Luis M. P. Ceríaco · Ricardo F. de Lima
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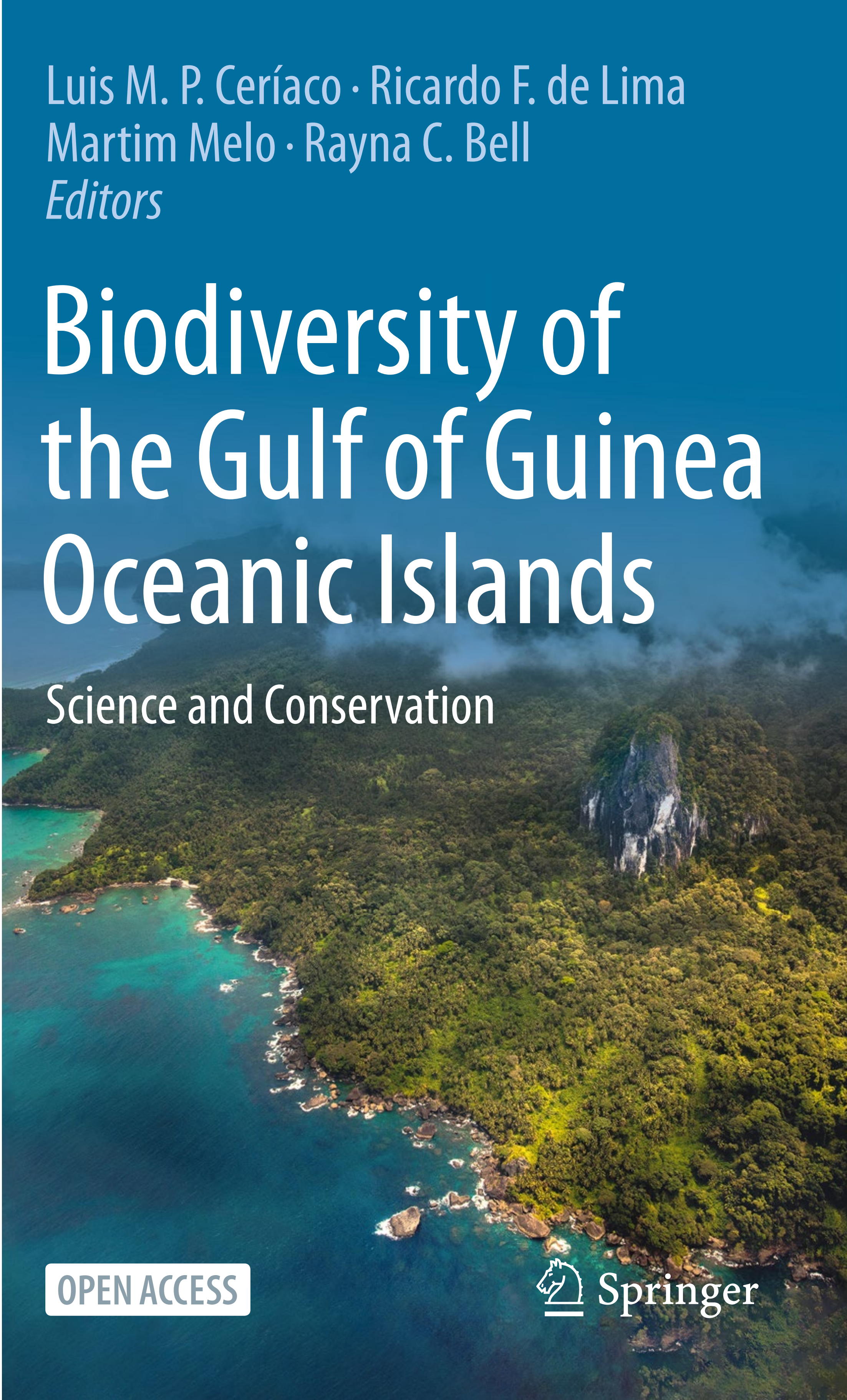
Editors

Biodiversity of the Gulf of Guinea Oceanic Islands

Science and Conservation



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Foreword 1

The islands of São Tomé and Príncipe emerged from relatively ancient volcanic activity, dating back 30 million years. Due to their isolation from the African continent, the fauna and flora are quite unique. The refuges that resulted from these volcanic phenomena gave rise to a high degree of endemic species, including bats, birds, reptiles, amphibians, butterflies, molluscs, as well as a great variety of flora. The richness of the islands' biodiversity is recognized by the scientific world, which considers the tropical forest of São Tomé and Príncipe as the second most important for the conservation of avifauna, among 75 African forests.

Biological diversity in São Tomé and Príncipe is manifested not only in terms of species richness and endemism. Despite the country's relatively small area, the diversity of its ecosystems is equally impressive, particularly in the forestry domain. The shade forests are particularly noteworthy as they house cocoa crops that support the national economy. Cocoa production requires the maintenance of forest cover to shade the plants, a practice that also helps to maintain high levels of forest biodiversity in producing countries.

With a total land area of around 1000 km^2, the islands of São Tomé and Príncipe are home to a great diversity of habitats ranging from savannas and mangroves in the coastal areas, to shade forests, low and medium altitude forests, and fog forests at altitudes of more than 2000 m. The forests are characterized by several endemic species, including the Giant Lobelia, *Lobelia barnsii* and many species of mammals, amphibians, reptiles, and insects. The birds are truly exceptional with more than 28 species of endemic birds including Maroon Pigeons, *Columba thomensis*, the São Tomé Green-Pigeon, *Treron sanctithomae*, the Sao Tome Ibis, *Bostrychia bocagei*, and the famous Sao Tome Prinia, *Prinia molleri*. The Prinia is also present in urban areas of the country and greets the islands' human inhabitants with its rhythmic wing flaps in the morning.

The Tinhosas islets, located 22 km from the island of Principe, are home to one of the largest colonies of seabirds in our African sub-region, which makes them the main nursery of seabirds in the Gulf of Guinea. This status, according to Birdlife International, makes them an area of worldwide importance for bird conservation.

The extraordinary biodiversity of the islands contributed to the island of Príncipe becoming part of the UNESCO World Network of Biosphere Reserves in 2012.

Throughout its existence, the population of São Tomé and Príncipe has been closely linked to the country's biological resources, through agriculture, fishing, harvesting, medicine, recreation, tourism, and also through cultural events. In recognition of the importance of biodiversity for the lives of the population, and that the issue of biodiversity conservation is a common concern for all of Humanity, the Democratic Republic of São Tomé and Príncipe became a signatory to the Convention on Biological Diversity in June 1992, in Rio de Janeiro. States must assume the main responsibility in the search for feasible and effective conservation.

After its ratification, several steps were taken at the international level to obtain the necessary means to implement the recommendations contained in Article 6 of the Convention, namely in terms of the elaboration and implementation of national strategies, plans and programmes aiming at conservation and sustainable use of biological diversity, as well as the integration of these same objectives in the specific framework of the different sectoral and intersectoral plans and programmes. The Biodiversity Action Plan of São Tomé and Príncipe aims for the local population to use natural resources in a way that contributes to poverty reduction and allows for sustainable socio-economic development.

The present work "The Biodiversity of the Oceanic Islands of the Gulf of Guinea" represents without a doubt, an important contribution to the knowledge of the rich biodiversity of São Tomé and Príncipe. Biodiversity is central to the current and future socio-economic development of the county, and there is a clear need to expand research that furthers knowledge of our biodiversity and identifies solutions that lead to its sustainable use.

I proudly provide a foreword to the present work, certain of its potential to encourage our national academia and inspire a new generation of researchers.

President of the Democratic Republic of São Tomé and Príncipe, Neves, São Tomé and Príncipe
December 2021

Carlos Vila Nova

Foreword 2

For more than 30 years, the EU and its partners have been supporting the preservation of biodiversity and fragile ecosystems in Central Africa, notably through the ECOFAC programme. ECOFAC was launched in 1993 with the objective to promote the conservation and rational use of Central Africa's forest heritage, taking into account the socio-economic and environmental particularities of its landscapes. This programme follows the intentions expressed in the "Lomé III" Convention (8 December 1984), between the European Economic Community and the African, Caribbean, and Pacific Group of States, aiming to strengthen cooperation for the economic, cultural, and social development of these States. In the Brazzaville Declaration of 31 May 1990, on the conservation and rational use of forest ecosystems in Central Africa, the representatives of seven countries submitted a request to the Commission, which was agreed on 26 October 1990. São Tomé and Príncipe has been benefitting directly from the Programme since its inception.

A great deal of knowledge has been gained over the last 30 years that has helped to shape the conservation sector in Central African countries. This knowledge has led to a better understanding of species diversity and ecosystems, the development of a sub-regional network of protected areas, and to valuable information for their effective management. The ECOFAC Programme has also played a pivotal role to build capacity and human capital in conservation in Central Africa. Over the course of these three decades, paradigms around protected areas have evolved. These areas were mainly oriented towards strict conservation in the beginning, but the approach is increasingly integrating the needs of human populations and the notion of landscape, establishing a new paradigm around "conservation for development". Fundamental and applied conservation research continues to be an essential component of the management of protected areas and their surroundings. This work encompasses a wide range of themes, and increasingly integrates socio-economic and biological research. Understanding how ecosystems and species respond to human pressures is essential as human population growth accelerates.

With continuous support from the European Union, the ECOFAC Programme is now in its sixth phase. This makes ECOFAC the oldest European programme in

Central Africa, a sign of the European Union's lasting political commitment to the region, specifically regarding conservation. The general objective of the ECOFAC 6 Programme is to improve the governance of natural resources and the management of protected areas, to contribute to a green economy characterized by endogenous, sustainable, and inclusive economic development. As the implementing partner of the ECOFAC 6 component for the Democratic Republic of São Tomé and Príncipe, BirdLife International has been working closely with park management authorities, government ministries, and communities to promote research, empowerment, and the conservation of threatened and unique birds and their habitats.

This book is an important step towards meeting these objectives, synthesizing centuries of research into a single volume that is freely accessible to researchers, educators, policy makers, and the public.

The oceanic islands of the Gulf of Guinea—Príncipe, São Tomé, and Annobón—are three small volcanic islands off the west coast of Central Africa. They are home to a remarkable number of unique species across the tree of life, including plants, mushrooms, spiders, butterflies, molluscs, amphibians, reptiles, birds, and mammals, inhabiting the forests that envelop the islands' inactive volcanic slopes. The surrounding marine ecosystems are also teeming with life, hosting diverse communities that include sea turtles, sharks, cetaceans, reef fishes, and marine invertebrates. The human populations on the islands are mostly concentrated along the coasts where they rely heavily on the balance of both terrestrial and marine environments.

On a global scale, biological diversity is declining and the rate of species extinction is accelerating, threatening the ecological processes that sustain life on Earth. Unfortunately, the ecosystems of the oceanic islands in the Gulf of Guinea have not been spared from the negative impacts of human activity. Centuries of intensive monoculture have left a lasting imprint on the island landscapes, and the human population has grown quickly over the last 50 years, which has increased the pressure on already vulnerable ecosystems. It is now widely recognized that biodiversity conservation is a fundamental element of sustainable development, increasing resilience and reducing environmental vulnerability.

The new European Green Deal adopted on 14 July 2021, identifies environmental degradation as an existential threat to the world. To overcome these challenges, the European Green Deal **is committed** to intensify the integration of environmental and climate change objectives, in particular the biodiversity, forests, oceans, and soils, across all sectors of cooperation. It is in this context that the EU has been fomenting the NaturAfrica initiative, aiming to support biodiversity conservation in Africa through an innovative, people-centred approach. NaturAfrica is the successor of ECOFAC and it consists of identifying key landscapes for conservation and development where the EU will focus its support for job creation, improved security, and sustainable livelihoods, while preserving ecosystems and wildlife that are vital to all. This initiative will directly benefit the island landscapes of Príncipe, São Tomé, and Annobón.

Moreover, the Global Gateway Strategy launched on 1 December 2021, stands for sustainable and trusted connections that work for people and the planet. It will help to tackle the most pressing global challenges, including fighting climate change.

Global Gateway is a great start to lead on climate action with developing countries, tackling climate change with a closing window of opportunity against global warming, taking into account the needs of partner countries and ensuring lasting benefits for local communities.

This book is the first synthesizing knowledge on the biodiversity of these islands. It is being published at a time when humanity is facing a serious ecological crisis due to the unprecedented collective impacts of human activities on nature, and the timely publication of this book will serve as an important resource to guide the next phase of biodiversity conservation of this unique archipelago.

Thus, the information in this book is fundamental to guide development strategies for the islands.

EU Ambassador in Gabon to São Tomé
and Príncipe and ECCAS, Gabon,
São Tomé and Príncipe

H. E. Rosario Bento Pais

Foreword 3

Ex Africa Semper Aliquid Novi

Some two decades ago, I found myself on a small aircraft en route to the island of São Tomé. I had just attended a meeting of the World Wildlife Fund in Libreville, Gabon and was now headed to meet an old San Francisco family friend. Ned Seligman, a former Peace Corps volunteer (later Country Director) and fellow lover of Africa had moved to the island and founded a non-profit organization called STeP UP that focused on education and health initiatives. He had been urging me to visit for some years. As a scientist with the California Academy of Sciences in San Francisco, I had by this time already travelled and worked in much of continental Africa, but I was unaware that one of the most meaningful and satisfying phases of my scientific career was about to begin; it would also be the last.

It has been said that nothing compares with the thrill of discovery. In the academic and scientific world, this might be a single novel idea or a series of related discoveries leading to a new understanding of a more complex whole. The Gulf of Guinea Islands are teeming with unique species of plants, animals, and fungi whose diversity and biology have inspired centuries of research, but the islands also present a unique geological setting in which to understand broader questions about how biodiversity evolves and accumulates on oceanic islands. Very early discoveries of the unique species inhabiting Gulf of Guinea Islands collected by early explorers such as Greef, Newton, and Fea, mostly during the nineteenth century, were tantalizing to biologists of the time. However, after a fruitful initial period of biological discoveries, the islands remained overlooked by the large majority of the scientific community. More recently, the spectacular Gulf of Guinea Islands opened again to collaborative biological exploration. The early results of this long overdue exploration and analysis include numerous intriguing, fascinating discoveries, many of which are presented in this volume.

While many of these results represent work by groups and individuals from scientific institutions in North America, Europe, and Brazil, they are most importantly the result of cooperation and efforts with the citizens and civic leaders of the islands. The islands' residents are the ultimate custodians of the biological wealth partially described herein. To that end, it must be mentioned that many of the results presented in this volume have already been and are still being transmitted directly to national and regional governmental entities. Past and ongoing efforts to spread environmental awareness to island residents of all ages and to inspire stewardship of the islands' biological heritage are also described in this volume.

The islands' residents are the custodians of something unique and special to the rest of the world. It has been the honour of my career to play a small role in advancing this new phase of discovery and collaboration.

SOMENTE AQUI! (ONLY HERE!)

Robert C. Drewes, PhD

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This synthesis is a direct result of sustained efforts in biodiversity research, conservation, and outreach that have taken place in the oceanic islands of the Gulf of Guinea over the last two decades. This new wave of work was only possible thanks to the interest and full institutional and logistic support of the authorities of São Tomé and Príncipe and of Equatorial Guinea. In São Tomé and Príncipe, this includes foremost the Direcção Geral do Ambiente (Dept. of the Environment), the Direcção de Florestas e Biodiversidade (Forestry and Biodiversity Dept.), the Ôbo Natural Park (São Tomé, Príncipe), and the University of São Tomé e Príncipe. The Regional Government of Príncipe has also been an important partner. In Equatorial Guinea this work is consistently supported by UNGE (National University of Equatorial Guinea) and INDEFOR-AP (National Institute of Forests and Protected Areas). Non-governmental organizations and other partners have also provided key support, including Associação Monte Pico (São Tomé), Fundação Príncipe (Príncipe), the Portuguese School of São Tomé and Príncipe (São Tomé), and the Bioko Biodiversity Protection Program (Equatorial Guinea). Most advances in the knowledge of the biodiversity of this region were only made possible with vast amounts of fieldwork, often in very challenging conditions. The success of this endeavour relied on the expertise, enthusiasm, and hard work of many field assistants throughout the years. Many others have provided crucial help along the way for different projects. These are specifically acknowledged in the respective chapters.

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Chapter 1
Biodiversity in the Gulf of Guinea Oceanic Islands: A Synthesis

Luis M. P. Ceríaco, Ricardo F. de Lima, Rayna C. Bell, and Martim Melo

Abstract The Gulf of Guinea oceanic islands (Príncipe, São Tomé, and Annobón) are among the most endemic-rich regions of the planet. Historical scientific studies of the islands' unique biodiversity are scattered in a variety of publications, many of which are difficult to access. More recently, there has been a growing interest in the islands, which is reflected in a burst of new studies, reports, and ongoing projects.

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Here we aim to provide an updated and comprehensive synthesis, covering all the key information and references on the biodiversity of these islands. The goal of the book is to be a comprehensive reference for students, researchers, and conservationists dedicated to the study and preservation of this unique biodiversity. It also intends to serve as a basis for local stakeholders to make informed decisions, namely regarding conservation actions. The book is divided into three main sections: (1) a general overview of the islands and their biodiversity, including aspects of natural and human history (six chapters); (2) detailed accounts on different taxonomic groups (16 chapters); and (3) the conservation, environmental education, and research challenges that lie ahead (three chapters).

Keywords Biogeography · Conservation · Ecology · Endemics · History of science · Taxonomy

Introduction

É realmente notável a fauna da ilha de S. Tomé e mais notável é ainda a diferença que faz da sua irmã o Príncipe. No Príncipe os animais que se encontram são em grande parte do continente, enquanto que em S. Tome há uma forma especial com bastantes espécies que julgo serem privativas da ilha. A distancia que há entre as duas ilhas é apenas de 90 milhas mas o cabo submarino lançado tem 120 milhas devido às ondulações de terreno no fundo do mar. Com relação à Atlântida, não serão as ilhas do Golpho da Guiné e mesmo as Canarias, Cabo verde, Stª Helena, Assumpção etc, restos d'esse grande continente?	*The fauna of S. Tome Island is truly remarkable, and it is even more remarkable the difference to its sister island of Príncipe. The animals that are found in Príncipe are mostly from the continent, while in S. Tomé there is a special form with several species that I believe are private to the island. The distance between the two islands is only 90 miles but the submarine cable has 120 miles due to the ruggedness of the sea floor. Regarding Atlantis, aren't the islands of the Gulf of Guinea, and even the Canaries, Cabo Verde, St. Helena, Ascension,* etc.*, the remains of that large continent?*

Francisco Newton, letter from São Tomé Island
23 January 1887

The Portuguese explorer Francisco Newton was one of the first naturalists to dedicate almost one decade to the study of the outstanding diversity of the Gulf of Guinea oceanic islands. The collections he made, in what was largely unexplored territory for science, allowed the description of dozens of new species and began to reveal intriguing biogeographic patterns. Gazing at the species he was collecting, many of which would turn out to be endemic, the naturalist found them so spectacular that he dared to suggest the islands could be the remains of the mythical continent of Atlantis. While this suggestion lacks any scientific basis, it is a perfect example of the sense of awe that the biodiversity of the Gulf of Guinea oceanic islands imparts to any naturalist who visits them. Although Newton's "Atlantis hypothesis" did not gain traction, other comparisons between these islands and other iconic places around the world have since been proposed. A quick search about these islands on the Internet, newspapers, popular magazines, or tourism advertisements will likely find them labeled as "a paradise on Earth" or "the Galapagos of Africa." The Galapagos archipelago in the Pacific Ocean is one of the most famous group of islands for naturalists and wildlife enthusiasts, especially due to their role in British naturalist Charles Darwin's (1809–1882) genesis of the theory of evolution through natural selection. The observation of the diverse environments, unique species, and incredible adaptations of the Galapagos fauna and flora were fundamental to Darwin's growing body of evidence, forever linking the Galapagos to the theory of evolution. Darwin never set foot in the Gulf of Guinea but the type of evidence he found in the Galapagos is also abundantly available in these oceanic islands. Thus, the label "the Galapagos of Africa" is certainly fitting.

Since their emergence millions of years ago, due to the activity of the Cameroon Volcanic Line, the islands of Príncipe, São Tomé, and Annobón have been isolated from the African continent. Their prolonged isolation and complex geological history led to the evolution of unique species that sustain distinctive ecosystems. Humans arrived approximately 500 years ago, when Portuguese navigators found these uninhabited islands teeming with biodiversity. Since then, human impact on the islands has increased considerably, with lasting impacts to both the landscape and biodiversity. The human impact on the biota has been considerable, and a number of species and ecosystems are now threatened.

The islands' unique biodiversity has attracted several generations of researchers working in a wide diversity of taxonomic groups and biological topics. Biodiversity research in the region received a renewed focus when in June 1993 the Jersey Wildlife Preservation in Jersey (UK) organized a workshop on the biodiversity of the Gulf of Guinea islands. The aim of this meeting was to synthesize the data available at the time, and led to the establishment of a network of experts: the Gulf of Guinea Conservation Group. Managed by Angus Gascoigne (1962–2012), a passionate British amateur naturalist who was living in São Tomé, it supported many scientific endeavors. The results of the meeting were published in a special edition of the journal *Biodiversity and Conservation* (Juste and Fa 1994). This issue became the major reference for the biodiversity of the islands for more than two decades, serving as the main source of data and theoretical support for the new generation of island biologists and conservationists, many of whom are contributors to this volume.

On October 16, 2020, a virtual meeting brought together several dozen scientists, conservationists, educators, and local stakeholders, all with shared interests in the biodiversity of the Gulf of Guinea oceanic islands. This meeting aimed to set the foundation for the Gulf of Guinea Biodiversity Center, a collaboration to satisfy the urgent needs of an ever-growing community to have an institution fully dedicated to the biodiversity of the islands. This new generation is dedicated to surveying the islands to document biodiversity, to understand and mitigate the current threats, and to raise local and global awareness for this unique natural heritage. This book aims to represent this new wave of research and to set the stage for the next phase of biodiversity research and conservation.

Historical Biodiversity Syntheses

Prior to the 1994 special issue of *Biodiversity and Conservation* (Jones 1994), efforts to synthesize knowledge on the biodiversity of the Gulf of Guinea islands were few and far between. Many tended to be taxonomically and geographically focused. In the early twentieth century, the Portuguese zoologist José Vicente Barbosa du Bocage (1823–1907) was the first to produce a synthesis on the land vertebrates of the Gulf of Guinea islands, based on the knowledge that had been amassed during the second half of the nineteenth century (Bocage 1903, 1905). According to him, the list of species for Príncipe included four mammals, 43 birds, ten reptiles, and two frogs, whereas that of São Tomé hosted 12 mammals, 64 birds, 11 reptiles, and five amphibians. For Annobón, the species list of Bocage (1903) recorded only two mammals, 14 birds, five reptiles, and no amphibians. Similar to Bocage's checklists of vertebrate fauna, the British botanist Arthur Wallis Exell (1901–1993) was the first to publish a checklist of the vascular flora of the Gulf of Guinea oceanic islands (Exell 1944). He benefited from the work of previous researchers, such as Júlio Henriques (1838–1928), former director of the herbarium of the University of Coimbra, providing an extensive series of publications (Exell 1956, 1958, 1959, 1963, 1973). By 1973 he had recorded 810 angiosperms for the islands (539 dicotyledons and 271 monocotyledons), of which 601 occurred on São Tomé, 314 on Príncipe, and 208 on Annobón (Exell 1973). Some taxonomic groups have received special attention in comparison to others. Birds, in particular, received regular syntheses through the years (Bocage 1889; Amadon 1953; Naurois 1994; Jones and Tye 2006; Lima and Melo 2021).

While many syntheses have been taxonomically oriented (vertebrates, angiosperms), others have focused on single islands. The work of Júlio Henriques on the natural history and agriculture of São Tomé (Henriques 1917) is a perfect example: across almost 300 pages, this monographic work aimed to cover all the aspects of the natural history of the island, listing its fauna, flora, geology, topography, agriculture, and even the organization of the local society. Other attempts to compile information on the biodiversity of the islands took place later on, including the bibliographic compilation of "pure and applied botany" of São Tomé and Príncipe by Fernandes (1982), and that on the fauna of the three oceanic islands by Gascoigne (1993, 1996).

Continuously updating species lists is vital for refining taxonomy, identifying knowledge gaps, recording changes in species composition, studying community ecology and biogeography, understanding ecosystem function, and supporting conservation decisions. Jones (1994) presented an updated overview of the number of vertebrate species and endemics on each island (Table 1.1). According to this compilation, the Príncipe species list of terrestrial vertebrates included four mammals, 35 birds, eight reptiles, and three frogs, that of São Tomé nine mammals, 49 birds, 14 reptiles, and six amphibians, and that of Annobón two mammals, nine birds, seven reptiles, and no amphibians (Table 1.1). Regarding plants, numbers would not be updated until the much more recent publication of bryophyte (Sérgio

Table 1.1 Comparison between confirmed extant resident terrestrial vertebrates since the previous synthesis (Jones 1994), considering all species, single-island endemics, and all endemics. The percentage of endemic species is shown in parenthesis. The number of species currently thought to be introduced is shown in the last column. A few cells are blank because those figures were not available in the previous synthesis

		Previous	Current	Previous	Current	Previous	Current	Current
	Island	Total		Single-island endemics		All endemics		Introduced
Amphibia	Príncipe	3	3	1 (33)	3 (100)	3 (100)	3 (100)	0
	São Tomé	6	6	4 (67)	6 (100)	6 (100)	6 (100)	0
	Annobón	0	0	0	0	0	0	0
	Total	7	9	5 (71)	9 (100)	7 (100)	9 (100)	0
Reptilia	Príncipe	8	14	2 (25)	8 (57)	7 (88)	10 (71)	2 (14)
	São Tomé	14	12	1 (7)	7 (58)	6 (43)	9 (75)	2 (17)
	Annobón	7	8	2 (29)	6 (75)	3 (43)	6 (75)	2 (25)
	Total		28	5	21 (75)	10	23 (82)	3 (11)
Aves	Príncipe	35	32	6 (17)	8 (25)	11 (31)	11 (34)	5 (16)
	São Tomé	49	50	15 (31)	17 (34)	20 (41)	20 (40)	17 (34)
	Annobón	9	11	2 (22)	1 (9)	3 (33)	2 (18)	3 (27)
	Total		66	23	26 (39)	28	29 (44)	17 (26)
Mammalia	Príncipe	9	12	1 (11)	2 (17)	1 (11)	2 (17)	5 (42)
	São Tomé	16	17	3 (19)	5 (29)	3 (19)	5 (29)	6 (35)
	Annobón		4	0	0 (0)	0	0 (0)	2 (50)
	Total		19	4	7 (37)	4	7 (37)	6 (32)
All	Príncipe	55	61	10 (18)	21 (34)	22 (40)	26 (43)	12 (20)
	São Tomé	85	85	23 (27)	35 (41)	35 (41)	40 (47)	25 (29)
	Annobón		23	4	7 (30)	6	8 (35)	7 (30)
	Total		122	37	63 (52)	49	68 (56)	26 (21)

and Gargia 2011), fern and lycophyte (Figueiredo 2002; Klopper and Figueiredo 2013), and angiosperm checklists (Figueiredo et al. 2011). There are noticeable differences in the number of species and endemics for taxa that have multiple checklists, reflecting the development of knowledge of the islands' biodiversity over the last century. New species continue to be added every year, even among the best studied groups, representing both species that are new to science and just newly recorded on the islands. Nevertheless, systematic and well-curated species checklists are still the exception for most taxa in the Gulf of Guinea oceanic islands. For many groups, notably terrestrial and marine invertebrates, there are still no comprehensive species checklists, or they were first published recently, highlighting how little is still known about the biodiversity of the islands (Lima 2016).

A New Synthesis

The outputs of the long history of research in the oceanic islands of the Gulf of Guinea are scattered in hundreds of publications—scientific papers, reports, and books. Most works published since the late eighteenth century to the present day are very specific, focusing on few taxa and on a single island, or even a single species and particular regions of an island. Publications are available in several different languages—Portuguese, Spanish, English, French, German, Italian, Latin, Russian—and formats—from books to peer-review scientific journals, theses, unpublished reports, and more recently also in non-printed media, such as online images, audio, and video. Access to many historical works has greatly improved in recent years, especially due to important online platforms, such as the Biodiversity Heritage Library (Gwinn and Constance 2009). However, this immense diversity of sources also makes it challenging to gain a complete and updated view on the biodiversity of these islands. Similarly, thousands of scientific specimens are held in natural history collections around the world, providing the baseline to our present knowledge and enabling exciting new findings and research. Many of these collections have not been included in recent studies and some have only recently been rehabilitated and once more made accessible to the scientific community (e.g., Monteiro et al. 2016; Ceríaco et al. 2021). For such a small area, the Gulf of Guinea oceanic islands may be one of the most intensively studied parts of Africa (e.g., Droissart et al. 2018). However, most of the scientific output and associated data are not synthesized or readily available.

This book attempts to compile the key information and references regarding the past and current knowledge on the biodiversity of the Gulf of Guinea oceanic islands. The goal is to be a comprehensive reference for students, researchers, and conservationists dedicated to the study and preservation of this unique biodiversity. It also intends to serve as a basis for local stakeholders to make informed decisions, namely regarding conservation actions. Above all, it is an act of celebration of the scientific achievements of several generations of biologists and conservationists, a manifest in support of the astonishing biodiversity of these islands, and a plea for its conservation.

Book Structure

The book is divided into three main sections: (1) a general overview of the islands and their biodiversity, including aspects of natural and human history (six chapters); (2) detailed accounts on different taxonomic groups (16 chapters); and (3) the conservation, environmental education, and research challenges that lie ahead (three chapters).

Section one starts with an outline of the physical geography, geological history, climate, and sea level evolution of the study area, providing also its political boundaries and administrative divisions (Chap. 2; Ceríaco et al. 2022a). This is followed by a revision of the classification and cartography of the terrestrial ecosystems (Chap. 3; Dauby et al. 2022). Chapter 4 (Muñoz-Torrent et al. 2022) analyzes the five centuries of human presence on the better-known island of São Tomé, presenting demographic trends, cultural heritage, and how the history of the main economic activities has impacted biodiversity. Chapter 5 (Ceríaco et al. 2022b) reviews the history of scientific research, from mid-eighteenth century to the twenty-first century. The fascinating evolutionary patterns that shaped the biodiversity of the "Galapagos of Africa" are presented in Chap. 6 (Melo et al. 2022a). In Chap. 7 (Soares et al. 2022), our current understanding of island species ecology is synthesized, including information about species distributions, habitat preferences, species assemblages, and the interactions that maintain functioning ecosystems.

The second section constitutes the bulk of the book and corresponds to the taxonomic chapters. The level of detail varies between chapters, mostly reflecting disparities in knowledge across taxonomic groups. However, all chapters have a similar structure, including an introduction to the group, a brief review of the history of research on the islands, an account of the group's diversity and endemism, an updated checklist, and a section on conservation. Most of these chapters also highlight important areas for future research.

Chapter 8 (Desjardin and Perry 2022) reports 260 species of mushrooms and allies of the Agaricomycetes lineages of the Basidiomycota in São Tomé and Príncipe. These correspond to 109 genera, 51 families, and 13 orders, and given how little scientific attention this group has received, species richness will likely increase with future work. Chapter 9 (Garcia et al. 2022) provides a review of the bryophytes of São Tomé and Príncipe, based on historical herbarium data complemented by the results of recent fieldwork. A preliminary list of 299 taxa (128 mosses, 171 liverworts and hornworts) is provided, and the authors note that several species likely remain undescribed or at least undocumented. Chapter 10 (Stévart et al. 2022) presents an updated checklist of vascular plants, combining data from historical material and bibliographic references with extensive new field surveys conducted since 2017. The current number of vascular plants includes

1285 taxa, with 164 endemics, of which at least 18 are new to science. A report on medicinal plants is also provided.

Six chapters focus on invertebrate groups. Chapter 11 (Crews and Esposito 2022) explores the diverse and little-known arachnid fauna of São Tomé and Príncipe, which includes 266 recorded species of six different orders. Chapter 12 (Nève et al. 2022) provides a first checklist for the beetles of the three oceanic islands, listing 403 species, of which 190 are endemic. The butterflies and skippers (Lepidoptera: Papilionoidea) are reviewed in Chap. 13 (Mendes and Bivar-de-Sousa 2022), with 91 confirmed taxa, and extensive discussion resolving previous doubtful records. Chapter 14 (Dijkstra and Tate 2022) notes the impoverished dragonfly and damselfly fauna of the islands, which includes only 22 confirmed records and one endemic species, from Príncipe. Chapter 15 (Loiseau et al. 2022) reviews the arthropod species that can act as vectors of diseases. Given the particularity of this group, the structure of this chapter is slightly different but its scientific relevance is undisputable due to the public health implications. The chapter also provides important insights into species interactions, and underscores the possibility of new vector-borne diseases arriving on the islands. Chapter 16 (Panisi et al. 2022) deals with the 96 species of land gastropods, of which 62 are endemic, providing new insights on the ecology, biogeography, and conservation of these species, including the famous endemic giant land snail *Archachatina bicarinata* Bruguière, 1792.

Regarding vertebrates, there are four taxonomic chapters for terrestrial groups and three for aquatic taxa. Chapter 17 (Costa et al. 2022) lists and discusses the more than 1000 species of fishes that potentially occur in the fresh and marine waters of the islands. Chapter 18 (Bell et al. 2022) deals with amphibians, which include three species on Príncipe and six on São Tomé, all of which are endemic (Annobón has no amphibians). The chapter provides a detailed overview of species biology, ecology, and biogeography. Chapter 19 (Ceríaco et al. 2022c) presents the 29 species of established terrestrial reptiles, reporting also historical and recent records of vagrant, doubtful, or introduced species. The five species of sea turtles that occur on the islands are reviewed in Chap. 20 (Ferreira-Airaud et al. 2022). All sea turtles are threatened, and this chapter includes extensive discussion of conservation successes and challenges. Chapter 21 (Melo et al. 2022b) revises information on birds, one of the best-known and most charismatic taxa from the islands that includes at least 29 endemic species. It summarizes historical data and provides updated insights into a group that has been at the forefront of research and conservation. Chapter 22 (Rainho et al. 2022) revises information on the 19 species of non-domesticated resident land mammals, including 11 bats, seven endemic species, and six introduced species. Finally, Chap. 23 (Carvalho et al. 2022) draws on new data collected since 2002 to present the updated list of the 12 cetaceans confirmed in the waters of the region, five of which are recent records. This chapter also provides a synthesis of the whaling history in the region.

The final section of the book focuses on the conservation, education, and future of research in the oceanic islands of the Gulf of Guinea. Chapter 24 (Lima et al. 2022) summarizes the state of conservation: from the cultural links to nature to the history of conservation initiatives. This chapter also lists priority species, sites, and actions.

Chapter 25 (Ayres et al. 2022) assesses recent strategies of formal and non-formal environmental education on São Tomé and Príncipe, which are vital to augment local capacity for conservation and scientific research. Chapter 26 (Bell et al. 2022) proposes a path toward biodiversity resilience for future naturalists, biologists, conservationists, and educators.

Current Numbers, Current Biases

Comparing the number of species presented in previous compilations, such as Bocage (1903, 1905) or Jones (1994), with those recorded in this book is not a straightforward task. The coverage of previous syntheses was taxonomically more limited than the present work, and methods for counting endemic and non-endemic species varied. In comparing the number of vertebrate species and endemics provided by Jones (1994) with those in the current synthesis, however, one major trend stands out—our improved understanding led to an increase in endemism across most taxa (Table 1.1). In many cases, this was due to recognizing that each island had a distinct endemic species, and that shared endemics are rare. While it is likely that these numbers change little for vertebrate groups, they will certainly keep changing for less studied taxa, such as fungi, plants, invertebrates, and marine vertebrates.

There are several other biases in our knowledge of the biodiversity of these islands. Annobón is by far the least studied island. Most of the chapters focus on terrestrial habitats and species, and while several teams and projects are currently focusing on marine biodiversity and conservation, knowledge is still very limited. The study of marine biomes in the Gulf of Guinea oceanic islands is of critical importance, not only because the region is likely an important hotspot for marine biodiversity, but also because human residents depend heavily on marine resources. Another major gap is the limited number of ecological and natural history studies. While there is now a considerable amount of traditional and modern taxonomic research—describing, naming, and listing the several thousands of species known from the islands—there are very few studies on the ecology and natural history of these taxa. For most species, almost nothing is known besides the diagnosis and a few anecdotal pieces of information about its ecology. This lack of information hinders the development of effective conservation measures, which are increasingly necessary to ensure a thriving future for this unique archipelago.

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Chapter 2
Physical Geography of the Gulf of Guinea Oceanic Islands

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Abstract The Gulf of Guinea, in the Atlantic coast of Central Africa, has three oceanic islands that arose as part of the Cameroon Volcanic Line. From northeast to southwest these are Príncipe (139 km^2), São Tomé (857 km^2), and Annobón (17 km^2). Although relatively close to the adjacent mainland, the islands have distinct climactic and geomorphologic characteristics, and have remained isolated throughout their geological history. Consequently, they have developed a unique biodiversity, rich in endemic species. We provide an integrated overview of the

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physical setting of the islands, including their geographic location, geological origin, topography, geology and soils, climate zones, and prevailing wind and ocean currents—key features that underlie the evolution of their biodiversity.

Keywords Annobón · Geology · Ocean currents · São Tomé · Príncipe · Soils · Volcanism

Introduction

The Gulf of Guinea is a major topographical feature of western equatorial Africa that marks the distinctive shape of the continent on its Atlantic coast (Fig. 2.1). The Gulf of Guinea has three oceanic islands (Príncipe, São Tomé, and Annobón), one land-bridge island (Bioko), and two seamounts, which together comprise the offshore part of the Cameroon Volcanic Line. The biodiversity of the oceanic islands is characterized by a small number of species but exceptional endemism (Jones 1994; Gascoigne 2004; Ceríaco et al. 2022). This chapter provides an introduction to the physical setting of the islands that created the conditions for the evolution of their unique biodiversity, including their geography and topography, geological history, geological substrates and soils, climate, and prevailing patterns of ocean sea currents.

Some of the most complete sources of data for these topics are found in works published under the seal of the Portuguese scientific colonial institute—the *Junta de Investigações do Ultramar*—during the 1950s, 1960s, and 1970s. Of these sources, Lains e Silva (1958) provides key information on climate, soils, vegetation, and agricultural potential of São Tomé and Príncipe islands (see also Lains e Silva and Cardoso 1958). Building on earlier work, Tenreiro (1961) further addressed some of these topics for São Tomé Island. Cardoso and Garcia (1962) is a key reference for the soils of São Tomé and Príncipe—providing detailed maps of the soils of each island. Rodrigues (1974) synthesized the information on climate and soils presented by Lains e Silva (1958) and Cardoso and Garcia (1962). Jones et al. (1991) provide a

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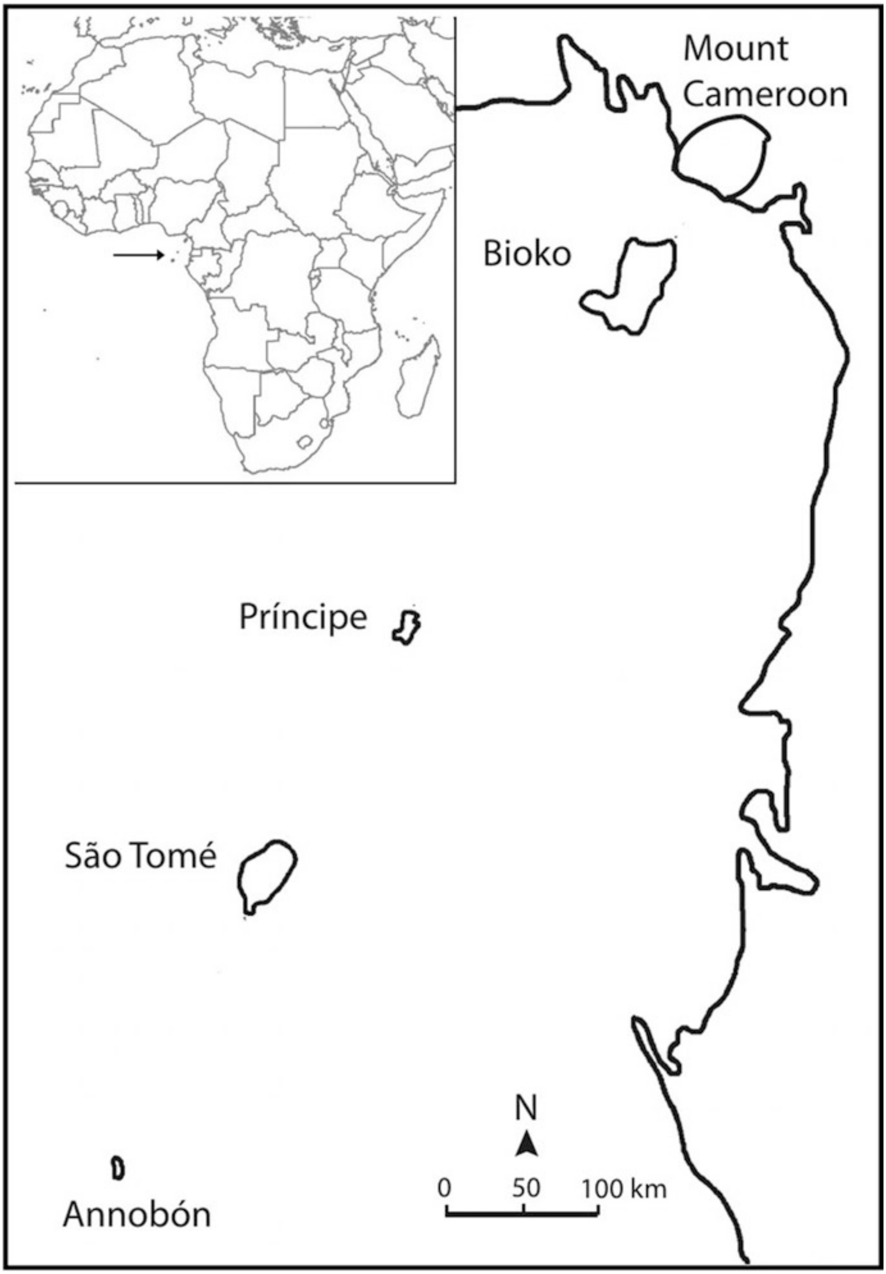

Fig. 2.1 Map of the Gulf of Guinea islands, western Central Africa. This system includes an ecological island (Mount Cameroon), a land-bridge island (Bioko), and the three oceanic islands, which are the focus of this book. Adapted from Jones and Tye (2006)

useful synthesis of background information available at the time. More recently, Diniz and Matos (2002) added to our understanding of the climate and soils of São Tomé and Príncipe islands, providing an updated and detailed map of the ecosystems and land-use types of the islands. A series of geological studies conducted by Munhá et al. (2002), Caldeira et al. (2003), Caldeira (2006), Munhá et al. (2006a, b, c, d, 2007), and Barfod and Fitton (2014) have provided important updates to our knowledge of the geology of São Tomé. Chou et al. (2020) provided the first modern analysis of the climate of São Tomé and Príncipe, downscaling global projections of climate change to these islands. For Annobón, the information is scarcer with initial geological works by Schultze (1913), petrological studies by Fuster Casas (1954) and Cornen and Maury (1980), work on volcanic geochemistry by Liotard et al. (1982), and a review by De Castro and De la Calle (1985), with subsequent additions by Fa (1991) and Velayos et al. (2014). Besides these island specific studies, several reviews summarize the main geophysical characteristics of the Gulf of Guinea islands (e.g., Lee et al. 1994; Jones 1994; Jones and Tye 2006; Juste and Fa 1994; Schlüter 2008).

Location, Extent, and Political Boundaries

The Gulf of Guinea island system (sensu lato) includes the ecological or "sky" island of Mount Cameroon, the land-bridge island of Bioko, and the three oceanic islands of Príncipe, São Tomé, and Annobón (Fig. 2.1). They are, from northeast to southwest:

Mount Cameroon, with an approximate area of 1750 km^2 (50 × 35 km), is an ecological island in the southwest province of the Republic of Cameroon. Mount Cameroon is the highest mountain in West Africa, with a peak elevation of 4095 m above sea level.

Bioko Island is a land-bridge island with an area of 2027 km^2 (roughly 35 km × 72 km). Bioko sits upon the continental shelf 32 km from the coast of Cameroon from which it is presently separated by a sea 60 m deep. During recent glacial periods, however, Bioko experienced recurring cycles of isolation and connectivity (Ali 2018), and was most recently connected c. 11,000 years ago (Einsentraut 1965; Lambert and Chappel 2001). Rising to an impressive 3011 m above sea level, Pico Basilé is the highest point of the island and one of its main landmarks.

The three oceanic islands that are the focus of this book have never been connected to the continent, and they are:

Príncipe Island (Fig. 2.2(1)) with a total area of 139 km^2 (c. 17 km × 8 km) is located 210 km SSW of Bioko and 220 km west of continental Africa. The island has six main satellite islets: Pedra da Galé, Mosteiros, and Bom-Bom in the north, Caroço (also known as the Jockey's Cap; Fig. 2.2(3)) in the southeast, and Tinhosa Grande and Tinhosa Pequena (Fig. 2.2(2)), which are about 20 km to the south. The highest point, Pico do Príncipe, is 942 m above sea level.

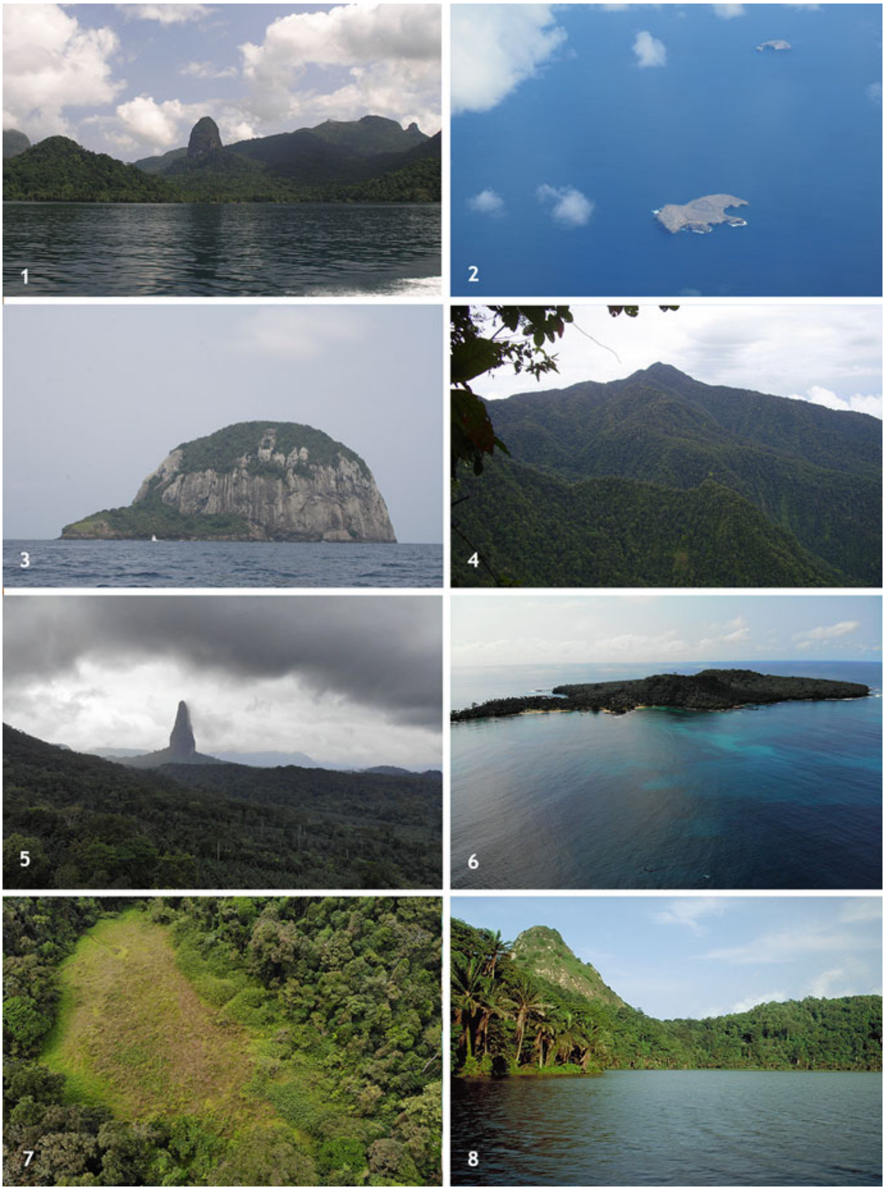

Fig. 2.2 (**1**) Pico Agulhas, Príncipe Island; (**2**) Tinhosa islets; (**3**) Jockey Bonet; (**4**) Pico São Tomé, São Tomé Island; (**5**) Pico Cão Grande, São Tomé Island; (**6**) Rolas islet; (**7**) Lagoa Amélia, São Tomé Island; (**8**) Lake A Pot, Annobón Island. Photo credits: (**1** and **8**) Martim Melo, (**2**, **3**, **5**–**7**) Luis M. P. Ceríaco; (**4**) Ricardo Lima

São Tomé Island with a total area of 857 km^2 (47 km × 28 km) lies 150 km SSW of Príncipe and 255 km west of Gabon. The island has several islets, of which Cabras to the north, Santana in the east, and Sete Pedras and Rolas (Fig. 2.2(6)) in the south

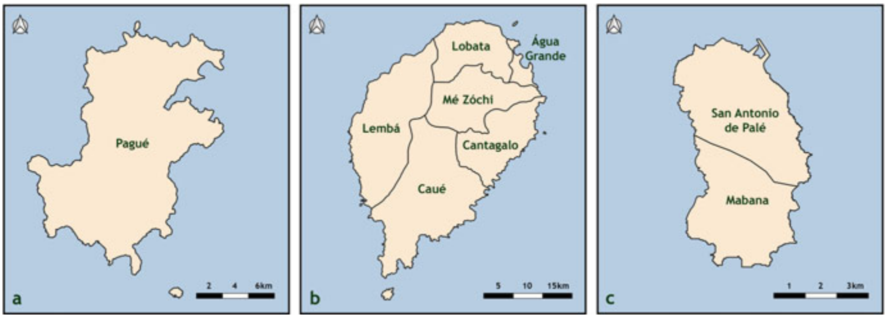

Fig. 2.3 Administrative divisions of Príncipe (**a**), São Tomé (**b**), and Annobón (**c**)

are the largest. The Equator passes through the center of Rolas Islet. The highest point, Pico de São Tomé (Fig. 2.2(4)), is 2024 m above sea level.

Annobón Island has an area of 17 km^2 (6 km × 3 km) and is the smallest and remotest of the Gulf of Guinea islands. It sits 180 km to the SSW of São Tomé and is about 340 km from the continent. The highest peak is Santa Mina, which rises 610 m above sea level.

Politically, the Gulf of Guinea oceanic islands belong to two countries: the Democratic Republic of São Tomé e Príncipe and the Republic of Equatorial Guinea. São Tomé e Príncipe is a nation state made up of Príncipe and São Tomé islands and the surrounding islets. It was once a colonial province of Portugal, from which it gained independence in 1975. It is one of the smallest countries in the world, with an approximate area of 1001 km^2. The country is internally organized into different levels of political and administrative divisions. São Tomé Island hosts the capital, the city of São Tomé, and is divided into six districts (Água Grande, Cantagalo, Caué, Lembá, Lobata, and Mé-Zóchi); Príncipe Island is an Autonomous Region, and is comprised of a single district, Pagué (Fig. 2.3).

Annobón (formerly known as Pagalu; Fig. 2.3), the smallest and most southwestern of the Gulf of Guinea oceanic islands, is one of eight provinces of Equatorial Guinea. This geographically disjunct country was a Spanish colony from 1778 to 1968. Equatorial Guinea is composed of a territory in continental Africa, Rio Muni, bordered by Cameroon to the north and Gabon in the east and south, the surroundings islets of Corisco, Elobey Chico, and Elobey Grande, the land-bridge island of Bioko (formerly known as Fernando Pó), where the country's capital is (Malabo), and finally the small oceanic island of Annobón. Whereas the mainland territory and Bioko have a long history of human occupation, Annobón was not peopled at the time of its discovery by the Portuguese, in 1473.

Geological History

The Gulf of Guinea islands form the southern part of the Cameroon Volcanic Line, a 1000-km line of volcanoes that has been active since the Cenozoic, and that extends from the Mandara Mountains on the Nigeria-Cameroon border to Annobón Island

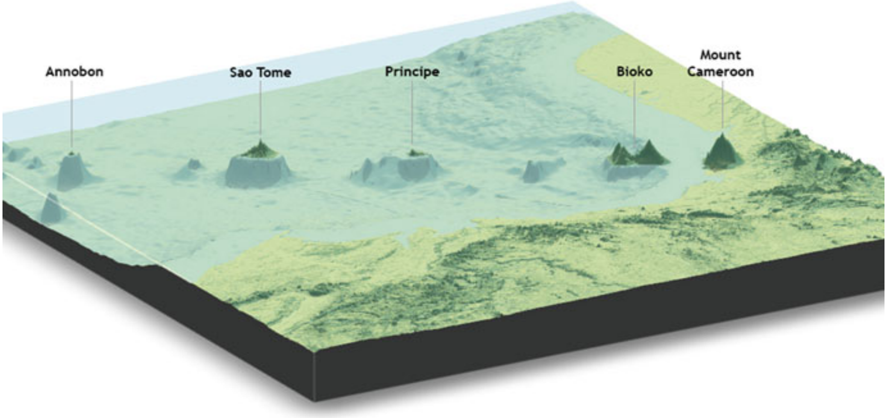

Fig. 2.4 Topographic representation of the offshore section of the Cameroon Volcanic Line. Figure created with the rayshader R package (Morgan-Wall 2021) using GEBCO data (GEBCO Compilation Group 2021)

(Burke 2001). This line runs in a NE-SW direction and includes four islands and two seamounts (Fig. 2.4). Onshore, there are four continental massifs (Mount Cameroon, Mount Manengouba, Mount Bambouto, and Mount Oku), all of which are in the Republic of Cameroon. Often, the Ngaoundéré and Biu swells, also in Cameroon, are considered part of the line, in which case the line becomes Y-shaped and 1600 km long (Fitton 1987; Lee et al. 1994; Fig. 2.5). Volcanic activity in the continental and oceanic sector has been more or less continuous since the Cretaceous (Fitton 1987; Lee et al. 1994; Burke 2001). There is no age progression in the line, except in the offshore section—with the oldest sub-aerial origins estimated at about 31 Ma for Príncipe, 15 Ma for São Tomé, and 6 Ma for Annobón (Lopes 2020).

The age of the oldest lava flows only provides estimates of the minimum age when each island was sub-aerial because older rocks may be buried under the most recent ones. For example, all the exposed lavas on Mount Cameroon are less than one million years old, but the mountain is built upon much older lava flows (Fitton 1987). Furthermore, volcanic activity persisted until recently on all the islands, and is still ongoing in Mount Cameroon and to a lesser extent in Bioko. This dynamic aspect of the islands is well illustrated in São Tomé, where the oldest rocks, at about 15.7 Ma, are from the small Cabras Islet, while the surface rocks of more than half of the island, including its highest peak, date between 1.5 and 0.4 Ma (Caldeira et al. 2003; Barfod and Fitton 2014). Although still poorly understood, the volcanic history of the Gulf of Guinea islands has no doubt played a major role in the assembly of their current biological communities. For instance, landslides or lava flows can split species ranges or cause extinctions, and distinct islands and islets may fuse and split over time (Milá et al. 2010; Gillespie and Roderick 2014; Ramalho et al. 2015).

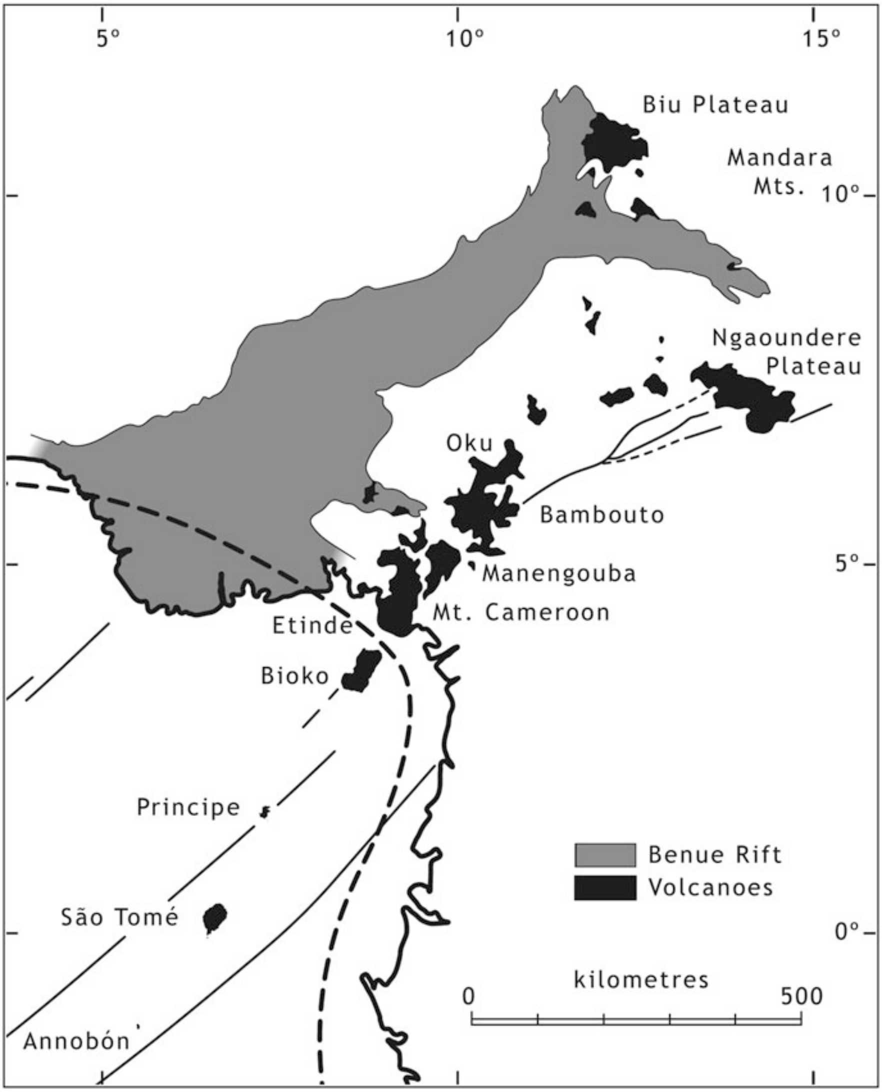

Fig. 2.5 The Cameroon line of volcanoes. Note the similarity in shape between the volcanic line (black) and the Benue Rift (grey). This was likely due to the rotation of the African plate c. 30–35 Ma that displaced the asthenospheric hot zone underlying the Benue Rift to its current position—resulting in a volcanic line without a rift and a rift without volcanoes, a unique feature on Earth. After decades of debate, the alignment of the volcanic centers is now thought to be controlled by the geometry of the northwest edge of the Congo Craton. Adapted from Lee et al. (1994)

Quaternary Sea-Level Fluctuations

Across the globe, glacial-interglacial sea-level fluctuations have shaped insular biodiversity and diversification by repeatedly connecting and isolating populations on coastal landmasses (e.g., Ali and Aitchison 2014; Rijsdijk et al. 2014; Fernández-Palacios 2016; Weigelt et al. 2016; Norder et al. 2018, 2019). Ceríaco et al. (2020) modeled the area of the islands throughout the last glacial period to the present day and demonstrated that the Gulf of Guinea islands show marked changes in area in response to eustatic sea-level fluctuations. During the exceptionally low sea level of the Last Glacial Maximum, as much as 134 m lower than present day (Lambeck et al. 2014), Bioko was connected to continental Africa, Annobón was five times its present size, Príncipe was about six times its present size, and São Tomé was approximately 50% larger than present day (Ceríaco et al. 2020; Fig. 2.6).

Topography and Hydrography

Due to recent volcanic activity, Príncipe, São Tomé, and Annobón are old islands that have the topography of young islands, including rugged mountains with steep slopes, deep valleys, volcanic chimneys, table mountains, and huge waterfalls (Figs. 2.7). The topography varies between islands. São Tomé is dominated by steep slopes and mountains across the majority of the island, with the exception of the flatter areas in the northeast (Figs. 2.7e, f). The maximum elevation reaches 2024 m at Pico de São Tomé, and several other mountain and peaks areas in the center of the island are well above 1000 m (Figs. 2.2(5), 2.7e). Príncipe has a plateau in the north but is mountainous in the south, where several peaks rise above 500 m, including Pico do Príncipe at 942 m (Figs. 2.7b). Annobón is small and steep, except for a small portion in the north, where most of the human population resides. The elevation rises considerably in the center and south, reaching 613 m at Santa Mina (Fig. 2.7h).

The available data on the terrestrial hydrography of the islands are limited. Both São Tomé and Príncipe are mostly covered by the hydrographic basin of a few large rivers in a dense network and also include several small coastal rivers (Fig. 2.7a, d). São Tomé Island has many small lagoons, estuaries, and mangroves, including the Malanza river estuary in the south, which forms the most extensive mangrove in the country. São Tomé also has a unique freshwater palustrine system in the crater of Lagoa Amélia (Fig. 2.2(7)), which is the source of the largest rivers in the north of the island (Fig. 2.7d). Annobón only has a few small streams, but Lago A Pot crater lake (Fig. 2.7g, shown in red; Fig. 2.2(8)) is a dominant feature of the island with a diameter of approximately 700 m at 150 m above sea level.

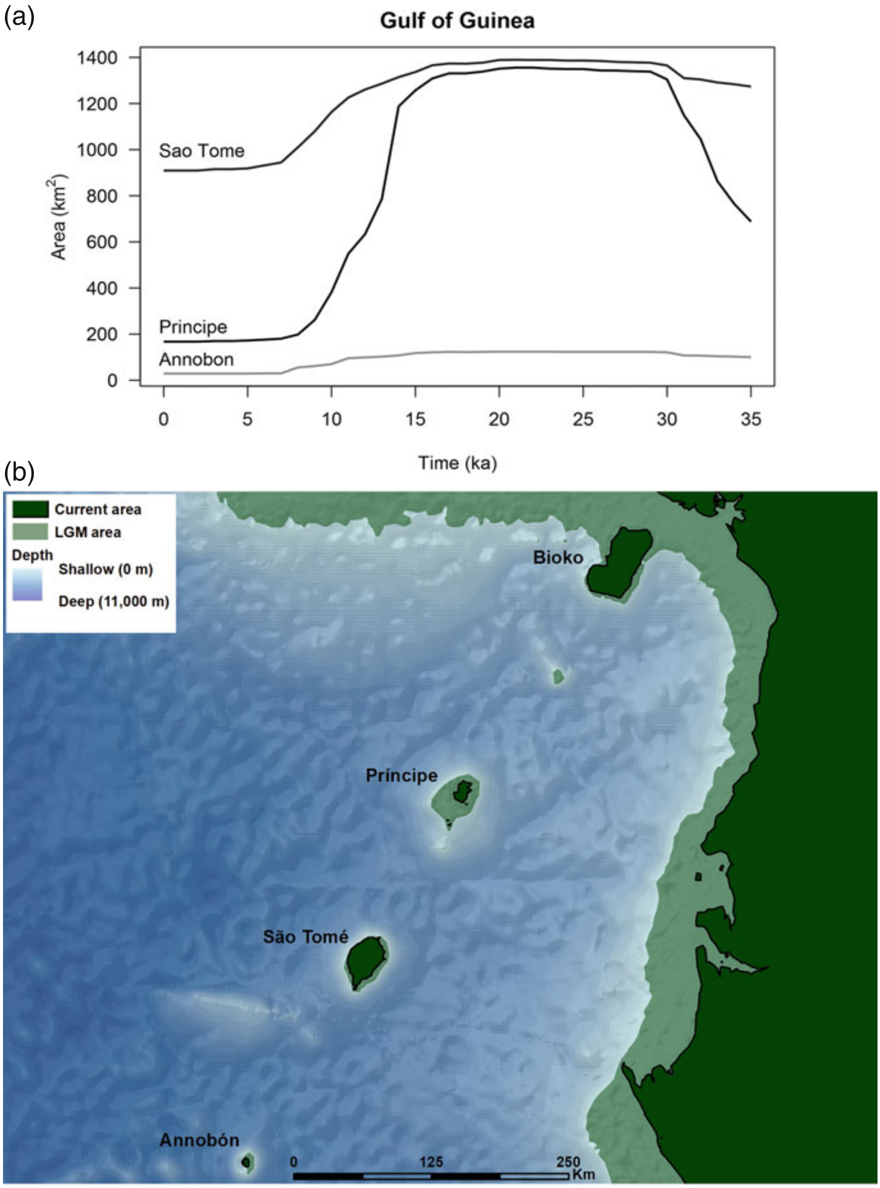

Fig. 2.6 Paleogeographic reconstructions of the Gulf of Guinea: (**a**) Area change curves of Príncipe, São Tomé, and Annobón islands; (**b**) area of islands today (dark green), and extreme area at the last glacial maximum (LGM, approximately 21 ka; light green). Adapted from Ceríaco et al. (2020)

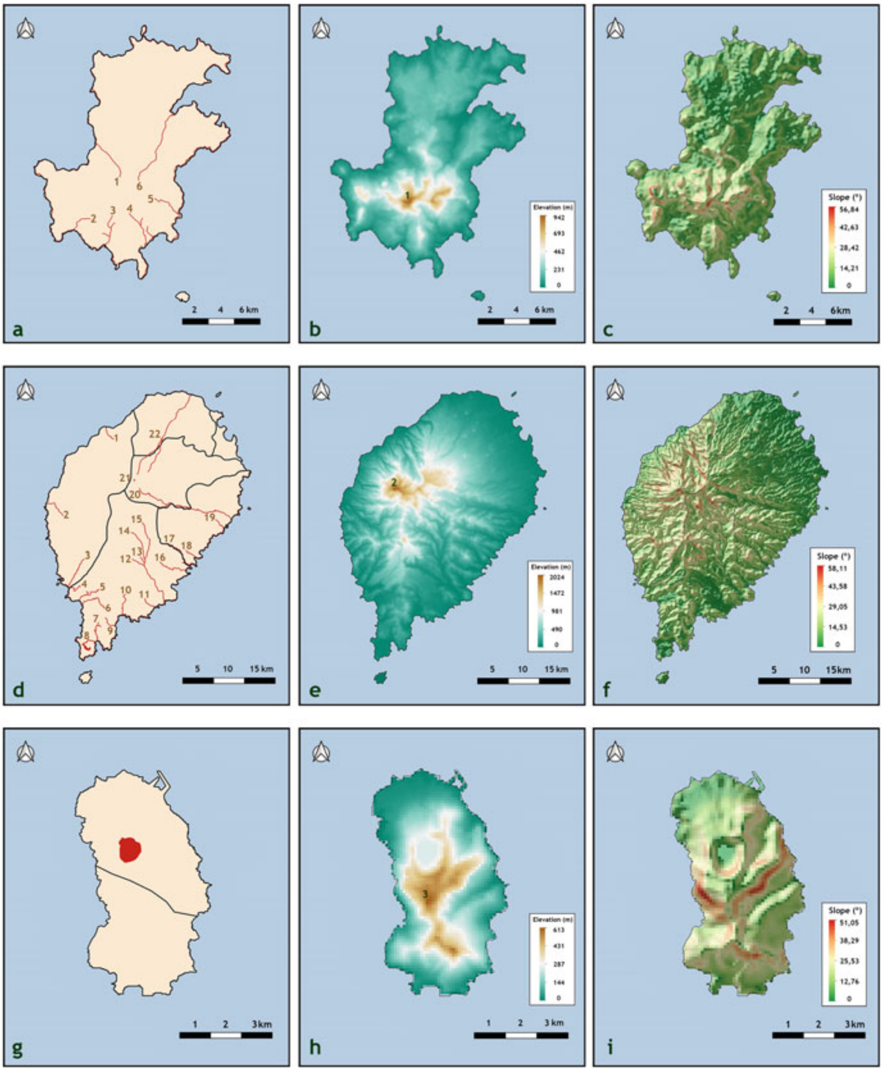

Fig. 2.7 Overview of the hydrography and topography of (**a**, **b**, **c**) Príncipe, (**d**, **e**, **f**) São Tomé, and (**g**, **h**, **i**) Annobón. For each island, elevation is presented in meters above sea level and steepness in degrees. Main rivers and waterbodies: São Tomé Rivers (**d**): 1—Provaz; 2—Lembá; 3—Xufexufe; 4—Quija; 5—Mussacavú; 6—Pedras; 7—Gumbela; 8—Malanza; 9—Gogô; 10—Caué; 11—Martim Mendes; 12—Miranda Guedes; 13—João Nunes; 14—Ana Chaves; 15—Ió Grande; 16—Angobó; 17—Angra Toldo; 18—Pedra Furada; 19—Ribeira Afonso; 20—Abade; 22—Ouro. São Tomé Crater Lake: 21—Lagoa Amélia. Príncipe Rivers (**a**): 1—Ribeira Banzú; 2—Ribeira São Tomé; 3—Ribeira Porco; 4—Chibala; 6—Papagaio. Annobón (**g**) has no significant rivers; the crater lake Lago A Pot is shown in red

Geology and Soils

The geology of São Tomé and Príncipe has been well studied since the early twentieth century. This is partly due to the importance of geology and soils for agriculture, which has been the major driver of the local economy for centuries (Lains e Silva 1958; Lains e Silva and Cardoso 1958; Rodrigues 1974). The first overview of the geology of São Tomé Island was provided by Carvalho *in* Henriques (1917), followed by a more detailed study on the microscopic characteristics of its rocks (Carvalho 1921). Teixeira (1948–1949, 1949) provided a more complete overview of the geology of the islands, followed by a petrological work by Pereira (1943). The most extensive and complete contributions to the geology of the islands were provided by the Portuguese geologist João Manuel Cotelo Neiva (1917–2015), whose work was fundamental to understanding the geochemistry and geomorphology (Neiva 1946, 1954, 1955a, b, 1956a, b, c; Neiva and Pureza 1956; Neiva and Neves 1956). Assunção (1956, 1957) and Barros (1960) also contributed to our understanding of the geochemistry. In the twenty-first century, new research on the geology of São Tomé (Munhá et al. 2002; Caldeira et al. 2003; Caldeira 2006) has resulted in updated geological maps (Munhá et al. 2006a, b, c, d, 2007). By contrast, the geology of Annobón has received far less attention. The first information on its geological history and composition was provided by Schultze (1913), followed by studies by Tyrrell (1934), Fuster Casas (1954), Cornen and Maury (1980), and Liotard et al. (1982). More recently, De Castro and De la Calle (1985) and Fa (1991) provided an overview of the geology of Annobón. On Príncipe, basaltic rocks predominate in the north and phonolites and tephrites in the south, whereas São Tomé and Annobón are mostly built by basaltic lavas (Fig. 2.8). A more detailed description of the geology of the islands is provided by Schlüter (2008).

Regarding the soils of Príncipe and São Tomé, Lains e Silva (1958) and Cardoso (1958) drafted the first maps, with a more comprehensive map and revision by Cardoso and Garcia (1962). Other works were done by Pissarra and Rocha (1963) and Pissarra et al. (1965). The dominant soil types of Príncipe and São Tomé are highly weathered, such as Ferralsols and Lixisols (Lains e Silva 1958; Cardoso and Garcia 1962; Diniz and Matos 2002), which are typical of tropical climates. Vertisols are restricted to the dry north and northeast of São Tomé, while Lithosols can be found everywhere on the island, often associated with ridges, steep slopes, and cliffs near the coast (Diniz and Matos 2002). Fluvisols, as expected, are mostly associated with riparian areas. Very little is known about the soils of Annobón, other than that they are ultrabasic with low silica and high proportions of ferromagnesian elements (De Castro and De la Calle 1985; Fa 1991).

The only reported fossils are from Príncipe and date to the Miocene (Teixeira 1949; Silva 1956a, b, 1958a, b; Serralheiro 1957). These include marine organisms such as gastropods, bivalve mollusks, coelenterates, echinoderms, and fishes' teeth, but also calcareous algae, radiolarians, and foraminifera. Modern foraminifera are known from both Príncipe and São Tomé beaches (Moura 1961). A palaeoecological study is currently taking place on Príncipe and São Tomé collecting data from

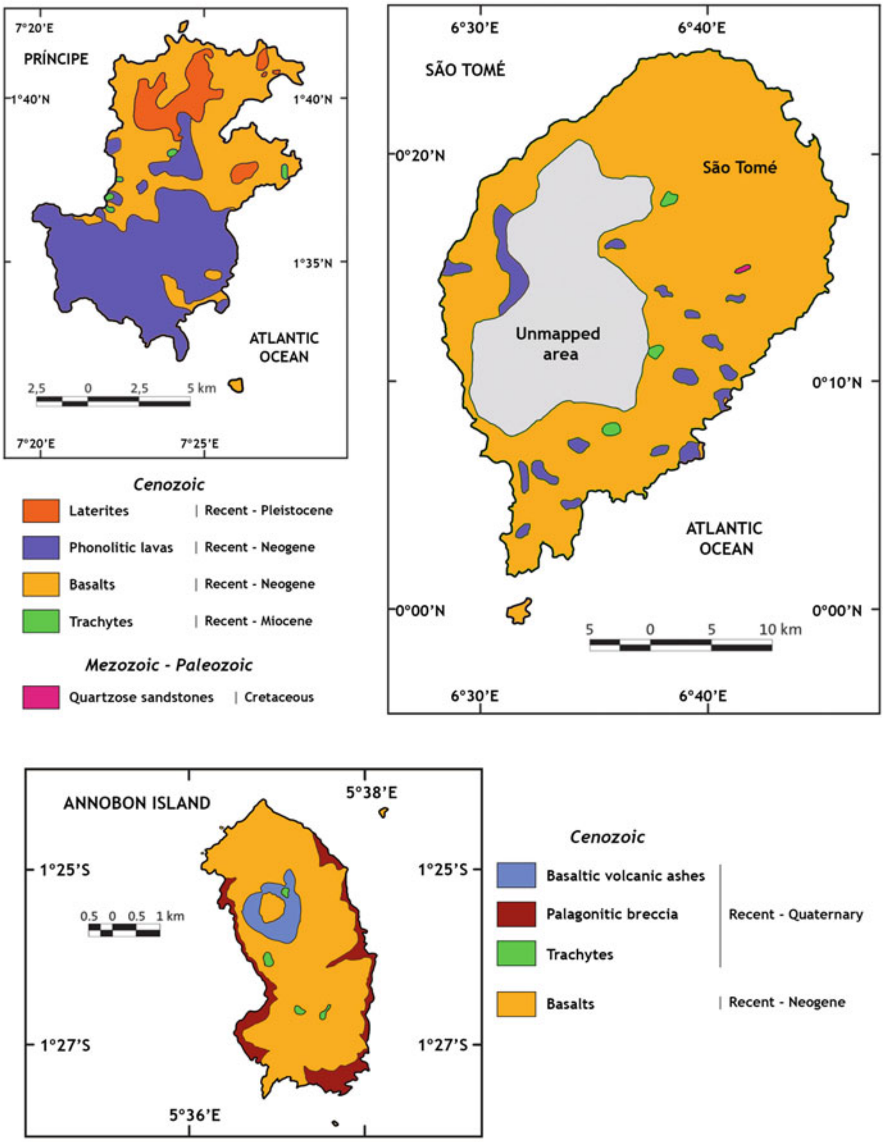

Fig. 2.8 Geological overview of the islands of Príncipe, São Tomé, and Annobón. Adapted with permission from Springer Nature Geological Atlas of Africa by Schlüter © Springer-Verlag Berlin Heidelberg 2006 (2008)

pollen, spores, charcoal, and sedimentology to reconstruct ecosystem changes associated with glacial cycles and the impacts of human activities (unpublished data by Alvaro Castilla-Beltrán).

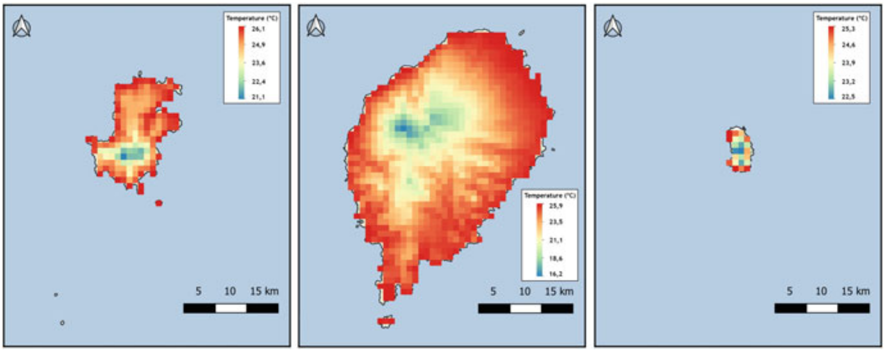

Fig. 2.9 Annual average temperature (in Celsius) for the islands of Príncipe, São Tomé, and Annobón. Data obtained from the Global Solar Atlas 2.0, provided by the World Bank Group

Climate

The Gulf of Guinea oceanic islands have an oceanic equatorial climate. Mean temperatures are above 25 °C at sea level but decrease with altitude (Fig. 2.9). The year is divided into rainy and dry seasons, which are determined by the Intertropical Convergence Zone, and by the interaction between the southern monsoon winds from the Atlantic Ocean and the northern dry harmattan winds from the Sahara. Seasons differ between the continental and the oceanic sectors. On Mount Cameroon and Bioko, the main dry season is from December to March, and a shorter dry season occurs from July to August (Juste and Fa 1994). In Príncipe and São Tomé, the long dry season, locally known as *gravana*, extends from June to mid-September, while a shorter dry season, the *gravanito*, lasts for a few weeks that may fall anywhere between mid-December and mid-March (Lains e Silva 1958). Annobón, south of the Equator, has a single extended dry season from mid-May to the end of October (Jones and Tye 2006).

Due to their small area and heterogeneity, modern rainfall and climate measurements based on remote sensing likely do not accurately describe the climate of Príncipe, São Tomé, and Annobón. To the best of our knowledge, until recently Annobón had no functional meteorological station, while there was only one on Príncipe and five on São Tomé, of which only one had been collecting long-term data systematically (Chou et al. 2020). This network was greatly improved over the last decade (https://www.thegef.org/project/strengthening-climate-information-and-early-warning-systems-sao-tome-and-Príncipe-climate), but detailed long-term information on the climate of the islands is still lacking.

The topography of Príncipe and São Tomé islands is similar, resulting in a similar distribution of climatic zones (Diniz and Matos 2002). The high relief areas of the south and center intercept the predominant warm and moist south-westerly winds, creating a striking north–south divide in precipitation (the Foehn effect). The southern-facing regions are "Super Humid," with annual precipitation above

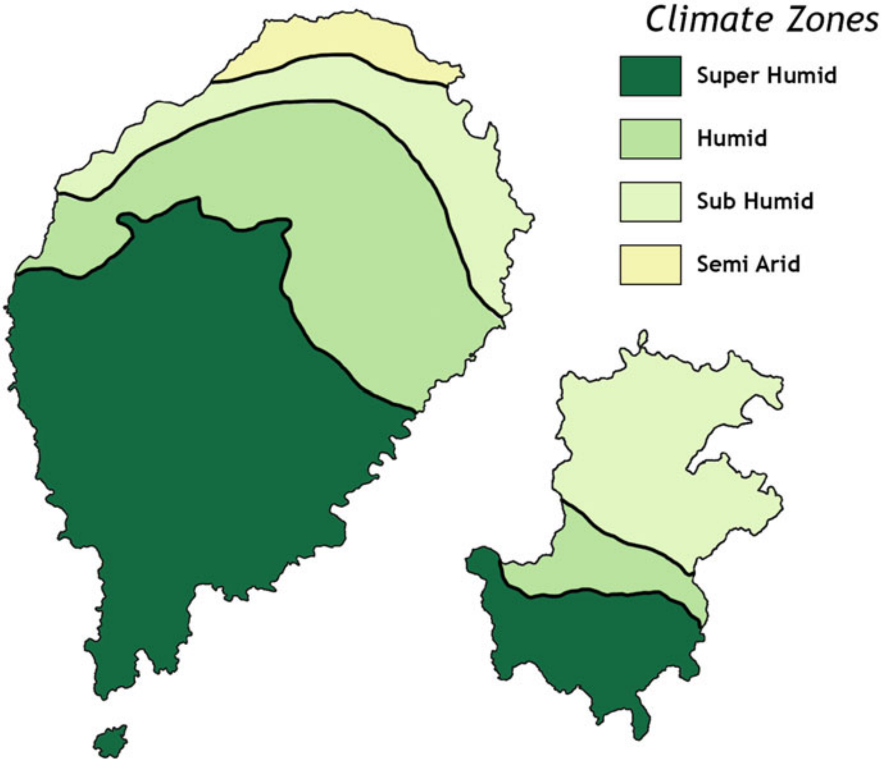

Fig. 2.10 Climatic zones for the islands of São Tomé (left) and Príncipe (right). Adapted from Diniz and Matos (2002)

3000 mm, and often much higher (c. 5000 mm on Príncipe, above 7000 mm on São Tomé—Diniz and Matos 2002), enhanced by extremely high humidity levels and low sun exposure (Fig. 2.10). The north, under the rain-shadow effect, has climatic belts associated with the decreasing levels of humidity with decreasing altitude. The higher slopes benefit from the monsoon winds that pass over the peaks, and have precipitation levels between 1500 and 3000 mm, making the "Humid" belt (Fig. 2.10). Lower down, from the coast to about 400 to 550 m, moderate slopes (below 15%) receive between 1000 and 1500 mm of rain per year, making up the "Sub-Humid" belt, which has a well-defined rainy season (Fig. 2.10). Finally, only on São Tomé, the littoral area in the flatter N-NE platform, below 1000 m, has a "Semi-Arid" belt that has annual precipitation levels between 600 and 1000 mm (Fig. 2.10). This general zonation, with more humid climates in the south and drier climates in the north, also seems to apply to Annobón and to the continental islands. Annual precipitation on the southwestern slopes of Mount Cameroon may be over 10,000 mm, and between 1500 and 2000 mm in the northern slopes. In the south of Bioko Island, annual precipitation can be over 11,000 mm (Juste and Fa 1994) while the capital Malabo, in the north, receives <2000 mm/year.

Wind and Ocean Currents

Understanding the wind and ocean currents is fundamental to infer potential colonization pathways for island fauna and flora. The prevailing winds in the Gulf of Guinea are the southwestern monsoon winds and the northern dry harmattan winds. The southwestern monsoon winds are unlikely to have dispersed colonizers from continental Africa but may have played a role in southwest-to-northeast dispersal between islands. During glacial cycles, the northern dry harmattan winds extended their influence southward, displacing the meteorological equator further south (Lézine et al. 1994), likely having a more important role in bringing colonizers to the island during those periods.

Data on sea surface currents originate from a combination of historical ship drifts, hydrographical data, surface-drifting buoy trajectories, and Argo floats surface drifts (Richardson and Walsh 1986; Arnault 1987; Stramma and Schott 1999; Renner 2004; Lumpkin and Garzoli 2005; Ollitrault and Rannou 2013). The Gulf of Guinea is dominated by two currents (northward and eastward) that follow the shoreline. In the north, the eastward current, also known as Guinea Current (GC), moves west to east along the southern coast of West Africa, and, when reaching the Biafra Bay, converges with the northward current and becomes more diffuse, turning back westward around the Equator (Feiler 1988; Haft 1993; Dupont et al. 2000; Fig. 2.11). In the southeast, the northward current, known as the Benguela Current (BC), moves along the northern coast of South Africa, the coast of Namibia, and is diverted west to the Atlantic around the mouth of the Cunene River, the natural and political border between Namibia and Angola. It also feeds the South Equatorial Current (SEC), which represents the northern limb of the South Atlantic Ocean subtropical gyre (Philander 2001; Rodrigues et al. 2007). Moving north, the coast of Angola is dominated by two different currents, the Benguela Coastal Current (BCC), a cold and less-saline northward flow, and the Angola Current (AC), a fast and narrow southward geostrophic flow of warm and saline water found between the equatorial band and about 15°S. The intersection of these two currents, around 15°S, is known as the Angola Benguela Front (Hopkins et al. 2013; Lass and Mohrholz 2008, their Fig. 1; Houndegnotono et al. 2021, their Fig. 1b). The discharge of the Congo River, which extends offshore as the Congo River plume, is a thin layer (3 m thick at the river mouth) of fresher/lower salinity water. This freshwater plume is entrained mostly westward, through Ekman-driven circulation in which the wind deflects surface water to the left of its direction in the southern hemisphere.

Ocean currents are important for understanding the biogeographic history of aquatic organisms and terrestrial organisms that disperse in water—such as some seed plants—but, in the Gulf of Guinea, they may also hold the key to understanding how many non-volant, non-swimming, or salt-intolerant species made their way to the islands (Melo et al. 2022). The prevailing hypothesis to explain the origin of such unlikely oceanic island taxa proposes that they came as passengers of natural rafts that drifted to the islands along "freshwater pathways" on the ocean surface (Measey et al. 2007). Such rafts would reach the islands along "freshwater pathways" created

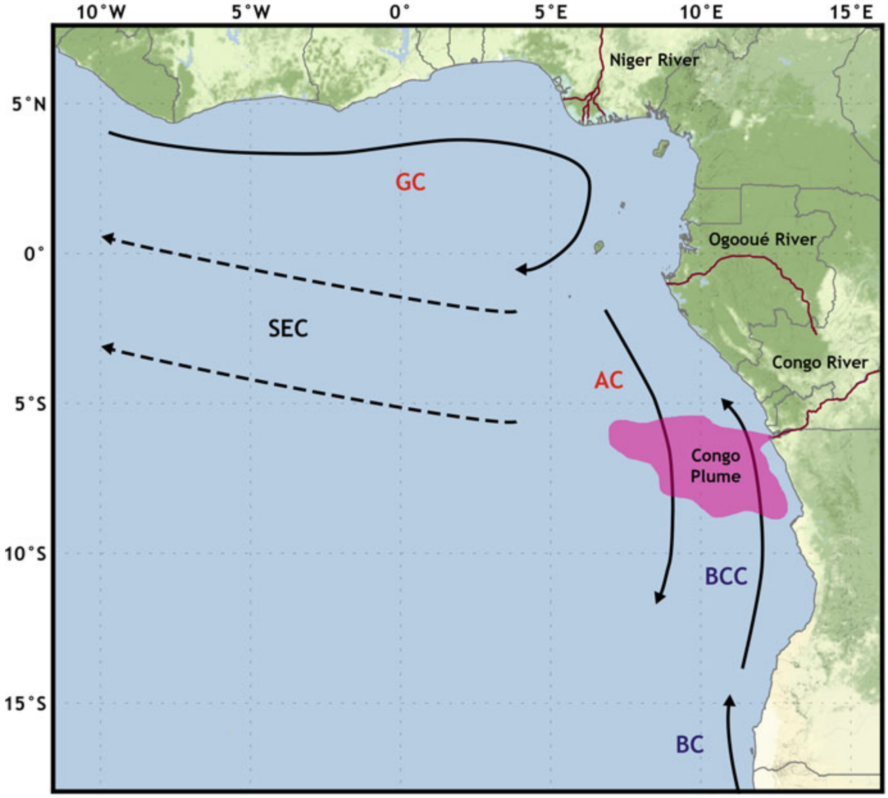

Fig. 2.11 Main ocean currents in the Gulf of Guinea. Angolan Current (AC), Benguela Current (AC), Benguela Coastal Current (BCC), Guinea Current (GC), and South Equatorial Current (SEC). Warm currents in red; cold currents in dark blue

by the large input of freshwater plumes and precipitation into the Gulf of Guinea (Fig. 2.11; Dessier and Donguy 1994; Large and Yeager 2009; Hopkins et al. 2013; Berger et al. 2014). Because saltwater is denser than freshwater, during the rainy season the ocean surface in the Gulf of Guinea exhibits reduced salinity—a well-known phenomenon by local fishermen (Measey et al. 2007; Hopkins et al. 2013). These "freshwater pathways" would give the rafts some protection against saltwater as they cross the sea.

The Gulf of Guinea receives the freshwater discharge of three major rivers that originate from different regions: the Niger in West Africa, the Congo in East-Central Africa, and the Ogooué in West-Central Africa (Fig. 2.12). The Congo River is only second to the Amazon in terms of discharge, having an average discharge of $40 \times 10^3\ m^3 s^{-1}$ (Mahé and Olivry 1999), while the Niger River has about $7 \times 10^3\ m^3 s^{-1}$ (Dai and Trenberth 2002). When reaching the ocean, these waters are directed toward the islands by the surface currents of the Atlantic Ocean.

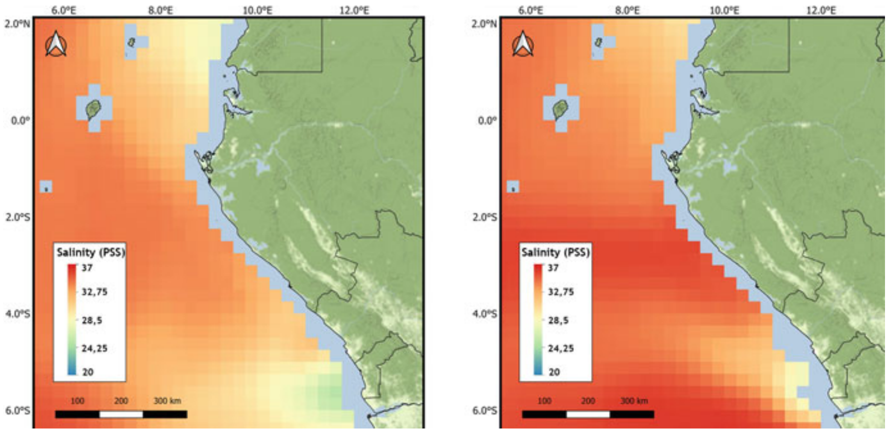

Fig. 2.12 Monthly average sea surface salinity for the months of February (left) and July (right) 2021. Values displayed with a range of 20 and 37 using the Practical Salinity Scale (PSS), roughly equivalent to parts per thousand of salt. Data from the Remote Sensing Systems SMAP Ocean Surface Salinities [Level 3 Monthly] Dataset, Version 4.0 validated release (Meissner et al. 2019)

Although the mouth of the Ogooué River is the closest to the islands (approximately 250 km), the currents in the Gulf of Guinea direct the freshwater plumes from the Niger and Congo rivers toward the islands (Richardson and Walsh 1986), such that vegetation rafts originating in the more distant West and East African drainages may also reach the islands.

Conclusions

Despite their small area, the oceanic islands of the Gulf of Guinea include a wealth of geological substrates and topographical features that underlie the development of diverse soils and micro-climates (Fig. 2.2). This diversity of geological features has been recognized by ten formations being proposed as geosites on São Tomé Island, which have a wide range of cultural, scientific, and scenic values (Henriques and Neto 2015). These landscapes have also promoted the appearance of distinct ecosystems (Dauby et al. 2022) and species (Melo et al. 2022). The location of the islands, at moderate distances from the mainland and at the crossroads of freshwater plumes from three large rivers, has likely further contributed toward the assembly of their rich biological communities. These rivers are thought to have been the source of natural rafts bringing species that would otherwise be unable to cross saltwater barriers.

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Chapter 3
Classification, Distribution, and Biodiversity of Terrestrial Ecosystems in the Gulf of Guinea Oceanic Islands

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Abstract The oceanic islands of the Gulf of Guinea display a large diversity of environmental conditions and biological communities, whose interactions have contributed to the development of a great variety of ecosystems, from mangroves to montane grasslands. Human activities have extensively and profoundly altered many of these natural ecosystems over the past five centuries. We review key studies to propose an updated classification map of terrestrial ecosystems, taking advantage of up-to-date spatial information on abiotic gradients and biological distributions. To guide future research and conservation programs, we highlight challenges and pending questions regarding our understanding of the structure, integrity, and dynamics of terrestrial ecosystems in these islands.

Keywords Abiotic gradients · Biological communities · Introduced species · Novel ecosystems · Topography · Vegetation types

Introduction

The oceanic islands of the Gulf of Guinea (GGOI) comprise three islands: Príncipe, São Tomé (together forming the Democratic Republic of São Tomé and Príncipe), and Annobón (part of the Republic of Equatorial Guinea). Despite their small size (c. 1000 km^2), their combined human population is ca. 225,000 inhabitants (INEGE 2017; INESTP 2020), and they are also host to a rich endemic fauna and flora (Jones 1994).

The tropical humid climate, complex topography, altitudinal gradients, and isolation (distance to mainland from 220 to 350 km) are often invoked to explain the endemic-rich biodiversity of these islands (Jones 1994). The abiotic gradients generate a diversity of habitats with distinct biological communities, whose interactions contribute to the development of a great variety of natural ecosystems, from mangroves to montane grasslands (Monod 1960). Over the past five centuries, human activities have profoundly altered most of these natural ecosystems across large areas (Eyzaguirre 1986). Impacts have varied in intensity across time and space among the three islands, but agricultural land use in particular has intensified (Jones et al. 1991), which has likely facilitated the expansion of introduced species (e.g., Soares et al. 2020).

The first attempts to delineate the ecosystems of the GGOI date back to the first half of the twentieth century, and aimed at documenting vegetation types (Henriques 1917; Chevalier 1938–1939; Exell 1944). These studies relied almost entirely on variations in vegetation physiognomy and on the degree of human interference. These authors paid particular attention to defining altitudinal vegetation belts. Other studies tried to identify phytogeographical units based mostly on the co-distribution of plant species, but ended up having to rely heavily on abiotic proxies (Stévart 1998; Ogonovszky 2003). Phytogeographical units can be misleading for identifying ecosystems because biogeographical processes can lead to different species assemblages in similar ecosystems. However, given the relatively small size of these islands, we can assume that the co-distributions of species within each island reflect environmental conditions and anthropogenic disturbances, while biogeographical processes, such as limited dispersal and speciation rates, are negligible.

Recently, many large-scale studies have inferred the integrity, distribution, and dynamics of ecosystems, taking advantage of the increasing availability of remote sensing data (e.g., Hansen et al. 2013; Gosling et al. 2020; Vancutsem et al. 2021). Unfortunately, these products are of little relevance for the GGOI, due to their coarse resolution and unavailability of high-quality aerial images without atmospheric obstructions, such as haze and aerosols.

In this chapter, we review the key studies that attempted to document the terrestrial ecosystems of the islands, and then propose an updated classification, taking advantage of up-to-date spatial information on abiotic gradients and biological communities to map proposed vegetation types. Finally, to guide future research and conservation efforts, we identify several challenges and pending questions regarding our understanding of the structure, integrity, and dynamics of the terrestrial ecosystems in the GGOI.

Ecological Setting and Previous Classifications

São Tomé Island

Abiotic Gradients

Rainfall measurements using remote sensing lack the accuracy required for a small and heterogeneous area like São Tomé (Chou et al. 2020). Thus, our understanding of rainfall patterns must still rely on the rough isohyets drawn from 50-year-old observations (Bredero et al. 1977). These isohyets show that annual rainfall varies strongly across the island, ranging from <1000 mm in the northeast to more than 7000 mm in the southwest (Fig. 3.1). Four seasons are recognized: a humid season from mid-September to mid-December, a mild dry season from mid-December to mid-march (“gravanito”), a humid season from mid-March to June, and a prolonged dry season from July to mid-September (“gravana”).

The rainfall pattern can be explained by the rugged topography and the resulting rain shadow (“foehn effect”; Ceríaco et al. 2022). Elevation reaches a maximum of 2024 m at Pico de São Tomé, to the northwest of the center of the island, which is surrounded by a multitude of smaller peaks, ridges, and steep slopes. Overall, the island is divided by a north–south ridge, extending from Pico de São Tomé to Cabumbé, which separates the island into a wetter west flank and a drier east flank. Apart from the northeast and a few flat areas and gentle slopes in the south and southeast, the topography of most of the island is complex and dominated by steep ridges and mountains (Fig. 3.1).

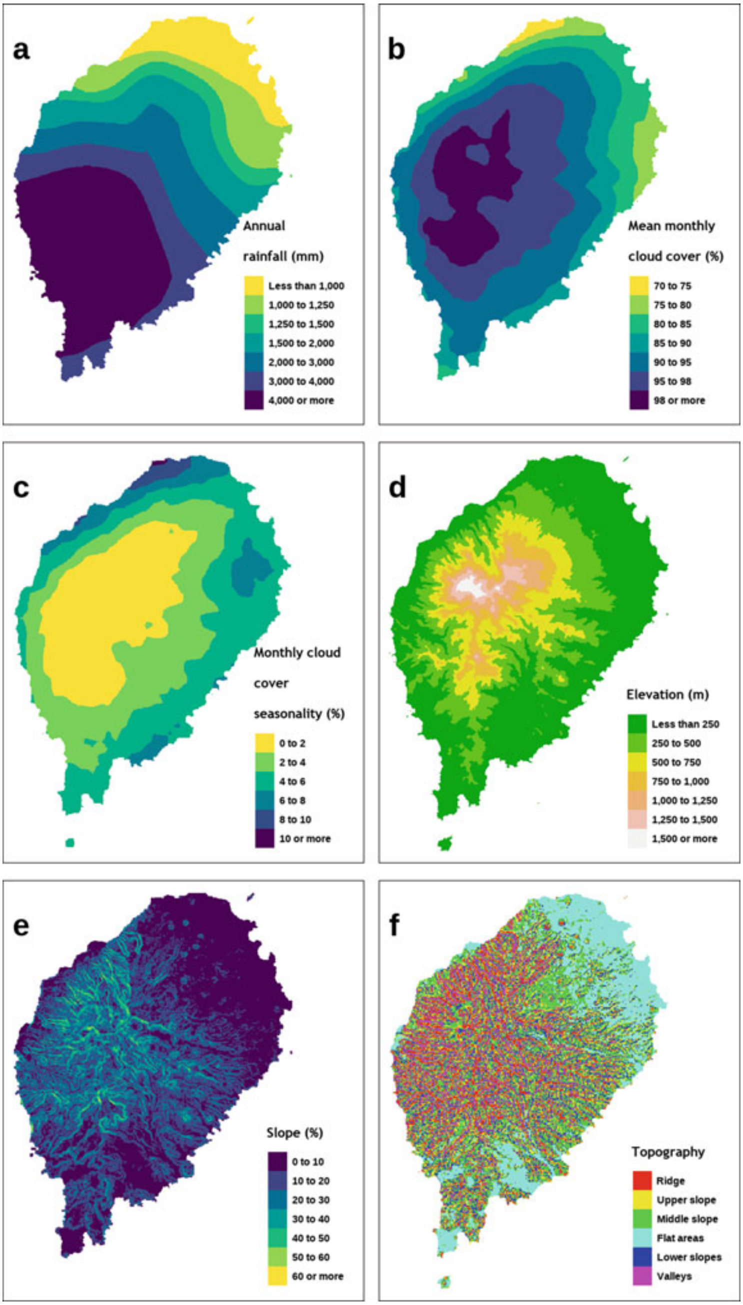

Fig. 3.1 Main physico-climatic gradients on São Tomé Island. Sources of data can be found on https://github.com/gdauby/stpa_ecosystems_review

Cloud cover influences biological processes and species distribution (Wilson and Jetz 2016). On São Tomé, according to remotely sensed data, the mean monthly cloud cover ranges from 70% in the extreme north to nearly permanent in the western highlands (Fig. 3.1). Rainfall and cloud cover do not fully coincide, although together they typify the constant high moisture on the west side of the island. Persistent cloud cover coincides with altitudes between 500 and 1500 m on the west flank, and above 1000 m on the south and east flanks as a result of the foehn effect. Intra-annual cloud cover varies little, but reflects the stronger seasonality in the north (Fig. 3.1).

São Tomé soils have been studied and mapped, and their properties are conditioned by topography and climate that often vary at fine scales (Cardoso and Garcia 1962). The most frequent soil types are highly weathered, such as Ferralsols and Lixisols, characteristic of tropical climates. Vertisols, Lithosols, and Fluvisols are noteworthy because they interact with vegetation. Vertisols are heavy clay soils frequently associated with grasslands and forests that develop deep wide cracks when dry, making them difficult to use for agriculture (Kovda 2020). This soil type is restricted to the dry north and northeast (Fig. 3.1). Lithosols are thin soils that have very little organic matter, and can be found everywhere on the island, often associated with ridges, steep slopes, and cliffs near the coast (Diniz and Matos 2002). Fluvisols, derived from alluvial deposits, are nutrient-rich, often associated with large riverbanks, and can be flooded or have weak drainage (IUSS Working Group WRB 2015).

Human Disturbance

Around three-quarters of the native vegetation of São Tomé has been lost, most of which was converted into large plantations (Fig. 3.2a; Soares et al. 2020). This transformation started in the late fifteenth century when humans began colonizing the island, clearing large extents of forest mostly in the dry northern coastal areas to establish sugarcane plantations (Eyzaguirre 1986). In the early sixteenth century, the island became a top producer of sugar globally, developing a cash crop economy that collapsed later that century (Garfield 1979), slowing down the deforestation rate. Throughout the seventeenth and eighteenth centuries, the island became an important slave trading post and the traditional "gleba" agroforestry system (based on tree and root crops grown in dense mixed stands with minimal tillage) expanded (Eyzaguirre 1986). In the nineteenth century, the deforestation rate increased and expanded further inland and upland, giving way to intensive plantations dedicated mostly to coffee and cacao, but also to oil palm, coconut, quinine, and cinnamon. This period saw the spread of shade plantations that can be defined as plantations where a canopy is maintained above crops (typically cacao or coffee). The canopy is often composed of introduced tree species (typically of the *Erythrina* genus).

Deforestation in São Tomé reached its peak early in the twentieth century, when the island became the world's largest producer of cacao. For various reasons, this system became economically unsustainable and during the late 1930s many

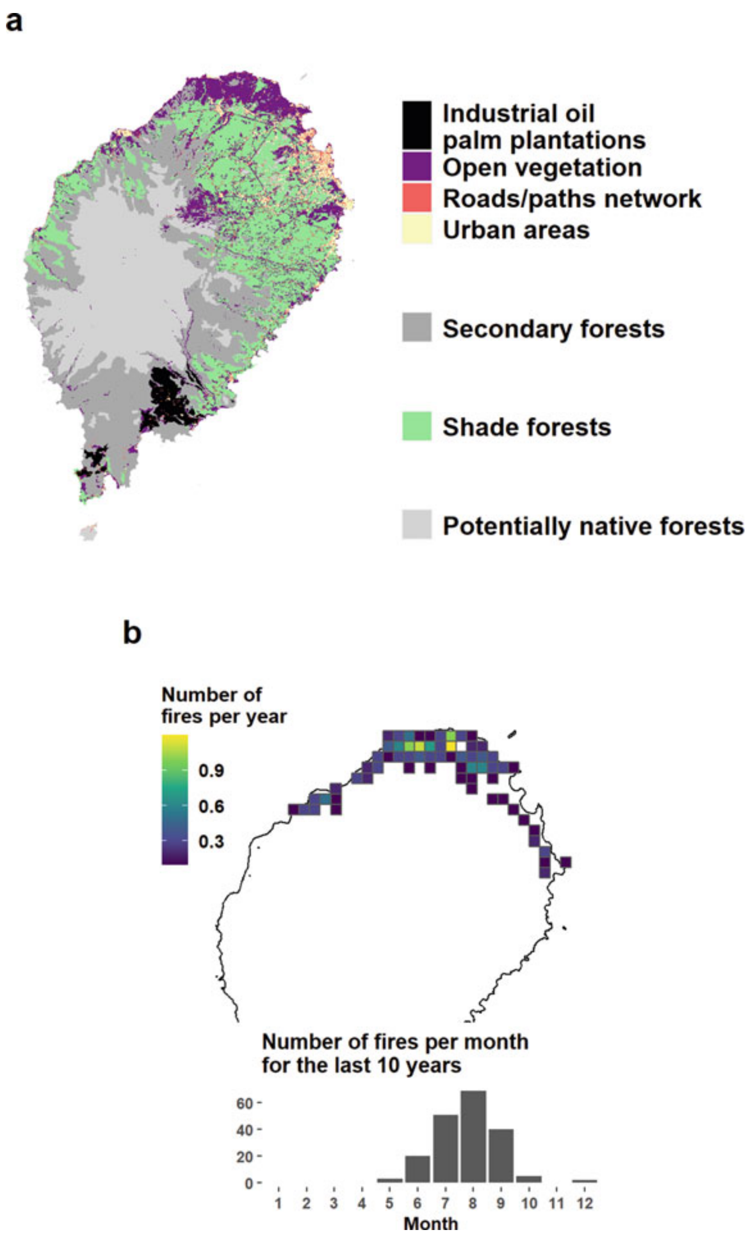

Fig. 3.2 (**a**) Degraded or transformed land cover on São Tomé. Note that the "open vegetation" category includes both agricultural lands and savanna-like vegetation (Adapted from Soares et al. 2020). (**b**) Annual fire frequency (data for the last 10 years). The inset barplot shows the distribution of fires along the year

Table 3.1 Total area and relative importance of transformed or degraded land cover in each island (Calculated from Norder et al. 2020; Soares et al. 2020; Frazer Sinclair and Yodiney dos Santos, unpublished data). Note that the open vegetation category also includes naturally open vegetation type

Land cover	Annobón	São Tomé	Príncipe
Open vegetation	2.8 km^2 (13.4%)	92.5 km^2 (10.9%)	6.6 km^2 (4.8%)
Urban areas	1.8 km^2 (8.5%)	23.3 km^2 (2.7%)	1.9 km^2 (1.4%)
Industrial palm plantations	–	23.4 km^2 (2.7%)	–
Roads/paths network	–	17.8 km^2 (2.1%)	2.9 km^2 (2.1%)
Secondary forest	–	240.6 km^2 (28.2%)	37.4 km^2 (26.8%)
Shade forest	–	218.6 km^2 (25.6%)	41.3 km^2 (29.6%)

plantations were abandoned, creating large extents of secondary forests in the higher altitudes, while the flatter lowland remained as plantations. Following independence in 1975, and especially after land privatization in the early 1990s, logging and residential areas expanded significantly, especially in the shade plantations. Meanwhile, swidden agriculture emerged to satisfy local food needs, producing horticultural crops such as potatoes, maize, cabbage, beans, and carrots (Eyzaguirre 1986). Strong demographic growth led to an increase in timber consumption (the main building material in the country), resulting in increasing pressure on forest resources (Salgueiro and Carvalho 2001). More recently, agro-industrial concessions to foreign companies have reconverted large areas of secondary forest to export crop plantations, such as oil palm, cacao, and coffee (Oyono et al. 2014).

This complex history led to the patchwork of land uses that characterizes the landscape on São Tomé (Fig. 3.2a, Table 3.1; Soares et al. 2020). Native forests (ca. 26.4% of the island) are mostly found in the rugged wetter areas at the center and southwest. Around these are mostly secondary forests (ca. 30.5%), resulting from agricultural abandonment, notably more widespread in the south. Agroforests (ca. 28.5%), comprising the traditional “glebas” but also more intensive shade plantations of cacao and coffee, are dominant in the northeast and in the south along the coast. The remainder of the island is characterized by non-forested land uses (ca. 14.5%), including urban areas and anthropogenic savannas in the northern coast and horticultural areas at higher altitudes. Terrain ruggedness predominantly shapes the extent of remaining native vegetation cover, suggesting that topography constrains human occupation across the island (Norder et al. 2020). Anthropogenic impacts have been felt mostly in the flat lowlands of the drier north, where fire maintains large extents of open vegetation, even though other areas are not spared. At higher altitudes, for instance, the distinct climate and fertile soil has promoted agricultural expansion of crops like quina, arabica coffee, cinnamon, and annuals, especially in the flatter areas around Monte Café.

Besides land-use change, human disturbance is also felt through more subtle modifications, namely through the exploitation of forest resources and the facilitation of introduced species. Logging (Espírito et al. 2020), hunting (Carvalho 2015), silviculture, and the gathering of other forest products such medicinal plants

(Madureira et al. 2008) are known to have impacts on the vegetation and overall functioning of forest ecosystems. Being at the crossroads of the Atlantic slave trade, having fertile soils and diverse ecological conditions, São Tomé was often used as an agricultural experimental ground, receiving crops from all over the world (Ferrão 2005), as well as many other species of flora (Figueiredo et al. 2011) and fauna (Dutton 1994). Agriculture greatly changed the ecology of the island, creating the conditions for many introduced species to expand across the island (Soares et al. 2020) that sometimes also became invasive in native undisturbed forests (Lima et al. 2014; Panisi 2017; De Menezes and Pagad 2020).

Previous Vegetation and Phytogeographical Classification

Previous works aimed to document vegetation types focused mostly on its physiognomy, the intensity and nature of anthropic impacts, and the use of abiotic gradients as proxies, such as altitude and precipitation (Table 3.2).

Chevalier (1938–1939) was the first to mention different vegetation types. However, it was Exell (1944) who proposed a delimitation and detailed description of several vegetation types. Exell recognized mangroves and coastal dunes as distinct and narrowly distributed vegetation types, and used three altitudinal belts to distinguish the remaining vegetation: low-altitude (mostly degraded) forests (up to 700 or 900 m), montane rainforests (between 800 and 1400 m), and mist forests (above 1400 m; Fig. 3.3).

Silva (1958) distinguished “primary” from “secondary” vegetation, and “climate-driven” from “edaphic-driven” vegetation, including summit shrubland and dry northern savannas in the latter (Fig. 3.3c). This approach also acknowledged the crucial role of human activities in transforming the landscapes of São Tomé.

Table 3.2 Key references proposing spatial delimitations of the islands in ecological, ecosystems, or phytogeographical units

References	Island(s)	Content	Criteria
Mildbraed (1922)	Annobón	Five vegetation types	Flora and vegetation physiognomy, elevation
Exell (1944)	São Tomé and Príncipe	Elevational belt	Abiotic gradients
Silva (1958)	São Tomé and Príncipe	Map of vegetation units	Elevation and land use
Monod (1960)	São Tomé and Príncipe	Documentation of vegetation type	Elevation, presence of endemic plant species
Peris (1962)	Annobón	Six vegetation types	Flora and vegetation physiognomy, elevation, agricultural activities
Stévart (1998)	São Tomé and Príncipe	Map of vegetation units	Elevation, annual rainfall, presence of orchids species
Diniz and Matos (2002)	São Tomé and Príncipe	Map of agro-ecological entities	Field observations, topography, edaphic properties, elevation

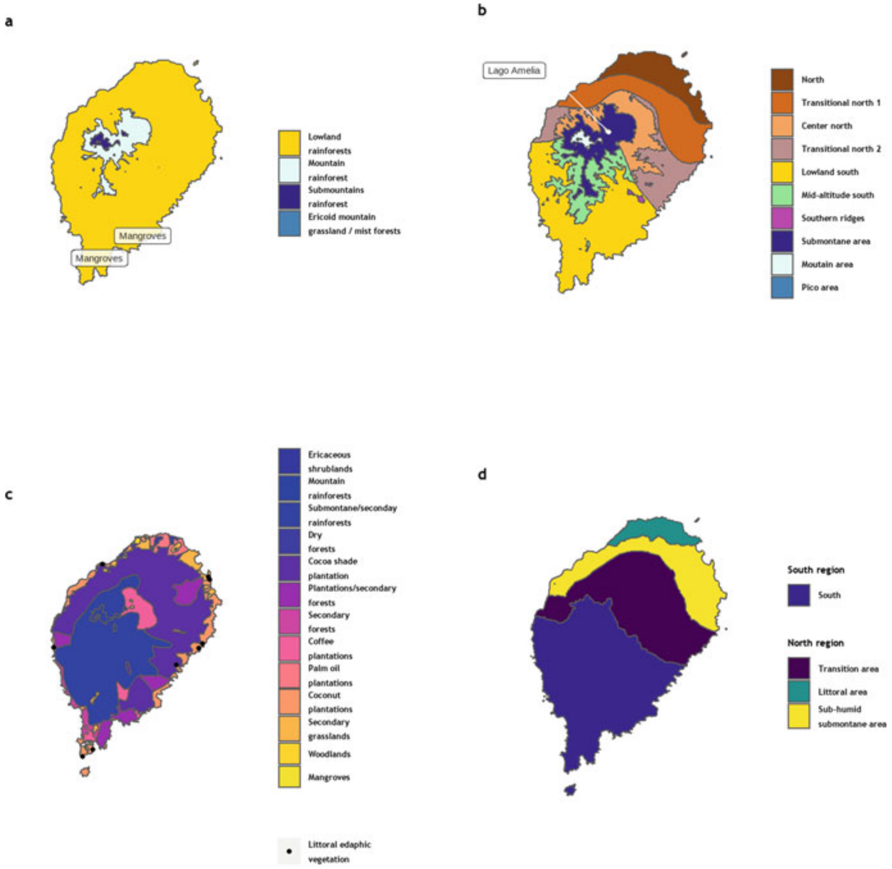

Fig. 3.3 Previous delimitations of vegetation types or phytogeographical territories on São Tomé Island. (a) According to Monod (1960) and Exell (1944); (b) According to Stévart (1998); (c) According to Silva (1958); (d) According to Diniz and Matos (2002). For the Diniz and Matos (2002) map, only the main regions are shown

Monod (1960) was especially interested in the altitudinal variation of vegetation. He extended previous classifications (Fig. 3.3a), highlighting the uniqueness of the high-altitude shrublands distributed in several small patches above 1900 m, which hosts some emblematic endemic plant species, such as *Erica thomensis* (Henriq) Dorr & E.G.H. Oliv. 1999 and *Lobelia barnsii* Exell 1944.

Stévart (1998) proposed a phytogeographical classification based on the distribution of orchid species and their auto-ecology (Fig. 3.3b). He was the first author to explicitly consider the rainfall pattern distinguishing the dry north and the wet south of the island, following the 3000 mm annual rainfall isohyet. He suggested that the area around Lagoa Amélia could be a distinct vegetation type. Stévart (1998) also pointed out that several ridges at lower elevation (below 800 m) in the southeast had a unique assemblage of orchid species. The floristic distinction of those ridges could be driven by the combination of topographic position and high precipitation, although data were very limited at the time.

Diniz and Matos (2002) provided a detailed map of 109 agro-ecological units distributed in two main regions (Fig. 3.3d). Although their primary goal was to assess the potential of each unit for agricultural production, they also provide detailed descriptions of vegetation and flora in each unit. The northern region broadly corresponds to the area with <2000 mm of annual rainfall, and is divided into three sub-regions; the littoral plain with a semi-arid climate, the transition area with a sub-humid climate, elevations between 300 and 550 m with slopes that do not exceed 15%, and the mountainous more humid area. The southern region is described as more homogenous, being characterized by the steep transition between the central mountainous highland and the littoral band, composed of ridges and deep valleys.

Príncipe Island

Abiotic Gradients

The mainland of Príncipe Island has a maximum length of 18.5 km (north to south) and 11 km in its maximum width (east to west), with an area of approximately 139 km^2. It is located 220 km off the West African coast and 146 km north of São Tomé (Diniz and Matos 2002; Dallimer and Melo 2010). The north of the island is relatively flat, whereas the south-center has the largest elevated area (>500 m), including Pico do Príncipe that reaches 942 m, and multiple peaks surrounded by steep slopes and ridges (Fig. 3.4).

Just like São Tomé, our knowledge of rainfall patterns still relies on rough isohyets drawn several decades ago. Annual rainfall ranges from more than 4000 mm in the southeast to <2000 mm in the northeast, which is a remarkable contrast in such a small area. Cloud cover follows broadly the same pattern as annual rainfall, highlighting the elevated and rugged area around the Pico Príncipe (Diniz and Matos 2002). Four seasons are also recognized for Príncipe, following the same patterns found in São Tomé.

Soils have been studied and mapped (Diniz and Matos 2002). Bedrocks are predominantly volcanic, mostly in the north, while Phonolite rocks are more common in the south. As on São Tomé, the most frequent soils are highly weathered such as Ferralsols and Lixisols (Cardoso and Garcia 1962).

Human Disturbance

The history of land occupation on Príncipe is broadly similar to that of São Tomé. However, contrary to São Tomé, no large areas are regularly burned. A peculiarity in the history of Príncipe is the intense deforestation campaign that took place between

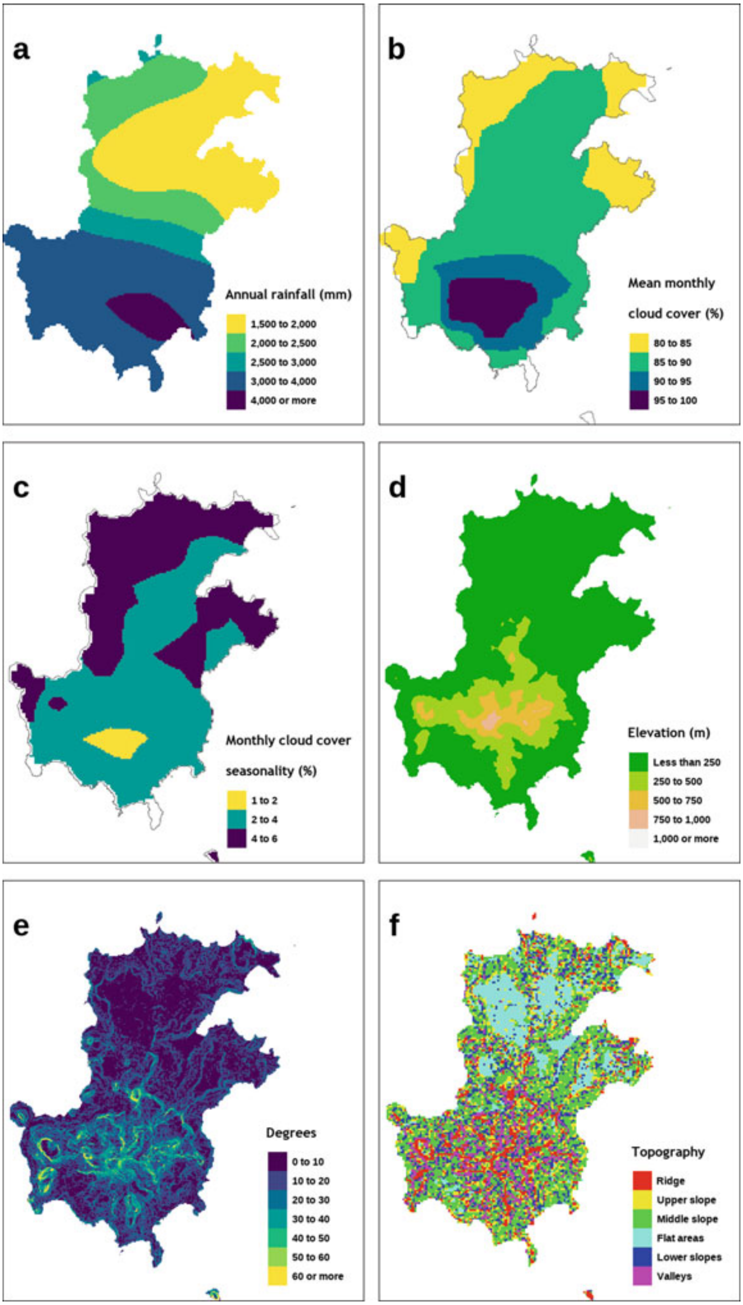

Fig. 3.4 Main physico-climatic gradients in Príncipe Island

1911 and 1916 to eradicate the tsetse fly vector of sleeping sickness (da Costa et al. 1916):

> The steps taken (. . .) consisted principally in the clearing away of herbaceous and bushy vegetation, in the opening out to the sun's rays of the margins of watercourses and swamps, straightening out and leveling the banks and the beds of these, draining and filling swamps, and forest fellings on a large scale.

More than 15 km^2 of native forests in the northern part of the island were deforested (11% of the island), while many plantations were also being abandoned (da Costa et al. 1916; da Silva 2019).

Nearly all lowland forests in Príncipe have been disturbed by human activity (Fig. 3.5), creating a mosaic of native and secondary forest, as well as active and abandoned agricultural lands (Dallimer et al. 2012). Most of the remaining native vegetation occurs at mid and high elevation and is included in the Príncipe Natural Park, a protected area created in 2006 that covers around 21% of Príncipe, mostly in the south (Ministry of Infrastructure, Natural Resources and Environment 2016).

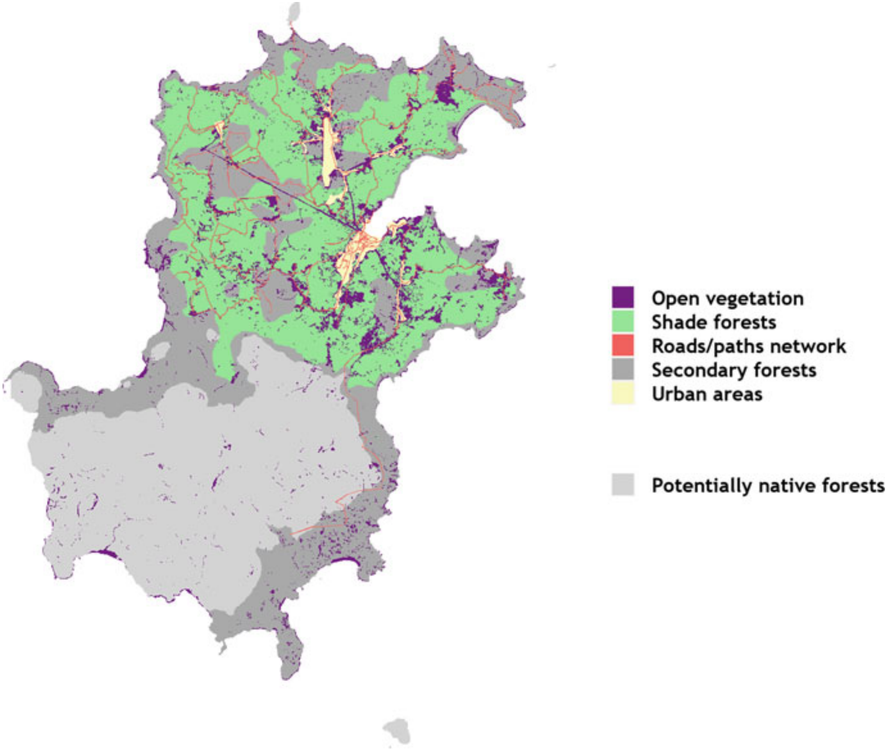

Fig. 3.5 Degraded or transformed land cover in Príncipe (Adapted from Frazer Sinclair and Yodiney dos Santos, unpublished data). Note that the "open vegetation" category includes both agricultural lands and savanna-like vegetation but also potentially natural edaphic open vegetation

The whole island was declared a UNESCO Man and Biosphere Reserve by 2012 (UNESCO 2021).

Previous Vegetation and Phytogeographical Classification

The distribution of forests on Príncipe was first depicted in a land cover map (IGC 1964) based on aerial photos and ground surveys. This map delimited the island according to land use in several categories, as natural forests or abandoned plantations, cacao plantations, coffee plantations, oil palm plantations, coconut plantations, agriculture, gardens, vegetable gardens or orchards, bush, undergrowth, or grasslands.

The native vegetation of Príncipe is similar to that of São Tomé, with plant families Rubiaceae, Euphorbiaceae, and Orchidaceae dominant (Figueiredo et al. 2011). It includes mangroves, but not savannas. Submontane forest is recorded only on the summit, at Pico do Príncipe, though Exell (1944) claimed that the composition of the vegetation at higher altitudes on Príncipe (namely Pico Papagaio; 680 m and Pico do Príncipe; 948 m) resembled that of lowland rainforest on São Tomé.

Diniz and Matos (2002) relied on climate, topography, and soil types to identify 28 agro-ecological units, which they described and delimited in detail. The vegetation is characterized by forests, ranging from primary ("obô") to secondary formations ("capoeira") and to strongly anthropized environments, including diverse types of plantations such as shaded cacao or coconut monocultures.

Forest tree communities were recently studied across the island, documenting floristic differentiation across north-south and altitudinal gradients (Fauna and Flora International 2018). These patterns were driven, at least partly, by a decrease in the relative abundance and diversity of tree species in secondary forests, highlighting the influence of past disturbances on forest tree composition.

Annobón Island

Abiotic Gradients

Of the three Gulf of Guinea Islands, Annobón is the smallest (17 km^2) and farthest from the mainland, located 360 km west of Gabon and 190 km southwest of São Tomé. Despite the small size, its geography is diverse. There is a 700 m wide crater at 150 m elevation, occupied by Lake A Pot, which has several adventitious cones, including the 400 m wide crater of Punta Manjob in the SE, the Quioveo and Santa Mina mountains, and northeast-southwest corridor that links the bays of San Pedro and Santa Cruz to the Anganchi river (Fig. 3.6). Santa Mina is the highest elevation at 613 m.

Annobón has an average temperature of 26 °C with little annual variation. Rainfall is primarily affected by the oceanic winds that cause a pronounced dry season from May to October, while the rest of the year is wet (Juste and Fa 1994). No accurate rainfall data is available, but maximum precipitation is around 3000 mm (Juste and Fa 1994; Velayos et al. 2014). Remotely sensed data suggests that intra-annual variability in cloud cover is less pronounced than on Príncipe or São Tomé, even though there is still a north-south humidity gradient, ranging from <70% in the north to almost 90% in the south (Fig. 3.6).

The soils of Annobón have not been thoroughly studied and mapped. However, they are ultrabasic and have the same volcanic origin as those of Bioko with lower silica and higher proportions of ferromagnesian elements (De Castro and De la Calle 1985).

Human Disturbance

Humans have modified most of the vegetation on Annobón (Fig. 3.7), except for the high peaks of Santa Mina and Quioveo. San Antonio de Palé or “Ambo,” located in the extreme north of the island, is the only permanent town. Most subsistence farms are on the fertile plains around the town, producing yuca (*Manihot esculenta* Crantz 1766), banana, and malanga (*Xanthosoma violaceum* Schott 1853). However, these small-scale plantations (“fincas”) can now be found everywhere on the island, even in steep slopes (Velayos et al. 2014), and their encroachment in the montane forests of Quioveo and Santa Mina is set to cause irreversible damage. Other villages are temporarily occupied during the dry season or holiday months. More recently, the expansion of the airport and seaport must have had considerable environmental impacts.

Previous Vegetation and Phytogeographical Classification

Only two studies attempted to delineate and document vegetation on Annobón. The first (Mildbraed 1922) proposed five vegetation types: (1) coastal “Sandstrand,” (2) “Vorland,” a savanna-like forest mixed with plantations, (3) “Buschwald,” oil palm artisanal plantations mixed with others tree species, (4) lowland dry forest, “Trockener Wald,” and (5) “Nebelwald,” a cloud forest found mostly above 500 m that is rich in orchid and fern species, including tree ferns *Alsophila* spp.

The second study (Peris 1962) proposed six vegetation types: (1) coastal, subdivided into rocky and sandy shores, (2) open vegetation strongly transformed by human activities, which was divided into herbaceous savanna-like vegetation, large-leaved savanna-like vegetation, cassava plantation, and shrubland, (3) dry forest, equivalent mostly to “trockener Wald,” (4) wet forest, also included in “trockener Wald” but distinguished by the presence of *Olea welwitschii* Gilg & G. Schellenb. 1913, (5) *Hymenophyllum* spp. cloud forest in the peaks of Santa Mina and Quioveo (see Fig. 3.8), and (6) tree fern areas in the summit of Santa Mina.

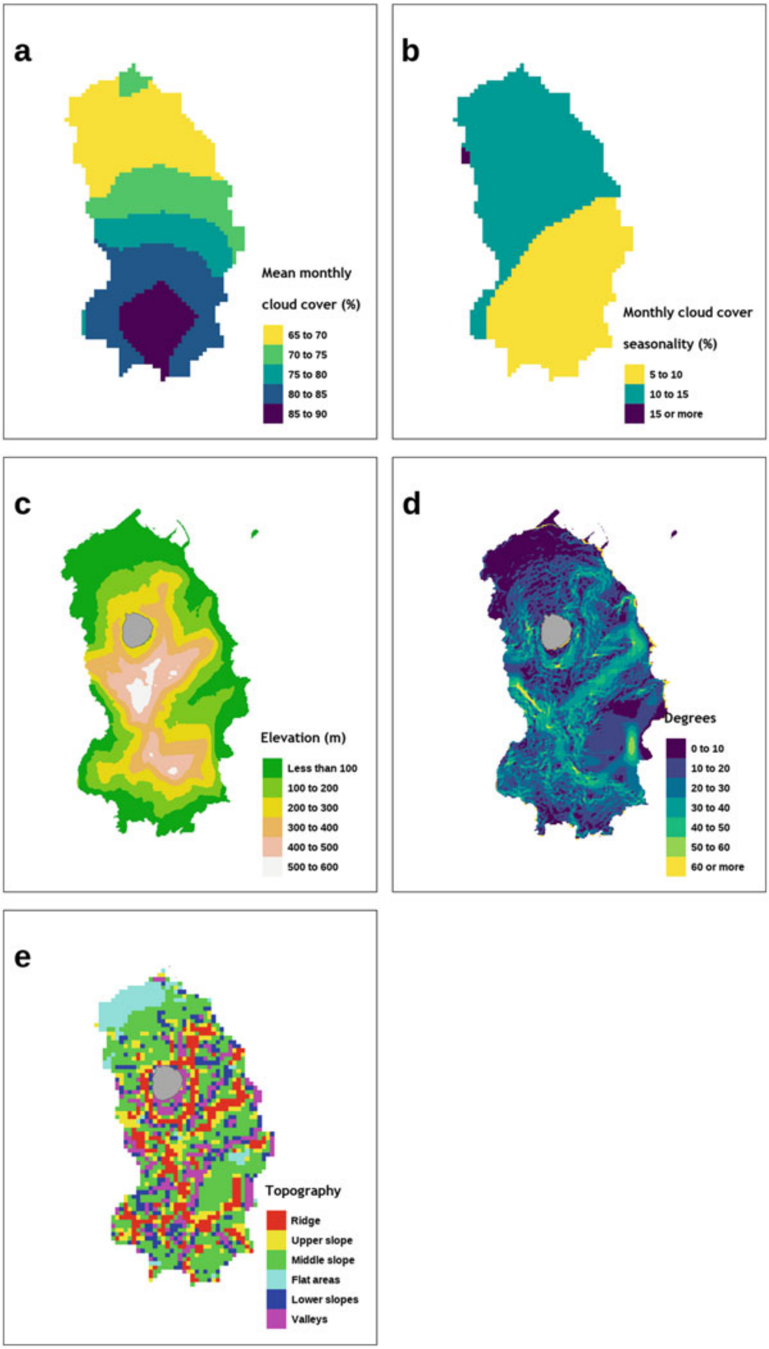

Fig. 3.6 Main physico-climatic gradients in Annobón island. The dark gray polygon represents the crater lake A Pot

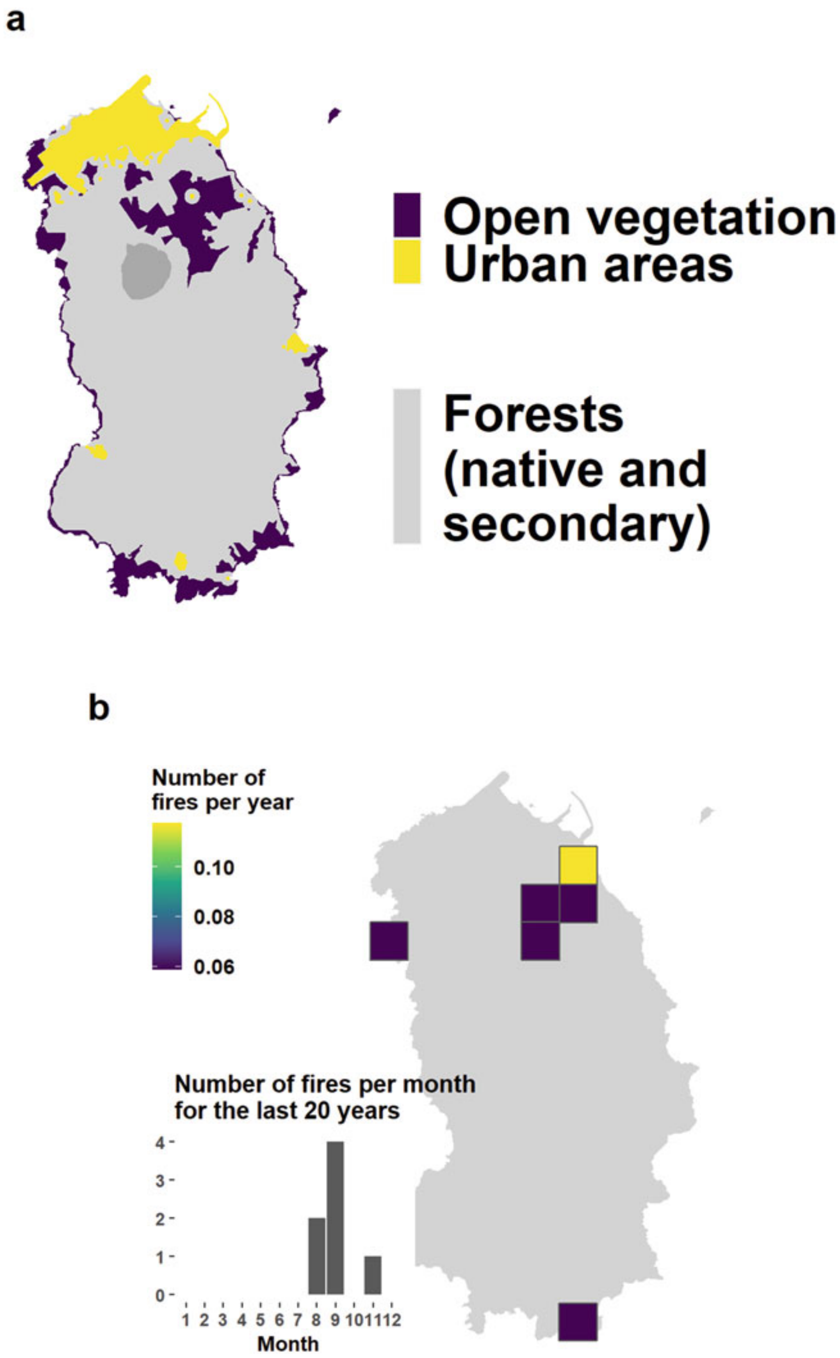

Fig. 3.7 (**a**) Degraded or transformed land cover on Annobón (Adapted from Norder et al. 2020). Note that the "open vegetation" category includes both agricultural lands and savanna-like vegetation but also naturally open vegetation type. (**b**) Annual fire frequency (data for the last 20 years). Inset barplot shows the distribution of these fires during the year

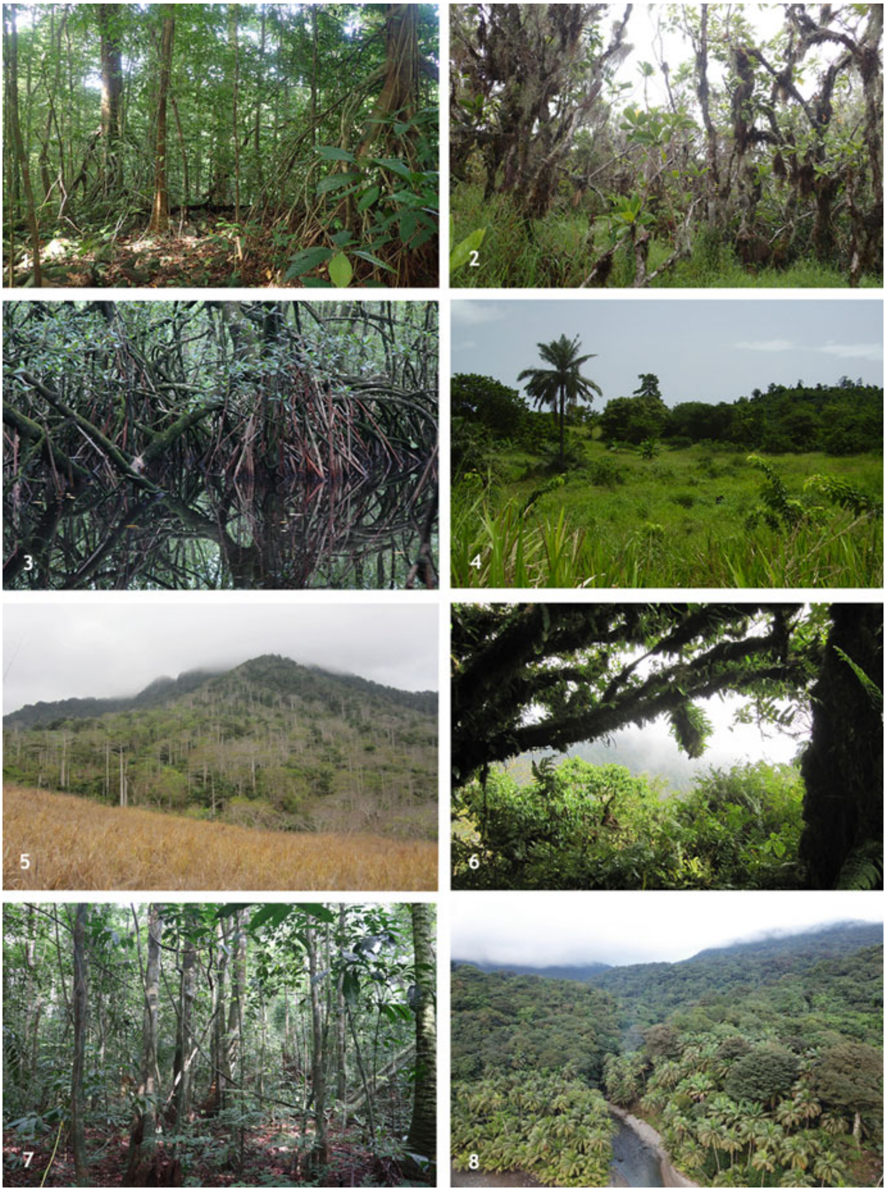

Fig. 3.8 Examples of terrestrial ecosystem types from the oceanic islands of the Gulf of Guinea. From top left to bottom right: (**1**) Mesic old-growth lowland rainforest in southwest São Tomé, where upper strata is dominated by *Uapaca vanhouttei* Pax 1908; (**2**) Vegetation on the Pico Pequeno characterized by small trees and shrub and the largest known population of *Erica thomensis* (Henriq.) Dorr & E.G.H. Oliv. 1999, endemic to this area; (**3**) typical mangrove with *Rhizophora* L. 1753 stilt roots in São Tomé; (**4**) the mosaic of lowland deciduous forest and savanna in the north of São Tomé; (**5**) lowland semi-deciduous forest in the background and savanna in the forefront, in Annobón; (**6**) rainforest in Annobón on the Quioveo peak above 500 m. According to the new classification, it is lowland rainforest, but the abundance of ferns and epiphyte suggests it is instead submontane rainforest similar to what can be found above 800 m in São Tomé; (**7**) Lowland

Classification Synthesis

Ecosystems are by definition open, dynamic, and scale-dependent, emerging from the interactions between organisms and the physical environment. Assuming that classifications are necessarily a simplification of reality, it makes sense to use variations in environmental conditions and biological communities to classify terrestrial ecosystems. Our goal here is to provide an updated classification, based on previous attempts and current knowledge, offering baselines for management and future scientific research on the dynamics of biodiversity.

Methodology

Spatial Information

We compiled previous classifications (Table 3.2) and mapped key ones, using QGIS (QGIS Development Team 2021) and R (R Core Team 2021) for georeferencing and analyzing spatial data. We retrieved several spatial features from Open Street Map (OSM) database using *"osmdata"* R package (Padgham et al. 2017) and other freely available shapefiles (see https://github.com/gdauby/stpa_ecosystems_review for further details on codes and data sources).

Synthetic Classification Mapping

We first considered abiotic gradients that drive potential natural ecosystems (e.g., temperature, rainfall, topography), and then vegetation types or proxies of anthropogenic impacts (e.g., secondary vegetation, shade tree plantation, fire frequency, urban area). This approach requires defining thresholds for characterizing ecosystems for continuous abiotic gradients, and acquiring spatial information on the distribution, nature, and intensity of human impacts. Thus, one map presents "potential natural ecosystems," which can be discussed in terms of potential vegetation types. A second map presents the developmental stages, resulting from natural or anthropogenic land-use changes. To analyze the relative importance of developmental stages in each ecosystem, we estimated the total area and proportion of each stage in each potential natural ecosystem. Spatial analyses were conducted in R using the packages "sf" (Pebesma 2018), "cleangeo" (Blondel 2019), and "sp" (Bivand et al. 2013) (see R codes here: https://github.com/gdauby/stpa_ecosystems_review).

Fig. 3.8 (continued) moist forest from the north of Príncipe, partly secondarized as indicated by the presence of *Elaeis guineensis* Jacq. 1763; (**8**) Lowland wet forest from the south of Príncipe. Photo credits: (1) G. Dauby, (2) D. U. Ikabanga, (3) Paula Chainho, (4) R. F. de Lima, (5,6) P. Barbéra, (7) L. Benitez, (8) T. Stévart

Annobón was excluded from this analysis because rainfall data was missing, but we still discuss similarities with the other islands.

Mapping Non-Forested Areas

To evaluate developmental stages of terrestrial ecosystems on Príncipe and São Tomé, an important first step was to identify forested and non-forested areas. To do so, we uploaded very high-resolution satellite images (sentinel-2) (https://peps.cnes.fr/rocket/) from the long dry season to minimize cloud cover. Then, we used eCognition software (Trimble Inc.) to segment spectrally homogeneous non-forest polygons based on thresholding normalized difference vegetation index. The resulting polygons were manually checked using Google Earth and added to a vector layer, which was combined with the land cover types retrieved from OSM, namely polygons identified as "scrub" and various built categories (residential, commercial). We also selected the "roads" tag polylines to be converted into polygons by adding a 10 m buffer. The final shapefiles distinguished non-forested "urban areas," "roads and path network," and "any other non-forested areas," which included agricultural land, deforested wastelands, but also naturally open vegetation types that could not be distinguished at fine scale.

High-quality satellite images were not available for Annobón, so we used the OSM shapefile to extract buildings and forest polygons. The "buildings" shapefile was edited based on Google Earth, and a 100 m buffer was added to identify areas impacted by urban activities.

Ecosystem Delimitations

The methodology is based on principles from the Ecosystemology approach recently proposed by Senterre et al. (2021). We defined regional-scale ecosystems based on relevant available abiotic gradients, namely altitude, precipitation, distance to coast, and cloud frequency. Within each of these units, we identified the distribution and extent of stand-scale units using abiotic gradients at a finer scale, such as topography, and soil features including humidity and salinity (Table 3.3). Thresholds were set based on the literature and on personal experiences and observations of the authors. Regional- and stand-scale ecosystems were listed, and their features discussed.

In parallel, we gathered spatial information on the distribution of human impacts on São Tomé and Príncipe (Fig. 3.2; Table 3.2), which were not included in the classification process, but were overlaid over the regional-scale units (Supp. Mat.). We estimated that secondary forests and shade plantations together cover over half of São Tomé and of Príncipe (28 and 27%, and 26 and 30%, respectively), while native vegetation covers around one-third or less (27 and 35%, respectively). Similar information was not available for Annobón, but recent observations suggest that native vegetation is mostly restricted to the highest peaks.

Table 3.3 Total area and relative importance of each stand-scale ecosystem defined for São Tomé and Príncipe

Ecosystem type	São Tomé	Príncipe
Montane forests	7.9 km^2 (0.9%)	–
Mesic	3.3 km^2 (0.4%)	–
On steep slope	3.1 km^2 (0.4%)	–
On ridge	1.5 km^2 (0.2%)	–
Montane low forest, grasslands, and shrublands	0.7 km^2 (0.1%)	–
Submontane rainforest	80.1 km^2 (9.4%)	0.8 km^2 (0.6%)
Mesic	39.9 km^2 (4.7%)	0.2 km^2 (0.1%)
In valley	4.5 km^2 (0.5%)	0.04 km^2 (0%)
On ridge	7.8 km^2 (0.9%)	0.1 km^2 (0.1%)
On steep slope	28 km^2 (3.3%)	0.5 km^2 (0.3%)
Lowland deciduous forests and woodlands	344.2 km^2 (40.4%)	43.4 km^2 (31.1%)
Mesic	248.6 km^2 (29.2%)	43.1 km^2 (30.9%)
On Vertisols	51.4 km^2 (6%)	–
In valleys	10.4 km^2 (1.2%)	0.1 km^2 (0.1%)
On steep slope	21.6 km^2 (2.5%)	0.2 km^2 (0.1%)
On Fluvisols	12.1 km^2 (1.4%)	–
Lowland moist and wet rainforests	459.7 km^2 (54%)	92.2 km^2 (66.2%)
Mesic	329.6 km^2 (38.7%)	74.3 km^2 (53.3%)
On ridge	30.7 km^2 (3.6%)	4.8 km^2 (3.4%)
On steep slope	63.6 km^2 (7.5%)	9.3 km^2 (6.7%)
In valleys	24.2 km^2 (2.8%)	3.8 km^2 (2.8%)
On Fluvisols	11.6 km^2 (1.4%)	–
Coastal ecosystems	10.4 km^2 (1.2%)	2.6 km^2 (1.9%)
Undifferentiated shores	9.2 km^2 (1.1%)	2.1 km^2 (1.5%)
Mangroves	0.9 km^2 (0.1%)	0.02 km^2 (< 0.1%)
Sandy shores	0.3 km^2 (< 0.1%)	0.4 km^2 (0.3%)
Palustrine areas	0.1 km^2 (< 0.1%)	0.1 km^2 (< 0.1%)

All classifications produced in this chapter and associated resources are accessible online (https://github.com/gdauby/stpa_ecosystems_review).

Coastal Ecosystems

The coasts of São Tomé, Príncipe, and Annobón are approximately 204, 100, and 35 km long respectively, and include mangroves, other palustrine areas, sandy coasts, and cliffs.

At the interface between terrestrial, freshwater, and marine realms, mangroves are the most distinctive coastal ecosystems on the islands (Herrero-Barrencua et al. 2017; Afonso 2019). On São Tomé, at least 14 mangroves areas persist (Fig. 3.8). Malanza and São João dos Angolares are the largest, and Malanza and Praia das

Conchas are the only ones within a protected area. In Príncipe, mangroves persist at Praia Caixão, Praia Grande, and Praia Salgada. Even though there is no estimate of the lost mangrove area, past distribution was certainly wider, especially in the north of São Tomé (Herrero-Barrencua et al. 2017). Mangroves are absent on Annobón (Juste and Fa 1994).

Other estuarine ecosystems often occupy similar conditions surrounding mangroves, some of which might have resulted from mangrove degradation on São Tomé. Sandy coasts are sparsely distributed across the three islands and host distinct psammophile communities.

Cliffs are frequent but their distribution and associated biota are poorly characterized. In the south of São Tomé, dense populations of *Pandanus thomensis* Henriq. 1887 frequently colonize them. Given its distinct edaphic properties, this ecosystem might be less impacted by human activities than others, but its vulnerability to invasive species remains unknown.

At least 15% of the coast of São Tomé and 12% of that of Príncipe have been strongly impacted and transformed into urban areas or roads. More than 50% of coastal ecosystems on São Tomé and 13% in Príncipe are covered by, or are next to secondary forests or shade plantations (Supp. Mat.).

Non-coastal Wetlands

Non-coastal wetlands include all habitats that are seasonally or permanently inundated by freshwater. We distinguished riverine forests, waterfalls, lowland swamp, and montane swamps.

Riverine forests can be defined as areas that are influenced by river soaking and flooding. Their distribution, extent, and associated biological communities are poorly characterized in the GGOI. Their width is expected to be small, considering most valleys are narrow, but this influence can be larger, particularly in flatter areas.

Waterfalls display specific geomorphic and micro-habitats features with strong but very localized, environmental heterogeneity and originality (Clayton and Pearson 2016). They also act as natural barriers, dividing streams and their associated biotas into distinct populations. Their biota characteristics and ecosystem functions have rarely been investigated in tropical regions, but some studies have highlighted their ecological and conservation significance (Baker et al. 2017). The distribution and ecological characteristics of waterfalls in the GGOI are not well known and deserve further attention, especially since they may be threatened by dams in the near future.

Lowland swamps are infrequent and small on São Tomé but seem to be somewhat more widespread in the northern plateau of Príncipe. This situation contrasts with continental central Africa, where swamp forests are frequent and harbor specific biological communities (e.g., Boupoya et al. 2017), but almost nothing is known about swamp forests in the GGOI. We do know, however, that large areas of Príncipe's swamps were drained during the tsetse eradication campaign in the early twentieth century (da Costa et al. 1916).

The only significant example of a montane swamp is the Lagoa Amélia, at c. 1400 m on São Tomé. Floristically, there is no evidence that this area has a distinct assemblage, but it represents a unique combination of environmental conditions in the GGOI, being a super humid, high-altitude swamp.

Inland Uplands

Inland uplands represent almost the entirety of the GGOI. In São Tomé and Príncipe, we divided them first by elevation, by thresholds at 800 m, 1400 m, and 1800 m, and then by the 2000 mm annual rainfall threshold. This allowed us to distinguish (1) lowland deciduous forests, (2) lowland moist and wet forests, (3) submontane rainforests, (4) montane forests, and (5) montane shrublands and grasslands. For each of these, we identified abiotic factors that may exacerbate or mitigate the local influence of temperature or water availability relative to the mesic environment. Namely, we considered specific soil types, slopes with steep gradients, and specific topographic categories, such as valleys and ridges. Steep slopes (> 30°) are likely to have superficial soils (Lithosols), increased susceptibility to erosion (landslides), and distinct micro-climate due to stronger (or weaker) insolation, depending on the aspect (Chapin III et al. 2011). They are also less directly threatened by anthropogenic activities.

Lowland Deciduous Forests

Occurring up to 800 m of elevation and registering <2000 mm of rainfall annually, these ecosystems are mostly found on the flat or gentle slopes of northern São Tomé. Given the limited rainfall, lower cloud frequency, and higher temperatures, water availability is probably the main limiting factor for vegetation growth. Vegetation composition and physiognomy also support the local influence of edaphic or topographical features. As such, we distinguished (1) forests on flat terrain and Fluvisols, (2) forests on flat terrain and Vertisols, (3) forests in valleys, and (4) forests on steep slopes. Almost none of this native forest vegetation remains, but we can assume the vegetation type in mesic conditions should have been a (semi)-deciduous or dry forest.

Fluvisols occur along large rivers on flat terrain, and are usually susceptible to occasional flooding. Native vegetation must have been moist semi-deciduous forest with higher frequency of species tolerant to poorly drained soils. This is the most disturbed ecosystem on São Tomé; ca. 23% are covered by roads and urban areas, and more than 30% by open agricultural land (Supp. Mat.). Fluvisols are infrequent on Príncipe (Diniz and Matos 2002).

Forest on flat terrain and Vertisols is only found on São Tomé, where it corresponds mostly to savanna-like vegetation. Soil moisture on Vertisols is highly variable, leaving plants vulnerable to drought. However, it is noteworthy that there are no indications that these savannas existed when human colonization started on

São Tomé, 500 years ago. It has been proposed that any such areas originally covered by the dry forest were lost to fires and sugarcane plantations (Diniz and Matos 2002). Later on, sugarcane production was mostly abandoned, but forests could not reestablish due to changes in soil properties and to regular fires during the dry season (Fig. 3.2). Nowadays, more than half of this area has open vegetation, mainly savanna-like but also agricultural lands, and around 15% has been converted to urban areas or to roads. Several plant communities occur in this mosaic of forest and savannas, where the landscape is locally dominated by the African baobab *Adansonia digitata* L. 1759. This complex mosaic might present some similarities with the north of Annobón, nowadays mostly occupied by urban areas.

In large and narrow valleys, particularly in the extreme north of São Tomé, water is less limited thanks to run-off from the central highlands. Floristic composition (Diniz and Matos 2002, personal observations) suggests that this specific topography holds distinct plant communities. This stand-scale ecosystem may also be significant for conservation as it might host the last remnant of lowland moist forests in the north of São Tomé, as almost all of these have been converted to shade cacao plantations, urban areas, and roads.

The forests surrounding the large valleys of São Tomé occur on the steep slopes, occupying a significant area (Table 3.3) that is less directly impacted by human activities, although most of these are nevertheless secondary forests.

Lowland Moist and Wet Rainforests

This regional-scale ecosystem includes all areas up to 800 m of elevation and above 2000 mm of annual rainfall, which are less limited by water availability due to lower seasonality. We considered topographic and soil features to distinguish forests (1) in valleys, (2) on ridges, (3) on steep slopes, and (4) on Fluvisols. Natural vegetation in mesic conditions is undoubtedly rainforest that still occupies most of São Tomé and Príncipe, even if most is secondary. On São Tomé, industrial palm plantations occupy more than 5% of this ecosystem. Overall, we estimate that native forests persist in <40% of its original area.

Forests in valleys occupy 4% of this region-scale ecosystem in Príncipe and 5% in São Tomé.

Forests on ridges have limited extent both on Príncipe and São Tomé but also seem to have been less impacted, due to their lower accessibility and reduced potential for agriculture. The biological communities here are poorly known. It has been suggested that lowland peaks, such as the Pico Maria Fernandes on São Tomé and Morro Fundão on Príncipe, host distinct plant assemblages that are more closely related to submontane vegetation than to surrounding lowland forests (Stévart 1998; Ogonovszky 2003). Biota and physico-climatic similarities of lowland ridges between the GGOI are likely and should be assessed. Indeed, these specific habitats are covered by low and open vegetation, close to those occurring on mainland inselbergs. However, the proximity to the ocean should increase moisture even during dry seasons, allowing for the development of a distinct vegetation type in these rocky places.

Forests on steep slopes occupy a significant extent and also seem to have been less impacted than other forest types due to their lower accessibility and potential for agriculture.

Forests on Fluvisols have only been identified in the large watersheds of Iô Grande and Xufe-Xufe on São Tomé. These correspond to flat lowland areas near the coast and that have thus been strongly impacted by human activities, namely by agricultural development.

Submontane Rainforest

Submontane rainforests include areas between 800 and 1400 m, and apart from mesic conditions, we distinguished forests (1) on ridges, (2) on steep slopes, and (3) in valleys. On São Tomé, we estimated that 9% of the potential area for submontane rainforest is currently non-forested, most of which is agricultural, while 15% is secondary forest and 2.5% shade forest. The extent on Príncipe is very limited (Table 3.3) but has been spared from human activities. A small portion of this territory (>5%) appears to be non-forested, probably due to natural treeless Lithosols. Annobón has no area above 800 m and thus submontane rainforests may not occur there (but see discussion).

Forests on ridges are often characterized by the endemic gymnosperm *Afrocarpus mannii* (Hook.) C.N. Page 1989. They represent nearly 10% of submontane forests on São Tomé, while forests on steep slopes represent almost 35%. Both these forest types are likely to be spared from direct human disturbances, even though natural disturbances, such as landslides, are probably frequent.

Montane Forests

The area between 1400 and 1800 m is restricted to São Tomé and includes mainly montane rainforests. This ecosystem is almost intact, although introduced plant species can be locally abundant (e.g., tree species *Cinchona* spp. L. 1753). We distinguished (1) forests on ridges, (2) forests on slopes and plateau, and (3) montane grasslands.

Montane forests on ridges occupy nearly 20% of this region and are similar to submontane ridge forests, as indicated by the sun-loving tree *Afrocarpus mannii*, but also by herbs such as *Begonia thomeana* C. DC. 1892 and *Mapania ferruginea* Ridl. 1887. Forests on slopes and plateaus remain poorly documented because of their limited accessibility, even though they represent nearly half of this region. Both submontane and montane forests are characterized by forest species like *Palisota pedicellata* K. Schum. 1897, *Homalium henriquesii* Gilg ex Engl. 1921 *Tabernaemontana stenosiphon* Stapf 1895, and *Craterispermum cerinanthum* Hiern 1877 (formerly *C. montanum* Hiern 1877 but considered as synonym by

Taedoumg (2020)). However, certain montane forest species, such as *Symphonia globulifera* L. f. 1782, can also be found on ridges at lower elevations, indicating that the transition between submontane and montane forest depends on the local topography, a topic that surely deserves attention in future studies. The physiognomy and the floristic composition of the montane grassland have been relatively well described, but its precise extent is unknown.

Montane Low Forest, Grasslands, and Shrublands

We consider this ecosystem above 1800 m as distinct from the Montane Forests because of its specific physiognomy characterized by the frequency of shrubby vegetation and smaller trees on ridges. Grass mat is also abundant along the ridges, but these grasslands can also be observed at lower altitude along ridges. The presence of plant taxa such as *Erica*, *Lobelia*, and the tree *Balthasaria mannii* (Oliv.) Verdc. 1969 makes this ecosystem as the most distinct in the GGOI, showing affinities to biological assemblages observed in other mountains ranges, such as on Bioko and in East Africa (Monod 1960). In addition to its unique species assemblage, the upper montane area of São Tomé also seems to display distinct abiotic properties. The “prevalent mist” of the “mist rainforests” is impressive but might be less important for the development of this specific community than the superficial soils (Exell 1944). Indeed, as Monod (1960) described, the area above 1800 m is often above the clouds and therefore tends to be relatively dry (especially during the dry season), while the montane and submontane forests at lower altitude remain wetter thanks to the nearly permanent mist (Fig. 3.1). Monod (1960) even noticed (in August, hence at the end of the dry season) that the vegetation was dry enough to be vulnerable to fires.

Besides ecotourism activity (which may bring seeds of invasive species, foster clearings along ridges, and provoke accidental fires during the dry season), this ecosystem has been mostly spared from direct human degradation. However, it may very well be one of the most threatened, considering its narrow distribution (ca. 0.66 km^2), the impact of climate change, and the spread of invasive species, in particular *Cinchona* spp. trees. This genus has been considered among the most invasive in many tropical islands (Jäger 2015), and especially in naturally treeless environments (Jäger et al. 2007). We do not know if these taxa are replacing native plant populations, but it is the dominant species (mono-dominant locally) along several ridges. This may be the consequence of vegetation clearings in the past and *Cinchona* plantings (Monod 1960).

Discussion

Defining ecosystems as discrete units is a simplification (Boitani et al. 2015) but can be useful to facilitate our understanding of a complex reality (Senterre et al. 2021). While the delineation of some ecosystems is straightforward, it is often not the case because transitions are usually not abrupt (Exell 1944; Monod 1960). The classification we propose tries to improve on existing classifications based on the best available data, to provide better baselines for management, and for testing hypotheses regarding biodiversity dynamics. This synthetic classification is thus likely to evolve as more data become available, namely regarding the distribution of ecosystems, and specifically of vegetation types on different islands. For future reference, all maps and spatial information are available on an open-access portal (https://github.com/gdauby/stpa_ecosystems_review).

Below, we point out several pending questions and challenges that became apparent during this exercise and that could help guide future research on the terrestrial ecosystems of the GGOI.

Is It Still Valid to Define Ecosystems Based on Altitude?

Most changes in large units of natural vegetation in the GGOI, and in the distribution of species, appear to be associated with altitude, explaining why the first naturalists (Exell 1944; Monod 1960) focused on the influence of this environmental gradient on biological communities. Altitude (i.e., a proxy for temperature pattern) interacts with topography and rainfall, creating micro-environmental conditions that can affect vegetation at a fine scale, and that remain poorly understood due to their subtle variations and complex effects on the distribution and abundance of species. Moreover, the intensity of anthropogenic disturbances interacts with this natural complexity, further complicating our understanding of ecosystem dynamics. As an example, these disturbances (and deforestation in particular) are typically more intense in the lowlands, where several populations of native species might have already been extirpated. In this scenario, their current distributions are artificially correlated with altitude, misguiding our understanding of the ecology of those species.

Even if altitude is still the best available proxy for delimiting large natural vegetation types, it may be hard to understand, or even misleading when trying to infer drivers of species distribution. For example, if those drivers are linked to precipitation or moisture, (sub)montane species may persist as satellite populations at lower altitudes where micro-habitats are sufficiently humid, such as deep valleys or riverine areas. Setting a threshold of 800 m for submontane forest, as we did, means this forest type does not occur on Annobón where the maximal altitude is 600 m. However, the description of the floristic and physiognomic features of the forest above 500 m (Peris 1962) does suggest some similarities with submontane forests found on São Tomé. If confirmed, this would suggest that humidity matters more than altitude for defining submontane forest. Comprehensive surveys of biota and physical features are still required across the islands to improve our understanding of the distribution of vegetation types and underlying environmental drivers.

What Is the Extent of Novel Ecosystems?

All three islands have high proportions of introduced species, whose frequency and abundance vary between ecosystems. Increasing proportions of introduced species can lead to changes in ecosystem functioning (Wardle et al. 2011). These taxonomic and functional turnovers can lead to the development of "novel" ecosystems resulting from human intervention; i.e., the ecosystem becomes self-sustaining in an alternative stable state (Hobbs et al. 2009; Morse et al. 2014). Applying these concepts for characterizing altered ecosystems is key for conservation and management, especially in oceanic islands where ecosystems are more prone to the threats posed by introduced species (Sax and Gaines 2008; Morse et al. 2014). Novel ecosystems, such as secondary vegetation and plantations, cover most of the GGOI and are far from homogenous, presenting a wide variety of species assemblages. The functioning of these new assemblages, whether they differ from that of native ecosystems and affect ecosystem services, remains to be investigated.

Which Factors Drive the Establishment of Novel Ecosystems?

The development of novel ecosystems results from the expansion of introduced species, which often but not always results from anthropogenic land-use changes (Morse et al. 2014). Novel ecosystems in the GGOI, and their accompanying introduced species, are probably more widespread in active and abandoned lowland agricultural areas, where historical land-use changes have been more significant (Muñoz-Torrent et al. 2022). This has already been shown for GGOI birds (Soares et al. 2020), and mollusk species assemblages (Panisi et al. 2022), for which invasion success is highest in the lowland areas. Nevertheless, although less abundant and diverse than in the lowlands, introduced species also occur in highland ecosystems where native vegetation largely dominates. Similar patterns are expected for other groups, such as plants. For example, species of *Cinchona* can be locally dominant in lower strata of montane and submontane forests, where it was planted for bark production (Chevalier 1938–1939). Populations of this species persist in old-growth forests, but it is unknown if they are spreading and replacing native species. In Estação Sousa on São Tomé, few individuals persist (unpublished results) in an area that was a plantation over 100 years ago (Chevalier 1938–1939). It is crucial to assess the vulnerability of highland ecosystems to introduced species, since these endemic-rich and diverse ecosystems have so far been the least impacted by human activities (Muñoz-Torrent et al. 2022).

How to Prioritize Conservation Efforts?

An understanding of the distribution of endemic and threatened species across ecosystems is necessary for allocating conservation efforts. Unfortunately, this information remains insufficient for several areas and clades (Stévart et al. 2022; Nève et al. 2022). Available data suggest that endemism tends to be higher in submontane and montane ecosystems (Stévart et al. 2022). On the other hand, lowland ecosystems are the most impacted and are often undersampled. For example, the extreme north of São Tomé hosts a complex mosaic of forest and savannas that is probably the best example of a novel ecosystem in the GGOI. Most scientists have focused on endemic-rich ecosystems, which at least partly explains why flora and fauna in the extreme north remain undersampled (Stévart et al. 2022). However, recent fieldwork (unpublished results) has led to the identification of some endemic plants, including two putative new species, suggesting that native biodiversity persists in these ecosystems. These discoveries highlight the importance of these areas for conservation, emphasizing the urgent need for further studies in novel ecosystems, particularly since native populations persisting in these areas may be some of the most vulnerable to extinction.

How to Improve Ecosystem Monitoring Through Space and Time?

Efficient ecosystem monitoring cannot rely solely on field observations, as these demand too many resources. The use of remote sensing data can help extend current assessments, in particular to document vegetation features and dynamics, but so far, these have been limited by their coarse resolution, which are not appropriate to study the complex landscapes of the GGOI. The availability of spectroscopic data and analytical tools is constantly improving and, in combination with in situ observations, might enable meaningful ecosystem monitoring in the near future (Cavender-Bares et al. 2020). For example, hyperspectral images could help characterize the dynamics of introduced plant species and thus infer the distribution of novel ecosystems.

The Need for a Unified Classification of Ecosystems for Central Africa

Island ecosystems are ideal natural experiments to test hypotheses regarding the links between biodiversity and ecosystem properties (Pimm 1984). To investigate these hypotheses, it is useful to define ecosystem units that are transferable across regions. In practice, such classification is challenging because there is no clear definition on how ecosystems should be identified (but see Senterre et al. 2021), despite international initiatives such as the Red List of Ecosystems (Keith et al. 2013). We support the development of an ecosystem classification that can be shared between the GGOI and continental Africa, as it would allow comparative studies that could greatly improve our understanding of regional biogeography and patterns of species diversity.

Conclusions

The three GGOI present similar humidity gradients, increasing from the northeast to the southwest due to the rugged topography and resulting foehn effect. These gradients, along with altitude and anthropogenic disturbance, can be used to identify distinct ecosystems and their distributions, and help to explain differences between islands. The high concentration of biotic and abiotic complexity in these small island territories creates unique combinations of features that shape ecosystem properties, making them ideal for studying the dynamics of tropical ecosystems. However, much of what is known about the GGOI is based mostly on São Tomé: by far the best known but also the most diverse island. Overcoming existing knowledge gaps will require multidisciplinary, collaborative frameworks and research agendas, which in turn rely on long-term observatories and capacity building. We hope that the synthetic ecosystem classification we have presented in this chapter, together with all the underlying resources that we have made available, will foster the future research needed for a better understanding and conservation of the tropical ecosystems of the GGOI.

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Chapter 4
Territory, Economy, and Demographic Growth in São Tomé and Príncipe: Anthropogenic Changes in Environment

Xavier Muñoz-Torrent, Ngouabi Tiny da Trindade, and Signe Mikulane

Abstract Nearly five centuries of human presence on the islands of the Gulf of Guinea have considerably marked the landscape with the replacement of natural habitats by *roças* (plantations) and other settlements, the introduction of numerous exotic plant and animal species, and the exploitation of resources needed for urban construction and daily life of the growing human population. Exponential population growth and, consequently, the urban sprawl are resulting in deforestation, illegal beach sand mining, exhaustion of natural resources, expansion of non-endemic species, and extermination of the endemic ones, thus causing immense resource exploitation and rapid environmental deterioration. The absence of an effective territorial planning amplifies the island's vulnerability and increases the fragility of the ecosystems, posing clear threats to the islands' unique biodiversity.

Keywords São Tomé and Príncipe · Biodiversity · Demographic growth · Economy · Environmental impact · Insularity · Environment-society interactions

Gulf of Guinea Oceanic Islands: A Biological Laboratory of Landscape Alteration

In the context of the European expansion, African islands in the Atlantic were prime spaces for experimentation of new agricultural species (Ferrão 2005). Since the early period of the European Age of Expansion, and especially for the Portuguese

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Colonial Empire, these islands became biological laboratories for the acclimatization of different economically interesting plants and animals from Europe and Africa, and even later from South and Central America and Asia. Initially, the most basic need for maritime expansions was the creation of safe ports for transoceanic trips, where horticultural commodities could restock the ships. The Gulf of Guinea Oceanic Islands served as a strategic base for the European colonial enterprise, especially because the islands of Príncipe, São Tomé, and Annobón were uninhabited (e.g., Seibert 2004). Here, we describe the history of the relationships between the human societies that inhabited these islands and their surrounding environment, with a focus on the island of São Tomé from which the most information is available.

According to the existing historiography, Portuguese navigators were the first humans to reach and colonize the oceanic islands of the Gulf of Guinea. São Tomé and Príncipe islands were discovered by the Portuguese navigators João de Santarém and Pêro Escobar on December 21, 1470, and January 17, 1471, respectively. The island of Annobón was discovered on January 1, 1473, by the Portuguese navigator Fernão do Pó who was attempting to find the maritime route to India. After a previous failed colonization attempt, in 1486 the Portuguese military leader Álvaro de Caminha became the third "donatário" (governor) of São Tomé and promoted the first successful colonization of São Tomé, establishing a small village in the area around Ana Chaves Bay, in the north-eastern part of the island (Seibert 2015). The original settlers included Europeans consisting of volunteers, exiles, and a group of Jewish children, as well as Africans, most of whom were enslaved (Seibert 2015). The island of Príncipe would only start to become populated in the early sixteenth century (Seibert 2015), and Annobón decades later, in 1592.

From these initial settlements until the mid-nineteenth century, the main economic activities of the islands were linked to the slave trade, in which the islands functioned as an important entrepôt for the transatlantic trade (especially until the mid-seventeenth century). The islands were also transformed by extensive sugarcane monoculture plantations (mainly throughout the sixteenth century), especially in the northeast of São Tomé (Seibert 2015). By the mid-sixteenth century, the island of São Tomé was the world's main producer of sugar, but the development of sugarcane cultivation in Brazil led to the collapse of São Tomé's plantations by the beginning of the seventeenth century (Seibert 2015). Revolts by enslaved Africans also contributed to this decline, such as those led by the iconic King Amador in 1595 that devastated a considerable number of sugar mills (Seibert 2015). With the end of the large sugarcane plantations, the islands' economy was reduced to the production of supplies to be sold to the ships that docked there. Many of these were linked to the slave trade, which was limited in 1836 and completely banned with the abolition of slavery in São Tomé and Príncipe in 1875, when enslaved plantation workers transitioned to a subsistence wage labor model (Seibert 2015).

Despite the impact of sugar mills on the local landscape, the human population during this early period was considerably low, with a total of 12,672 people on the islands of São Tomé and Príncipe in 1758, of which only 53 were white Europeans (Seibert 2015). From the second half of the nineteenth century onward, the islands would witness the rapid expansion of coffee and cocoa crops, which came to

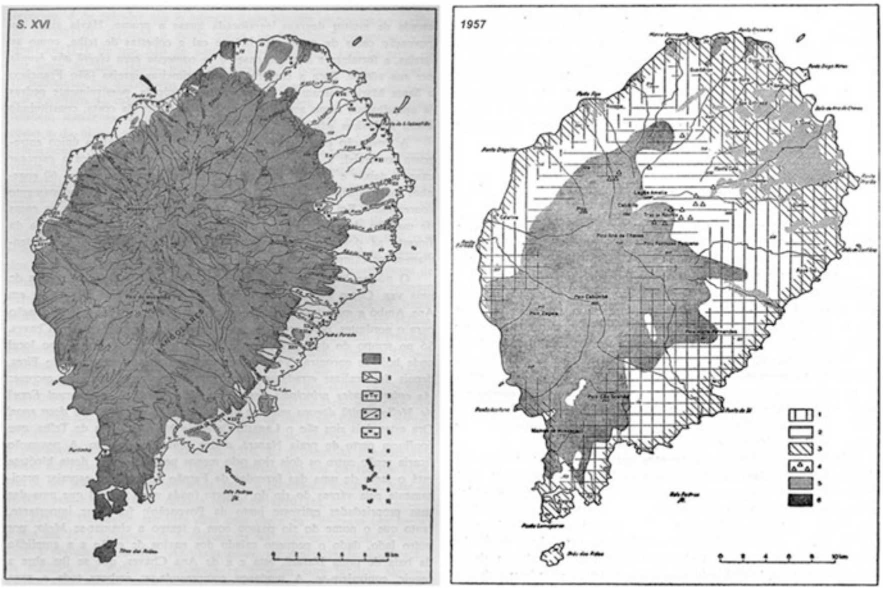

Fig. 4.1 Evolution of land occupation in São Tomé Island from the late sixteenth century (left: 1 *Obô*—forests, 2 sugarcane plantations and fields, 3 coconut palm and banana, 4 factories and sugar mills, 5 wetlands) to 1957 (right: 1 cocoa, 2 coffee, 3 oleaginous trees, 4 quinines, 5 quintal cultures, family horticulture, 6 *Obô*—forests). The diminishing cover of the *Obô* (dark gray area) is evident. Tenreiro (1961)

dominate the economy and landscape through the establishment of dozens of *roças* (plantations and their dependencies; Seibert 2015). According to available historical data, cocoa plantations in 1913 occupied about three-fourths of the surface of São Tomé and Príncipe islands, a proportion that would gradually start to decline after the First World War, due to the infestation of cocoa trees by pests, soil erosion, and expansion of cocoa cultivation in other regions (Seibert 2015). This decrease in cocoa cultivation was such that by the time São Tomé and Príncipe became independent in 1975, the total planted area was only one-fourth of the country's territory (Seibert 2015). Nearly five centuries of human presence on the islands have considerably marked the landscape with the replacement of natural habitats by *roças,* the introduction of numerous exotic plant and animal species, and the exploitation of resources needed for urban construction and daily life of the growing human population.

Similar to other Atlantic islands off the coast of Africa, the recent ecological and landscape history of Sao Tomé and Príncipe is strongly linked to the growth of human activity, including the degradation of native ecosystems and the establishment of alien species. This process was strongly associated with cycles of agricultural development, initially the production of sugarcane, and then coffee and cocoa (Eyzaguirre 1986—Fig. 4.1). Cocoa in particular was decisive for the economic development of the islands, with regressive stages leading to the generation of secondary forest, or scrub, which emerged mainly as a result of agricultural abandonment. More recently, ecosystems continue to be altered, namely by the installation of extensive areas of oil palm monoculture (Oyono et al. 2014).

By the end of the 1950s, the geographer Francisco Tenreiro noted that the original forests of São Tomé were no longer found below 1400 m altitude and thus that only 1/140 of the total land on the island was covered by the original vegetation. He denounced that "by clearing the woods, degrading spontaneous formations, even replacing them entirely with new formations, men almost completely transformed the primitive physiognomy of the island" (Tenreiro, 1961; Fig. 4.2). These dramatic changes had pronounced impacts on the islands' biological diversity, adding several alien species (Muñoz-Torrent 2013) and likely eradicating many natives ones. Landscape transformations were associated with the process of developing human settlements, such as the drainage of swamps, the creation of dams and canalization of river courses, the construction of buildings and roads (especially on the coastal fringes), and overexploitation of natural resources, both on land and at sea. Some species were directly targeted for extirpation, such as attempts to eradicate species that transmit diseases like the tsetse fly (Costa 1913) and more modern attempts to eliminate malaria. These eradication campaigns employed methods including deforestation, draining swamps, and harsh chemicals that likely contributed to significant ecological loss. Thus, the presence of humans on the islands from the early colonization to the present day has dramatically shaped the landscape and ecosystem ecology.

In São Tome, Tenreiro compared landscape units to reconstruct the changes that occurred throughout the island's colonization history: from the closed forest of the *Obô* (Creole term referring to the original forest, called *Obô jiji* when it is dense and impenetrable) to the sugarcane fields (which emerged in the sixteenth to seventeenth centuries), passing through secondary forests and plantations of cocoa, coffee, oilseeds, and bananas (which emerged from the nineteenth century onward). The intensive agricultural use resulted in the gradual impoverishment of soils, giving rise to a savanna area in the north of São Tomé that is dotted with palm groves, riparian forests, and *micondos* (local name given to baobab trees) (Fig. 4.2—Diniz and Matos 2002; Figueiredo et al. 2011).

Despite these landscape alterations, the first impression of those arriving to the Gulf of Guinea islands is lush rainforest, which in some places reaches the coastline giving the landscape an appearance of dense and untouched forest, almost limitless (Fig. 4.2a). That first impression gives contemporary visitors the idea that they are in front of the original landscape of the *Obô,* never altered. The reality, however, is that plant diversity across the landscape varies not only as a function of climate, relief, and soils, but also as a function of the history of human occupation and, in particular, of the different plantation regimes that existed on the islands. These islands clearly illustrate the consequences of an incessant landscape modification: how demographic expansion and economies based on intensive cash crop monocultures and forest cultures impact the climate, environment, and biodiversity. Thus, addressing contemporary environmental challenges must account for the reality that the landscape is fundamentally different than it was 500 years ago and the biological

Fig. 4.2 The different processes that modified the São Tomé landscape, from the original humid jungles to drier savannahs with *micondós* (baobabs) and palm groves. Top: the mountainous and more humid regions that preserve dense forests (photo © Rogério Nave—2003). Middle: the most intense deforestation in the coastal and drier areas of the island, which reached its first peak between the late nineteenth century and early twentieth century. In the photo, corn plantation fields among coconut palm groves (photo © Orlando Ribeiro—1955). Bottom: drier area of the northern parts of the island, which currently presents a very modified vegetation, as is the case of the human-made savannahs (photo © Thomas Schenk—2007)

communities now include many introduced species that have since become acclimated.

Furthermore, even for those with a deep understanding of landscape richness and biological diversity, the impression of leafiness, of dense forest which is stubbornly resisting to humanization, induces a misleading perception about the islands' dimensions, making them bigger than they really are. Therefore, when addressing environmental issues, both the original vegetal landscape, that most Santomean people never stepped on, and also the current landscape constituted mainly of non-native species must be taken into account. In other words, when we are talking about ecosystems and biodiversity of the Gulf of Guinea Ocean Islands, biological and landscape evolution has to be regarded in a wider sense, considering also the adaptation of introduced species and not only the endemic ones, although, in any case, the latter are those which distinguish the islands' ecologic richness.

Despite the intense landscape transformation experienced since the first human settlements, the diversity of both plant and animal species that can only be found on these islands is extraordinary. The latest report on the biodiversity of São Tomé and Príncipe states that 15% of the vascular plant species catalogued on the islands are endemic, while 57% of birds in São Tomé and 54% in Príncipe, 44% of reptiles, and 100% of amphibians are also endemic (MIRNASTP 2016). However, many of the species presently found on the islands were introduced, constituting an important source of products that make up the traditional basic diet of the population, as well as their housing (wood) and energy source (firewood and charcoal). Likewise, agricultural crops are non-native and are a key driver of the national economy, both in terms of the domestic and export markets (Oliveira 1993).

This is especially important considering the exponential growth of the population in recent decades and also the projected growth for the decades to come, which, following the improvement in living standards, will certainly continue to intensify territorial uses and result in further landscape changes. Future risks include further deforestation due to increased demand for building materials and agricultural production, and depletion of fisheries and other natural resources. Accelerated growth, which is often poorly planned and rarely monitored, constitutes a real—and in some cases already imminent—threat to the islands' extraordinary biological richness and the people who rely on the ecosystem services they provide.

Demographic Growth, Territory, and Urban Sprawl

Until the 1960s, 32% of the up to 65,000 inhabitants of São Tomé and Príncipe lived in the Mé-Zóchi district (in the center of the island), where many of the most populated agricultural fields were concentrated (INESTP 2012a). From 1970 onward, the distribution of the population began to change, with the district of Água Grande becoming the most populous. This is where the capital city, São Tomé, is located, and this change in distribution clearly reflects the decline in the plantation economy and the trend toward urbanization. There was also an inversion in the structure of the resident population, which became female-biased. This phenomenon was due to the reduction of men brought to work in the fields and emigration of men searching for better working and living conditions abroad. Meanwhile, with the proclamation of independence in 1975, thousands of people left the country, including many of the most educated and prominent members of society. At the same time, many of those who had left in search of better

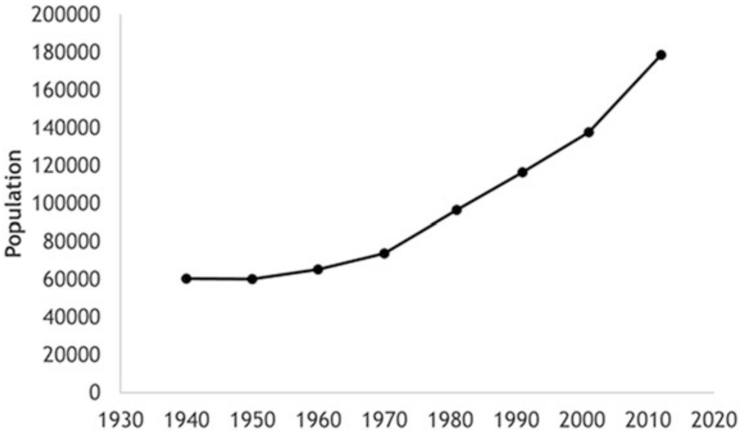

Fig. 4.3 Human population growth in São Tomé and Príncipe (source: INESTP 2012a)

opportunities abroad began to return to São Tomé and Príncipe due to the war in Angola. Comparing immigration and emigration around the time of independence, it appears the population grew, and became more concentrated around the capital city and other urban centers. Data from the last Portuguese census, in 1970, and from the first censuses of independent São Tomé and Príncipe illustrate these changes (Fig. 4.3).

Between 1976 and 1991, the colonial infrastructure was largely intact and in full operation, and the majority of the population remained in the rural areas, where the *roças* constituted authentic autonomous villages. Drops in production from former plantations, associated with the depletion of trees and production resources, together with increased competition and lower prices on the international cacao market, resulted in a collapse of the economic structure. Many of the agricultural companies that had become nationalized after the independence were privatized again, but most of them failed and became abandoned, intensifying the regression of intensive crops and the expansion of capoeira areas (scrubs, shrubby habitat). In 1981, the general population and housing census reported 96,566 inhabitants in the country, representing an increase of 30.8% compared to 1970. In the following decade, this rate of growth dropped to 20.6%, to reach a resident population of 116,504 inhabitants in 1991. It was during this period that the rural exodus toward the urban centers of the country further intensified, in particular to the outskirts of the city of São Tomé, resulting from the agrarian reform financed by the World Bank (INESTP 2012a). Between 1992 and 2020, there were two censuses, one in 2001 and the other in 2012 (INESTP 2012a). Between 1991 and 2012, the population increased by 53.41%, to 178,739 people, an increase of 62,235 inhabitants in just 21 years and almost double the population at independence. The average annual growth rate between 2001 and 2012 was 2.45%. At the district level, this index reveals that Lembá had the highest growth rate (2.96%), followed by Água Grande (2.74%), while the lowest was Caué (0.86%). These values illustrate the trend toward

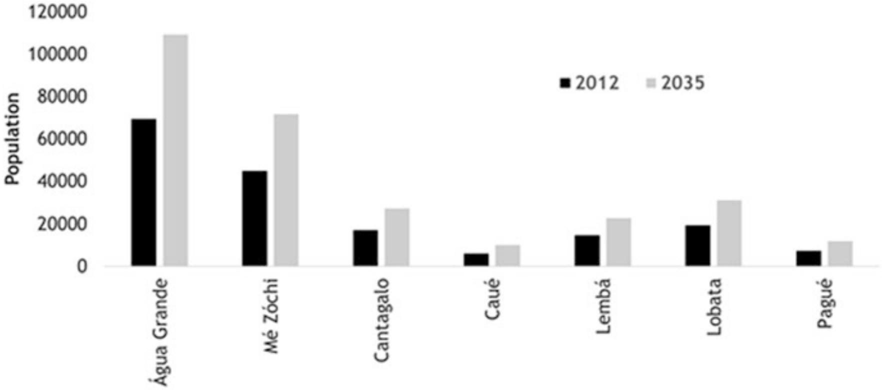

Fig. 4.4 Distribution of São Tomé and Príncipe population in each district (2012 and projections for 2035) (Source: INESTP 2012a)

population concentration around urban areas, especially around the São Tomé-Trindade axis, as seen in recent studies.

Average growth rates make it possible to carry out population projections to better understand demographic dynamics and design a more realistic territorial planning. Between 2012 and 2015, the annual population growth was 2.03%, and between 2012 and 2025, annual population growth is projected to be 2.08%, and 2.01% from 2025 to 2035. Consequently, population growth is projected to be approximately 26% between 2012 and 2035, which would place the total population at 284,293 inhabitants by 2035 (INESTP 2012c).

The demographic increases have taken place mainly in the suburbs of urban areas. In the 1990s, the number of agricultural workers, most of them residing in farmland and other rural areas, decreased from 14,500 to 8860 (INESTP 2012b). This trend was likely in response to the agrarian reform promoted and financed by the World Bank, which encouraged the government to dismantle large plots of land. These were divided into small parcels and distributed among 8735 former agricultural workers, under a usufruct regime (Oliveira 1993). The implementation of this policy had perverse effects on urban centers, namely in conditioning the capacity and sustainability of the country's current structures and basic services, increasing its population density, and clearly unbalancing the distribution of the population across the national territory (Seibert 2015). However, this trend is expected to be attenuated in the near future: if in 2012 67% of the population lived in urban areas, in 2035 it is estimated that it will reach only 70% (INESTP 2012c). The rural exodus reached its greatest extent in 1991 with the land reform, but it did not stop and has only decreased in intensity. The extreme poverty of rural areas was the main reason for this exodus, forcing populations to move in search of better living conditions, which resulted in the saturation of urban areas. It is estimated that 38.9% of the population will reside in the district of Água Grande by 2035, where the capital is located, and that by then its population will exceed 100,000 inhabitants (INESTP 2012a—Fig. 4.4). The rapid emergence of high population densities concentrated around a few urban areas has created several environmental problems, with clear implications for human well-being, such as intense road traffic and high concentrations of noise, light, and chemical pollution, as well as a deregulation of urban expansion and exploitation of resources, with far broader environmental implications.

Several indicators already point to a "demographic transition" (see Thompson 1929) in São Tomé and Príncipe. The large difference between high birth rates and low mortality rates provides a marked growth, which explains the observed rapid demographic expansion. On the other hand, the exacerbated increase in urban development, the widespread use of contraceptive methods, the evident appearance of women in the formal employment market, the costs associated with educating children, the improvement in the level of education, and the increase in family planning point to a reduction in the birth rate, which will soon approach the death rate and lead to the stabilization of the population. Other demographic indicators reveal these same trends: the average age of the population will go from 19 years old in 2012 to 26 years old in 2035 and the time needed for the population to double will go from 35 to 38 years. In any case, despite the trend of the main demographic indicators, the population of São Tomé will maintain a high population growth rate, and it is estimated that it will reach a synthetic fertility rate of 2.01 in 2030.

The districts of Água Grande, Mé-Zóchi, and Lobata, in the north of the island of São Tomé, have three-fourths of the national population, despite corresponding to less than one-fourth of the country's area (INESTP 2012a). The highest density in 2012 was in the district of Água Grande, with 4209 inhab./km^2 in 16.5 km^2. At the opposite extreme, was the district of Caué, with 23 inhab./km^2 in 267 km^2, illustrating the great territorial imbalance in terms of population distribution, which also affects the available services and the type of economic activity in each region. Since 2001, the entire district of Água Grande has been considered urban, which homogenizes the analyses referring to the capital, although it is clear that some regions within this district maintain elements of rurality. In the 2012 census, population distribution was georeferenced for the first time, which will constitute an important tool for understanding its evolution (Fig. 4.5). The urban expansion is very evident, using as main axes the national roads that leave the capital, connecting it with residential neighborhoods in Trindade to the west, in Santana to the south, and several villages in the north, toward Guadalupe. This trend is particularly evident along national road 3, from the neighborhood of Madredeus and industrial areas in Água Grande to the village of Trindade and beyond in the district of Mé-Zóchi, which effectively constitute an urban continuum. This expansion entails an increasing urban sprawl, the impacts of which are especially significant because the Santomean residential tradition is not compact, consisting mainly of detached single-family houses built of wood on family plots, known as *quintais*.

Between 2012 and 2035, the rural population is expected to continue to decline, in contrast to urban population growth. Underlying these trends is an increase in the territory's vulnerability, especially given the scarcity of effective regulatory instruments that control urban expansion and the use of natural resources. In other words, the population is becoming even more urban, reaching 70% of the total population in 2020, which will especially affect the forecast of needs for basic services and

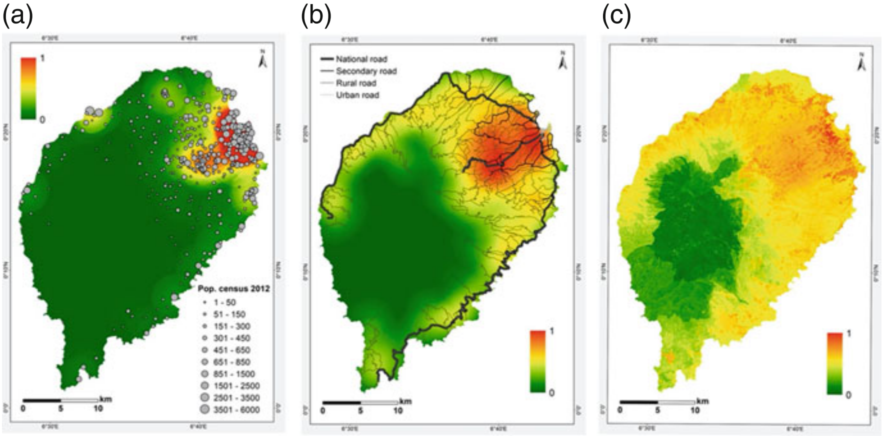

Fig. 4.5 (**a**) Population density derived from the 2012 census, (**b**) road density, and (**c**) landscape vulnerability based on a multifactorial analysis of São Tomé Island in Mikulane (2019). The coloration for all three graphs represents linear standardization

mobility, which will be greater. At the same time, this presupposes, following the traditional settlement and housing model, a clear tendency to occupy more territory: the city of São Tomé, which had an orthogonal plan of origin, will tend to grow sharply, irregularly, and haphazardly rather than a compact model in line with sustainable urbanism. However, the National Plan for Spatial Planning PNOT, currently under preparation (MIRNASTP 2020a), may be an important guide to improve territorial management, as long as they are able to support regulated and enforceable public policies in planning and controlling growth in urban and suburban areas, which take into account the demographic and occupation dynamics of the territory that we have just described.

Culture and the Concepts of *Obô* and *Omali*: When Conservation Collides with Development

Anthropogenic pressure on the environment should not only be measured in terms of demographic expansion and the occupation of space, but also in terms of income levels, traditional uses, and the population's perception of the ecological wealth of the islands (Boya-Busquet 2008a, b, Mikulane 2019). Furthermore, the same anthropic pressure must be contextualized in the awareness of the pernicious impact of uncontrolled growth in demographic terms, and in terms of an economy that does not respect the environment and instead follows the trends of a globalized capitalist system. This is increasingly the reality on these islands, where the extreme poverty of most families, an unstable economy, low wages, low saving capacity, etc., are all at play. These constraints mean that even in the most urban environments, traditional cultures persist with basic livelihoods that are largely supported by agriculture and the extraction of resources from the natural environment. The *Obô* still provides wood for construction and to make canoes, furniture and other utensils, firewood and charcoal for cooking, fruits, condiments, medicinal herbs, and sources of animal protein. *Omali* (sea) provides fish and shellfish, vital protein sources on the islands, as well as sand for construction. The highly informal and poorly quantified domestic market largely depends on these predominantly extractive activities. For example, it was estimated that in 2014 alone, São Tomé and Príncipe bakeries consumed around 5000 tons of firewood, mostly obtained from illegal harvesting in national forests (MOPIRNASTP 2019).

As an illustrative example of a prevailing mentality among islanders, the following testimony of a resident from Porto-Real, Príncipe, states: “Here [in Príncipe] there are no jobs, but there is *moandim* (a local tree) in the woods to make charcoal. Coal is easy money. If you take it to the market, it is sold straight away. If you cut a bunch of bananas, where do you sell them? With a sack of charcoal, I haven’t even arrived in the city yet and I’m already doing business” (Temudo 2008). In other words, the forest is a sure source of income for families, frequently used by many of the island’s inhabitants. Consequently, *Obô* and the *Omali* are seen by most islanders as an inexhaustible source of easily accessible resources, unlike plantations that are largely operated by the state or large agricultural companies, or existing jobs in the city, often with uncertain profit or low pay. It is the combination of a deficient family economy with abundant natural resources that reinforces the inhabitants’ direct dependence on natural resource extraction. This relationship was once more respectful and balanced, forming part of the animist beliefs themselves. For example, it was customary for fishermen to ask Mother Nature’s permission in advance and the tree’s forgiveness, before cutting it to make a canoe (Torres 2005). Currently, strong social changes, largely due to increased contact with the outside world, but also due to population growth itself, put at risk not only nature but also cultural identity. This interdependence between society and nature creates a certain perception of citizenship, which plays a crucial role in the conservation of ecosystems (Boya-Busquet 2008a).

The dense forests, in addition to being a source of resources, are also an unknown, dark, hidden, changing space for many islanders. This is where witches and sorcerers live, where outlaws hide, where the fearsome *cobra-preta* dwells (endemic to São Tomé), and where there is danger of illness or death. It is also in the depths of the forest that the spirits of the deceased live and are invoked, where uncertainty and fear are generated. It is wild place that at the same time imposes and deserves respect and challenges men to dominate it, as it is the antithesis of the civilized, the known, the controlled, which all originated from the devastation of this dark place. This feeling is also experienced in other cultures, at other times and under different circumstances (e.g., Urteaga González 1987). For instance, in school surveys (Boya-Busquet 2008a), drawings express the prejudice about the unknown space of forests, streams, and seas, and in which there is a clear ladder of values—evolving from the forest to the *roça* and to the city, as an evolution from a wild place to a civilized one. In any case, the same representations demonstrate the perception of the existence within the

Obô jiji, of an indomitable, still virgin place, where it is possible to find spirits, from which new knowledge, certain remedies, occult magic or the power of healers can be found.

There is, therefore, a great contradiction that can be explained by the generational shift (or disinterest) in relation to ancient beliefs and by the relativization of the importance of animism for the conservation of Nature. In essence, the impenetrable *Obô* is a place to respect, so perhaps it is not strange to think that the majority of the modest population considers the *Obô* (and the *Omali* as well) as a kind of "open bar," "an immense and inexhaustible cornucopia" (Valverde 2000), a place to civilize and explore. As such, it is difficult to think of valuing biodiversity if it is not recognized as a shared and finite heritage, which if it disappears as a result of economic development will take with it a large part of the unique identity of the peoples of the oceanic islands of the Gulf of Guinea.

The strongly impregnated idea that natural resources are infinite and for the enjoyment and benefit of the immediate needs of its inhabitants, associated with rapid demographic growth, the exchange of habits and social references, and the liberalization of access to land, have caused the destruction of natural resources to accelerate in recent decades, making it urgent to apply a strict policy of conservation and modification of territorial planning standards. A multifactorial analysis of the elements that are affecting the ecosystems of the island of São Tomé revealed that more than two-thirds of the island have a high degree of landscape vulnerability (Fig. 4.5—Mikulane 2019). This approach reveals the long-evident trend of degradation (Tenreiro 1961), even in areas protected by law.

The awareness of the unique value of the forests, rivers, beaches, and seas of these islands by its inhabitants is relatively new, and becoming more widespread since the beginning of the twenty-first century. This transition was largely externally inspired, stemming from international programs such as ECOFAC (Albuquerque and Carvalho 2015), but is currently reflected in several national strategic documents (e.g., MIRNASTP 2016, MIRNASTP 2020a, b), which identify the values to be protected in coastal and marine ecosystems, inland waters, forestry, and agrarian ecosystems, and from which the establishment of the Obô Natural Park was derived (DGA 2006a, b). Despite clearly pointing out threats and challenges, awareness programs on these values have not been satisfactorily established or implemented, starting with the low presence of this topic in school curricula (Carvalho et al. 2010).

Despite legal regulations and strategies created to promote responsible environmental management, poor enforcement results in widespread transgressions in illegal activities such as systematic cutting of trees in protected areas without authorization (Espírito et al. 2020), indiscriminate extraction of sand from beaches, poaching of protected species, or fishing with prohibited gear. Awareness of the value of biodiversity as a shared heritage remains poorly rooted, or is outweighed by necessity, and the debate about its importance continues to have little practical effect.

Agricultural and urban land use are also often at odds with environmental protections. In addition to the expansion and intensification of small-scale agriculture carried out mainly by small owners, there are strong pressures inflicted by large concessions (Oyono et al. 2014). This is true both on the part of agricultural corporations, which work to recover and intensify plantations, and on the part of urban interests, sometimes linked to tourism, which have even intruded into protected areas. As already denounced long ago (Tenreiro 1961), the development of intensive agriculture, concerned with above all profit and export, has been at the expense of natural ecosystems. In addition to the direct impacts of agriculture, the impact of improving the network of roads and other infrastructures has also resulted in further land use intensification. All these elements of modernization will continue to require more land; for example, continued horizontal expansion of single-family homes at the current urban growth rate is unsustainable.

Deforestation means not only an abrupt landscape change in the context of the islands, but also a change in climate regimes, with implications for the islands' ecology (Henriques 1917). These changes can be especially notable in terms of rainfall and, therefore, water supply. In this context, it is evident that it is difficult to strike a balance between conservation and development. As such, in the medium and long term, the prospect of retaining functional ecosystems on the islands is sobering. With the continued decline of local biological diversity, and, in particular, of endemic species, the islands' ecosystems will likely become increasingly fragile.

On the island of Príncipe, low demographic pressure and lower accessibility, associated with a more pro-conservationist policy, provide some hope for the preservation of its biodiversity and landscape integrity. The island was declared a UNESCO Biosphere Reserve in 2012 (UNESCO 2013), which is paired with a tourism model that leverages the unique landscape and cultural heritage. These circumstances have also attracted the interest of scientists and conservationists, leading to the description of new endemic species and the implementation of several successful conservation programs (e.g., Fundação Príncipe 2021). This approach seems to have influenced a more positive perception of biodiversity and stronger enforcement of environmental regulations, halting the trend of environmental degradation. These changes end up benefiting an economic model that centers nature conservation, although perhaps the benefits for the local population are less clear: so far, this theory has not been associated with changes in population demography or urban planning. One important consequence, however, is growing social inequalities created by strong foreign investment that has led to an increase in prices on the island. In addition, the small size of Príncipe means the species on this island are much more vulnerable to anthropogenic pressure, as they have much smaller distributions.

As a consequence of all of this, the first draft of the PNOT (MIRNASTP 2020a) outlines a more solid basis for the delimitation of uses in the territory and the urban expansion model. These include strict safeguarding of natural habitats and ensuring the balance of biophysical systems, and the sustainability of hydrological cycles, both those that constitute a forest or fish reserve and their buffer zones and agricultural regime zones. This document highlights a chapter on establishing the planning model that adopts the culture of territorial management, and a second chapter on measures to protect the environmental and cultural system. Proposed measures include the promotion of institutional and population awareness to preserve and enhance the notable natural and cultural elements, and the establishment of a national policy for the environment, nature conservation, and protection of biodiversity, very much in line with correcting the effects of uncontrolled growth described above. It is therefore an encouraging instrument, or at the very least a basic statement of good intentions.

The Limits of Environmental Change: A Dystopian Panorama?

Given the current moment of social and economic development, the outlook for biodiversity conservation in the islands of the Gulf of Guinea is not very optimistic. In particular, the exponential growth of the population and, consequently, the increasing pressure exerted on natural resources suggest the future scenario will be one of rapid environmental degradation, with the ultimate outcome being the general depletion of the territory, deforestation, disappearance of beaches, the gradual erosion of ecosystems, and disappearance of endemic species, but also threats to the persistence of the allochthonous richness already adapted to the territory.

Is it possible to put limits on this Malthusian drama in these jewels of the Atlantic? Is it really impossible to think of an economic development that is not based on the exhaustion of territory? Will the islands' unique biological diversity persist? There is still time to promote effective territorial planning, to which must be added demographic containment, and the implementation of a rigorous environmental policy, based on good management of uses, but also on awareness and, primarily, on basic education. There is great difficulty in reconciling the management of resources recommended by specialists with local practices, needs, and interests, and even private or corporate ones. In this sense, there is still a lot of work to be done, and it will be a great challenge to overthrow many of the vested interests. Keeping up with the current pace, the current landscape of the islands may become unrecognizable in a short time. To curb the prospects created by the current development path and avoid the most devastating environmental scenarios, it is necessary to increase social and economic equity, allowing access to sufficient income to help change the population model and demographic and social growth. The ultimate goal is a shift in mentality that positively influences the valorization of the islands' unique biodiversity as a common heritage, which is in fact the clearest pillar for a differentiated and long-term sustainable economic and social development model.

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Chapter 5
The History of Biological Research in the Gulf of Guinea Oceanic Islands

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Abstract The oceanic islands of the Gulf of Guinea (Príncipe, São Tomé, and Annobón) have been the focus of biological research for over two hundred years. Following small surveys that generated modest collections in the eighteenth and early mid-nineteenth century, European institutions commissioned several exploratory missions to the region that resulted in the first major catalogues of its biodiversity. The following century brought a new wave of research investment, mostly driven by the colonial interests. After the independence of both Equatorial Guinea

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and São Tomé and Príncipe, novel research trends focusing on conservation aspects of biodiversity research emerged. Here we present a chronological review of the zoological and botanical expeditions to the region, commenting on their major results, collectors, and the naturalists who studied them.

Keywords Expeditions · Herbaria · History of science · Natural history collections · Taxonomy

Introduction

From the beginning, humans have tried to understand, classify, and master the biodiversity that surrounds them. Through time, and across different civilizations and cultural groups, different approaches and classification schemes have been proposed to try to classify the natural world. Despite many attempts, the creation of a natural, objective, and replicable system to classify nature was only achieved in the mid-eighteenth century, with the seminal works of the Swedish naturalist Carl Linnaeus (1707–1778). The works of Linnaeus are universally recognized as marking the birth of modern natural history and all its resulting subdisciplines (biology, ecology, etc.). As supporting evidence for its foundational importance in the current international zoological and botanical codes of nomenclature, valid scientific names are those starting in the 1750s, following the works of Linnaeus. For zoological nomenclature, the fixed starting point is 1758 (ICZN 1999), which corresponds to the publication of the tenth edition of Linnaeus' *Systema Naturae* (Linnaeus 1758). For botanical nomenclature, this point is only five years before, in 1753 (Turland et al. 2018), corresponding to the publication of the first edition of Linnaeus' *Species Plantarum* (Linnaeus 1753). Although this renders all the previous works invalid, from the narrow point of view of biological nomenclature, this does not mean that earlier work does not provide important information and insights regarding the natural world. In addition, many important contributions to scientific knowledge throughout history (and today) are made outside of the formal scientific literature. For the oceanic islands of the Gulf of Guinea, the reports made by some of the earliest Portuguese navigators in the late fifteenth and early sixteenth centuries are teeming with information about the nature of these islands and the surrounding sea. This is the case of the report produced by the Portuguese navigator Gonçalo Pires (dates of birth and death unknown), transcribed by Valentim Fernandes (ca. 1450–1519) and subsequently published by Baião (1940), in which the author describes the geography, fauna, and flora of the three oceanic islands in considerable detail.

This chapter aims to provide a general overview of more than two centuries of scientific research on the biodiversity of the oceanic islands of the Gulf of Guinea. Due to the impossibility of providing a fully detailed account on the life and work of every naturalist or explorer that worked on the biodiversity of these islands, some of which would be sufficiently rich and detailed to write an entire chapter or book about, this text intends to be mostly a commented guide to the available publications. In a way, it is an updated and commented version of the important bibliographic compilations provided by Exell et al. (1952), Fernandes (1982) and Figueiredo

(1994a) for plants and by Gascoigne (1993, 1996) for animals, but it also aims to present the major research trends regarding biodiversity of the oceanic islands of the Gulf of Guinea across time. Despite the historical importance of older records, such as those of Gonçalo Pires, we do not include them here and focus solely on works published after the Linnean revolution, as the latter ones are those more readily accessible to the present-day researcher and student.

Eighteenth Century to Mid-Nineteenth Century

Formal zoological research in the Gulf of Guinea did not begin until the latter half of the nineteenth century, although in the late eighteenth century and earlier decades of the nineteenth century small collections made their way into Europe. Naturalists like the Danish zoologist Otto Friedrich Müller (1730–1784), the Dutch merchant and entomologist Pieter Cramer (1721–1776), and the French zoologist Jean Guillaume Bruguiére (1749–1798) studied them and described the first known species of insects and molluscs from the islands (Müller 1774; Cramer 1775/76; Bruguière 1792). Most notably, the French Naval officer Sander Rang (1793–1844) docked the naval brig *La Champenoise* in Príncipe for a month, where he collected terrestrial molluscs, which he later described (Rang 1831). During these early days of the modern era, much of the collecting and research was conducted in a framework of private collections and a dilettante approach to science, but these first records can be seen as the beginning of taxonomic research in the region.

The oldest record of plants collected from the Gulf of Guinea Islands dates from 1787 and was collected by the French naturalist Ambroise Marie François Joseph Palisot de Beauvois (1752–1820), during his stay in Príncipe Island while he was ill (Exell 1944). Out of the four species he collected, *Asplenium emarginatum*, *Aeschynomene indica*, *Tristemma hirtum,* and *Agrostis tropica*, the last has never been collected again on Príncipe and no other specimen is known (Figueiredo et al. 2011). After Beauvois' initial study, botanical specimens were only collected again in the Gulf of Guinea during the nineteenth century. The Scotsman George Don (1798–1856) spent three weeks collecting plants in São Tomé (15 May to 11 June 1822). All the sailors who accompanied him ashore died from a tropical disease after leaving the island (Exell 1944). It was a good collection for the time, with about twenty species new to science, some of which have not been found again in São Tomé (Figueiredo et al. 2011). These "missing" species may in part be because some of them, such as *Cichorium intybus* and *Pluchea sagittalis* (*Epaltes brasiliensis*), were alien weeds (from Europe and South America, respectively) that did not become established (Exell 1944) or were, perhaps, misidentified.

Later, Andrew Beveridge Curror (1811–1844), a British naval surgeon and naturalist, visited Annobón between 1839 and 1843, where he reportedly collected two species of plants, *Begonia annobonensis* and *Vernonia amygdalina* (Exell 1944). Figueiredo and Smith (2020a) cite the holotype of *Begonia annobonensis* [*Curror 9* (K000242508), Annobón 1841]. At Herb. K there is also a herbarium sheet with several specimens of *Vernonia amygdalina* from Annobón, two of which were collected by Burton (Oct. 1863) and one by Curror (*Curror 8*, 1841). It is likely that Curror made more collections in Annobón. Curror died of "remittent fever", during his last expedition (in 1844), off the coast of Gabon (Figueiredo and Smith 2020a). Curror also travelled to the island of Príncipe on four different occasions during 1839 (Figueiredo and Smith 2020a). Even though none of Curror's collections at Herb. K are labelled as originating from Príncipe, one of his collections is, without a doubt, from that island, consisting of the fern *Alsophila camerooniana* var. *currorii*, which is endemic to Príncipe (Figueiredo and Smith 2020a).

Near the end of this period, Désiré Edélestan Stanislas Aimé Jardin (1822–1896), a clerk in the service to the French Navy, collected plants in Tropical West Africa between 1845 and 1848 and visited Príncipe. Amongst the plants (about 50 species) he mentioned from this island (Jardin 1850/51), he refers one *Combretum* without the specific name. Exell (1944), who did not see the collection, referred to it as *Combretum platypterum*, which has not been found again in Príncipe. This information was given to him by Georges Le Testu (Exell 1944), who, at Exell's request, had searched the Jardin collection, then held at Herb. CN and later transferred to the Herb. P. The only species of *Combretu*m recorded in Príncipe is *Combretum paniculatum* (Figueiredo et al. 2011).

Mid-Nineteenth Century to Early Twentieth Century

From the mid-nineteenth century forward, a wave of interest in African territories prompted several European institutions into commissioning naturalist expeditions to the continent. The need to catalogue the colonial possessions, together with the broader interest to uncover the planet's biodiversity, led to the flourishing of taxonomy. Most of the publications and research outputs of this time came in the form of species descriptions, checklists, and catalogues.

The first publication was that of the Swedish mycologist Elias M. Fries (1794–1878), who was the first naturalist to report fungi from São Tomé (Fries 1851), namely six Agaricomycetes species collected by Krebs (no additional collector information). This publication is of special relevance not only as the first published account of fungi of the oceanic islands of the Gulf of Guinea, but also as the first major bibliographical record to feature a report on the biodiversity of the region following the investment boom in the continent.

In 1853, while *en route* to a botanical expedition to Angola, the Austrian botanist Friedrich Welwitsch (1806–1872) collected specimens on the islands of São Tomé and Príncipe, doing the same seven years later upon returning from the trip (Figueiredo and Smith 2020b). He visited Príncipe between 15 and 22 September 1853. Almost all the species he collected were new records for the island, except the fern *Alsophila camerooniana* var. *currorii* found years before by Curror in 1839 and those species collected by Jardin. On 23 September of the same year, he paid a short visit to São Tomé. In December 1860, on the return trip from Angola to Lisbon, Welwitsch stayed in São Tomé for some days and amassed a very good collection of plants, with interesting new records and new species, some of which he described (Exell 1944). The mollusc specimens collected by Welwitsch on the islands were studied and published by Morelet (1868), and later mentioned in Crosse's (1868) compilation of known land molluscs from São Tomé. Pierre Marie Arthur Morelet (1809–1892) was a renowned French naturalist specializing in molluscs, whereas Joseph Charles Hippolyte Crosse was a French conchologist, co-editor of the publication *Journal de Conchyliologie*. Additional malacological fauna collections resulting from expeditions into the area undertaken by various naturalists were studied by Morelet (1848, 1858, 1860, 1873).

During the seven years between Welwitsch's two visits to these islands (i.e. between 1853 and 1860) only the Scottish gardener Charles Barter (1821–1859), collector on William Baikie's second Niger Expedition (1857–1863), visited Príncipe. In 1858, he made a small but important botanical collection, primarily comprised of orchids (Exell 1944; Figueiredo and Smith 2020b). He caught dysentery and died on 15 July 1859 at Rabba, Nigeria. Barter was replaced on this expedition by Gustav Mann (1835–1916), a German botanist, who collected a great number of plants during the three years he participated in the expedition (1859–1862). In August 1861, Mann collected across a large area of São Tomé and reached Pico de São Tomé, discovering several new species and various interesting plants that would be studied by Hooker (1863, 1864). Later, Mann collected on Príncipe (22 September–26 October 1861), again uncovering new species and novelties for the flora of the island (Exell 1944). A few years later, Richard Francis Burton (1821–1890), who served as the British Consul in Bioko from 1861 to 1864, visited Annobón (October 1863) on his way back to Bioko from the Niger–Congo rivers expedition (August–October 1863) and made a small collection, currently held at Herb. K (Burton 1876).

In 1865, the German explorer Heinrich Wolfgang Ludwig Dohrn (1838–1913) spent six months in Príncipe, where he collected birds, reptiles, and snails. The results were later published by him and by other specialists (Dohrn 1866a, b, c; Keulemans 1866; Heynemann 1868; Peters 1868). Subsequently, the German zoologist Richard Greeff visited São Tomé and Rolas Islet between 1879 and 1880, where he collected extensively and obtained important specimens that contributed to the description of a considerable number of new species by him and others (Peters 1881; Greeff 1882a, b, c, d, 1884, 1886; Bocage 1886a; Koch 1886; Krauss 1890).

In 1871, the Portuguese naturalist Félix António Brito Capello (1828–1879) published the first list of fishes from the Portuguese islands of Madeira and Azores, with the inclusion of fishes from its overseas possessions Angola, Cabo Verde, Mozambique, and São Tomé and Príncipe (Brito Capello 1871). After his death, António Roberto Pereira Guimarães continued Capello's analysis of the material extant in the Lisbon Museum and published two additional papers on the topic (Guimarães 1882, 1884).

In 1885, Adolfo Frederico Moller (1842–1920; Fig. 5.1), chief gardener of the Botanical Garden of the University of Coimbra, was sent by the institution to collect natural history specimens in São Tomé. Despite it being a short four-month

Fig. 5.1 Portraits of Adolfo Moller (left) and Júlio Henriques (right). Moller's portrait from Henrique Eusébio Moller private family álbum, adapted from Gouveia (2014). Henriques' portrait reproduced with the permission of the Botanical Archive—Department of Life Sciences, University of Coimbra, Portugal (PT-UC-FCT-DCV-ABUC-S2.13)

exploratory stint (23 May–25 September), Moller found time to teach Francisco Quintas (dates of birth and death unknown), the son of a Portuguese owner of coffee and cocoa plantations, how to continue his botanical collection (Gouveia 2014; Figueiredo and Smith 2019). Quintas travelled and made remarkable collections in the west and south of São Tomé between 1885 and 1889 and also in Príncipe between January and March 1889 (Figueiredo and Smith 2019). Bedriaga (amphibians and reptiles: Bedriaga 1892, 1893a, b), Bocage (amphibians and reptiles: Bocage 1893b), Moller (sponges: Moller 1894, studied by Weltner in Berlin), Nobre (land molluscs: Nobre 1886b, 1894), Osório (fish: Osório 1891a), Verhoeff (Chilopoda and Diplopoda: 1892, 1893), and Vieira (insects, spiders, and birds: Vieira 1886, 1887a, b, 1894) published the majority of the zoological results from the expedition. The botanical material was deposited at the Herb. COI and studied by the botanist Júlio Augusto Henriques (1838–1928; Fig. 5.1) for his publications on the flora of São Tomé and Príncipe.

Francisco Newton (1864–1909; Fig. 5.2), working for the Natural History Museum of Lisbon, fruitfully explored the Gulf of Guinea for a decade between 1885 and 1895 (Santos and Ceríaco 2021). The collections amassed by Newton during that period proved crucial in the first extensive faunal catalogues and the description of new species from the region, resulting in numerous works. Of special

Fig. 5.2 Portrait of Francisco Newton and a watercolour he painted of a *Leptopelis palmatus* from Príncipe Island. Source: Arquivo Histórico do Museu Bocage

importance were those published by José Vicente Barbosa du Bocage (1823–1907), director of the zoological section of the Natural History Museum of Lisbon. Bocage provided the first comprehensive checklists of the islands' vertebrate fauna, as well as the description of several species new to science, including amphibians, reptiles, birds, and mammals (Bocage 1886a, b, c, 1887a, b, c, 1888a, b, c, d, 1889a, b, c, 1891a, b, c, 1893a, b, c, 1895a, b, c, d, e, 1896, 1903, 1905). The butterflies collected by Newton were studied and published by Emily Mary Sharpe (1893), while the land molluscs were studied by Arruda Furtado (Furtado 1888), Girard (1893a, b, 1894, 1895), and Augusto Nobre (Nobre 1886a, 1887, 1909). Balthazar Osório studied both crustaceans and fishes (Osório 1887, 1888, 1889 1890, 1891a, b, 1892a, b, 1893, 1895a, b, c, d, e), Júlio Bettencourt Ferreira was responsible for the reptiles (Ferreira 1897, 1902), and the birds were studied by David Armitage Bannerman (1931), José Augusto de Sousa (1887, 1888) and Richard Bowdler Sharpe (1892). While Newton's zoological collections were sent to Lisbon, his botanical specimens were sent to the University of Coimbra where they were studied by Júlio Henriques. An extensive collection of letters from Newton to Bocage and Osório is still extant in the collections of the *Museu Nacional de História Natural e da Ciência*, Lisbon, and are being processed for a future publication (Ceríaco and Santos, in prep.).

Despite the few publications on the islands' botany published in the previous decades, the research programme established by Henriques can be considered the birth of systematic botanical studies in the islands. The first contact Henriques had with the flora of São Tomé was through a few specimens collected by Newton in 1881 (Henriques 1884a; Figueiredo et al. 2019a). After the return of Moller from São Tomé, Henriques highlighted future plans for the study of the collections from the island (Henriques 1895). For the first instalment of what Henriques would call "Flora de S. Thomé" (Henriques 1886), he invited other specialists to identify and describe the collections in his possession (i.e. those from Newton, Moller, and Quintas). Henriques (1886) had the contributions of Charles Fuller Baker (ferns: in Henriques 1886, pp. 149–158 + 2 plates), Carl Muller (mosses: in Henriques 1886, pp. 159–169), Franz Stephani (liverworts: in Henriques 1886, pp. 170–184 + 3 plates), Heinrich Georg Winter (fungi: in Henriques 1886, pp. 185–204 + 3 plates), William Nylander (lichens: in Henriques 1886, pp. 205–217), and C. Agardh, O. Nordstedt, F. Hauck, and Charles Flahault (algae: in Henriques 1886, pp. 217–221).

This series of publications continued in the following years. In 1887, Henriques coordinated two additional papers, one based on Newton's collections (among other collectors that were active in the African mainland; Henriques 1887a), and another based on the collections of Welwitsch, Moller, and Quintas (Henriques 1887b). For the latter, Henriques collaborated with foreign botanists such as Ernst Haeckel (grasses), Henry N. Ridley (sedges and orchids), the Count Solms-Laubach (*Pandanus*), and Cornelis A. Backer who made general reviews and corrections to the manuscript. For the paper on Newton's collections, Henriques (1887a) had once again contributions of Franz Stephani (liverworts: in Henriques 1887a, pp. 224–225) and William Nylander (lichens: in Henriques 1887a, pp. 221–222).

Other contributions were published in 1889 by Henriques (1889a, b). Following the strategy used in the 1886 instalment, besides his own contributions and identifications, Henriques sent material to other European botanists, who subsequently provided the results of their observations. Henriques (1889b) had the collaboration of Karl August Otto Hoffmann (Capparidaceae: in Henriques 1889b, p. 224; Lithrarieae in Henriques 1889b, p. 229), Célestin A. Cogniaux (Melastomataceae: in Henriques 1889a, p. 226; Cucurbitaceae: in Henriques 1889b, p. 227), and Robert Allen Rolfe (Orchideae: in Henriques 1889b, pp. 236–238). In the same year, Augusto Nobre was able to study some fresh material of *Afrocarpus mannii* collected by Moller in Lagoa Amélia and sent to him by Henriques (Nobre 1889). This was the second study on this endemic and enigmatic conifer. Roumeguère (1889), Saccardo and Berlese (1889), Bresadola and Roumeguère (1889), and Bresadola (1890, 1891) studied and described several species of fungi from the collections sent to them by Henriques. The bryophytes collected by Quintas were studied, described, and published by Brotherus (1890).

Based on new material sent to Henriques by Quintas, Henriques (1891) published a further article with the contributions of Hoffmann (Crassulaceae: in Henriques 1891, p. 135) and Rolfe (Orchideae: in Henriques 1891, pp. 137–143). Henriques' last contribution to the flora of São Tomé in the nineteenth century (Henriques 1892) stretched for about 160 pages and covered several families of plants. It included several contributions: Cogniaux (Melastomataceae: in Henriques 1892, pp. 118–119; Cucurbitaceae: in Henriques 1892, pp. 119–122), Casimir de Candolle

(Begoniaceae: in Henriques 1892, pp. 122–124); Piperaceae: in Henriques 1892, pp. 152–155), Adolf Engler (Anacardiaceae: in Henriques 1892, p. 110), Gustav Lindau (Acanthaceae: in Henriques 1892, pp. 145–148), Ferdinand A. Pax (Euphorbiaceae: in Henriques 1892, pp. 156–161), Jules E. Planchon (Ampelideae: in Henriques 1892, pp. 108–109), and Karl M. Schumann (Rubiaceae: in Henriques 1892, pp. 126–134).

Sobrinho (1953a) refers some plants from Príncipe Island collected by Jacinto Augusto de Souza Junior in February 1880. These collections were not included in the revisions of Henriques. Efforts to identify this collector have yielded no results besides his name and herbaria where his collections are deposited: Herb. COI and LISU (Exell 1962, Liberato 1994). One of the most enigmatic results of Souza Junior works in São Tomé and Principe is the description of the species *Justicia thomensis* by Landau (Holotype at COI: COI00005706), a species of Acanthaceae that has never been collected again since its original description, raising questions if the specimens were in fact collected in the islands, or if the species may have become extinct (Figueiredo et al. 2011). Portuguese museums also received several small collections of zoological specimens from the Gulf of Guinea, mostly collected and offered by Portuguese military personnel deployed in the area, studied by various specialists (Bocage 1880a, b, 1887d; Nobre 1891, 1894, 1901; Osório 1887; Santos 1882).

The English diatomist John Rattray (1858–1900) participated in the *Buccaneer* steamship 1885–1888 expedition that combined plans to conduct sound operations and lay a telegraph line along the West African coast (Bencker 1930; Figueiredo et al. 2019b) with the collection of biological specimens. A brief stop during early 1886 in the Gulf of Guinea resulted in a small zoological collection, the results of which were later published by Hoyle (1887), Scott (1893), and Stebbing (1895), and botanical collections.

Leonardo Fea (1852–1903), an experienced Italian naturalist, explored the Gulf of Guinea from 1901 to 1902 under the sponsorship of the Museo Civico di Storia Naturale of Genoa (Fea 1902). This was his last expedition before passing away in 1903. His results were studied in the following years by Boulenger (reptiles: 1905, 1906), Breuning (insects: 1955, 1956), Germain (molluscs: 1912a, b, 1915, 1916), Griffini (Orthoptera: 1905), Kerremans (Buprestidae: 1905), Lewis (Histeridae: 1905), Lesne (1905), Martin (Odonata: 1908), Salvadori (birds: 1903a, b, c), Silvestri (Thysanura: 1908), and Simon (Arachnids: 1907).

During the second half of the nineteenth century, besides the taxonomically oriented works, several authors focused on the agricultural capacities and potential of São Tomé (Castro 1867; Henriques 1884, 1898; Nogueira 1885; Moller 1899). This resulted in the publication of several works related to coffee (Almeida 1858; Carvalho 1858; Castro 1857–1858), cinchona (Henriques 1876, 1878, 1880a, b, 1882), fruits (Almeida 1865), and timbers (Castro 1894). These topics, especially those related to coffee, would be explored in much more detail in the following decades. Plant uses and vernacular names were addressed by Almada Negreiros (1895, 1901) in publications that are arguably the first on ethnography of São Tomé.

Early Twentieth Century to the Independence of Equatorial Guinea (1968) and São Tomé and Príncipe (1975)

The taxonomic cataloguing efforts of the nineteenth century carried on into the first decades of the twentieth century. Some new research trends started to emerge, becoming quite prevalent in the mid-twentieth century and until the independence of the two colonies. These trends were mostly dedicated to what was known as "colonial sciences"—research dedicated to the improvement of the colonial enterprise in its different activities (but especially agriculture), as well the well-being of the colonists and native populations. Therefore, studies dedicated to economic entomology, fisheries, and parasites became the dominant focus. Traditional taxonomic work also continued on several groups.

The botanical collections amassed during the mid-nineteenth century contributed to increased botanical interest in the islands of the Gulf of Guinea. To continue his studies of the flora of São Tomé, Júlio Henriques in 1903 at the age of 65, fulfilled his dream of travelling to São Tomé. Henriques travelled through a large part of the island, but the weather conditions prevented him from ascending to the Pico. From his trip to São Tomé and the consolidation of his already vast knowledge of the island he published one of his most iconic monographs entitled "A ilha de S. Tomé sob o ponto de vista histórico-natural e agrícola" [The Island of S. Tomé from the historical-natural and agricultural point of view] (Henriques 1900, 1917). The study of the material collected in the previous century continued (e.g. Hariot 1908, with a revision of the algae collected by Moller and Quintas).

Exell (1944) gave a comprehensive account of botanical collecting in São Tomé, Príncipe, and Annobón, naming all collectors recorded up to that date. In the account he mentioned a "valuable collection" made by the Portuguese engineer "I. Campos" in 1907 on São Tomé, mostly deposited at Herb. COI. It included specimens of *Adinandra manni* re-collected on Pico de São Tomé, and three specimens which were described in Exell (1944) as three species new to science: *Urophyllum camposii*, *Lachnopylis thomensis,* and *Peddiea thomensis*. According to the data on the label of the specimens the collector is E. Campos. This is likely Ezequiel de Campos (1874–1965), an engineer who worked in São Tomé and Príncipe from 1899 (Campos 1920). He was later a professor and a member of Parliament in Lisbon. Much later, in 1954, Campos became the chief of *Missão Científica de São Tomé* (see below).

Among the most relevant collections referred by Exell (1962) is the one made by Auguste Chevalier (1873–1956), a French explorer and botanist who visited São Tomé and made collections from August to October 1905. Chevalier made over 700 collections (Chevalier 1914) in São Tomé that are deposited in the Herb. P, COI, K, and LY (Exell 1962, Liberato 1994). In 1909, the agronomist José Joaquim de Almeida (1862–1933), the first director of the Colonial Garden in Lisbon, made a study visit to São Tomé, collecting some plants that he later deposited in Herb. COI and LISJC (meanwhile integrated into LISC) (Exell et al. 1952, Liberato 1994).

An extensive botanical collection from Annobón was made by the German botanist Johannes Gottfried Wilhelm Mildbraed (1879–1954) under the auspices of the *Deutsche Zentral Afrika-Expedition* (1910–1911) in 1911, including 32 pteridophyte species. Mildbraed spent over a month on the island of Annobón from 5 September to 13 October 1911 collecting almost everything that was in flower or in fruit at the time. His collection was mainly kept at Berlin (Herb. B) but unfortunately, it was almost completely destroyed during the allied bombings of Berlin in World War II. Nevertheless, there are duplicates of Mildbraed's collections at Herb. HBG, K, and BM. Mildbraed published his results (Mildbraed 1922) which were later reviewed by Exell (1944, 1963).

A new array of zoologists visited the islands in the following years. French zoologist Charles Gravier (1865–1938) was entrusted to lead a scientific mission to São Tomé (C.C.A.M. 1938), with several papers resulting from his collections (Polychaeta: Billard 1907; molluscs: Germain 1908; corals: Gravier 1906, 1907a, b, 1909, 1910; bivalves: Lamy 1907). The British Lieutenant of the Rifle Brigade, Boyd Alexander (1873–1910), was a renowned explorer and ornithologist who journeyed through the Gulf of Guinea in 1909 accompanied by his faithful Portuguese colleague José Lopes (Bannerman 1914). Alexander's bird collections were subsequently studied and published by Bannerman (1914, 1915a, b). Additionally, mollusc specimens were sent to the British Museum around the same time, collected by amateurs working in the Gulf of Guinea and later studied by Tomlin and Shackleford (1912, 1913a, b, 1914/15, 1915), and Tomlin (1923). Seabra (1922) studied the insects collected by Sousa da Câmara (1871–1955) in São Tomé, on behalf of the *Instituto Superior de Agronomia* in Lisbon, and sent some material to be studied in the Imperial Bureau of Entomology. This material was reviewed a year later by Herbert Campion (1923). While on leave in Europe, the Trinidadian entomologist Frederick William Urich (1870–1937) carried out a short expedition to São Tomé in 1920, in which he rediscovered a parasitic dipteran species in its original bat host (Urich et al. 1922). The English explorer Thomas Alexander Barns (1881–1930) collected on behalf of the amateur entomologist James John Joicey (1870–1932) in the region of the Gulf of Guinea during the end of 1925 and 1926, on what was his third and last expedition (Talbot 1932). The results of this expedition were published by Joicey and Talbot (1926, 1927), Prout (1927a, b) and Riley (1928). José Correia (1881–1954; Fig. 5.3) and Virginia Correia (1900–1987), a husband-and-wife team of collectors, explored the Gulf of Guinea during 1928 and 1929 on a trip funded by S. Brinckerhoff Thorne, trustee of the American Museum of Natural History. Amadon (1953) published the ornithological results of their expedition.

From October 1932 to March 1933, the entomologist Willie Horace Thomas Tams (1891–1980) and the acclaimed botanist Arthur Wallis Exell (1901–1993) conducted a scientific mission to the Gulf of Guinea on behalf of the British Museum, sponsored by the Percy Sladen Memorial Fund and Godman Trusts Fund (Tams 1934). The zoological specimens collected in this expedition were examined and published by several authors (Diptera: Edwards 1934; Collembola: Maldwyn-Davis 1935; Microlepidoptera: Meyrick 1934; Odonata: Longfield 1936). During the four-month long British Museum expedition, Exell made extensive botanical collections in São Tomé (mostly in the mountains), Príncipe, Bioko

Fig. 5.3 The Portuguese naturalist José Correia, during his bird-collecting mission to the Gulf of Guinea (1928–1929). Courtesy of the Ornithological Archives of the American Museum of Natural History

(Moka region), and Annobón. Exell deposited his specimens at Herb. BM and sent duplicates to Herb. COI and BR (Exell 1962); his collections include bryophytes, algae, lichenes, and fungi (Exell 1944). Resulting from this collecting trip, Exell published a catalogue of the vascular plants of the three islands (Exell 1944), in which 75 new names were published (36 being for new species) and several new records noted (Figueiredo et al. 2011). In the following years, Exell published a supplement to the catalogue (Exell 1956), and a checklist of the angiosperms for the four islands in the Gulf of Guinea (Exell 1973a). Although he visited and collected on the four islands, Exell made use of earlier collections when compiling the plant catalogues of these islands, namely from Herb. COI where he spent some time in 1934 (Figueiredo et al. 2018; Fig. 5.4). In addition to having intensively and extensively collected and studied the botany of the islands of the Gulf of Guinea, while using the existing collections in comparative studies with his own specimens,

Fig. 5.4 From left to the right (including background), the botanists Luis Grandvaux Barbosa, Maria Leonor Gonçalves, Arthur Exell, Mildred Exell, Abílio Fernandes, Rosette Fernandes, and A. V. Bogdan in the Botanical Garden of Coimbra, September 1960

Exell was responsible for reviewing and re-organizing many of the pre-existing collections, such as that of Herb. COI (Exell 1944, 1962; Figueiredo and Smith 2019). For the supplement of the catalogue, Exell (1956) studied some old collections that had not been examined previously or that he reassessed, and some recent ones. A substantial collection made by Newton in 1893 in Annobón is included in this supplement. The recent material consists mostly of the collections made by Espírito Santo (see below) in São Tomé. A few specimens collected by the agronomist Branquinho de Oliveira (1904–1983) and E. Noronha in 1951 in São Tomé (listed by Sobrinho 1953b), likely *en route*, were also included, consisting mostly of weeds and aliens.

Exell was one of the most prolific figures when it came to the cataloguing of the flora of the islands of the Gulf of Guinea. From 1944 to 1973, he produced a dozen publications, some of which became classic references (Exell 1944, 1952, 1956, 1958, 1959, 1962, 1963, 1968, 1973a, b; Exell et al. 1952; Exell and Rozeira 1958). Like Henriques, Exell also received the contributions of numerous botanists who identified the collections: 16 botanists were acknowledged in Exell (1944) and

21 botanists in Exell (1973b). Arthur Hugh Garfit Alston (1902–1958) who authored the treatment of the pteridophytes (Alston 1944) in Exell's Catalogue (1944) also contributed with the pteridophytes for the Supplement (Alston 1956) and for two additional articles (Alston 1958, 1959).

The algae of São Tomé and Príncipe, that had not been revised since 1908, were finally treated by Rodrigues (1960).

Other plant collectors in the first half of the twentieth century were the Swiss botanist John Gossweiler (1873–1952), who collected in Príncipe during stopovers of his numerous trips between Angola and Portugal, in 1913, 1914, and 1938 (Liberato 1994), and the American botanist David H. Linder (1899–1846) on an expedition by Harvard University from 1926 to 1927, the specimens of which are deposited in Herb. GH (Exell 1944, Liberato 1994). On the zoological side, an ornithological team from Oxford University went on a short visit to São Tomé and Príncipe between September and October of 1949, providing additional notes about several species, in the first major contribution on the subject since the works of José Correia (Snow 1950).

In the second half of the twentieth century, the 1959 Peris-Álvarez Expedition to Annobón (Alvarado and Álvarez 1964), headed by entomologist Salvador V. Peris (1922–2007) and Julio Álvarez Sanchez, although short in duration, was fruitful in advancing knowledge regarding the fauna of the area (Anthribidae: Hoffman 1959; Nematoda: Gadea 1960a, b; Gastropoda: Ortiz de Zárate and Álvarez 1960; Collembola: Selga 1960, 1962; fishes: Lozano Cabo 1961; Rodentia: Peris SJ 1991; Muscidae: Peris SV 1961, 1963; Odonata: Sart 1962; Orthoptera: Llorente 1968; Oribatida: Pérez-Iñigo 1969, 1982, 1983, 1984). Commissioned by the Institute of Marine Science at the University of Miami, a team of scientists lead by Gilbert L. Voss (1918–1989), Frederick M. Bayer (1921–2007), and C. Richard Robins (1928–2020) conducted a deep-sea biological investigation to the Gulf of Guinea aboard the R/V Pillsbury between 1964 and 1965 (Voss 1966). In subsequent years, despite difficulties caused by the loss of manuscripts to a fire in December 1967, the results were eventually published (Echinoidea: Chesher 1966; shrimp: Holthuis 1966; Opisthobranchia: Marcus and Marcus 1966; birds: Robins 1966b, 1970; fishes: Courtenay 1970, Gibbs and Staiger 1970, Robins 1966a, 1970, Robins and Nielsen 1970, Emery 1970, Fraser and Robins 1970, Iwamoto 1970; Decapoda: Holthuis and Manning 1970; Foraminifera: Adegoke et al. 1971; Brachiopoda: Cooper 1975; Stomatopoda: Manning 1970).

The French research vessel "Calypso" undertook a short exploratory stint to the Gulf of Guinea in 1956, with a multitude of new publications resulting from the material collected (Pycnogonida: Fage 1959; Polychaeta: Fauvel and Rullier 1959; molluscs: Franc 1959; Chaetognatha: Furnestin 1959; Porifera: Levi 1959; Annelida: Wesenburg-Lund 1959; Foraminifera: Mangin 1959; Crustacea: Forest 1959, 1966, Stubbings 1961, Crosnier and Forest 1966, Forest and Guinot 1966, Manning 1973, de Saint Laurent and Le Loeuff 1979; Octocorallia: Tixier-Durivault 1961; fishes: Arnoult 1966; Amphipoda: Mateus and Mateus 1986). As part of a Calypso expedition, Rose and Denizot made several botanical collections in São Tomé and Príncipe, including living material; herbarium specimens were deposited at Herb. P (Figueiredo 1998; Figueiredo et al. 2009).

The French National Museum of Natural History in Paris commissioned several excursions throughout the twentieth century to the Gulf of Guinea region, also resulting in many new studies (Diptera: Alexander 1957; amphibians and reptiles: Angel 1920; Tenebrionidae: Ardoin 1958; Coleoptera: Basilewsky 1957, 1958; Orthoptera: Chopard 1958; Osoriinae: Fagel 1958; Lepidoptera: Herbulot 1958; Dermaptera: Hincks 1958; Orthoptera: Kraus 1960; Trichoptera: Marlier 1959; insects: Viette 1956, 1957, 1958; Coleoptera: Villiers 1957). After the creation of the Institut fondamental d'Afrique noire [Fundamental Institute of Black Africa] (IFAN) by the French naturalist Théodore Monod (1902–2000), its academic journal published several papers regarding the Gulf of Guinea (*Anthocleista*: Monod 1957; bryophytes: Potier de la Varde 1959; Annelida: Rullier 1965; fish: Blanc et al. 1968; Lepidoptera: Darge 1970; insects: Kumar 1975; Decapoda: Monod 1975).

In 1936, in an effort to better understand the biological richness of its overseas colonies, Portugal launched a scientific project for their study, *Junta das Missões Geográficas e de Investigações Coloniais* (later renamed *Junta de Investigação do Ultramar* and later still *Junta de Investigações Científicas do Ultramar*) (Marques et al. 2018). The zoologist Fernando Frade [Viegas da Costa] (1898–1983; Fig. 5.5) was in charge of the *Centro de Zoologia de Lisboa*, the zoological division under the

Fig. 5.5 A party of the participants of *Missão Científica de São Tomé e Principe*, in 1954 in São Tomé, including the zoologist Fernando Frade (1), Isolina Campos (2) accompanying the husband Ezequiel de Campos (3), and "Jaime" (4). Courtesy of the Herb. PO, Museu de História Natural e da Ciência, Universidade do Porto

Junta. During the 1950s and 1960s, several zoological expeditions were commissioned by the institution and from these expeditions important publications were produced by an extended network of researchers up to present day (insects: Bacelar 1948, 1950, 1956a, b, Castel-Branco 1955a, b, 1956a, b, c, 1958a, b, c, 1963a, b, c, 1964, 1965, 1969, 1970a, 1972, Alves 1956a, b, 1965, Castel-Branco and Alves 1957, 1958, Tendeiro 1956a, b, c, d, 1957, Tordo 1956, 1969, 1974, Schmidt 1967a, b, Fernandes 1974; Diptera: Dias 1955, Azevedo et al. 1956, 1961, 1962, Gandara 1956, Pinhão and Mourão 1961; birds, insects, and mammals: Frade 1955a, 1956; fishes: Frade and Correia da Costa 1956, Correia da Costa 1959, Alves and Castel-Branco 1962, Almeida and Alves 2019; Copepoda: Marques 1956, 1960, 1965, 1975; diseases: Mourão 1964; Miocene fauna: Silva GH 1956a, b, 1958a, b, Serralheiro 1957; amphibians and reptiles: Manaças 1958, 1973; Foraminifera: Reis Moura 1961; Hymenoptera: Diniz 1964; Arachnida: Cabral and Carmona 1968/69, Dias 1958, 1988; Aphidoidea: Ilharco and Van Harten 1975, Van Harten 1976; birds: Frade 1959, Frade and Santos 1977; Gastropoda: Simões 1989; Chiroptera: Lopes and Crawford-Cabral 1992).

From 1954 to 1955, Frade and Armando Castel-Branco (1909–1977) conducted an expedition to the archipelago of São Tomé and Príncipe (Frade 1955b). This expedition was part of the so-called *Missão Científica de São Tomé e Principe*. The mission was conceived in 1954, comprising multiple scientific subjects and had the specific aim of providing data to the International West African Conference (Conferência Internacional dos Africanistas Ocidentais—C.I.A.O.) held in 1956 in São Tomé. It was created by the *Junta*, with the objective of studying various aspects of natural history, ethno-sociology, and economics of São Tomé and Príncipe (Vieira and Viegas 2019). In 1956, C.I.A.O. started to work under the aegis of C.C.T.A./C.S.A. (Commission for Technical Co-operation in Africa South of the Sahara/Scientific Council for Africa South of the Sahara), international organizations aiming to promote the application of science to the resolution of African problems and that included several African and European countries (Anonymous 1956). This mission was led by the previously mentioned Ezequiel de Campos. Campos, already in his 80s, returned to São Tomé and Príncipe (Fig. 5.5), where he had begun his professional activities. He collected new data, which together with his previous knowledge of the islands resulted in important works about changes in the environment, ecological disturbances, and landscape changes that he had observed over the preceding decades (Campos 1956a, b, 1958).

The botanist Arnaldo Rozeira (1912–1984)—born in São Tomé and raised in Portugal (Porto)—professor at the University of Porto, joined the *Missão Científica de São Tomé e Principe*, as Mission Assistant and Chief of the *Brigada de Sociologia Botânica* [Botanical Sociology Brigade]. During his participation in this mission Rozeira visited São Tomé and Príncipe at least three times, in 1954, 1957, and 1958. In 1957, the Portuguese botanist Jorge Martins d'Alte (1912–death unknown) accompanied the botanical expedition, making botanical collections (Costa 2020). As a result of this mission a great diversity of material was collected and deposited in Herb. PO. It comprised vascular plants (including pteridophytes), bryophytes, lichens, algae, and a wood collection (Vieira and Viegas 2019). The singularity of these collections lies in the fact that Rozeira carried out the first botanical collections on Pico do Príncipe, the highest mountain on the island which had scarcely been accessed in earlier times. Furthermore, it was during these expeditions that species collected by Barter were re-collected for the first time.

The African botanical collections at Herb. PO were only recently subject to an inventory (Costa 2020), but some of these have been cited in previous works, namely by Exell and Rozeira (1958; which included one species new to science and new records for the islands, with pteridophytes identified by Alston), Rozeira (1958), Barros-Ferreira (1963, 1965,1968a, b, Begoniaceae, Malvaceae, Melastomataceae; including a new species of *Tristemma*), and Sampaio (1958, 1962, cyanophytes). The Portuguese collector and naturalist Joaquim Sampaio (1899–1981) again published about cyanophytes (Sampaio 1963), but this time on specimens collected by Joaquim R. dos Santos Júnior (1901–1990) from Príncipe (specimens at Herb. PO).

During the C.I.A.O. in 1956, several authors who had been working on the islands of the Gulf of Guinea presented communications dedicated to botanical topics (Campos 1956b; Almeida and Morais 1958a, b, c; Boughey 1958). Both the French naturalist Théodore Monod (1902–2000) and the English botanist Charles Aubrey Thorold (1906–1998) visited São Tomé and Príncipe during C.I.A.O. and made botanical collections (specimens at Herb. BM and COI; Exell 1962, Liberato 1994). The pteridophytes were studied by Alston (1959), with several new records being added to the flora of the islands (Figueiredo 1998). Exell (1959) published the novelties for the Flora, referring to Monod's material as "excellent collections". Exell (1959) referred to collections from Espírito Santo (see below). The majority of the bryophytes collected by Monod and Thorold constituted the basis for the publication by Robert André Léopold Potier de la Varde (1878–1961) (1959). It was Monod (1960) who established and proposed the most commonly used classification of São Tomé vegetation, based on species composition (Figueiredo et al. 2011).

Between 1956 and 1973, the Santomean Joaquim Viegas da Graça Espírito Santo (1901–unknown) made numerous botanical collections in São Tomé and Príncipe (Espírito Santo 1970, 1974), with duplicates at Herb. COI, LISC, BM, and K, including endemic plants (Figueiredo 1994c). In 1968, he was appointed by the *Brigada de Fomento Agro-Pecuária de S. Tomé* to undertake botanical prospecting, a task he executed for six months (Exell et al. 1952, Figueiredo 1994c, d, Liberato 1994).

In 1956, Helder Lains e Silva (1921–1984) and José Carvalho (dates of birth and death unknown) also made a considerable collection in São Tomé and Príncipe. The list of their collections was published by Silva HL (1958b). These collections were made under the auspices of the *Junta de Exportação do Café* and are housed at Herb. LISC (Exell, 1962, Silva HL 1958b, Sobrinho 1959, Liberato 1994).

Thomas Christopher Wrigley (1935–) and Fenella Ann Melville (later Mrs. Wrigley) (1936–), both English botanists, participated in a joint Spanish-British expedition to Bioko and Annobón in July and August 1959, together with Julio Álvarez (dates of birth and death unknown), a Spanish zoologist. It was the most significant biological expedition to Annobón since that of Mildbraed in 1911. They collected 316 specimens which are at Herb. K, with duplicates at Herb. BM, BR, MPU, and MA. This collection was identified and published by Exell (1963). Although Exell identified the majority of the collection, the pteridophytes had not been studied until recently (Figueiredo et al. 2009). These collections were kept at Herb. BM but had not been incorporated into the main collection (Figueiredo et al. 2009).

The French botanist Bernard Marie Descoings (1931–2018) collected in Annobón from 24 February to 3 March 1964, as part of an expedition with several researchers. There are 233 specimens of his collections deposited at Herb. MPU, including 56 pteridophytes (Figueiredo et al. 2009; Velayos et al. 2014).

In cooperation with the *Junta*, the *Brigada de Fomento Agro-Pecuário de São Tomé e Príncipe* (established in 1964) carried out studies regarding the fauna of the islands, with special relevance to the Entomologists' meeting in São Tomé and Príncipe in August of 1967 (Quinta 1967; Carvalho 1968). The results of those missions were published in the journal with the same name as the initiative (e.g., Castel-Branco 1967a, b, c, d, e, f, 1970b, 1971; Ferreira 1967a, b, c, d, 1968, 1969, 1971; Quinta 1967).

René de Naurois (1906–2006), a World War II veteran and catholic priest turned ornithologist, authored dozens of papers and books regarding the birds of the coast of West Africa and its offshore islands. From the early 1970s to the late 1990s, Naurois thoroughly studied the ornithological fauna of the Gulf of Guinea and published the results of his research (Naurois 1972a, b, 1973a, b, 1975a, b, 1979, 1980, 1981, 1982, 1983a, b, 1984a, b, c, d, 1985a, b, 1987a, b, c, 1988a, b, 1994; Naurois and Antunes 1973; Naurois and Wolters 1975; Fry and Naurois 1984), which culminated with the "Les oiseaux des îles du Golfe de Guinée: São Tomé, Prince et Annobon" published in 1994. On behalf of the zoologist Henri Heim de Balsac (1889–1979), Naurois also collected shrew specimens, in addition to his work with birds (Heim de Balsac and Hutterer 1982).

Up until 1974, several more incursions to the Gulf of Guinea were commissioned, with the extent of their collections resulting in important publications from various taxonomic groups. Aurélio Basilio conducted an expedition to Annobón in 1957 (Basilio 1957) and some years later, in 1961, C.H. Fry did the same (Fry 1961). The entomologist Jacques O. Derron, with the *Brigada,* spent three years (1972–1975) studying the insects associated with cacao plantations in São Tomé, from which stemmed several publications (Fursch 1974; Badonnel 1976; Wirth and Derron 1976).

On the years leading up to the independence of the country, many of the collections in herbaria were revisited and studied by other researchers, or compared to new material, resulting in new publications often focusing on a particular group, family, genus, or even a species (e.g. *Calvoa robusta*: Cogniaux 1908/09; Fungi: Henriques 1922; Câmara and Luz 1938; botanic collections: Romariz 1952; vascular plants: Sobrinho 1952; Hepaticae: Arnell 1956; Algae: Rodrigues 1960; marine algae: Steentoft 1967; *Achyranthes*: Cavaco 1968; Loranthaceae: Balle 1964;

Nicandra, *Physalis,* and *Withania*: Fernandes 1969; *Erythrina*: Bocquet and Derron 1976; *Uvaria*: Paiva 1978/79).

In 1972, Maria Cândida Liberato (1944–) and Espírito Santo began taxonomic revisions of families of the flora of the islands with the objective of producing a Flora of São Tomé and Príncipe (Liberato and Espírito Santo 1972–1982). The project was never completed, and only a few families were published (Papilionaceae, Mimosaceae, Caesalpiniaceae, Connaraceae, Rosaceae: Liberato 1972, 1973, 1976, 1980a, b, 1982; Aquifoliaceae, Alangiaceae: Espírito Santo 1973a, b).

The common names of the plants of this archipelago were not neglected, being the subject of multiple publications (Rozeira 1958; Silva HL 1959a; Espírito Santo 1969a). These approaches were often included in studies dedicated to the use of plants for medicinal purposes. Several works and research were dedicated to pharmacology/pharmacognosy and uses of medicinal plants across this period (Alves and Prista 1958, 1959, 1960; Prista and Alves 1958, 1959; Prista et al. 1960; Alves et al. 1961, 1962; Alves et al. 1960; Espírito Santo 1969b).

In geographical and economic studies undertaken on these islands, it was common to include an analysis of vegetation, ecology, landscape change, and productive aptitude, providing data on vegetation cover and habitats (Chevalier 1906, 1910, 1938/39; Campos 1920, 1956a, 1958; Tenreiro 1961; Rodrigues 1971; White 1983/84). Throughout the twentieth century, there were several studies and reviews of applied botany, namely with an agronomic perspective, addressing topics such as agricultural suitability, crops and associated problems (e.g. Câmara and Coutinho 1923; Cortesão 1956/57; Silva HL 1958a, 1959b; Ascenso 1964; Mariano 1966; Espírito Santo 1973c; Rodrigues 1974), with a special focus on cocoa, coffee, and quinine crops (e.g. cocoa: Cortesão 1921; Thorold 1955, 1959; Silva HL 1960; Ascenso 1963, 1965; quinine: Costa 1941, 1944; coffee: Silva HL 1958b; coffee and cocoa: Vieira da Silva 1960).

The First Decades of Independence

Following independence from Portuguese rule in 1975, São Tomé and Príncipe was engulfed in a wave of political unrest that hindered the possibility of new biological missions in the area (Jones 1994). Although the taxonomic enterprise continued, the 1970s saw the birth of the modern nature conservation movement and the raise of public and scientific concerns regarding human impacts on the natural world. This has led to an almost radical change of interests in the research community, who became much more dedicated to the conservation aspects of biodiversity research, which in the Gulf of Guinea archipelago translated to the study of the ecology and conservation status of vertebrates.

In 1984, a team of zoologists from the Zoology and Anthropology Sections of the Faculty of Sciences of the University of Lisbon led by entomologist Luis Mendes (1946–) conducted a one-month zoological expedition to São Tomé (Mendes et al. 1988). The resulting publications were published by himself and other authors

(Diptera: Grácio 1988, 1999; insects: Mendes 1988a, b, c; Mendes et al. 1988; Drosophilidae: Rocha Pité 1993; Culicidae: Ramos and Capela 1988, Ramos et al. 1989, 1994; Ribeiro 1993, Ramos et al. 1994; Serrano et al. 1995; Ribeiro et al. 1998). Most of the vertebrates collected were not studied until very recently (see Ceríaco et al. 2022).

From 1987 onwards, the International Council for Bird Preservation (ICPB) sponsored several projects for the study of endemic birds of São Tomé and Príncipe (Jones and Tye 1987, 1988; Burlinson and Jones 1988), one of them in cooperation with the University of East Anglia (UEA) (Atkinson et al. 1991, 1994), as well as the creation of a conservation educational programme with the support of the European Economic Community (Harrison and Steel 1989). With the information Atkinson and colleagues were able to gather in the UEA expedition, Dave E. Sargent travelled with other birders in 1989 and 1991, publishing the results of their observations (Sargent et al. 1992; Sargent 1994), which included the rediscovery of the São Tome Grosbeak *Crithagra concolor*, 101 years after the previous record.

After a one-week trip to São Tomé, Eccles (1988) published the results of his ornithological observations, highlighting the rediscovery of São Tome Short-tail *Motacilla bocagii*. A short research stint to Annobón was conducted by Michael J. S. Harrison in March 1989, as a part of a larger mission to São Tomé and Príncipe sponsored by ICPB. The visit resulted in an updated bird checklist of some parts of the island (Harrison 1990). The Polish entomologist Tomasz W. Pyrcz conducted two small expeditions in 1989 (January–March) and 1990 (July–September) to São Tomé and Príncipe aiming to create the first checklist for the butterfly species in the archipelago, which resulted in three publications (Pyrcz 1991, 1992a, b). In cooperation with the Natural History Museum (NHM), the entomologist Janusz Wojtusiak (1942–2012) was entrusted to lead a project to identify and catalogue the macrolepidoptera species of São Tomé extant at the NHM as well as those collected in September of 1990 in a small trip to the island (Honey and Wojtusiak 1994; Wojtusiak and Pyrcz 1995; Wojtusiak 1996a, b, c). Other entomological expeditions to the region resulted in the description of new species and contributed to the growth of knowledge regarding the entomofauna of the Gulf of Guinea (Pinhey 1974; Villiers 1976; Darge 1991; Allard 1990; Herbulot 1991a, b; Antoine 1992; Basquin 1992; Bomans 1992; Canu 1994).

In the late 80s and early 90s, teams of Spanish researchers began working in the Gulf of Guinea, some of them under the Spanish programme "Research and Nature Conservation Programme in Equatorial Guinea" (Castroviejo et al. 1994b). Those expeditions led to several publications on insects (Viejo 1984, 1990), mammals (Juste and Ibañez 1993a, b, c, 1994), molluscs (Fernandes and Rolan 1989, 1992; Kosuge and Fernandes 1989; Gofas and Fernandes 1991; Rolan and Fernandes 1990, 1991, 1992, 1995; Rubio and Rolan 1990; Rolan and Templado 1993; Rolan 1996), and sea turtles (Castroviejo et al. 1994a).

Funded by *Cooperación Española* and led by the *Associación Amigos de Doñana*, a Spanish expedition including the botanist Manuel Fidalgo de Carvalho (dates of birth and death unknown) visited the island of Annobón. Between September and October of 1987, Carvalho collected 113 specimens, now deposited at Herb. MA (Figueiredo et al. 2009; Velayos et al. 2014). In August 1986, in an expedition to São Tomé organized by the *Secció de Petits Països del CIDOB*, Neus Gabaldá Casado (dates of birth and date unknown) and Núria García Jacas (1961–) collected specimens of 114 taxa, including pteridophytes; the specimens are deposited at Herb. COI and BC (Gabaldá and Jacas 1988).

Herpetological expeditions to São Tomé and Príncipe from 1989 and 1991 led by Catherine Loumont (1942–) resulted in reviews of the amphibians and reptiles of these islands (Loumont 1992; Schätti and Loumont 1992). Previously, Ronald Nussbaum (1942–) and Michael Pfrender (1960–) had collected herpetological specimens during June and July of 1988, with a particular special focus on caecilians. Those collections are currently extant in the University of Michigan's Museum of Zoology.

In the spring of 1991, a team of researchers from the University of Dresden (Germany) conducted an exploratory mission to the Gulf of Guinea, with numerous publications resulting (amphibians, reptiles and arachnids: Haft 1992, 1993a, b; amphibians and reptiles: Schatti and Loumont 1992; amphibians and arachnids: Fahr 1993a, b; Feiler 1993; mammals: Feiler et al. 1993, Dutton and Haft 1996; Cnidaria: Kock 1993; Phthiraptera: Mey 1993; birds: Feiler and Nadler 1992, Nadler 1993; Nadler and Feiler 1993; reptiles: Nill 1993; Gastropoda: Schniebs 1993; Lepidoptera: Schutz 1993; Myriapoda: Spelda 1993; Teleostei: Zarske 1993; amphibians: Haft and Franzen 1996). Previously, Feiler and Günther had travelled to the region and published several papers regarding the mammals of the Gulf of Guinea (Feiler 1984, 1988; Günther and Feiler 1985).

Although the ichthyofauna of the islands is quite diverse, after the pioneering work of Balthazar Osório there was a lack of further studies. Russian expeditions in 1983 and 1986 (Domanevskaya 1987, 1988) provided additional information on the biodiversity and were followed by *Project d'Évaluation des Ressources Halieutiques*, which resulted in important publications for improved baseline knowledge (Worms 1996a, b; D'Almeida 1996; Afonso et al. 1999).

The work of the English zoologist Angus Robin Gascoigne (1962–2012), who lived in São Tomé for many years (Melo 2012), greatly contributed to the knowledge of the molluscan fauna and other aspects of the biodiversity of the Gulf of Guinea (Gascoigne 1993, 1994a, b, c 1995a, b). He also collected plants that were deposited at Herb. LISC and co-authored some papers on flora (Figueiredo and Gascoigne 2001; Figueiredo et al. 2009).

A collaboration between the European Community conservation programme for the forest ecosystems of central Africa (ECOFAC) and the U.S. Peace Corps originated the first major survey on the sea turtles of the Gulf of Guinea (1994–1996), which resulted in baseline information to move towards conservation programmes (Graff 1996; Rosseel 1997). The ECOFAC programme is associated with generating interest in the flora of these islands among the Belgium academic community, which resulted in numerous collections made and the description of new species (e.g. La Croix and Brune 1997; Cribb et al. 1999; Stévart and Geerinck 2000; Joffroy 2001).

Continuing the dynamics implemented by the ECOFAC programme on São Tomé, further botanical inventories took place in the 1990s, notably those carried out by the botanist Jean Lejoly (1945–) and his students between 1994 and 1998, and by the Angolan agronomist Gilberto Cardoso de Matos (1935–) from 1994 to 1999. These collections are deposited at Herb. BRLU and LISC. Some duplicates are also deposited at Herb. STPH (Figueiredo et al. 2011). Matos was one of the main collectors active in São Tomé and Príncipe in the 1990s, amassing ca. 3000 specimens during several expeditions. He often collected with Kathleen Van Essche (fl. 1991–2001). Matos also produced agro-ecological and vegetation maps for São Tomé and Príncipe with the agronomist Alberto Castanheira Diniz (1923–2008) (Diniz and Matos 2002a, b).

Some collecting initiatives focused on orchids were developed by Belgian botanist Tariq Stévart (1974–). With the collaboration of Faustino de Oliveira (1963–) he carried out a systematic survey of the island throughout 1998, after two preliminary missions. On the island of Príncipe, three surveys were organized with the aim of carrying out botanical inventories in the southwestern parts of the island. The results were published in several papers and a guide to orchids of São Tomé and Príncipe (Stévart et al. 2000; Stévart and Oliveira 2000).

The botanist Jorge Paiva (1933–) who undertook over 20 collecting expeditions to São Tomé and Príncipe deposited his collections at Herb. COI. Many of his botanical surveys and collections took place within the scope of diverse projects. For instance, between 1989 and 1993, he collaborated on a project funded by the European Communities Commission regarding the impact of coffee nematodes in the different cultivars (Abrantes 1993).

Additionally, there are collections made in the 1990s by many others, such as the Santomeans Sabino Pires Carvalho (1959–) and Oliveira, at Herb. BRLU and LISC, Estrela Figueiredo (1963–; collected from 1993 to 2002) at Herb. K and LISC, Gascoigne (collected in 1999) at Herb LISC, Maria Fernanda Pinto Basto (1938–; collected in 1990) at Herb. LISC, and Maria do Céu Madureira (1961–) and Ana Paula Martins (1962–) at Herb. COI. Most collections made in the 1990s were deposited at Herb. BRLU, COI, and LISC.

By the end of the twentieth century, a series of taxonomic revisions of the flora of the islands was initiated with the publication of a catalogue of pteridophytes (Figueiredo 1998) and several revisions produced for Equatorial Guinea (e.g. Fernández Casas 1992, Hepper 1992, Morales 1992, Leeuwenberg 1992). These revisions would later give rise to the *Flora de Guinea Ecuatorial*.

In 1993, an ethnopharmacological study was initiated in São Tomé and Príncipe in collaboration with the Ministry of Health of the country (Madureira 2006, 2012; Madureira et al. 2008; Martins 2002). This study involved a survey of species and had the collaboration of Paiva for the identification of the plant collections. Further projects of applied botany ensued, including the doctoral project of Cristina Galhano (1969–) (Galhano 2006) during which collections were made by Paiva in 1996. In Bom Sucesso Botanical Garden (São Tomé), a tribute is paid to many of the botanists mentioned here, who developed work on the flora of the arquipelago (Fig. 5.6).

OS BOTÂNICOS QUE PARTICIPARAM
NO CONHECIMENTO DA BIODIVERSIDADE
VEGETAL DE SÃO TOMÉ E PRÍNCIPE

EXELL A.W.	INGLêS	1944	ESTUDO DA FLORA E VEGETAÇÃO.
CHEVALIER A.	FRANCêS	1906	RECOLHA BOTÂNICA.
COGNIAUX A.	FRANCêS	1909	ESTUDO DO GéNERO . CALVOA.
FERREIRA J.B.	PORTUGUêS	1965	ESTUDO DAS MALVáCEAS E BEGONIA.
FIGUEIREDO E.	PORTUGUêSA	1994	ESTUDOS DOS FETOS.
LEJOLY J.	BELGA	1993	INVENTÁRIO FLORESTAL.
LIBERATO M.C	SANTOMENSE	1972	ESTUDOS DAS FABáCEAS, DICHAPETALACEAS E OUTRAS.
MATOS G.C.	PORTUGUêS	1955	ESTUDO DA FLORA E VEGETAÇÃO.
PAIVA J.A.R.	PORTUGUêS	1978	ESTUDO DO GéNERO UVARIA.
ROZEIRA A.	PORTUGUêS	1958	NOMES POPULARES DE PLANTAS DE STP.
SANTO J.E.	SANTOMENSE	1969	USO DE PLANTAS.
SILVA H.L.	PORTUGUêS	1959	ESTUDOS AGRONOMOS.
SOBRINHO L.G	PORTUGUêS	1953	ESTUDOS DE PLANTAS VASCULARES.
STEVART T.	BELGA	1997	ESTUDOS DE ORQUIDáCEAS DE S.T.P.
WHITE T.	INGLêS	1983	ESTUDOS DE S.P.AFROMONTANHOSOS.
WELWISTCH	INGLêS	1953	FLORA.

Fig. 5.6 Commemorative plate on the botanists who studied São Tomé and Príncipe flora, funded by ECOFAC and placed in the Bom Sucesso Botanical Garden. Photo credits: Luis Ceríaco

In December 1994, the journal *Biodiversity and Conservation* published a special issue dedicated exclusively to the review of old and new data regarding the Gulf of Guinea's species richness and endemism (Juste and Fa 1994). This publication was based on works presented at the workshop "Biodiversity and Conservation of the Gulf of Guinea Islands", held in June 1993 at the Jersey Wildlife Preservation Trust (Butnyski and Koster 1994; Castelo 1994; Castroviejo et al. 1994a, b; Colell et al. 1994; Del Val Pérez et al. 1994; Dutton 1994; Gascoigne 1994c; Jones 1994; Juste and Fa 1994; Juste and Ibañez 1994; Peet and Atkinson 1994; Schaaf 1994; Figueiredo 1994b; Sequeira 1994).

In the 1990s, environmental awareness initiatives stimulated the emergence of publications dedicated to biodiversity conservation, such as the book *Conservação dos ecossistemas florestais na República Democrática de São Tomé e Príncipe* (Jones et al. 1991). Figueiredo (1997) produced a preliminary assessment of the conservation status of 38 trees of São Tomé and Príncipe in a report for the World Conservation Monitoring Centre (Oldfield et al. 1998).

Following the work of Espírito Santo (1969a, b) and Silva HL (1959a), the medicinal uses and the common names of plants continued to be studied and compiled (Sequeira 1994). Studies of agronomic content were also continued, some directed to particular products (seeds: Ferrão 1979, Ferrão and Ferrão 1984; plant uses: Roseira 1984; woods: Freitas 1987).

Twenty-First Century: A New Generation of Researchers

Taxonomic research initiated in the previous century continued well into the twenty-first century, with several revisions and checklists being published. The flora of Annobón was treated in a series of checklists of the flora of Equatorial Guinea (e.g. Fero et al. 2003; Parmentier and Geerinck 2003; Cabezas et al. 2004) and in the volumes of *Flora de Guinea Ecuatorial,* an on-going project with the first volume being issued in 2008 (Velayos et al. 2008). Regarding São Tomé and Príncipe, several papers on pteridophytes (Figueiredo 2001, 2002; Figueiredo and Gascoigne 2001; Figueiredo and Roux 2008; Figueiredo et al. 2009) and a checklist of the pteridophytes and lycophytes (Klopper and Figueiredo 2013) were published. A new catalogue of the flora of São Tomé and Príncipe that updated the over 35-years-old checklist produced by Exell (1973b) was finally published (Figueiredo et al. 2011). In the same year a catalogue of the bryophytes was also published (Sérgio and Garcia 2011). The Rubiaceae, one of the dominant families of the flora, was treated in a series of revisions (Alves et al. 2005; Figueiredo 2005; Davies and Figueiredo 2007). Applied botany studies integrated into environmental protection strategies also continued (e.g. Martins 2002; Madureira 2006; Madureira et al. 2008).

At the dawn of the new century, a new wave of biodiversity researchers hit the islands. Furthering knowledge gathered by the previous generations, this new generation has not only continued to contribute to cataloguing the still undocumented and undescribed fauna and flora of the oceanic islands of the Gulf of Guinea, but also implemented new techniques, methodologies, and approaches. Other topics, such as biodiversity conservation, ethnobiology, ecosystem health, and ecology have experienced a considerable growth. This research has been conducted by an increasingly diverse group of international and national researchers and is mostly covered in the subsequent chapters of the volume. Nevertheless, some aspects of this new wave of research need to be highlighted here—both because they represent an important turning point on the study and preservation of the local biodiversity, but also due to the dimension and intensity of some of these activities.

One fundamental difference in the research carried out in the twenty-first century is the use of molecular methods to study the taxonomy, phylogenety, and biogeography of the biodiversity of the islands. While this has not yet been applied to all taxonomic groups, the use of molecular methods has been widely applied to the study of the island's herpetofauna (Bell et al. 2022; Ceríaco et al. 2022), birds (Melo et al. 2022) and, to a lesser extent, plants (Plana et al. 2004; Soares et al. 2010). The growing importance of ecological and conservation studies has also marked the research landscape in the oceanic islands of the Gulf of Guinea, with dozens of works and theses produced on the topic, especially at the University of Lisbon (see Lima et al. 2022, Soares et al. 2022), but also the seminal works on marine turtles (see Ferreira-Airaud et al. 2022), plants (see Stevart et al. 2022), and even land molluscs (see Panisi et al. 2022). Finally, a revival of field expeditions to further catalogue the diversity and distribution of islands' species has resulted in important modern collections, many of which have not yet been fully studied. Of critical importance is the programme led by the California Academy of Sciences (CAS), whose activities started in 2001. This programme, led by Robert "Bob" Drewes, has conducted over a dozen expeditions to the islands and involved researchers from across the world with expertise in a wide array of taxonomic groups. A considerable part of the recently produced knowledge on the archipelago's biodiversity stems from this programme.

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Chapter 6
Biogeography and Evolution in the Oceanic Islands of the Gulf of Guinea

Martim Melo, Luis M. P. Ceríaco, and Rayna C. Bell

Abstract As with most archipelagos, geography played a central role in the assembly and evolution of the endemic-rich biological communities of the Gulf of Guinea oceanic islands. The islands are located at moderate distances from the species-rich African continent that surrounds them to the east and north. This proximity facilitated colonization by many branches of the tree of life, but gene flow between the islands and continent was low enough that many lineages evolved in isolation once they reached the archipelago, resulting in many endemic species. Furthermore, several of the island taxa belong to groups typically considered to be "poor dispersers" across sea barriers, which strongly supports a role for natural rafts in seeding the islands. Oceanic currents, including the freshwater pathways that extend from large river drainages into the Gulf of Guinea during the rainy season, also support this hypothesis. The distances between the islands are equivalent to those between the islands and the continent such that inter-island dispersal events appear

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to be relatively rare and thus few taxa are shared between them. Still, the islands present multiple cases of secondary contact leading to hybridization and genetic introgression between closely related lineages—providing several models to study the role and consequences of gene flow in evolution. Most taxa for which molecular estimates of divergence time have been derived are much younger than the ages of the islands. This pattern is consistent with high species turnover, likely resulting from a combination of small island sizes, proximity to the African continent and a long history of intense volcanic activity. The Gulf of Guinea oceanic islands provide multiple examples of classical adaptations to island life (the "island syndrome"), including giants and dwarves, ornament and color loss, among others. In addition, emerging studies of birds are highlighting the importance of competition regimes in driving phenotypic change—with examples of both character release (low inter-specific competition) and character displacement (inter-specific competition upon secondary contact). Collectively, the Gulf of Guinea oceanic islands offer unique opportunities to study adaptation and speciation in a range of taxa and contexts.

Keywords Adaptation · Biogeography · Endemism · Gene flow · Island syndrome · Speciation

Introduction

Islands, and oceanic islands in particular, have always occupied a special place in human imagination (cf. Schalansky 2010). Their isolation and well-defined borders make them worlds apart, microcosms often populated by unique and peculiar creatures. For the naturalist, oceanic islands are one of the most fruitful settings for the study of evolutionary and ecological processes, including adaptation, speciation, and community assembly (Losos and Ricklefs 2009; Whittaker et al. 2017). Charles Darwin hinted at islands serving as "natural laboratories" in his account of the *Beagle* expedition, after having visited the Galapagos in September 1835 (Darwin 1845: 377–378). It was Alfred Russel Wallace, however, who put it clearly in his fundamental work aptly named *Island Life* under the section *Importance of Islands in the Study of the Distribution of Organisms* (Wallace 1880: 234):

> In islands we have the facts of distribution often presented to us in their simplest forms, along with others which become gradually more and more complex; and we are therefore able to proceed step by step in the solution of the problems they present. (. . .) [W]hen we have mastered the difficulties presented by the peculiarities of island life we shall find it comparatively easy to deal with the more complex and less clearly defined problems of continental distribution.

The depiction of islands as natural laboratories arises from their inherent simplicity (systems with well-defined boundaries, generally small, and with a depauperate biota), together with being striking centers of evolutionary change and diversification by virtue of their isolation and specific environmental constraints (Wallace 1880; Carlquist 1965; Grant 1998a; Emerson 2002; Losos and Ricklefs 2009; Whittaker et al. 2017). Both these characteristics are particularly evident in the spectacular radiations of the most isolated island systems, as illustrated by the

Hawaiian *Drosophila* in which up to 1000 species may have evolved from just one or two species (Carson and Kaneshiro 1976; Kaneshiro et al. 1995). Correspondingly, much progress on the study of evolution on islands has stemmed from remote islands such as the Hawaiian archipelago (Wagner and Funk 1995; Craddock 2000) and the Galápagos (Grant and Grant 2008). More recently, it has become clear that island systems closer to continents have the potential to significantly advance our understanding of the processes driving diversification.

As one approaches the mainland, the complexity of island systems increases as dispersal and gene flow between the mainland and the island populations become more frequent (cf. Fig. 1.1 in Whittaker 1998). "Intermediate island systems" are those archipelagos that lie between remote islands systems, virtually independent from the mainland, and systems so close to the mainland that speciation in situ is not possible (Melo 2007; Ricklefs and Bermingham 2007). Intermediate island systems are promising natural laboratories as they may provide a simple setting to investigate the role of gene flow in evolution, which remains a question of fundamental importance in evolutionary biology (Dowling and Secor 1997; Seehausen 2004; Pinho and Hey 2010; Feder et al. 2012; Abbott et al. 2013; Buerkle 2014; Arnold 2015; Taylor and Larson 2019; Matute and Cooper 2021). In addition, the faunas of intermediate island systems are typically derived from several distinct families (independent replicates for evolutionary studies), rather than being dominated by a few species-rich genera that have adaptively radiated. Consequently, patterns of community assembly in such archipelagos are likely more similar to those of continents than are those of more isolated archipelagos where most of the diversity is derived from a few extensive radiations (Melo 2007; Ricklefs and Bermingham 2007).

Here we provide an overview of the biogeography and evolution of the biota of the oceanic islands of the Gulf of Guinea (Príncipe, São Tomé, and Annobón), highlighting their potential to advance our understanding of the processes generating diversity: from population divergence to speciation to community assembly. In addition, this setting provides several excellent models to study the role of gene flow with respect to the evolution of divergent phenotypes and patterns of genome-wide differentiation. Readers will likely notice that this overview is limited and biased towards terrestrial vertebrates. For other taxonomic groups, the diversity of the islands is still incompletely documented and described (Ceríaco et al. 2022a), and thus building the essential foundation for future hypothesis-driven studies is still a work in progress for these other taxa. A brief overview of marine biogeography in the Gulf of Guinea is described in Costa et al. (2022).

Biogeography

The Importance of Geography

The updated checklists for terrestrial groups in the oceanic islands of the Gulf of Guinea (reference list in Ceríaco et al. 2022a) reveal a few principal patterns:

(1) high levels of endemism; (2) wide representation across the tree of life; (3) in situ radiations are rare and result in few species; and (4) the biological communities of each island are largely unique, with few endemics shared between them. With the exception of the Odonata (dragonflies and damselflies), which have relatively low species diversity in the Gulf of Guinea and just one endemic species (Dijkstra and Tate 2022), the three islands have some of the highest concentrations of endemic species in the world for several groups, including mosquitoes (Loiseau et al. 2019), amphibians (Bell et al. 2022), terrestrial reptiles (Ceríaco et al. 2022b), and birds (Melo et al. 2022). These patterns are particularly remarkable in relation to the small size of these islands (just over 1000 km^2 combined) and are likely a consequence of their favorable geographic setting.

Just in the Right Place: Close, But Not Too Close, to a Large and Species-Rich Continent

The diversity of unique genera and families in the archipelago across taxonomic groups from fungi to frogs is indicative of a large number of colonizations from the mainland. High levels of endemism, once again across many taxonomic groups, indicate that many of these island colonizers have subsequently diverged from their mainland counterparts. The islands are therefore close enough to the continent to receive a diverse array of mainland dispersers but far enough away for these to diverge once they arrive to the islands. These are two defining traits of intermediate island systems: the likelihood of colonizations is higher than on remote systems and the conditions for population divergence are preserved (Melo 2007; Ricklefs and Bermingham 2007). For groups such as birds, where the concentration of island endemics is the highest in the world (Melo et al. 2022), it is as if the oceanic islands of the Gulf of Guinea are located at the perfect distance from the mainland to optimize the balance between colonization (as a source of new lineages) and isolation (reduced gene flow to allow for genetic differentiation). Such an optimal distance will likely vary among taxonomic groups according to their dispersal potential.

The adjacent African continent also hosts the species-rich Congolian rainforests and the Guinean Forests of the West Africa biodiversity hotspot (IUCN 2015), which surround the islands to the east and north, respectively. Thus, the islands are proximal to extensive coastlines of a large and biodiverse landmass. Being situated adjacent to a large landmass is the most important predictor of global plant species diversity on islands (Weigelt and Kreft 2013). In addition, the islands and much of the adjacent mainland share similar habitats (notably rainforest), which increases the chance of successful establishment following sweepstakes dispersal events (Weigelt and Kreft 2013).

Colonization Outweighs In Situ Diversification as a Source of New Species Diversity

Independent colonizations from the mainland, rather than in situ diversification, is the dominant process by which species diversity accumulated in the archipelago (Box 6.1). For example, the 29 endemic bird species present on the three oceanic islands derive from 20 to 22 separate colonizations from the mainland, and only three are shared between islands (Melo et al. 2022). Of the 164 endemic vascular plant taxa of the Gulf of Guinea islands only a small subset is shared between more than one island, and an even more diminutive number is shared with Bioko (Figueiredo 1994; Stévart et al. 2022). Likewise, all nine amphibian species are endemic to a single island, and five are the sole representative of their family on their respective island (Bell et al. 2022). Dispersal between islands, and subsequent isolation, has also been a source of further endemic species in some vertebrate groups including *Hyperolius* reed frogs (Bell et al. 2015a, b), *Hemidactylus* geckos (Miller et al. 2012), *Trachylepis* skinks (Ceríaco et al. 2016), *Boaedon* house snakes (Ceríaco et al. 2021) and birds, of which the five-species radiation of *Zosterops* white-eyes is the best example (Melo et al. 2011, 2022). However, for most organisms, each island is closer to an independent unit rather than part of a tight-knit archipelago.

The extensive evolutionary radiations described from remote archipelagos are facilitated by inter-island dispersal events within the archipelago followed by divergent adaptation to fill open ecological niches (Schluter 2000; Gillespie et al. 2020). In the case of the oceanic islands of the Gulf of Guinea, the dearth of adaptive radiation may be a consequence of low inter-island colonization (due to the large distances that separate them), limited opportunities to adapt to novel ecological space (due to the high phylogenetic and ecological diversity of colonizers from the mainland; Schluter 2000; Ricklefs and Bermingham 2007; Rundell and Price 2009; Gillespie et al. 2020), and reduced dispersal ability of island species (Box 6.2).

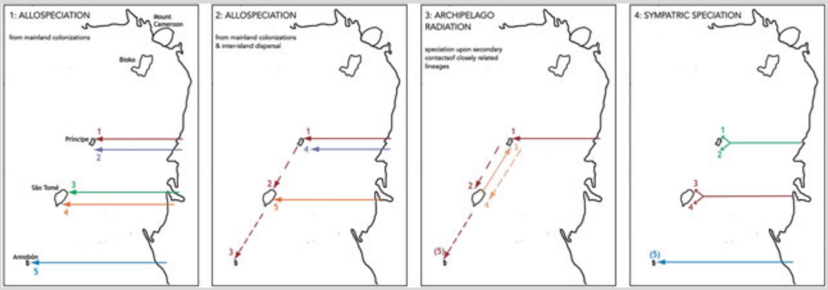
Box 6.1 Speciation on Oceanic Islands

The most detailed model of how populations diversify on oceanic islands was proposed more than 100 years ago by the British naturalist Robert C. L. Perkins (Grant 2000, 2001). His “archipelago radiation model” (Perkins 1913) was derived from his work on the radiation of Hawaiian honeycreepers (Aves: Fringillidae; Perkins 1901), and subsequently strengthened with his studies of other Hawaiian vertebrates (Perkins 1903) and insects (Perkins 1913). In Perkin’s archipelago radiation model (Panel 3 of figure below), speciation is initiated by population subdivision (isolation: allopatry), which leads to selection-driven divergence, potentially aided by random factors (the concept of drift had not yet been formulated). In a second stage, populations diverging in isolation may meet on the same island (secondary contact: sympatry). They may either interbreed, obscuring the divergence and merging

(continued)

Box 6.1 (continued)

into a single population once more, or they may co-exist as increasingly distinct entities even if some interbreeding occurs. In this case, competition between the two populations will lead to further divergence resulting in ecological character displacement. In other words, the most similar individuals of each species suffer the strongest competition, such that extreme phenotypes are favored by selection and intermediate phenotypes are selected against (Brown and Wilson 1956; Grant 1972). Two things are surprising regarding this model: (1) how complete and specific it is and (2) how it was forgotten by most evolutionary biologists in the ensuing decades (Grant 2000, 2001). The deep insights of Perkins, including the central role of competition in driving phenotypic divergence, are particularly impressive considering that his archipelago radiation model is very similar to the "ecological speciation model" proposed in the twenty-first century (Rundle and Nosil 2005; Nosil 2012).



Pathways for speciation in oceanic archipelagos—using the Gulf of Guinea as an example. In this schematic, the single endemic species on Annobón has always arisen by allospeciation

In many archipelagos, speciation is achieved by divergence in isolation (allospeciation: Mayr and Diamond 2001), the first step of the radiation model (Panels 1 and 2 of figure above). This may even be the case for most archipelagos, as recently confirmed for birds in a global analysis of diversification on islands (Valente et al. 2020). It may also be deemed the most passive, or trivial, speciation mode as permanently isolated populations will always follow distinct evolutionary paths. Phenotypic diversification is often limited in this setting, especially when the mainland and island provide similar habitats. At the other extreme, populations may diverge and speciate fully in sympatry (Panel 4 of figure above; sympatric speciation). This mechanism is not included in Perkins' model and although much work has been devoted to demonstrating speciation without any sort of geographic isolation, it has been extremely difficult to find convincing cases in nature (Coyne and Orr 2004;

(continued)

Box 6.1 (continued)

Coyne 2007; Bolnick and FitzPatrick 2007). Often, even the best candidates have experienced an initial period of isolation—even a short one—just as in the archipelago radiation model (Feder et al. 2003; Martin et al. 2015a).

The composition of the community across an archipelago can reveal which of the above scenarios played a major role in the origin of endemic species. For instance, the number of families represents the minimum number of colonizations from the mainland, whereas single representatives from mainland groups provide unambiguous cases of allospeciation. The presence of sympatric congeneric endemic species in an archipelago indicates the groups where molecular-based studies are needed, as such species could be the result of any of the speciation modes. There are several such instances in the Gulf of Guinea oceanic islands that have not yet been investigated with molecular data including among several groups of plants (Garcia and Shevock 2022; Stévart et al. 2022), mollusks (Panisi et al. 2022), mushrooms (Desjardin and Perry 2022), arachnids (Crews and Esposito 2022), and insects Mendes and Bivar-de-Sousa 2022; Nève et al. 2022). An important limitation of molecular studies, however, is that they cannot account for the possibility that undetected extinctions have removed the true sister species of extant species. In the volcanic islands of the Gulf of Guinea, no suitable fossil ground has yet been found and hence the extent to which extinctions may confound our inferences of speciation mode is unknown.

Getting There: Modes of Active and Passive Dispersal

Although the location of the oceanic islands of the Gulf of Guinea is favorable to colonization from the continent, it is still a considerable distance to travel for many organisms. The task is made easier for active flyers, such as birds, bats, or large insects. For organisms that disperse passively in the air—the aerial plankton—the dominant wind currents determine the most likely sources of colonizers. In the Gulf of Guinea, these are the southwestern monsoon winds, responsible for the high precipitation that sustains the rainforests, and the northern dry harmattan winds (Ceríaco et al. 2022c). It is the meeting of these two air masses that determines the position of the meteorological equator. The southwestern winds are unlikely to have dispersed colonizers from continental Africa but may have promoted inter-island dispersal from the southwest to the northeast (i.e., Annobón to São Tomé to Príncipe). Passive wind-dispersing organisms are therefore more likely to have originated from West Africa, to the north of the archipelago, and this is indeed the case for angiosperms (Exell 1973) and Simuliidae black-flies (Mustapha et al. 2006). Dispersal via the northern harmattan winds is likely to have been more prominent during glacial cycles, when they displaced the meteorological equator further south (Lézine et al. 1994) and thus extending further into the Gulf. These hypotheses regarding both the direction, timing, and periodicity of colonization for wind-dispersed taxa can be tested with molecular phylogenetic analyses.

Ocean currents determine the most likely sources of aquatic organisms and of terrestrial organisms that disperse in water, including some seed plants and marine fishes that became secondarily adapted to the freshwater bodies of the islands (Costa et al. 2022). These currents have also likely played a major role in facilitating the arrival of many non-volant, non-swimming, and salt-intolerant animals via passive dispersal on floating vegetation rafts (e.g., Ali and Fritz 2021). These include all amphibians (Bell et al. 2022), several fossorial reptiles (Ceríaco et al. 2022b), and the two species of endemic shrews (Rainho et al. 2022). Likewise, plants with low dispersal ability also likely reached the islands via rafting, for instance, the unusual plant *Sciaphila ledermannii*, a mycoheterotroph that obtains its nutrients by a symbiotic relationship with fungi and lacks obvious structures for either wind or animal dispersal of its seeds (Daniel 2010). Other species that likely reached the islands in this way include species pairs with tight ecological associations unlikely to be maintained by independent dispersal events, such as the hypothesized simultaneous colonization of São Tomé by the sheet-web tarantula *Allothele* and its kleptoparasitic spider *Isela* (Charles Griswold, pers. comm.).

Several factors come together in the Gulf of Guinea to support the rafting hypothesis (Measey et al. 2007; Ceríaco et al. 2022c). First, three large rivers (from north to south: Niger, Ogooué, and Congo) drain into the Gulf of Guinea in the vicinity of the islands. These rivers are among the largest in the world with exceptional freshwater discharge during the rainy season. Second, tropical Africa receives very high precipitation levels during the rainy season that can lead to occasional downfalls of river margins, resulting in rafts of vegetation and soil—a necessary requisite for different groups of animals and plants, such as fossorial amphibians and reptiles that made it to the islands (Bell et al. 2022; Ceríaco et al. 2022b). During the rainy season, high freshwater discharge leads to a large outflow of the rivers into the sea, creating extensive freshwater plumes that create a superficial low-salinity layer in the sea (Richardson and Walsh 1986; Jourdin et al. 2006), and protect the rafts from the intrusion of saltwater. Finally, the dominant ocean currents in the Gulf of Guinea direct the freshwater plumes of the Niger and Congo rivers towards the islands. In summary, the ocean currents together with the top layer of freshwater create “freshwater paths” that carry floating natural rafts from West and Central African river drainages towards the islands (Measey et al. 2007).

The dispersal histories of island species can be inferred using molecular data to build phylogenies and identify the most closely related species or populations on the continent. For instance, a phylogeographic approach revealed that the Gray Parrot *Psittacus erithacus* first reached Príncipe Island from West Africa (c. 1 Ma ago), and that in contemporary times new colonizers arrived from Central African populations (Melo and O'Ryan 2007). By contrast, phylogenetic studies of the endemic São Tomé caecilians suggest they are the product of a single dispersal event (c. 1 Ma ago) from East Africa (Loader et al. 2007). Likewise, the House Snakes *Boaedon* are the product of a single dispersal event to the archipelago from Southern Africa (Ceríaco et al. 2021). The rare instances of inter-island dispersal can be a bit more challenging to decipher from molecular data (e.g., Melo et al. 2011). Such studies will typically require population-level genetic sampling to estimate patterns of genetic diversity for each island (e.g., Bell et al. 2015b; Weinell et al. 2019) with the assumption that each successive colonization event from the source population represents a bottleneck, leading to sequential reductions in genetic diversity along the island chain (Clegg et al. 2002). Thus far, such biogeographic studies have primarily been conducted for many of the islands' amphibians, reptiles, and birds with results supporting instances of dispersal from West, Central, East, and Southern Africa, as well as some cases of inter-island dispersal (Bell et al. 2022; Ceríaco et al. 2022b; Melo et al. 2022). As more phylogenetic and population genetic studies become available from a greater diversity of taxa, we will start to gain a better understanding of the dominant continent-to-island and inter-island dispersal pathways and likely mechanisms.

The Temporal Setting

The oceanic islands of the Gulf of Guinea originated from the activity of the Cameroon Volcanic Line, which began c. 30 my ago (Burke 2001). As such they are a relatively old island system, with the age of Príncipe estimated at 31 Ma, São Tomé at 15 Ma, and Annobón at 6 Ma (Ceríaco et al. 2022c). For comparison, the ages of the islands of the Hawaiian archipelago range from 5 to 0.5 Ma (Carson and Clague 1995) and the Galapagos from less than 0.5 to 3 Ma (Harpp and Geist 2018). Thus, in theory, the islands of the Gulf of Guinea have had extensive evolutionary time to accumulate species diversity and endemism. The tempo at which species richness has accrued, however, may have been influenced by many global climatic factors (e.g., changes in sea level and exposed coastline of the African continent), as well as local geological factors (e.g., devastating volcanic eruptions). As the fossil record in the region is poor, molecular clock approaches can be employed to estimate divergence times between the island endemics and their closest mainland relatives. In turn, these dated phylogenies can be used to infer the corresponding colonization time frame for a given lineage (Fig. 6.1) and reconstruct the timeline of community assembly.

The currently available divergence dating studies suggest that the old age of the islands has not necessarily translated to an abundance of very old lineages. In plants, although afromontane paleo-endemics are present, these co-exist with a large assemblage of neo-endemics (Figueiredo 1994). Likewise, for other groups, most molecular estimates of divergence times indicate that many endemics are much younger than the ages of the islands. For example, from 22 divergence time estimates for endemic birds, 18 occurred within the last 2 Ma, 3 within the last 3–5 Ma, and the oldest dates to 8 Ma (Table 24.1 in Melo et al. 2022). The endemic fruit fly *Drosophila santomea* (Llopart et al. 2002; Turissini and Matute 2017), caecilians (Loader et al. 2007), and shrews (Nicolas et al. 2019) also represent recent colonization and speciation events within the last 2 Ma, while inferred colonization dates for reed frogs (Bell et al. 2015a), the ridged frog *Ptychadena newtoni* (Zimkus et al.

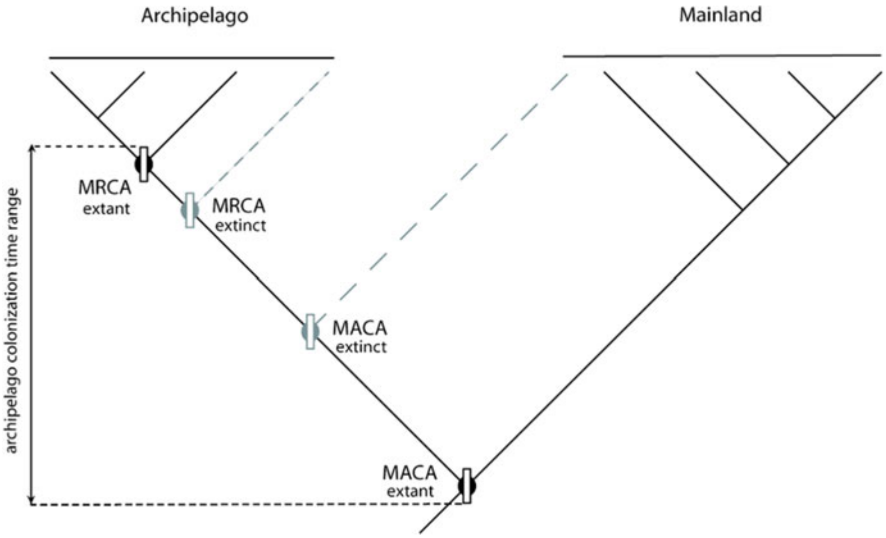


Fig. 6.1 The colonization date of an archipelago lies between the time of most ancient common ancestor (MACA) and the time of most recent common ancestor (MRCA). Time of MACA assumes that the appearance of the insular lineages was simultaneous with colonization. Time of MRCA does not take into account post-colonization demographic effects on genetic diversity. Even if the true MACA and/or MRCA went extinct (or were not sampled) they would be located within this interval. Adapted from Vences (2005) and Hayward and Stone (2006)

2017), and skink *Trachylepis thomensis* (Weinell et al. 2019), date to the Late-Miocene.

Although divergence estimates are not yet available for many groups on the oceanic islands of the Gulf of Guinea, the emerging pattern supports high species turnover. This turnover likely arises as a product of the small size of the islands, moderate distances to the continental pool of new potential dispersers, and the intense recent volcanism of the islands. Small island size is associated with high extinction rates (MacArthur and Wilson 1967). Proximity to the mainland increases colonization rates, in particular for more mobile organisms, such as birds, which is expected to favor taxon cycle dynamics. According to the taxon cycle hypothesis, successful colonizers tend to be generalists that will outcompete specialized endemics, but these generalists then evolve into endemic specialists that will themselves be outcompeted when new generalists reach the island (Wilson 1961; Ricklefs and Bermingham 1999, 2002). In the oceanic islands of the Gulf of Guinea, the community assembly of avian blood parasites is concordant with the taxon cycle hypothesis (Loiseau et al. 2017). This is particularly interesting as the co-evolutionary arms race between pathogens and their hosts has been proposed as a factor that could be driving taxon cycle patterns in the macro-fauna (Ricklefs and Bermingham 1999, 2002; Ricklefs et al. 2016). It is unclear whether such a pattern is present in other taxonomic groups in the Gulf of Guinea.

Volcanism in the continental and oceanic sector of the Cameroon Volcanic Line has been contemporaneous and more or less continuous since the Cretaceous (Fitton 1987; Lee et al. 1994; Burke 2001). Volcanic activity persisted until recently on the islands (0.1 Ma: Lee et al. 1994; 0.036 Ma: Barfod and Fitton 2014—see also Ceríaco et al. 2022c) and is still present for Mount Cameroon, and to a lesser extent, Bioko. Only faint signatures of volcanic activity remain on São Tomé in the form of hot springs (Henriques and Neto 2015), but the intensity of recent volcanic activity is still clearly visible in the orography, which is marked by high mountains and steep slopes, characteristic of young islands. For example, the peak of São Tomé, rising at 2024 m, was formed 1.5 Ma together with most of the central mountain massif of the island (Caldeira et al. 2003). These major volcanic events have likely driven species to extinction on multiple occasions, contributing to accelerating species turnover. Volcanic eruptions could also contribute to diversification and speciation, however, by dividing the ranges of previously panmictic populations with lava flows. The distributions of the two endemic sister caecilian lineages—*Schistometopum ephele* and *S. thomense* on São Tomé align with this hypothesis (Stoelting et al. 2014, O'Connell et al. 2021), as do patterns of genetic variation in the skink *Trachylepis thomensis* (Jesus et al. 2005).

The prevalence of species derived from recent speciation events attests to the Gulf of Guinea islands being diversification centers rather than simple "museums" where continental species found refuge from habitat changes associated with glacial cycles. Yet, the presence of species whose arrivals date to earlier times of island formation, and of Afromontane paleo-endemic plants in particular, supports the hypothesis that the islands offered a stable climatic environment during glacial cycles (Plana et al. 2004). As more dated phylogenetic studies become available from a greater diversity of taxa, we will start to gain a better understanding of the tempo of island colonization and in situ diversification.

Hybridization and Speciation in the Gulf of Guinea

The role of hybridization in evolution, and in speciation in particular, remains one of the most fundamental questions in evolutionary biology (Abbott et al. 2013; Seehausen et al. 2014; Taylor and Larson 2019). The consequences of hybridization between two lineages range from the extinction of one lineage (via the fusion of the two) to the origin of a new "hybrid" lineage. In between these extremes, hybridization can lead to different levels of genetic introgression across species boundaries, with the potential of accelerating, rather than hindering, the evolutionary process (Anderson and Stebbins 1954; Arnold and Emms 1998). In intermediate island systems, such as the oceanic islands of the Gulf of Guinea, a mainland lineage may colonize the islands more than once and at different points in time. Such cases are likely to lead to hybridization between the diverging island and mainland lineages. These rare and episodic hybridization events provide clear-cut models to study the consequences of hybridization in lineage divergence and speciation. In the oceanic islands of the Gulf of Guinea, several examples of hybridization between species have been detected. Interestingly, several of these cases were only detected with molecular data, suggesting that several other cases are likely to be uncovered with the increasing use of genetic data in the region. Here we highlight some of the better studied examples.

The *Drosophila santomea* x *D. yakuba* Hybrid Zones The genus *Drosophila*, with c. 1500 species, includes the most widely used model organism for the study of genetics, *D. melanogaster*. Interestingly, up until the discovery and description of the endemic species from São Tomé, *D. santomea* (Lachaise et al. 2000), stable hybrid zones within the genus were unknown. The description of this hybrid zone in *Drosophila* quickly led to the search, and discovery, of others such as on the island of Bioko (Cooper et al. 2018) and the Seychelles (Matute and Ayroles 2014). On São Tomé, the island endemic co-occurs with its sister species, the widespread Sub-Saharan *D. yakuba*. The endemic species is mostly restricted to mist forest at higher elevations, whereas the cosmopolitan species prefers more open habitats at lower elevations. Although the two species diverged between c. 400,000 (Llopart et al. 2002) and 1 million years ago (Turissini and Matute 2017), hybridization occurs at a rate of about 1% where their ranges meet, at intermediate elevations (Lachaise et al. 2000; Llopart et al. 2005a). This hybrid zone became an important model for research on the genetic basis of phenotypic differences (Llopart et al. 2002); the evolution of reproductive barriers (Coyne et al. 2002; Moehring et al. 2006a, b; Turissini et al. 2015); the impacts of introgression on the genome, including the replacement of the mitochondrial DNA of *D. santomea* by that of *D. yakuba* (Llopart et al. 2005a; Turissini et al. 2015); and, more generally, on the role of hybridization and introgression in speciation (Turissini and Matute 2017; Matute et al. 2020). The hybrid zone is unusual in that a population of hybrid males is restricted to the higher elevations of São Tomé, away from the ranges of both parental species (Llopart et al. 2005b). The origins of this hybrid male population are still unclear.

The *Hyperolius thomensis* x *H. molleri* Hybrid Zone Two endemic species of reed frogs occur on São Tomé—*H. thomensis* mostly restricted to the native closed-canopy forests, and *H. molleri* associated with more open habitats, including human modified ones (Bell et al. 2015b, 2022). Although closely related (c. 0.5–1.5 Ma; Bell et al. 2015a), they are clearly phenotypically distinct species differing in size, coloration, advertisement call, and reproductive biology (Drewes and Wilkinson 2004; Gilbert and Bell 2018; Bell and Irian 2019). In spite of this, hybridization occurs where the two species meet at the interface of closed-canopy forest and more open habitats, resulting in a mosaic hybrid zone (Bell et al. 2015b; Bell and Irian 2019). This hybrid zone is ripe for investigations of the genetic basis of phenotypic differences, reproductive barriers, the scale and pattern of introgression across species boundaries, and the impact of gene flow on genome architecture and phenotypic evolution. Although the geographic and temporal extent of hybridization between these species is incompletely understood, recent evidence suggests that hybridization may be a direct result of human-driven habitat changes, and of deforestation in particular (Bell and Irian 2019). The hybrid zone of the two *Drosophila* species from São Tomé also coincides with the transition from agricultural areas to native forest habitats, and therefore may also be a result of changes in habitat structure (Lachaise et al. 2000).

Mitochondrial Introgression in Parrots and Pigeons Mitochondrial data used to infer phylogenetic and phylogeographic relationships of most endemic bird species in the archipelago (Melo 2007; Melo et al. 2022) uncovered several instances of mitochondrial introgression (Box 21.1 in Melo et al. 2022): (1) the Gray Parrot *Psittacus erithacus*, where a distinct Príncipe lineage hybridized with recent arrivals from the mainland (Melo and O'Ryan 2007); (2) the Lemon Dove *Columba larvata*, where, as with the parrot, a distinct island lineage was recently joined by a new wave of mainland colonizers (Hugo Pereira and Martim Melo, unpublished data); (3) from the Sao Tome Green-Pigeon *Treron sanctithomae* to the Príncipe subspecies of the African Green-Pigeon *Treron calvus virescens* (Pereira 2013). These are all species with strong flying abilities—making them typical oceanic island colonizers—and as such, secondary contact and inter-island dispersal events are not surprising. Genomic studies are required to better understand the extent of introgression derived from interbreeding between the diverging lineages.

The Saga of the Canaries *Crithagra concolor x C. rufobrunnea* The islands of Príncipe and São Tomé host two endemic canaries (Fringillidae: *Crithagra*). The Principe Seedeater *C. rufobrunnea* is present on Príncipe, Boné de Jóquei Islet (c. 2.5 km from Príncipe), and São Tomé. Gene flow between the three allopatric populations is reduced and phenotypic differentiation has evolved, justifying their current treatment as three distinct subspecies (Melo 2007). The Sao Tome Grosbeak *C. concolor* is restricted to the primary forests of São Tomé, where it is the rarest or, at least, the most difficult bird species to find. The São Tomé population of the Principe Seedeater occurs across the entire island, from primary forest to urban areas—whenever trees are present. The phenotype of the grosbeak has often misled taxonomists, who episodically considered it to be a weaver (Ploceidae; cf. Melo et al. 2022). More recently, molecular evidence confirmed not only that it is a *Crithagra* canary, but that it is sister to the Principe Seedeater (Melo et al. 2017). The surprising twist to this story is that molecular data, from multiple loci (2 mitochondrial markers, 33 nuclear introns and exons, 34 microsatellites, and c. 10,000 single nucleotide polymorphisms—SNPs) consistently indicated that the São Tomé population of the seedeater is more closely related to the grosbeak than to its conspecific allopatric populations on Príncipe and Boné de Jóquei Islet (Melo 2007; Stervander 2009, 2015). The paraphyly of the seedeater was concordant with the grosbeak and seedeater having speciated in sympatry on São Tomé—a very unlikely scenario for birds, with the only another potential case described in the *Nesospiza* buntings (Thraupidae) from the Tristan da Cunha archipelago (Ryan et al. 2007). Clarification of this pattern was only possible using a large-scale genomic approach (Stervander 2015; Stervander et al. 2022). Mapping of over 130,000 SNPs across the genome revealed that the “sympatric speciation pattern” was the consequence of an extensive degree of genetic introgression between the two species. For the subset of

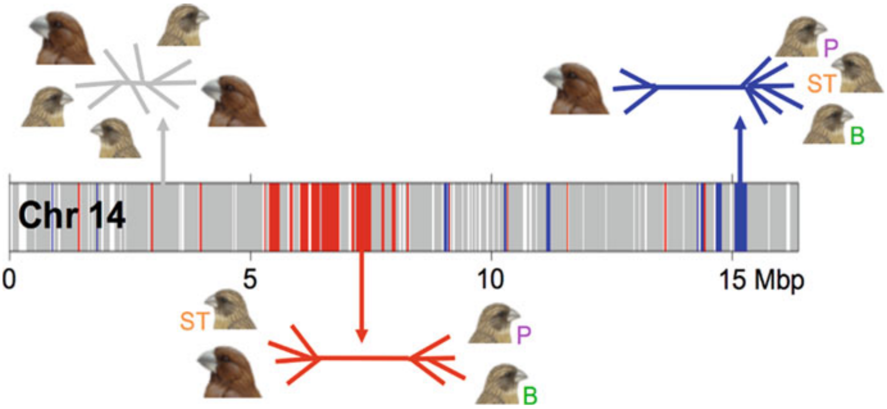


Fig. 6.2 Genomic patterns of differentiation and introgression between the Sao Tome Grosbeak and the Principe Seedeater, exemplified by data from chromosome 14. Three classes of phylogenetic signatures are distributed across the genome: Chromosomal segments that are phylogenetically inconclusive are gray ("inconclusive"; 89.1% of all segments across the genome that were assigned a local phylogeny); Segments representing a preserved phylogenetic signal (not introgressed during secondary contact of the grosbeak and seedeater on São Tomé), where the three seedeater populations are sister taxa and form a distinct lineage from the grosbeak, are blue ("preserved" 4.6%); Segments representing introgression from the grosbeak to the São Tomé population of Príncipe seedeater are red ("introgressed"; 6.3%). The latter suggest the sympatric populations of the grosbeak and the seedeater on São Tomé are sister taxa, and divergent from the other seedeater populations. Example topologies representative of each of the three genomic classes are drawn in corresponding colors, with the three seedeater populations abbreviated as ST (São Tomé; orange font; sympatric with the grosbeak), P (Príncipe; purple), and B (Boné de Jóquei; green). Figure from Stervander et al. (2022)

phylogenetically informative SNPs, more SNPs supported the sympatric speciation pattern ("introgressed markers") than allopatric speciation (i.e., where the three seedeater populations make a monophyletic group, sister to the grosbeak; "preserved markers"; Fig. 6.2). Many of the SNPs supporting allopatric speciation were associated with coding regions, including those harboring genes underlying bill size and shape, suggesting a strong role for natural selection against hybrids with intermediate bills (Stervander 2015; Stervander et al. 2022).

Evolution on Islands

The "Island Syndrome"

Island organisms often capture the imagination of scientists and non-scientists alike, as "museums of curiosities." They are lands of "dragons" (Komodo dragon *Varanus komodoensis*) and of other fantastical creatures such as the Dodo *Raphus cucullatus* (Hume 2012), a giant flightless pigeon encountered by Alice in her adventures in wonderland (Carroll 1865). Naturalists noticed early on that organisms on islands across the world appear to have shared suites of unusual characteristics (Darwin 1859; Wallace 1880; Carlquist 1965; Grant 1998b; Whittaker 1998). These common evolutionary paths have been described for many traits and grouped under the "island syndrome" umbrella (Grant 1998b; Losos and Ricklefs 2009; Burns 2019; Baeckens and Van Damme 2020). Such island syndrome traits include:

1. increased longevity and lower fecundity (e.g., Adler and Levins 1994; Covas 2012; Novosolov et al. 2013);
2. wider ecological niches (Grant 1965a, 1998b; Blondel 2000; Covas 2016; Scott et al. 2003; Amorim et al. 2017);
3. small species becoming larger and large species becoming smaller (Grant 1965a; Lomolino 2005; Clegg 2010; Lomolino et al. 2013; Novosolov et al. 2013; Biddick et al. 2019; Benítez-López et al. 2021);
4. species becoming more sedentary, with the evolution of flightlessness in animals (Diamond 1981; Wright et al. 2016; Leihy and Chown 2020) and the transition away from wind-dispersal in plants (Cody and Overton 1996; Kavanagh and Burns 2014);
5. animals becoming less territorial, allowing them to live in higher densities (density compensation: MacArthur et al. 1972), which is also likely associated with the evolution of increased "tameness" on islands;
6. birds losing colorful ornaments (Grant 1965b; Doutrelant et al. 2016).

Most of the hypotheses proposed to explain the convergent evolution of a wide suite of traits on oceanic islands are linked to the defining abiotic factors of oceanic islands: isolation, small size, and a stable and mild climate associated with the buffer influence of the sea (Grant 1998a, b; Whittaker 1998; Blondel 2000; Covas 2016; Baeckens and Van Damme 2020). Isolation and small size underlie the defining biotic feature of oceanic islands: lower species richness relative to mainland areas of equivalent size (MacArthur and Wilson 1967). This depauperate biota translates to lower levels of inter-specific competition which contributes to ecological release (Herrmann et al. 2020). Lower species richness also translates to fewer predators and parasites, allowing species to evolve in ways that are generally not possible on the mainland—including growing towards their metabolic optimum size or losing dispersal abilities.

The Gulf of Guinea islands present several potential cases of the island syndrome across different groups, albeit studies on this subject have focused primarily on birds (Box 6.2). Gigantism is the most striking, with examples found in plants, amphibians, reptiles, and birds, and dwarfism in the only endemic bird descending from a large continental species, the Sao Tome Ibis *Bostrychia bocagei*. Many of the island syndromes can only be identified once the island endemics are placed in the evolutionary context of the continental lineage they arose from. For instance, the endemic giant lobelia, *Lobelia barnsii*, found near the peak of São Tomé, is most likely part of the monophyletic clade that groups all giant *Lobelia* of the world (Antonelli 2008, 2009: *L. barnsii* not included in the analyses) and, if so, the large size of the island endemic will reflect shared history rather than convergent evolution towards island gigantism. By contrast, the Principe Giant Tree Frog *Leptopelis* *palmatus* does not appear to be closely related to the largest continental species in the genus and may therefore represent a true case of island gigantism (Jaynes et al. 2021). The house snakes, *Boaedon bedriagae* from São Tomé and *B. mendesi* from Príncipe, may also be island giants as they are considerably larger than their mainland relatives in the *B. capensis* complex in southern Africa (Ceríaco et al. 2021). Within an archipelago, selective pressures of the island condition may be stronger in smaller islands. This likely applies to the gigantism and tameness of the Tinhosa Grande islet population of *Trachylepis adamastor*. Recently described as a unique species due to its large size and dark coloration (Ceríaco 2015), molecular data indicate that the populations on Tinhosas and Príncipe are not genetically differentiated (Ceríaco et al. 2016, 2020). Such rapid phenotypic changes have been observed in just a few generations in other island lizards (e.g., Amorim et al. 2017). Likewise, out of the three populations of the endemic Principe Seedeater (São Tomé, Príncipe, Boné de Jóquei Islet), it is the birds from the small 40 ha islet that have evolved by far the largest body mass and bill and have lost more of their flying abilities (sedentariness) and anti-predator behavior (tameness) (Box 6.3).

Box 6.2 The Island Syndrome in the Birds of the Gulf of Guinea Oceanic Islands

Wider niches: Bird song is a trait directly linked to fitness for its role in mate attraction and territory defense (Collins 2004). Hence, song is a signal under strong selection for efficient transmission. In species-rich communities, competition for acoustic space is expected to be high—as overlap of different songs masks the signals and impairs the efficacy of their transmission (Wollerman and Wiley 2002). Thus, mainland species tend to partition the acoustic space into narrow temporal and spatial (frequency bandwidth) windows to minimize interference (Planqué and Slabbekoorn 2008; Weir et al. 2012). By contrast, the acoustic space of species-poor islands is predicted to be less saturated. Comparisons of bird communities of São Tomé and Cameroon revealed that the species-poor island communities live in an acoustic environment with less acoustic interference (both from birds and insects) than those on the mainland, that island species spend more time vocalizing alone, and that acoustic overlap is lower (Robert et al. 2019, 2021). This lower competition for acoustic space translates into the songs of island species occupying a broader frequency bandwidth than the songs of their mainland counterparts (Robert et al. 2021)—a pattern that is consistent with the character release hypothesis predicted from the lower levels of inter-specific competition (Grant 1972; Herrmann et al. 2020).

Island rule: The trends of body size evolution in the endemic birds of the Gulf of Guinea fit the predictions of the island rule very closely. Most small and medium birds increased in size, with three "island giants" including the world's largest sunbird (Sao Tome Sunbird *Dreptes thomensis*), weaver (Giant Weaver *Ploceus grandis*), and canary (Sao Tome Grosbeak *Crithagra*

(continued)

Box 6.2 (continued)

rufobrunnea). The few exceptions where small birds decreased slightly in size occur in those species that co-exist with a congeneric species and, therefore, represent the few cases in which inter-specific competition is present and character displacement may be at play (see main text and Fig. 6.3). The exceptions to this rule appear to be limited to the Sao Tome Paradise-Flycatcher *Terpsiphone atrochalybeia* and the Sao Tome Short-tail *Motacilla bocagii*, which are smaller than their mainland relatives but do not have any close relatives on the island. By contrast, the only endemic derived from a group of large birds, the Sao Tome Ibis *Bostrychia bocagei*, is the smallest representative of its group and one of the smallest ibises in the world.

Dispersal loss: Darwin hypothesized that sedentariness on islands evolves because dispersing individuals are unlikely to return (Darwin 1859). Under this hypothesis, the smaller the island, the stronger the selection favoring individuals that do not disperse. One study investigated the evolution of flying potential among populations of the endemic Principe Seedeater *Crithagra rufobrunnea* in the early stages of divergence. This species occurs in three allopatric populations: Príncipe, Boné de Jóquei Islet (c. 2.5 km off Príncipe), and São Tomé. Gene flow between the three populations is very restricted and phenotypic differentiation is significant (Melo 2007). The population on the smallest island (the 40 ha Boné de Jóquei Islet) had the lowest flying potential, as inferred from its small wing length: body mass ratio (Melo 2007; Box 6.3).

Color loss: The loss of coloration, color patches, and even sexual dimorphism in island birds has long attracted the attention of ornithologists (Grant 1965b). This pattern is consistent across distinct taxonomic groups and island systems (Doutrelant et al. 2016). A trend for increased melanism has also been suggested for island birds (Uy and Vargas-Castro 2015)—and for reptiles (Novosolov et al. 2013)—but has not yet been as extensively studied. As with the island rule, color loss is on full display in the endemic birds of the oceanic islands of the Gulf of Guinea. Lipochromes (yellow and green pigments) present in mainland relatives have mostly been lost in the island endemics: Sao Tome Oriole *Oriolus crassirostris*, the five white-eye species (*Zosterops* sp.; Melo et al. 2011), the Sao Tome Sunbird, and the Principe Sunbird *Anabathmis hartlaubi* (Newton's Sunbird *A. newtonii* being the exception). Additionally, the male of the Sao Tome Paradise-Flycatcher is entirely black, and melanin predominates in the plumage of the Principe Seedeater and the endemic São Tomé subspecies of the Western Barn Owl *Tyto alba thomensis*.

Several hypotheses have been put forward to explain the loss of color in island birds including that (1) species-poor communities may relax the need for elaborate signals used in species recognition (Martin et al. 2010, 2015a, b); (2) long-lived species have higher levels of parental care, which is associated with lower investment in sexual signals (Covas 2012); (3) sexual selection is

(continued)

Box 6.2 (continued)

relaxed as a consequence of both the reduced genetic diversity (Frankham 1997) and higher relatedness within island populations (Griffith 2000). Most work on the Gulf of Guinea islands has focused on the hypothesis that colors in birds are honest signals of immune condition as they often depend on the acquisition of carotenoids from the diet, which are also essential co-adjuvants of the immune system (Hamilton and Zuk 1982). From a pathogen perspective, islands are thought to be more benign environments because the decrease in species richness is expected to also extend to parasites. If this expectation is correct, the inter-individual variation in health condition on islands should be very narrow, and hence color would no longer hold information regarding individual condition.

A survey of avian blood parasites indicated that parasite diversity and prevalence is lower on Príncipe and São Tomé relative to the adjacent mainland (Loiseau et al. 2017). Proxies of acquired immune function were lower on islands (Lobato et al. 2017), and genes from the Major Histocompatibility Complex (also involved in acquired immunity) were found to be under relaxed selection (Barthe et al. 2022), consistent with low exposure to pathogens. Other important genetic components of the immune system, however, were impacted by small population sizes and drift rather than by relaxed selection (Barthe et al. 2022). Demonstrating a direct link between the reduction in parasites and color loss in the avian community is more challenging. Although many of the island endemics have lost coloration and many of the more recent arrivals have not, the birds of Príncipe and São Tomé do not provide enough data points along the gradient of time since colonization to conclusively support the Hamilton and Zuk hypothesis.

Box 6.3 Evolution on an Island of an Island

Boné de Jóquei Islet (**1**) is only about 600 x 900 m and lies c. 2.5 km off the southeast coast of Príncipe (**2**), from which it has been separated since the last glaciation, c. 10,000 years ago. It holds an endemic subspecies of the Principe Seedeater *Crithagra rufobrunnea fradei* (**3**), which occurs at very high densities (**4**). Two other subspecies occur on Príncipe and on São Tomé Islands, respectively. The birds from Boné have the smallest wing relatively to their mass, indicating the loss of dispersal ability. They have evolved a high degree of tameness, reflecting evolution in a predator-free environment. They have stouter bills, which have likely evolved due to the reliance of their diet on the resources provided by the oil palm *Elaeis guineensis*, which constitutes the dominant vegetation. They feed both on the pollen of the male inflorescences

(continued)

Box 6.3 (continued)

(**5**) and on the fruit (**6**, **7**). The oil palms of Boné produce giant fruits, which appear to have no parallel worldwide—and are not found on neighboring Príncipe, where both species also co-occur. The large fruits may have co-evolved as a defense against the strong predation pressure exerted by the seedeater, or as an adaptation against dispersal. (**6**) Large fruits from Boné oil palms in comparison with typical fruits; 15 cm ruler shown. Photo credits: Martim Melo.

Inter-Specific Competition Accelerates Phenotypic Evolution

Low levels of inter-specific competition characterize species-poor island assemblages, resulting in high levels of intra-specific competition. Both factors likely contribute to the evolution of many traits associated with the island syndrome. Research on bird speciation in the oceanic islands of the Gulf of Guinea (Melo

2007; Melo et al. 2022), however, reveals an important role for rare cases of inter-specific competition that occur when closely related lineages meet on the same island (see also: Grant 1965c)—an event that may be not so infrequent in intermediate island systems. Molecular phylogenies have shown that in most cases the most phenotypically divergent species are those that (1) evolved in sympatry with a close relative (both evolutionarily and ecologically) and (2) represent the most recent speciation events, instead of deriving from the oldest colonization events as previously assumed (Melo et al. 2022). For example, the two most phenotypically "aberrant" white-eyes, the Principe Speirops *Zosterops leucophaeus* and the São Tomé Speirops *Z. lugubris*, are sister species derived from the most recent speciation events in the Gulf of Guinea white-eye radiation (Box 21.2 in Melo et al. 2022). Furthermore, in this radiation, when two species meet it is the newcomer that changes the most (Melo et al. 2011), in a process of asymmetrical character displacement that had been predicted by theory (Doebeli and Dieckmann 2000), and confirmed in the radiation of Darwin's finches (Petren et al. 2005).

The evolution of true giants among the Gulf of Guinea island birds seems to have resulted from the sequential effects of character release (Herrmann et al. 2020) and character displacement (Brown and Wilson 1956; Grant 1972). The three giant birds (weaver, sunbird, canary) all evolved in sympatry with a closely related lineage (the sister lineage in the case of the canary). This suggests the following history for the evolution of gigantism in the Gulf of Guinea birds, as previously suggested by Amadon (1953): (1) a colonizer arrives to an island; (2) with no direct competitors it evolves towards a generalist diet (character release), which in birds is associated with an increase in bill size and, correspondingly, body size (Grant 1965a; Blondel 2000); (3) a related lineage colonizes the island and inter-specific competition ensues; (4) for co-existence to be possible, selection drives a reduction in competition through character displacement, (5) the larger species evolves to become even larger. Morphometrics of the five-species radiation of the white-eyes of the oceanic islands of the Gulf of Guinea is strongly suggestive of character displacement as a driver of phenotypic differentiation, although in this case the larger species evolved from the secondary arrivals (Fig. 6.3).

Collectively, these studies point to the importance of inter-specific competition in driving and accelerating phenotypic divergence in island birds, and even in the speciation process.

Concluding Remarks

The Gulf of Guinea oceanic islands are an exciting example of an intermediate island system, such that they are close enough to the continent to receive a diverse array of mainland dispersers but far enough away for these to diverge once they arrive to the islands. Thus, the archipelago holds great potential for testing classic hypotheses of island biogeography by providing a wide array of independent evolutionary replicates, something that is missing from more remote archipelagos dominated by few

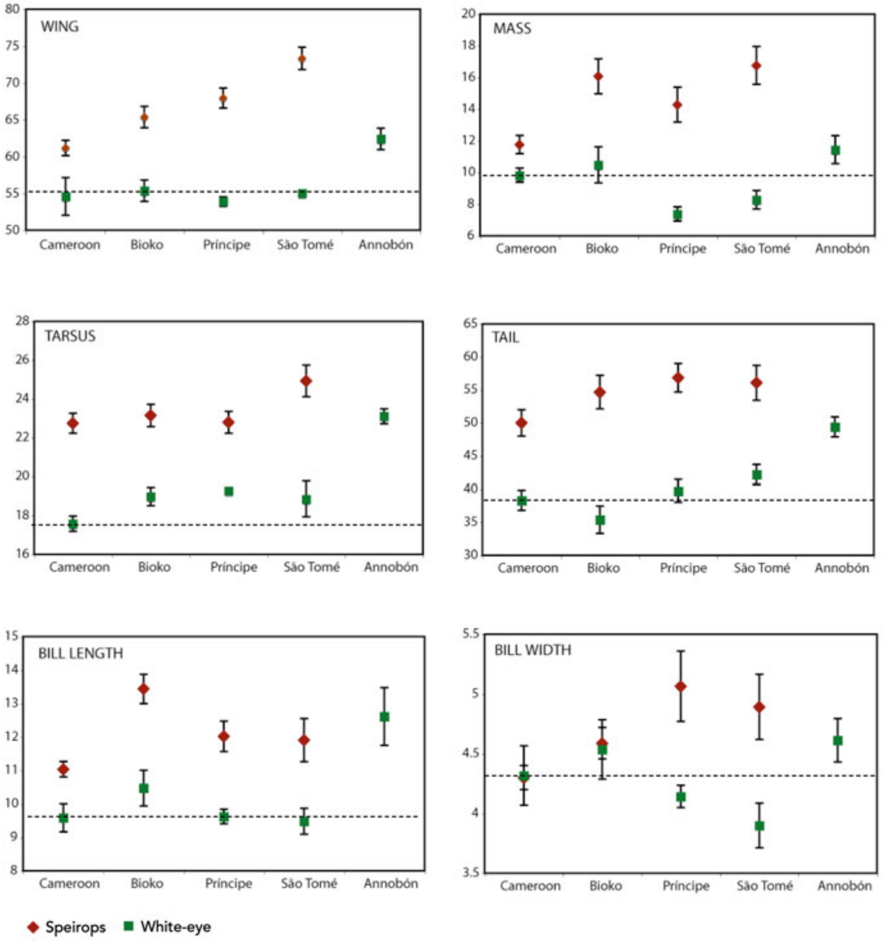


Fig. 6.3 Evidence for character displacement? Morphometrics of the white-eyes (Zosteropidae) of the Gulf of Guinea, including the five-species radiation of the oceanic islands and the three species radiation of Bioko and Mount Cameroon. White-eyes generally occur as single allopatric species, but in the Gulf of Guinea there are four instances of co-occurrence of two species. On Annobón there is only one species, which has evolved a larger size than its mainland counterpart (broken line) in accordance with the island rule. In all other cases, where two species meet in sympatry, the secondary arrival (red) increased significantly in size, while the first colonizers (green) did not change much or decreased in size relative to their closest mainland relatives (depicted, approximately, by the broken line). In addition, the secondary arrivals evolved strikingly different colors from those of the typical white-eye template (Box 21.2 in Melo et al. 2022). These patterns of phenotypic divergence in this group support the process of asymmetric character displacement. The large phenotypic differences of the secondary arrivals led them to be originally placed in a separate genus, *Speirops*

lineages, and for investigating the role of gene flow in speciation and diversification. Likewise, the archipelago presents the opportunity to disentangle mechanisms of community assembly in a setting that is intermediate between the complex communities of continents, with high phylogenetic diversity, and the simple communities of more isolated archipelagos, in which most of the diversity is derived from a few extensive radiations. Finally, the archipelago's endemics exhibit many of the unusual phenotypes that have long captured the attention of scientists and non-scientists, alike. As taxonomic and systematic research advances for the archipelago's lesser known groups, hypothesis-driven studies investigating speciation and phenotypic evolution will be possible in a more representative subset of the remarkable diversity of the Gulf of Guinea oceanic islands.

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Chapter 7
Species Ecology in the Gulf of Guinea Oceanic Islands: Distribution, Habitat Preferences, Assemblages, and Interactions

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Abstract The oceanic islands of the Gulf of Guinea (Príncipe, São Tomé, and Annobón) are an exceptional centre of endemism for flora and fauna. Remarkable progress has been made in biological research during the last few decades: from species being described and reported for the first time, to general patterns of species-habitat associations found across terrestrial, coastal, and marine taxa. Despite this increase in knowledge, key aspects of Gulf of Guinea species ecology remain poorly

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understood. This chapter reviews existing knowledge on the biodiversity of the islands, focusing on species distributions, population abundance estimates, traits, habitat associations and interactions. To promote these islands as ecological models, and to ensure the future of their endemic-rich biodiversity, it is essential to overcome current knowledge gaps and reduce existing taxonomic, spatial, and temporal biases in the information available. Therefore, future studies should favour systematic island-wide surveys and prioritize understudied areas and taxonomic groups. Moreover, long-term monitoring studies are urgently needed to assess biodiversity trends and to advise conservation actions. The future of ecological research and conservation of the unique biodiversity of these islands must increasingly rely on the development of local biodiversity-focused scientific expertise, through outreach, capacity building, and advanced training, paired with international collaborations and the development of local organizations.

Keywords Annobón · Conservation · Exotic species · Príncipe · São Tomé · Seasonality

Introduction

The oceanic islands of the Gulf of Guinea (Príncipe, São Tomé, and Annobón) have long been recognized for the high levels of endemism of their flora and fauna (Jones 1994). This in itself makes them an important model of ecological research, but studying ecology in these unique islands may also provide invaluable insights into evolutionary and ecological processes, since islands can be used as natural experiments to extrapolate to wider scales (Whittaker et al. 2017).

The description of the biodiversity in the archipelago began in the late eighteenth century and was intensified during the late nineteenth and twentieth centuries (Ceríaco et al. 2022b). Since then, the islands have captured the imagination and efforts of biologists, prompting scientific studies across multiple disciplines, many of which aim to clarify different aspects of ecology (e.g., Lima 2016), such as species distributions and habitat associations. Up to the 1990s, virtually all zoological publications focused on taxonomy (Gascoigne 1993), and this is still mostly the case for plants (Stévart et al. 2022) and most invertebrates. Despite an increase in ecological research over the last few decades, key aspects of the ecology of species occurring in the Gulf of Guinea islands remain poorly documented, such as the influence community diversity and composition has on ecosystem processes. Progress is often halted by major knowledge gaps in areas fundamental to ecology, such as taxonomy. This has been the case for most invertebrates, as unresolved taxonomy halts progress in other areas of research. Take the example of terrestrial molluscs, in which an updated taxonomy opened the doors for several ecological studies (Panisi et al. 2022).

Here, we review existing information on the ecology of species from the oceanic islands of the Gulf of Guinea. Specifically, we address current knowledge on species distributions, population abundance, traits, habitat associations and interactions. We also provide key references for each island and taxonomic group and identify current knowledge gaps to direct future research.

Distribution

Information on the distributions of species on the oceanic islands of the Gulf of Guinea has been an important feature of initial studies. Some are even associated with the first descriptions of the islands themselves: a report of São Tomé in 1506, made by the Portuguese navigator Gonçalo Pires and written by Valentim Fernandes, describes an abundance of kites and the occurrence of a crocodilian that has since been extirpated from the island (Monod et al. 1951). However, much of the data on species distributions available today is still limited to the brief reports included in species descriptions (e.g. Ceríaco et al. 2015), species catalogues (e.g. Stévart and de Oliveira 2000; Csuzdi 2005; Sérgio and Garcia 2011; Mendes and Bivar-de-Sousa 2012), or studies focusing on various aspects of their biology (e.g. Drewes and Stoelting 2004). These are usually based on opportunistic observations, rather than on systematic surveys of the islands, and often only mention the islands where the species occur. When such studies provide details on the distribution of a given species, they tend to be biased towards well preserved accessible sites (Atkinson et al. 1991, Stévart et al. 2022).

Few studies have compiled geographically explicit information on species locations. Some exceptions include pteridophytes (Figueiredo 2002), endemic plants (Joffroy 2000; Stévart et al. 2022), land snails (Holyoak et al. 2020), and birds (Jones and Tye 2006). In some cases, information and even maps are shown, but details on how these were obtained are missing, as is the case for amphibians and reptiles (Pollo 2017) and threatened endemic birds (IUCN 2020a).

Even fewer species assemblages have been systematically surveyed across any of the islands. Some exceptions include plants (Fundação Príncipe 2019; Stévart et al. 2022), terrestrial snails (Tavares 2020), benthic reefs and fishes (Maia et al. 2018b), sea turtles (Ribeiro 2018; Hancock 2019), birds (Fundação Príncipe 2019; Soares et al. 2020), and bats (Rainho et al. 2010). Bird surveys informed some of the first island-wide assessments of the distribution of community traits, such as species richness, composition, and structure (e.g. Lima et al. 2013; Soares 2017; Fig. 7.1). Documenting plant species assemblages to classify vegetation is ongoing (Dauby et al. 2022), although the main gradients have been described (Monod 1960; Stévart 1998; Ogonovszky 2003).

The scarcity of historical records hampers the detection and quantification of temporal changes in the distribution of species on the oceanic islands of the Gulf of Guinea. However, sometimes even sporadic records allow assessing trends, such as the retraction of native species and the expansion of introduced species. For instance, localities linked to herbarium samples have provided convincing evidence for the disappearance of many plant species from large portions of the north of São Tomé and Príncipe, such as *Aerangis flexuosa* (Ridl.) Schltr, 1887. Interviews in rural and

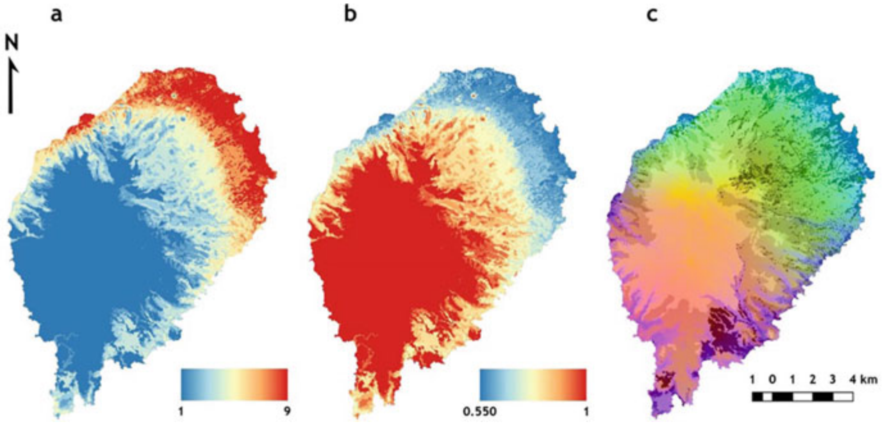

Fig. 7.1 Maps showing the distribution of (**a**) non-native bird species richness, (**b**) proportion of native bird species (Soares et al. 2020), and (**c**) compositional dissimilarity (Soares 2017). There was a clear opposing pattern in the distribution of non-native species richness and proportion of native species: non-native bird species thrive particularly well in land use types most influenced by humans (**a**), whereas native bird species dominate the best-preserved forests (**b**). Species composition largely coincides with the distinct land use types (**c**)

coastal communities suggest distribution areas for populations of giant land snails (Panisi 2017) and fishes (Maia et al. 2018a) have shifted. Historical distribution data reveal strong declines in the ranges of the endemic Obô Giant Land Snail *Archachatina bicarinata* (Bruguière, 1792) (Dallimer and Melo 2010), of the endemic São Tomé Shrew *Crocidura thomensis* (Bocage, 1887) (Lima et al. 2016), and of the number of beaches where sea turtles nest on São Tomé (Graff 1996; Ribeiro 2018). The number of recorded extinctions and extirpations is very small, with the only documented cases being an unknown species of crocodile on São Tomé (Ceríaco et al. 2018), an endemic subspecies of Olive Ibis on Príncipe (Lima and Melo 2021), and two orchid species (IUCN 2020). However, as for most other oceanic islands, vegetation clearance and the introduction of species are likely to have caused extinctions and extirpations before taxonomic studies started, and those may remain unknown, especially considering the poor fossil or subfossil record of the islands.

Population Estimates

To date, there has not been an attempt to estimate plant population sizes. The first attempts to characterize plant species abundance on Príncipe provided valuable information on population dynamics of threatened species (Benitez et al. 2018). This study also revealed a higher abundance of species than previously thought, with high levels of regeneration for *Grossera elongata* Hutch, 1944, *Santiria balsamifera*

Oliv., 1886, and *Mesogyne henriquesii* Engl., 1894, and a lack of regeneration for *Strephonema* sp. nov. and *Carapa gogo* A. Chev. ex Kenfack, 2011.

The scarcity of quantitative surveys has resulted in very few reliable population size estimates for animal species. These include estimates made for birds (Dallimer and King 2007; Dallimer et al. 2009, 2010, 2012; Fundação Príncipe 2019), particularly for species of conservation concern, such as the Critically Endangered Dwarf Olive Ibis *Bostrychia bocagei* (Chapin, 1923) (Azevedo 2015), all pigeon species on São Tomé (Carvalho 2014), the Endangered Grey Parrot *Psittacus* sp. on Príncipe (Valle 2015), and the undescribed Príncipe Scops-Owl *Otus* sp. (Freitas 2019). Recent studies have also attempted to estimate population sizes for the Hawksbill Turtle *Eretmochelys imbricata* (Linnaeus, 1766) (Hancock 2019) and the Obô Giant Land Snail (Panisi 2017; Fundação Príncipe 2019), both on Príncipe and on São Tomé. On land, the difficult terrain and dense vegetation have greatly hampered the use of methods to account for detectability, such as distance sampling (but see: Dallimer and King 2007). In marine ecosystems abundances are even harder to sample, partly because many of the important species in these environments are migratory and have complex life cycles.

The very few long-term population studies that have been conducted include attempts to determine population trends of reef fishes, sea turtles, seabirds, and the Grey Parrot on Príncipe. The study of reef fish on São Tomé revealed worrisome declines (Maia et al. 2018b). Underwater visual census and photo-quadrats across six sites around São Tomé allowed researchers to explore the relative importance of exposure, depth, and topographic complexity as drivers of fish and benthic reef communities. Species richness, abundance, and biomass of reef fish were higher in deeper sites, which suffer less influence from human activities and are under the direct influence of a constant thermocline resulting from the intrusion of cold waters from the Benguela current.

Breeding female sea turtles have been monitored on Príncipe and São Tomé since the early 1990s (Ribeiro 2018; Hancock 2019). However, incomplete temporal and spatial coverage has led to high levels of uncertainty and hindered the quantification of critical parameters to estimate abundances. Recent advances in population modelling are overcoming this problem (Hancock et al. 2019), and standardized surveys carried out on both islands since 2012 will allow even more accurate estimates in the future. Techniques such as genetic analyses have also been used to estimate operational sex-ratios and assess population changes over time, such as reductions in effective population sizes in the Olive Ridley Turtle *Lepidochelys olivacea* (Eschscholtz, 1829), and migration rates in the Green Turtle *Chelonia mydas* (Linnaeus, 1758) (Hancock et al. 2019).

Local seabird colonies are the most important in the tropical Eastern Atlantic (BirdLife International 2020), primarily due to the large breeding colonies on the Tinhosas islets (Monteiro et al. 1997; Valle et al. 2016; Bollen et al. 2018; Lima and Martins 2020). These small islets (<25 ha) host around 140,000 breeding pairs of Sooty Tern *Onychoprion fuscatus* (Linnaeus, 1766), 10,000 pairs of Brown Noddy *Anous stolidus* (Linnaeus, 1758), and important breeding populations of Black Noddy *Anous minutus* Boie, 1844, and Brown Booby *Sula leucogaster* (Boddaert, 1783). Large population decreases have been reported for these colonies, but it is not yet clear whether these represent real declines or natural variations between years. Breeding and non-breeding seabird population sizes were first assessed in 1997, for most islets and small islands around Príncipe and São Tomé (Monteiro et al. 1997). More recently, the Tinhosas have been monitored quarterly to refine population estimates and trends, and to gain a better understanding of the breeding seasonality of these species (Valle et al. 2016; Bollen et al. 2018; Lima and Martins 2020).

Finally, the population of Grey Parrot on Príncipe has so far been the only one targeted by a population viability analysis (Valle 2015). Counts suggest that the species has recovered since the 2005 trade ban, now numbering around 8000 individuals, and that adult survivorship is critical to ensure population persistence, since the species can sustain relatively high levels of chick harvesting.

Species Traits

From early on, researchers showed an interest in describing the temporal trends in the evolution and selection of species traits (Hortal et al. 2015). Many initial descriptions of biodiversity provided the first data on species traits that are vital for ecological studies. Biological collections, in particular, play a fundamental role in enriching trait databases, and can even lead to unexpected discoveries. In the oceanic islands of the Gulf of Guinea, morphological analyses of more than 2500 plant specimens collected in 2019 and 2020 have yielded many new species, while rediscovering rare species and finding new records for the islands (Stévart et al. 2022). Despite strong research effort in the 2000s (Figueiredo et al. 2011), ongoing studies on orchids are still leading to the description of new species, especially for the genus *Tridactyle*. Moreover, museum specimens allow the quantification of traits and trait variability, which are key to understanding the ecological function of species (e.g., Heleno et al. 2021). These collections are particularly relevant for species that might be harder to find and offer a historical reference that allows an assessment of temporal changes in traits, an aspect that remains poorly explored in these and other islands.

Species traits can be measured not only on museum specimens but also in the field, on living specimens that are not collected. This has begun to be carried out extensively in plants, but the amount of information available varies greatly between islands and specific groups (Exell 1944; Figueiredo et al. 2011; Sérgio and Garcia 2011; Klopper and Figueiredo 2013; Velayos et al. 2014), and, overall, information about plant traits remains scarce. This is not surprising considering that much of the plant taxonomy remains unresolved, and many species are still being reported and described as new to the islands (Benitez et al. 2018; Stévart et al. 2022). Ongoing work focused on threatened plant species has been collecting important information on species traits (Stévart et al. 2019).

A new checklist of land snails of São Tomé and Príncipe provided some information on these species' traits (Holyoak et al. 2020). Despite limitations, both on the types of the traits characterized and on the number of species that have been assessed (Tavares 2020), this remains one of the few studies providing species traits for invertebrate taxa.

Sea turtle and bird traits have been studied much more extensively on the islands. The long-term monitoring of sea turtles in Príncipe and São Tomé since the 1990s collected data on female size that captured both spatial and temporal variation (Ribeiro 2018; Hancock 2019). Bird banding activities on the islands, although sporadic, have allowed collecting trait data, mostly on activity, morphometric measurements, and coloration, which have improved our understanding of sexual dimorphism, spatial trait variability, and daily and annual life cycles (King and Dallimer 2003; Madeira 2018).

High endemism rates and island syndromes hinder the use of the increasingly available global trait databases to assess species traits for island species, which have to be gathered locally (e.g., Covas 2016). In addition, behavioural, physiological, and life-history traits are often less easily recorded than morphological traits and remain an important knowledge gap (Hortal et al. 2015). Finally, to interpret current ecosystems under the lens of long-term ecology it is also vital to understand which species are native (Nogué et al. 2017).

Habitat Associations

Until recently, local information on species-habitat associations was very scarce (e.g., Exell 1944; de Naurois 1994), but the situation has greatly improved since the 1990s. Some of the first studies from this period reported associations between species occurrence and local environmental variables, producing brief descriptions of habitat preferences (e.g., Atkinson et al. 1991; Joffroy 2000; Jones and Tye 2006). This was followed by more detailed and accurate descriptions for the best-studied groups, such as mammals (e.g., Dutton and Haft 1996) and birds (e.g., Dallimer and King 2007).

In recent years, a few studies have used geographically explicit information on environmental variables to model the distribution of terrestrial snails and birds on Príncipe (Fundação Príncipe 2019; Rebelo 2020) and on São Tomé (Lima et al. 2017; Panisi 2017; Soares 2017). Some of these studies have also assessed how local variables, often related to the vegetation, affect the distribution of species and species assemblages at smaller scales. Most of these have focused on vertebrates, such as amphibians (e.g., Strauß et al. 2018) and birds (e.g., Lima et al. 2013; Carvalho et al. 2015; Margarido 2015; Lewis et al. 2018; Alves 2019; Freitas 2019), but also on land snails (Panisi 2017; Rebelo 2020; Tavares 2020).

Native species, and especially endemic and threatened species, tend to be strongly associated with ecosystems that have been less disturbed by human activities. This pattern is common to terrestrial, coastal, and marine realms, and to distinct groups, including birds (Lima et al. 2013; Soares et al. 2020), tree frogs (Strauß et al. 2018), sea turtles (Hancock 2019), land snails (Panisi 2017; Tavares 2020), and even earthworms (Csuzdi 2005) in the Gulf of Guinea.

In terrestrial groups, species distributions are strongly determined by land use, which in turn has been shaped mostly by topography (Jones et al. 1991; Norder et al. 2020). The best-preserved native forests, on which most native species depend, tend to persist in rainy, remote, and rugged areas (e.g., Soares et al. 2020). However, some native species, and even a few endemics, managed to adapt to novel ecosystems created by humans, including some birds (Dallimer et al. 2009; Lima et al. 2013; Carvalho 2014; Alves 2019), mammals (Rainho et al. 2010), frogs (Strauß et al. 2018), and land snails (Tavares 2020). Among novel ecosystems, those that maintain dense tree cover and mimic the structure of the native vegetation seem to be preferred by native species (Jones and Tye 2006; Lima et al. 2014). These include secondary forests, which result from vegetation regrowth after logging and agricultural abandonment, and agroforest systems, such as coffee and cocoa shade plantations, which integrate trees and agricultural crops (Jones et al. 1991; Oyono et al. 2014; Dauby et al. 2022). Unfortunately, it is also clear that many taxa do not cope well in these novel ecosystems (e.g., Fundação Príncipe 2019; Soares et al. 2020). In contrast with native terrestrial species, introduced species tend to be associated with more intensive land uses, many of which are located in the drier lowlands (Jones et al. 1991). On São Tomé, introduced birds are mainly small granivore species that rely on anthropogenic land uses (Soares et al. 2020), while introduced mammals seem to be less restricted to these environments (Dutton 1994).

Altitude might be less relevant to explain the distribution of mobile terrestrial organisms with broad ecological niches, such as most birds (e.g., Soares et al. 2020; but see: Dallimer et al. 2009; Lima et al. 2017), but it is crucial for other groups, such as snails (Tavares 2020), and notably plants (Exell 1944; Monod 1960; Stévart et al. 2022). Since plants are key components of terrestrial ecosystems, altitude has thus fundamental implications for how ecosystems are distributed across the islands (Dauby et al. 2022).

In reef ecosystems, depth and wave exposure appear to be the most important factors to explain changes in fish diversity (Tuya et al. 2018) and in the composition of fish and benthic communities (Morais and Maia 2017; Maia et al. 2018b). For highly mobile marine megafauna, such as sea turtles and cetaceans, species distributions vary among groups and appear to be related mostly to ecosystem type, food availability, depth, and sea surface temperature. For example, species of cetaceans that are quite similar, such as the Pantropical Spotted Dolphin *Stenella attenuata* (Gray, 1846), and the Common Bottlenose Dolphin *Tursiops truncatus* (Montagu, 1821), show clearly distinct habitat preferences related with bathymetry (Picanço et al. 2009). In the case of sea turtles, the habitat associations are strongly related to life stage. Juvenile Green and Hawksbills sea turtles feed on seagrasses or algal beds and coral and/or rocky reefs respectively, all year long (Monzón-Argüello et al. 2011; Ferreira et al. 2018; Hancock et al. 2018). By contrast, most adult turtles are found in coastal waters only during the reproductive season and are seldom observed feeding. The northern beaches of São Tomé are dominated by the Olive Ridley, which is extremely rare in the south of the island and on the island of Príncipe

(Hancock et al. 2015). On the other hand, the Green Turtle is clearly the dominant nesting sea turtle species on Príncipe, and on the eastern and southern shores of São Tomé. This is linked to the preference of Green Turtle for narrow and steeper beaches associated with strong erosive processes, while Olive Ridley prefers unobstructed access to wide beaches with gentle slopes. The Hawksbill Turtle typically prefers small, protected beaches composed mainly of coralline sand and surrounded by vegetation, hence occurring mostly on the Rolas Islet off São Tomé, and along the northern coast of Príncipe (Hancock 2019).

Species Interactions

Interactions between species are often complex, but they are the structure that supports biodiversity, and thus their study is fundamental to understand ecosystem functioning (Thébault and Fontaine 2010). Since they rely on detailed knowledge of basic aspects of the ecology of species and are often difficult to quantify, few species interactions have been studied in-depth on these islands, and the information available in the literature is often still limited to brief descriptions (e.g., Jones and Tye 2006; Wirtz and d'Udekem d'Acoz 2008; Vasco-Rodrigues et al. 2017).

We drafted a qualitative vertebrate food web for terrestrial ecosystems in São Tomé and Príncipe, distinguishing native and non-native species (Fig. 7.2). This was based solely on information on trophic interactions described for the islands for introduced mammals (Dutton 1994), birds (Jones and Tye 2006), bats (Rainho et al. 2010), shrews (Ceríaco et al. 2015; Lima et al. 2016), amphibians and reptiles (Ceríaco et al. 2018), the undescribed Príncipe Scops-Owl (Freitas 2019), and on more generic sources for other species (IUCN 2020). Nevertheless, even this simplistic approach, which excludes humans from the equation, illustrates major disruptions of trophic interactions by non-native species. Beyond the obvious changes in the topography of trophic interactions, the impact of introduced species is further heightened by their distinctive traits (Capellini et al. 2015). This food web provides a starting point for studies to deepen our understanding of trophic linkages and how they may be disrupted by introduced species.

A more quantitative, community-level approach enabled building a multi-guild seed dispersal network for São Tomé (Heleno et al. 2021). This showed that non-native species can disrupt this important component of ecosystem functioning, especially large mammals, which are seldom native on oceanic islands. Other quantitative studies at the community level have assessed how reef microhabitats mediate fish agonistic interactions (Canterle et al. 2020), and how land use and host species influence richness, prevalence, and co-infection patterns of haemosporidian bird parasites (Reis et al. 2021). A quantitative, species-specific study used stable isotopes to reveal that juvenile São Tomé Green Turtles adapt their diet preferences to the available food sources and, in contrast with expectations, are not strict herbivores (Hancock et al. 2018). Further quantitative studies at the community and species level across terrestrial and marine ecosystems are sorely needed.

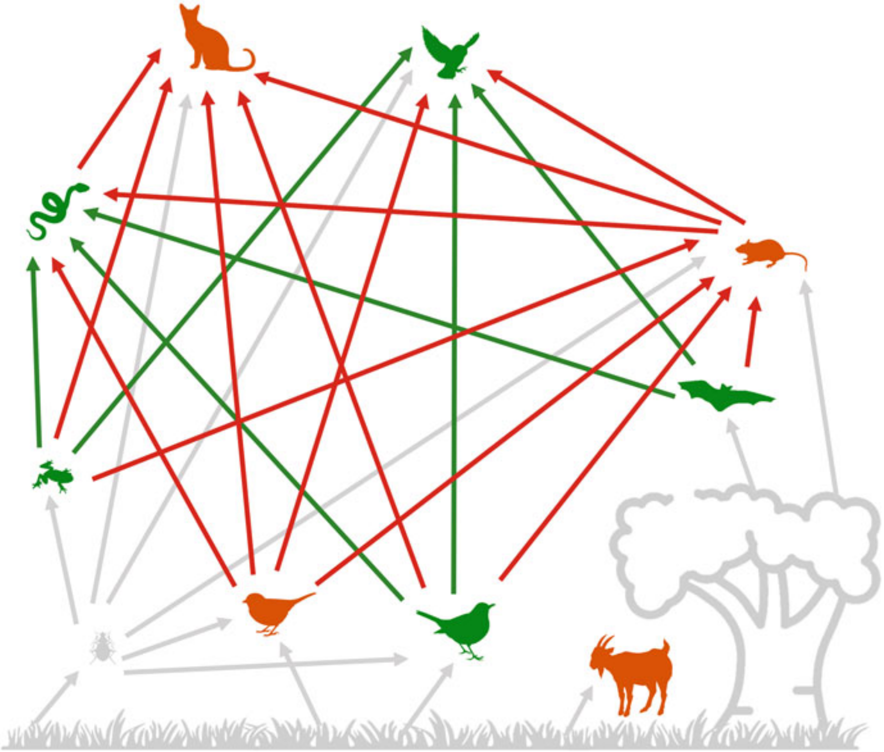

Fig. 7.2 Generalized São Tomé and Príncipe terrestrial vertebrate food web. Each icon represents a group of native or non-native species in the same trophic level. Arrows signal energy transfers through trophic interactions. Green symbolizes native species and interactions, red symbolizes non-native ones and grey symbolizes non-vertebrate components of the food web, namely plants and invertebrates. Native herbivores include fruit bats, pigeons, and parrots, while non-native include several ungulates, Rock Pigeon *Columba livia* J.F. Gmelin, 1789, and Laughing Dove *Streptopelia senegalensis* (Linnaeus, 1766). Native omnivores include several species of pigeons and perching bird species, while non-native include rodents, Mona Monkey *Cercopithecus mona* (Schreber, 1775), African Civet *Civettictis civetta* (Schreber, 1776), Pig *Sus scrofa* Linnaeus, 1758, fowls, and other bird species. Native insectivores include amphibians, geckos, skinks, shrews, bats, and a few bird species, while non-native include geckos, skinks; the Palm Swift *Cypsiurus parvus* (M.H.K.Lichtenstein, 1823), an insectivore that colonized the islands recently. Native carnivores include Dwarf Olive Ibis *Bostrychia bocagei* (Chapin, 1923), owls, and Black Kite *Milvus migrans* (Boddaert, 1783), while Cattle Egret *Bubulcus ibis* (Linnaeus, 1758) is the only non-native carnivore bird. Snakes are the only native vertivores, while Cat *Felis catus* Linnaeus, 1758, Dog *Canis familiaris* Linnaeus, 1758, and Least Weasel *Mustela nivalis* Linnaeus, 1766 are all non-native vertivores. Humans have been omitted from the figure, but they participate in all trophic levels that are represented. Decomposers have also been omitted

Concluding Remarks

Species are still being described from the Gulf of Guinea on a regular basis (Lima 2016), clearly showing that much taxonomic work is still needed to understand the biodiversity of these islands. In recent years, careful reviews combined with intensive island surveys and advances in molecular analyses have led to the description of several new endemic species. Terrestrial vertebrates are certainly the best-studied taxa, but since 2000 two amphibians (Uyeda et al. 2007; Bell 2016), six reptiles (Ceríaco et al. 2022a), and one mammal species (Ceríaco et al. 2015) have been newly described as endemic to the islands. Many widespread species have also been reported for the first time, including plants (Stévart et al. 2019), land snails (Holyoak et al. 2020), fishes (Costa et al. 2022), and birds (Lima and Melo 2021). A few have also regained species status (e.g., Melo et al. 2010), while many others remain undescribed, even among plants (e.g. Stévart et al. 2022), land mammals (Rainho et al. 2022), and birds (Melo et al. 2022). This incomplete knowledge is a serious handicap to develop a more in-depth understanding of the ecology of the islands.

Furthermore, ecological studies have been biased towards certain groups, such as terrestrial vertebrates, and notably birds. This bias occurs because the taxonomy of these groups is mostly resolved, both locally (Jones and Tye 2006) and globally (Billerman et al. 2020). Such studies have been particularly relevant for the recognition of the biological importance of these islands at the global scale (e.g. Le Saout et al. 2013). Conversely, very few ecological studies have been dedicated to invertebrate groups, exceptions including very recent research on land snails (Panisi et al. 2022) and mosquitoes (Reis et al. 2021). Biases persist even within taxonomic groups, since studies tend to focus on conspicuous and easily detectable species. Even among birds, the existence of the Príncipe Scops-Owl was only confirmed in 2016 (Verbelen et al. 2016), and the taxonomy of the Gulf of Guinea Storm Petrel remains uncertain (Flood et al. 2019). Although often rarer and harder to find, threatened and endemic species are targeted by more studies than expected (Lima et al. 2011), because they tend to be the focus of conservation studies (e.g., Lima et al. 2017).

There are also important spatial research biases, within and across the islands. The most evident is the scarcity of studies on Annobón, the smallest and least accessible of the main islands. Within Príncipe and São Tomé, the most remote areas have also been less surveyed. Marine species are often less known, simply because they are more challenging to study. This is especially true for those living away from the coast and at greater depths.

Finally, there are also multiple temporal biases. Certain groups tend to be studied primarily during certain seasons, as it is the case for plants (e.g., Benitez et al. 2018) and sea turtles (Ribeiro 2018; Hancock 2019), which are mostly monitored during the breeding season. Out of convenience, many other taxa tend to be studied during the dry seasons, such as birds (Lima et al. 2017), even though this is not their breeding season (Madeira 2018). These biases may ultimately constrain the broader understanding of the ecology of the islands and a conscious effort to study species throughout the year would help alleviate this bias.

Relatively few studies have addressed community ecology, focusing instead on individual species, even when multiple species are included in the same study. In some cases, this has resulted from methodological limitations to gather comparable data from multiple species simultaneously. Nevertheless, in recent years, there have been several community ecology studies, including birds (Lima 2012; Soares et al. 2020), land snails (Tavares 2020), plants (Fundação Príncipe 2019), and bird–plant interactions (Heleno et al. 2021).

To promote these islands as models for understanding ecological processes, it is necessary to overcome knowledge gaps and research biases, which generate uncertainty and limit extrapolation to broader contexts. To do so, future studies should include systematic island-wide surveys, or prioritize understudied areas, such as Annobón, less accessible areas within the islands, and marine environments. Likewise, research must focus on understudied taxonomic groups, such as invertebrates. For most of these groups many fundamental ecological aspects, such as distribution and environmental associations, remain fully unknown. Furthermore, studies at the community level and focusing on species interactions are needed to understand the functioning of ecosystems and ultimately help protect the unique biodiversity of these islands.

To ensure the future of the endemic-rich biodiversity of these islands, it is evident that protecting remaining natural ecosystems and preventing the degradation of human-modified ecosystems, such as secondary forests, are key priorities. Additionally, the over-exploitation of native species and the introduction and spread of non-native species must be curbed, and conservation strategies need to be continuously refined and implemented. These include Red Listing (IUCN 2020), species-specific action plans for threatened species (e.g., Ndang'ang'a et al. 2014a, b; Panisi et al. 2020; Fundação Príncipe 2021), the expansion of the existing network of protected areas (BirdLife International 2020), and their management plans. Long-term monitoring studies are urgently needed to assess biodiversity trends, promptly identify declines, and inform conservation actions.

Finally, it is crucial to raise public awareness about the unique biodiversity of these islands, both internationally and locally. Local biodiversity education has greatly improved in recent years (Ayres et al. 2022), but the development of local scientific expertise through outreach, capacity building, and advanced training is still lacking and should be promoted through international collaborations.

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Chapter 8
Fungi of São Tomé and Príncipe Islands: Basidiomycete Mushrooms and Allies

Dennis E. Desjardin and Brian A. Perry

Abstract Mushrooms and allies belong to the Agaricomycetes lineage of Basidiomycota. A total of 260 species, belonging in 109 genera, 51 families and 13 orders have been reported from São Tomé and Príncipe between 1851 and 2020, of which 66 were described as new species. They range in body forms from agarics and boletes to polyporoid, clavarioid, coralloid, thelephoroid, stereoid, corticioid, hydnoid, cantherelloid, gasteroid, and jelly fungi. The vast majority are saprotrophs, a small number are plant pathogens, and a rare few may be ectomycorrhizal. Sixty species, 23%, can be classified putative endemics. The current state of knowledge of the Agaricomycetes from the nation is based on fewer than ten expeditions in the past 170 years and represents only a snapshot of the actual diversity that is likely present.

Keywords Agaricomycetes · Fungal diversity · Mycota · Taxonomy

Introduction

This chapter constitutes a preliminary accounting of the mushrooms and allied taxa (Fungi, Basidiomycota) that occur in the West African island nation São Tomé and Príncipe (ST&P). Herein, we treat only organisms currently recognized as belonging to the Agaricomycetes lineage, comprising most mushroom-forming taxa. These charismatic megafungi are recognized easily in the field although understudied in tropical Africa. The names associated with each species are based historically on morphological features of their sexual reproductive structures, i.e., the mushrooms, supplemented now with molecular sequence data.

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The Agaricomycetes comprises organisms commonly called gilled fungi (agarics), boletes, polypores, club and coral fungi, thelephoroid and stereoid fungi, corticioid fungi (resupinates), tooth fungi, cantherelloid fungi, gasteroid fungi (puffballs, stinkhorns, bird's nest fungi, earthstars) and jelly fungi. They form sexual reproductive structures (basidiomes) large enough to be observed with the naked eye and broadly defined as mushrooms (= macrofungi). Their vegetative, mycelial stage serves numerous ecological roles as saprotrophs, mixotrophs, pathogens, endophytes, and mycorrhizae, and aids in soil generation, erosion control, biofiltration, nutrient retention and other important bioprocesses. Their sporulating stage, beyond functioning as the dispersal and reproductive phase, serves as a food source for myriad organisms. Many lineages produce basidiomes harvested by indigenous cultures in West Africa (e.g., chanterelles, boletes, oyster mushrooms, wood ears, etc.) and used for food, medicine, textile dyeing, a source of income and other sociological aspects (entheogens) (Osarenkhoe et al. 2014). Although the mycota of the region is diverse and abundant, only limited research has been published on the fungi of ST&P, primarily because few mycologists have visited the islands. Several expeditions in the late nineteenth century, a single excursion in the twentieth century, and several in the twenty-first century constitute the total acquisitions upon which our current knowledge of the diversity of Agaricomycetes from ST&P is based.

History of Agaricomycetes Research

The first published account of Agaricomycetes from São Tomé was a report by Elias M. Fries (1851) of six species collected by Krebs (no further collector information was provided) in a paper entitled *Novarum Symbolarum Mycologicarum Mantissa*. Four of these were described as new species, viz., *Agaricus papularis* Fr., *A. macromastes* Fr., *Panus troglodytes* Fr., and *Lentinus flaccidus* Fr., the first three of which have not been treated since, and their taxonomic placement is uncertain. This was followed by a more substantive contribution from G. Winter (1886) based on his study of specimens collected from São Tomé in 1885 by A. Moller, Inspector of the Botanical Garden of Coimbra, and Francisco A. Dias Quintas and F. Newton, Portuguese botanists. Winter's (1886) paper was an accounting of 100 species of Fungi as part of the *Flora de S. Thomé, Contribuições para o Estudo da Flora d'Africa*, compiled by J. Henriques (1886). Of these, 29 represented species of Basidiomycota; none were new species. Roumeguère (1889) examined a number of the fungal specimens collected from São Tomé by Moller, Quintas and Newton and reported four species of Basidiomycota, of which one, *Stereum amphirhytes* Sacc. & Berl. was reported as new (published again that same year by Saccardo and Berlese). The species has not been treated since. Saccardo and Berlese (1889) also studied some Moller and Newton specimens from ST&P and reported 13 species of Basidiomycota, of which six represented new species. In a paper on Fungi from Cameroon, Bresadola (1890) reported three species of *Polyporus* from São Tomé, including one new species, *P. squamulosus* Bres. The most significant early accounting of Fungi from ST&P were the papers by Bresadola and Roumeguère (1890) and Bresadola (1891), which comprised a re-examination of the material reported by Winter (1886) and inclusion of additional taxa from specimens not treated by Winter. Collectively, these two papers reported 83 species of Basidiomycota from ST&P, of which 9 were new taxa. The specimens reported from ST&P between 1886 and 1891, representing 113 species, were deposited in the Herbarium of the Botanic Garden and Botanical Museum Berlin-Dahlem (B), but unfortunately were destroyed in a fire in 1943, making taxonomic confirmation now impossible. Consequently, the taxonomic placement of the new species is uncertain, and the occurrence on ST&P of many of the other species reported, which were based primarily on European epithets, is questionable.

During the twentieth century, the only significant contribution to our knowledge of Fungi from ST&P was that of António Xavier Pereira Coutinho, Professor of Horticulture at the Instituto Superior de Agronomia, Universidade de Lisboa. Coutinho (1925) reported 74 Basidiomycota and two Ascomycota from São Tomé, based on material collected in 1920 by his son Martinho de França Pereira Coutinho, and Professor Manuel de Sousa da Câmara, Head of Section and Director, respectively, of the Laboratory of Plant Pathology at the same Institute. Eighty-two percent of the species were collected at Água-Izé. Ten of the Basidiomycota represented new species.

Contemporary treatments of Agaricomycetes from ST&P based on newly collected specimens and molecular systematic approaches did not begin until the early twenty-first century. In 2001, Dr. Robert C. Drewes, Curator of Herpetology at the California Academy of Sciences, led a multidisciplinary research expedition to ST&P, the beginning of two decades of intensive exploration of the islands to document their biodiversity (Drewes 2002). In April 2006 (2 weeks) Desjardin, and in April 2008 (3 weeks), Desjardin and Perry conducted extensive fieldwork on ST&P, documenting the diversity of macrofungi (fleshy Agaricomycetes, excluding polypores and corticioid fungi). To honor Robert Drewes, who has dedicated more than 40 years of his life to research in Africa, and who introduced us to the island nation, we described *Phallus drewesii* Desjardin & B.A. Perry (Phallaceae, Fig. 8.1–5) in our premier paper (Desjardin and Perry 2009). Subsequently, partial results of these expeditions were published in nine additional papers (Desjardin and Perry 2015a, b, 2016, 2017, 2018, 2020; Desjardin et al. 2017; Cooper et al. 2018; Grace et al. 2019), reporting 126 species of Agaricomycetes, including 36 new species. This research is ongoing—78 additional specimens, representing approx. 50 species, await publication. Several other researchers have documented macrofungi from the region over the past decade. Decock (2011) described *Truncospora oboensis* Decock (Polyporaceae, Fig. 8.1–4) and *Coltricia oboensis* Decock (2013) (Hymenochaetaceae) as new from material collected from high elevation cloud forests on São Tomé. Degreef et al. (2013) reported two rare Phallaceae, *Blumenavia angolensis* (Welw. & Curr.) Dring and *Mutinus zenkeri* (Henn.) E. Fisch., from São Tomé. Most of the species included in these contemporary publications are

Fig. 8.1 Representative Agaricomycetes from São Tomé and Príncipe: (**1**) *Marasmius laranja* (Agaricales); (**2**) *Gymnopus rodhallii* (Agaricales); (**3**) *Cyathus poeppigii* (Agaricales); (**4**) *Truncospora oboensis* (Polyporales); (**5**) *Phallus drewesii* (Phallales); (**6**) *Geastrum schweinitzii* (Geastrales); (**7**) *Scytinopogon havencampii* (Trechisporales); (**8**) *Aphelaria subglobispora* (Cantharellales). Scale bar = 10 mm. Photo credits: (**1–3**, **5**, **6**, **8**) B. Perry, (**4**) C. Decock (**7**) W. Eckerman

represented by single or very few specimens, although the specimens are deposited in herbaria and accessible for future studies.

Diversity and Endemism

Our knowledge of the diversity of fungi globally is incomplete due to their unique biology (cryptic mycelium producing often inconspicuous, short-lived sporulating structures upon which their names are based) and difficulty in identification (Willis 2018). In ST&P, documentation of the diversity of Agaricomycetes is rather depauperate as a direct result of limited fieldwork conducted there to date. Fungal species reported prior to 1925 is a reflection of the peregrinations of itinerant botanists, not the result of a concerted effort to document the fungi from the region. Their serendipitous encounters with mushrooms produced exsiccati that were often squashed between paper and blotters in plant presses and dried amongst the plant specimens that were the focus of early expeditions. Subsequent research in the twentieth century (Coutinho 1925) produced better quality specimens, but as with earlier expeditions, focused primarily on easily collected and preserved polypores and allies. It was not until the twenty-first century that a concerted effort was made to document the Agaricomycetes from the nation, supported by well documented fungarium specimens and molecular data (research of Desjardin, Perry and colleagues). Combining the unsubstantiated early reports with new vouchered reports, we account for 260 species of Agaricomycetes from ST&P, representing 109 genera, 51 families and 13 orders (Appendix).

It is difficult to compare these numbers with those of Agaricomycetes recorded from neighboring countries of West Africa (Piepenbring et al. 2020). We recognize that what we are presenting herein is only a snapshot of the actual mushroom diversity from the islands. More effort needs to be focused on documenting the polypores and similar taxa with persistent basidiomes whose early reports are not vouchered, and continued work on taxa with fleshy, putrescent basidiomes in understudied lineages.

Determining the distribution status of fungi is fraught with difficulties. Many areas of the world have not been explored for fungi, and documentation from tropical Africa is especially limited. It is premature to state unequivocally that any species is "endemic" until we have more data on the diversity of fungi from understudied areas. For this treatise, if a species was described as new from São Tomé or Príncipe and it has not yet been reported from elsewhere, we recognize the taxon as a putative endemic and annotate as such in the Appendix. Under this scenario, 66 new species have been described from material collected on ST&P, of which six species have been reported as occurring elsewhere. Hence, 60 species can be considered as putative endemics, or a 23% level of endemism in the Agaricomycetes from ST&P.

Species reports, where identification was based on molecular phylogenetic data, indicate that ST&P mushrooms or their closest relatives occur in neighboring West and Central African countries (Cameroon, Sierra Leone, DR Congo), other parts of continental Africa and Madagascar, South East and South-Central Asia, and tropical America (pers. obs.). No attempt was made to rate species as resident, migrant, vagrant or introduced as such categorizations would be only speculative. We recognize that the mushrooms commonly collected in habitats dominated by introduced plants, such as coastal cacao-banana groves, coffee plantations and other agricultural sites, most likely represent introduced species, however, we have not annotated them as such. Interestingly, a number of the species that we encountered in human-altered lowland habitats, either also occur in or have their closest known relatives in the Caribbean region. This could indicate unidirectional or bidirectional introduction of fungal species associated with aspects of the slave or agricultural trade.

Ecology and Conservation

The macrofungi of ST&P are primarily saprotrophic, decomposing leaf litter and woody substrates. A number of species may be pathogens, associated with root or heart rot of woody plants (e.g., *Bjerkandera*, *Fomes*), while a rare few are biotroph associates of mosses (*Cotylidia*). The ectomycorrhizal status of ST&P fungi is unknown, but we suspect that there are very few because of the paucity of ectotrophic host plant genera. A cross-reference of the annotated list of Angiosperms for ST&P (Figueiredo et al. 2011) with a list of global ectotrophic host plant genera (Brundrett 2009), yielded only six potential ectotrophic host plant genera in ST&P, viz., *Casuarina* (Casuarinaceae), *Lonchocarpus* and *Acacia* (Fabaceae), *Eucalyptus* and *Melaleuca* (Myrtaceae), and *Manilkara* (Sapotaceae), which include only ten local species. Of these ten, six are introduced species, and only four may represent native species, viz., *Lonchocarpus sericeus* (Poir.) Kunth, *Acacia kamerunensis* Gand., *Acacia pentagona* (Schumach.) Hook. and *Manilkara obovata* (Sabine & G. Don) J.H. Hemsl. Whether these potential plant host species are ectotrophic has not been determined.

Mushrooms and allies require adequate moisture and appropriate nutritional substrates for survival. Many species, whether saprotrophic, pathogenic, or mycorrhizal, are host specific (at various levels of specificity). When their habitats change due to changes in water availability (rain, humidity), anthropogenic disturbance, or an alteration in plant community structure, the abundance and diversity of fungi changes as well. Conservation efforts focused on fungi are in their infancy globally. Of the 135,000 species of fungi described to date (Kirk 2019), as noted by Piepenbring et al. (2020), only 91 have been evaluated for the global Red List established by the International Union for Conservation of Nature (IUCN). None of the species reported from ST&P are included in the list.

Agaricomycetes of São Tomé and Príncipe

An accounting of the history and diversity of ST&P mushrooms in each order is presented below, organized in accordance with the phylogenetic tree of Agaricomycetes adapted from Varga et al. (2019) (Fig. 8.2).

Order Agaricales

Approximately half of the known Agaricomycetes from ST&P belong to the Agaricales, this accounting primarily the result of recent research published by Desjardin and Perry. To date, 133 species of Agaricales have been reported from ST&P, belonging to 46 genera in 24 families. This order is comprised mainly of

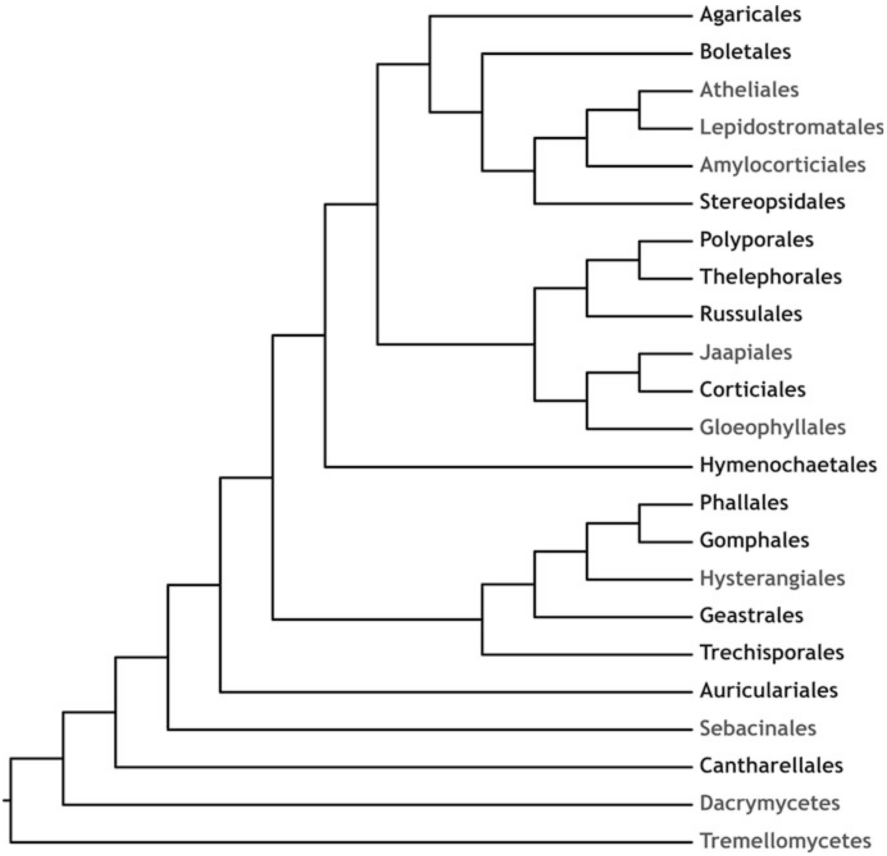

Fig. 8.2 Phylogenetic tree of Agaricomycetes adapted from Varga et al. (2019). Orders containing taxa reported from São Tomé and Príncipe are in bold

gilled mushrooms, i.e., basidiomes with the hymenium (spore-producing tissue) located on radiating plate-like structures (gills = lamellae) suspended under a cap (pileus), and together typically elevated by a stem (stipe). A few families in the order contain species with clavarioid (club-shaped), coralloid (branched, coral-shaped), gasteroid (enclosed, puffball-like) or corticioid (crust-like, with smooth, resupinate hymenophores) basidiomes. These mushrooms are typically putrescent, lasting from only a few hours to a few days, then wither and disappear. They form only after abundant moisture is available, usually during the wet season, and encountering them is often serendipitous. To obtain quality specimens for study and determination, basidiomes must be collected fresh, their taxonomically important features documented, and then dried immediately for long-term preservation. This procedure presents many difficulties in understudied tropical habitats and most likely accounts for the limited number of early reports. Between 1851 and 1891, only 19 species of Agaricales were reported from ST&P, four of which were new species, and two of the latter remain *incertae sedis* (Fries 1851; Winter 1886; Roumeguère 1889; Saccardo and Berlese 1889; Bresadola and Roumeguère 1890; Bresadola 1891). Coutinho (1925) reported 17 gilled mushroom species from São Tomé, of which six were new species and two of these are currently of unknown taxonomic placement. Most of the known Agaricales from ST&P were reported by Desjardin, Perry and colleagues, viz., 101 species of which 32 were new to science. They provided comprehensive coverage of clavarioid and gasteroid species in the Clavariaceae, Lycoperdaceae and Nidulariaceae (Desjardin and Perry 2015b), dark-spored species in the Bolbitiaceae, Crepidotaceae, Hymenogastraceae, Psathyrellaceae and Strophariaceae (Desjardin and Perry 2016), gymnopoid species in the Agaricaceae, Catathelasmataceae, Hydropoid clade, Hygrophoraceae, Marasmiaceae, Mycenaceae, Omphalotaceae, Physalacriaceae and Tricholomataceae (Desjardin and Perry 2017, Desjardin et al. 2017), species of *Pluteus* of Pluteaceae (Desjardin and Perry 2018), mycenoid species in the Hydropoid clade and Mycenaceae (Cooper et al. 2018), marasmioid species in the Marasmiaceae (Grace et al. 2019), and hygrophoroid species in the Hygrophoraceae (Desjardin and Perry 2020). Additional specimens collected during the 2008 expedition await diagnosis.

Order Boletales

Most members of order Boletales are ectomycorrhizal and require specific plant hosts to support their mutualistic symbiosis. As noted in the section on ecology, few ectotrophic plant species occur on ST&P, and accordingly, ectomycorrhizal Agaricomycetes are rare. Most Boletales form putrescent basidiomes with a thick fleshy cap supporting a tubular hymenophore with the hymenium lining the inside of the vertically oriented tubes, and all elevated on a stipe—a body form known as a bolete. A few lineages form gasteroid basidiomes, while others form corticioid (crust-like, resupinate with smooth or wrinkled hymenophore) basidiomes. Only a single species of Boletales has been reported from Príncipe, the gasteroid

Scleroderma dictyosporum Pat. (Sclerodermataceae) (Desjardin and Perry 2015b). We are aware of several boletes that occur on São Tomé, although official reports have not yet been published. Desjardin and Perry (unpubl.) have collected a single specimen of a *Tylopilus* sp. (deposited in SFSU) and have seen photographs of a probable *Phlebopus* sp. (no specimens retained). Whether these taxa are ectomycorrhizal or saprotrophic is currently unknown.

Order Stereopsidales

Members of order Stereopsidales form corticioid or thelephoroid (tough, with a smooth or wrinkled hymenophore) basidiomes. Only a single species from the order, the thelephoroid *Stereopsis radicans* (Berk.) D.A. Reid (Stereopsidaceae) has been reported, apparently collected twice on São Tomé, once on wood by F. Quintas in 1885 (Bresadola and Roumeguère 1890), and once on soil in 1920 (Coutinho 1925).

Order Polyporales

The first fungi collected and repeatedly reported from West African countries were mostly polypores, belonging mainly to the Polyporales and Hymenochaetales (Piepenbring et al. 2020). This is because of their persistent basidiomes, which may be encountered throughout the year when fleshy species are not apparent, and due to the ease of collecting, drying and transporting specimens. Basidiomes are typically tough and woody, with a tubular hymenophore, lack a stem, and grow on woody substrates as saprotrophs or pathogens. Seventy-one species of order Polyporales have been documented from ST&P; 55 of these were reported prior to 1925, of which six represented new species, viz., *Daedalea newtonii* Bres. & Roum. (Fomitopsidaceae), *Tyromyces squamulosus* (Bres.) Ryvarden (Incrustoporiaceae), and *Favolus jacobeus* Sacc. & Berl., *Polyporus torquescens* Sacc. & Berl. and *Trametes discolor* Sacc. & Berl. (Polyporaceae) (Saccardo and Berlese 1889; Bresadola 1890; Bresadola and Roumeguère 1890). *Stereum pulchellum* Sacc. & Berl. was described as new from Príncipe, but is currently accepted as a synonym of *Podoscypha involuta* (Klotsch ex Fr.) Imazeki (Podoscyphaceae). Apparently, the specimen vouchers of these 55 species were destroyed in the 1943 fire at the Berlin Herbarium. Coutinho (1925) added another 16 species to the list, including two new species, *Fomes ferrugineobrunneus* Cout. and *Lentinus thomensis* Cout. (Polyporaceae). Since then, only a single species of Polyporales has been reported from São Tomé, the new species *Truncospora oboensis* Decock (Polyporaceae, Fig. 8.1–4) (Decock 2011). Although many species of polypores were observed on ST&P during the expeditions by Desjardin and Perry (in 2006 and 2008), this fungal group was not the focus of their research and no specimens were collected. Future research should focus on documenting order Polyporales from ST&P, to verify early reports with vouchered material and to clarify polypore diversity for the region.

Order Thelephorales

Members of this order form tough, stipitate basidiomes with a smooth hymenophore (thelephoroid) and stipitate or sessile basidiomes with a toothed hymenophore (hydnoid). Only a single species has been reported from São Tomé, the new sessile hydnoid taxon *Phaeodon thomensis* Cout. (Bankeraceae) (Coutinho 1925). The species is known from a single collection made in 1920 and has not been reported since from West Africa.

Order Russulales

Species of order Russulales are quite common and abundant in Africa. They develop basidiomes with a great variety of body forms, from gilled and poroid to hydnoid, corticioid, clavarioid and coralloid. Many are ectomycorrhizal, while others are saprotrophs or plant pathogens. Unfortunately, the speciose ectomycorrhizal genera *Russula* and *Lactarius*, so common in the miombo woodlands of Western Africa, are lacking in ST&P because of the near absence of ectotrophic host plants. Only 14 species of Russulales have been documented from ST&P, all but one species reported before 1925 (Winter 1886; Saccardo and Berlese 1889; Bresadola and Roumeguère 1890). Most of these represent saprotrophic or pathogenic taxa with corticioid or stereoid (sessile, with a cap and smooth hymenophore) basidiomes in the Hericiaceae, Peniophoraceae and Stereaceae, although two *Lentinellus* species are gilled fungi in Auriscalpiaceae. Only two species were described as new from São Tomé, the corticioid *Scytinostroma quintasianum* (Bres. & Roum.) Nakasone (Peniophoraceae), named after the early Portuguese collector F. Quintas (Bresadola and Roumeguère 1890), and the stereoid *Stereum amphirhytes* Sacc. & Berl. (Stereaceae) (Saccardo and Berlese 1889).

Order Hymenochaetales

Similar to the Polyporales, the ST&P representatives of order Hymenochaetales form primarily persistent basidiomes with tubular hymenophore and saprotrophic or pathogenic ecology (Hymenochataceae), but the order also contains an unusual lineage with small, fleshy basidiomes with gilled or smooth hymenophore (Rickenellaceae) that are associated with mosses. Twelve species have been documented from São Tomé, ten of which were reported prior to 1925 (Winter

1886; Roumeguère 1889; Bresadola and Roumeguère 1890), whose material has been lost, although four of these species were recollected and reported again by Coutinho (1925). Two lignicolous species were described as new, *Polystictus albocinereus* Cout. (Coutinho 1925) and *Coltricia oboensis* Decock (Hymenochaetaceae) (Decock 2013). This is another group that needs attention from contemporary researchers.

Order Phallales

The Phallales constitute the "stinkhorns," a lineage of bizarrely-shaped mushrooms with a dispersal strategy symbiotic with insects. All basidiomes are initially globose or egg-shaped with the hymenophore enclosed (gasteroid), and as they mature, the outer peridium layer ruptures, and the inner sporulating structure erupts into a plethora of shapes, allowing for common names like octopus stinkhorn, basket stinkhorn, Devil's horn, etc. The spores are produced in a gelatinous, putrid-scented mass on the elevated structure. The often carrion-like odor attracts insects, primarily flies, who lay their eggs in the stinkhorn to provide a food source for their larvae, and the adults also consume the spores which pass through their digestive system and when defecated, aid in stinkhorn dispersal. Six species belonging to the Phallaceae have been documented from ST&P. The first reported was a new species, *Clathrus parvulus* Bres. & Roum., a very small (<20 mm diam), reddish basket stinkhorn that has not been reported since first discovery (Bresadola and Roumeguère 1890). The remaining five species are recent reports (Degreef et al. 2013; Desjardin and Perry 2015b), including a new species, *Phallus drewesii* (Fig. 8.1–5).

Order Gomphales

Three families comprise the order Gomphales, but only members of the Gomphaceae have been reported from ST&P. The family contains species with funnel-shaped basidiomes with wrinkled to venous or gilled hymenophore (cantharelloid) and coralloid basidiomes. Only a single genus of coralloid species has been reported from São Tomé, representing three species of *Ramaria*. Two represent new species described in 1890 that have not been recollected, viz., *Ramaria henriquesii* (Bres. & Roum.) Corner (*ut Clavaria*), and *Ramaria mollerianum* (Bres. & Roum.) Corner (*ut Lachnocladium*) (Bresadola and Roumeguère 1890), both named after the early Portuguese botanists who conducted fieldwork on São Tomé. The genus *Ramaria* is ectomycorrhizal in other parts of the world, but the nutritional status of the São Tomé species is unknown.

Order Geastrales

The order Geastrales, with the single family Geastraceae, are commonly known as the “Earthstars.” The basidiomes, initially fully enclosed (gasteroid), rupture, and the outer layers split and fold back into ray-shaped arms (star-like), exposing the interior puffball, which opens by a central apical pore to passively release the internal spores. Three species of *Geastrum* were recently reported from ST&P (Desjardin and Perry 2015b), the most unusual being *Geastrum schweinitzii* (Berk. & M.A. Curtis) Zeller (Fig. 8.1–6), which forms very small earthstar basidiomes that arise from a thick membranous sheet of mycelium (subiculum) that covers the substrate.

Order Trechisporales

Members of this order form corticioid basidiomes (type genus *Trechispora*) or coralloid basidiomes (*Scytinopogon*). Only a single species from the group has been recently reported, the new species *Scytinopogon havencampii* Desjardin & B.A. Perry (Fig. 8.1–7), described from material collected on Príncipe (Desjardin and Perry 2015a). Although it grows from the soil, we suspect that it is a saprotroph. The genus *Scytinopogon* with coralloid basidiomes was recently accepted as a synonym of *Trechispora*, a genus composed primarily of corticioid species, based on multi-gene analyses (Meiras-Ottoni et al. 2021).

Order Auriculariales

The “jelly fungi” is a heterogeneous assemblage of fungi representing numerous lineages, wherein the basidiomes are rubbery-gelatinous and hydrophilic/hygroscopic. Order Auriculariales comprises a number of families, several of which contain species that form such basidiomes. Members of the Auriculariaceae often form lignicolous, ear-shaped basidiomes that are commonly known as “wood ear” mushrooms, which are edible and both wild-harvested and artificially cultivated. Three species of *Auricularia* were documented early from São Tomé (Winter 1886; Bresadola and Roumeguère 1890; Bresadola 1891) and reported again by Coutinho (1925) from additional specimens. We have no information on whether local cultures consume these commonly encountered mushrooms.

Order Cantharellales

Basidiome morphology is quite variable in order Cantharellales, and includes clavarioid, coralloid, cantharelloid (funnel-shaped with decurrent gills or veins), and hydnoid body forms. Three species, one from each of three families (Aphelariaceae, Cantharellaceae, Hydnaceae), have been reported from ST&P. The earliest report was for *Craterellus crispus* (Bull.) Berk. (Bresadola 1891), accepted now as a synonym of *Pseudocraterellus undulatus* (Pers.) Rauschert. This species is considered ectomycorrhizal, and given the paucity of ectotrophic plant species on São Tomé, we question the original identification by Bresadola (1891). The two additional reports of Cantharellales are from recently collected specimens, viz., *Aphelaria subglobispora* P. Roberts (Fig. 8.1–8) and *Clavulina vanderystii* (Bres.) Corner (Desjardin and Perry 2015b).

Summary and Future Research

Although the Gulf of Guinea oceanic islands of São Tomé (13+ my) and Príncipe (31+ my) are volcanic in origin and have never been part of or connected by a land bridge to continental Africa (Lee et al. 1994), they are rich in Agaricomycetes diversity. The fungal species or their ancestors reached the islands by wind, avian or human-mediated dispersal, or on flotsam. Only a handful of expeditions have been conducted since 1851, which produced specimens of Agaricomycetes that allowed documentation of mushroom diversity from the islands. To date, 260 species, belonging in 109 genera, 51 families and 13 orders have been reported from ST&P, providing only a snapshot of the estimated actual diversity of this important fungal group. Twenty-three percent of these may represent endemic species. Reported taxa represent myriad body forms, from agarics and boletes, to polypores, club and coral fungi, thelephoroid, stereoid, corticioid, hydnoid and cantherelloid fungi, puffballs, stinkhorns, bird's nest fungi, earthstars, and jelly fungi. Nearly half (113 spp.) of the recorded 260 species are known only from published reports, as their vouchered specimens were destroyed during World War II, and hence the accuracy of their determinations is questionable. The majority of reported species are saprotrophic, functioning as important litter and wood decomposers, while a number are plant pathogens and a rare few are putatively ectotrophic. The islands provide a wide variety of native and human-disturbed habitats that undoubtedly house hidden Agaricomycetes diversity. Future research should focus on recollecting the lineages containing unvouchered species reports (polypores, thelephoroid, stereoid, corticioid fungi), on identifying available specimens belonging to difficult taxonomic groups (e.g., lepiotoid, entolomatoid, hemimycenoid taxa), and on further intensive fieldwork conducted monthly in undisturbed native forests. Our knowledge of the mushrooms and allies from ST&P is in its infancy, and additional field and lab work will surely yield surprises, new distribution records and new taxa.

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Appendix

List of Agaricomycetes reported from Príncipe (P) and São Tomé (ST). Author abbreviations and nomenclature are according to Index Fungorum (www.indexfungorum.org). Phylogenetic placement and synonymy are based on current literature, or as reported in Species Fungorum (www.speciesfungorum.org) and Mycobank (www.mycobank.org). E—putative endemic

Currently accepted name	Name reported in literature	Citation	P	ST
ORDER AGARICALES				
Agaricaceae				
Agaricus subflabellatus Cout.	*Agaricus subflabellatus* Cout.	Coutinho (1925)		E
Agaricus sylvaticus Schaeff.	*Psalliota sylvatica* (Schaeff.) P. Kumm.	Coutinho (1925)		X
Phellorinia herculeana (Pers.) Kreisel	*Phellorinia delestrei* (Durieu & Mont.) E. Fisch.	Coutinho (1925)		X
Ripartitella brasiliensis (Speg.) Singer	*Ripartitella brasiliensis* (Speg.) Singer	Desjardin and Perry (2017)		X
Tulostoma mollerianum Bres. & Roum.	*Tylostoma mollerianum* Bres. & Roum.	Bresadola and Roumeguère (1890)		E
Bolbitiaceae				
Conocybe zeylanica (Petch) Boedijn	*Conocybe zeylanica* (Petch) Boedijn	Desjardin and Perry (2016)		X
Catathelasmataceae				
Callistosporium cystidiatum (T.J. Baroni, Lodge & D.L. Lindner) Vizzini, Consiglio & M. Marchetti	*Pleurocollybia cystidiata* T.J. Baroni, Lodge & D.L. Lindner	Desjardin and Perry (2017)		X
Callistosporium elegans Desjardin & B.A. Perry	*Callistosporium elegans* Desjardin & B.A. Perry	Desjardin and Perry (2017)		E
Callistosporium praemultifolium (Murrill) Vizzini, Consiglio & M. Marchetti	*Pleurocollybia praemultifolia* (Murrill) Singer	Desjardin and Perry (2017)	X	

(continued)

Currently accepted name	Name reported in literature	Citation	P	ST
Clavariaceae				
Clavaria phoenicea Zoll. & Moritzi	*Clavaria phoenicea* Zoll. & Moritzi	Desjardin and Perry (2015b)	X	
Clavulinopsis amoena (Zoll. & Moritzi) Corner	*Clavulinopsis amoena* (Zoll. & Moritzi) Corner	Desjardin and Perry (2015b)	X	
Crepidotaceae				
Crepidotus hemiphlebius (Berk. & M.A. Curtis) Murrill	*Agaricus hemiphlebius* Berk. & M.A. Curtis	Coutinho (1925)		X
Crepidotus kangoliformis Desjardin & B.A. Perry	*Crepidotus kangoliformis* Desjardin & B.A. Perry	Desjardin and Perry (2016)		E
Crepidotus nephrodes (Berk. & M.A. Curtis) Sacc.	*Crepidotus nephrodes* (Berk. & M.A. Curtis) Sacc.	Desjardin and Perry (2016)	X	
Simocybe centunculus (Fr.) P. Karst.	*Simocybe centunculus* (Fr.) P. Karst.	Desjardin and Perry (2016)		X
Cyphellaceae				
Chondrostereum purpureum (Pers.) Pouzar	*Stereum purpureum* Pers.	Bresadola and Roumeguère (1890)		X
Entolomataceae				
Entoloma mammosum (L.) Hesler	*Hyporrhodius mammosus* (L.) J. Schröt.	Coutinho (1925)		X
Entoloma papillatum (Bres.) Dennis	*Nolanea papillata* Bres.	Bresadola (1891)		X
Hydropoid Clade				
Clitocybula intervenosa A.C. Cooper, Desjardin & B.A. Perry	*Clitocybula intervenosa* A.C. Cooper, Desjardin & B.A. Perry	Cooper et al. (2018)		E
Hydropus globosporus A.C. Cooper, Desjardin & B.A. Perry	*Hydropus globosporus* A.C. Cooper, Desjardin & B.A. Perry	Cooper et al. (2018)		E
Hydropus murinus A.C. Cooper, Desjardin & B.A. Perry	*Hydropus murinus* A.C. Cooper, Desjardin & B.A. Perry	Cooper et al. (2018)		E
Trogia anthidepas (Berk. & Broome) Corner	*Trogia anthidepas* (Berk. & Broome) Corner	Desjardin and Perry (2017)	X	
Trogia aff. *brevipes* Corner	*Trogia* aff. *brevipes* Corner	Desjardin and Perry (2017)		X
Trogia buccinalis (Mont.) Pat.	*Cantharellus buccinalis* Mont.	Bresadola and Roumeguère (1890)		X
Trogia delicata Corner	*Trogia delicata* Corner	Cooper et al. (2018)		X
Trogia aff. furcata Corner	*Trogia* aff. *furcata* Corner	Desjardin and Perry (2017)		X
Trogia infundibuliformis Berk. & Broome	*Trogia infundibuliformis* Berk. & Broome	Desjardin and Perry (2017)	X	
Hygrophoraceae				
Arrhenia cystidiata Desjardin & B.A. Perry	*Arrhenia cystidiata* Desjardin & B.A. Perry	Desjardin and Perry (2017)		E
Cuphophyllus laranja Desjardin & B.A. Perry	*Cuphophyllus laranja* Desjardin & B.A. Perry	Desjardin and Perry (2020)		E
Cuphophyllus pratensis (Fr.) Bon	*Cuphophyllus pratensis* (Fr.) Bon	Desjardin and Perry (2020)	X	
Hygrocybe macambrarensis Desjardin & B.A. Perry	*Hygrocybe macambrarensis* Desjardin & B.A. Perry	Desjardin and Perry (2020)		E
Hygrocybe aff. *miniata* (Fr.) P. Kumm.	*Hygrocybe* aff. *miniata* (Fr.) P. Kumm.	Desjardin and Perry (2020)	X	
Hygrocybe sp.	*Hygrocybe* sp.	Desjardin and Perry (2020)	X	
Hymenogastraceae				
Galerina makereriensis Pegler	*Galerina makereriensis* Pegler	Desjardin and Perry (2016)		X

(continued)

Currently accepted name	Name reported in literature	Citation	P	ST
Galerina physospora Singer	*Galerina physospora* Singer	Desjardin and Perry (2016)		X
Gymnopilus aculeatus (Bres. & Roum.) Singer	*Pholiota aculeata* Bres. & Roum.	Bresadola and Roumeguère (1890), Coutinho (1925)		E
Gymnopilus aureobrunneus (Berk. & M.A. Curtis) Murrill	*Naucoria aureobrunnea* (Berk. & M.A. Curtis) Cout.	Coutinho (1925)		X
	Gymnopilus aureobrunneus (Berk. & M.A. Curtis) Murrill	Desjardin and Perry (2016)		X
Gymnopilus delipis (Berk. & Broome) Singer	*Naucoria delipis* (Berk. & Broome) Cout.	Coutinho (1925)		X
Gymnopilus purpureosquamulosus Høiland	*Gymnopilus purpureosquamulosus* Høiland	Desjardin and Perry (2016)	X	X
Naucoria brevipes Cout.	*Naucoria brevipes* Cout.	Coutinho (1925)		E
Naucoria chrysotricha (Berk. & M.A. Curtis) Cout.	*Naucoria chrysotricha* (Berk. & M.A. Curtis) Cout.	Coutinho (1925)		X
Naucoria fusco-olivacea Bres. & Roum.	*Naucoria fusco-olivacea* Bres. & Roum.	Bresadola and Roumeguère (1890)		E
Naucoria papularis (Fr.) Sacc.	*Naucoria papularis* (Fr.) Sacc.	Coutinho (1925)		X
Inocybaceae				
Inocybe hystrix (Fr.) P. Karst.	*Inocybe hystrix* (Fr.) P. Karst.	Coutinho (1925)–doubtful (see Desjardin and Perry (2016))		E
Inocybe reticulata Cout.	*Inocybe reticulata* Cout.	Coutinho (1925)–doubtful (see Desjardin and Perry (2016))		E
Lycoperdaceae				
Lycoperdon molle Pers.	*Lycoperdon molle* Pers.	Desjardin and Perry (2015b)	X	
Marasmiaceae				
Campanella buettneri Henn.	*Campanella buettneri Henn.*	Desjardin et al. (2017)	X	
Campanella burkei Desjardin & B.A. Perry	*Campanella burkei* Desjardin & B.A. Perry	Desjardin and Perry (2017)	E	
Lactocollybia variicystis D.A. Reid & Eicker	*Lactocollybia variicystis* D.A. Reid & Eicker	Desjardin and Perry (2017)		X
Marasmius albisubiculosus C.L. Grace, Desjardin & B.A. Perry	*Marasmius albisubiculosus* C.L. Grace, Desjardin & B.A. Perry	Grace et al. (2019)	E	
Marasmius aff. *apatelius* Singer	*Marasmius* aff. *apatelius* Singer	Grace et al. (2019)	X	
Marasmius collinus (Scop.) P. Kumm.	*Collybia collina* (Scop.) P. Kumm.	Bresadola and Roumeguère (1890)		X
Marasmius colorimarginatus Antonín	*Marasmius colorimarginatus* Antonín	Grace et al. (2019)	X	
Marasmius corrugatiformis Singer	*Marasmius corrugatiformis* Singer	Grace et al. (2019)		X
Marasmius diversus C.L. Grace, Desjardin & B.A. Perry	*Marasmius diversus* C.L. Grace, Desjardin & B.A. Perry	Grace et al. (2019)		E
Marasmius elaeocephaliformis C.L. Grace, Desjardin & B.A. Perry	*Marasmius elaeocephaliformis* C.L. Grace, Desjardin & B.A. Perry	Grace et al. (2019)		E
Marasmius elaeocephalus Singer	*Marasmius elaeocephalus* Singer	Grace et al. (2019)		X

(continued)

Currently accepted name	Name reported in literature	Citation	P	ST
Marasmius grandisetulosus Singer	*Marasmius grandisetulosus* Singer	Grace et al. (2019)		X
Marasmius aff. *guyanensis* Mont.	*Marasmius* aff. *guyanensis* Mont.	Grace et al. (2019)	X	
Marasmius haediniformis Singer	*Marasmius haediniformis* Singer	Grace et al. (2019)		X
Marasmius laranja C.L. Grace, Desjardin & B.A. Perry	*Marasmius laranja* C.L. Grace, Desjardin & B.A. Perry	Grace et al. (2019)		E
Marasmius leptocephalus C.L. Grace, Desjardin & B.A. Perry	*Marasmius leptocephalus* C.L. Grace, Desjardin & B.A. Perry	Grace et al. (2019)		E
Marasmius aff. *megistus* Singer	*Marasmius* aff. *megistus* Singer	Grace et al. (2019)		X
Marasmius nodulocystis Pegler	*Marasmius nodulocystis* Pegler	Grace et al. (2019)	X	X
Marasmius palmivorus Sharples	*Marasmius palmivorus* Sharples	Desjardin and Perry (2017)		X
Marasmius paratrichotus C.L. Grace, Desjardin & B.A. Perry	*Marasmius paratrichotus* C.L. Grace, Desjardin & B.A. Perry	Grace et al. (2019)		X
Marasmius rotalis Berk. & Broome	*Marasmius rotalis* Berk. & Broome	Grace et al. (2019)		X
Marasmius segregatus C.L. Grace, Desjardin & B.A. Perry	*Marasmius segregatus* C.L. Grace, Desjardin & B.A. Perry	Grace et al. (2019)		E
Marasmius subarborescens Singer	*Marasmius subarborescens* Singer	Grace et al. (2019)		X
Marasmius subruforotula Singer	*Marasmius subruforotula* Singer	Grace et al. (2019)	X	
Marasmius suthepensis Wannathes, Desjardin & Lumyong	*Marasmius suthepensis* Wannathes, Desjardin & Lumyong	Grace et al. (2019)	X	
Marasmius tenuisetulosus (Singer) Singer	*Marasmius tenuisetulosus* (Singer) Singer	Grace et al. (2019)		X
Mycenaceae				
Favolaschia auriscalpium (Mont.) Henn.	*Laschia auriscalpium* Mont.	Winter (1886), Bresadola and Roumeguère (1890)		X
Filoboletus pallescens (Boedijn) Maas Geest.	*Filoboletus pallescens* (Boedijn) Maas Geest.	Cooper et al. (2018)	X	
Heimiomyces tenuipes (Schwein.) Singer	*Heimiomyces tenuipes* (Schwein.) Singer	Desjardin and Perry (2017)	X	
Mycena alphitophora (Berk.) Sacc.	*Mycena alphitophora* (Berk.) Sacc.	Cooper et al. (2018)		X
Mycena antennae A.C. Cooper, Desjardin & B.A. Perry	*Mycena antennae* A.C. Cooper, Desjardin & B.A. Perry	Cooper et al. (2018)		E
Mycena breviseta Höhnel	*Mycena breviseta* Höhnel	Cooper et al. (2018)	X	
Mycena brunneoviolacea A.C. Cooper, Desjardin & B.A. Perry	*Mycena brunneoviolacea* A.C. Cooper, Desjardin & B.A. Perry	Cooper et al. (2018)		E
Mycena aff. *discobasis* Métrod	*Mycena* aff. *discobasis* Métrod	Cooper et al. (2018)		X
Mycena discogena Singer	*Mycena discogena* Singer	Cooper et al. (2018)	X	
Mycena galopus (Pers.) P. Kumm.	*Mycena galopus* (Pers.) P. Kumm.	Cooper et al. (2018)		X

(continued)

Currently accepted name	Name reported in literature	Citation	P	ST
Mycena aff. *holoporphyra* (Berk. & M.A. Curtis) Singer	*Mycena* aff. *holoporphyra* (Berk. & M.A. Curtis) Singer	Cooper et al. (2018)		X
Mycena lamprospora (Corner) E. Horak	*Mycena lamprospora* (Corner) E. Horak	Cooper et al. (2018)	X	
Mycena lasiopus Maas Geest. & de Meijer	*Mycena lasiopus* Maas Geest. & de Meijer	Cooper et al. (2018)	X	X
Mycena longinqua A.C. Cooper, Desjardin & B.A. Perry	*Mycena longinqua* A.C. Cooper, Desjardin & B.A. Perry	Cooper et al. (2018)	E	
Mycena oboensis A.C. Cooper, Desjardin & B.A. Perry	*Mycena oboensis* A.C. Cooper, Desjardin & B.A. Perry	Cooper et al. (2018)		E
Mycena phaeonox A.C. Cooper, Desjardin & B.A. Perry	*Mycena phaeonox* A.C. Cooper, Desjardin & B.A. Perry	Cooper et al. (2018)		E
Mycena rosea Gramberg	*Agaricus roseus* Schaeff.	Coutinho (1925)		X
Mycena solis A.C. Cooper, Desjardin & B.A. Perry	*Mycena solis* A.C. Cooper, Desjardin & B.A. Perry	Cooper et al. (2018)		E
Mycena tintinnabulum (Paulet) Quél.	*Mycena tintinnabulum* (Paulet) Quél.	Bresadola and Roumeguère (1890)		X
Nidulariaceae				
Cyathus limbatus Tul. & C. Tul.	*Cyathus limbatus* Tul. & C. Tul.	Desjardin and Perry (2015b)		X
Cyathus poeppigii Tul. & C. Tul.	*Cyathus poeppigii* Tul. & C. Tul.	Desjardin and Perry (2015b)	X	
Omphalotaceae				
Gymnopus billbowesii Desjardin & B.A. Perry	*Gymnopus billbowesii* Desjardin & B.A. Perry	Desjardin and Perry (2017)		X
Gymnopus aff. *brunneigracilis* (Corner) A.W. Wilson & Desjardin	*Gymnopus* aff. *brunneigracilis* (Corner) A.W. Wilson & Desjardin	Desjardin and Perry (2017)		X
Gymnopus cervinus (Henn.) Desjardin & B.A. Perry	*Gymnopus cervinus* (Henn.) Desjardin & B.A. Perry	Desjardin and Perry (2017)	X	X
Gymnopus gibbosus (Corner) A.W. Wilson, Desjardin & E. Horak	*Gymnopus gibbosus* (Corner) A.W. Wilson, Desjardin & E. Horak	Desjardin and Perry (2017)		X
Gymnopus hirtelloides Desjardin & B.A. Perry	*Gymnopus hirtelloides* Desjardin & B.A. Perry	Desjardin and Perry (2017)	E	
Gymnopus hirtellus (Berk. & Broome) Desjardin & B.A. Perry	*Gymnopus hirtellus* (Berk. & Broome) Desjardin & B.A. Perry	Desjardin and Perry (2017)	X	
Gymnopus irresolutus Desjardin & B.A. Perry	*Gymnopus irresolutus* Desjardin & B.A. Perry	Desjardin and Perry (2017)		E
Gymnopus melanopus A.W. Wilson, Desjardin & E. Horak	*Gymnopus melanopus* A.W. Wilson, Desjardin & E. Horak	Desjardin and Perry (2017)		X
Gymnopus mustachius Desjardin & B.A. Perry	*Gymnopus mustachius* Desjardin & B.A. Perry	Desjardin and Perry (2017)		E
Gymnopus ocellus Desjardin & B.A. Perry	*Gymnopus ocellus* Desjardin & B.A. Perry	Desjardin and Perry (2017)	E	
Gymnopus ocior (Pers.) Antonín & Noordel.	*Agaricus xanthopus* Fr.	Coutinho (1925)		X
Gymnopus pleurocystidiatus Desjardin & B.A. Perry	*Gymnopus pleurocystidiatus* Desjardin & B.A. Perry	Desjardin and Perry (2017)	E	

(continued)

Currently accepted name	Name reported in literature	Citation	P	ST
Gymnopus aff. *polygrammus* (Mont.) J.L. Mata	*Gymnopus* aff. *polygrammus* (Mont.) J.L. Mata	Desjardin and Perry (2017)		X
Gymnopus quercophilus (Pouzar) Antonín & Noordel.	*Marasmius splachnoides* (Hornem.) Fr.	Bresadola and Roumeguère (1890)		X
Gymnopus rodhallii Desjardin & B.A. Perry	*Gymnopus rodhallii* Desjardin & B.A. Perry	Desjardin and Perry (2017)	E	E
Gymnopus ugandensis (Pegler) Desjardin & B.A. Perry	*Gymnopus ugandensis* (Pegler) Desjardin & B.A. Perry	Desjardin and Perry (2017)		X
Marasmiellus ramealis (Bull.) Singer	*Marasmius amadelphus* (Bull.) Fr.	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Mycetinis ignobilis (Berk. & Broome) Desjardin & B.A. Perry	*Mycetinis ignobilis* (Berk. & Broome) Desjardin & B.A. Perry	Desjardin and Perry (2017)		X
Setulipes afibulatus Antonín	*Setulipes afibulatus* Antonín	Desjardin and Perry (2017)		X
Physalacriaceae				
Cyptotrama asprata (Berk.) Redhead & Ginns	*Cyptotrama asprata* (Berk.) Redhead & Ginns	Desjardin and Perry (2017)	X	X
Pleurotaceae				
Pleurotus tuber-regium (Fr.) Singer	*Lentinus tuber-regium* (Fr.) Fr.	Coutinho (1925)		X
	Lentinus descendens Afzel ex Fr.	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Pluteaceae				
Pluteus albidus Beeli	*Pluteus albidus* Beeli	Desjardin and Perry (2018)		X
Pluteus albostipitatus (Dennis) Singer	*Pluteus albostipitatus* (Dennis) Singer	Desjardin and Perry (2018)		X
Pluteus chrysaegis (Berk. & Broome) Petch	*Pluteus chrysaegis* (Berk. & Broome) Petch	Desjardin and Perry (2018)		X
Pluteus hirtellus Desjardin & B.A. Perry	*Pluteus hirtellus* Desjardin & B.A. Perry	Desjardin and Perry (2018)		E
Pluteus losulus Justo	*Pluteus losulus* Justo	Desjardin and Perry (2018)	X	
Pluteus thomensis Desjardin & B.A. Perry	*Pluteus thomensis* Desjardin & B.A. Perry	Desjardin and Perry (2018)		E
Psathyrellaceae				
Candolleomyces albipes (Murrill) Wächter & A. Melzer	*Psathyrella albipes* (Murrill) A.H. Sm.	Desjardin and Perry (2016)		X
Candolleomyces cacao (Desjardin & B.A. Perry) Wächter & A. Melzer	*Psathyrella cacao* Desjardin & B.A. Perry	Desjardin and Perry (2016)		E
Coprinellus aureogranulatus (Uljé & Aptroot) Redhead, Vilgalys & Moncalvo	*Coprinellus aureogranulatus* (Uljé & Aptroot) Redhead, Vilgalys & Moncalvo	Desjardin and Perry (2016)		X
Coprinellus disseminatus (Pers.) J.E. Lange	*Coprinellus disseminatus* (Pers.) J.E. Lange	Desjardin and Perry (2016)		X
	Coprinarius disseminatus (Pers.) P. Kumm.	Coutinho (1925)		X
	Psathyrella disseminata (Pers.) Quél.	Bresadola and Roumeguère (1890)		X
Coprinopsis afronivea Desjardin & B.A. Perry	*Coprinopsis afronivea* Desjardin & B.A. Perry	Desjardin and Perry (2016)		E
Coprinopsis cinerea (Schaeff.) Redhead, Vilgalys & Moncalvo	*Coprinus cinereus* (Schaeff.) Gray	Saccardo and Berlese (1889)		X

(continued)

Currently accepted name	Name reported in literature	Citation	P	ST
Psathyrella oboensis Desjardin & B.A. Perry	*Psathyrella oboensis* Desjardin & B.A. Perry	Desjardin and Perry (2016)		E
Pterulaceae				
Pterulicium xylogenum (Berk. & Broome) Corner	*Pterula subaquatica* Bres. & Roum.	Bresadola and Roumeguère (1890)		X
Schizophyllaceae				
Schizophyllum commune Fr.	*Schizophyllum commune* Fr.	Winter (1886)		X
	Schizophyllum commune var. *multifidum* (Batsch) Cooke	Bresadola and Roumeguère (1890)		X
	Schizophyllum alneum (L.) J. Schröt.	Coutinho (1925)		X
Strophariaceae				
Deconica overeemii (E. Horak & Desjardin) Desjardin & B.A. Perry	*Deconica overeemii* (E. Horak & Desjardin) Desjardin & B.A. Perry	Desjardin and Perry (2016)		X
Deconica protea (Kalchbr.) Desjardin & B.A. Perry	*Deconica protea* (Kalchbr.) Desjardin & B.A. Perry	Desjardin and Perry (2016)		X
Hypholoma aff. *subviride* (Berk. & M.A. Curtis) Dennis	*Hypholoma* aff. *subviride* (Berk. & M.A. Curtis) Dennis	Desjardin and Perry (2016)		X
Tricholomataceae s.l.				
Tricholomopsis aurea (Beeli) Desjardin & B.A. Perry	*Tricholomopsis aurea* (Beeli) Desjardin & B.A. Perry	Desjardin and Perry (2017)		X
ORDER BOLETALES				
Sclerodermataceae				
Scleroderma dictyosporum Pat.	*Scleroderma dictyosporum* Pat.	Desjardin and Perry (2015b)	X	
ORDER STEREOPSIDALES				
Stereopsidaceae				
Stereopsis radicans (Berk.) D.A. Reid	*Thelephora radicans* Berk.	Bresadola and Roumeguère (1890), Coutinho (1925)		X
ORDER POLYPORALES				
Cerrenaceae				
Cerrena hydnoides (Sw.) Zmitr.	*Trametes hydnoides* (Sw.) Fr.	Bresadola and Roumeguère (1890)		X
Fomitopsidaceae				
Antrodia albida (Fr.) Donk	*Trametes sepium* Berk.	Coutinho (1925)		X
Daedalea newtonii Bres. & Roum.	*Daedalea newtonii* Bres. & Roum.	Bresadola and Roumeguère (1890), Coutinho (1925)	E	E
Daedalea quercina (L.) Pers.	*Daedalea quercina* (L.) Pers.	Bresadola and Roumeguère (1890)		X
Ranadivia modesta (Kunze ex Fr.) Zmitr.	*Polyporus atypus* Lév.	Bresadola and Roumeguère (1890)		X
Incrustoporiaceae				
Tyromyces albogilvus (Berk. & M.A. Curtis) Murrill	*Polyporus albogilvus* Berk. & M.A. Curtis	Winter (1886), Coutinho (1925)		X
Tyromyces squamulosus (Bres.) Ryvarden	*Polyporus squamosus* Bres.	Bresadola (1890)		E
Irpicaceae				
Flavodon flavus (Klotzsch) Ryvarden	*Irpex flavus* Klotzsch	Bresadola and Roumeguère (1890), Coutinho (1925)		X

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Currently accepted name	Name reported in literature	Citation	P	ST
Meripilaceae				
Rigidoporus lineatus (Pers.) Ryvarden	*Polyporus zonalis* Berk.	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Rigidoporus microporus (Sw.) Overeem	*Polyporus auberianus* Mont.	Winter (1886), Bresadola and Roumeguère (1890), Coutinho (1925)		X
Meruliaceae				
Steccherinum rawakense (Pers.) Banker	*Hydnum rawakense* Pers.	Saccardo and Berlese (1889)		X
Phanerochaetaceae				
Bjerkandera adusta (Pers.) P. Karst.	*Polyporus adusta* (Willd.) Fr.	Bresadola (1890)		X
Bjerkandera fumosa (Pers.) P. Karst.	*Polyporus imberbis* (Bull.) Fr.	Bresadola (1890)		X
Porostereum spadiceum (Pers.) Hjortstam & Ryvarden	*Stereum spadiceum* var. *venosum* Quél.	Bresadola and Roumeguère (1890)		X
Terana caerulea (Schrad. ex Lam.) Kuntze	*Corticium caeruleum* (Schrad. ex Lam.) Fr.	Bresadola and Roumeguère (1890)		X
Podoscyphaceae				
Podoscypha involuta (Klotzsch ex Fr.) Imazeki	*Stereum involutum* Klotzsch ex Fr.	Bresadola and Roumeguère (1890)	X	
	Stereum pulchellum Sacc. & Berl.	Saccardo and Berlese (1889)	X	
Polyporaceae				
Asterotus dealbatus (Berk.) Singer	*Lentinus sprucei* (Berk.) Cout.	Coutinho (1925)		X
	Panus sprucei Berk.	Bresadola and Roumeguère (1890)		X
Coriolopsis badia (Berk.) Murrill	*Trametes badia* Berk.	Bresadola and Roumeguère (1890)	X	
Coriolopsis occidentalis (Klotzsch) Murrill	*Polystictus occidentalis* (Klotzsch) Sacc.	Coutinho (1925)		X
Coriolus sprucei (Berk.) G. Cunn.	*Trametes sprucei* Berk.	Coutinho (1925)		X
Earliella scabrosa (Pers.) Gilb. & Ryvarden	*Trametes sanguinea* (Klotzsch) Pat.	Coutinho (1925)		X
	Daedalea sanguinea Klotzsch	Winter (1886)		X
Favolus grammocephalus (Berk.) Imazeki	*Favolus multiplex* Lév.	Bresadola and Roumeguère (1890), Coutinho (1925)		X
	Polyporus grammocephalus Berk.	Winter (1886)		X
Favolus jacobeus Sacc. & Berl.	*Favolus jacobeus* Sacc. & Berl.	Saccardo and Berlese (1889), Bresadola and Roumeguère (1890)	E	E
Favolus platyporus Berk. & M.A. Curtis	*Favolus platyporus* Berk. & M.A. Curtis	Bresadola and Roumeguère (1890)		X
Favolus tenuiculus P. Beauv.	*Favolus tesselatus* Mont.	Coutinho (1925)		X
	Hexagonia tenuicola (P. Beauv.)	Bresadola and Roumeguère (1890)		X
	Favolus brasiliensis (Fr.) Fr.	Bresadola (1891)		X
Fomes amboinensis (Lam.) Cooke	*Fomes amboinensis* (Lam.) Cooke	Coutinho (1925)		X

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Currently accepted name	Name reported in literature	Citation	P	ST
Fomes ferrugineobrunneus Cout.	*Fomes ferrugineobrunneus* Cout.	Coutinho (1925)		E
Fomes fulvellus (Bres.) Sacc.	*Ganoderma fulvellum* Bres.	Bresadola and Roumeguère (1890)		X
Funalia caperata (Berk.) Zmitr. & Malysheva	*Polyporus caperatus* Berk.	Winter (1886)		X
Ganoderma amboinense (Lam.) Pat.	*Ganoderma amboinense* (Lam.) Pat.	Bresadola and Roumeguère (1890)		X
Ganoderma applanatum (Pers.) Pat.	*Fomes applanatus* (Pers.) Fr.	Coutinho (1925)		X
Ganoderma australe (Fr.) Pat.	*Ganoderma australe* (Fr.) Pat.	Bresadola and Roumeguère (1890)		X
	Polyporus australis Fr.	Winter (1886)		X
Ganoderma lucidum (Curtis) P. Karst.	*Ganoderma lucidum* (Curtis) P. Karst.	Bresadola and Roumeguère (1890)		X
	Fomes lucidus (Curtis) Sacc.	Coutinho (1925)		X
	Polyporus lucidus (Curtis) Fr.	Winter (1886)		X
Ganoderma multiplicatum (Mont.) Pat.	*Ganoderma multiplicatum* (Mont.) Pat.	Bresadola and Roumeguère (1890)	X	
	Fomes multiplicatus (Mont.) Sacc.	Coutinho (1925)		X
Ganoderma ochrolaccatum (Mont.) Pat.	*Ganoderma ochrolaccatum* (Mont.) Pat.	Bresadola and Roumeguère (1890)		X
	Fomes ochrolaccatus (Mont.) Pat.	Coutinho (1925)		X
Ganoderma oerstedii (Fr.) Torrend	*Fomes oerstedii* (Fr.) Cooke	Coutinho (1925)		X
Hexagonia cucullata (Mont.) Murrill	*Favolus cucullatus* Mont.	Bresadola and Roumeguère (1890)		X
Hexagonia purpurascens (Berk. & M.A. Curtis) Murrill	*Favolus purpurascens* Berk. & M.A. Curtis	Winter (1886)		X
Leiotrametes menziesii (Berk.) Welti & Courtec.	*Polystictus kurzianus* Cooke	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Lentinus striatulus Lév.	*Lentinus flaccidus* Fr.	Fries (1851)		X
Lentinus thomensis Cout.	*Lentinus thomensis* Cout.	Coutinho (1925)		E
Lentinus villosus Klotzsch	*Lentinus villosus* Klotzsch	Winter (1886), Bresadola and Roumeguère (1890)	X	X
Lenzites applanatus (Klotzsch) Fr.	*Lenzites applanatus* (Klotzsch) Fr.	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Lenzites asperus (Klotzsch) Fr.	*Lenzites asperus* (Klotzsch) Fr.	Winter (1886), Bresadola and Roumeguère (1890), Coutinho (1925)		X
Lenzites deplanatus Fr.	*Lenzites deplanatus* Fr.	Winter (1886)		X
Lenzites repandus Fr.	*Lenzites repandus* Fr.	Winter (1886), Coutinho (1925)		X
Lopharia cinerascens (Schwein.) G. Cunn.	*Lopharia lirellosa* Kalchbr. & MacOwen	Coutinho (1925)		X
Microporus affinis (Blume & T. Nees) Kuntze	*Polystictus affinis* (Blume & T. Nees) Fr.	Roumeguère (1889)		X
	Polyporus flabelliformis Klotzsch	Winter (1886)		X
	Polystictus flabelliformis Fr.	Bresadola and Roumeguère (1890), Coutinho (1925)		X

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Currently accepted name	Name reported in literature	Citation	P	ST
	Polystictus carneoniger (Berk. ex Cooke) Cooke	Bresadola and Roumeguère (1890)	X	
Microporus xanthopus (Fr.) Kuntze	*Polystictus xanthopus* (Fr.) Fr.	Saccardo and Berlese (1889), Bresadola and Roumeguère (1890)	X	
Panus neostrigosus Drechsler-Santos & Wartchow	*Lentinus strigosus* Fr.	Bresadola and Roumeguère (1890)	X	
Perenniporia ohiensis (Berk.) Ryvarden	*Trametes ohiensis* Berk.	Coutinho (1925)		X
Polyporus amboinensis Fr.	*Polyporus amboinensis* Fr.	Winter (1886)		X
Polyporus dictyopus Mont.	*Polyporus dictyopus* Mont.	Bresadola and Roumeguère (1890)		X
Polyporus philippinensis Berk.	*Favolus philippinensis* (Berk.) Sacc.	Coutinho (1925)		X
Polyporus rugulosus Lév.	*Polyporus rugulosus* Lév.	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Polyporus torquescens Sacc. & Berl.	*Polyporus torquescens* Sacc. & Berl.	Saccardo and Berlese (1889)		E
Polyporus venezuelae Berk. & M.A. Curtis ex Cooke	*Polyporus venezuelae* Berk. & M.A. Curtis ex Cooke	Winter (1886)		X
Pseudofavolus polygrammus (Mont.) G. Cunn.	*Hexagonia polygramma* (Mont.) Fr.	Winter (1886)		X
Pycnoporus sanguineus (L.) Murrill	*Polystictus sanguineus* (L.) G. Mey.	Coutinho (1925)		X
Szczepkamyces campestris (Quél.) Zmitr.	*Trametes campestris* Quél.	Bresadola and Roumeguère (1890)		X
Trametes cubensis (Mont.) Sacc.	*Trametes cubensis* (Mont.) Sacc.	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Trametes discolor Sacc. & Berl.	*Trametes discolor* Sacc. & Berl.	Saccardo and Berlese (1889)	E	
Trametes gibbosa (Pers.) Fr.	*Trametes gibbosa* (Pers.) Fr.	Coutinho (1925)		X
Trametes hirsuta (Wulfen) Lloyd	*Polystictus hirsutus* (Wulfen) Fr.	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Trametes meyenii (Klotzsch) Lloyd	*Daedalea ochracea* Kalchbr.	Coutinho (1925)		X
Trametes pubescens (Schumach.) Pilát	*Polystictus velutinus* (Pers.) Sacc.	Saccardo and Berlese (1889), Bresadola and Roumeguère (1890), Coutinho (1925)		X
Trametes strumosa (Fr.) Zmitr., Wasser & Ezhov	*Polyporus strumosus* Fr.	Coutinho (1925)		X
Trametes versicolor (L.) Lloyd	*Polysticus versicolor* (L.) Fr.	Bresadola and Roumeguère (1890)		X
Trametes villosa (Sw.) Kreisel	*Polystictus pinsitus* (Fr.) Fr.	Fries (1851)		X
Truncospora oboensis Decock	*Truncospora oboensis* Decock	Decock (2011)		E
Xenasmataceae				
Xenasmatella vaga (Fr.) Stalpers	*Phlebia vaga* Fr.	Coutinho (1925)		X
ORDER THELEPHORALES				
Bankeraceae				
Phaeodon thomensis Cout.	*Phaeodon thomensis* Cout.	Coutinho (1925)		E
ORDER RUSSULALES				

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Currently accepted name	Name reported in literature	Citation	P	ST
Auriscalpiaceae				
Lentinellus cochleatus (Pers.) P. Karst	*Lentinus cochleatus* var. *occidentalis* (Pers.) Fr.	Fries (1851)		X
Lentinellus flabelliformis (Bolton) S. Ito	*Lentinus flabelliformis* (Bolton) Fr.	Coutinho (1925)		X
Hericiaceae				
Laxitextum bicolor (Pers.) Lentz	*Stereum bicolor* (Pers.) Fr.	Bresadola and Roumeguère (1890)		X
Peniophoraceae				
Scytinostroma duriusculum (Berk. & Broome) Donk	*Stereum duriusculum* Berk. & Broome	Bresadola and Roumeguère (1890)		X
Scytinostroma quintasianum (Bres. & Roum.) Nakasone	*Corticium quintasianum* Bres. & Roum.	Bresadola and Roumeguère (1890)		E
Stereaceae				
Stereum amphirhytes Sacc. & Berl.	*Stereum amphirhytes* Sacc. & Berl.	Saccardo and Berlese (1889), Roumeguère (1889)		E
Stereum bellum (Kunze) Sacc.	*Stereum bellum* (Kunze) Sacc.	Winter (1886), Bresadola and Roumeguère (1890)		X
Stereum hirsutum (Willd.) Pers.	*Stereum hirsutum* (Willd.) Pers.	Bresadola and Roumeguère (1890)		X
Stereum kalchbrenneri Sacc.	*Stereum kalchbrenneri* Sacc.	Saccardo and Berlese (1889), Bresadola and Roumeguère (1890)		X
Stereum lobatum (Kunze ex Fr.) Fr.	*Stereum lobatum* (Kunze ex Fr.) Fr.	Winter (1886), Bresadola and Roumeguère (1890), Coutinho (1925)		X
Stereum obliquum Mont. & Berk.	*Stereum obliquum* Mont. & Berk.	Bresadola and Roumeguère (1890)		X
Stereum ostrea (Blume & T. Nees) Fr.	*Stereum fasciatum* (Schwein.) Fr.	Winter (1886), Bresadola and Roumeguère (1890), Coutinho (1925)	X	X
Stereum versicolor (Sw.) Fr.	*Stereum versicolor* (Sw.) Fr.	Winter (1886)		X
Xylobolus subpileatus (Berk. & M.A. Curtis) Boidin	*Stereum subpileatum* Berk. & M.A. Curtis	Winter (1886), Bresadola and Roumeguère (1890)		X
ORDER HYMENOCHAETALES				
Hymenochaetaceae				
Coltricia oboensis Decock	*Coltricia oboensis* Decock	Decock (2013)		E
Fuscoporia ferruginosa (Schrad.) Murrill	*Poria ferruginosa* (Schrad.) P. Karst.	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Fuscoporia senex (Nees & Mont.) Gohb.-Nejh.	*Fomes senex* (Nees & Mont.) Cooke	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Hydnoporia tabacina (Sowerby) Spirin, Miettinen & K.H. Larss.	*Hymenochaete tabacina* (Sowerby) Lév.	Bresadola and Roumeguère (1890)		X
Hymenochaete damicornis (Link) Lév.	*Hymenochaete damicornis* (Link) Lév.	Bresadola and Roumeguère (1890)		X
Hymenochaete tenuissima Berk.	*Hymenochaete tenuissima* Berk.	Bresadola and Roumeguère (1890)		X
Inonotus sideroides (Lév.) Ryvarden	*Polystictus sideroides* (Lév.) Cooke	Coutinho (1925)		X
Phellinus gilvus (Schwein.) Pat.	*Polyporus gilvus* (Schwein.) Fr.	Roumeguère (1889), Saccardo and Berlese		X

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Currently accepted name	Name reported in literature	Citation	P	ST
		(1889), Bresadola and Roumeguère (1890)		
	Polyporus gilvus var. *scruposus* (Fr.) Henn.	Bresadola and Roumeguère (1890)		X
	Polyporus scruposus Fr.	Winter (1886)		X
	Polyporus scruposus var. *isidioides* (Berk.) Cooke	Winter (1886)		X
	Polyporus licnoides Mont.	Bresadola and Roumeguère (1890)		X
Phellinus igniarius (L.) Quél.	*Polyporus igniarius* (L.) Fr.	Winter (1886)		X
	Fomes igniarius (L.) Fr.	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Phylloporia pectinata (Klotzsch) Ryvarden	*Fomes pectinatus* (Klotzsch) Gillet	Bresadola and Roumeguère (1890), Coutinho (1925)		X
Polystictus albidocinereus Cout.	*Polystictus albidocinereus* Cout.	Coutinho (1925)		E
Polystictus russogramme (Berk.) Cooke	*Polyporus russogramme* Berk.	Winter (1886)		X
Rickenellaceae				
Cotylidia aurantiaca (Pat.) A.L. Welden	*Thelephora aurantiaca* Pers.	Bresadola and Roumeguère (1890)		X
	Thelephora affinis Berk. & M.A. Curtis	Winter (1886)		X
ORDER PHALLALES				
Phallaceae				
Blumenavia angolensis (Welw. & Curr.) Dring	*Blumenavia angolensis* (Welw. & Curr.) Dring	Degreef et al. (2013), Desjardin and Perry (2015b)		X
Clathrus parvulus Bres. & Roum.	*Clathrus parvulus* Bres. & Roum.	Bresadola and Roumeguère (1890)		E
Mutinus bambusinus (Zoll.) E. Fisch.	*Mutinus bambusinus* (Zoll.) E. Fisch.	Desjardin and Perry (2015b)	X	
Mutinus zenkeri (Henn.) E. Fisch.	*Mutinus zenkeri* (Henn.) E. Fisch.	Degreef et al. (2013), Desjardin and Perry (2015b)	X	X
Phallus drewesii Desjardin & B.A. Perry	*Phallus drewesii* Desjardin & B.A. Perry	Desjardin and Perry (2009)		E
Phallus indusiatus Vent.	*Phallus indusiatus* Vent.	Desjardin and Perry (2015b)	X	
ORDER GOMPHALES				
Gomphaceae				
Ramaria henriquesii (Bres. & Roum.) Corner	*Clavaria henriquesii* Bres. & Roum.	Bresadola and Roumeguère (1890)		X
Ramaria molleariana (Bres. & Roum.) Corner	*Lachnocladium mollerianum* Bres. & Roum.	Bresadola and Roumeguère (1890)		X
Ramaria polypus Corner	*Ramaria polypus* Corner	Desjardin and Perry (2015b)		X
ORDER GEASTRALES				
Geastraceae				
Geastrum fimbriatum Fr.	*Geastrum fimbriatum* Fr.	Desjardin and Perry (2015b)		X

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Currently accepted name	Name reported in literature	Citation	P	ST
Geastrum schweinitzii (Berk. & M.A. Curtis) Zeller	*Geastrum schweinitzii* (Berk. & M.A. Curtis) Zeller	Desjardin and Perry (2015b)	X	X
Geastrum velutinum Morgan	*Geastrum velutinum* Morgan	Desjardin and Perry (2015b)		X
ORDER TRECHISPORALES				
Hydnodontaceae				
Trechispora havencampii (Desjardin & B.A. Perry) Meiras-Ottoni & Gibertoni	*Scytinopogon havencampii* Desjardin & B.A. Perry	Desjardin and Perry (2015a)	E	
ORDER AURICULARIALES				
Auriculariaceae				
Auricularia auricula-judae (Bull.) Quél.	*Auricularia auricula-judae* (Bull.) Quél.	Coutinho (1925)		X
	Hirneola auricula-judae (Bull.) Berk.	Bresadola (1891)		X
	Laschia tremellosa Fr.	Winter (1886)		X
Auricularia fuscosuccinea (Mont.) Henn.	*Auricularia fuscosuccinea* (Mont.) Henn.	Coutinho (1925)		X
	Hirneola fuscosuccinea (Mont.) Sacc.	Bresadola and Roumeguère (1890)		X
Auricularia nigricans (Sw.) Birkebak, Looney & Sánchez-García	*Auricularia polytricha* (Mont.) Sacc.	Coutinho (1925)		X
	Hirneola polytricha (Mont.) Fr.	Bresadola and Roumeguère (1890)		X
ORDER CANTHARELLALES				
Aphelariaceae				
Aphelaria subglobispora P. Roberts	*Aphelaria subglobispora* P. Roberts	Desjardin and Perry (2015b)	X	
Cantharellaceae				
Pseudocraterellus undulatus (Pers.) Rauschert	*Craterellus crispus* (Bull.) Berk.	Bresadola (1891)		X
Hydnaceae				
Clavulina vanderystii (Bres.) Corner	*Clavulina vanderystii* (Bres.) Corner	Desjardin and Perry (2015b)	X	
INCERTAE SEDIS—**insufficient data, problematic nomenclature**				
Agaricus (*Collybia*) *diffractus* Cout. *nom. illeg.*	Competing epithet; not treated since publication	Coutinho (1925)		E
Agaricus (*Galera*) *macromastes* Fr.	Not treated since publication	Fries (1851) (see Desjardin and Perry (2016))		E
Agaricus (*Mycena*) *rufescens* Cout. *nom. illeg.*	Competing epithet; not treated since publication	Coutinho (1925) (see Cooper et al. (2018))		E
Agaricus (*Naucoria*) *papularis* Fr.	Not treated since publication	Fries (1851) (see Desjardin and Perry (2016))		E
Panus troglodytes Fr.	Not treated since publication	Fries (1851)		E
Polystictus affinis var. *cyathoidea* Sacc. & Berl.	Not treated since publication	Saccardo and Berlese (1889), Roumeguère (1889)		E
Polystictus mollerianus Sacc., Berl. & Roum.	Not treated since publication	Saccardo and Berlese (1889)		E

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Chapter 9
The Bryophyte Flora of São Tomé and Príncipe (Gulf of Guinea): Past, Present and Future

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Abstract This chapter aims to present a review of the knowledge of the bryological flora for the São Tomé and Príncipe Islands (Gulf of Guinea). An updated catalogue is presented, as well as a brief overview of the first expeditions conducted by the University of Coimbra. The labels of the historical herbarium collections and correspondence were analyzed, which provides an important source of data contributing toward research in taxonomy and conservation of these oceanic islands. Since 2007, exploratory fieldwork was carried out in different habitats of this archipelago along an altitudinal gradient, aiming to improve the knowledge of the ecology and distribution patterns of its bryophyte flora. A total of 304 taxa of bryophytes (133 mosses, 164 liverworts and seven hornworts) are currently reported, of which 21 are endemic to São Tomé and Príncipe and 144 species are shared endemics with the African continent. Several vouchers, especially in the herbaria of the University of Lisbon and of the California Academy of Sciences, are still under study and will likely provide further insights and new discoveries.

Keywords Africa · Biodiversity · Bryophytes · Conservation · Expeditions · Herbaria

Introduction

Bryophytes are a group of land plants that includes mosses, liverworts, and hornworts, and with over 20,000 described species, they are the second most speciose group of higher plants, after angiosperms (Patiño and Vanderpoorten 2018; Song

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et al. 2021). Bryophytes are a common component of tropical forests and provide important ecosystem functions. In tropical regions during rainstorms numerous bryophyte species can quickly absorb (and retain) many times their dry weight in water. The absorbed water is then slowly released over time back into the environment, thereby reducing the erosive effects of heavy rain and allowing other plants and animals to benefit from the rain and the humid environment for a longer period (Pócs 1982). Bryophytes are widely distributed in terrestrial ecosystems (St Martin and Mallik 2017), and islands provide an exceptional natural laboratory for ecological and evolutionary research in this group of terrestrial plants that is often poorly studied. Oceanic tropical islands usually host amazing bryophyte diversity, including endemic species, especially in the montane forests favoured by ideal climatic conditions, such as frequent rainfall and permanent fog (Ah-Peng et al. 2012).

The first known bryophyte collections of São Tomé and Príncipe were made by Friedrich Welwitsch (1806–1872) in 1853 and 1860, as part of the expeditions supported by the Portuguese government to Angola (Dolezal 1974), followed by Charles Barter (1821–1859) and Gustav Mann (1836–1916), botanists with special interest in vascular flora (Sérgio and Garcia 2011). One of the greatest Portuguese mentors of Botany in Africa was Júlio Augusto Henriques (1838–1928) and he outlined a plan for studying the flora of São Tomé and Príncipe (Coutinho 1929–30). Throughout his life, Henriques remained deeply invested in understanding the botanical diversity of the archipelago, which motivated his tireless research as professor and director of the Botanical Garden of the University of Coimbra for more than 50 years. His initial interest in the botanical study of São Tomé and Príncipe was likely related to cultivation of the Cinchona tree (*Chinchona* spp.) and other medicinal plants at the Coimbra Botanical Garden (Perpétuo et al. 2012). At the age of 65, Henriques led an expedition to the island of São Tomé to study the island's flora, departing from Lisbon on June 23, 1903. The research based on this visit culminated in an important publication (Henriques 1917). During his stay in the archipelago, Henriques was received by the owners of many farms (*roças*), taking notes and obtaining important data on the natural history of the island. Fernandes (1980, 1986) noted that when Henriques planned the study of the flora of São Tomé and Príncipe in the 1880s, he implemented a set of measures that proved to be extremely important for the enrichment of the University of Coimbra herbarium (currently, Herbário do Instituto Botânico de Coimbra, Coimbra, Portugal - COI). First, he promoted and intensified the development of the Coimbra herbarium and trained qualified botany specialists. It was to this end that he appointed Adolpho Frederico Möller (1842–1920), a renowned collector of flora in Portugal and later in São Tomé and Príncipe (four months in 1885), and in turn Francisco Joaquim Dias Quintas (1864–1909) in botanical field studies in São Tomé and Príncipe. Second, Henriques sent material collected on these expeditions to the greatest bryologists at the time. Their results were published in the "Boletim da Sociedade Broteriana", a scientific journal dedicated to Botany and co-published by the University of Coimbra and the Broterian Society (Sociedade Broteriana).

Herbarium Specimens and Associated Documentation

Numerous naturalists passing through or purposefully visiting São Tomé and Príncipe gathered biological collections, some of which were then published in different scientific outlets. The Austrian naturalist and explorer Friedrich Welwitsch visited São Tomé in 1853 and 1860, during stopovers at the beginning and end of his botanical survey of Angola (Sérgio and Garcia 2011). The major scientific expeditions during the nineteenth century were performed by Adolpho Möller in 1885 (Henriques 1917; Sérgio and Garcia 2011), Francisco Quintas from 1888 to 1889, and Francisco Newton (1864–1909) between 1885 and 1895 (Sérgio and Garcia 2011). Casual collections were made by different naturalists, for example, the French botanist Auguste Jean Baptiste Chevalier (1873–1956) in 1905 (Exell 1944).

In all these field studies, botanical collections were organized, and duplicates were distributed to different herbaria. These included COI, and the herbaria of the Museu Nacional de História Natural e da Ciência da Universidade de Lisboa, Lisbon, Portugal (LISU), of the Natural History Museum, London, United Kingdom (BM), of the Muséum National d'Histoire Naturelle de Paris, France (PC), of the Instituto de Investigação Científica Tropical - ULisboa (LISC), and of the Conservatoire et Jardin botaniques de la Ville de Genève, Geneve Switzerland (G), and the Brotherus Herbarium (H-BR) of the Finnish Museum of Natural History University of Helsinki, Finland (H) (Herbaria acronyms according to Thiers 2016). The original herbarium collections, details presented in field notes, draft descriptions of species, and the extensive correspondence between the collectors and the specialists that studied the biological material are a valuable source of data and a base for modern studies regarding São Tomé and Príncipe flora.

Presently, COI and LISU herbaria hold most of the bryophyte specimens cited in the bibliography for São Tomé and Príncipe, corresponding mostly to the collections of Friedrich Welwitsch, Möller, Quintas and Newton, in addition to the smaller collections of Júlio Henriques. However, duplicates of these collections are also found in other European herbaria (Sérgio and Garcia 2011). The bryological collections resulting from the expeditions organized by Júlio Henriques were studied by several experts. The liverworts were sent to Franz Stephani (1842–1927) between 1886 and 1913. The mosses were first sent to Carl Müller (1818–1889) in Halle (between 1885 and 1887) and later to Viktor Ferdinand Brotherus (1849–1929) in Helsinki (between 1889 and 1904). The letters that Henriques sent to Stephani and Brotherus (Biblioteca Digital de Botânica da Universidade de Coimbra 2021) list all the specimens exchanged. Thus, specimens originating from these collections were progressively divvied up and disseminated by several international herbaria at the discretion of the authors who studied them.

In this study, by cross-checking the LISU database referring to the aforementioned studied herbaria, we were able to confirm where the reference material and most of the respective nomenclatural types are currently located (Sérgio and Garcia 2011). Additionally, we also gathered and compared all available information on

Fig. 9.1 Two specimens (**1**, **2**) of *Bryum coronatum* Schwägr., corresponding to the same Welwitsch specimen (n° 126, Insula de S. Thomé loco called Monte Caffé) collected in December 1860, and (**3**, **4**) *Sendtnera mollis* Steph. Typus, Slopes of Pico de São Tomé, 1500-2100 m, 1885, Adolpho Möller 23. (**1**) At BM herbarium with "Inter Angolense" labels, with original iconography; (**2**) At LISU herbarium without iconography but with a handwritten label by Welwitsch; (**3**) At COI herbarium with the Möller label; (**4**) At BM herbarium (BM000745048) of Stephani's herbarium and handwritten data by the same author

where the voucher specimens from São Tomé and Príncipe are currently housed (e.g., Figs. 9.1 and 9.2).

Most of the material of each specimen in the COI herbarium is abundant and generally corresponds to isotypes found also in BM, G, H or PC. The labels in COI are generally not the original and must have been written by Möller or Quintas (Fig. 9.2), who organized the collections, with many duplicates sent to other herbaria. Arthur Wallis Exell (1901–1993) first landed on São Tomé Island in October 1932 to initiate a botanical expedition of the islands of the Gulf of Guinea (e.g., Fig. 9.3.1–2). He visited the four principal islands (São Tomé, Príncipe, Bioko

Fig. 9.2 Brotherus specimen identifications. Two specimens of *Ectropothecium drepanophyllum* corresponding to the same specimen from Quintas, n° 23: (**1**) Holotypus in H herbarium (H-BR1415–022) with Brotherus handwriting; (**2**) Isotypus in COI herbarium with a handwritten label from Quintas

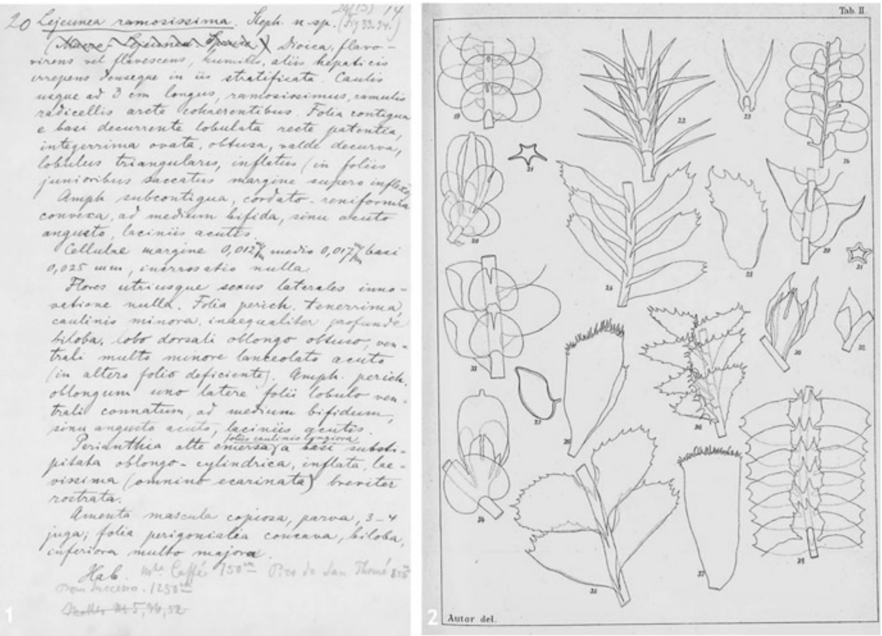
and Annobón), and the results of this expedition were published in 1944, in the Catalogue of the Vascular Plants of São Tomé (Exell 1944).

There are also numerous other specimens with labels based on the printed text of the work published by Carl Müller (1886a), such as the mosses collected by Adolpho Frederico Möller in 1885 and published in the Boletim da Sociedade Broteriana. We also verified the presence of specimens with original handwritten labels by Stephani and Brotherus in COI herbarium collections (Fig. 9.3.3–4), although some labels have two handwritings with the numbering of localities corresponding to Adolpho Möller manuscripts and the identifications handwritten by Stephani (Figs. 9.3.3–4 and 9.4) or Carl Müller.

The historical specimens from São Tomé and Príncipe archived in the Stephani collection in the herbarium of Genève (G) (Geissler 1982) have duplicates at COI. However, some taxa collected by Newton and Quintas were not returned to Coimbra, at least those studied after 1900. These correspond to the specimen references indicated in the most recent volumes of the Index Hepaticarum (Stephani 1901–1906, 1905–1909, 1909–1912, 1912–1917, 1917–1925). Likewise, there are a considerable number of specimens collected during Júlio Henriques career in the herbarium of Paris (PC), either included in the collections of Jules Cardot (1860–1934), Ferdinand Renauld (1837–1910) or Robert Potier de La Varde (1878–1961), that are often cited in revisionary studies of bryophyte genera.

Fig. 9.3 Arthur Exell (**1**, **2**) and Francisco Quintas specimens (**3**, **4**). (**1**) *Octoblepharum albidum*, Esperança, circa 350 ft., 1932, Exell 675 in the herbarium of Coimbra (COI); (**2**) *Hygrolejeunea pulcherrima*, Santa Maria, circa 4200 ft., 1932, Exell 197 in the London (BM) collections; (**3**) Isotypus of *Metzgeria thomeensis* (BM); (**4**) The same material in COI, isotypes. Both labels (**3**, **4**) correspond to Stephani's manuscripts

At the Helsinki herbarium (H), a significant part of material from São Tomé was found in the Brotherus (H–BR) collections, particularly type specimens collected in this archipelago (Sérgio and Garcia 2011), corresponding almost exclusively to Quintas and Möller collections. However, some of the specimens originally studied by Brotherus are now at BM, PC or COI herbaria and were not found at H herbarium (e.g., *Leucobryum homalophyllum* Broth.). It should be noted that, contrary to Stephani, Brotherus returned all the material he studied to Coimbra, mostly with handwritten labels.



20 Lejeunea ramosissima. Steph. n. sp. (Fig 33. 34.) 24(15) 14

(~~[illegible]~~) Dioica, flavovirens vel flavescens, humilis, aliis hepaticis irrepens denseque in iis stratificata. Caulis usque ad 3 cm longus, ramosissimus, ramulis radicellis arcte cohaerentibus. Folia contigua e basi decurrente lobulata recte patentia, integerrima ovata, obtusa, valde decurva, lobulus triangularis, inflatus (in foliis junioribus saccatus margine supero inflexo)

Amph. subcontigua, cordato-reniformia convexa, ad medium bifida, sinu acuto angusto, laciniis acutis.

Cellulae margine 0,012 mm medio 0,017 mm basi 0,025 mm, incrassatio nulla.

Flores utriusque sexus laterales innovatione nulla. Folia perich. tenerrima, caulinis minora, inaequaliter profunde biloba, lobo dorsali oblongo obtuso, ventrali multo minore lanceolato acuto (in altero folio deficiente). Amph. perich. oblongum uno latere folii lobulo ventrali connatum, ad medium bifidum, sinu angusto acuto, laciniis acutis.

Perianthia alte emersa (folia caulinis longiora) a basi substipitata oblongo-cylindrica, inflata, laevissima (omnino ecarinata) breviter rostrata.

Amenta mascula copiosa, parva, 3–4 juga; folia perigonialia concava, biloba, inferiora multo majora.

Hab. Mte Caffé 150m Pico de San Thomé 850
Monte Macerio. 1250m
~~Moller~~ 45, 46, 52

Fig. 9.4 (**1**) Original description of *Lejeunea ramosissima* Steph. included in the archives of the Botanical Institute of Coimbra Library as part of the letter dated 25 February 1886, and (**2**) Iconography of several species, including *L. ramosissima* Steph. (33 and 34) and *Sendtneria mollis* Steph. (22 and 23) by Stephani (1886)

Historical Correspondence

The correspondence between naturalists who studied bryophyte specimens collected by Möller, Quintas and Newton, is largely housed in the archives of the University of Coimbra at present. The documentation referring to Welwitsch's correspondence, currently in Lisbon at the Museu Nacional de História Natural e da Ciência (MUHNAC) of the University of Lisbon, does not provide any mention of bryophytes, despite the existence of bryophyte herbarium specimens of Welwitsch's expeditions in LISU herbarium (MUHNAC). Among this documentation are lists of the identified species and, in some cases, the original descriptions of species are also included.

Although it was not possible to study all Júlio Henriques' correspondence in some foreign institutions (except for the one in the library of the University of Helsinki and in the Botanical Garden of Geneva), we analyzed the correspondence exchanged between him and several specialists that is filed at the University of Coimbra (Biblioteca Digital de Botânica da Universidade de Coimbra). Some important parts of this correspondence are transcribed below.

Correspondence from Júlio Henriques to Franz Stephani

Henriques' first letter referring sending material to Stephani, was on 8 January 1885. The first publication of Stephani concerning the liverworts of São Tomé (Stephani 1886) refers to the A. Moller 1885 collections, so the specimen identifications must have been rather hasty. It describes 19 new species, in addition to other taxa, such as those already described by Mitten from the Cameroon Mountains (Mitten 1863) (e.g., *Radula bipinnata* Mitt.). Among the first records for São Tomé and Príncipe there was, for example, *Lejeunea ramosissima* Steph. (Fig. 9.4), *Plagiochila integerrima* Steph., *Sendtnera mollis* Steph. and *Anthoceros pinnatus* Steph., all currently still considered as distinct species with valid names. In the letter of 25 February 1886, Stephani sent along a list referencing the figures with the iconographies that were included in the same publication of Stephani (1886).

Correspondence from Júlio Henriques to Carl Müller

The correspondence sent by C. Müller from Halle to Henriques is very sparse and consists only of four letters between 1885 and 1887. C. Müller's second letter, dated 21 March 1886 (UC Digitalis 2021), is the most important as it includes a list of about 50 taxa, corresponding to the identification of the specimens cited in Müller (1886a, b). These specimens include more than 25 new species, some of them still recognized as species, as in the case of *Funaria acicularis* Müll.Hal and *Leucobryum leucophanoides* Müll.Hal.

Correspondence from Júlio Henriques to Viktor Ferdinand Brotherus

Sérgio and Garcia (2011) analyzed much of the correspondence between Henriques and Brotherus. Henriques' first letter dated 31 January 1889, refers to sending (on 24 January 1889) a package including mosses from São Tomé to Copenhagen and then to Helsinki. The exchange of bryological material continued and Henriques must have sent a second package that also included material from Portugal. In Brotherus's letter to Coimbra, sent on 19 August 1889, he states "*J'ai reçu en bon état, il ya quelque jours, la quaisse avec des mousses du Portugal et j'irais à leurs déterminations et révision aussitôt qu'il me sera possible. Les mousses de l'île S. Thomé de votre second envoi j'ai déjà examinés et vous communique le nom des espèces. Sont-elles aussi recueillies par M. Quintas"?* ["I received in good condition, a few days ago, the case with mosses from Portugal and I will make their identifications and revision as soon as possible. The mosses of the island S. Thomé of your second shipment I have already examined and communicated to you the names of the species. Were they also collected by Mr. Quintas"?] (UC Digitalis 2021).The reprints referenced in these letters correspond to the 1890 article, published in the "Boletim da Sociedade Broteriana" (Brotherus 1890), where 29 new species are described, some still considered valid species, including several endemics, such as *Leucobryum homalophyllum* Broth. and *Ectropothecium drepanophyllum* Broth (Fig. 9.2).

Correspondence from Júlio Henriques to Francisco Quintas

Although there are no extant records of correspondence from Möller to Henriques, a set of letters from Quintas sent from São Tomé to Henriques in Coimbra are still extant (Biblioteca Digital de Botânica da Universidade de Coimbra 2021). From most of this correspondence, it is evident that Quintas kept Henriques apprised of his research and situation on the island, attaching lists of the material he sent to Coimbra.

Although there is no specific numbering for the bryophyte specimens, there were indications of the boxes that contained cryptogams. For instance, the attachment to the letter issued on 21 July 1888 (UC Digitalis 2021). In that same letter, he also mentioned that mushroom specimens were listed separately. There are many bryophyte specimens collected by Quintas, which correspond to about 70 different bryophyte taxa, some of them corresponding to new species, such as *Plagiochila flabellata* Steph., *P. amplifolia* Steph. Among the liverworts and numerous species of mosses (ca. 31) described as new by Brotherus in 1890, we have the examples of *Pilotrichella calomicra* Broth., *Porotrichum quintasii* Broth., *P. caudatum* Broth., *Trichosteleum dicranelloides* Broth., among other new taxa.

Correspondence from Francisco Newton to Júlio Henriques

Some correspondence between Henriques and Newton is available in the historical archives of MUHNAC, but none of these letters has any reference to bryophytes. In Coimbra University, there is a letter sent by Newton to Henriques about his 1885 upcoming mission to Africa. Based on this letter, dated 23 August 1885, Newton makes Henriques aware of certain material from Angola (UC Digitalis 2021). He also confirms in that letter that he proposed to make a stop at Príncipe Island and then São Tomé. Ultimately, Newton arrived in São Tomé on 24 September 1885 (Guedes 2021).

Strangely, most of the bryophyte material collected by Newton and found in the different herbaria (BM, FH, G, JE and M herbaria) corresponds to specimens collected in 1887 on Príncipe and only a few are indicated to be from São Tomé. In fact, in the different publications concerning Newton, specimens correspond to Príncipe Island, excluding two references corresponding to São Tomé, in Angolares (Stephani 1888a, b). It is also interesting to note that the bryophyte specimens collected on Príncipe Island were only shipped in September of 1885 (Newton 1885), after this letter, but Newton should have sent more material later.

Apparently, Newton did not organize the numbering of his bryophyte specimens and the labels are very uninformative. The numbering of specimens was made when the plants arrived in Coimbra. However, it should be noted that based on Newton's collections, some liverwort species were described by Stephani (1888a, b), as *Microlejeunea africana* Steph., *Lejeunea newtonii* Steph. (now included in *Cheilolejeunea newtonii* Steph. ex Schiffn.), *Plagiochila thomeensis* Steph. (currently a synonym for *Plagiochila terebrans* Nees et Mont. ex Lindenb); *Cheilolejeunea principensis* Steph. (synonymized to *Cheilolejeunea serpentina* (Mitt.) Mizut.), and *Lophocolea newtonii* Steph. (synonymized to *Lophocolea martiana* Nees).

Historical Collecting Localities

Based on the data associated with the aforementioned collections, the location (exact or approximate) of the historical collecting activities by the first naturalists dedicated to the study of bryophytes in São Tomé Island was georeferenced (Fig. 9.5), and used as a starting point for the most recent fieldwork performed by the authors.

Exell's 1944 plant catalogue (Exell 1944) includes all the species known at the time and new reports of some taxa for the islands (Figueiredo 1994, 2005; Figueiredo and Gascoigne 2001), including diverse bryophytes. He was based in Vanhulst (Macambrará), in the Roça Zampalma and collected most of the bryophyte material in this region. This bryophyte collection was the basis for two publications, in which about 40 taxa of liverworts and mosses are listed (Exell 1944). Most of Exell's specimens are stored in BM, except for some specimens that are kept at COI.

After the Exell expedition, other collections were obtained in 1956 by the French naturalist Théodore Monod (1902–2000) and C. A. Thorold (1906–1998) in São Tomé and Príncipe, mainly in Pico de Príncipe, during the "6th Conférence lnternationale des Africanistes de I'Ouest" (Monod 1960). Most of this material is hosted in PC and was the basis of the publication of Potier de la Varde (1959). Arnaldo Roseira also collected in the islands between 1954 and 1958, corresponding to 79 specimens of three taxa in the PO herbarium (Universidade do Porto) (Costa 2020).

Recent Studies

Since the middle of the twentieth century and after the works of Exell, the study of bryophytes of São Tomé and Príncipe came to a halt. Only more recently has a new effort emerged through the project Bryotome (Sérgio and Garcia 2011). During this project, the first author carried out fieldwork in São Tomé and Príncipe in 2007 and

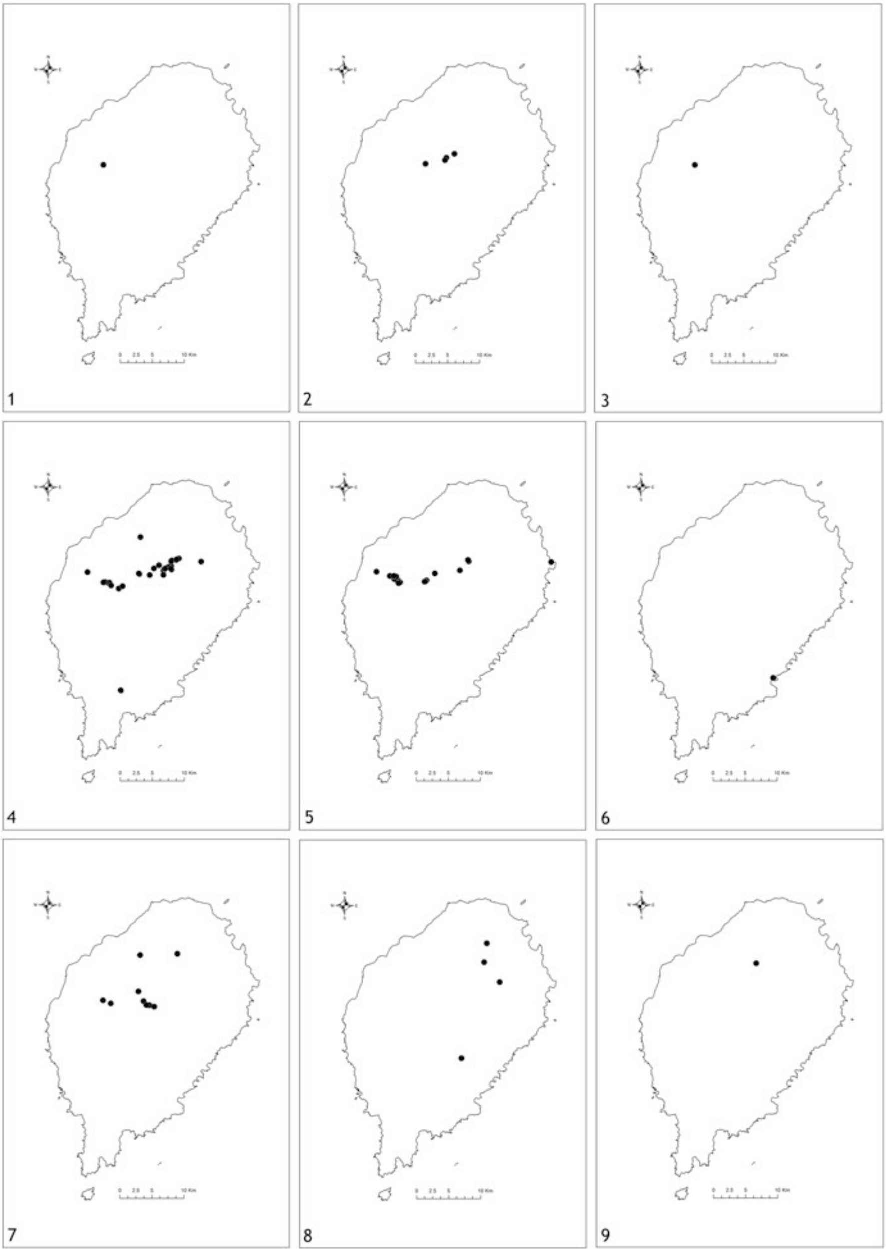


Fig. 9.5 Historical collecting localities of naturalists who collected bryophytes specimens on São Tomé Island from the mid-nineteenth century to mid-twentieth century: (**1**) Auguste Jean Baptiste Chevalier (1873–1956), (**2**) Arthur Wallis Exell (1901–1993), (**3**) Gustav Mann (1836–1916), (**4**) Adolpho Frederico Möller (1842–1920), (**5**) Théodore Monod (1902–2000), (**6**) Francisco Newton (1864–1909), (**7**) Francisco Joaquim Dias Quintas (1864–1909), (**8**) Charles Aubrey Thorold (1906–1998), (**9**) Friedrich Welwitsch (1806–1872)

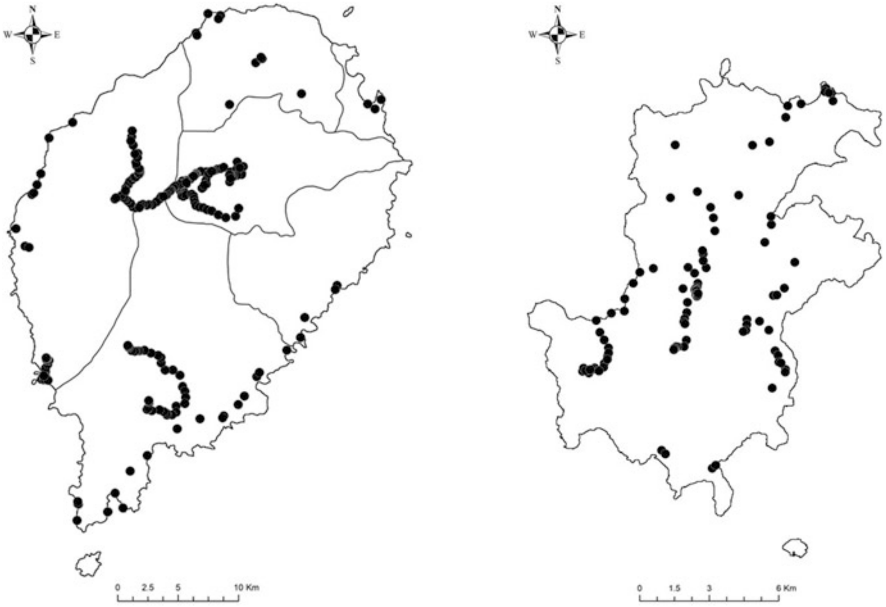


Fig. 9.6 Study localities in 2007, 2008, 2010, 2013 and 2016 for the enrichment of the University of Lisbon (LISU) and the California Academy of Science (CAS) herbaria

2008, collecting about 6000 specimens at various altitudes, including Pico de São Tomé. This project enabled the study of herbarium specimens, georeferencing historical specimens, planning new fieldwork more effectively, and studying different substrates (epiphytic, epiphyllous, rupicolous, terricolous and humicolous) to better determine specific microhabitats of species across the islands. In 2010, 2013 and 2016, expeditions sponsored by the California Academy of Sciences were carried out (Fig. 9.6). During these new expeditions, several species were discovered, including new records for the archipelago and the African continent, as well as species new to science (Figs. 9.7 and 9.8). One of the new species discovered was particularly interesting: *Dendroceros paivae* is distinct from most other species of the genus in its ecology, gametophyte, and sporophyte characters, resembling only the Bornean *D. foliicola* J. Haseg. In comparison to the type material of *D. foliicola, D. paivae* has a narrower sporophyte diameter. The thallus of *D. paivae* does not form rosettes, the cuticle is weakly papillose, and apices are plane to undulate, while *D. foliicola* forms rosette-like patches with strong crispate margins, even at branches apices, and the cuticle is slightly papillose (Garcia et al. 2012).

Fig. 9.7 Liverworts and hornworts from São Tomé and Príncipe: (**1**, **2**) *Dendroceros paivae* C.A. Garcia, Sérgio & J. C. Villarreal. (hornworts) at the type locality (LISU 237201) (Garcia et al. 2012); (**3**, **4**) *Megaceros flagellaris* (Mitt,) Steph. (hornworts) growing on a tree trunk in the first known locality in São Tomé and Príncipe and the second one reported for the African Continent (LISU 237200); (**5**) *Anthoceros pinnatus* Steph. (hornworts); (**6**) *Phaeoceros carolinianus* (Michx.) Prosk. (hornworts); (**7**) *Colura* sp. (liverworts); (**8**) *Cyathodium cavernarum* Kunze (liverworts)

Fig. 9.8 Liverworts and mosses from São Tomé and Príncipe. (**1**) *Marchantia pappeana* Lehm. subsp. *pappeana* (liverworts). (**2**), *Plicanthus hirtellus* (F. Weber) R.M. Schust. (liverworts). (**3**), *Calymperes lonchophyllum* Schwägr. (mosses). (**4**), *Octoblepharum albidum* Hedw. (mosses). (**5**), *Orthostichella* sp. (mosses). (**6**), *Trematodon longicollis* Michx. (mosses). (**7**), *Macromitrium sulcatum* var. *sulcatum* (Hook.) Brid. (mosses). (**8**), *Calymperes palisotii* Schwägr. (mosses)

Diversity, Composition and Endemism

In recent years, several papers resulting from these last expeditions have been published. These included the study of secondary metabolism compounds (Figueiredo et al. 2010) and the description of new species and new genera of bryophytes (Enroth and Shevock 2011; Müller et al. 2011; Garcia and Sérgio 2012a, b, c, d, e; Shevock et al. 2013; Pócs et al. 2015; Sollman et al. 2016; Enroth and Shevock 2017a, b; Müller and Shevock 2018; Müller et al. 2019).

These works allowed revising the number of species and endemics for each island individually and for the two islands combined (Table 9.1 and Appendix). One hundred and forty-four species of bryophytes occurring on the islands are currently considered endemic to Africa, 21 of which are endemic to the archipelago, including seven liverworts or hornworts and 14 mosses. One of these species is the hornwort *Dendroceros paivae* C.A. Garcia, Sérgio & J. C. Villarreal. (hornworts), endemic to São Tomé Island (Garcia et al. 2012) and found only in a single location, in a very restricted area.

The known bryophyte species diversity of the islands has increased markedly as specimens of various families are critically examined. For example, prior to fieldwork by the authors, only three species of the moss genus *Fissidens* (Fissidentaceae) were reported (O'Shea 2006). Now, *Fissidens* Hedw. is the most species-rich bryophyte genus in the archipelago with 24 known species (Shevock et al. 2013). The liverwort genera, *Lejeunea* Lib. and *Plagiochila* (Dumort.) Dumort. are also quite diverse with 19 and 18 species respectively (Müller et al. 2011; Pócs et al. 2015). A similar story of species additions for the islands was provided in a recent study of the moss families Neckeraceae (Enroth and Shevock 2011, 2017a, b) and

Table 9.1 Bryophyte species diversity and endemism for each island individually and for the two islands combined

	Príncipe	São Tomé	P&ST
MARCHANTIOPHYTA and ANTHOCEROTOPHYTA Liverworts and hornworts			
Total species/taxa	108	138	171
Island endemism	4	4	7
African endemism	52	65	80
DIVISION BRYOPHYTA Mosses			
Total species/taxa	41	114	133
Island endemism	1	13	14
African endemism	16	59	64
TOTAL BRYOPHYTES Liverworts, hornworts and mosses			
Total species/taxa	149	252	304
Island endemism	5	17	21
African endemism	68	124	144

Liverworts and hornworts, according to Wigginton (2018), and mosses, according to O'Shea (2006)

Pottiaceae (Sollman et al. 2016). Ongoing work on the moss family Calymperaceae also has discovered several new species for these islands. We anticipate species additions for these islands will continue for many years to come. Most studies were carried out on existing trails to reach higher areas, and several regions have not yet been surveyed (Figs. 9.5 and 9.6) due to the difficult terrain. Additional species will likely be documented and discovered as more remote cloud forest environments can be systematically surveyed. Our updated summary for the bryoflora of the islands reveals the documented diversity has increased significantly since the last reports of the mosses (O'Shea 2006) and of the liverworts and hornworts (Wigginton 2018). Thus, the 304 bryophytes documented for the archipelago at this time are likely a vast underestimate of the true diversity (Appendix).

The species catalogue of the bryophyte flora of the islands of São Tomé and Príncipe presented in this work (Appendix) is based on all known published literature. All the literature on bryophytes of São Tomé and Príncipe Islands was surveyed, including liverworts, hornworts, and mosses. The delimitation of families follows the latest version of the Checklist of sub-Saharan Africa of Wigginton (2018) for liverworts and hornworts and O'Shea (2006) for mosses. Taxa are presented in alphabetical order of all the accepted names (including subspecies and varieties). Taxa with synonymies (homotypic and heterotypic synonyms) whose type locality corresponds to São Tomé and Príncipe are designated in a second column with respective authors and the year of publication for São Tomé and Príncipe. The most accurate information about the original description, as well as the relevant synonyms, were considered with general taxonomic criteria. The present table includes only records published up until June 2020 (unpublished data of the authors, including new species and localities, are not included). The catalogue is not a taxonomic document, and no new taxonomic nor nomenclatural acts are published here. Synopses of families and genera are placed alphabetically within each order.

Final Remarks

The known bryoflora of São Tomé and Príncipe includes at least 304 species. Based on our ongoing studies and the number of specimens still awaiting critical study, this number will increase in the coming years as the diversity of this group becomes more comprehensively documented. The apparently low number of known species may be explained by the logistical and practical difficulties of carrying out fieldwork in dense forests and in areas of rough terrain, a reality that affects most of the scientists working in the region. Bryophytes are also generally very small plants, and many species occur in small populations. Therefore, during fieldwork some species can easily be overlooked or may occupy exceedingly specialized microhabitats that are difficult to find (e.g., fine twigs in the tree canopy). Further difficulty originates from the fact that the taxonomy of different bryophyte families is not well developed in the tropics, and world experts in bryophyte taxonomy are also starting to become scarce, especially those dedicated to the study of tropical species. Many bryophyte species reported from Africa are known only from type specimens or based on a handful of collections. Almost 45 bryophyte taxa reported for São Tomé and Príncipe have not been resampled since the nineteenth century. For a large number of bryophyte species, the ecology and habitat specificity are not well known or not known at all, and also the distribution patterns, elevational range, and abundance for most species remain to be determined.

The threats affecting forest habitats in São Tomé and Príncipe, such as habitat destruction or competition by invasive species, may affect the survival of bryophytes. One major threat to biodiversity conservation in the archipelago, particularly to the cryptogamic communities, forest structure, and habitat diversity along the altitudinal gradients is deforestation, especially that associated with the plantations of oil palm *Elaeis guineesis* Jacq. In the Emolve region (southern region of São Tomé), there is a monoculture of more than 600 ha of oil palm that is expected to continue growing, which would result in a significant loss in biodiversity (bryophytes and other taxonomic groups), especially to forests at lower elevations. By contrast, ancestral *roças* (old colonial farms), with *Cofeea* spp. and *Theobroma cacao* L. plantations, seem to preserve a high diversity of bryophyte species, mainly epiphytic taxa.

New bryological studies are urgently needed, especially in areas that have never been surveyed. Together with the recently collected material that is currently being studied by the coauthors and other colleagues, these new surveys will continue to increase our knowledge of distributions, species diversity and the particularities of bryophyte endemism in the country. A more comprehensive and updated species list will be essential to inform a future IUCN Red List assessment of bryophytes from São Tomé and Príncipe and to designate priority areas for conservation.

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Appendix

Updated catalogue of bryophytes from São Tomé and Príncipe Islands. A: African endemics. E: Island endemism.

Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
DIVISIONS **Marchantiophyta and Anthocerotophyta** Liverworts and Hornworts				
Acrolejeunea emergens (Mitt.) Steph. var. *emergens*		X	X	2015/ 2011
Aneura pinguis (L.) Dumort. sens. lat.		X	X	1956/ 1886
Aneura latissima Spruce		X	X	1888/ 2011
Anthoceros pinnatus Steph.	*Anthoceros pinnatus* Steph. 1886		A	1886
Bazzania decrescens subsp. *molleri* (Steph.) E.W.Jones	*Mastigobryum molleri* Steph. 1886	X	X	2015/ 1886
Bazzania nitida (F.Weber) Grolle			X	2011
Brachiolejeunea laxifolia (Taylor) Schiffn.	*Brachiolejeunea thomeensis* Steph. 1912		X	1912
Calypogeia fissa (L.) Raddi			X	1970
Calypogeia peruviana Nees et Mont.			X	1976
Caudalejeunea africana (Steph.) Schiffn.		X	X	2011
Caudalejeunea dusenii Steph.			A	2015
Caudalejeunea hanningtonii (Mitt.) Schiffn.		A	A	2000/ 2000
Caudalejeunea lehmanniana (Gottsche) A.Evans		X		2015
Ceratolejeunea cornuta (Lindenb.) Steph.		X	X	1960/ 2015
Ceratolejeunea floribunda Steph.	*Ceratolejeunea floribunda* Steph. 2013 1913		E	1913
Cheilolejeunea intertexta (Lindenb.) Steph.	*Cheilolejeunea newtonii* Steph. ex Schiffn. 1893	X		2015/ 1893
Cheilolejeunea montagnei (Gottsche) R.M.Schust.	*Euosmolejeunea thomeensis* Steph. 1914		X	1863
Cheilolejeunea rigidula (Nees ex Mont.) R.M.Schust.	*Cheilolejeunea principensis* Steph. ex Paris 1888	X		1888
Cheilolejeunea surrepens (Mitt.) E. W.Jones			X	2015

(continued)

Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Cheilolejeunea trifaria (Reinw. et al.) Mizut.	*Lejeunea grandistipula* Steph. 1886	X	X	2015/ 1886
Chiloscyphus difformis (Nees) J.J. Engel et R.M.Schust.	*Lophocolea molleri* Steph. 1886		X	1886
Cololejeunea africana (Steph.) R. M.Schust.	*Physocolea africana* Steph. 1915		A	1916
Cololejeunea cuneifolia Steph.		A		2015
Cololejeunea iradieri Infante et Heras			A	2015
Cololejeunea lanceolata E.W.Jones		A		2015
Cololejeunea leloutrei (E.W.Jones) R.M.Schust.			A	1960
Cololejeunea mocambiquensis S. W.Arnell		A		2015
Cololejeunea obliqua (Nees et Mont.) Schiffn.	*Cololejeunea crenatiflora* Steph. 1891	X	X	2011/ 1891
Cololejeunea obtusifolia (E.W. Jones) Tixier		A		2015
Cololejeunea papilliloba Steph.		X		2015
Cololejeunea platyneura (Spruce) A.Evans			X	2015
Cololejeunea pusilla Steph.		A		2015
Cololejeunea zenkeri (Steph.) E.W. Jones		A	A	2000/ 2015
Colura calderae Pócs			A	2011
Colura digitalis (Mitt.) Steph.		A	A	1958/ 1953
Colura hattoriana Pócs			A	2015
Colura obesa Jovet-Ast		A	A	2015
Colura tenuicornis (A.Evans) Steph.		X	X	2015/ 1958
Colura thomeensis Pócs		E	E	2015/ 2011
Conoscyphus trapezioides (Sande Lac.) Schiffn.	*Lophocolea devexa* Mitt. 1863	X	X	2015/ 1863
Cryptolophocolea martiana (Nees) L.Söderstr., Crand.-Stotl. et Stotler subsp. *martiana*	*Lophocolea newtonii* Steph. 1907	X	X	1953
Cyathodium cavernarum Kunze			X	1952
Dendroceros crispatus Nees			X	1863
Dendroceros herasii M.Infante			A	2010
Dendroceros paivae C.Garcia, Sérgio & J.C. Villarreal			E	2012

(continued)

Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Dibrachiella africana (Steph.) X.Q. Shi, R.L.Zhu et Gradst.		A		2000
Dibrachiella autoica (Vanden Berghen) X.Q.Shi, R.L.Zhu et Gradst.		A		2015
Diplasiolejeunea cavifolia Steph.	*Lejeunea cavifolia* Steph. 1886		X	1886
Drepanolejeunea capulata (Taylor) Steph.			A	2011
Drepanolejeunea cultrella (Mitt.) Steph.	*Drepanolejeunea molleri* Steph. 1913	A	A	2015/ 1913
Drepanolejeunea physifolia (Gottsche) Pearson	*Prionolejeunea fissistipula* Steph. 1913	A	A	1960/ 1913
Dumortiera hirsuta (Sw.) Nees		X	X	1960/ 1886
Folioceros incurvus (Steph.) D.C. Bharadwaj		A	A	1888/ 1889
Fossombronia indica Steph.		X		2019
Fossombronia sp.		X		2011
Frullania angulata Mitt. var. *angulata*	*Frullania angulata* Mitt. 1863*; F. subatrata* Steph. 1911; *F. cordifolia* Steph. 1911		A	1863
Frullania apicalis Mitt.	*Frullania laceriloba* Steph. 1911	A	A	2015/ 1911
Frullania apiculata (Reinw. et al.) Nees			X	2011
Frullania caffraria Steph.	*Frullania molleri* Steph. 1894 (Probably synonym)		X	1894
Frullania diptera (Lehm.) Drège			A	1886
Frullania ericoides (Nees) Mont.		X	X	1886/ 1863
Frullania obscura (Sw.) Mont.	*Frullania thomeensis* Steph. 1910		X	1910
Frullania obscurifolia Mitt.		X	X	2015/ 2004
Frullania purpurea Steph.			X	1976
Frullania rio-janeirensis (Raddi) Ångstr.	*Frullania africana* Steph. 1891	X	X	1976/ 1891
Frullania serrata Gottsche var. *serrata*			X	1886
Frullania spongiosa Steph.		X	X	2011/ 2011
Fuscocephaloziopsis connivens subsp. *fissa* (Steph.) Váňa et L. Soderstr.		X	X	1988/ 1988
Herbertus dicranus (Taylor ex Gottsche, Lindenb. et Nees) Trevis.	*Sendtnera mollis* Steph. 1886	X	X	2011/ 1886

(continued)

Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Heteroscyphus dubius (Gottsche) Schiffn.		X		1888
Heteroscyphus spectabilis (Steph.) Schiffn.	*Isotachis perfoliata* Steph. 1886 *Chiloscyphus thomeensis* Steph. 1893 nom. nud.?	A	A	2015/ 1886
Lejeunea abyssinica (Gola) Cufod.		A	A	2015/ 2015
Lejeunea acuta Mitt.		A	A	2019/ 1960
Lejeunea anisophylla Mont.		X	X	2011/ 2011
Lejeunea brenanii E.W.Jones			A	2015
Lejeunea cf. *obtusata* Gottsche			X	2011
Lejeunea conformis Nees et Mont.			A	2011
Lejeunea eckloniana Lindenb.		X		2015
Lejeunea flava (Sw.) Nees		X	X	1888/ 1960
Lejeunea grossecristata (Steph.) E. W.Jones	*Hygrolejeunea grossecristata* Steph. 1896; *Taxilejeunea longirostris* Steph. 1914		A	1896
Lejeunea helenae Pearson		X		2015
Lejeunea ibadana A.J.Harr. et E.W. Jones		A	A	2015/ 2015
Lejeunea jungneri (Steph.) Steph.		A		1901
Lejeunea lyratiflora Steph.			A	2015
Lejeunea papilionacea Prantl			X	2011
Lejeunea phyllobola Nees et Mont.		X		2011
Lejeunea pulchriflora (Pearson) G.E. Lee, Bechteler, Pócs, Schäf-Verw. & Heinrichs		X		2015
Lejeunea ramosissima Steph.	*Lejeunea ramosissima* Steph. 1886	X	X	1996/ 1886
Lejeunea setacea (Steph.) Steph.		A	A	1969/ 1969
Lejeunea tuberculosa Steph.		X		2011
Lepidozia succida Mitt.		A	A	2011/ 1891
Lepidozia ubangiensis Steph.		A	A	2015
Leptolejeunea astroidea (Mitt.) Steph.		A		2015
Leptolejeunea epiphylla (Mitt.) Steph.	*Leptolejeunea quintasii* Steph. 1891	X	X	2015/ 1891
Leptolejeunea maculata (Mitt.) Schiffn.	*Lejeunea thomeensis* Steph. 1886; *Drepanolejeunea gomphiae* Steph. 1913	X	X	2015/ 1886

(continued)

Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Lopholejeunea nigricans (Lindenb.) Schiffn.		X	X	2011/ 2011
Lopholejeunea subfusca (Nees) Schiffn.		X	X	2015/ 2011
Marchantia debilis Goebel			A	2011
Marchantia pappeana Lehm. subsp. *pappeana*	*Marchantia planiloba* Steph. 1886		A	1886
Marchesinia excavata (Mitt.) Schiffn.	*Homalolejeunea henriquesii* Steph. 1888		A	1886
Marchesinia principensis Frank Müll. et Shevock		A		2018
Mastigophora diclados (Brid. ex F. Weber) Nees		X	X	2015/ 1886
Megaceros flagellaris (Mitt.) Steph.			X	2012
Metalejeunea cucullata (Reinw. et al.) Grolle		X		2015
Metzgeria furcata (L.) Dumort.	*Metzgeria thomeensis* Steph. 1891	X	X	2004/ 1891
Metzgeria leptoneura Spruce	*Metzgeria recurva* Steph. 1886	X	X	2004/ 1886
Metzgeria lindbergii Schuffn.		X		2015
Microlejeunea africana Steph.	*Microlejeunea africana* Steph. 1888	A	A	1888/ 1891
Microlejeunea ankasica E.W. Jones		A	A	2015
Microlejeunea kamerunensis Steph.	*Microlejeunea cochlarifolia Steph 1888* (probably synonymy)	A	A	1990/ 1888
Neurolejeunea breutelii (Gottsche) A.Evans var. *africana* Pócs		E		2015
Notoscyphus lutescens (Lehm. et Lindenb.) Mitt.			X	2015
Odontolejeunea lunulata (F.Weber) Schiffn.	*Odontolejeunea thomeensis* Steph. 1912		X	2004/ 1912
Pallavicinia lyellii (Hook.) Carruth.	*Pallavicinia pilifera* Steph. 1891		X	1891
Phaeoceros carolinianus (Michx.) Prosk.			X	2011
Plagiochila barteri Mitt.	*Plagiochila triangularis* Steph. 1886; *P. quintasii* Steph. 1904	A	A	1962/ 1886
Plagiochila barteri var. *valida* (Steph.) Vanden Berghen		A	A	1981/ 1981
Plagiochila brunneola Steph.	*Plagiochila brunneola* Steph. 1904		A	1904
Plagiochila divergens var. *capensis* (Steph.) E.W. Jones			X	1962
Plagiochila flabellata Steph.	*Plagiochila flabellata* Steph. 1886; *P. molleri* Steph. 1886	A	A	2011/ 1886
Plagiochila fusifera Taylor	*Plagiochila amplifolia* Steph. 1901		X	1901

(continued)

Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Plagiochila gibbiflora Steph.	*Plagiochila gibbiflora* Steph. 1904		E	1904
Plagiochila heterostipa Steph.		A		2015
Plagiochila integerrima Steph.	*Plagiochila integerrima* Steph. 1886	X	X	2011/ 1886
Plagiochila loloensis Steph.	*Plagiochila rotundifolia* Steph. 1904	A	A	2011/ 1904
Plagiochila moenkemeyeri Steph.		A	A	2011/ 1960
Plagiochila neckeroidea Mitt.		A	A	2011/ 1904
Plagiochila pectinata Willd. ex Lindenb.		A	A	2011/ 1960
Plagiochila pinniflora Steph.			A	2011
Plagiochila praemorsa Steph.	*Plagiochila cacuminis* Steph. 1918	X	X	1888/ 1918
Plagiochila sarmentosa (Lehm. et Lindenb.) Lindenb.	Requires confirmation			
Plagiochila strictifolia Steph.		A	A	1962/ 1962
Plagiochila terebrans Nees et Mont. ex Lindenb.	*Plagiochila thomeensis* Steph. 1886	A	A	2011/ 1886
Pleurozia gigantea (F.Weber) Lindb.			X	1863
Plicanthus hirtellus (F.Weber) R.M. Schust.			X	1886
Porella abyssinica var. *hoehnelii* (Steph.) Pócs.			A	2011
Porella subdentata (Mitt.) E.W. Jones var. *subdentata*	*Madotheca thomeensis* Steph. 1910	A	A	1963/ 1910
Porella subdentata var. *camerunensis* E.W.Jones			A	2011
Prionolejeunea grata (Gottsche) Schiffn.		X	X	1960/ 1960
Prionolejeunea principensis Vanden Berghen		E		1960
Radula ankefinensis Gottsche ex Steph.		A	A	2011/ 2015
Radula appressa Mitt.	*Radula angustata* Steph. *1886;* *R. molleri* Steph. 1910	A	A	1910/ 1886
Radula boryana (F.Weber) Mont.	*Radula tamariscina* Mitt. 1863; *R. bipinnata* Mitt. 1863	X	X	1996/ 1863
Radula flaccida Lindenb. et Gottsche		X	X	1939/ 1939

(continued)

Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Radula fulvifolia (Hook.f. et Taylor) Gottsche et al.		X	X	2001/ 2011
Radula stenocalyx Mont.		X	X	2015/ 1910
Riccardia amazonica (Spruce) Schiffn. ex Gradst. et Hekking		X	X	2015/ 2011
Riccardia erosa (Steph.) E.W.Jones	*Aneura erosa* Steph. 1891	A	A	2011/ 1891
Riccardia limbata (Steph.) E.W. Jones	*Aneura reticulata* Steph. 1891	A	A	2011/ 1891
Riccardia longispica (Steph.) Pearson		A	A	2015/ 2011
Riccia congoana Steph.			X	2012
Riccia discolor Lehm. et Lindenb.		X		2015
Riccia lanceolata Steph.		A		2015
*Riccia moenkemeyer*i Steph.			A	2012
Riccia stricta (Lindenb.) Perold			X	2012
Schiffneriolejeunea occulta (Steph.) Gradst.		A	A	2015/ 2011
Schiffneriolejeunea pappeana (Nees) Gradst. var. *pappeana*	*Ptychocoleus quintasii* Steph. 1912		A	1912
Schiffneriolejeunea polycarpa (Nees) Gradst.	*Phragmicoma amplectens* Steph. 1886 = *P. molleri* Steph. 1886		X	1886
Solenostoma borgenii (Gottsche ex Pearson) Steph.			A	1974
Solenostoma dusenii (Steph.) Váňa, Hentschel et Heinrichs.		X	X	2019/ 1974
Spruceanthus abbreviatus (Mitt.) X. Q.Shi, R.L.Zhu et Gradst.		X		2015
Spruceanthus floreus (Mitt.) Sukkharak et Gradst.		A		1891
Stictolejeunea balfourii (Mitt.) E. W.Jones		X		2015
Symphyogyna podophylla (Thunb.) Mont. et Nees			X	2011
Syzygiella manca (Mont.) Steph.	*Jungermannia geminiflolia* Mitt. 1863		X	1863
Telaranea coactilis (Spruce) J.J. Engel et G.L.Merr.			X	2011
Telaranea nematodes (Gottsche ex Austin) M.Howe	*Lepidozia quintasii* Steph. 1922		X	1922
Thysananthus auriculatus (Wilson) Sukkharak et Gradst. var. *auriculatus*		X	X	2011/ 1949

(continued)

Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Thysananthus humilis (Gottsche) Sukkharak et Gradst.		X	X	2014/ 1888
Thysananthus nigrus (Steph.) Sukkharak et Gradst.	*Mastigolejeunea nigra* Steph. 1891	A	X	2015/ 1891
Thysananthus turgidus (Steph.) Sukkharak et Gradst.	*Mastigolejeunea turgida* Steph.	A	X	1983/ 1917
DIVISION Bryophyta Mosses				
Afrothamnium stipitatum (Mitt.) Enroth			X	1982
Anoectangium aestivum (Hedw.) Mitt.			X	2016
Anoectangium stracheyanum Mitt.			X	2016
Barbula cf. *seramensis* H.Akiyama			X	2016
Brachymenium leptophyllum (Bruch & Schimp. ex Müll.Hal.) Bruch & Schimp. ex A.Jaeger			X	1972
Brachymenium nepalense Hook.			X	1972
Brachymenium subuliferum (Mitt.) A.Jaeger	*Bryum subuliferum* Mitt. 1863; *Bryum molleri* Müll.Hal. 1886		A	1863
Brachymitrion moritzianum (Müll. Hal.) A.K.Kop.	*Orthodon thomeanus* Broth. 1890*;* *Tayloria thomeana* Broth. 1903		X	1890
Bryum apiculatum Schwägr.	*Bryum areoblastum* Müll.Hal. 1886		X	1886
Bryum argenteum Hedw. var. *argenteum*	*Bryum squarripilum* Müll.Hal. 1886		X	1886
Bryum coronatum Schwägr.	*Bryum erythrostegum* Müll.Hal. 1886		X	1886
Bryum huillense Welw. & Duby	*Bryum quintasii* Broth.1890		X	1890
Bryum thomeanum P. de la Varde	*Bryum thomeanum* P.de la Varde 1959		E	1959
Caduciella mariei (Besch.) Enroth		X		2017
Callicostella brevipes (Broth.) Broth.			A	1952
Callicostella chionophylla (Müll. Hal.) Broth.	*Hookeria chionophylla* Müll.Hal. 1886		E	1886
Callicostella fissidentella (Besch.) Kindb.	*Hookeria thomeana* Broth. 1890	A	A	1890/ 1890
Callicostella perpapillata Broth. & P.de la Varde		X		1944
Callicostella salaziae (Besch.) Broth.	*Hookeria quintasi* Broth. 1890		A	1890
Calymperes afzelii Sw.	*Calymperes quintasi* Broth. 1890		X	1863
Calymperes lonchophyllum subsp. *saxatile* (Müll. Hal. ex Besch.) S.R. Edwards		A		1944

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Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Calymperes palisotii Schwägr.		X		1987
Calymperes pintasii Müll.Hal. ex Besch.			A	1896
Calymperes tenerum Müll.Hal.	*Calymperes principis* Broth. 1890	X	X	1890/ 1959
Calyptothecium acutifolium var. *breviusculum* (Müll.Hal. ex Dusén) Argent			A	2011
Campylopus flexuosus (Hedw.) Brid var. *flexuosus*.	*Campylopus quintasii* Broth. 1890		X	1890
Campylopus savannarum (Müll. Hal.) Mitt.	*Dicranum divaricatum* Mitt. 1863; *Campylopus erythrocaulon* Broth. 1890	X	X	1890/ 1863
Chionoloma bombayense (Müll. Hal.) P. Sollman			X	2016
Cyclodictyon filicuspis P.de la Varde		X		1944
Cyclodictyon laetevirens (Hook. & Taylor) Mitt.			X	1944
Deslooveria quintasii (Broth.) Enroth	*Porotrichum quintasii* Broth. 1890		A	1890
Deslooveria saotomensis (Enroth & Shevock) Enroth	*Porotrichum saotomense* Enroth and Shevock (2011)		E	2011
Dicranella falcularia Müll.Hal. ex Dusén		A		1944
Ectropothecium brevifalcatum (Müll.Hal.) Kindb.	*Hypnum brevifalcatum* Müll.Hal. 1886		A	1888
Ectropothecium diffusum (Mitt.) A. Jaeger	*Stereodon diffusus* Mitt. 1863	A		1863
Ectropothecium drepanophyllum Broth.	*Ectropothecium drepanophyllum* Broth. 1890		E	1890
Fissidens asplenioides Hedw.			X	2013
Fissidens borgenii Hampe		A	X	2013/ 2013
Fissidens crispulus Brid. var. *crispulus*		X	X	2013/ 2013
Fissidens crispulus var. *robinsonii* (Broth.) Z. Iwats.& Z.-H. Li		X	X	2013/ 2013
Fissidens crispus Mont.			X	2013
Fissidens darntyi Schimp.			A	2013
Fissidens enervis Sim		A	A	2013/ 2013
Fissidens flaccidus Mitt.		X	X	2013/ 2013
Fissidens glaucissimus Welw. & Duby	*Fissidens subglaucissimus* Broth. 1890	A	A	1890/ 1890

(continued)

Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Fissidens intramarginatus (Hampe) A.Jaeger			X	2013
Fissidens metzgeria (Müll.Hal.) Broth.			A	2013
Fissidens microcarpus Mitt.		A		2013
Fissidens ovatus Brid.			A	2013
Fissidens pallidinervis Mitt.			X	2013
Fissidens palmatus Hedw		X		2013
Fissidens pellucidus Hornsch.		X	X	2013/ 2013
Fissidens porrectus Mitt.		A	A	2013/ 2013
Fissidens punctulatus Sande Lac.			X	1890
Fissidens ramulosus Mitt.		A	A	2013/ 2013
Fissidens sciophyllus Mitt.	*Fissidens purpureocaulis* Müll. Hal. 1900	A	A	2013/ 2013
Fissidens serratus Müll.Hal. var. *serratus*		X		2013
Fissidens submarginatus Bruch			X	2013
Fissidens usambaricus Broth.			A	2013
Fissidens zollingeri Mont.		X		2013
Floribundaria floribunda (Dozy & Molk.) M.Fleisch.			X	2011
Floribundaria vaginans (Welw. & Duby) Broth.	*Papillaria patentissima* Müll.Hal. 1886		A	1886
Funaria acicularis Müll.Hal.	*Funaria acicularis* Müll.Hal. 1886		E	1886
Funaria hygrometrica Hedw. var. *hygrometrica*			X	1901
Gymnostomiella erosula (Müll.Hal. ex Dusén) Arts			A	2016
Gymnostomiella vernicosa (Hook.) M.Fleisch.			X	2016
Hydrogonium consanguineum (Thwaites & Mitt.) Hilp.		X	X	2016/ 2016
Hydrogonium orientale (F. Weber) Kucera		X		2016/ 1987?
Hymenostylium recurvirostrum (Hedw.) Dixon var. *recurvirostrum*			X	2016
Hyophila involuta (Hook.) A.Jaeger		X	X	2016/ 2016
Hypopterygium tamarisci (Sw. ex Sw.) Brid. ex Müll.Hal.	*Hypopterygium brevifolium* Broth. 1890	X	X	1997/ 1863
Isopterygium nanoglobum (Müll. Hal.) Paris	*Hypnum nanoglobum* Müll.Hal. 1886		E	1886

(continued)

Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Lepidopilum lastii Mitt.			A	1944
Lepidopilum niveum (Müll.Hal.) Kindb.	*Hookeria niveum* Müll.Hal. 1886		A	1886
Leptodontium viticulosoides (P. Beauv.) Wijk & Margad. var. *viticulosoides*			X	2016
Leucobryum fouta-djalloni Paris & Cardot			A	1959
Leucobryum homalophyllum Broth.	*Leucobryum homolophyllum* Broth. 1890		E	1890
Leucobryum leucophanoides Müll. Hal.	*Leucobryum leucophanoides* Müll. Hal. 1886		E	1886
Leucoloma gracilescens Broth.	*Leucoloma gracilescens* Broth. 1890		A	1890
Leucoloma secundifolium Mitt.	*Leucoloma secundifolium* Mitt.1863		A	1863
Leucomium strumosum (Hornsch.) Mitt.			X	1944
Leucophanes molleri Müll.Hal.	*Leucophanes molleri* Müll.Hal. 1886		X	1886
Leucophanes unguiculatum Mitt.	*Leucophanes unguiculatum* Mitt.1863	A		1863
Lopidium struthiopteris (Brid.) M. Fleisch.	*Hypopterygium subtrichocladum* Broth. 1890	X	X	1890/ 1997
Macromitrium sulcatum (Hook.) Brid. var. *sulcatum*	*Macromitrium undatifolium* Müll. Hal. 1886	X	X	1917/ 1886
Mesonodon flavescens (Hook.) W.R. Buck		X		2011
Mittenothamnium leptoreptans (Broth.) Cardot	*Microthamnium leptoreptans* Broth. 1890		E	1890
Neckeromnion lepineanum (Mont.) S.Olsson, Enroth, Huttunen & D. Quandt		X	X	2017/ 2017
Neckeropsis disticha (Hedw.) Kindb.		X	X	2011/ 1993
Octoblepharum albidum Hedw.		X	X	1944/ 1959
Orthostichella rigida (Müll. Hal.) B.H.Allen & Magill	*Pilotrichella leptoclada* Müll.Hal. 1886*; P. calomicra* Broth. 1890		X	1886
Orthostichella versicolor (Müll. Hal.) B.H. Allen & W.R. Buck	*Pilotrichella inflatifolia* Müll.Hal. 1886		X	1886
Orthostichidium involutifolium subsp. *thomeanum* (Broth.) Argent	*Hildebrandtiella thomeana* Broth.1890; *Orthostichidium thomeanum* (Broth.) Broth. 1906	A	A	1996/ 1890
Orthostichidium involutifolium (Mitt.) Broth. subsp. *involutifolium.*			A	1959

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Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Philonotis nanothecia (Müll.Hal.) Kindb.	*Bartramia nanothecia* Müll.Hal. 1886		A	1886
Philonotis trichodonta (Müll.Hal.) Kindb.	*Bartramia trichodonta* Müll.Hal. 1886		E	1886
Pinnatella minuta (Mitt.) Broth.	*Hypnum africanum* Welw. & Duby 1872	X	X	1917/ 1872
Pinnatidendron piniforme (Brid.) Enroth		X	X	2011/ 2011
Plagiomnium rhynchophorum (Hook.) T.J.Kop. var. *rhynchophorum*.			X	1944
Pogonatum gracilifolium Besch.	*Polytrichum rubentiviride* Müll. Hal. 1886; *P. molleri* Müll.Hal. 1886	A	A	1944/ 1886
Pogonatum usambaricum (Broth.) Paris			A	1989
Pyrrhobryum spiniforme (Hedw.) Mitt.			X	1886
Racopilum orthocarpioides Broth.	*Racopilum orthocarpioides* Broth. 1890		A	1890
Racopilum thomeanum Broth.	*Rhacopilum thomeanum* Broth. 1890		A	1890
Radulina borbonica (Bél.) W.R. Buck	*Trichosteleum subpycnocylindricum* Broth. 1890		X	1890
Rhacopilopsis trinitensis (Müll. Hal.) E.Britton ex Dixon	*Microthamnium subelegentulum* Broth. 1890		X	1890
Rhizofabronia persoonii (Schwägr.) M.Fleisch var. *persoonii*.			A	1863
Rhynchostegium hopfferi (Welw. & Duby) A.Gepp	*Hypnum hopfferi* Welw. & Duby 1872		E	1872
Scabrellifolium elongatum (Welw. & Duby) Enroth	*Hypnum molleri* Müll.Hal. 1886		A	1886
Scabrellifolium substriatum (Hampe) Enroth	*Porotrichum caudatum* Broth. 1890		X	1890
Sematophyllum amblystegiocarpum (Müll.Hal.) Broth.	*Hypnum amblystegiocarpum* Müll. Hal. 1886		E	1886
Splachnobryum obtusum (Brid.) Müll.Hal.			X	2016
Symphyodon pygmaeus (Broth.) S. He & Snider			X	2011
Syrrhopodon gardneri (Hook.) Schwägr.	*Syrrhopodon quintasii* Broth. 1890		X	1890
Syrrhopodon lamprocarpus Mitt.			A	1886
Tayloria solitaria (Hedw.) T.J.Kop. & W.Weber			A	1972

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Taxon species/subspecies/variety	Synonyms (basionyms) based in São Tomé and Príncipe collections	P	ST	Year of first ref. P/ST
Thamnobryum corticola (Kindb.) De Sloover			A	1902
Thuidium involvens subsp. *thomeanum* (Broth.) Touw	*Thuidium thomeanum* Broth. 1890		A	1890
Trachypodopsis serrulata (P. Beauv.) M.Fleisch. var. *serrulata*	*Trachypodopsis quintasiana* Broth. 1909		A	1909
Trachypus bicolor var. *viridulus* (Mitt.) Zanten	*Papillaria molleri* Müll.Hal. 1886		X	1886
Trematodon divaricatus Bruch	*Trematodon flexifolius* Müll.Hal. 1886??		A	1886
Trematodon longicollis Michx.	*Trematodon flexifolius* Müll.Hal. 1886		X	1886
Trichosteleum dicranelloides Broth.	*Trichosteleum dicranelloides* Broth. 1890		A	1890
Vesicularia glaucula (Broth.) Broth.	*Ectropothecium glauculum* Broth. 1890		A	1890
Vesicularia scaturigina (Brid.) Broth.			A	1863
Vesicularia strephomischos (Welw. & Duby) Broth.	*Hypnum strephomischos* Welw. & Duby 1872		A	1872
*Wijkia monodi*i (P.de la Varde) H. Akiyama	*Gollania monodii* P.de la Varde 1959		E	1959
Wijkia trichocoleoides (Müll.Hal.) H.A.Crum	*Hypnum trichocoleoides* Müll.Hal. 1886		A	1886

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Chapter 10
Diversity of the Vascular Plants of the Gulf of Guinea Oceanic Islands

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Abstract Despite a long history of botanical collecting in the three oceanic islands of the Gulf of Guinea, no recent studies have documented floristic patterns. This chapter summarizes information on the vascular plants of the islands, including inventories conducted on Príncipe and São Tomé since 2017, as well as two recent expeditions to Annobón. An updated database of the vascular flora was compiled, which includes 14,376 records representing 1285 species and infraspecific taxa (1028 native). Príncipe has 445 species and infraspecific taxa (394 native), São Tomé has 1044 (842 native), and Annobón has 344 (274 native). Recent inventory work has generated collections of more than 90% of the endemic woody species. Several very rare taxa were rediscovered, including *Balthasaria mannii* (Oliv.) Verdc., 1969 (Pentaphylacaceae) and *Psychotria exellii* R. Alves, Figueiredo and A.P. Davis, 2005 (Rubiaceae), neither of which had been seen for more than 50 years. At least 17 species new to science were also discovered on Príncipe and São Tomé. Of the 1028 indigenous taxa, 164 (16%) are currently considered endemic to the islands. Of the 285 species evaluated according to the IUCN Red List criteria, 2 (0.7%) were Data Deficient, 226 (79.3%) Least Concern or Near Threatened, 55 (19.3%) threatened (including 3 Critically Endangered, 21 Endangered, and 31 Vulnerable), and 2 (0.7%) Extinct. On São Tomé and Príncipe, 325 plant species are used in traditional medicine, 37 of which are endemic. These results should be used to identify new priority sites for conservation, including on Annobón, where priority sites are less well defined.

Keywords Collecting effort · Endemism · Flora · IUCN red list · Species richness

Despite a long history of collecting in the three oceanic islands of the Gulf of Guinea (Príncipe, São Tomé, and Annobón), no recent studies have documented their floristic patterns. In this chapter, we synthesize current knowledge on their diversity of vascular plants: (1) briefly reviewing the history of botanical exploration, (2) documenting the spatial distribution of sampling, species richness, and endemism within and between the islands, (3) reviewing risk of extinction assessments for plant species, using the IUCN Red List criteria, and (4) providing an account of plants used in traditional medicine in São Tomé and Príncipe.

Sampling Efforts Through Time

São Tomé

Despite the relatively small area occupied by São Tomé and Príncipe compared to other African countries, their flora has been the subject of many publications (Figueiredo 1994b; Figueiredo et al. 2011; Droissart et al. 2018). The first comprehensive studies of the flora of São Tomé and Príncipe, primarily focused on São Tomé, were undertaken by Júlio Henriques from the University of Coimbra (e.g.,

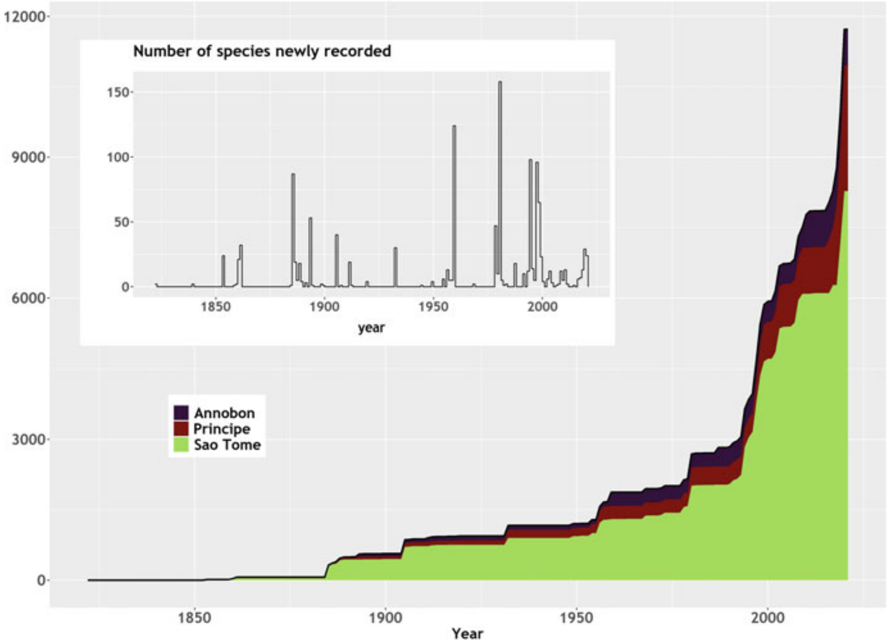

Fig. 10.1 Collecting effort in the oceanic islands of the Gulf of Guinea, showing numbers of species and records accumulated through time. Insert figure shows the number of species newly recorded per year. Specimens were excluded if they had an estimated georeferencing precision greater than or equal to 4 km. A total of 2600 records were excluded because they lacked information on the year of collection

Henriques 1892, 1917), who worked on the collections made during the 1880s by Francisco Newton, Adolfo Moller and Francisco Quintas (Figueiredo and Smith 2019; Ceríaco et al. 2022). In 1932–1933, Arthur Wallis Exell visited the three islands, collecting extensively and publishing the seminal catalogue of vascular plants (Exell 1944), in which many new species were described and several new records noted. Exell subsequently published a few additional papers (e.g., Exell 1956, 1959; Exell and Rozeira 1958), and finally produced a preliminary checklist of the Angiosperms of the islands (Exell 1973). Fieldwork largely stopped for the next 20 years, followed by an extensive period of collecting (Fig. 10.1), supported for the first 10 years by the ECOFAC project, which was funded by the European Commission. The Bom Sucesso Botanical Garden and the National Herbarium (STPH) were established on São Tomé during this period, and a few papers were published on the flora of the islands (e.g., Stévart et al. 2000; Stévart and Oliveira 2000; Stévart and Cribb 2004). In 2011, a new checklist was published, providing a good synthesis of the history of botanical studies, and the current state of knowledge of the flora with citations of herbarium specimens (Figueiredo et al. 2011). A significant collecting effort since 2016 justifies a new synthesis on the diversity of vascular plants of these islands (Fig. 10.1).

Príncipe

The history of floristic surveys on Príncipe is largely similar to that of São Tomé. During the nineteenth and twentieth century, Príncipe was visited by several collectors during expeditions to São Tomé or Annobón (Exell 1944; Figueiredo 1994a; Figueiredo and Smith 2019, 2020; Ceríaco et al. 2022). The flora of Príncipe was included in several checklists and publications (Exell 1944, 1956, 1959, 1973; Exell and Rozeira 1958; Figueiredo et al. 2011). A few collecting expeditions were conducted in the late 1990s with support from the ECOFAC project, followed by sporadic collections during the subsequent 20 years. In 2016, a project aiming to describe the tree diversity of Príncipe was initiated, which included exhaustive collecting, especially in the southern part of the island, and the production of the first forest classification ever proposed for Príncipe (Benitez et al. 2018). This initiative also supported the creation of an unofficial herbarium at the Príncipe Natural Park headquarters, built local botanical capacity, conducted Red List assessments, and made floristic data available online (Tropicos 2021).

Annobón

An account of the history of botanical studies on Annobón was presented in its most recent checklist (Velayos et al. 2013a). The oldest collections from the island are probably those made during the nineteenth century by the British botanists Andrew B. Curror (1839–1843) and Richard Burton (1861–1864). The first study specifically dealing with the flora of Annobón was published by the German botanist Johannes Mildbraed from the Botanical Garden of Berlin, based on his collection made in 1911 (Mildbraed 1937) during the 1910–1911 Deutsche Zentral-Afrika-Expedition. As mentioned above, Exell also published on its flora (Exell 1944, 1956, 1963, 1973), including ca. 40 specimens he collected in 1933. Luís G. Sobrinho studied the material collected by Francisco Newton between November 1892 and January 1893 (Sobrinho 1953). Finally, in 2010 and 2011, botanists of the Real Jardín Botánico Madrid and the Universidad Nacional de Guinea Ecuatorial collected exhaustively on the island, subsequently publishing an updated catalogue of the plants of Annobón with citations of herbarium specimens (Velayos et al. 2013a).

Spatial Distribution of Collecting Effort

The Database

Recent data on the flora of Príncipe, São Tomé, and Annobón were included in an updated version of the RAINBIO database (Dauby et al. 2016). The quality and accuracy of georeferencing of all specimen records were assessed first by verifying whether they fell within the limits of the islands and, if not, at what distance from the coast, using the CoordinateCleaner R package (Zizka et al. 2019). When errors or inaccuracies were detected, or when coordinates were entirely missing, georeferencing was corrected or added manually using the locality information indicated on specimen labels. A scale from one to nine was used to indicate the precision of the georeferencing of each record, assigned based on label coordinates, either manually or automatically (Dauby et al. 2016). When the elevation was provided on the specimen label, it was recorded in the database, otherwise it was retrieved from an elevation raster based on the geo-coordinates. The resulting database includes 14,376 records, among which 12,077 represent collections identified to the species level, and 12,790 are georeferenced, constituting the largest and most comprehensive dataset ever compiled for the islands.

Collecting Effort

Collecting effort is highly heterogeneous on all islands (Fig. 10.2). In Príncipe, most fieldwork has been concentrated at higher elevations, centered on Pico Papagaio and near Pico do Príncipe. The same is true for São Tomé, where they are concentrated around Pico de São Tomé and between Bom Sucesso and Lagoa Amélia. In Annobón, they have focused around Lake Apot, but also on the coast near Punta Yalba. All of these locations but the last are at higher altitudes and harbor relatively intact vegetation (Dauby et al. 2022). When standardized by area (Fig. 10.3), highlands clearly appear as the most intensely collected, while the lowlands and the rugged central portions of the islands are the most under-collected (Fig. 10.2). This pattern of collection suggests that botanists tend to conduct fieldwork in accessible areas that have less impacted vegetation, while more heavily impacted areas at lower elevations or very remote locations remain undersampled.

Species richness has a bimodal distribution with respect to elevation gradient on São Tomé. It should be stated that this decrease is *only* due to the fact that elevated areas are much less extensive. In fact, when you look at areas of comparable size (Fig. 10.2) the diversity is *higher* in elevated areas. Species richness is, however, also well correlated with sampling effort, so it is not clear to what extent these patterns are biased by sampling. The second explanation is obviously the correct one: 1100–1200 m is the area where lowland and montane species overlap, hence the higher diversity.

On Príncipe, Pico de Príncipe was relatively less well collected than Pico Papagaio because it is less accessible, the trail being uncovered by the first modern field surveys during the ECOFAC project in the 1990s (Baillie 1999). The southern part of the island was poorly collected until recently because it is usually accessed by boat. The recent field expedition conducted as part of the Global Tree Campaign allowed surveying the flora around Rio Porco, where the last remaining example of original littoral forest can be found on the islands (Benitez et al. 2018).

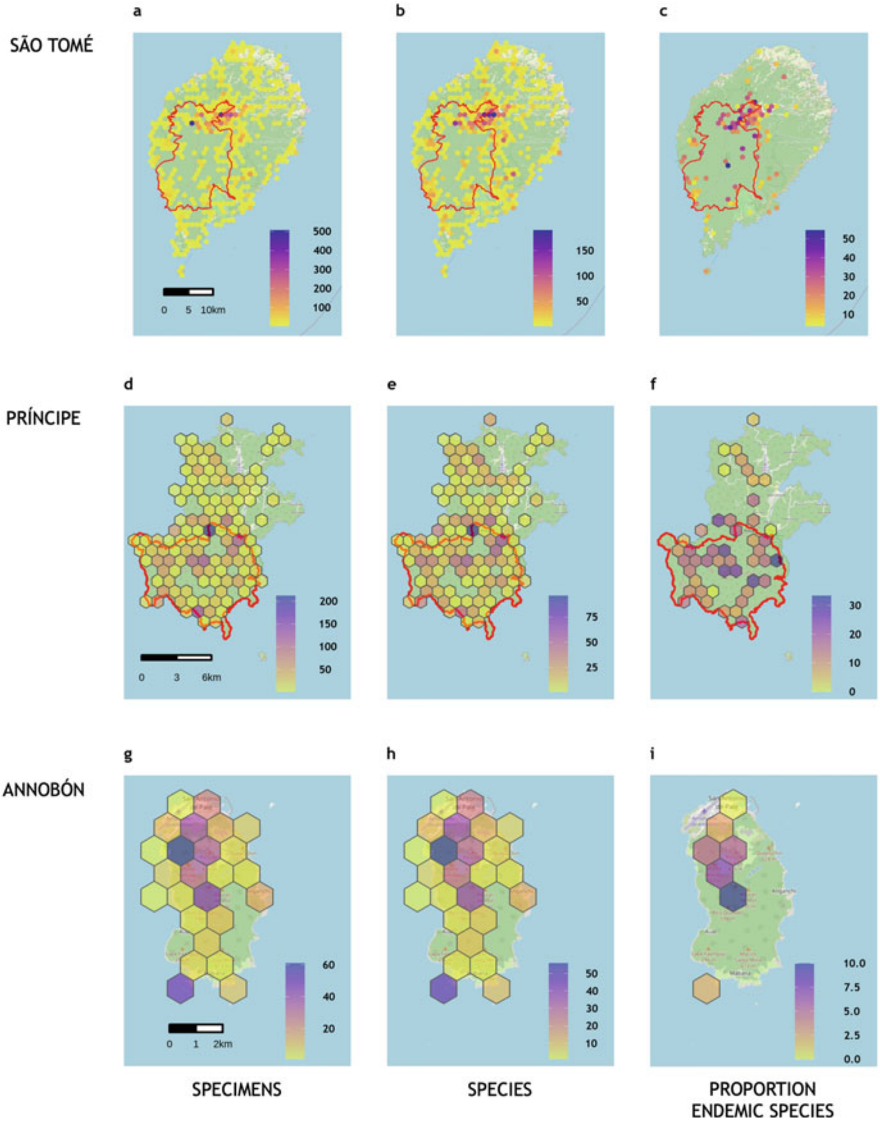

Fig. 10.2 Maps of Príncipe, São Tomé, and Annobón, showing the number of specimens, number of species, and proportion of endemic species per 1 km-sided hexagon. The proportion of endemic species is only shown in hexagons with at least 25 specimen records for Annobón and 20 elsewhere. Specimens whose estimated georeferencing precision is greater than 4 km were excluded. The red outline demarks the boundaries of Natural Parks

On São Tomé, some lowland areas have been relatively well explored, namely around São Miguel, São João dos Angolares, and the mouths of Xufe-Xufe or Iô Grande River. These have been less sampled than the highlands, thus remaining

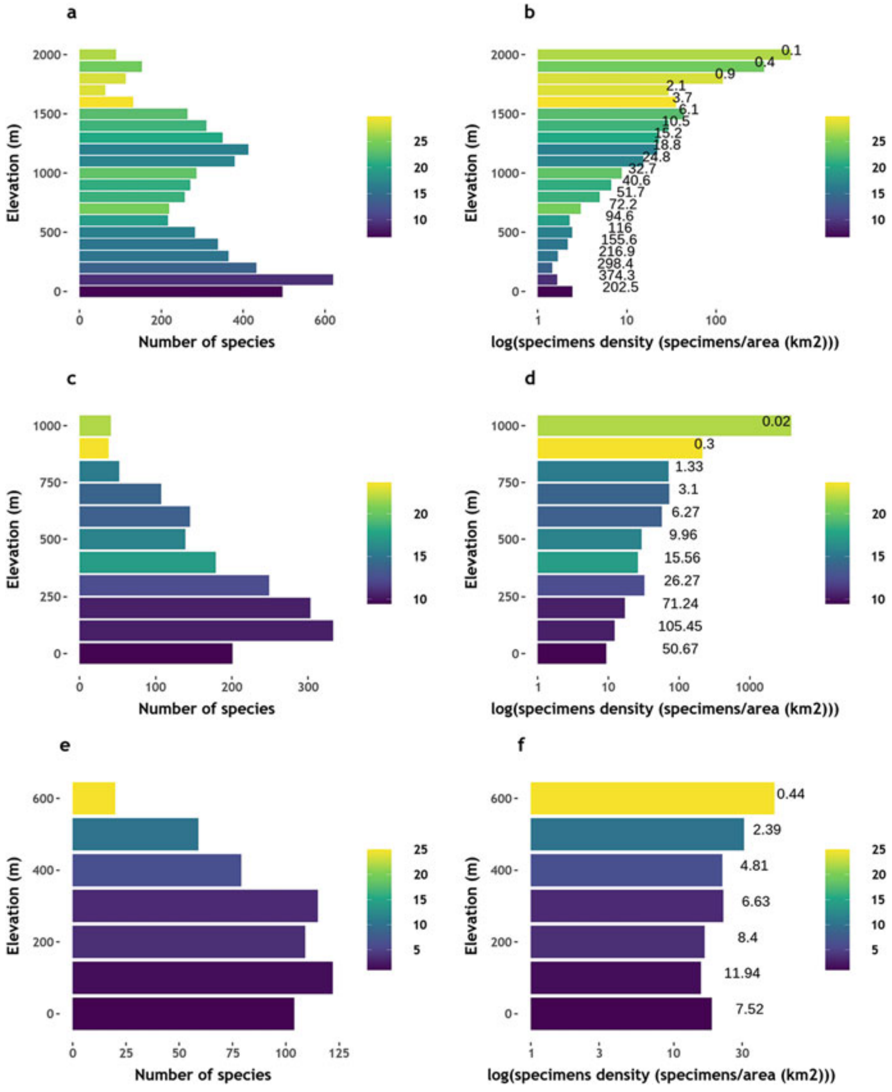

Fig. 10.3 (**a, c, e**) Number of species and (**b, d, f**) sampling effort relative to area along 100 m elevational bands for (**a**, **b**) São Tomé, (**c**, **d**) Príncipe and (**e**, **f**) Annobón. Sampling effort was obtained from specimen density per unit of area, and numbers indicate the area covered by each elevational band in km^2. The color scale represents the proportion of endemic species. Specimens whose estimated georeferencing precision is greater than 4 km were excluded. When available, elevation was retrieved from the specimen label, otherwise it was estimated from the elevation raster based on coordinates

overall poorly sampled given their much larger area (Fig. 10.3). Observed species richness on São Tomé (Fig. 10.2b) is particularly high around the Pico de São Tomé, Lagoa Amélia, and Bom Sucesso, but is also highly correlated with specimen density

(Pearson correlation $R = 0.94$) and is therefore certainly underestimated in most other parts of the island.

On Annobón, the number of species per 1 km-sided hexagons is also correlated with collecting effort (Fig. 10.2g–h), but the proportion of endemic plants is higher in the elevated area of the island (Figs. 10.2i and 10.3).

Floristic Diversity

The numbers of vascular plant taxa recorded from São Tomé and Príncipe were indicated in the most recent checklist (Figueiredo et al. 2011): 135 families (of which 29 are introduced), 624 genera (172 introduced), and 1104 species (301 introduced), along with 12 infraspecific taxa, including 119 endemic taxa (107 species and 12 infraspecific taxa). However, these figures only concern São Tomé and Príncipe, and extensive inventories have since been conducted on Príncipe (Benitez et al. 2018) and on São Tomé (Flora Ameaçada 2021). An updated calculation indicates that 1285 species and infraspecific taxa (1028 native) are known to occur on the three islands (Table 10.1). Príncipe has 445 species and infraspecific taxa (394 native), São Tomé has 1044 (842 native), and Annobón has 344 (274 native). Príncipe has the highest proportion of native flora (88.5%), followed by São Tomé (80.7%), while Annobón has the lowest (79.7%).

The three most species-rich families are Orchidaceae (163 taxa), Rubiaceae (94 taxa), and Fabaceae (86 taxa); however, many of the Fabaceae are not native (Table 10.2). Euphorbiaceae *s.l.*, as previously delimited, was one of the most speciose families, but its members have recently been divided among Euphorbiaceae *s.str*. (44 taxa) and Phyllanthaceae (27 taxa).

The genera with the most species and infraspecific taxa are *Asplenium* L. (28), *Bulbophyllum* Thouars (27), and *Polystachya* Hook. (26) (Table 10.3), all of which are wind-dispersed.

Table 10.1 Family, genus, species, and infraspecific taxon richness on each of the three oceanic islands of the Gulf of Guinea

	Príncipe	São Tomé	Annobón	Total
Families	94	143	90	**155**
Genera	264	561	241	**627**
Species and infraspecific taxa richness (SR)	445	1044	344	**1285**
SR native	394	842	274	**1028**
% of the flora which is native	88.5	80.7	79.7	**80.0**
Individuals	1876	8182	773	**11,388**

The number of native species or infraspecific taxa is given as well as the native proportion of each island’s flora

Table 10.2 The most species-rich families on the oceanic islands of the Gulf of Guinea

	SR	Príncipe	São Tomé	Annobón	Grand total
Orchidaceae	163	85	125	25	**235**
Rubiaceae	94	46	73	18	**137**
Fabaceae	86	14	70	38	**122**
Poaceae	46	4	40	24	**68**
Euphorbiaceae	44	14	32	12	**58**
Cyperaceae	34	8	25	14	**47**
Asteraceae	31	2	28	9	**39**
Aspleniaceae	28	14	25	5	**44**
Phyllanthaceae	27	14	20	6	**40**
Malvaceae	26	1	21	12	**34**

Numbers indicate specific and infraspecific taxon richness (SR) for all islands taken together and for each individual island. The grand total represents the total number of species-presences recorded across the islands

Table 10.3 The most species-rich genera on the oceanic islands of the Gulf of Guinea

	SR	Príncipe	São Tomé	Annobón	Grand total
Asplenium	28	14	25	5	**44**
Bulbophyllum	27	14	20	4	**38**
Polystachya	26	12	21	6	**39**
Cyperus	22	2	16	11	**29**
Psychotria	13	4	12	2	**18**
Ipomoea	12	2	8	4	**14**
Begonia	11	5	10	2	**17**
Ficus	11	3	10	3	**16**
Pteris	11	7	9	1	**17**
Desmodium	10	1	9	9	**19**

Numbers indicate specific and infraspecific taxon richness (SR) for all islands taken together and for each individual island. The grand total represents the total number of species-presences recorded across the islands

Main Findings of the Botanical Expeditions on São Tomé and Príncipe, 2019–2020

To improve the documentation of the current floristic diversity of São Tomé and to identify conservation priorities, several botanical expeditions were undertaken between 2019 and 2021 (Flora Ameaçada 2021). Various localities across the island were visited, from the dry North to the wet South, and from the coast to the summit of the Pico de São Tomé at 2024 m, covering most vegetation types. More than 90% of the endemic woody species were seen during this fieldwork. Some very rare species were rediscovered, including *Balthasaria mannii* (Oliv.) Verdc., 1969 (Pentaphylacaceae) (Fig. 10.4.2–4), and *Psychotria exellii* R. Alves, Figueiredo and A.P. Davis, 2005 (Rubiaceae), both restricted to near the summit of the Pico

Fig. 10.4 Species endemic to São Tomé and Príncipe: (**1**) *Santiria balsamifera* Oliv., 1887 (Burseraceae); (**2–4**) *Balthasaria mannii* (Oliv.) Verdc., 1969 (Theaceae); (**5**) *Cleistanthus sp. nov.* (Euphorbiaceae); (**6**) *Impatiens manteroana* Exell, 1944 (Balsaminaceae). Photos credits: (**1**, **6**) Tariq Stévart, (**3–5**) Olivier Lachenaud, (**2**) Gilles Dauby

de São Tomé and not seen for more than 50 years. Even more interesting is the finding of at least 17 species new to science—a number likely to increase as the ongoing identification of specimens continues. The most remarkable of these is a new species of *Cleistanthus* Hook. f. ex Planch., 1848 (Phyllanthaceae) (Fig. 10.4.5), which is the dominant tree of dry forest remnants in the North of the island. Several earlier collections of this species are deposited in herbaria, but they had not yet been identified. Although locally abundant, the new species of *Cleistanthus* is highly threatened by wood exploitation and charcoal production, and its habitat is in need of protection. In addition, 42 species represent new country records for São Tomé and Príncipe, most of which are widespread on the mainland. One of them, *Phyllocosmus sessiliflorus* Oliv., 1868 (Ixonanthaceae), is the first record of its family from the islands. Other species previously known from the country are new island records, namely five for São Tomé and 26 for Príncipe.

Complementing the efforts undertaken since 2016 to understand tree diversity in the southern forests of Príncipe (Benitez et al. 2018), since 2019, several botanical expeditions have focused on the drier North (Flora Ameaçada 2021). This work included areas of secondary or presumably degraded forest, extending from coastal and lowland forests to the northern plateau of the island, but also involved collecting in areas in the south that had not been assessed during previous years, such as the summit of Pico do Príncipe (947 m). These inventories resulted in the discovery of eight species new to science, six of which are only known from Príncipe.

Endemism

The flora of the Gulf of Guinea Islands comprises approximately 1700 indigenous species of angiosperms (Figueiredo 1994b), and is well known for its high level of endemism. Bioko is a continental island, while Príncipe, São Tomé and Annobón are oceanic, never having been connected to the mainland or to one another. It is therefore not surprising that Bioko has a more speciose flora (1558 species, Velayos et al. 2013b), but exhibits much lower levels of endemism (3.6% according to Exell 1973).

Of the 1028 indigenous species and infraspecific taxa documented from Príncipe, São Tomé, and Annobón, approximately 164 are endemic (Table 10.4, Figs. 10.4, 10.5, 10.6 and 10.7), yielding a rate of endemism of about 16%. Estimates for endemism on Príncipe have varied significantly over the years, from 12.7% (Exell 1944), to 9.9% (Exell 1973), and to the current 14.7% for vascular plants (Table 10.4). Calculations of endemism in São Tomé have decreased from 19.4% (Exell 1944) to 15.4% (Exell 1973) and the current 14.5% (Table 10.4). On Annobón, they are estimated to be at 6.9% (Table 10.4).

The families with the largest numbers of endemic taxa are Orchidaceae (30), Rubiaceae (29), and Euphorbiaceae *s.str.* (15) (Table 10.5). The genera *Polystachya* (Orchidaceae), *Begonia* L., 1753 (Begoniaceae) and *Psychotria* L., 1759 (Rubiaceae) have the largest numbers of endemic species (Table 10.6). Some

Table 10.4 Plant endemism in the oceanic islands of the Gulf of Guinea (including 17 putative new species)

	Príncipe	São Tomé	Annobón	Total
Single-island endemic species	28	90	14	**132**
Shared endemics between islands	30	32	5	**32**
Total endemics	58	122	19	**164**
Indigenous species	394	842	274	**1028**
Endemic rate (3 islands)	14.7	14.5	6.9	**16.0**
Endemic rate (strict)	7.6	3.8	1.8	**3.1**

emblematic endemic species are the gigantic species *Begonia baccata* Hook.f., 1866 and *Begonia crateris* Exell, 1944, which can reach a height of 4 m. *Afrocarpus mannii* (Hook.) C.N. Page, 1988 (Podocarpaceae), the only native gymnosperm, is endemic to São Tomé and is widely grown in many botanic gardens around the world. The proportion of endemic species tends to increase with elevation with an endemic rate between 20 and 25% in the highlands of the three islands (Fig. 10.3).

Conservation

From 1998 to 2020, risk of extinction assessments were performed for 285 native and introduced plant species from Príncipe, São Tomé, and Annobón Islands (IUCN 2021). These taxa belonged to 207 genera and 86 families, and over 13% are endemic to São Tomé and Príncipe. *Cyperus* L., 1753 (Cyperaceae) is the best-represented genus, with twelve species assessed; the remaining genera are represented by between one and four species each. Seven families have more than ten species assessed: Orchidaceae (34.9% of all species assessed), Fabaceae (29.1%), Cyperaceae (24.4%), Rubiaceae (23.3%), Euphorbiaceae (17.4%), Apocynaceae and Phyllanthaceae (11.6% each). Thirty-two assessments were made in 1998 and 62 more were done between 2000 and 2017. The number of species assessed has more than doubled between 2018 and 2020 (Fig. 10.8). Of the 285 species evaluated to date, 0.7% are Data Deficient, 19.3% are threatened (3 Critically Endangered, 21 Endangered, and 31 Vulnerable), and 78.3% are Least Concern or Near Threatened. Two Orchidaceae species (*Angraecopsis dolabriformis* (Rolfe) Schltr., 1918 and *Angraecum astroarche* Ridl., 1887) are considered Extinct (Simo et al. 2018a, b), since they were not recorded after intensive surveys in the locations where they had previously been documented. The number of species assessed as threatened per year has decreased over time, even though the total number of assessments performed each year has increased: 22 of 32 species were assessed as threatened in 1998, compared to just 21 of 191 assessments done over the last three years (Fig. 10.7; Table 10.7). This is partly due to numerous recent assessments on widespread non-threatened tree species (e.g., *Symphonia globulifera* L. f., 1782, *Xylopia aethiopica* (Dunal) A. Rich., 1845, *Cola digitata* W. Mast.,

Fig. 10.5 Species endemic to São Tomé and Príncipe: (**1**) *Carapa gogo* A. Chev. ex Kenfack, 2011 (Meliaceae); (**2–3**) *Palisota pedicellata* K.Schum., 1897 (Commelinaceae); (**4**) *Polystachya expansa* Ridl., 1887 (Orchidaceae); (**5**) *Pandanus thomensis* Henriq., 1887 (Pandanaceae); (**6–7**) *Lobelia barnsii* Exell, 1944 (Campanulaceae); (**8–9**) *Impatiens buccinalis* Hook.f., 1864 (Balsaminaceae). Photo credits: (all, except **6**) Tariq Stévart, (**6**) Gilles Dauby

Fig. 10.6 Species endemic to São Tomé and Príncipe: (**1**) *Thunbergianthus quintasii* Engl., 1897 (Scrophulariaceae); (**2**) *Costus giganteus* Welw. ex Ridl., 1887 (Costaceae); (**3**) *Rhipidoglossum pendulum* (la Croix & P.J.Cribb) Farminhão & Stévart, 2018 (Orchidaceae); (**4**) *Dicranolepis thomensis* Engl. & Gilg, 1894 (Thymelaeaceae); (**5**) *Tabernaemontana stenosiphon* Stapf, 1895 (Apocynaceae); (**6**) *Leea tinctoria* Lindl. ex Baker, 1868 (Leeaceae); (**7**) *Elatostema thomense* Henriq., 1892 (Urticaceae); (**8**) *Begonia crateris* Exell, 1944 (Begoniaceae); (**9**) *Erica thomensis* (Henriq.) Dorr & E.G.H.Oliv., 1999 (Ericaceae). Photo credits: (all, except **8**) Tariq Stévart, (**8**) Olivier Lachenaud

Fig. 10.7 Species endemic to São Tomé and Príncipe: (**1**) *Erica thomensis* (Henriq.) Dorr & E.G. H.Oliv., 1999 (Ericaceae); (**2**) *Chytranthus mannii* Hook.f., 1867 (Sapindaceae); (**3**) *Strephonema sp. nov.* (Combretaceae). Photo credits: (**1**) Davy Ikabanga, (**2**) Laura Benitez, (**3**) Tariq Stévart

1868, and *Santiria trimera* (Oliv.) Aubrév., 1948) (Fig. 10.4.1). Some species require better knowledge before they can be assessed (e.g., *Santiria trimera*) or are outside of their native range (*Coffea arabica* L., 1753), and therefore their presence

Table 10.5 The ten families with the largest number of endemic species and infraspecific taxa on the three oceanic islands of the Gulf of Guinea

Family	Príncipe	São Tomé	Annobón	Total
Orchidaceae	10	22	2	**30**
Rubiaceae	10	21	3	**27**
Euphorbiaceae	6	11	2	**15**
Begoniaceae	2	5		**6**
Melastomataceae		5	2	**6**
Sapotaceae	2	2		**4**
Violaceae	1	3		**4**
Acanthaceae		3		**3**
Aspleniaceae	1	2	1	**3**
Balsaminaceae	1	2		**3**

Numbers indicate specific and infraspecific taxon richness (SR)

Table 10.6 The ten genera with the largest number of endemic species and infraspecific taxa on the three oceanic islands of the Gulf of Guinea

Genus	Príncipe	São Tomé	Annobón	Total
Polystachya	4	5	1	**8**
Psychotria		8		**8**
Begonia	2	4		**6**
Diaphananthe	2	2		**4**
Rinorea	1	3		**4**
Tristemma		3	1	**4**
Asplenium	1	2	1	**3**
Cassipourea	1	1	1	**3**
Chassalia	2	2		**3**
Dryopteris		2	1	**3**

Numbers indicate specific and infraspecific taxon richness (SR)

on these islands is irrelevant for Red Listing, and they were not included in this analysis. For example, a recent taxonomic revision of *Santiria* Blume, 1850, in Africa revealed that a threatened species (*S. balsamifera* Oliv., 1886) occurs on São Tomé and Príncipe (Ikabanga et al. 2019). Additional efforts will be needed to assess other endemic and range-restricted species to enable a more accurate assessment of the true proportion of threatened plant species on the oceanic islands of the Gulf of Guinea.

Recent Red List activities and field expeditions have shown that the flora of São Tomé and PrÚncipe is highly threatened, in addition to historical threats that have ceased, such as large-scale plantations that profoundly changed the natural vegetation of the two islands (Muñoz-Torrent et al. 2022). On Príncipe, current threats are relatively limited and not clearly defined, but certainly include the development of infrastructure for tourism (Lima et al. 2022), whose impact on the flora remains to be quantified. The development of human activities adds pressure on the remaining forests in the north, which are already threatened by small-scale agriculture, charcoal production, firewood collection, and logging (D'Avis 2022). The collection and use of medicinal plants are also subjecting some species to the risk of local extinction.

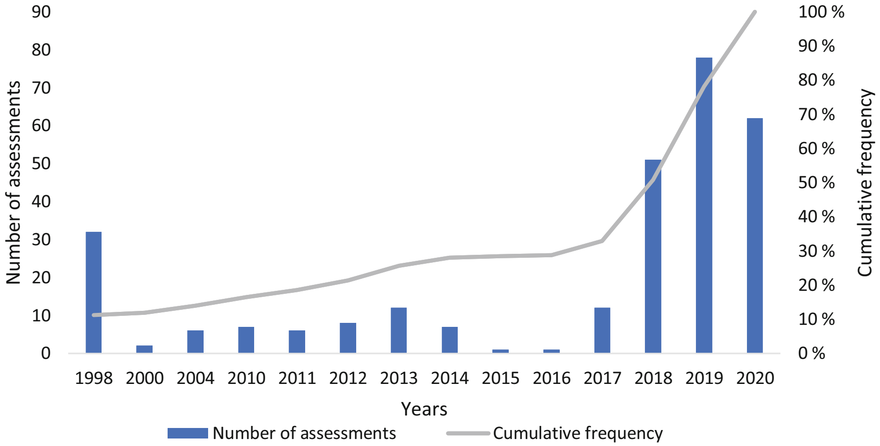

Fig. 10.8 Progress of the number of risk of extinction assessments made for species occurring on Príncipe, São Tomé, and Annobón islands from 1998 to 2020

Table 10.7 Number of threatened species recorded on Príncipe, São Tomé, and Annobón islands from 1998 to 2020

	Threatened species			
Years	CR	EN	VU	Total
1998	0	1	21	22
2000	1	0	0	1
2004	0	2	4	6
2013	0	1	1	2
2014	0	1	3	4
2018	2	9	0	11
2019	0	1	1	2
2020	0	6	1	7
Total threatened species				**55**

Indeed, most of the plants harvested by traditional healers and by commercial sellers who collect medicinal plants for alcoholic beverages come from forests, and very few plants are cultivated for medicinal purposes. On São Tomé, threats include local logging around the parks, and the widespread presence of invasive species (Lima et al. 2022). These threats do not affect most species directly, but they impact the quality of their habitat. The most severe current threats on São Tomé are, however, the presence of an oil palm plantation in the southwest of the island, and charcoal production is also an important threat, especially in the north (Oyono et al. 2014). These activities have expanded in recent years and directly impact populations of plant species. On Annobón, plants occurring in almost all parts of the island are threatened by small-scale agriculture. The dry northern part of the island, from the sea to Lake Apot, is particularly heavily impacted by agriculture, urbanization, and infrastructure construction (Norder et al. 2020).

The Medicinal Plants of São Tomé and Príncipe

Many medicinal plants have been used for centuries on São Tomé and Príncipe and are often the only available therapeutic agents. Until the end of the twentieth century, uses were not well documented, and few ethnopharmacological studies had been conducted on the medicinal plants used by the population of the two islands. Between 1993 and 2001, an exhaustive collection of the medicinal flora was conducted to record ethnomedical information from the most renowned local traditional healers. More than 350 taxa were identified, for which voucher specimens were deposited at the University of Coimbra herbarium (COI), and more than 1000 traditional preparation procedures and their respective uses were recorded (Madureira et al. 2003). Exhaustive bibliographic research was also conducted, resulting in a monograph for each species containing traditional uses and scientific data (Madureira et al. 2003; Madureira 2006, 2010).

These investigations show a strong correlation between the traditional use of most medicinal plants and their proven pharmacological activity, demonstrating that many of them have a recognized efficacy: e.g., *Spermacoce verticillata* L., 1753, *Desmodium adscendens* (Sw.) DC., 1825, *Dracaena arborea* (Willd.) Link, 1821, *Phyllanthus amarus* Schumach. & Thonn., 1827, *Phyllanthus urinaria* L., 1753, *Piper capense* L.fil., 1781, *Scoparia dulcis* L. 1753 (Madureira 2006, 2008), along with *Tithonia diversifolia* (Hemsl.) A. Gray, 1883, an introduced species that has antimalarial activity and could be a very interesting alternative to commercially available antimalarials (Madureira 2010). An analysis of the composition of essential oils from eighteen species widely used in traditional medicine for the treatment of infections was carried out, and the preliminary study of the antibacterial and antifungal activities of these essential oils proved their activity, highlighting the oils of *Cymbopogon citratus* (DC.) Stapf, 1906, *Ocimum gratissimum* l., 1753, *Santiria balsamifera* and *Zingiber officinale* Roscoe, 1807, which showed the best activities (Martins 2002). Some of these medicinal plants have been studied for their antiviral properties (*Phyllanthus amarus*, *Scoparia dulcis*, *Momordica charantia* L., 1753, and *Margaritaria discoidea* (Baill.) G.L. Webster, 1967). Other species have shown some promising results regarding their antitumor activity, such as *Desmodium adscendens*, *Piper capense*, and *Momordica charantia* (Madureira 2008), and more recently the identification of natural compounds from *Voacanga africana* Stapf, 1894, that show multiple biological activities of interest for Alzheimer's disease (Currais et al. 2014).

The families with the largest numbers of species used for medicinal purposes are Euphorbiaceae (13 species), Asteraceae (12), Rubiaceae (11), Moraceae (10), Malvaceae (9), Rutaceae (8), and Apocynaceae (7). The fact that many families (57) and genera (134) are represented on the list of medicinal species illustrates the high level of knowledge of the flora among traditional healers, and it is possible to infer that there are a great variety of chemical structures and pharmacological activities among the medicinal plants collected in the region.

The traditional uses of the medicinal plants are highly diverse: analgesic, anti-inflammatory or anti-rheumatic action represent the main group of traditional records (218), followed by diseases of the digestive system (204); diseases related to the respiratory system represent the third group with 179 traditional records; genito-urinary system (134); skin diseases (97); traditional medicines for the treatment of febrile conditions (38) and malaria (23); diseases of the cardiovascular system (43); 14 preparations for the treatment and control of diabetes, and 16 indications for diseases of the central nervous system. Finally, on São Tomé and Príncipe, many medicinal plants are also used for food, representing about 15.0% of the total species collected for medicinal purposes (Madureira 2012).

Among the 350 medicinal species used, 37 are endemic to the islands of the Gulf of Guinea (e.g., *Tabernaemontana stenosiphon*, *Begonia baccata*, *Croton stellulifer* Hutch. 1944, *Hernandia beninensis* Welw. ex Henriq., 1892, *Staudtia pterocarpa* Warb., 1897, *Pandanus thomensis* Henriq., 1887, *Afrocarpus mannii*, *Chytranthus mannii* Hook.f., 1867, and *Costus giganteus* Welw. ex Ridley, 1887), which indicates an evident dynamism of the local traditional medicine, with traditional healers maintaining and perfecting their traditional therapeutic wisdom, and taking advantage of the native available resources of São Tomé and Príncipe.

Improving Local Botanical Practices and Knowledge

The literature review for this chapter revealed a heavy reliance on a few key publications for the identification of medicinal plant species based on local vernacular names (Rozeira 1958; Roseira 1984; Figueiredo 2002; Figueiredo et al. 2011), the majority of which lack the citation of voucher specimens. Vernacular names are important for identification of plants locally, but to be reliable and of use for scientific studies, they must be unambiguously linked to scientific names, which requires the collection and storage of voucher specimens. This need is particularly pressing considering that local names vary from region to region, sometimes multiple species having the same name, or multiple names referring to a single species (e.g., Figueiredo et al. 2011). This is especially true in the case of medicinal plant parts that are sold in the markets, for which accurate identification to species is even more difficult, but also for ecological studies such as tree inventories, which have so far mostly used local names (e.g., Salgueiro and Carvalho 2001).

Basic botanical skills are also largely lacking, especially with respect to plant taxonomy and botanical nomenclature. The correct botanical name of an individual plant, linked to a voucher specimen, is the sine qua non of phytomedical research. Without the unique taxonomic identifier, research cannot accurately be linked to the existing literature. This uncertainty, thus obstructs the accuracy and reproducibility of results—a cornerstone of science. It is therefore vital to increase local scientific literacy, and continue training local botanists with different skills, from field identification, to the management of herbarium specimens, and more advanced scientific capacities to ensure increased local autonomy for research and conservation. To overcome these handicaps, the publication of a practical field guide to facilitate plant identification and stimulate the interest for botany is highly recommended.

Concluding Remarks

Significant collecting effort, especially since 2016, has created a huge updated wealth of information for the islands, which is readily available online (Tropicos 2021). Nevertheless, this information is still being compiled and will require extensive taxonomic work and numerous publications until it can produce an updated vascular plant checklist for the islands. The same is true for Red List assessments, many of which seem to be focusing on species that are widespread, while endemic and range-restricted species that are more likely to be threatened remain unassessed. This calls for a major, consolidated focus on conservation assessments, which are currently being conducted through several mostly uncoordinated projects. The results of this work could and should then be used to identify new priority sites for conservation (D'Avis 2022; Lima et al. 2022), including on Annobón, where priority sites are less well defined.

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Chapter 11
A Checklist of the Arachnids from the Gulf of Guinea Islands (Excluding Ticks and Mites)

Sarah C. Crews and Lauren A. Esposito

Abstract While historic efforts to document the arachnofauna of the Gulf of Guinea islands have primarily been the result of fortuitous collecting by non-specialists, recent efforts have been made to provide a more thorough documentation using systematic, targeted collecting methods. Results from those preliminary efforts indicate that the current formal scientific knowledge of the fauna is significantly underreported. Here, we present the first checklist of all arachnid species, excluding mites and ticks, for the Gulf of Guinea islands. We hope that this will serve as a guide to begin the immense work of documenting the true diversity represented in this unique archipelago.

Keywords Diversity · Scorpion · Spider · Survey

Introduction

This chapter provides a preliminary account of the arachnids that occur on the islands of Bioko, Príncipe, São Tomé, and Annobón. We treat our assessment as preliminary because to comprehensively determine which arachnids inhabit a place, systematic, multi-year, seasonal surveys are critical. For many arachnid species, the annual lifecycle is temporal, often with adult males and females more common at particular times of the year (Cardoso et al. 2009). Standardized collecting methods have been proposed for arachnids, which allow for a more effective estimate of species richness when collecting efforts are limited (e.g., Malumbres-Olarte et al. 2016). To date, however, this type of surveying for arachnids has not been undertaken on any of the Gulf of Guinea islands. In fact, nearly all of the historical collectors of arachnids in the region, including West and Central Africa, collected them opportunistically while making general collections of flora and fauna or targeting other organisms. The lack of methodical collecting across much of the

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African continent and the monumental work needed for subsequent taxonomic investigation also hinders our ability to discern whether species recorded from the islands are endemic or are also present on the mainland. Consequently, our current knowledge of the arachnid fauna of the islands is far from complete given the few historical or contemporary surveys dedicated to documenting arachnid diversity and minimal taxonomic study of most major groups. Here we summarize what is (and likely is not) known about the arachnid diversity of the Gulf of Guinea archipelago in the hopes that it will inspire and guide future research on this understudied group.

Arachnids are a diverse and ancient group (>430 my old) of primarily terrestrial arthropods. There are 11 extant orders, all of which are known from mainland Africa, with 8 known from the Gulf of Guinea islands. While Acari, or ticks and mites, are present, we do not discuss them here. They are typically treated separately in arachnid faunal overviews and surveys because, although they are arachnids, they are extremely diverse and even more poorly known than other arachnids. Their life histories and habits differ greatly from the other arachnids in that many are plant or animal parasites or live in soil.

There are three orders of arachnids that have not yet been found on the Gulf of Guinea islands, although they are known from the adjacent mainland. One of these orders is the Palpigradi, or microwhip scorpions, which are very small, pale, eyeless animals that live interstitially in leaf litter, caves, or cracks deep in the ground. They are found worldwide, but due to their cryptic habits and small size, fewer than 100 species have been described (Harvey 2013a). The other two orders, however, are not minute. These are the Solifugae, or sun spiders, and the Thelyphonida, or whip scorpions. The former consists of about 1000 species that are primarily found in dry habitats, while the latter has only about 100 species described from a wide variety of tropical and sub-tropical ecosystems (Harvey 2013e; Murienne et al. 2013). Although they are not small, whip scorpions are burrowers, thus not easily detected, and there is only a single species known from Africa (Huff and Prendini 2009). Below, we discuss the seven other orders: Amblypygi or whip spiders, Opiliones or harvestmen, Pseudoscorpiones or pseudoscorpions, Ricinulei or hooded tickspiders, Schizomida or short-tailed whip scorpions, Scorpiones or scorpions, and include a focused discussion of the most diverse group, the Araneae or spiders.

A Brief History of Arachnological Research

In the 1700s and 1800s, most arachnid collecting in the Gulf of Guinea was done by naturalists making general collections of extant flora and fauna as well as fossils. The specimens were then sold or donated to European museums, where they were divvied up and given to experts on the various groups, who then described new species and/or published a species list. Ferdinand Karsch (1884) was likely the first arachnologist to focus specifically on arachnids from the Gulf of Guinea islands. He received the specimens for his study from Professor Richard Greeff of Marburg, who had lived on São Tomé and Príncipe islands for several months in 1879–1880.

Greeff made some of the first maps of the islands and collected everything from crinoids (echinoderms) to sipunculids (peanut worms) to geckos and published his results in 1884. Other authors published smaller works on the island fauna, including Vieira (1893) and Pocock (1900), the latter of whom described some theraphosid spiders that had been purchased by trustees of the British Museum.

Leonardo Fea from the Museum of Natural History in Genoa, Italy made trips to Asia and Africa in the late 1800s to the early 1900s, spending 1900–1902 on São Tomé and Príncipe, Bioko, and Annobón, and 1902 in Cameroon and the French Congo (now the Republic of Congo, Gabon, and Central African Republic). Although primarily collecting specimens for his malacological and geological research, he also collected several arachnids. These specimens eventually made their way to perhaps the most prolific arachnologist of all time, Eugene Simon from the Natural History Museum in Paris. In the early 1900s, Simon began describing and cataloging a large collection that comprises the most comprehensive arachnid publications of the region (1907, 1909–1910), where he included a brief tribute to Fea who had died in 1904.

Following Simon's work, there were a number of important publications in the 1900s. Hansen (1921) described harvestmen and other small arachnid groups primarily from the Fea collection. Roewer later described many of the harvestmen from Fea's collection in a series of papers (1927, 1942, 1949). Additional research was conducted by Amélia Bacelar (1956), the first woman to formally study Gulf of Guinea arachnids, and also by Otto Kraus (1960). The latter was on an expedition to the "Gulf of Guinee" led by Herrn P. Viette on the Calypso (The Calypso was owned by Jacques Cousteau, purchased in 1950, so he also was likely on this trip, but there is no mention of him specifically). Prieto more recently published on the harvestmen of Bioko and Annobón (Prieto 1999). In 1998, arachnologist Darrell Ubick of the California Academy of Sciences (CAS) visited Bioko. Ubick's 1998 collection from Bioko was the first targeted collection of arachnids in the region, resulting in over 5000 specimens that are deposited at CAS. A preliminary report published on the material identified 372 morphospecies, with 9 families and 5 genera otherwise undocumented from the region (Griswold et al. 1999). A series of trips to São Tomé and Príncipe have been made by other CAS arachnologists, including Charles Griswold and Joel Ledford in 2001, Tamas Szűts in 2013, and Lauren Esposito in 2016, and will likely yield undescribed species.

Arachnids of the Gulf of Guinea Islands

Here we have compiled a list of spider, scorpion, whip spider, harvestmen, hooded tickspider, pseudoscorpion, and short-tailed whipscorpion species from the Gulf of Guinea islands based on the published works mentioned above, community science observations documented using iNaturalist (iNaturalist 2021), the World Spider Catalog (WSC 2021), and the Western Australian Museum catalogs for the smaller arachnid groups (Harvey 2013a, b, c, d, e, f). The majority of specimens mentioned or described in publications are singletons—single individuals from unique localities. However, there are many caveats. For example, in Simon's papers, specimens are listed as being from specific localities (i.e., a particular island), whereas in the WSC, the available information is provided at the country level without further specificity, with Bioko often included only as Guinea. Two of the species described from Fea's material were not associated with any locality data beyond the region as a whole; consequently, due to the large geographic scope of his surveys, they could have originated from any of the islands and/or the mainland. Given the paucity of data from the region, we chose to err on the side of inclusion for compiling a list of arachnids from the Gulf of Guinea oceanic islands. In particular, we include taxa reported from the land-bridge island in the archipelago, Bioko, because species reported from this island may also occur on the oceanic islands. We have also analyzed publication information to assess the quantity of research conducted on arachnid fauna of the area as a way of beginning a conversation on the remaining work required before major evolutionary questions (i.e., biogeography) can be addressed within these diverse lineages.

Order Amblypygi

The amblypygids or whip spiders are a modestly diverse group of predatory arachnids with approximately 150 extant species found in tropical and sub-tropical regions around the world (Harvey 2013f). All amblypygids lack silk glands and are not venomous. Their first pair of legs are highly modified sensory organs that give the appearance of antennae or whips, and their chelicerae are modified into raptorial claw-like structures (Fig. 11.1). Amblypygids are often found in leaf litter and caves, and all species are nocturnal. Four species in two genera (*Charinus*, *Damon*) are known from the Gulf of Guinea islands, three of which (all *Damon*) are confirmed to also occur in continental Africa (Appendix) (Harms 2018).

Order Araneae

The Araneae or spiders are the most diverse arachnid group, with nearly 50,000 described species (WSC 2021). Spiders have chelicerae with fangs, and most species use these to inject venom into their prey, which range from insects to other spiders and small vertebrates (Fig. 11.1). Although the venom of some species can be dangerous to humans, most species do not pose a risk. Spiders also have spinnerets that extrude silk, which is used to build webs for prey capture, make retreats and egg sacs, for mating purposes, as well as dispersal via ballooning.

A total of 213 spider species have been recorded from the Gulf of Guinea islands, encompassing 48 families and 136 genera (Appendix). The most speciose spider families from the islands are Araneidae (40 species), Salticidae (33), Tetragnathidae

Fig. 11.1 Representative Arachnids from the Gulf of Guinea islands: (**1**) *Hysterocrates sp.* (spider); (**2**) *Gasteracantha thomasinsulae* (spider); (**3**) Assamiidae (harvestman); (**4**) *Damon medius* (whip spider); (**5**) *Nilus* sp. (spider) predating on frog; (**6**) pseudoscorpion; (**7**) *Pandinus imperator* (scorpion); (**8**) *Ricinoides* sp. (hooded tickspider). Photo credits: (**1**) Guy Tansley, (**2**) Brian Simison, (**3**, **6**) Gonzalo Giribet, (**4**) John Sullivan, (**5**) Andrew Stanbridge, (**7**) Nik Borrow, (**8**) Beat Akeret

(15), and Lycosidae (12). All other families have fewer than ten recorded species, which likely reflects poor collecting of several groups, including good dispersers or those with cryptic ecologies. Singleton families (families from which only a single species is known) make up 35% of the familial diversity on the islands. Several dozen species were described based on material collected from the oceanic islands in the archipelago and are not known to occur in continental Africa, suggesting they may be island endemics.

Order Opiliones

The Opiliones are commonly referred to as harvestmen and contain over 6500 described species distributed worldwide. Although they appear superficially similar to spiders (Araneae), they are not closely related and do not possess venom glands (Fig. 11.1). They also do not have silk glands and thus do not build webs. Collectively, 34 species in 7 families are known from the Gulf of Guinea islands, 10 of which are confirmed to also occur in continental Africa (Appendix).

Order Pseudoscorpionida

Pseudoscorpionida, commonly known as pseudoscorpions, are small arachnids, typically around 3 mm in length, with pincer-like pedipalps similar to those of scorpions (Fig. 11.1); however, unlike scorpions, some pseudoscorpions deliver venom with their pedipalps rather than a stinger on a tail, which they lack. This group includes over 3300 described species that occur in many kinds of environments, but they are often overlooked due to their size (Harvey 2013b). Pseudoscorpions spin silk from a specialized gland in their jaws to produce a cocoon. Thirteen species in four families are known from the Gulf of Guinea islands, eight of which are confirmed to also occur in continental Africa (Appendix).

Order Ricinulei

The Ricinulei are commonly known as hooded tickspiders but are not true spiders (Fig. 11.1). This group is not very diverse, with ~75 extant species described from tropical Africa and the Neotropics (Harvey 2013c). One species, *Ricinoides crassipalpe,* is documented from Bioko Island, and it is also found in continental Africa (Appendix). It is unclear whether any representatives of this enigmatic order occur on the oceanic islands in the Gulf of Guinea.

Order Scorpiones

The Scorpiones, commonly known as scorpions, are easily recognized by their grasping pincers and curved, segmented tail with a stinger (Fig. 11.1). This group includes over 2500 described species that can be found in a variety of habitats around the globe (Fet et al. 2000). Because their exoskeletons contain fluorescent compounds, scorpions glow under ultraviolet light, facilitating detection at night. Although all scorpions produce venom, most species do not pose a risk to humans. Three species in two families are known from the Gulf of Guinea islands (Appendix), all of which are also found in continental Africa. The only species known from an oceanic island in the archipelago is *Isometrus maculatus*, which is introduced on São Tomé (see below).

Order Schizomida

The Schizomida, commonly known as short-tailed whipscorpions, superficially resemble true scorpions but have a short tail that lacks a stinger, and their first pair of legs is antenniform. This group includes over 230 described species that can be found in tropical and sub-tropical habitats worldwide, with a few species occupying temperate habitats (Harvey 2013d). Only one species is known from the Gulf of Guinea islands, *Schizomus parvus*, which is documented from both São Tomé and Bioko islands (Appendix).

Diversity, Endemism, and Introduced Species

Based on the current literature, araneids are the most species-rich arachnid group in the Gulf of Guinea. Araneidae are the most diverse spider lineage on many tropical islands (e.g., Caribbean: Crews et al. 2015; Crews and Yang 2016), though some studies of tropical island spider diversity have found higher numbers of salticid species (Caribbean: Crews et al. 2019; Southeast Asia: Ponce et al. 2021). Salticids and some araneids (e.g., *Gasteracantha,* nephilines) are diurnal, the latter often with large aerial webs that would be more obvious to a non-spider specialist, whereas many of the other families have species that are nocturnal or that do not build aerial webs. Thus, for the Gulf of Guinea, it is difficult to know whether the large number of salticid and araneid species reported is due to a collecting artifact (i.e., non-targeted collecting) or if it is representative of the true diversity. For instance, sub-tropical island surveys employing standardized collecting have reported the highest species diversity of small and cryptic linyphiid spiders, underscoring the limitations of extrapolating from opportunistic sampling efforts (Macaronesia: Malumbres-Olarte et al. 2016, 2020). Likewise, although crab spiders (Thomisidae) and lynx spiders (Oxyopidae) are diurnal, they are generally cryptic or ground-living and easily overlooked. Targeted collecting methods to comprehensively survey arachnid diversity include vegetation beating, leaf litter sifting combined with malaise or Winkler traps, visual night searching for nocturnal arachnids using white and ultraviolet light, turning rocks and logs, and pitfall traps.

Of particular note in the Gulf of Guinea archipelago is the high diversity of tetragnathid species, likely owing to their relatively good dispersal ability and the extremely high humidity and abundance of freshwater on the islands, and mygalomorph families (Barychelidae, Cyrtaucheniidae, Ischnothelidae, Migidae, Theraphosidae). A preliminary report on a targeted spider collection on Bioko identified 81 theridiid morphospecies, 45 salticid morphospecies, 39 araneid morphospecies, and 32 linyphiid morphospecies. This far exceeds the 8, 14, 25, and 5 species, respectively, that have been formally documented from the island (Griswold et al. 1999).

The total number of spider species on each island is somewhat unclear because the literature and WSC often provide the country or general region rather than a specific island. What we do know is that São Tomé and Príncipe together have 130 recorded species, and that 33 (33%) of the 101 species that have specific locality data are from Príncipe and 51 (50%) from São Tomé. Ten species are known from Annobón and 91 from Bioko. Of the 211 species documented from the archipelago, 113 also occur on the mainland. The remaining ~100 species may be endemic to one or more of the islands, but more comprehensive sampling of continental diversity is needed to confirm their endemic status.

Based on the available records, however, Príncipe has 20 endemic species in 13 families (17 genera), and 61% of the families and 82% of the genera are represented from singletons. São Tomé has 23 endemic species (only slightly more than Príncipe based on the depauperate data) in 9 families and 13 genera, and 69% of the families and 82% of the genera are singletons. Bioko has 27 endemic species in 16 families and 27 genera, with 69% of families and 93% of genera represented by singletons. Annobón has two endemic species recorded: *Thoriosa taurina* (Simon 1909) (Ctenidae) and *Hogna furva cingulipes* (Simon 1909) (Lycosidae).

We can also examine the arachnid fauna of each island for instances of multiple closely related endemic species, which may point to within-island species radiations and provide further evidence that the taxa are indeed island and/or archipelago endemics. The only (non-introduced) genera shared between São Tomé, Príncipe, and Bioko are *Castianeira* (Corinnidae) (São Tomé and Bioko), *Mallinella* (Zodariidae) (Príncipe and Bioko), and *Tetragnatha* and *Leucauge* (Tetragnathidae) (São Tomé, Príncipe and Bioko). Genera with multiple species on a single island occur in the salticids *Maltecora* (2 in Príncipe, 1 on São Tomé) and *Belippo* (3 on São Tomé), and the theraphosid *Hysterocrates* (3 on São Tomé, 1 on Bioko). A number of (likely) introduced species are also documented in the literature, many of them cosmopolitan or cosmotropical, and almost all are associated with human construction or agriculture (indicated in Appendix). Most of the introduced species were collected from multiple localities, and some mentions date back to at least the 1800s, indicating that the introductions are not recent.

What We Know of the Arachnid Fauna, and Likely Do Not

To gauge the level of scientific activity on the Gulf of Guinea arachnid taxa through time, we used publication data and taxonomic changes as a proxy (i.e., the number of years from original description that a species has been idle). Because spiders are the most speciose arachnid group present on the islands, our conclusions are drawn from spider-specific taxonomic data. The average number of years since a species had been studied was 83.4, with the most recent being within the past year (*Araneus apricus* (Karsch 1884), *Peplometus biscutellatus* (Simon 1887)) (Dippenaar-Schoeman et al. 2020; Wesołowska et al. 2020). The two species with the longest period of inactivity (137 years) were both described by Karsch (1884): *Singa concinna* (Araneidae), described from an immature specimen but still considered valid, and *Philodromus morsus* (Philodromidae). At least 55 (of 210) species are only known from the original description (26.2%), with 22 (10.5%) having been mentioned in publications from the past 10 years, 70 (33.3%) in the past 50 years, and 88 (41.9%) in more than 50 years. The majority of species (58%) are known from both sexes, which is surprisingly high and could be explained by some of the most prolific collectors having spent long periods of time on the islands. The remaining species (41.3%) are known only from female (31.9%), immature (1.4%), or male specimens (8.1%). These differences are likely because males are often only active for part of the year.

Although our knowledge is incomplete, there are some interesting emerging patterns for arachnid diversity on the Gulf of Guinea islands. For one, three orders of arachnids appear to be entirely missing from the fauna, though all are present on the mainland: Thelyphonida (whip scorpions), Palpigradi (micro whip scorpions), and Solifugae (wind scorpions). Two additional orders are apparently absent from the oceanic islands: Ricinulei (hooded tickspiders) and Scorpiones (aside from an introduced species). The absence of some of these groups is unexpected for islands of this size and age (scorpions, whip scorpions), while the absence of others may be attributable to a gap in collecting effort (e.g., microwhip scorpions).

A thorough understanding of arachnids on the Gulf of Guinea islands is still severely lacking. The majority of species descriptions were made in the first half of the twentieth century, there have been very few collections made by arachnologists, and none made using standardized methods of collection that would allow for a better assessment of the proportion of described versus undescribed fauna (Cardoso et al. 2009). Additionally, nearly all of the arachnid research to date has focused on alpha taxonomy and has not included the use of any modern tools or technologies to expedite the rate of discovery and description (i.e., molecular methods). Taxonomic training programs for local naturalists or students and partnerships with global experts would likely go a long way in closing this knowledge gap.

Appendix

Checklist of the arachnids of the Gulf of Guinea: including the three oceanic islands, the land-bridge island (Bioko), and the adjacent mainland

SPECIES	SEX	A	ST	P	STP	B	MA
ORDER AMBLYPYGI							
Family **Charinidae**							
Charinus africanus Hansen 1921		X			X		
Family **Phrynichidae**							
Damon johnstonii (Pocock 1894)						X	X
Damon medius (Herbst 1797)					X		X
Damon tibialis (Simon 1876)					X		X
ORDER ARANEAE							
Family **Agelenidae***							
Agelenidae sp.						*	
Family **Anapidae***							
Anapidae sp.						*	
Family **Araneidae**							
Aetrocantha falkensteini Karsch 1879	MF					X	X
Agalenatea redii (Scopoli 1763)	MF				I		I
Araneus aethiopissa Simon 1907	MF					X	X
Araneus apricus (Karsch 1884)	F				X		X
Araneus catospilotus Simon 1907	F			X	X		X
Araneus cereolus (Simon 1886)	MF					X	X
Araneus principis Simon 1907	F			E	X		
Aranoethra cambridgei (Butler 1873)	MF					X	X
Argiope flavipalpis (Lucas 1858)	MF				X		X
Argiope lobata (Pallas 1772)	MF				X		X
Argiope trifasciata (Forsskål 1775)	MF	I				I	I
Caerostris sexcuspidata (Fabricius 1793)	MF					X	X
Cyclosa circumlucens Simon 1907	F	X			X	?	X
Cyclosa formosa Karsch 1879	F	X				?	X
Cyrtarachne bigibbosa Simon 1907	F		X		X	X	
Cyrtarachne nodosa Thorell 1899	F					X	X
Cyrtophora citricola (Forsskål 1775)				I	I	?	
Gasteracantha curvispina (Guérin 1837)	MF				X	X	X
Gasteracantha sanguinolenta C.L. Koch 1844	MF		X		X		X
Gasteracantha thomasinsulae Archer 1951	F				X		
Megaraneus gabonensis (Lucas 1858)	MF					X	X
Metepeira labyrinthea (Hentz 1847)	MF		I		I		
Neoscona chiarinii (Pavesi 1883)	MF					X	X
Neoscona moreli (Vinson 1863)	MF	X		X	X	X	X
Neoscona novella (Simon 1907)	F					E	

(continued)

SPECIES	SEX	A	ST	P	STP	B	MA
Neoscona penicillipes (Karsch 1879)	MF			X	X	X	X
Neoscona rufipalpis (Lucas 1858)	MF		X		X		X
Neoscona simoni Grasshoff 1986	F					X	X
Neoscona subfusca C.L. Koch 1837	MF			I	I	I	I
Nephila constricta Karsch 1879	MF					X	X
Nephilingis cruentata (Fabricius 1775)	MF		X		X	X	X
Pararaneus perforatus (Thorell 1899)	MF		X		X		X
Poltys caelatus Simon 1907	F		X		X	?	X
Poltys fornicatus Simon 1907	F			E	X		
Pseudartonis semicoccinea Simon 1907	F		E		X		
Singa concinna Karsch 1884	Imm.				E		
Singafrotypa acanthopus (Simon 1907)	MF					X	X
Trichonephila clavipes (Linnaeus 1767)	MF				I		I
Trichonephila fenestrata venusta (Blackwall 1865)	MF	X	X		X	X	X
Trichonephila turneri (Blackwall 1833)	MF					X	X
Family **Barychelidae**							
Cyphonisia manicata Simon 1907	Imm.					X	
Cyphonisia nesiotes Simon 1907	MF				E		
Cyphonisia obesa Simon 1889	MF					X	X
Family **Cheiracanthiidae**							
Cheiracanthium furculatum Karsch 1879	MF					X	X
Cheiracanthium joculare Simon 1909	F			E	X		
Family **Clubionidae**							
Clubionidae sp.						*	
Clubiona haplotarsa Simon 1909	M		E		X		
Family **Corinnidae**							
Castianeira formosula Simon 1909	M					E	
Castianeira thomensis Simon 1909	MF		E		X		
Creugas gulosus Thorell 1878	MF		I		I		X
Procopius ensifer Simon 1909	F					X	X
Procopius gentilis Simon 1909	MF					X	X
Procopius granulosus Simon 1903	F					X	X
Procopius laticeps Simon 1909	F					E	
Pseudocorinna septemaculeata Simon 1909	F					X	X
Pseudocorinna ubicki Jocqué and Bosselaers 2011	MF					E	
Family **Ctenidae**							
Africactenus fernandensis (Simon 1909)	F					X	
Anahita mamma Karsch 1884	MF				X		X
Ctenus potteri Simon 1901	F					X	X
Ctenus capulinus (Karsch 1879)	MF					X	X
Thoriosa fulvastra Simon 1909	F		X		X		X
Thoriosa spadicea (Simon 1909)	F				E		
Thoriosa spinivulva (Simon 1909)	MF		E		X		

(continued)

SPECIES	SEX	A	ST	P	STP	B	MA
Thoriosa taurina (Simon 1909)	MF	E					
Family **Cyatholipidae**							
Buibui kankamelos Griswold 2001	MF					X	X
Wanzia fako Griswold 1998	MF					X	X
Family **Cyrtaucheniidae**							
Acontius humiliceps (Simon 1907)	F					E	
Family **Deinopidae**							
Deinopis anchietae Brito Capello 1867	MF				X	X	X
Family **Dictynidae**							
Dictynidae sp.						*	
Anaxibia difficilis (Kraus 1960)	M				E		
Family **Dipluridae***							
Dipluridae sp.						*	
Family **Gnaphosidae**							
Gnaphosidae sp.						*	
Aphantaulax ensifera Simon 1907	MF		E		X		
Echemus lacertosus Simon 1907	F			E	X		
Poecilochroa haplostyla Simon 1907	MF			E	X		
Family **Hahniidae**							
Hahnia eidmanni (Roewer 1942)	F					E	
Family **Hersiliidae**							
Hersilia occidentalis Simon 1907	MF			X	X	?	X
Family **Ischnothelidae**							
Lathrothele catamita (Simon 1907)	F				E		
Family **Linyphiidae**							
Afroneta sp.						*	
Araeoncus femineus (Roewer 1942)	F					E	
Hypomma clypeatum Roewer 1942	F					E	
Linyphia karschi Roewer 1942	MF				E		
Mecynidis sp.						*	
Microlinyphia sp.						*	
Family **Liocranidae***							
Hortipes sp.						*	
Family **Lycosidae**							
Arctosa bacchabunda (Karsch 1884)	F				E		
Alopecosa sublimbata Roewer 1960	MF					E	
Edenticosa edentula (Simon 1909)	F					E	
Geolycosa minor (Simon 1909)	F					E	
Hogna ferox (Lucas 1838)	MF				I		I
Hogna furva (Thorell 1899)	MF					X	X
Hogna furva cingulipes (Simon 1909)	F	E					
Hogna karschi (Roewer 1951)	F				X		
Hogna principum (Simon 1909)	MF			E	X		

(continued)

SPECIES	SEX	A	ST	P	STP	B	MA
Hogna thetis (Simon 1909)	F			E	X		
Loculla rauca Simon 1909	F		E		X		
Loculla rauca minor Simon 1909	F		E		X		
Family **Migidae**							
Moggridgea anactenidia Griswold 1987						*	X
Moggridgea occidua Simon 1907	F			E	X		
Family **Mimetidae**							
Mimetidae sp.						*	
Anansi insidiator (Thorell 1899)	MF		E		X		X
Kratochvilia pulvinata (Simon 1907)	F			E	X		
Family **Miturgidae***							
Miturgidae sp.						*	
Family **Mysmenidae***							
Mysmenidae sp.						*	
Family **Nesticidae**							
Nesticidae sp.						*	
Nesticus inconcinnus Simon 1907	F		E		X		
Family **Ochyroceratidae***							
Ochyroceratidae sp.	F					*	
Family **Oonopidae**							
Triaeris equestris Simon 1907	F			E	X		
Xestaspis parmata Thorell 1890	MF		I		I		
Xestaspis sertata Simon 1907	MF					E	
Family **Oxyopidae**							
Oxyopes brachiatus Simon 1909	MF					X	X
Oxyopes campestratus Simon 1909	MF		X		X	X	X
Oxyopes obscurifrons Simon 1909	F		E		X		
Family **Palpimanidae**							
Palpimanus hesperius Simon 1907	F		E		X		
Sarascelis luteipes Simon 1887	MF		X		X	?	X
Scelidocteus baccatus Simon 1907	F		E		X		
Scelidocteus pachypus Simon 1907	MF				X	?	X
Family **Philodromidae**							
Philodromus morsus Karsch 1884	F				X		X
Philodromus albofrenatus Simon 1907	F					E	
Family **Pholcidae**							
Artema atlanta Walckenaer 1837	MF				I		
Leptopholcus obo Huber 2011	MF				E		
Leptopholcus tipula (Simon 1907)	MF					X	X
Pholcus batepa Huber 2011	MF				E		
Pholcus circularis Kraus 1960	MF				E		
Pholcus moca Huber 2011	MF					X	X
Smeringopina fon Huber 2013	MF				X		X

(continued)

SPECIES	SEX	A	ST	P	STP	B	MA
Smeringopus principe Huber 2012	MF				E		
Smeringopus thomensis Simon 1907	MF		E		X		
Family **Pisauridae**							
Dolomedes fernandensis Simon 1909	F					E	
Nilus curtus O. Pickard-Cambridge 1876	MF			X	X	?	X
Tetragonophthalma vulpina (Simon 1898)	MF		X		X		X
Family **Salticidae**							
Baryphas eupogon Simon 1902	M		E		X		
Belippo anguina Simon 1909	F		E		X		
Belippo calcarata (Roewer 1942)	MF					X	X
Belippo nexilis (Simon 1909)	MF		E		X		
Belippo viettei (Kraus 1960)	M		E		E		
Bokokius penicillatus Roewer 1942	M					E	
Cosmophasis tricincta Simon 1909	MF					E	
Heliophanus congolensis Giltay 1935	MF				X		X
Holcolaetis vellerea Simon 1909	MF		X		X		X
Hyllus holochalceus Simon 1909	M					E	
Hyllus leucomelas (Lucas 1858)	MF			X	X	X	X
Maltecora chrysochlora Simon 1909	M			E	X		
Maltecora divina Simon 1909	M			E	X		
Maltecora janthina Simon 1909	MF		E		X		
Menemerus bivittatus (Dufour 1831)	MF				I		
Myrmarachne confusa Wanless 1978	M				X		X
Myrmarachne eidmanni Roewer 1942	M					X	X
Myrmarachne hesperia (Simon 1887)	MF			X	X	X	X
Myrmarachne nigeriensis Wanless 1978	MF				X		X
Natta horizontalis Karsch 1879	MF		X		X		X
Nigorella albimana (Simon 1902)	MF		X		X		X
Pachyballus flavipes Simon 1909	MF					X	X
Peplometus biscutellatus (Simon 1887)	MF					X	X
Plexippus paykulli (Audouin 1826)	MF				I		
Pochyta insulana Simon 1909	MF			E	X		
Portia africana (Simon 1886)	MF			X	X		X
Thiratoscirtus capito Simon 1903	MF					X	X
Thyene hesperia (Simon 1909)	MF	X					X
Thyene ocellata (Thorell 1899)	MF					X	X
Thyene sexplagiata (Simon 1909)	F		E		X		
Thyenillus fernandensis Simon 1909	MF					E	
Tomomingi silvae Szűts & Scharff 2009	M					E	
Viciria scintillans Simon 1909	MF					X	X
Family **Scytodidae**							
Scytodes longipes Lucas 1844	MF					I	I
Scytodes punctipes Simon 1907	MF			E	X	X	

(continued)

SPECIES	SEX	A	ST	P	STP	B	MA
Scytodes velutina Heineken & Lowe 1832	MF		X		X	X	X
Family **Segestriidae**							
Ariadna laeta Thorell 1899	F			X	X	?	X
Ariadna rapinatrix Thorell 1899	F				E	?	X
Family **Selenopidae**							
Selenops intricatus Simon 1910	MF				E		X
Selenops radiatus Latreille 1819	MF			I	I		
Family **Sparassidae**							
Barylestis insularis Simon 1909	F					X	X
Heteropoda venatoria (Linnaeus 1767)	MF				I		
Thelcticopis scaura (Simon 1909)	F				E		
Thelcticopis truculenta Karsch 1884	MF				E		
Family **Symphytognathidae***							
Symphytognathidae sp.						*	
Family **Telemidae***							
Telemidae sp.	F					*	
Family **Tetragnathidae**							
Dolichognatha petiti (Simon 1884)	MF					X	X
Leucauge argenteanigra (Karsch 1884)	F				E		
Leucauge cabindae (Brito Capello 1866)	F			X	X	X	X
Leucauge isabela Roewer 1942	M					E	
Leucauge nigrocincta Simon 1903	MF				X	X	X
Leucauge opiparis Simon 1907	MF				E		
Leucauge thomeensis Kraus 1960	M				E		
Leucauge undulata (Vinson 1863)	MF				X		X
Leucauge ungulata (Karsch 1879)	MF		X		X	X	X
Mecynometa argyrosticta Simon 1907	F	X	X		X		X
Tetragnatha clavigera Simon 1887	MF					X	X
Tetragnatha filum Simon 1907	MF		X		X	X	X
Tetragnatha hastula Simon 1907	MF			X	X		X
Tetragnatha macrops Simon 1907	F			E	X		
Tylorida seriata Thorell 1899	F		X		X		X
Family **Theraphosidae**							
Hysterocrates apostolicus Pocock 1900	MF		E		X		
Hysterocrates didymus Pocock 1900	F		E		X		
Hysterocrates ederi Charpentier 1995	MF					E	
Hysterocrates greeffi (Karsch 1884)	MF				X		X
Hysterocrates scepticus Pocock 1900	F		E		X		
Phoneyusa manicata Simon 1907	MF			E	X		
Phoneyusa principium Simon 1907	F			E	X		
Family **Theridiidae**							
Achaearanea sp.						*	
Argyrodes argyrodes (Walckenaer 1841)	MF					X	X

(continued)

SPECIES	SEX	A	ST	P	STP	B	MA
Argyrodes zonatus (Walckenaer 1841)	MF		X		X	X	X
Latrodectus hesperus Chamberlin & Ivie 1935	F				I		
Nesticodes rufipes (Lucas 1836)	MF		I		I		I
Rhomphaea nasica (Simon 1873)	MF		I		I		I
Steatoda carbonaria (Simon 1907)	MF		X		X	X	X
Steatoda rubrocalceolata (Simon 1907)	F					E	
Theridion derhami Simon 1895	F					X	X
Theridion eugeni Roewer 1942	MF					E	
Theridion fernandense Simon 1907	F					E	
Tidarren scenicum (Thorell 1899)	F		X		X		X
Family **Theridiosomatidae**							
Theridiosomatidae sp.						*	
Wendilgarda atricolor (Simon 1907)	F			E	X		
Family **Thomisidae**							
Ansiea tuckeri thomensis (Bacelar 1958)	M		E		X		
Borboropactus noditarsis (Simon 1903)	Imm.					X	X
Diaea puncta Karsch 1884	MF		X		X		X
Holopelus albibarbis Simon 1895	MF					X	X
Runcinia tropica Simon 1907	MF	X					X
Stiphropus dentifrons Simon 1895	F					X	X
Synema jaspideum Simon 1907	M					X	X
Thomisops sulcatus Simon 1895	MF					X	X
Thomisus tripunctatus Lucas 1858	MF					X	X
Tmarus cancellatus Thorell 1899	M					X	X
Family **Trachelidae**							
Orthobula sp. Simon, 1897	MF		E				
Family **Udubidae**							
Raecius asper (Thorell 1899)	MF					X	X
Family **Uloboridae**							
Uloboridae sp.						*	
Zosis geniculata (Olivier 1789)	MF		I		I		I
Family **Zodariidae**							
Mallinella leonardi (Simon 1907)	MF			E	X		
Mallinella octosignata (Simon 1903)	F					E	
Mallinella submonticola (Van Hove & Bosmans 1984)	MF				X		X
Systenoplacis septemguttatus Simon 1907	MF						X
ORDER OPILIONES							
Family **Assamiidae**							
Bueana quadridentata Prieto 1999 *nomen nudem?*						E	
Cerea feai Roewer 1927						X	X
Chilon horridus (Roewer 1912)						X	X
Chilon robustus Sørensen 1896						X	X
Eupodauchenius luteocruciatus (Loman 1910)						X	X

(continued)

SPECIES	SEX	A	ST	P	STP	B	MA
Euselenca feai Roewer 1927						X	X
Henriquea spinigera Roewer 1927				E			
Izea pectinata Roewer 1927			E				
Musola longipes Roewer 1927						E	
Palmanella tigrina Roewer 1927					E		
Selencasta minuscula (Roewer 1927)						E	
Selencula filipes (Roewer 1927)						E	
Thomecola quadrispina (Roewer 1927)			E				
Family **Biantidae**							
Biantomma nigrospinosum Roewer 1942						E	
Lacurbs fernandopoensis Prieto 1999 *nomen nudem*						E	
Lacurbs nigrimana Roewer 1912			X	X			
Metabiantes insulanus (Roewer 1949)				E			
Metabiantes pumilio Roewer 1927				E			X
Family **Ogoveidae**							
Ogovea nasuta Hansen 1921						E	
Family **Neogoveidae**							
Paragovia sironoides Hansen 1921						E	
Family **Phalangiidae**							
Dacnopilio insularis Hansen 1921						E	
Megistobunus longipes Hansen 1921						E	
Family **Pyramidopidae**							
Conomma annobonum Roewer 1949		E					
Conomma feae Roewer 1927				E			
Conomma fortis Loman 1902		X		X		X	X
Conomma minima Roewer 1912		X				X	X
Conomma oedipus Roewer 1949						E	
Conomma principeum Roewer 1949				E			
Conomma sorianoi Prieto 1999 *nomen nudem*						E	
Opconomma hirsuta Roewer 1927			E				
Pyramidops albimana Roewer 1927						E	
Pyramidops biseriata Roewer 1949						E	
Pyramidops raptator (Sørensen 1896)						X	X
Family **Samoidae**							
Microconomma armatipes Roewer 1915						X	X
ORDER PSEUDOSCORPIONIDA							
Family **Atemnidae**							
Cyclatemnus equestroides (Ellingsen 1906)			X	X		X	X
Micratemnus pusillus (Ellingsen 1906)			X				X
Parachernes cocophilus (Simon 1901)						?	
Paratemnoides pallidus (Balzan 1892)			X			X	X
Tamenus camerunensis (Tullgren 1901)						X	X
Tamenus insularis Beier 1932						E	

(continued)

SPECIES	SEX	A	ST	P	STP	B	MA
Titanatemnus sjoestedti (Tullgren 1901)						X	X
Titanatemnus thomeensis (Ellingsen 1906)			E				
Family **Olpiidae**							
Minniza vermis Simon 1881						?	
Family **Tridenchthoniidae**							
Ditha (Paraditha) sinuata (Tullgren 1901)					X		X
Tridenchthonius addititius Hoff 1950			X				X
Family **Withiidae**							
Stenowithius angulatus (Ellingsen 1906)				E			
Withius simoni (Balzan 1892)					X	X	X
ORDER RICINULEI							
Family **Ricinoididae**							
Ricinoides crassipalpe (Hansen and Sørensen 1904)						X	X
ORDER SCORPIONES							
Family **Buthidae**							
Isometrus maculatus (De Geer 1778)			I			I	I
Family **Scorpionidae**							
Opisthacanthus lecomtei (Lucas 1858)						X	X
Pandinus dictator (Pocock 1888)						X	X
ORDER SCHIZOMIDA							
Family **Hubbardiidae**							
Schizomus parvus (Hansen 1921)			X			X	X

A: Annobón - ST: São Tomé - P: Príncipe - STP: locality given as “São Tomé and Príncipe” - B: Bioko - MA: Mainland Africa. X: present; I: introduced; E: endemic: ? the literature is unclear; *: a morphospecies has been reported (Griswold et al. 1999). The sex of the collected or photographed specimens is given (F: female; M: male)

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Chapter 12
The Beetles (Coleoptera) of Príncipe, São Tomé and Annobón

Gabriel Nève, Patrick Bonneau, Alain Coache, Artur Serrano, and Gérard Filippi

Abstract The known beetle fauna of Príncipe, São Tomé, and Annobón amounts to 403 species and subspecies, of which 190 (47%) are endemic. The most diverse families of beetles are the Cerambycidae (61 species), the Tenebrionidae (57 species), the Carabidae (45 species), the Scarabaeidae (34 species), and the Coccinellidae (31 species). Most records come from São Tomé, with 297 species. In comparison, Príncipe, with 151 recorded species, and especially Annobón, with 16 recorded species, still require extensive faunistic investigations. The families Staphylinidae and Curculionidae probably hold numerous undescribed species and should be the focus of future research. Most of the endemic species live in forests. Therefore, the continued conservation of large forest areas on the islands is key to the long-term survival of their unique beetle fauna. As elsewhere, the beetle fauna will likely suffer from the effects of climatic change, and high-altitude species are likely to be the most severely affected.

Keywords Biodiversity · Checklist · Coleoptera · Conservation · Endemism · Gulf of Guinea

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Introduction

The islands of Príncipe, São Tomé, and Annobón, in the equatorial Atlantic ocean, have a volcanic origin and have never been connected to the African continent (Fitton and Dunlop 1985). Their isolation led to the evolution of numerous endemic species, but also to a fauna that is less diverse than that of continental Africa, lacking many continental species that were unable to cross the stretch of Atlantic ocean isolating the islands. Before human colonization, which started in the late fifteenth century, the islands were almost entirely covered by forests (Jones et al. 1991).

Entomological research in the islands started in the beginning of the nineteenth century, with the first descriptions of endemic species by Hope (1833) and Klug (1835). The fauna was subsequently investigated by entomologists from various European countries who later published their findings in journals from their respective countries, making it difficult to produce a synthesis. The main additions to the knowledge of the local beetle fauna came in waves (Fig. 12.1). Karsch (1881) mentioned 53 species, including 21 he described as new to science. The Italian explorer and zoologist Leonardo Fea (1852–1903) collected extensively on São Tomé and Príncipe in 1900–1901, and 12 beetle species from the archipelago still bear his name, such as *Pseudammus feae* (Fig. 12.2.3). The French entomologist Léon Fairmaire (1820–1906) published revisions of the fauna of São Tomé (1891, 1892, 1902). The Portuguese botanist Júlio Augusto Henriques (1838–1928) published an important geographical description of São Tomé (1917) that included a list of all species then known to the island, unfortunately mentioning several species based on dubious identification or with erroneous names. Later publications were usually focused on a single family, such as Tenebrionidae (Gebien 1921, 1942) and Coccinellidae (Fürsch 1974). Castel-Branco (1963) studied the insects feeding

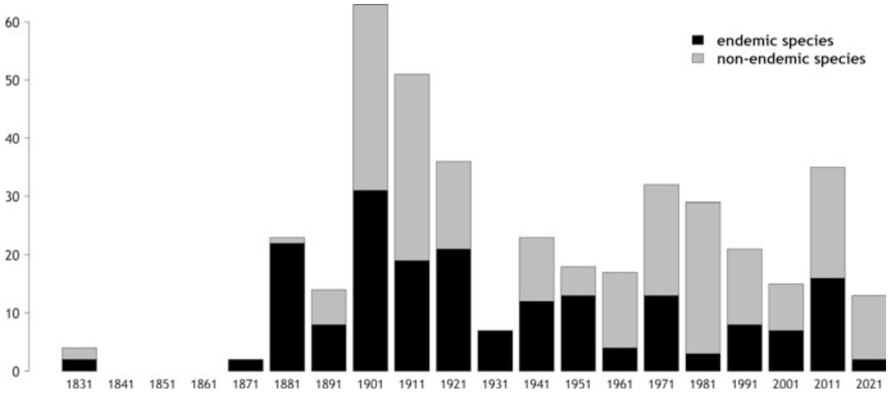

Fig. 12.1 Number of named beetle species added per decade to the fauna of Príncipe, São Tomé, and Annobón

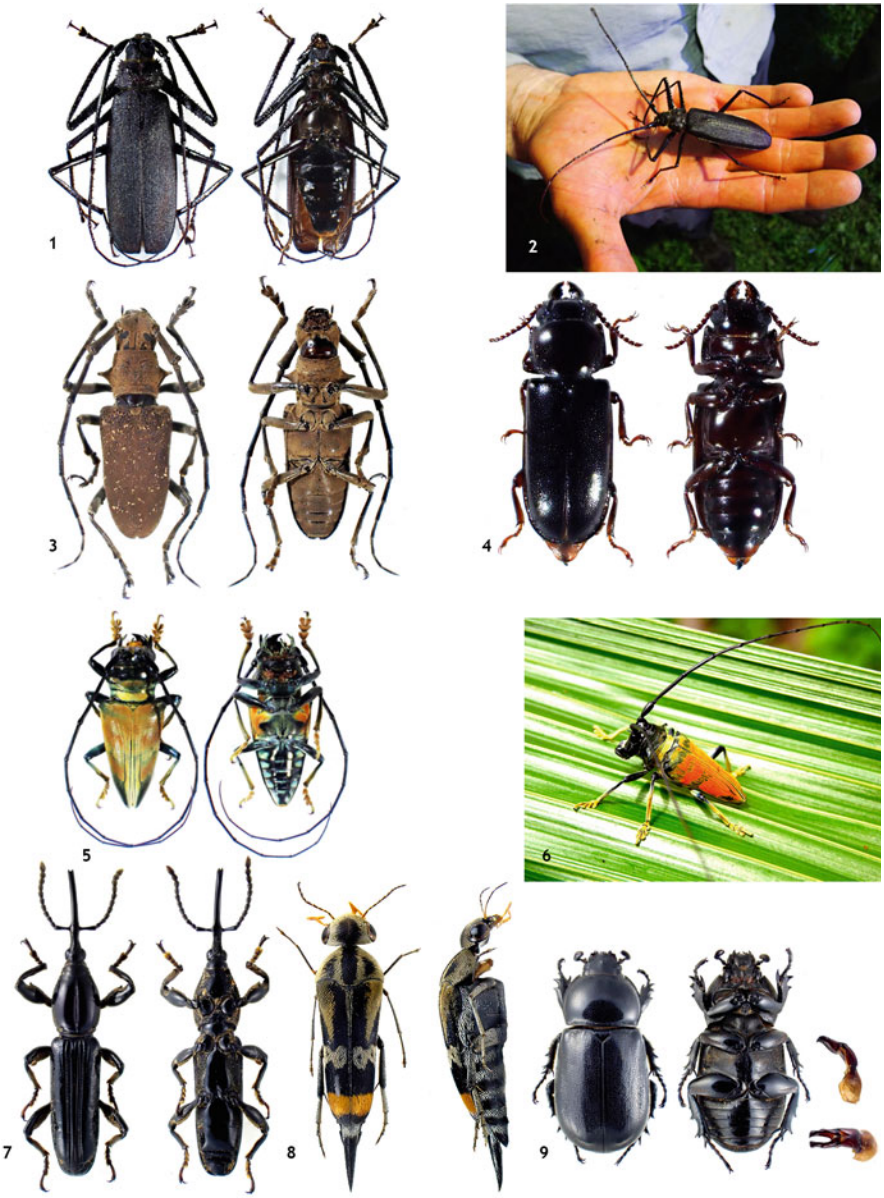

Fig. 12.2 Photos of charismatic beetle fauna from the oceanic islands of the Gulf of Guinea. Cerambycidae: (**1–2**) *Macrotoma hayesii*; (**3**) *Pseudammus feae*; (**4**) *Acutandra delahayi*; (**5**) *Sternotomis ducalis*; (**6**) *Sternotomis rufozonata*. Brentidae: (**7**) *Cerobates sennae*. Mordellidae: (**8**) *Ophthalmoglipa horaki*. Dynastinae: (**9**) *Rhizoplatys cedrici* (insert: genitalia). Photo credits: (**1**, **3–5**, **7–9**) Patrick Bonneau, (**2**) Gabriel Nève, (**6**) Artur Serrano

on *Theobroma cacao*, and listed a series of predators, including several labybirds (Coccinellidae).

Several expeditions to the islands were completed in the 1900s. Sousa da Camara visited São Tomé in 1920 (Seabra 1922); Fernando Frade (*Missão Científica a São Tomé*) visited São Tomé in November and December 1954 (Gomes Alves 1956); Pierre Viette, from the *Muséum National d'Histoire Naturelle* (Paris) visited the three islands in June and July 1956 (Viette 1956); and Guy Schmitz from the Royal Museum of Central Africa (Tervuren, Belgium) visited São Tomé in October and November 1973 (Basilewsky 1975). A zoological mission by entomologists and ornithologists from the *Faculdade de Ciências* and *Museu Nacional de História Natural* (Lisboa) took place in São Tomé and Príncipe in June and July 1984 (Mendes et al. 1988; Rocha Pité 1993; Serrano 1995; Zuzarte and Serrano 1996a). Charles E. Griswold and Joel M. Ledford from the California Academy of Sciences visited São Tomé and Príncipe in 2001 (Kavanaugh 2005), Clive R. Turner and Tõnis Tasane from the African Natural History Research Trust (Herefordshire, England) and the Natural History Museum (London) visited São Tomé in 2016 (Darby 2020). Several other entomologists visited the islands since 1980, and published descriptions of their findings, notably Jean-Guy Canu from Príncipe between 1989 and 1991 (Allard 1990; Antoine 1992) and Norbert Delahaye between 2013 and 2016 (Delahaye and Camiade 2016). The French NGO Microland also visited São Tomé in February and October 2019, the latter expedition including a week on Príncipe, and whose results on Coleoptera are published here for the first time.

The local *Brigada de Fomento Agro-Pecuário*, and later the *Centro de Investigação Agronómica e Tecnológica de São Tomé e Príncipe* (CIAT-STP) commissioned numerous entomological studies, mostly related to agriculture (Fürsch 1974). CIAT-STP holds a collection of insects mainly obtained between the 1950s and 1975, when the former Portuguese colony gained independence. Otherwise, specimens from São Tomé and Príncipe are now deposited in several European and American institutions, as well as in numerous private collections.

The aim of this chapter is to compile a list of all Coleoptera species known from the islands of Príncipe, São Tomé, and Annobón. For this, we relied on indexes of entomological publications, and, for Cerambycidae, on the TITAN database (Tavakilian and Chevillotte 2020). Drawing from published material and our experience on the islands, we analyze this list highlighting the distinctiveness of the beetle fauna, possible threats, and main gaps in knowledge. Coleoptera families followed recent publications (Bouchard et al. 2011; López-López and Vogler 2017), and species nomenclature followed recent revisions (Appendix). Nomenclature for Carabidae follows Lorenz (2005).

Diversity of the Beetle Fauna

The fauna that we find today in the archipelago is the result of successive colonization and extinction events throughout geological time. Colonization can be active, in which flight has a dominant role, or passive, such as on floating rafts, or carried by other animals or by air currents. Extinction can be derived from natural physical mechanisms, such as catastrophic volcanism, or by ecological processes, such as predation and competition between species, and in more recent history by anthropogenic actions, such as the destruction of habitats. In the last 500 years, since the Portuguese first arrived on these islands, we cannot neglect the accidental introduction of exotic species through human activity, namely on the ballast of boats, through the introduction of plant species of agricultural interest, or on imported goods.

The beetle fauna of Príncipe, São Tomé, and Annobón currently includes 403 species and subspecies (Appendix), which is certainly an underestimate of the richness of the local fauna. A total of 297 species are known from São Tomé, while only half of this number (151) has been listed for Príncipe, which most likely remains understudied. For example, 20 species of Curculionidae are known from São Tomé, but only 1 from Príncipe and 1 from Annobón. Only 16 Coleoptera species have been reported for the latter island, which is clearly in need of further investigations.

The most diverse families of beetles on Príncipe, São Tomé, and Annobón are the Cerambycidae (61 species), the Tenebrionidae (57 species), the Carabidae (45 species), the Scarabaeidae (34 species), and the Coccinellidae (31 species) (Fig. 12.3). The Cerambycidae, Carabidae, and Scarabaeidae have been actively studied by numerous collectors over several decades and there are recent syntheses by Serrano (1995, 2008, 2010), and Zuzarte and Serrano (1996b), while the Tenebrionidae have been the subject of an in-depth study by Gebien (1921, 1942), and the Coccinellidae by Fürsch (1974). The high number of Coccinellidae, 31 species, 8% of the known beetles on the islands, is probably the result of two factors: (1) the family has been the subject of a systematic study on the archipelago, and (2) their flight ability facilitates colonization from continental Africa, compared to other beetle families (half of the species known on the islands also occur on the African mainland).

The Staphylinidae has only 11 species recorded on the islands, accounting to less than 3% of their known beetle fauna, but are likely more diverse than the current estimates. For instance, Réunion, a partly forested equatorial island in the Indian ocean, has 206 species listed, which amounts to one-fifth of the local beetle fauna, about half of which are endemic (Gomy et al. 2016; Fig. 12.3). Two species of Dytiscidae are known from São Tomé, which is most certainly an underestimate since this family has not been the subject of a specialized study. Again, for comparison, this group is represented by 19 species on Réunion Island. Since Gebien (1921, 1942) listed 46 species of Tenebrionidae, only seven were added by Ardoin (1958, 1962) and Robiche (2000), plus two linked with imported goods (Luna de Carvalho 1984) and one newly found on São Tomé in 2019 (Laurent Soldati, pers. comm.).

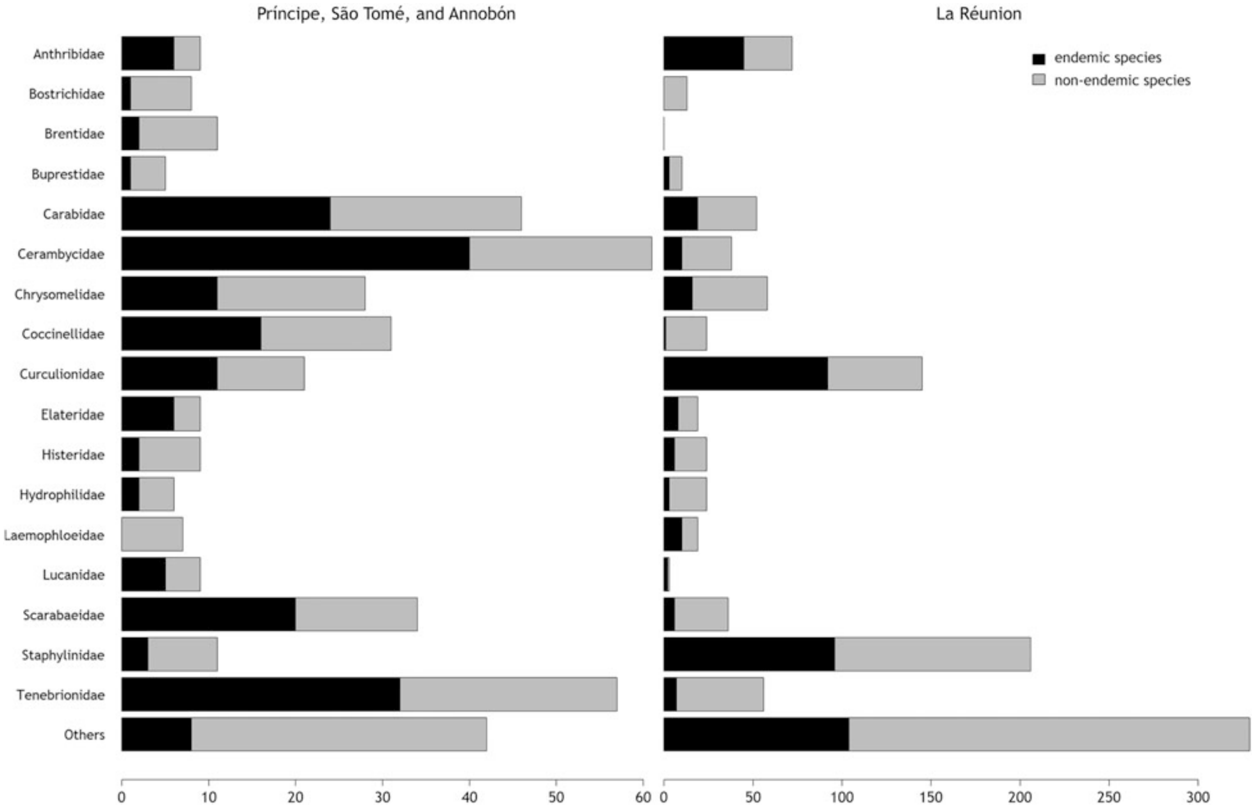

Fig. 12.3 Left: Distribution of known species of beetles from São Tomé, Príncipe, and Annobón, with the proportion in each family; families with less than six species are grouped as "Others." Right: distribution of species known on Réunion Island among the same families (Gomy et al. 2016). Note the differences in scale between the two graphs

Distinctiveness of the Beetle Fauna

Out of 403 species recorded, 190 (47%) are known only from these islands and are therefore considered endemic (Table 12.1). The Cerambycidae has 40 endemic species, the highest number of all beetle families, followed by the Tenebrionidae (32) and the Carabidae (24).

Lycidae (2 species) is the only family that is fully composed of endemic species on the islands. The families that have the highest numbers of endemic species, Tenebrionidae and Cerambycidae, occur mainly in forests (Barclay 2006; Rejzek 2006), which remain abundant on the islands.

The endemicity of several species has been recognized in their names; 16 species bear the adjective *thomensis*, *saotomense* or one of their derivatives, 7 bear the adjective *principis*, *principensis* or *principiensis,* and 3 bear the adjective *annobonae*. The genus *Saotomia* was given to an endemic species of weevil (Curculionidae), and the adjective *amadori* was recently given to a ground beetle (Carabidae) to honor Rei Amador, a hero in São Tomé history.

Knowledge Gaps

The assignment of species to a particular island is sometimes problematic. For example, Karsch (1882) described *Apogonia insulana* based on a specimen collected by Erdmann in Príncipe. Kolbe (1899) doubted the locality and suggested it came from the coast of Guinea. This uncertainty could only be solved when the species was rediscovered on Príncipe in 2019 (Patrick Bonneau and Marc Lacroix, unpublished; Fig. 12.4.1). In addition, some species mentioned in old references were likely based on misidentifications (Table 12.2). The compilation of all Coleoptera species listed for the islands by various authors over two centuries also led to numerous synonymies, some of which remain unresolved, as no systematic revision has been done. This is the case of *Grammopyga marginicollis*, described as endemic for São Tomé, but which may be a synonym of *G. cincticollis*, mentioned for Príncipe and widely distributed in Africa. Biphilidae, Limnichidae, and Ptilodactylidae are known to occur on the islands but the material has not yet been identified at the species level (Appendix). Other poorly known families are also likely present, such as Scydmaenidae.

In total, 37 families of beetles are known from Príncipe, São Tomé, and Annobón whereas 70 are known from Réunion Island, which is larger (2511 km^2) but also far more distant from continents (Gomy et al. 2016). The known beetle fauna of Reunion Island holds 1128 species, of which 428 (38%) are endemic (Gomy et al. 2016). Thus, there seems to be a gap in the knowledge of the Gulf of Guinea beetle families that are studied by few entomologists. Focused research by specialist entomologists, training local scientists, and conducting comprehensive surveys with multiple trapping methods will be necessary to close this gap. For instance,

Table 12.1 Number of known named Coleoptera species in each family for the islands of Príncipe, São Tomé, and Annobón (All: All species; END: Endemics)

	Príncipe		São Tomé		Annobón		Total	
Family	All	END	ALL	END	All	END	All	END
Anthribidae	7	5	7	5	0	0	9	6
Biphyllidae	0	0	?	?	0	0	?	?
Bostrichidae	4	1	5	0	2	0	8	1
Brentidae	10	1	7	2	0	0	11	2
Buprestidae	2	1	4	0	0	0	5	1
Carabidae	19	10	32	14	0	0	45	24
Cerambycidae	18	9	45	27	7	5	61	40
Chrysomelidae	19	8	16	7	0	0	28	11
Cicindelidae	2	0	2	0	0	0	3	0
Ciidae	0	0	1	0	0	0	1	0
Cleridae	0	0	1	0	0	0	1	0
Coccinellidae	6	2	27	14	0	0	31	16
Curculionidae	1	0	20	10	1	1	21	11
Dryophthoridae	0	0	4	0	0	0	4	0
Dytiscidae	2	0	1	0	0	0	2	0
Elateridae	2	1	8	6	0	0	9	6
Endomychidae	0	0	1	0	0	0	1	0
Gyrinidae	0	0	1	0	0	0	1	0
Histeridae	6	2	8	1	0	0	9	2
Hybosoridae	0	0	1	0	0	0	1	0
Hydrophilidae	3	1	3	1	1	0	6	2
Laemophloeidae	0	0	7	0	0	0	7	0
Limnichidae	0	0	?	?	0	0	?	?
Lucanidae	5	2	4	2	1	1	9	5
Lycidae	1	1	1	1	0	0	2	2
Lymexylidae	0	0	1	0	0	0	1	0
Mordellidae	1	1	2	1	0	0	3	2
Mycteridae	0	0	1	0	0	0	1	0
Nitidulidae	0	0	3	0	0	0	3	0
Oedemeridae	0	0	3	2	0	0	3	2
Passalidae	1	1	2	1	0	0	2	1
Ptiliidae	0	0	2	0	0	0	2	0
Ptilodactylidae	0	0	?	?	0	0	?	?
Ptinidae	0	0	2	0	0	0	2	0
Scarabaeidae	16	8	20	12	0	0	34	20
Silvanidae	0	0	3	0	0	0	3	0
Staphylinidae	0	0	11	3	0	0	11	3
Tenebrionidae	24	11	37	21	4	2	57	32
Trogossitidae	0	0	3	1	0	0	3	1
Zopheridae	2	0	1	0	0	0	3	0
TOTAL	**151**	**65**	**297**	**131**	**16**	**9**	**403**	**190**

Doubtful species and genera with unnamed species (Chrysomelidae: *Longitarsus* sp. and *Manioba* sp. and Curculionidae: *Sternuchopsis* sp.) are not listed. Families with unnamed species are indicated by '?'

Table 12.2 List of species mentioned in old references that were most likely mistakenly reported for the islands

Family	Subfamily	Species	Synonyms	References	Comment	Revision reference
Carabidae	Brachininae	*Pheropsophus angolensis* (Erichson, 1843)		Henriques, 1917	Probable confusion with *Pheropsophus amadori*	Present revision
Carabidae	Harpalinae	*Selenophorus atratus* Klug, 1862	*Progonochaetus caffer* (Boheman, 1848)	Henriques 1917	Unconfirmed record	Present revision
Carabidae	Lebiinae	*Pentagonica conradti* Kolbe, 1898		Straneo, 1945	Straneo's specimen could not be assigned unambiguously to this species	Serrano, 1995
Cerambycidae	Cerambycinae	*Philematium festivum* (Fabricius, 1775)		Henriques, 1917	Probable confusion with *Philematium greeffi*	Present revision
Cerambycidae	Lamiinae	*Ceroplesis bicincta* (Fabricius, 1798)		Henriques, 1917	Unconfirmed record	Present revision
Cerambycidae	Parandrinae	*Acutandra gabonica* (Thompson, 1858)	*Parandra gabonica* Thompson, 1857	Hintz, 1919; Villiers, 1957	Probable confusion with other *Acutandra* species	Bouyer et al. (2012)
Cicindelidae	Cicindelinae	*Habrodera nidula* (Dejean, 1825)		Henriques, 1917	Unconfirmed record	Present revision
Coccinellidae	Coccinellinae	*Cheilomenes lunata* (Fabricius, 1775)		Henriques 1917; Seabra 1922; Castel-Branco 1963	Probable confusion with *C. sulphurea*	Fürsch, 1974
Dytiscidae	Dytiscinae	*Hydaticus capricula* Anlar.		Henriques, 1917	No other reference to this name found. *Nomen nudum.*	Nilsson & Hájek, 2018
Lymexylidae	Atractocerinae	*Atractocerus brasiliensis* Lepeletier de Saint Fargeau & Audinet-Serville, 1825		Seabra, 1922	Probable confusion with *Atractocerus brevicornis*	Present revision
Scarabaeidae	Dynastinae	*Oryctes obuncus* Karsch		Henriques, 1917	No other reference to this name found. *Nomen nudum.*	Endrődi, 1985

(continued)

Table 12.2 (continued)

Family	Subfamily	Species	Synonyms	References	Comment	Revision reference
Scarabaeidae	Dynastinae	Temnorhynchus coronatus diana (Palisot de Beauvois, 1805)	*Temnorhynchus diana*	Henriques, 1917	Probable confusion with *T. tridentatus*	Present revision
Tenebrionidae	Tenebrioninae	Gonocephalum aequale (Erichson, 1843)	*Opatrum aequale*	Henriques, 1917	Dubious record	Iwan et al., 2010
Tenebrionidae	Tenebrioninae	Gonocephalum granicolle Gebien, 1920		Gebien, 1942	Dubious record	Iwan et al., 2010

we are currently working on the description of new species of Curculionidae from São Tomé, and a revision of this family on the islands will probably yield several new species. The Hydrophilidae, quite common in forest pools probably include more than the six currently recognized species, and a revision of these would likely reveal local endemism, as has been shown recently in the Neotropics (Smith and Short 2020).

Soil Coleoptera

The soil fauna includes both endogean and epigean Coleoptera. The former spend all or most of their life cycle within the soil, are not very conspicuous and in most cases are poorly or almost entirely unknown due to their small size (mainly <2 mm) and secretive way of life. Epigean beetles live on the ground, and are active mainly by night or at twilight, while during the day they rest or hide in the litter, under rocks and logs, sometimes burying themselves in the soil. The endogean beetles of Príncipe, São Tomé, and Annobón, are completely unknown to science, hence the absence of records of Scydmaenidae and Pselaphiinae. We do not know of any research directed to their collection and study on the islands.

Most epigean beetles are predators such as Cicindelidae (e.g., *Myriochila melancholica*), some ground Carabidae (e.g., *Notiobia sanctithomae* and *Scarites fatuus*) and Staphylinidae. Many epigean beetles are saprophagous, such as Tenebrionidae, or leaf litter dwellers (e.g., Curculionidae: *Titilayo* spp.). On the other hand, the dung beetle fauna of the islands includes only four Onthophagini species despite being extremely biodiverse in the continent. Other groups that have not yet been reported from the islands include carrion (Silphidae), hide (Dermestidae), and skin (Trogidae) beetles, as well as some families that have representatives that typically occur on the ground (e.g., Cucujidae, Cryptophagidae, Latridiidae, Mycetophagidae, etc.). Considering that this fauna is closely associated with substrate, vegetation cover, and abiotic factors, such as humidity and temperature, we foresee that this group contains an enormous component of undocumented diversity in these islands.

Epiphytic Coleoptera

The aerial parts of plants constitute an enormous spatial matrix, varying through time in their different components (stems, leaves, inflorescences, and fruits). A high percentage of the known beetles, both larval and adult, are phytophagous in the broad sense of the term. Since São Tomé and Príncipe maintain almost 30% of the original forest cover (Jones et al. 1991), it is not surprising that they host a rich and diverse fauna of Coleoptera associated with the vegetation, including the subterranean and the aerial parts of plants. Most Chrysomelidae and Curculionidae species are phytophagous, sometimes having numerous species within a genus, probably linked to different host species, as in the case of the six species of *Aspidomorpha* (Curculionidae) recently recorded on Príncipe (Coache and Rainon 2020). Nitidulidae (*Carpophilus* spp.) and Bruchinae species are found in abundance on flowers and mainly on fruits. Plant saps attract a multiplicity of species belonging to different families, such as adults of Lucanidae (e.g., *Prosopocoilus downesi*, Figs. 12.4.5–6), Cetoniinae (e.g., *Chlorocala viridicyanea*, *Pachnoda* spp.) and Cerambycidae (e.g., *Macrotoma hayesii*, *Sternotomis* spp.). Finally, some species are predators of other insects dwelling on vegetation, of which the Coccinellidae are the best known and richest family in São Tomé and Príncipe.

Coleoptera Associated with Decaying Wood

Woodborer Coleoptera larvae and adults that live within the wood (xylophages) or under bark (subcortical) can be predators, saprophagous or even phytophagous species that seek refuge there. These are surely one of the most diverse and abundant ecological Coleoptera groups in São Tomé and Príncipe, as almost all Coleoptera families present species in these biotopes. Woodborer larvae include numerous species of Anthribidae, Bostrichidae, Brentidae, Buprestidae, Cerambycidae, Curculionidae, Elateridae, Lucanidae, Scarabaeidae, Tenebrionidae, among others. Adult beetles found in this habitat encompass most of the endemic Carabidae (e.g., *Metagonum insulanum*, *Pseudobatenus straneoi*, *Abacetus* spp., *Camptogenys trisetosa*), as well as Histeridae, Laemophloeidae (e.g., *Cryptolestes* spp., *Placonotus* spp.) and Staphylinidae (e.g., *Afrosorius* spp.). It is sometimes possible to find numerous species of most families mentioned above side-by-side in the same tree trunk.

Freshwater Coleoptera

São Tomé and Príncipe exhibit a wide range of freshwater biotopes, including streams, rivulets, lagoons, pools, and phytotelmata, which are habitat to several families of beetles (e.g., Gyrinidae, Haliplidae, Hygrobiidae, Dytiscidae, Hydrophilidae and Hydraenidae). So far, only a few species of Gyrinidae, Dytiscidae, and Hydrophilidae have been recorded from Príncipe, São Tomé, and Annobón, but considering the abundance of freshwater biotopes on the islands, many more likely remain to be discovered.

Coleoptera of Agricultural Importance

A few beetle species are known to be of agricultural importance, either as pests of cultivated species, or as predators of pests. *Lamprocopa occidentalis* (Chrysomelidae), which we documented in 2019 on both São Tomé and Príncipe, is known as a serious pest on several cultivated Cucurbitacae (Adja et al. 2014). Some species were deliberately introduced for the control of aphids and other insects that are detrimental to agriculture. Among these, the Coccinellidae *Rodolia cardinalis* was introduced by Castel-Branco (1963) specifically to control the aphid *Toxoptera aurantii* (Boyer de Fonscolombe, 1841), which feeds on *Theobroma cacao*, and seems now to have been extirpated. Other introduced pest predators became established, such as *Cryptognatha nodiceps*, which feeds on the Cottony Cushion Scale *Icerya puchasi* Makell, 1878 (Hemiptera) (Fürsch 1974).

Remarkably, the endemic ladybird species *Chilocorus pilosus, Nephus derroni*, and *N. theobromae* were also found on cultivated plants, notably *Coffea arabica, Theobroma cacao* and *Cocos nucifera* (Fürsch 1974). This must be the result of local adaptations of either the ladybird species or of their prey, since the host plants are introduced to cultivated plants. The natural habitat and feeding habits of these species are not known.

Some Charismatic Species

The Príncipe endemic *Macrotoma hayesii* (Figs. 12.2.1–2) is the largest Cerambycidae species in Africa (up to 12 cm), occurring in forests, where *Pentaclethra macrophylla* has been described as its host plant (Tordo 1956). *Macrotoma hayesi* is always rare, and the size of its imago, the adult life stage of beetles, suggests a life cycle lasting several years. Its conservation requires maintaining old growth forests with decaying trees in the Príncipe Natural Park, including Azeitona. Another Cerambycidae, *Ceratocentrus oremansi*, reported in 1998 (Delahaye and Camiade 2016), is much smaller (3.2 to 5.5 cm) and has been found in several forest areas on São Tomé Island.

The Lucanidae fauna of São Tomé and Príncipe is well known and includes nine species and subspecies. *Prosopocoilus antilopus* has a distinct endemic subspecies on each oceanic island: *P. antilopus insulanus* on São Tomé, *P. antilopus beisa* on Príncipe and *P. antilopus amicorum* on Annobón. Eight additional subspecies have been described from Senegal to the Democratic Republic of Congo (Bartolozzi and Werner 2004). *Prosopocoilus downesii* is known from São Tomé, Príncipe and Bioko. Specimens of *Prosopocoilus*, especially males, are known to vary in size (Fig. 12.4), depending on larval growth conditions (Bartolozzi and Werner 2004), with large males sometimes having proportionally long mandibles, as in the case of “mesodonte” *P. antilopus* males (Gomes Alves 1956).

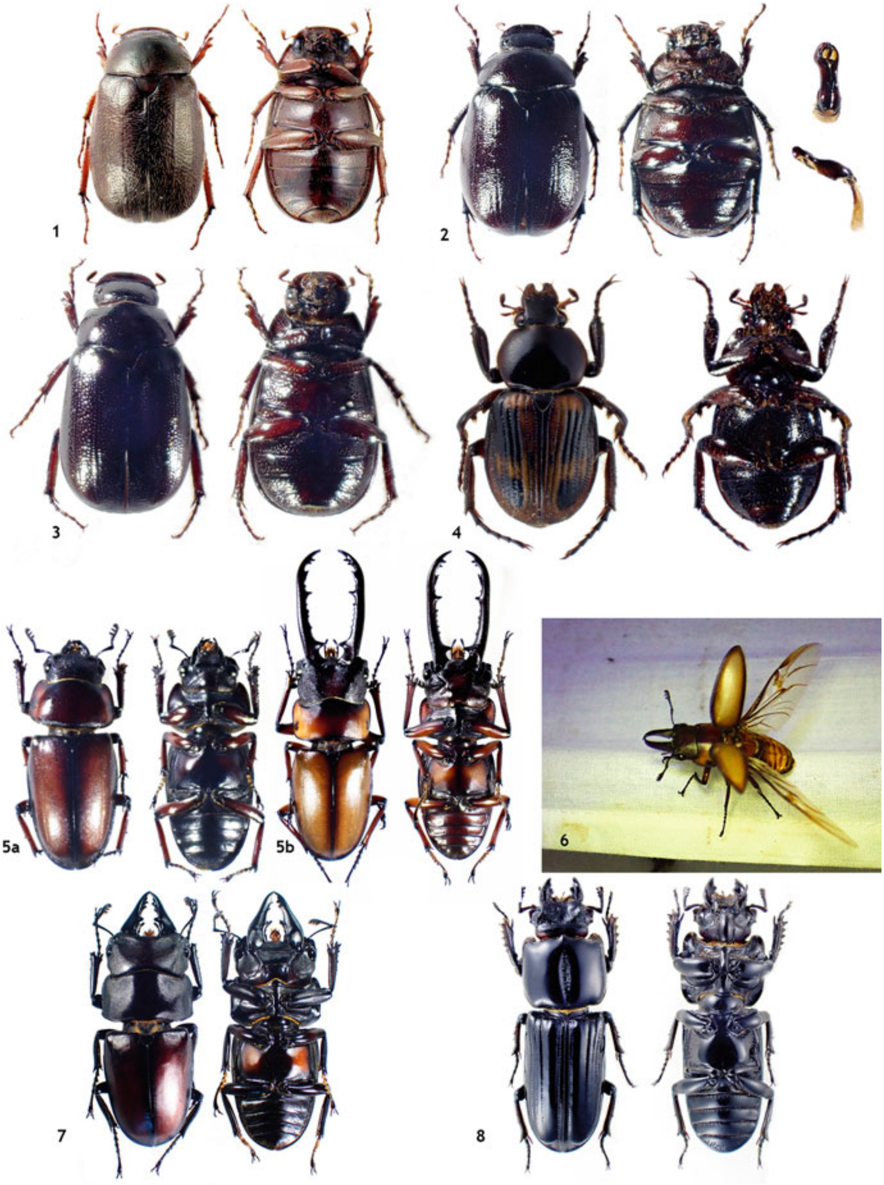

Fig. 12.4 Photos of charismatic beetle fauna from the oceanic islands of the Gulf of Guinea (cont.). Scarabaeidae: (**1**) *Apogonia insulana*; (**2**) *Apogonia tomeensis* (insert: genitalia); (**3**) *Apogonia decellei*; (**4**) *Clastocnemis quadrimaculatus oremansi*. Lucanidae: (**5**) *Prosopocoilus downesi* (left: female, right: male, mesodonte form); (**6**) *Prosopocoilus downesi* (male, prosodonte form); (**7**) *Prosopocoilus antilopus insulanus*; (**8**) *Figulus decipiens*. Photo credits: (1–5, 7–8) Patrick Bonneau, (6) Gabriel Nève

The Cetoniinae *Uloptera canui* (Scarabaeidae) is a typical example of a remarkable species that has a restricted distribution. It was described in 1992 based on a few specimens from two areas in Príncipe at ca. 500 m altitude: Pico Mesa and Pico Dois Irmãos. Given the peculiar ecological conditions of these locations, it is unlikely that the species occurs at lower altitudes. Of the other 12 Cetoniinae species known from São Tomé and Príncipe, 8 are endemic, either at the species or sub-specific level (Table 12.1). Their poor ability to fly long distances likely explains why there are so few species on the islands. One of these, the São Tomé endemic *Stenosternus costatus*, is thought to be the result of an ancient colonization from the Neotropics, since it is the only African species of the tribe Orphnini (Orphninae, Scarabaeidae – Frolov 2013).

Carabidae are generally predators of smaller insects and other arthropods, and sometimes of mollusks. Forty-five species are known from São Tomé and Príncipe. The genus *Pseudobatenus* illustrates an interesting biogeography, since it is only represented by the São Tomé endemic *Pseudobatenus straneoi* and two other species, *P. camerunicus* (Burgeon, 1942) and *P. longicollis* Basilewsky, 1951, which are restricted to Mt. Cameroon (Basilewsky 1975). These three species are most likely altitudinal relicts of a widespread ancestral species. The Cerambycidae *Bangalaia thomensis* has a similar distribution, being found only on São Tomé and in Cameroon, although it occurs at low altitudes (Lepesme and Breuning 1956).

Concluding Remarks

Príncipe, São Tomé, and Annobón host 403 named species and subspecies of beetles, plus an unknown number of undescribed species. Many of these species are endemic and very little is known about them. For instance, several endemics, such as *Nesopatrum josephii* (Tenebrionidae) and *Panoptes convexus* (Curculionidae), were described from Ilhéu das Rolas by Karsch (1881), and there are no records from São Tomé Island itself. Given the development of touristic infrastructure and overall environmental degradation on Ilhéu das Rolas, it is not known if these species persist. An improved knowledge of the fauna of the archipelago would require a variety of sampling techniques deployed in a wide range of habitats, including some low-cost canopy trapping (Bar-Ness et al. 2011). The main task, however, would be identification, which would require engaging specialists of the various families. The establishment of a local reference collection would be an important asset to train and raise awareness of the beetle fauna.

The long-term conservation of the beetle fauna, as for most of the endemic terrestrial fauna of Príncipe, São Tomé, and Annobón relies on effective conservation of native forests. These still cover about 30% of the islands, an unusually high percentage that is linked to the rugged topography (Norder et al. 2020). The capture and export of beetles should also be controlled, namely of endemic species that might be particularly vulnerable, such as the endemic as *Macrotoma hayesii* (Fig. 12.2.1–2), which occurs at low densities. This and several other endemic beetle species, such *Rhizoplatys canui* and *Figulus decipiens* (Figs. 12.4.4 and 12.4.8) are emblematic and could serve as flagship species for the conservation of their habitats, especially old growth forests, where standing dead old trees are key habitat for the larvae. Visits to the forests and producing conservation educational material using beetle fauna may play an important role in educating the public about the uniqueness and exceptional biodiversity of the islands.

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Supplementary Material

A full text format of Appendix and Table 12.2, with references to the occurrence of all species in Príncipe, São Tomé, and Annobón, together with the main synonyms is available on https://doi.org/10.5281/zenodo.5151308.

Appendix

Appendix List of Coleoptera taxa known from the islands of Príncipe, São Tomé, and Annobón. "Microland" refers to species added to the known São Tomé and Príncipe fauna during our two expeditions in February and October 2019. E: endemic species, I: introduced species, R: resident on the islands, *: species recorded during the 2019 Microland expeditions (ML)

Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Family **Anthribidae** Billberg, 1820							
Subfamily **Anthribinae** Billberg, 1820							
Acorynus Schönherr 1833	*Acorynus benitensis* Jordan, 1903	R			Jordan, 1920		
Apatenia Pascoe 1859	*Apateni benina* Jordan, 1920	E	E		Jordan, 1920		
Cenchromorphus Fairmaire, 1893	*Cenchromorphus fulvum* Jordan, 1903		R		Jordan, 1920		*Derographium fulvum*
Gynandrocerus Lacordaire, 1866	*Gynandrocerus thomensis* Jordan, 1911	E	E		Jordan, 1911		
Litocerus Schönherr, 1833	*Litocerus beninus* Jordan, 1920	E	E		Jordan, 1920		
Phloeobius Schönherr, 1823	*Phloeobius hypoxanthus* Jordan, 1911	E	E		Jordan, 1911		
Xylinada Berthold, 1827	*Xylinada princeps* Jordan, 1920	E			Jordan, 1920		*Xylinades princeps*
	Xylinada thomasius Jordan, 1911		E		Jordan, 1911		*Xylinades thomasius*
Subfamily **Choraginae** Kirby, 1819							
Araecerus Schönherr, 1823	*Araecerus fasciculatus* (Degeer, 1775)	R	R		Jordan, 1920		
Family **Biphyllidae** Le Conte, 1861							
	Unidentified species		R?		Microland	*	
Family **Bostrichidae** Latreille, 1802							
Subfamily **Apatinae** Jacquelin du Val, 1861							
Apate Fabricius, 1775	*Apate cephalotes* (Olivier, 1790)	R	R		Microland	*	*Phonapate frontalis*
	Apate degener Murray, 1867		R		Lesne, 1906		
	Apate monachus Fabricius, 1775		R	R	Lesne, 1906	*	
	Apate terebrans (Pallas, 1772)	R			Lesne, 1906		
Phonapate Lesne, 1895	*Phonapate discreta* Lesne, 1906	E			Lesne, 1906		

(continued)

Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Subfamily **Bostrichinae** Latreille, 1802							
Bostrychoplites Lesne, 1899	*Bostrychoplites cornutus* (Olivier, 1790)		R		Lesne, 1906		
Xylionulus Lesne, 1901	*Xylionulus transvena* (Lesne,1900)			R	Lesne, 1906		
Subfamily **Dinoderinae** C.G. Thomson, 1863							
Rhyzopertha Stephens, 1830	*Rhyzopertha dominica* (Fabricius, 1792)	R	R		Luna de Carvalho, 1984		
Family **Brentidae** Billberg, 1820							
Subfamily **Brentinae** Billberg, 1820							
Adidactus Senna, 1894	*Adidactus striolatus* (Fairmaire, 1897)	R			Calabresi, 1920	*	
Cerobates Schönherr, 1840	*Cerobates sennae* Calabresi, 1920	R	R		Calabresi, 1920	*	
	Cerobates sulcatus sulcirostris Thomson, 1858	R	R		Calabresi, 1920		
Eumecopodus Calabresi, 1920	*Eumecopodus fuliginosus* Calabresi, 1920		E		Calabresi, 1920		
Gynandrorhynchus Lacordaire, 1866	*Gynandrorynchus vittipennis* (Fåhraeus, 1871)	R	R		Calabresi, 1920	*	*Mygaleicus vittipennis*; *Mygaleicus vittipennis nitida*
Microtrachelizus Senna, 1893	*Microtrachelizus aethiopicus* Calabresi, 1920	R			Calabresi, 1920	*	
Orphanobrentus Damoiseau, 1962	*Orphanobrentus picipes* (Olivier, 1791)	R			Damoiseau, 1963		
Pseudomygaleicus de Muizon, 1960	*Pseudomygaleicus georgei* (Karsch, 1881)	E	E		Karsch, 1881		*Ceocephalus georgei*
Rhinopteryx Lacordaire, 1865	*Rhinopteryx foveipennis* (J.Thomson, 1858)	R	R		Calabresi 1920	*	
Spatherhinus Power, 1879	*Spatherhinus longiceps* Kolbe, 1888	R			Calabresi, 1920		

Usambius Kolbe, 1892	*Usambius advena* (Pascoe, 1866)	R	R		Calabresi, 1920		*Usambius conradti*
Family **Buprestidae** Leach, 1815							
Subfamily **Agrilinae** Laporte, 1835							
Agrilus Curtis, 1825	*Agrilus feae* Kerremans, 1906	E			Kerremans, 1906		
Subfamily **Buprestinae** Leach, 1815							
Chrysobothris Eschscholtz, 1829	*Chrysobothris dorsata* (Fabricius, 1787)		R		Kerremans, 1906		
Megactenodes Kerremans, 1893	*Megactenodes westermanni* (Gory et Laporte, 1838)		R		Kerremans, 1906		
Subfamily **Chrysochroinae** Laporte, 1835							
Lampetis Dejean, 1833	*Lampetis zona* (Thomson, 1858)		R		Kerremans, 1914		*Damarsila zona*
Parataenia Kerremans, 1892	*Parataenia chrysochlora* (Palisot de Beauvois, 1805)	R	R		Kerremans, 1906		
Family **Carabidae** Latreille, 1802							
Subfamily **Brachininae** Bonelli, 1810							
Brachinulus Basilewsky, 1958	*Brachinulus viettei* Basilewsky, 1958	E			Basilewsky, 1958		
Pheropsophus Solier, 1833	*Pheropsophus* (*Stenaptinus*) *amadori* Lassalle & Roux, 2021		E		Lassalle & Roux, 2021		
	Pheropsophus (*Stenaptinus*) *fastigiatus* (Linnaeus, 1764)		R		Basilewsky, 1975		
Subfamily **Harpalinae** Bonelli, 1810							
Idiomela Tschitscherine, 1900	*Idiomelas* (*Egaploa*) *crenulatus* (Dejean, 1829)		R		Basilewsky, 1975		*Egaploa crenulata*
Notiobia Perty, 1830	*Notiobia* (*Diatypus*) *sanctithomae* (Serrano, 1995)		E		Serrano, 1995		

(continued)

Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Progonochaetus G. Müller, 1938	*Progonochaetus* (*Progonochaetus*) *planicollis* (Putzeys, 1882)		R		Basilewsky, 1975		*Dichaetochilus planicollis*
Siopelus Murray, 1859	*Siopelus* (*Pseudosiopelus*) *pulchellus* (Dejean, 1829)		R		Basilewsky, 1975		*Aulacoryssus pulchellus*
Stenolophus Dejean, 1821	*Stenolophus* (*Egadroma*) *scapularis* (Dejean, 1831)		R		Basilewsky, 1975		*Stenolophus scapulare*
Subfamily **Lebiinae** Bonelli, 1810							
Anaulacus W.S. MacLeay, 1825	*Anaulacus* (*Microus*) *mocqueryzi* (Chaudoir, 1878)	R	R		Serrano, 1995		*Microus mocqueryzi*
Calleida Latreille, 1824	*Calleida* (*Stenocallida*) *ruficollis* (Fabricius, 1801)		R		Serrano, 1995		
Dromius Bonelli, 1810	*Dromius* (*Klepterus*) *basilewskyi* (Serrano, 1995)		E		Serrano, 1995		
Pentagonica Schmidt-Göbel, 1846	*Pentagonica boavistensis* Serrano, 1995		E		Serrano, 1995		
	Pentagonica nigritula Straneo, 1943	E			Straneo, 1943		
Perigona Laporte de Castenau, 1835	*Perigona* (*Euripogena*) *congoana* Burgeon, 1935	R			Basilewsky, 1989		
	Perigona (*Perigona*) *pallida* Laporte, 1835		R		Basilewsky, 1975		
	Perigona (*Perigona*) *parallela* Chaudoir, 1878	R	R		Basilewsky, 1989		
	Perigona (*Perigona*) *principensis* Serrano, 2008	E			Serrano, 2008		
	Perigona (*Trechicus*) *nigriceps* (Dejean, 1831)		R		Basilewsky, 1975		*Trechicus nigriceps*
	Perigona (*Trechicus*) *schmitzi* (Basilewsky, 1989)		R		Basilewsky, 1989		*Trechicus schmitzi*

Subfamily **Licininae** Bonelli, 1810							
Chlaenius Bonelli, 1810	*Chlaenius* (*Lissauchenius*) *assecla* Laferté-Senectere, 1851	R	R		Basilewsky, 1975		
Melanchiton Andrewes, 1940	*Melanchiton laevisulcis* Straneo, 1950		R		Basilewsky, 1975		*Melanchiton laeviscus*
Subfamily **Panagaeinae** Bonelli, 1810							
Euschizomerus Chaudoir, 1850	*Euschizomerus buquetii* Chaudoir, 1850	R	R		Serrano, 1995		
Microcosmodes Strand, 1936	*Microschemus vicinus* (Murray, 1857)		R		Basilewsky, 1975		*Microcosmodes vicinus*
Subfamily **Paussinae** Latreille, 1807							
Carabidomemnus Kolbe, 1924	*Carabidomemnus* (*Carabidomemnus*) *feae* (Gestro, 1902)	E			Gestro, 1902		
Sphaerostylus Chaudoir, 1848	*Sphaerostylus* (*Afrozaena*) *feai* (Basilewsky, 1949)		E		Basilewsky, 1949		
	Sphaerostylus (*Afrozaena*) *insularis* (Basilewsky, 1949)		E		Basilewsky, 1949		*Pseudozaena insularis*
Subfamily **Platyninae** Bonelli, 1810							
Euplynes Schmidt-Gobel, 1846	*Euplynes brunneus* Straneo, 1943	E			Straneo, 1943		*Euplynes bruneus*
Metagonum Jeannel, 1948	*Metagonum insulanum* Basilewsky, 1948		E		Basilewsky, 1948		
Pseudobatenus Basilewsky, 1951	*Pseudobatenus straneoi* Basilewsky, 1957		E		Basilewsky, 1957		
Straneoa Basilewsky, 1953	*Straneoa collatata* (Karsch, 1881)		E		Karsch, 1881		*Zargus collatatus*; *Platynus opacipennis*; *Straneoa opacipennis*
	Straneoa seligmani Kavanaugh, 2005		E		Kavanaugh, 2005		

(continued)

Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Subfamily **Pterostichinae** Bonelli, 1810							
Abacetus Dejean, 1828	*Abacetus amplithorax* Straneo, 1940	E			Straneo, 1940		
	Abacetus feai Straneo, 1940		E		Straneo, 1940		
Caelostomus MacLeay, 1825	*Caelostomus* (*Caelostomus*) *striatocollis* (Dejean, 1831)		R		Straneo, 1941–1942	*	
	Caelostomus (*Drimostomellus*) *punctifrons* (Chaudoir, 1850)	R	R		Basilewsky, 1975		*Drimostomellus punctifrons*
Camptogenys Tschitscherine, 1899	*Camptogenys trisetosa* (Serrano, 1995)		E		Serrano, 1995	*	*Caelostomus* (*Camptogenys*) *trisetosus*
Dromistomus Jeannel, 1948	*Dromistomus complanatus levistriatus* (Straneo, 1941–1942)	E			Straneo, 1941–1942		*Caelostomus complanatus* var. *levistriatus*
Monodryxus Straneo, 1941–1942	*Monodryxus crassus* (Straneo, 1941–1942)		E		Straneo, 1941–1942		
Morion Latreille, 1810	*Morion guineensis* Imhoff, 1843	R	R		Henriques, 1917		*Morion guineense*
Pachyroxochus Straneo, 1941–1942	*Pachyroxochus subquadratus* Straneo, 1941–1942	E			Straneo, 1941–1942		
Platyxythrius Straneo, 1941–1942	*Platyxythrius insularis* Straneo, 1956	E			Straneo, 1941–1942		*Platyxythrius laevicollis*
Subfamily **Scaritinae** Bonelli, 1810							
Dyschirius Bonneli, 1810	*Dyschirius* (*Dyschiriodes*) *zanzibaricus palmeni* Kult, 1954		R		Basilewsky, 1975		*Dyschirius palmeni*
Scarites Fabricius, 1775	*Scarites fatuus* Karsch, 1881		E		Karsch, 1881		
	Scarites feanus Bänninger, 1937	E			Bänninger, 1937		
Subfamily **Trechinae** Bonelli, 1810							
Tachyta Kirby, 1837	*Tachyta subvirens* Chaudoir, 1878	R			Serrano, 2008		

Family **Cerambycidae** Latreille, 1802							
Subfamily **Cerambycinae** Latreille, 1802							
Achryson Audinet-Serville, 1833	*Achryson surinamum* (Linnaeus, 1767)	I	I		Zuzarte & Serrano, 1996	*	
Calanthemis Thomson, 1864	*Calanthemis thomensis* Aurivillius, 1910		E		Aurivillius, 1910		
Chlorida Miers, 1880	*Chlorida festiva* (Linnaeus, 1758)	I	I		Henriques, 1917	*	*Callichroma festivum*
Chromalizus Schmidt, 1922	*Chromalizus* (*Callichromalizus*) *fragrans aldbaueri* Delahaye & Juhel, 2018		E		Delahaye & Juhel, 2018		
	Chromalizus (*Chromalizus*) *rhodoscelis* (Jordan, 1903)		E		Jordan, 1903		*Cloniophorus rhodoscelis*; *Callichroma rhodoscelis*
Diaspila Jordan, 1903	*Diaspila periscelis* Jordan, 1903		R		Jordan, 1903		
Neoplocaederus Sama, 1991	*Neoplocaederus fucatus* (Thomson, 1858)	R	R		Villiers, 1957	*	
Philematium Thomson, 1864	*Philematium greeffi* Karsch, 1881		E		Karsch, 1881		
Philomeces Kolbe, 1893	*Philomeces thomensis* (Aurivillius, 1910)		E		Aurivillius, 1910		
Phrosyne Murray 1870	*Phrosyne brevicornis* (Fabricius, 1775)	R			Henriques, 1917		*Euporus brevicornis*
Xylotrechus Chevrolat, 1860	*Xylotrechus aedon* Jordan, 1903		E		Jordan, 1903		
Xystrocera Audinet-Serville, 1834	*Xystrocera interrupta* Jordan, 1903		R		Jordan, 1903	*	*Hystrocera interrupta*
	Xystrocera nigrita Audinet-Serville, 1834		R		Zuzarte & Serrano, 1996		
Subfamily **Lamiinae** Latreille, 1825							
Acmocera Dejean, 1835	*Acmocera conjux* Thomson, 1858		R		Henriques, 1917		*Achmocera anthriboides*
	Acmocera insularis Breuning, 1940		E		Breuning, 1940		
	Acmocera lutosa Jordan, 1903		E		Jordan, 1903		

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Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Acridoschema Thomson, 1858	*Acridoschema thomense* Jordan, 1903		E		Jordan, 1903		*Acridoschema thomensis*
Ancylonotus Dejean, 1835	*Ancylonotus tribulus* (Fabricius, 1775)		R		Jordan, 1903		
Bangalaia Duvivier, 1890	*Bangalaia thomensis* Breuning, 1947		R		Breuning, 1947		
Coptops Serville, 1835	*Coptops aedificator* (Fabricius, 1793)		R		Jordan, 1903		*Coptops fusca*; *Lamia fusca*
	Coptops annobonae Aurivillius, 1910			E	Aurivillius, 1910		*Pterolophia annobonae*
	Coptops hypocrita Lameere, 1892	R	R		Aurivillius, 1910		
Eunidia Erichson, 1843	*Eunidia thomensis* Breuning, 1970		E		Breuning, 1970		
Frea Thomson, 1858	*Frea maculicornis* Thomson, 1858		R		Lepesme, 1948		
	Frea puncticollis Jordan, 1903		E		Jordan, 1903		
Glenea Newman, 1842	*Glenea thomensis* Breuning, 1958		E		Breuning, 1958		
Insulochamus Dillon & Dillon, 1961	*Insulochamus annobonae* (Aurivillius, 1928)			E	Aurivillius, 1928		
	Insulochamus thomensis (Jordan, 1903)		E		Jordan, 1903		*Monochamus thomensis*
Jordanoleiopus Lepesme & Breuning, 1955	*Jordanoleiopus* (*Polymitoleiopus*) *feai* Breuning, 1955	E			Breuning, 1955		
Monochamus Dejean, 1821	*Monochamus* (*Ethiopiochamus*) *ruspator* (Fabricius, 1781)	R	R		Jordan, 1903		
	Monochamus nubilosus Hintz, 1919			E	Hintz, 1919		
	Monochamus principis Breuning, 1956	E			Breuning, 1956		
	Monochamus rubiginosus Teocchi, Sudre & Jiroux, 2014		E		Fairmaire, 1892		*Monohommus rubigineus*

Phryneta Dejean, 1835	*Phryneta verrucosa* (Drury, 1773)			I	Villiers, 1957		*Phryneta vietti*
Phrynetopsis Kolbe, 1894	*Phrynetopsis thomensis principis* Breuning, 1952	E			Villiers, 1957		
	Phrynetopsis thomensis thomensis (Jordan, 1903)		E		Jordan, 1903		*Pachystola trituberculata thomensis*
Prosopocera Dejean, 1835	*Prosopocera* (*Alphitopola*) *insularis* Breuning, 1936		E		Breuning, 1936		
Protonarthron Thomson, 1858	*Protonarthron microps* (Jordan, 1903)		R		Jordan, 1903		*Plectonarthron microps*
Pseudhammus Kolbe, 1894	*Pseudhammus* (*Litigiosus*) *feae* Aurivillius, 1910		E		Aurivillius, 1910	*	
Pterolophia Newman, 1842	*Pterolophia* (*Annobonaepraonetha*) *annobonae* Aurivillius, 1910			E	Aurivillius, 1910		
	Pterolophia (*Insularepraonetha*) *ferrugineotincta* Aurivillius, 1926	E			Zuzarte & Serrano, 1996		
	Pterolophia (*Insularepraonetha*) *insularis* Breuning, 1938		E		Zuzarte & Serrano, 1996		
	Pterolophia (*Principipraonetha*) *principis* Aurivillius, 1910	E			Aurivillius, 1910		
	Pterolophia (*Principipraonetha*) *pseudoprincipis* Breuning, 1943		E		Breuning, 1943		
	Pterolophia (*Pterolophia*) *thomensis* Breuning, 1938		E		Breuning, 1938		
Ropica Pascoe, 1858	*Ropica thomensis* Breuning, 1970		E		Breuning, 1970		
Steirastoma Lepeletier & Audinet-Serville, 1830	*Steirastoma stellio* Pascoe, 1866		I		Zuzarte & Serrano, 1996	*	
Sternotomis Percheron, 1836	*Sternotomis* (*Pseudolemur*) *rufozonata* Fairmaire, 1902		E		Fairmaire, 1902	*	*Pseudolemur rufozonata*
	Sternotomis (*Ultiolemur*) *ducalis* (Klug, 1835)	R		R	Henriques, 1917	*	*Ultiolemur ducalis*

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Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Tragocephala Dejean, 1835	*Tragocephala guerinii* White, 1856		R		Lepesme & Breuning, 1950		
Subfamily **Parandrinae** Blanchard, 1845							
Acutandra Santos-Silva, 2002	*Acutandra barclayi* Bouyer, Drumont & Santos-Silva, 2012		E		Bouyer et al., 2012		
	Acutandra dasilvai Bouyer, Drumont & Santos-Silva, 2012	E			Bouyer et al., 2012		
	Acutandra delahayei Bouyer, Drumont & Santos-Silva, 2012	E	E		Bouyer et al., 2012	*	
	Acutandra oremansi Bouyer, Drumont & Santos-Silva, 2012		E		Bouyer et al., 2012		
Subfamily **Prioninae** Latreille, 1802							
Ceratocentrus Aurivillius, 1903	*Ceratocentrus oremansi* Delahaye & Camiade, 2016		E		Villiers, 1957		*Acanthophorus spinicornis*
	Ceratocentrus principiensis (Nýlander, 2000)	E			Nýlander, 2000		
Macrotoma Audinet-Serville, 1832	*Macrotoma hayesii* Hope, 1833	E			Tordo, 1956	*	*Telotoma hayesi*
	Macrotoma palmata (Fabricius, 1793)	R	R		Tordo, 1956		
Mallodon Lacordaire, 1869	*Mallodon downesii* Hope, 1843	R	R		Fairmaire, 1891	*	
Sarothrogastra Karsch, 1881	*Sarothrogastra edulis* (Karsch, 1881)		E		Karsch, 1881		*Macrotoma edulis*
	Sarothrogastra feai (Lameere, 1912)			E	Lameere, 1912		
Family **Chrysomelidae** Latreille, 1802							
Subfamily **Bruchinae** Latreille, 1802							
Callosobruchus Pic, 1902	*Callosobruchus maculatus* (Fabricius, 1775)		I		Luna de Carvalho, 1984		

Pachymerus Thunberg, 1805	*Pachymerus nucleorum* (Fabricius, 1792)		I		Castel-Branco, 1966		*Pachymerus lacerdae*
Zabrotes Horn, 1885	*Zabrotes subfasciatus* (Boheman, 1833)		I		Luna de Carvalho, 1984		
Subfamily **Cassidinae** Chapuis, 1875							
Aspidomorpha Hope, 1840	*Aspidimorpha* (*Afroaspidimorpha*) *nigromaculata* (Herbst, 1799)	R			Coache & Rainon, 2020		
	Aspidimorpha (*Aspidimorpha*) *isparetta* Boheman, 1854	R			Coache & Rainon, 2020		
	Aspidimorpha (*Aspidimorpha*) *obovata* (Klug, 1835)	R			Coache & Rainon, 2020		
	Aspidimorpha (*Aspidimorpha*) *quinquefasciata* (Fabricius, 1801)	R	R		Henriques, 1917		
	Aspidimorpha (*Aspidimorpha*) *submutata* Weise, 1899	R			Coache & Rainon, 2020		
	Aspidimorpha (*Aspidocassis*) *confinis* (Klug, 1835)	R			Coache & Rainon, 2020		
Chiridopsis Spaeth, 1922	*Chiridopsis aubei* (Boheman, 1855)	R			Coache & Rainon, 2020	*	
Laccoptera Boheman, 1855	*Laccoptera* (*Orphodella*) *corrugata* (Sahlberg, 1823)		R		Microland	*	*Laccoptera corrugata*
Subfamily **Criocerinae** Latreille, 1804							
Hatita Fairmaire, 1891	*Hatita limbatella* Fairmaire, 1891		E		Fairmaire, 1891		
Lema Fabricius, 1798	*Lema rubricollis* Klug, 1835		R		Jordan, 1903		
Subfamily **Eumolpinae** Hope, 1840							
Afroeurydemus Selman, 1965	*Afroeurydemus variicolor* (Berlioz, 1919)	E	E		Berlioz, 1919	*	
Cheiridella Jacoby, 1904	*Cheiridella principis* Zoia, 2017	E	E		Zoia, 2017		

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Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Paraivongius Pic, 1936	*Paraivongius* (*Micromenius*) sp.	E			Zoia, 2017		
	Paraivongius (*Paraivongius*) *inexspectatus* Zoia, 2017	R			Zoia, 2017		
Rhembastus Harold, 1877	*Rhembastus piceus* Zoia, 2017	E			Zoia, 2017		
Subfamily **Galerucinae** Latreille, 1802							
Lamprocopa Hincks, 1949	*Lamprocopa delata* (Erichson, 1843)		R		Jordan, 1903		*Anlacophora delata*; *Aulacophora delata*
	Lamprocopa occidentalis Weise, 1895	R	R		Microland	*	
Longitarsus Latreille, 1829	*Longitarsus* sp.		R?		Microland	*	
Manobia Jacoby, 1885	*Manobia* sp.		R?		Microland	*	
Nisotra Baly, 1864	*Nisotra theobromae* Laboissière, 1920	E	E		Laboissière, 1920	*	
Notomela Jacoby, 1899	*Notomela joliveti* Biondi & D'Alessandro, 2015	E			Biondi & D'Alessandro, 2015		
Subfamily **Hispinae** Gyllenhal, 1813							
Dactylispa Weise, 1897	*Dactylispa aculeata* (Klug, 1835)	R			Gestro, 1905		
	Dactylispa cavicollis Gestro, 1905		E		Gestro, 1905		
	Dactylispa incredula Gestro, 1905		E		Gestro, 1905		
	Dactylispa nigricornis Gestro, 1905	E			Gestro, 1905		
Platypria Guérin-Méneville, 1840	*Platypria* (*Dichirispa*) *paucispinosa* Gestro, 1905	R	R		Gestro, 1905		*Platypria feae*
Thomispa Würmli, 1975	*Thomispa feae* (Gestro, 1906)	E	E		Gestro, 1905	*	*Trichispa feae*

Family **Cicindelidae** Latreille, 1802							
Subfamily **Cicindelinae** W. Horn, 1926							
Cylindera Westwood, 1831	*Cylindera* (*Ifasina*) *octoguttata* (Fabricius, 1787)	R			Serrano, 2008		
Lophyra Motschulsky, 1861	*Lophyra neglecta* (Dejean, 1825)		R		Gomes Alves, 1956		*Lophyra discoidea*
Myriochila Motschulsky, 1862	*Myriochila melancholica* (Fabricius, 1798)	R	R		Jordan, 1903		*Myriochile melancholica*; *Cicindela melancholica*
Family **Ciidae** Leach, 1819							
Subfamily **Ciinae** Leach, 1819							
Xylographus Melli,, 1849	*Xylographus nitidissimus* Pic, 1916		R		Pic 1916		
Family **Cleridae** Latreille, 1802							
Subfamily **Korynetinae** Laporte, 1836							
Necrobia Olivier, 1800	*Necrobia rufipes* (De Geer, 1775)		I		Luna de Carvalho, 1984		
Family **Coccinellidae** Latreille, 1807							
Subfamily **Chilocorinae** Mulsant, 1846							
Chilocorus Leach, 1815	*Chilocorus cacti* (Linnaeus, 1767)		R		Castel-Branco, 1963		
	Chilocorus pilosus Sicard, 1920		E		Sicard, 1920		
Endochilus Weise, 1898	*Endochilus plagiatus* Sicard, 1920		E		Sicard, 1920		
	Endochilus styx Sicard, 1911	E			Sicard, 1911		
Exochomus Redtenbacher, 1843	*Exochomus flavipes* (Thunberg, 1781)		R		Sicard, 1920		*Exochomus nigromaculatus insulicola*
	Exochomus nigrifrons Gerstäcker, 1871		R		Fürsch, 1974		*Brumus nigrifrons*
Subfamily **Coccinellinae** Latreille, 1807							
Cheilomenes Mulsant, 1850	*Cheilomenes sulphurea* (Olivier, 1791)	R	R		Henriques, 1917		

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Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Coccinella Linnaeus, 1758	*Coccinella intermedia* (Crotch, 1874)		E		Gordon, 1987		
Micraspis Chevrolat in Dejean, 1836	*Micraspis striata* (Fabricius, 1792)		R		Hounkpati et al., 2020		*Alesia striata*
Oenopia Mulsant, 1850	*Oenopia doderoi* (Sicard, 1911)		E		Sicard, 1911		*Coccinella doderoi*; *Synharmonia doderoi*
Thea Mulsant, 1846	*Thea moniqueae* Fürsch, 1974		E		Fürsch, 1974		
Subfamily **Epilachninae** Mulsant, 1846							
Chnootriba Dejean, 1835	*Chnootriba elaterii* (Rossi, 1794)		R		Hounkpati et al., 2020		
Subfamily **Exoplectrinae** Crotch, 1874							
Aulis Mulsant, 1850	*Aulis nigricordis* Fürsch, 1974		E		Fürsch, 1974		
Subfamily **Microweiseinae** Leng, 1920							
Scymnomorphus Weise, 1897	*Scymnomorphus minuta* Fürsch, 1974		E		Fürsch, 1974		*Sukunahikona minuta*
	Scymnomorphus principiensis Gomes Alves & Castel-Branco, 1962	E			Gomes Alves & Castel-Branco, 1962		
Subfamily **Ortaliinae** Mulsant, 1850							
Rodolia Mulsant, 1850	*Rodolia cardinalis* (Mulsant, 1850)		I		Castel-Branco, 1963		
	Rodolia seabrai Sicard, 1920		E		Sicard, 1920		
	Rodolia vulpina Fürsch, 1974		E		Fürsch, 1974		
Subfamily **Scymninae** Mulsant, 1846							
Cryptognatha Mulsant, 1850	*Cryptognatha nodiceps* Marschall, 1912	I			Castel-Branco, 1963		
Nephus Mulsant, 1846	*Nephus derroni* Fürsch, 1974		E		Fürsch, 1974		
	Nephus theobromae Fürsch, 1974		E		Fürsch, 1974		

Platynaspis Redtenbacher, 1843	*Platynaspis capicola* Crotch, 1874		R		Fürsch 1974		
Scymnus Cuvier, 1816	*Scymnus levaillanti* Mulsant, 1850		R		Fürsch, 1974		
	Scymnus nubilus Mulsant, 1850		R		Hounkpati et al., 2020		*Scymnus canariensis*
	Scymnus oblongoides Fürsch, 1974		E		Fürsch, 1974		
	Scymnus scapuliferus Mulsant, 1850	R	R		Gomes Alves, 1973		
	Scymnus senegalensis Mader, 1955		R		Hounkpati et al., 2020		
Stethorus Weise, 1885	*Stethorus chazeaui* Fürsch, 1974		E		Fürsch, 1974		
Subfamily **Sticholotidinae** Weise, 1901							
Pharoscymnus Bedel, 1906	*Pharoscymnus exiguus* Weise, 1913	R			Gomes Alves, 1973		
	Pharoscymnus tetrastictus Sicard, 1930		R		Fürsch, 1974		
	Pharoscymnus tomeensis Fürsch, 1974		E		Fürsch, 1974		
Family **Curculionidae** Latreille, 1802							
Subfamily **Conoderinae** Schönherr, 1833							
Panoptes Gerstaecker, 1860	*Panoptes convexus* Karsch, 1881		E		Karsch, 1881		
Subfamily **Cryptorhynchinae** Schönherr, 1825							
Cyamobolus Schönherr, 1837	*Cyamobolus greeffi* Karsch, 1881		E		Karsch, 1881		*Cyanobulus greeffi*
Mechistocerus Fauvel, 1862	*Mechistocerus nubeculosus* Fairmaire, 1891		R		Fairmaire, 1891		*Mecictocerus nubeculosus*
Subfamily **Entiminae** Schönherr, 1823							
Phyllobius Germar, 1824	*Phyllobius verruculatus* Karsch, 1881		E		Karsch, 1881		

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Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Saotomia Borovec & Anderson, 2021	*Saotomia tuberculata* Borovec & Anderson, 2021		E		Borovec & Anderson, 2021		
Subfamily **Molytinae** Schönherr, 1823							
Aethiopacorep Voisin, 1992	*Aethiopacorep africanus* (Hustache, 1932)			E	Cristóvão & Lyal, 2018		
Sternuchopsis Heller, 1917	*Sternuchopsis* sp.		R?		Microland	*	
Titilayo Cristóvão & Lyal, 2018	*Titilayo barclayi* Cristóvão & Lyal, 2018		E		Cristóvão & Lyal, 2018		
	Titilayo perrinae Cristóvão & Lyal, 2018		E		Cristóvão & Lyal, 2018		
	Titilayo saotomense Cristóvão & Lyal, 2018		E		Cristóvão & Lyal, 2018		
	Titilayo turneri Cristóvão & Lyal, 2018		E		Cristóvão & Lyal, 2018		
Subfamily **Platypodinae** Shuckard, 1839							
Chaetastus Nunberg 1953	*Chaetastus tuberculatus* (Chapuis, 1865)		R		Beaver & Löyttyniemi, 1985		
Costaroplatus Nunberg, 1963	*Costaroplatus pernix* (Schedl, 1941)		E		Wood & Bright, 1992		*Platyscapus pernix*
Doliopygus Browne, 1962	*Doliopygus erichsoni* (Chapuis, 1865)		R		Beaver & Löyttyniemi, 1985		*Crossotarsus erichsoni*
	Doliopygus ibex Schedl, 1941		E		Wood & Bright, 1992		
Periommatus Chapuis, 1866	*Periommatus excisus* Strohmeyer, 1912	R	R		Wood & Bright, 1992		

Platypus Herbst, 1793	*Platypus hintzi* Schaufuss, 1897		I		Wood & Bright, 1992		
	Platypus intermedius (Schedl, 1937)		R		Wood & Bright, 1992		*Stenoplatypus intermedius*
	Platypus parallelus (Fabricius, 1801)		I		Wood & Bright, 1992		
Subfamily **Scolytinae** Latreille, 1804							
Hapalogenius Hagedorn, 1912	*Hapalogenius dubius* Eggers, 1920		R		Medler, 1980		*Hylesinopsis dubius*
Hypothenemus Westwood, 1836	*Hypothenemus hampei* (Ferrari, 1867)		I		Kaden, 1930		*Stephanoderes hampei*
Xyleborus Eichhoff, 1864	*Xyleborus ferrugineus* (Fabricius, 1801)		I		Luna de Carvalho 1984		
Family **Dryophthoridae** Schönherr, 1825							
Subfamily **Dryophthorinae** Schönherr, 1825							
Cosmopolites Chevrolat, 1885	*Cosmopolites sordidus* (Germar, 1824)		R		Jordan, 1903		*Sphenophorus sordidus*; *Sphenophorus striatus*
Sitophilus Schönherr, 1838	*Sitophilus oryzae* (Linnaeus, 1763)		I		Luna de Carvalho, 1984		
Subfamily **Rhynchophorinae** Schönherr, 1833							
Metamasius Horn, 1873	*Metamasius hemipterus* Linnaeus, 1758		R		Microland	*	
Temnoschoita Chevrolat, 1885	*Temnoschoita quadrimaculata* Csiki, E., 1936		R		Henriques, 1917		
Family **Dytiscidae** Leach, 1815							
Subfamily **Copelatinae** Van den Branden, 1885							
Copelatus Erichson, 1832	*Copelatus pallidus* Régimbart, 1895	R			Régimbart, 1904	*	

(continued)

Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Subfamily **Dytiscinae** Leach, 1815							
Cybister Curtis, 1827	*Cybister* (*Melanectes*) *vulneratus* Klug, 1834	R	R		Jordan, 1903		*Trogus binotatus*; *Melanectes vulneratus*; *Cybister binotatus*
Family **Elateridae** Leach, 1815							
Subfamily **Agrypninae** Candèze, 1857							
Calais Laporte de Castelnau, 1836	*Calais controversa* (Karsch, 1881)		E		Karsch, 1881	*	*Ctenicera controversa*; *Alaus chalcolepidinus*
Elasmosomus Schwarz, 1903	*Elasmosomus mocquerysi* (Fleutiaux, 1902)	E	E		Girard, 2017		
Lanelater Arnett, 1952	*Lanelater glabratus* (Gyllenhall, 1817)	R			Girard, 2017	*	*Lanelater substriatus*
Subfamily **Denticollinae** Stein & Weise, 1877							
Melanoxanthus Dejean, 1833	*Melanoxanthus inaequalis* Candèze, 1881		R		Girard, 2017		
Subfamily **Elaterinae** Leach, 1815							
Propsephus Hyslop, 1921	*Propsephus athoides* (Candèze, 1881)		R		Fairmaire, 1891		
	Propsephus campyloides (Candèze, 1897)		E		Fairmaire, 1891		*Psephus athoides*
	Propsephus melanotoides (Fairmaire, 1891)		E		Fairmaire, 1891		
	Propsephus scitulus Schwarz, 1909		E		Girard, 2017		
Subfamily **Lissominae** Laporte, 1835							
Lissomus Dalman, 1824	*Lissomus francisci* Karsch, 1881		E		Karsch, 1881	*	
Family **Endomychidae** Leach, 1815							
Subfamily **Lycoperdininae** Bromhead, 1838							
Ancylopus Costa, 1854	*Ancylopus meridionalis* Stroheker, 1962		R		Microland	*	

Family **Gyrinidae** Latreille, 1810							
Subfamily **Gyrininae** Latreille, 1810							
Orectogyrus Régimbart, 1884	*Orectogyrus* (*Lobogyrus*) *lionotus* Régimbart, 1884		R		Régimbart, 1904		
Family **Histeridae** Gyllenhal, 1808							
Subfamily **Dendrophilinae** Reitter, 1909							
Platylomalus Cooman, 1948	*Platylomalus digitatus* (Wollaston, 1867)		R		Gomy, 2004		
	Platylomalus longicornis (Lewis, 1906)	E	E		Lewis, 1906		
Subfamily **Histerinae** Gyllenhal, 1808							
Apobletes Marseul, 1861	*Apobletes macer* (Lewis, 1906)	E			Lewis, 1906		*Platysoma macer*
Corticalinus Gomy, 2004	*Corticalinus minusculus* (Schmidt, 1893)	R	R		Gomy, 2004		
Hololepta Paykull, 1811	*Hololepta syntexis* Lewis, 1900	R	R		Lewis, 1900	*	
Pachycraerus Marseul, 1854	*Pachycraerus chlorites* Lewis, 1900		R		Lewis, 1900		
	Pachycraerus cyanescens Erichson, 1834	R	R		Gomy, 2004	*	
Platylister Lewis, 1892	*Platylister* (*Ricinodendrus*) *foliaceus* (Paykull, 1811)	R	R		Gomy, 2004	*	
Teretrius Erichson, 1834	*Teretrius braganzae* Lewis, 1900		R		Lewis, 1900		
Family **Hybosoridae** Erichson, 1847							
Subfamily **Hybosorinae** Erichson, 1847							
Hybosorus MacLeay, 1819	*Hybosorus illigeri* Reiche, 1853		R		Kuijten, 1983		
Family **Hydrophilidae** Latreille, 1802							
Subfamily **Sphaeridiinae** Latreille, 1802							
Coelostoma Brullé, 1835	*Coelostoma rufitarse* (Boheman, 1851)			R	Régimbart, 1907		

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Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Dactylosternum Wollaston, 1854	*Dactylosternum abdominale* (Fabricius, 1792)		R		Régimbart, 1907		
	Dactylosternum intermedium Régimbart, 1907	R			Régimbart, 1907		
	Dactylosternum profundum Régimbart, 1907		E		Régimbart, 1907		
Megasternini Mulsant, 1844	Unidentified species		R?		Microland	*	
Pachysternum Motschulsky, 1863	*Pachysternum capense* (Mulsant, 1844)	R	R		Régimbart, 1907		
Pelosoma Mulsant, 1844	*Pelosoma buccalis* (Régimbart, 1907)	E			Régimbart, 1907		
Family **Laemophloeidae** Ganglbauer, 1899							
Subfamily **Laemophloeinae** Ganglbauer, 1899							
Cryptolestes Ganglbauer, 1899	*Cryptolestes atulus* Lefkovitch, 1962		R		Lefkovitch, 1962		
	Cryptolestes ferrugineus (Stephens, 1831)		I		Luna de Carvalho, 1984		
	Cryptolestes pusillus (Schönherr, 1817)		I		Luna de Carvalho, 1984		
Placonotus Mac Leay, 1871	*Placonotus bolivari* (Grouvelle, 1905)		R		Lefkovitch, 1962		
	Placonotus politissimus (Wollaston, 1867)		R		Lefkovitch, 1962		
	Placonotus testaceus (Fabricius, 1787)		I		Luna de Carvalho, 1984		
Xylolestes Lefkovitch, 1962	*Xylolestes unicolor* (Grouvelle, 1908		R		Lefkovitch, 1962		
Family **Limnichidae** Erichson, 1846							
	Unidentified species		R?		Microland	*	

Family **Lucanidae** Latreille, 1804							
Subfamily **Lucaninae** Latreille, 1804							
Figulus MacLeay, 1819	*Figulus anthracinus* Klug, 1832	R			Griffini, 1906		*Figulus sublaevis*
	Figulus decipiens Albers, 1884		E		Gomes Alves, 1973	*	*Figulus sublaevis decipiens*
Nigidius MacLeay, 1819	*Nigidius bubalus* (Swederus, 1787)		R		Klug, 1835		*Nigidius auriculatus*
	Nigidius endroedi Gomes Alves, 1973	E			Gomes Alves, 1973		
Prosopocoilus Westwood, 1845	*Prosopocoilus antilopus amicorum* Matsumoto, 2019			E	Matsumoto, 2019		
	Prosopocoilus antilopus beisa Kriesche, 1919	E			Griffini, 1906		*Prosopocoelus antilopus*
	Prosopocoilus antilopus insulanus Kriesche, 1919		E		Fairmaire, 1891	*	*Prosopocoelus antilopus*
	Prosopocoilus downesii savagei (Hope, 1835)	R	R		Griffini, 1906	*	*Metopodontus downesii*
	Prosopocoilus senegalensis (Klug, 1835)	R			Bartolozzi & Werner, 2004		
Family **Lycidae** Laporte de Castelnau, 1838							
Subfamily **Lycinae** Laporte, 1836							
Flagrax Kasantsev, 1992	*Flagrax bifoveolatus* Pic, 1924	E			Pic, 1926	*	
Stadenus Waterhouse, 1879	*Stadenus auberti sensifulvus* Fairmaire, 1891		E		Fairmaire, 1891		*Stadenus semiflavus*; *Stadenus auberti semufulvus*
Family **Lymexylidae** Fleming, 1821							
Subfamily **Atractocerinae** Laporte, 1840							
Atractocerus Palisot de Beauvoir, 1801	*Atractocerus brevicornis* (Linnaeus, 1766)		R		Jordan, 1903		*Atractocerus africanus*; *Atractocerus frontalis*; *Atractocerus brevicornis africanus*

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Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Family **Mordellidae** Latreille, 1802							
Subfamily **Mordellinae** Latreille, 1802							
Glipostena Ermisch, 1941	*Glipostena nemoralis* Franciscolo, 1962		R		Microland	*	
Ophthalmoglipa Franciscolo, 1952	*Ophthalmoglipa horaki* Ruzzier, 2015	E			Ruzzier, 2015	*	
	Ophthalmoglipa leblanci Ruzzier, 2015		E		Ruzzier, 2015		
Family **Mycteridae** Oken, 1843							
Subfamily **Hemipeplinae** Lacordaire, 1854							
Hemipeplus Latreille, 1825	*Hemipeplus africanus* Grouvelle, 1915		R		Microland	*	
Family **Nitidulidae** Latreille, 1802							
Subfamily **Carpophilinae** Erichson, 1842							
Carpophilus Stephens, 1830	*Carpophilus dimidiatus* (Fabricius, 1792)		I		Luna de Carvalho, 1984		
	Carpophilus hemipterus (Linnaeus, 1758)		I		Luna de Carvalho, 1984		
Subfamily **Epuraeinae** Kirejtshuk, 1986							
Epurea Erichson, 1845	*Epureae ocularis* Fairmaire, 1849		R		Microland	*	*Epureae* (*Haptoncus*) *ocularis*
Family **Oedemeridae** Latreille, 1810							
Subfamily **Oedemerinae** Latreille, 1810							
Alloxanthoides Svihla, 1985	*Alloxanthoides lateritincta* (Pic, 1920)		R		Serrano unpublished data		
Ditylomorphula Svihla, 1985	*Ditylomorphula bicolorites* (Pic, 1922)		E		Pic, 1922		
Monosigynes Vazquez, 2004	*Monosigynes semipiceus* (Karsch, 1881)		E		Karsch, 1881		*Danerces semipicea*

Family **Passalidae** Leach, 1815							
Subfamily **Passalinae** Leach, 1815							
Didymus Hincks, 1933	*Didymus laevis* (Klug, 1835)	E	E		Gomes Alves, 1965	*	
Pentalobus Kaup, 1868	*Pentalobus barbatus* (Fabricius, 1801)		R		Jordan, 1903		*Pselaphus barbatus*
Family **Ptiliidae** Heer, 1843							
Subfamily **Acrotrichinae** Reitter, 1909							
Acrotrichis Motschulsky, 1848	*Acrotrichis* (*Ctenopteryx*) *discoloroides* Johnson, 1969		R		Darby, 2020		
	Acrotrichis tersa Johnson, 1969		R		Darby, 2020		
Family **Ptilodactylidae** Laporte de Castelnau, 1836							
	Unidentified species		R?		Microland	*	
Family **Ptinidae** Latreille, 1802							
Subfamily **Anobiinae** Fleming, 1821							
Stegobium Motschulsky, 1860	*Stegobium paniceum* (Linnaeus, 1758)		I		Luna de Carvalho, 1984		
Subfamily **Xyletininae** Gistel, 1848							
Lasioderma Stephens, 1835	*Lasioderma serricorne* (Fabricius, 1792)		I		Luna de Carvalho, 1984		
Family **Scarabaeidae** Latreille, 1802							
Subfamily **Bolboceratinae** Mulsant, 1842							
Bolbocaffer Vulcano,Martinez & Pereira 1969	*Bolbocaffer pallens* (Kolbe, 1835)		R		Paulian, 1941		*Odontaeus pallens*
Subfamily **Cetoniinae** Leach, 1815							
Chlorocala Kirby, 1828	*Chlorocala viridicyanea* (Palisot de Beauvois, 1821)	R			Janson, 1907		
Diplognata Gory & Percheron, 1833	*Diplognata* (*Diplognatha*) *gagates* Forster, 1771		R		Jordan, 1903		

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Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Dischista Burmeister, 1842	*Dischista rufa* (De Geer, 1778)		R		Jordan, 1903		*Pachnoda rufa*; *Cetonia rufa*
Grammopyga Kolbe, 1895	*Grammopyga cincticollis* (Hope, 1842)	R			Janson, 1907		
	Grammopyga marginicollis (Moser, 1904)		E		Moser, 1904		
Leucocelis Burmeister, 1842	*Leucocelis feana* Janson, 1907		E		Janson, 1907		
Pachnoda Burmeister, 1842	*Pachnoda canui* Rigout & Allard, 1992	E			Rigout & Allard, 1992		
	Pachnoda prasina Karsch, 1881		E		Karsch, 1881		*Cetonia prasina*
Phaneresthes Kraatz, 1894	*Phaneresthes flavosignata* (Moser, 1904)		E		Moser, 1904		
Pseudoheterophana Allard, 1990	*Pseudoheterophana canui* Allard, 1990	E			Allard, 1990		
Pseudotephraea Kraatz, 1882	*Pseudotephraea ancilla ancilla* (Harold, 1879)		E		Harold, 1879		
	Pseudotephraea ancilla canui Antoine, 1992	E			Jordan, 1903		*Tephraea ancilla*
Uloptera Burmeister, 1842	*Uloptera canui* Antoine, 1992	E			Antoine, 1992		
Subfamily **Dynastinae** MacLeay, 1819							
Cyphonistes Burmeister, 1847	*Cyphonistes camurus* Karsch, 1881		E		Karsch, 1881		
Oryctes Hellwig, 1798	*Oryctes* (*Rykanes*) *capucinus* Arrow, 1937	R			Vesco et al., 1999		
	Oryctes (*Rykanes*) *latecavatus* Fairmaire, 1891		E		Fairmaire, 1891		
	Oryctes (Rykanoryctes) monoceros Olivier, 1789		I		Vargas Ferreira, 1967		

Rhizoplatys Westwood, 1842	*Rhizoplatys canui* Dechambre, 1983	E			Dechambre, 1983		
	Rhizoplatys mucronatus cedrici Dechambre, 1983	E			Dechambre, 1983	*	
Temnorhynchus Hope, 1837	*Temnorhynchus* (*Temnorhynchus*) *coronatus diana* (Palisot de Beauvois, 1805)		R		Henriques, 1917		*Temnorhynchus diana*
	Temnorrhynchus (*Temnorhynchus*) *tridentatus* Lansberge, 1886		R		Krell, 1994		
Subfamily **Melolonthinae** MacLeay, 1819							
Apogonia Kirby, 1819	*Apogonia decellei* Lacroix, 2008		E		Lacroix, 2008	*	
	Apogonia insulana Karsch, 1882	E			Karsch, 1882	*	
	Apogonia tomeensis Lacroix, 2008		E		Lacroix, 2008	*	
Subfamily **Orphninae** Erichson, 1847							
Stenosternus Karsch, 1881	*Stenosternus costatus* Karsch, 1881		E		Karsch, 1881		*Mecistoceros costatus*
Subfamily **Scarabaeinae** Latreille, 1802							
Onthophagus Latreille, 1802	*Onthophagus* (*Onthophagus*) *sellatus* Klug, 1845	R	R		d'Orbigny, 1905		
	Onthophagus (*Trichonthophagus*) *juvencus* Klug, 1835	R			d'Orbigny, 1905		
Paraphytus Harold, 1877	*Paraphytus africanus* Boucomont, 1923	R	R		Paulian, 1949	*	
Phalops Erichson, 1848	*Phalops fimbriatus* (Klug, 1835)	R			d'Orbigny, 1913		
Proagoderus Lansberge, 1883	*Proagoderus laticollis* Klug, 1835	R			d'Orbigny, 1913		

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Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Subfamily **Trichiinae** Fleming, 1821							
Clastocnemis Burmeister & Schaum, 1840	*Clastocnemis quadrimaculatus oremansi* Antoine, 2005		E		Antoine, 2005	*	
	Clastocnemis quadrimaculatus principis Antoine, 2005	E			Antoine, 2005		
Comythovalgus Kolbe, 1884	*Comythovalgus aemulus* Kolbe, 1897		R		Janson, 1907		
Cryptodontus Burmeiester, 1847	*Cryptodontus latreilleanus desaegeri* Burgeon, 1946		E		Henriques, 1917	*	
Family **Silvanidae** Kirby, 1837							
Subfamily **Silvaninae** Kirby, 1837							
Ahasverus Gozis, 1881	*Ahasverus advena* (Waltl, 1834)		I		Luna de Carvalho, 1984		
Cryptamorpha Wollaston, 1854	*Cryptamorpha* sp.		R?		Microland	*	
Oryzaephilus Ganglbauer, 1899	*Oryzaephilus mercator* (Fauvel, 1889)		I		Luna de Carvalho, 1984		
	Oryzaephilus surinamensis (Linnaeus, 1758)		I		Luna de Carvalho, 1984		
Family **Staphylinidae** Lameere, 1900							
Subfamily **Osoriinae** Erichson, 1839							
Afrosorius Fagel, 1958	*Afrosorius assiniensis* (Fauvel, 1903)		R		Ferreira, 2014		
	Afrosorius curtipennis Fagel, 1958		E		Fagel, 1958		
	Afrosorius strigifrons (Kolbe, 1889)		R		Ferreira, 2014		
	Afrosorius viettei Fagel, 1958		E		Fagel, 1958		
Nacaeus Blackwelder, 1942	*Nacaeus aethiops* (Eppelsheim, 1895)		R		Fauvel, 1903		

Subfamily **Paederinae** Fleming, 1821							
Paederus Fabricius, 1775	*Paederus angusticeps* Bernhauer, 1915		R		Fagel, 1966		
Rugilus Leach, 1819	*Rugilus rubelloides* (Fagel, 1951)		R		Fagel, 1953		*Stilicus rubelloides*
Tracypum Fagel, 1977	*Tracypum vietteanum* Fagel, 1977		E		Fagel, 1977		
Subfamily **Staphylininae**, Latreille, 1802							
Philonthus Stephens, 1826	*Philonthus longicornis* Stephens, 1832		R		Ferreira, 2014		
	Philonthus peregrinus Fauvel, 1866		R		Ferreira, 2014		
Subfamily **Tachyporinae** MacLeay, 1825							
Tachinomorphus Kraatz, 1859	*Tachinomorphus africanus* (Eppelsheim, 1895)		R		Fauvel, 1903		
Family **Tenebrionidae** Latreille, 1802							
Subfamily **Diaperinae** Latreille, 1802							
Ceropria Laporte & Brullé, 1831	*Ceropria anthracina* Quedenfeldt, 1885		R		Gebien, 1921		
	Ceropria romandi Laporte & Brullé, 1831	R			Gebien, 1921		
Gnathidium Gebien, 1920	*Gnathidium cephalotes* Gebien, 1921	E			Gebien, 1921		
Hypophloeus Fabricius, 1790	*Hypophloeus insularis* Gebien, 1921	R			Gebien, 1942		*Corticeus insularis*
	Hypophloeus piceus Gebien, 1921	E			Gebien, 1921		
	Hypophloeus sternalis Gebien, 1914	E	E		Gebien, 1914		*Corticeus sternalis*
Ischnarthron Gebien, 1920	*Ischnarthron longipes* Gebien, 1921		E		Gebien, 1921		

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Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Microcrypticus Gebien, 1921	*Microcrypticus scriptipennis* (Fairmaire, 1875)		R		Gebien, 1942		
Platydema Laporte de Castelnau & Brullé, 1831	*Platydema capucinum* Gebien, 1921	E			Gebien, 1921		
Stomylus Fåhraeus, 1870	*Stomylus maculosus* (Thomson, 1858)		R		Gebien, 1942		*Pselaphidion macularium*; *Pselaphidion maculosum*; *Platydema maculosum*
Subfamily **Lagriinae** Latreille, 1825 (1820)							
Luprops Hope, 1833	*Luprops chalceus* Gebien, 1921		R		Microland	*	
Physolagria Fairmaire, 1891	*Physolagria molleri* Fairmaire, 1891		E		Fairmaire, 1891	*	
Prioscelis Hope, 1840	*Prioscelis haesitans* Kolbe, 1903		E		Jordan, 1903	*	*Prioscelis serrata haesitans*
Subfamily **Phrenapatinae** Solier, 1834							
Afrotagalus Gebien, 1942	*Afrotagalus viettei* Ardoin, 1958		E		Ardoin, 1958		
Subfamily **Stenochiinae** Kirby, 1837							
Alcyonotus Pascoe, 1882	*Alcyonotus insularis* Ardoin, 1958	E			Ardoin, 1958		
Derosphaerus Thomson, 1858	*Derosphaerus globicollis* Thomson, 1858	R	R	R	Gebien, 1942		
	Derosphaerus morosus (Motschulsky, 1872)	R	R		Gebien, 1921		
Eremobatodes Gebien, 1943	*Eremobatodes crux* (Gebien, 1921)		E		Gebien, 1942	*	*Eremobates crux*
	Eremobatodes metallicus (Ardoin, 1958)		E		Ardoin,1958		*Eremobates metallicus*
Menephilus Mulsant, 1854	*Menephilus carbonatus* Gebien, 1921	E	E		Gebien, 1921		
	Menephilus conquinatus Karsch, 1881		E		Karsch, 1881	*	

Nesosphaerotus Gebien, 1921	*Nesosphaerotus aeneus* Gebien, 1921		E		Gebien, 1921	*	
	Nesosphaerotus egena Gebien, 1921		E		Gebien, 1921		
	Nesosphaerotus justi Karsch, 1881		E		Karsch, 1881	*	*Derosphaerus justi*
	Nesosphaerotus kulzeri Ardoin, 1962		E		Ardoin, 1962		
	Nesosphaerotus marquesi Karsch, 1881		E		Karsch, 1881		*Derosphaerus marquesii*
	Nesosphaerotus simplicifrons Gebien, 1921	E			Gebien, 1921		
	Nesosphaerotus striatipennis Gebien, 1921		E		Gebien, 1921		
	Nesosphaerotus viettei Ardoin, 1958		E		Ardoin, 1958	*	
Strongylium Ditmar, 1809	*Strongylium camiadei* Robiche, 2000	E			Robiche, 2000		
	Strongylium feai Gebien, 1921		E		Gebien, 1921	*	
Subfamily **Tenebrioninae** Latreille, 1802							
Alphitobius Stephens, 1829	*Alphitobius laevigatus* (Fabricius, 1781)		I		Luna de Carvalho, 1984		
	Alphitobius viator Mulsant & Godart, 1868	R			Gebien, 1942		
Amenophis Thomson, 1858	*Amenophis insularis* Gebien, 1921			E	Gebien, 1921		
	Amenophis minor Gebien, 1921		E		Gebien, 1921		
	Amenophis striata Gebien, 1921	E			Gebien, 1921		
Cryphaeus Klug, 1833	*Cryphaeus taurus* (Fabricius, 1801)	R	R		Jordan, 1903	*	*Toxicum taurus*; *Cryphaeus aries*
Diaclina Jacquelin du Val, 1861	*Diaclina parallela* (Thomson, 1858)	R			Gebien, 1921		

(continued)

Higher taxonomy	Species	P	ST	A	Reference	ML	Synonyms
Gonocephalum Solier, 1834	*Gonocephalum angolense subtilistriatum* Kolbe, 1887		R		Gebien, 1921		*Gonocephalum granicolle*
	Gonocephalum calcaripes (Karsch, 1881)		R		Karsch, 1881		*Opatrum calcaripes*
	Gonocephalum feae Gebien, 1921			E	Gebien, 1921		
	Gonocephalum prolixum (Erichson, 1843)	R	R	R	Gebien, 1921		
	Gonocephalum simplex (Fabricius, 1801)		R		Gebien, 1942		
Hoplonyx Thomson, 1858	*Hoplonyx insularis* Gebien, 1921	E			Gebien, 1921		
Megacantha Westwood, 1843	*Megacantha dentata* (Fabricius, 1801)	R			Gebien, 1921		
Nesopatrum Gebien, 1921	*Nesopatrum josephii* (Karsch, 1881)		E		Karsch, 1881		*Opatrinus josephi*
Palorus Mulsant, 1854	*Palorus carinicollis* Gebien, 1921		R		Gebien, 1921		*Platyotus carinicollis*
	Palorus subdepressus (Wollaston, 1864)		R		Gebien, 1921		
Peltoides Laporte de Castelnau, 1832	*Peltoides senegalensis* Laporte de Castelnau, 1832	R			Gebien, 1921		
Tenebrio Linnaeus, 1758	*Tenebrio* (*Afrotenebrio*) *guineensis* Imhoff, 1843	R			Gebien, 1921		
	Tenebrio legalli Robiche, 2009		E		Robiche, 2009		
Tribolium Macleay 1825	*Tribolium castaneum* (Herbst, 1797)		I		Luna de Carvalho, 1984		
	Tribolium semicostata Gebien, 1921		R		Gebien, 1921		*Tenebrioloma semicostata*
Uloma Dejean, 1821	*Uloma collaris* Gebien, 1921	E			Gebien, 1942		
	Uloma costae Karsch, 1881		E		Karsch, 1881	*	
	Uloma laesicollis Thomson, 1858	R			Gebien, 1921		

Zidalus Mulsant & Rey, 1852	*Zidalus latipes* (Sahlberg, 1823)	R			Gebien, 1921		*Opatrinus atratus*; *Opatrinus opacus*
Family **Trogossitidae** Latreille, 1802							
Subfamily **Trogossitinae** Latreille, 1802							
Temnoscheila Westwood, 1830	*Temnocheila patricioi* (Karsch, 1881)		E		Karsch, 1881		*Trogossita patricioi*; *Trogosita patricioi*
Tenebroides Piller & Mitterpacher, 1783	*Tenebroides maroccanus* Reitter, 1884		I		Luna de Carvalho, 1984		
	Tenebroides mauritanicus (Linnaeus, 1758)		I		Luna de Carvalho, 1984		
Family **Zopheridae** Solier, 1834							
Subfamily **Colydiinae** Billberg, 1820							
Bitoma Herbst, 1793	*Bitoma siccana* (Pascoe, 1863)	R			Pope, 1961		*Bitoma lyctiformis*
Mecedanum Erichson, 1845	*Mecedanum auberti* (Fairmaire, 1882)	R			Serrano, unpublished data		
Microprius Fairmaire, 1868	*Microprius rufulus* (Motschulsky, 1863)		R		Pope, 1961		*Microprius confusus*

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Chapter 13
Butterflies and Skippers (Lepidoptera: Papilionoidea) of the Gulf of Guinea Oceanic Islands

Luís F. Mendes and António Bivar-de-Sousa

Abstract The three Gulf of Guinea oceanic islands, Príncipe, São Tomé, and Annobón, have always remained isolated from the African continent and correspond to the westernmost peaks of the Cameroon Volcanic Line, while the island of Bioko, part of the same ridge, was connected to the mainland during glaciations. Despite the small area of the oceanic islands, their relief and remoteness have enabled the evolution of remarkable ecological and biological diversity. Concerning diurnal Lepidoptera, 91 species and subspecies are known from the oceanic islands: 46 from Príncipe, 64 from São Tomé, and 8 from Annobón; and 35 are endemic: 17 to Príncipe, 23 to São Tomé, and only 5 shared among islands. Further species have been reported in error, either due to misidentification or to mislabelling. A revised checklist of the species and subspecies of the Gulf of Guinea oceanic islands Papilionoidea is presented as is a summary of their taxonomy, distribution, and ecology.

Keywords Africa · Conservation · Ecology · Endemism · Taxonomy

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Introduction

The Gulf of Guinea Oceanic Islands (GGOI), Príncipe, São Tomé, and Annobón (=Pagalu), represent the Cameroon Volcanic Line's westernmost peaks; they have never been connected to one another nor to the mainland. Bioko (=Fernando Poo), on the other hand, is a continental island that was connected to mainland Africa during glaciations, most recently, ca. 11,000 years (Lambert and Chappel 2001). Annobón is part of Equatorial Guinea, and with ca. 17 km^2, it is located ca. 180 km SSW from São Tomé and 340 km W from Gabon (Jones and Tye 2006). The maximum altitude of this small island is ca. 600 m (Quioveo peak) and its biodiversity (Exell 1944, 1956, 1973; Heras et al. 2002), Papilionoidea included, is much lower than that of the other GGOI. Príncipe is the smaller of the Democratic Republic of São Tomé e Príncipe main islands. With ca. 140 km^2, it is ca. 210 km SSW off Bioko and 140 km NNE of ST with a maximum altitude ca. 935 m (Pico Príncipe). It was, however, much larger historically and extended to the SSW (Jones and Tye 2006), including the plantless Tinhosas Islets. The Tinhosas are currently a breeding colony of sea birds, a Ramsar site, from which no Papilionoidea are known. São Tomé is ca. 860 km^2, and lies almost 150 km SW of Príncipe, 180 km NNE of Annobón and ca. 255 NW of Gabon, with a maximum altitude (Pico São Tomé) ca. 2024 m. the Equator crosses Rolas Islet, which is just South of São Tomé.

The predominant natural ecosystem type of the GGOI was described as rainforest (Exell 1944, 1973) or tropical moist broadleaf forest (Gascoigne 2004), which is stratified into lowland (0–800 m), montane (800–1400 m), and mist forest (1400–2024 m), the last category being absent from Príncipe. In Annobón the three types appear compressed in its small altitudinal range as in the lower São Tomé southern peaks (Ogonovszky 2003). Due to rain shadow, NW São Tomé has a dry forest, which is rich in endemic butterfly species.

In relation to diurnal Lepidoptera, the skippers (Hesperiidae) were formerly placed in the superfamily Hesperioidea, independent from the butterflies, but Heikkilä et al. (2012), supported by morphological and genetic data, demonstrated that they are part of the same evolutionary group, the superfamily Papilionoidea. Their diversity and endemism in São Tomé and Príncipe has been the focus of several notable studies (Pyrcz 1992a; Mendes and Bivar-de-Sousa 2012a) and a further contribution is currently in preparation (Mendes et al. in prep.). Here we provide an updated checklist of the Papilionoidea of the GGOI and review previously incorrectly cited taxa.

The Papilionoidea of the Gulf of Guinea Oceanic Islands: Data Sources

The first references to the Papilionoidea of Annobón were given by Aurivillius (1910), who reported *Borbo fatuellus* (sub *Baoris*), and Kheil (1910) who noted *Leptotes pirithous* (sub *Syntarucus*), *A. zetes* (as monotypic) and *Telchinia pharsalus* (sub *Acraea*). Aurivillius (1928) and Bacelar (1948) recorded *Euchrysops osiris* (sub *Cupido*). D'Abrera (1980) described *Acraea zetes annobona* (type locality), which also occurs in São Tomé and Príncipe, being endemic to the three islands. Viejo (1984) added *Melanitis leda*, *Danaus chrysippus*, *Hypolimnas misippus* and *Telchinia pharsalus* (sub *Acraea*) to the list of species of these islands but some of the samples were reported only from "Spanish Guinea". Olano and Marcos (1993) report the species assigned by Viejo (1984) but consider *D. chrysippus* as restricted to Rio Muni and Bioko while *Euchrysops osiris* is assigned to the mainland only. *Acraea zetes annobona* is not recognized by Olano and Marcos (1993) despite Annobón being its type locality. These authors also question the presence in the islands of *Sevenia boisduvalli insularis* (today considered a São Tomé endemic) and of *Dixeia piscicollis* reported by D'Abrera (1980) from Equatorial Guinea but later considered as a São Tomé endemic (D'Abrera 1997). These are the only data known on the Papilionoidea of the most remote and less diverse GGOI. An even lower diversity is known from the remote Saint Helena that, while not part of the Cameroon Volcanic Line, lies eastwards of the Mid-Atlantic chain (Ashmole and Ashmole 2000): *Lampides boeticus*, *Danaus chrysippus*, *Vanessa cardui* and *Hypolimnas misippus*, all widely ranged migratory species.

The scientific knowledge of butterfly and skipper diversity of the GGOI has increased intermittently since Cramer (1775–1776). It (almost) stabilized during the eighteenth century (1850–1870) but suddenly increased from the turn of the nineteenth until the twentieth century with the contributions of Aurivillius, Joicey and Talbot, Sharpe and Snellen. After another hiatus, several additional phases of discovery followed, firstly due to the work of Amélia Bacelar (Bacelar 1948, 1958) in the mid-twentieth century, and then, toward the end of the century the contributions of Libert (2004, 2011), Pyrcz (1991a–c) and our work in São Tomé and Príncipe (Mendes et al. 1988, 2018; Mendes and Bivar-de-Sousa 2006, 2012a, b).

Some large collections, which are mostly currently housed in the Museu Nacional de História Natural e da Ciência (MUHNAC), in Lisbon, Portugal, were studied by Mendes and Bivar-de-Sousa 2006, 2012a, b; Mendes et al. 2018, but the revised checklist (Appendix) takes into account bibliographic records that have been reviewed and confirmed by newly collected data. The bibliographic data considered for assembling this checklist originated from the following references: Cramer (1775–76—who reports the first species for São Tomé and for the GGOI: *Acraea medea*), Snellen (1873), Sharpe (1893), Holland (1896), Aurivillius (1898, 1910), Rothschild and Jordan (1900), Eltringham (1912), Le Cerf (1924), Joicey and Talbot (1926, 1927), Hawker-Smith (1928), Riley (1928), Evans (1937), Bacelar (1948), Someren (1971a, b, 1972, 1974, 1975), Pinhey (1972), D'Abrera (1980, 1997, 2004, 2009), Plantrou (1983), Hancock (1984), Henning (1988), Pyrcz (1991a, b, c, 1992a, b), Canu (1994), Wojtusiak and Pyrcz (1995, 1997), Pierre et al. (2002), Hecq (2003a, b), Turlin (2005a, b, 2007a, b, c), Anonymous (2007), Bonfim and Carvalho (2009), Koçak and Kemal (2009), Williams (2008, 2015), Velzen et al.

(2009), Libert (2011), Oremans (2012), Pierre and Bernaud (2013, 2014), Collins and Larsen (2013), Wikipedia (2014), Collins (2015) and Awanao et al. (2018).

Specimens deposited in the Museu Bocage (MB), a precursor institution of present-day MUHNAC, were also partially studied by the authors. However, all of MB specimens were destroyed in the fire that engulfed the collections, library, and associated structures on March 28, 1978. Among the destroyed collections were Sharpe (1893) São Tomé type specimens, as had been recorded by Fernandes (1958), the holotype of *Pyrrhiades bocagei* (sub *Rhopalocampta*), three specimens of *Leptotes sanctithomae* (as *Catochrysops sancti-thomae*), comprising holotype and allotype, as well as the holotypes of *Acraea niobe*, *Telchinia insularis* (sub *Acraea*) and *Telchinia newtoni* (sub *Acraea*).

Most of the information concerning newly identified and re-examined specimens is based on the analysis of specimens from São Tomé and Príncipe collected by the zoological expeditions held in 1954–1955 by the Centro de Zoologia (CZ) of the Junta de Investigações do Ultramar and a mission to São Tomé Island in 1984 by MB and the Faculty of Sciences of the Lisbon University (Mendes et al. 1988). These studies were followed by Mendes and Bivar-de-Sousa (2006, 2012a, b) and Mendes et al. (2018) contributions, all based on newly collected specimens between 2004 and 2019. Some of these specimens were collected during a 2015 California Academy of Sciences funded expedition, to which the senior author was invited by Dr. Robert (Bob) Drewes to participate. Some other material was studied, namely that available in the collections of the Centro de Investigação Agronómica e Tecnológica de São Tomé e Príncipe (CIAT) in Potó, São Tomé Island. This collection was established by members of the CZ before the country gained independence in 1975. Data available from the private collections of the second co-author of this study, as well as those of António Figueira (1924–2017; now housed in the collections of the Museu de História Natural e da Ciência da Universidade do Porto, Porto, Portugal) and Carlos da Silva were also used. Information from local collaborators, especially those of Rato Cabinda, are also included in this revised checklist.

Incorrectly Recorded Taxa

Despite most of the known references being scientifically trustworthy, several reported taxa are based on misidentified or mislabelled specimens of species and subspecies that are mostly typical from savanna and Sahel-biotopes (see Appendix):

Hesperiidae *Sarangesa phidyle*, *Spialia diomus*, *S. spio*, *Gomalia elma*, *Borbo gemella* and *Pelopidas mathias* were recorded for the islands but do not occur there (Appendix). Evans (1937) and Chiba (2009) consider *Coeliades hanno* as present in São Tomé, but the only brown *Coeliades* confirmed in São Tomé and Príncipe is the morphologically similar *C. forestan*.

Papilionidae *Papilio dardanus sulfurea* is a Bioko endemic whose type locality was wrongly considered to be Príncipe (Palisot de Beauvois 1805–1821). Its occurrence on Príncipe Island was also recorded by Canu (1994) and by Koçak and Kemal (2009—sub *princeps*), but all the recent authors consider it a Bioko endemic. *Graphium angolanus baronis*, *G. latreillianus theorini* and *G. ridleyanus*, which are large and unmistakable taxa occurring in continental Africa have also been recorded from São Tomé based on some specimens in the collections of the Natural History Museum (NHM) of London (Smith and Vane-Wright 2001); however, the location of these specimens is likely mislabelled, as no other records of these taxa exist for the island.

Pieridae Larsen (2005) considers *Colotis doubledayi*, noted for instance by Ackery et al. (1995) and D'Abrera (1997) as occurring in São Tomé, as a misidentification. Berger (1981) is the only record of *Belenois gidica* for São Tomé. The single reference of *Appias phaola* to the island of São Tomé (Bacelar 1948) refers to three males and one female that were subsequently destroyed during the MB fire. These likely represented records of *A. epaphia aequatorialis*, later described from the island (Mendes and Bivar-de-Sousa 2006). *Leptosia medusa*, reported also by Bacelar (1948, four males, one female) from São Tomé corresponds to a misidentified *L. alcesta* (Mendes and Bivar-de-Sousa 2012a, b). All the São Tomé records of species of the genus *Mylothris*, except those of *M. rembina*, are putative misidentifications and were partially rectified: *M. asphodelus* by Bacelar (1948); *M. bernice* by Sharpe (1893); *M. nubila* by Schultze (1917); *M. poppea* by Viejo (1984); *M. rhodope* and *M. spica* by Berger (1979); and *M. sulphurea* by Pyrcz (1992a, who stresses the muddled knowledge of the genus in São Tomé).

Lycaenidae *Hypolycaena philippus*, *Anthene amarah*, *Azanus moriqua*, *Azanus ubaldus*, *Leptotes brevidentatus*, *L. jeannelli*, and *Zizula hylax* were recorded for the islands but do not occur there (Appendix). *Liptena evanescens* f. *xanthis* reported by Stempffer et al. (1974) from São Tomé either represents a mislabeled specimen or a locally extirpated population. Libert (2004) reports the presence of *Hypomyrina fournieri* either in São Tomé or in Príncipe (material not seen, occurrence not mapped), but the species is not mentioned as occurring in the GGOI by Ackery et al. (1995) nor by D'Abrera (2009). Sharpe (1893) reports *Rubropelates aruma* in São Tomé, but this record may represent a non-established population or a misidentified specimen of *Deudorix lorisona*. In addition, Sharpe (1893) registers *Leptotes pulchra* in São Tomé but does not consider the quite common *L. pirithous*.

Nymphalidae *Bicyclus dorothea concolor, B. funebris* and *B. martius sanaos* were recorded for the islands but do not occur there (Appendix). Furthermore, *B. italus* was mapped in São Tomé by Condamin (1973), but all these records may have been based on a misidentified *B. medontias,* a similar forest species whose presence on the island was unknown until recently (Larsen 2005). *Precis hierta*, *Precis orithya*, *Salamis anacardii* (currently a species of *Protogoniomorpha*), *Byblia ilithyia* and *Hamanumida daedalus* are certainly not present in São Tomé and Príncipe. *Neptis serena* is listed by Koçak and Kemal (2009) for São Tomé and Príncipe, but these authors do not report the endemic *Neptis larseni* from Príncipe; indeed, *N. serena* is only assigned to Príncipe when that endemic was described (Wojtusiak and Pyrcz 1997). Pyrcz (1992a) reports an undetermined red *Cymothoe* that Canu (1994) assigned to São Tomé, but was unable to find the specimens later; several species of the *C. sangaris* group are known from Central and West Africa and thus this information is insufficient to consider its presence in the GGOI. The same must be stated about the references of several "*acraea*" species (currently *Acraea* and *Telchinia*) reported by Bacelar (1958), Mendes and Bivar-de-Sousa (2012a, b), Pierre and Bernaud (1999, 2009a, b), Pierre et al. (2002), Pyrcz (1992a), Snellen (1873) and Viejo (1984), namely *Acraea pseudegina, Telchinia e. encedon, T. esebria, T. pentapolis,* and *T. vesperalis*. *Telchinia jodutta* was reported from São Tomé and Príncipe by several authors—first reference by Aurivillius (1910)—though Oremans (2012) describes its insular vicariant, *A. severina*, with one subspecies in São Tomé and another in Príncipe. Bacelar (1958) refers *A. eponina latifasciata* but she did not have access to new specimens, while Pyrcz (1992a) questioned its presence in São Tomé and Príncipe and Pierre et al. (2002) did not report the species as occurring in the GGOI despite its huge African range. Bacelar (1948) reports *Acraea monteironis* from São Tomé based upon one male whose identification we could not confirm—if the specimen was in MB it was certainly destroyed in 1978; this species, described from Angola, was never recorded again from the island. Viejo (1984), based in Bacelar (1948), was the only subsequent author who considers *Acraea monteironis* to occur in São Tomé, without providing further comments. According to Bacelar (1948), the reference of Aurivillius (1928, Figs, 57d–e) of an *A. esebria* form shall represent *T. severina* instead, a taxon that has been until recently considered a synonym of *T. esebria* (Eltringham 1912; Ackery et al. 1995; Williams 2008; Pierre and Bernaud 2014). This is, however, certainly not true in the GGOI—it may, indeed, belong to *T. s. severina* synonymy in the case of its reference to São Tomé. Reports of *Phalanta phalantha aethiopica* in the GGOI must represent the morphologically similar forest dweller *P. eurytis*, known from Príncipe, São Tomé, and Rio Muni (Viejo 1984).

Composition, Diversity, and Endemism of the GGOI Papilionoidea

Isolation, geological age, area, catching-area, relief, climate, and diversity of biotopes are fundamental to the potential biodiversity and endemism of an island (Whittaker et al. 2017). Among the families of Papilionoidea known in Sub-Saharan Africa, only Riodinidae has not been recorded in the GGOI. Most of the subfamilies assigned from the region occur both in Príncipe and in São Tomé (the scant diversity of Annobón was already discussed). The currently known number of species (in parentheses) per family and respective subfamily is as follows: Hesperiidae (nine): Coeliadinae (two), Pyrginae (one), and Hesperiinae (six);

Papilionidae (four): Papilioninae (four); Pieridae (12): Coliadinae (five) and Pierinae (seven); Lycaenidae (21): Miletinae (one), Aphnaeinae (five) and Polyomatinae (15); and Nymphalidae (45): Libytheinae (one), Danainae (one), Satyrinae (two), Charaxinae (eight), Nymphalinae (10), Cyrestinae (one), Biblidinae (two), Limenetidinae (four) and Heliconiinae (16). There are no Papilionoidea genera that are endemic from the GGOI. The Nymphalidae is the most diverse family (ca. 45% of the Papilionoidea) and the Heliconiinae (ca. 35%) its most diverse subfamily.

According to Gascoigne (1995), the Lepidoptera endemicity for São Tomé is 38.3% (47 taxa: 11 endemic species, 7 endemic subspecies) and 21.4% for Príncipe (42 taxa: six endemic species, three endemic subspecies). These estimates, based on Pyrcz (1991a, b), did not include the Hesperiidae, lumped the São Tomé and Príncipe species of the genus *Neptis* to a single species (*N. eltringhami*), and considered *Leptotes terrenus* and *Chilades sanctithomae* as independent taxa.

Currently, based on the specimens we have examined and bibliographic references, 91 species and subspecies are considered to occur in the GGOI: 46 are known for Príncipe, 64 (though three in need of revision) for São Tomé, and eight for Annobón (Appendix). All the taxa known for Annobón also occur in São Tomé and Príncipe, with the exception of *Telchinia pharsalus*, identified as *T. p. carmen*, but putatively referring to a still undescribed Annobón subspecies (Kheil 1910; Viejo 1984). The subspecies *Acraea zetes annobona* is the single taxon that is endemic to the three islands. The species that occur both in São Tomé and Príncipe are mostly those with the largest distributions. Regarding endemics (Fig. 13.1), 17 taxa are endemic for Príncipe (almost 37%), 23 for São Tomé (ca. 36%), and five are endemic to more than one island. These estimates approach those of Pyrcz (1991a, b), especially after considering that he did not consider skippers.

Conservation

Modifications of the natural environment associated with human expansion and climatic change have impacted the diversity of butterflies and skippers around the globe. Activities with detrimental impacts range from deforestation, fires, charcoal production, introduction of invasive weeds or of animal pests, use of chemicals, water, air and soil pollution, expanse of cultivated fields and of monocultures (agriculture or forestry) and human expansion in its strict sense. The considerable taxonomic knowledge and data available for lepidopteran distributions and ecological requirements make them important indicators for environmental change and for monitoring the health of ecosystems (Parmesan 2019).

In the GGOI, population sizes of species with high sensitivity to ecological changes may be important to monitor, especially under current climate change. Some of the GGOI species are very common while others seem to be restricted to

Fig. 13.1 Some endemic Papilionoidea of the Gulf of Guinea oceanic islands. R: recto (dorsal), V: verso (ventral): (**1**) *Pyrrhiades bocagei*, ♂R; (**2**) Ibid, V. (**3.**) *Papilio nerminae*, ♂R; (**4**) *Graphium leonidas santamarthae*, ♂R; (**5**) *Dixeia piscicollis*, ♂R; (**6**) *Deudorix* (*Virachola*) *odana chalybeate*, ♂R; (**7**) *Charaxes antiques*, ♂R; (**8**) Ibid, V; (**9**) *Pseudacraea gamae*, ♀R; (**10**) *Acraea zetes annobona*, ♂R; (**11**) Ibid, V; (**12**) *Acraea medea*, ♂R; (**13**) Ibid, V. Photo credits: (**1–3**, **5**, **10–13**) António Bivar-de-Sousa and Luís Mendes, (**4**, **6–9**) Carlos da Silva. Photos not to scale

small areas or associated to specific biotopes (Mendes et al. in prep.). As noted elsewhere, most of these more rare and poorly distributed taxa are endemics and strictly associated with natural biotopes, although some exceptions are remarkable: we frequently found images of the São Tomé endemic *Acraea niobe* pollinating cultivated introduced coffee plants *Coffea* sp. (Rubiaceae) or, as firstly noted Pierre et al. (2002), feeding on the nectar of the introduced Mexican sunflower, *Tithonia diversifolia* (Asteraceae). These observations suggest that some endemic species may be resilient to some ecological changes.

The observation that some species are known from only a small number of individuals may be the consequence of two fundamental and unrelated mechanisms. First, some species are considered rare when they occur in quite localized areas, they fly during a short period, or they are restricted to particular biotopes, and thus challenging to locate. However, these species with patchy distributions may be geographically widespread and common in other parts of their range. Second, insect abundance is known to fluctuate from year to year according to annual ecological conditions and in the GGOI some areas are quite complicated to access. Thus, temporal and geographic biases in survey effort may partly explain why some taxa appear to be rare. However, some species may be considered threatened because they are truly rare and at real risk of extirpation or extinction due to environmental pressures. We note that these concepts apply to both endemic and non-endemic species.

One good example of a rare endemic species is *Dixeia piscicollis*, which is restricted to the São Tomé dry forest and known from a small number of specimens. However, at the end of the dry season, locally known as *gravana*, it may be quite abundant, even becoming the dominant or the only butterfly in the area—although it is restricted to this area. Some endemic *Charaxes* restricted to the São Tomé or Príncipe highland forests also fit this description. Likewise, the insular subspecies of *Graphium leonidas* are both rare and limited to precise biotopes and seem to fly during a short period only.

A certain number of threatened species in São Tomé and Príncipe were reported by Gascoigne (1995). However, this list included taxa that even if rare, may not be threatened, as is the case of *Pyrrhiades bocagei* (sub *Coeliades*) which is noted as vulnerable, and despite being present on both islands, is reported only for São Tomé. Both *Graphium leonidas* subspecies are listed as endangered; *Leptotes terrenus* and *Chilades sanctithomae*, *Pseudacraea gamae* are "undetermined," while *Epamera bellina maris* and *Charaxes defulvata* are said to be extinct, despite Pyrcz (1992a) recording live specimens of both. The threatened community of Lagoa Azul in São Tomé is discussed, with special attention on *Coeliades bocagei*, the "endemic *Charaxes*" (species not discriminated), and *Neptis eltringhami* that occur there. *Dixeia piscicollis* was also considered to be threatened though it is common along the northwestern dry forest.

The statuses of species considered endemic or almost endemic are in dire need of new data to update assessments, as several of them may be threatened or even extinct. This is the case for *Andronymus thomasi*, treated as a subspecies from

Andronymus neander by Gascoigne (1995) and possibly others. *Iolaus bellina maris* and *Charaxes defulvata* if not extinct, likely occur only in very small numbers.

Potential Future Discoveries and Research

Given the current knowledge of the GGOI Papilionoidea, the intermittent increase in the number of recognized species over time, and the considerable bias of knowledge toward São Tomé and Príncipe when compared with Annobón, several areas of future research are needed. Fieldwork in Annobón is essential, as the known taxonomic diversity is likely incomplete. São Tomé and Príncipe have been more extensively surveyed, but large areas of their most pristine forest, where endemics are expected to have evolved, have been little explored due to the difficult access, high rainfall, and dense vegetation. As such, new species for the islands (and even for science) are expected to be found, and populations of some of the species considered as (almost) extinct may be rediscovered. Information on the range and abundance of each species is essential to establish their conservation status. This is especially urgent for the rare island endemics. Although some information already exists about the activity periods of caterpillars and imagoes, more data are needed to allow the implementation of effective protection measures. For instance, the morphology of the caterpillar life stage is unknown for most of the tropical species, particularly the endemics. Likewise, knowledge of caterpillar host-plants is also incomplete. In the non-endemic taxa, the caterpillar food-plants may be different from those of populations in mainland Africa, while for some of the insular endemics they simply remain unknown. Genetic studies on GGOI Papilionoidea are virtually inexistent. They are fundamental to taxonomical and phylogeographic studies and are key to investigating the biogeographic history of this unique island fauna.

Appendix

Commented checklist of Papilionoidea recorded from the Gulf of Guinea oceanic islands. Names of the 91 species and subspecies considered correctly assigned to Príncipe (**P**), São Tomé (**ST**) and Annobón (**A**) are numbered. Taxa considered incorrectly assigned to the GGOI, as justified in the text, are not numbered. K&K (2009): Koçak and Kemal; M&BS: Mendes and Bivar-de-Sousa. Endemic taxa (**E**), if shared by P and ST and/or A, respectively as **E-1**, **E-2** and **E-3** according to their topotypical island. Samples examined by the authors are marked in the **SS** column (studied specimens) with a ●; 17 species are known only from reliable bibliographic references. Preferred habitats (**H**): **A**—Humid lowland forest; **B**—Humid highland forest; **C**—Dry forest, forest margins, and somewhat degraded biotopes; **D**—Several types of forest; **U**—Ubiquitous or almost ubiquitous; **?**—Doubtful

Families and species/subspecies	First reference	SS	P	ST	A	H
Fam. **HESPERIIDAE**						
1. *Pyrrhiades bocagei* (Sharpe, 1893)	Sharpe (1893)	●	**E**	**E-2**		**D**
2. *Coeliades forestan* (Stoll, 1784)	Sharpe (1893)	●	**X**	**X**		**C, D**
Coeliades hanno (Plötz, 1879)	Riley (1928)					
3. *Tagiades flesus* (Fabricius, 1871)	Sharpe (1893)	●	**X**	**X**		**A, C**
Sarangesa phydile (Walker, 1870)	K&K (2009)					
Spialia diomus (Hopffer, 1855)	K& K (2009)					
Spialia spio (Linnaeus, 1764)	K&K (2009)					
Gomalia elma (Trimen, 1862)	K&K (2009)					
4. *Andronymus thomasi* Riley, 1928	Riley (1928)	●	**E**	**E-2**		**A**
5. *Artitropa principetome* Collins and Larsen 2013	(Collins and Larsen 2013)		**E-1**	**E**		**A**
Pelopidas mathias (Fabricius, 1798)	K&K (2009)					
6. *Borbo borbonica* (Boisduval, 1833)	Aurivillius (1910)	●	**X**	**X**		**C**
7. *Borbo detecta* (Trimen, 1893)	Riley (1928)	●	**X**	**X**		**C**
8. *Borbo f. fatuellus* (Hopffer, 1855)	Aurivillius (1910)	●	**X**	**X**	**X**	**C**
Borbo gemella (Mabille, 1884)	K&K (2009)					
9. *Afrogegenes letterstedti* (Wallengren, 1857)	Sharpe (1893)	●	**X**	**X**		**C**
Fam. **PAPILIONIDAE**						
10. *Papilio nerminae* Koçak, 1983	Sharpe (1893)	●		**E**		**A, B**
Papilio dardanus sulfurea Palisot de Beauvois 1806	Palisot de Beauvois (1806)					

(continued)

Families and species/subspecies	First reference	SS	P	ST	A	H
11. *Papilio d. demodocus* Esper, 1798	Snellen (1873)	●	**X**	**X**		**U**
Graphium angolanus baronis (Ungemach, 1932)	Smith and Vane-Wright (2001)					
Graphium latreillianus theorini (Aurivillius, 1831)	Smith and Vane-Wright (2001)					
12. *Graphium leonidas santamarthae* Joicey and Talbot, 1927	Joicey and Talbot, (1927)	●	**E**			**A, C**
13. *Graphium leonidas thomasius* Le Cerf 1924	Le Cerf (1924)	●		**E**		**A, C**
Graphium ridleyanus (White, 1843)	Smith and Vane-Wright (2001)					
Fam. **PIERIDAE**						
14. *Catopsilia florella* (Faricius, 1775)	Bacelar (1958)	●	**X**	**X**		**U**
15. *Eurema b. brigitta* (Stoll, 1780)	K&K (2009)	●	**X**	**X**		**C**
16. *Eurema hecabe solifera* (Butler, 1875)	Snellen (1882)	●	**X**			**C**
17. *Eurema floricola leonis* (Butler, 1886)	Snellen (1882)	●	**X**			**D**
18. *Eurema senegalensis* (Boisuval, 1836)	Sharpe (1893)	●	**X**	**X**		**A**
Colotis doubledayi (Hopffer, 1872)	Ackery et al. (1995)					
Belenois gidica Godart, 1819	Berger (1981)					
19. *Belenois c. creona* (Stoll, 1780)	M&BS (2012)	●		**X**		**C**
20. *Dixeia piscicollis* Pinhey, 1972	Pinhey (1972)	●		**E**		**C**
21. *Appias epaphia aequatorialis* Mendes & Bivar-de-Sousa, 2006	M&BS (2006)	●		**E**		**C**
22. *Appias epaphia piresi* Mendes & Bivar-de-Sousa, 2006	M&BS (2006)	●	**E**			**C**
Appias phaola (Doubleday, 1847)	Bacelar (1948)					
23. *Leptosia a. alcesta* (Stoll, 1781)	Snellen (1873)	●	**X**			**A**
Leptosia medusa (Cramer, 1777)	Bacelar (1948)					
24. *Leptosia n. nupta* (Butler, 1873)	Sharpe (1873)	●	**X**	**X**		**A, B**
Mylothris asphodelus Butler, 1888	Bacelar (1948)					
Mylothris bernice (Hewitson, 1862)	Sharpe (1893)					
Mylothris nubila (Möschler, 1884)	Schutze (1917)					
Mylothris popea (Cramer, 1777)	Viejo (1984)					
25. *Mylothris rembina* (Plötz, 1880)	Schutze (1917)	●	**X**	**X**		**A**
Mylothris rhodope (Fabricius, 1775)	Berger (1979)					
Mylothris spica (Möschler, 1884)	K&K (2009)					
Mylothris sulphurea (Aurivillius, 1895)	K&K (2009)					

(continued)

Families and species/subspecies	First reference	SS	P	ST	A	H
Fam. **LYCAENIDAE**						
26. *Spalgis l. lemolea* Druce, 1890	Pyrcz (1992)	●	**X**			**A, C**
Liptena evanescens xanthis (Holland, 1890)	Stempffer (1974)					
27. *Iolaus* (*Epamera*) *bellina maris* (Riley, 1928)	Riley (1928)			**E**		**A?**
Hypomyrina fournieri Gabriel, 1939	Libert (2004)					
Hypolycaena phillippus (Fabricius, 1793)	K&K (2009)					
28. *Deudorix (Virachola) l. lorisona* (Hewitson, 1862)	Hawker-Smith (1928)	●	**X**	**X?**		**A**
29. *Deudorix (Virachola) a. antalus* (Hopffer, 1855)	Pyrcz (1992)	●	**X**	**X**		**C**
30. *Deudorix (Virachola) caliginosa* Lathy,1903	Libert (2004)			**X**		**C?**
31. *Deudorix (Virachola) odana chalybeata* (Joicey and Talbot, 1926)	Joicey and Talbot (1926)	●	**E**	**E-2**		**A**
Rubropelates a. aruma (Hewitson, 1873)	Sharpe (1893)					
Anthene amarah (Guérin-Méneville,1849)	K&K (2009)					
32. *Anthene l. lunulata* (Trimen, 1894)	Viejo (1984)	●	**X**	**X?**		**A, B**
33. *Anthene prínceps* (Butler, 1876)	Pyrcz (1992)	●	**X**	**X**		**A, B**
34. *Pseudonacaduba s. sichela* (Wallengren, 1857)	Mendes et al. (*ad.Prep.*)	●	**X**			**C**
35. *Lampides boeticus* (Linnaeus, 1767)	Bacelar (1958)	●	**X**	**X**		**D**
36. *Cacyreus lingeus* (Stoll, 1782)	Joicey and Talbot (1926)	●	**X**	**X**		**A, C**
37. *Leptotes p. pirithous* (Linnaeus, 1767)	Kheil (1910)	●	**X**	**X**	**X**	**C, D**
Leptotes brevidentatus (Tite, 1958)	K&K (2009)					
Leptotes jeanneli (Stempffer, 1935)	K&K (2009)					
Leptotes pulchra (Murray, 1874)	Sharpe (1893)					
38. *Leptotes pyrczi* Libert, 2011	Libert (2011)	●	**E**			**A**
39. *Leptotes sanctithomae* Sharpe, 1893 *(= L. terrenus* (Joicey and Talbot, 1926)*)*	Sharpe (1893)			**E**		**B?**
40. *Zizeeria knysna* (Trimen, 1862)	Joicey and Talbot (1926)	●	**X**	**X**		**A, C**
41. *Zizina otis antanossa* (Mabille, 1877)	Pyrcz (1992)	●	**X**	**X**		**A, C**
Zizula hylax (Fabricius, 1775)	K&K (2009)					
42. *Azanus mirzá* (Plötz, 1880)	Pyrcz (1992)	●		**X**		**C, D**
Azanus moriqua (Wallengren, 1857)	K&K (2009)					
Azanus ubaldus (Stoll, 1782)	K&K (2009)					
43. *Eicochrysops hippocrates* (Fabricius, 1793)	Pyrcz (1992)	●	**X**	**X**		**D**
44. *Euchrysops malathana* (Boisduval, 1833)	Aurivillius (1928)	●	**X**	**X**		**C, D**

(continued)

Families and species/subspecies	First reference	SS	P	ST	A	H
45. *Euchrysops* cf. *osiris* (Hopffer, 1855)	Aurivillius (1928)	●	**X**	**X?**	**X**	**C, D**
46. *Chilades trochylus* (Freyer, 1844)	K& K (2009)	●		**X**		**D**
Fam. **NYMPHALIDAE**						
47. *Libythea l. labdaca* Westwood, 1851	Sharpe (1893)	●	**X**	**X**		**A, C**
48. *Danaus c. chrysippus* (Linnaeus, 1758)	Snellen (1873)	●	**X**	**X**	**X**	**U**
49. *Melanitis leda* (Linnaeus, 1758)	Sharpe (1893)	●	**X**	**X**	**X**	**C, D**
Bicyclus dorothea concolor Condamin and Fox, 1964	Condamin and Fox (1964)					
Bicyclus funebris (Guérin-Méneville, 1844)	Condamin (1973)					
Bicyclus italus (Hewitson, 1865)	Condamin (1973)					
50. *Bicyclus medontias* (Hewitson, 1873)	Larsen (2005)			**X**		**B?**
Bicyclus martius sanaos (Hewitson, 1866)	Condamin (1973)					
51. *Bicyclus vulgaris* (Butler, 1868)	Aurivillius (1910)	●	**X**			**C**
52. *Charaxes defulvata* (Joicey and Talbot, 1926)	Joicey and Talbot (1926)			**E**		**A?**
53. *Charaxes c. candiope* (Godart, 1824)	Plantrou (1983)		**X**	**X**		**A, C**
54. *Charaxes thomasius* Staudinger, 1886	Staudinger (1886)	●		**E**		**B**
55. *Charaxes lemosi* (Joicey and Talbot, 1927)	Aurivillius (1910) as *C. lucretius*	●	**E**			**B**
56. *Charaxes odysseus* Staudinger 1892	Staudinger (1892)			**E**		**A?, B**
57. *Charaxes antiquus* Joicey and Talbot 1926	Joicey and Talbot (1926)			**E**		**B**
58. *Charaxes barnsi* Joicey and Talbot, 1927	Joicey and Talbot (1927)		**E**			**A**
59. *Charaxes monteiri* Staudinger 1886	Staudinger (1886)			**E**		**B**
60. *Vanessa cardui* (Linnaeus, 1758)	Pyrcz (1992)	●	**X**	**X**		**C**
Precis hierta crebrene (Trimen, 1870)	K&K (2009)					
Precis orythia madagascariensis (Guenée, 1865)	K&K (2009)					
61. *Precis pelarga* (Fabricius, 1775)	Aurivillius (1910)	●	**X**	**X**		**B, C**
62. *Precis s. sinuta* Plötz, 1880	Sharpe (1893)	●		**X**		**C, D**
63. *Hypolimnas a. anthedon* (Doubleday, 1845)	Sharpe (1893)	●	**X**	**X**		**C, D**

(continued)

Families and species/subspecies	First reference	SS	P	ST	A	H
64. *Hypolimnas misippus* (Linnaeus, 1764)	Snellen (1873)	●	**X**	**X**	**X**	**C**
65. *Hypolimnas m. monteironis* (Druce, 1874)	Pyrcz (1992) as *H. salmacis*	●	**X**			**A, B**
66. *Hypolimnas salmacis thomensis* Aurivillius, 1910	Aurivillius (1910)	●		**E**		**A, B**
Protogoniomorpha anacardi (Linnaeus, 1758)	K&K (2009)					
67. *Junonia cymodoce lugens* (Schultze, 1912)	Bacelar (1958)	●	**X**			**A**
68. *Junonia o. oenone* (Linnaeus, 1758)	Bacelar (1958)	●	**X**	**X**		**C, D**
69. *Junonia t. terea* (Drury, 1773)	Aurivillius (1910)	●	**X**			**A, B**
70. *Cyrestis c. camillus* (Fabricius, 1781)	Bacelar (1958)	●	**X**			**A**
Byblia ilithyia (Drury, 1773)	K&K (2009)					
71. *Sevenia amulia principensis* Mendes & Bivar-de-Sousa, 2018 **n.stat.**	Bacelar (1958)—no ssp	●	**E**			**A, B**
72. *Sevenia boisduvali insularis* (Joicey & Talbot 1926)	Sharpe (1893)	●		**E**		**B**
73. *Pseudacraea gamae*	Joicey and Talbo (1926)		**E**			**A**
Neptis serena Overlaet, 1955	K&K (2009)					
74. *Neptis eltringhami* Joicey and Talbot 1926	Joicey and Talbot (1926)			**E**		**A?**
75. *Neptis larseni* Wojtuziak and Pyrcz, 1997	Pyrcz (1991) as *N. eltringhami*	●	**E**			**A, C**
76. *Cymothoe caenis* (Drury, 1773)	van Velzen et al. (2009)		**X**			**A?**
Cymothoe sp. ("sangaris-group")	Pyrcz (1992)—after Canu					
Hamanumida daedalus (Fabricius, 1775)	K&K (2009)					
77. *Acraea n. neobule* Doubleday, 1847	K&K (2009)	●		**X**		**C, D**
78. *Acraea q. quirina* (Fabricius, 1781)	Aurivillius (1910)	●	**X**	**X**		**A**
79. *Acraea zetes annobona* D'Abrera, 1980	Snellen (1873)—no ssp	●	**E**	**E**	**E-3**	**A, C**
80. *Acraea e. egina* (Cramer, 1775)	M&BS (2012)	●	**X**			**A, B**
81. *Acraea medea* (Craner, 1775)	Cramer (1775)	●	**E**			**A, B**
82. *Acraea niobe* Sharpe, 1893	Sharpe (1893)	●		**E**		**A, B**
Acraea pseudegina Westwood, 1852	Pyrcz (1992)					
83. *Acraea alcinoe racaji* Pyrcz, 1991	Snellen (1873) as *A. esebria*		**E**			**A, B**
84. *Telchinia alciope* (Hewitson, 1852)	Pierre (1985)		**X**	**X**		**A**
Telchinia esebria (Hewitson, 1861)	Snellen (1873)					

(continued)

Families and species/subspecies	First reference	SS	P	ST	A	H
Telchinia encedon (Linnaeus, 1758)	K&K (2009)					
85. *Telchinia insularis* (Sharpe 1893)	Sharpe (1893)	●		**E**		**A**
Telchinia j. jodutta (Fabricius, 1793)	Aurivillius (1910)					
86. *Telchinia lycoa* (Godart, 1819)	Aurivillius (1910)	●	**X**			**A, C**
Telchinia p. pentapolis (Ward, 1871)	Pierre and Bernaud (1999)					
87. *Telchinia pharsalus carmen* (Pyrcz, 1991)	Aurivillius (1910)—no ssp	●	**E**		**X**?	**A, B**
Telchinia serena (Fabricius, 1775)	Snellen (1873) as *A. manjaca*					
88. *Telchinia severina severina* (Ouremans, 2012)	Berger (1986) as *A. jodutta*	●		**E**		**A, B**
89. *Telchinia severina terreirovelhoensis* (Ouremans, 2012)	Aurivillius (1910) as *A. jodutta*	●	**E**			**A, B**
Telchinia vesperalis (Grose-Smith, 1890)	Pyrcz (1992)					
90. *Telchinia newtoni* (Sharpe 1893)	Sharpe (1893)	●		**E**		
Acraea monteironis Butler, 1874	Bacelar (1958)					
91. *Phalanta e. eurytis* (Doubleday, 1847)	Pyrcz (1992)		**X**	**X**		**A**
Phalanta phalantha (Drury, 1773)	K&K (2009)					

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Chapter 14
Dragonflies and Damselflies (Odonata) of Príncipe, São Tomé, and Annobón

Klaas-Douwe B. Dijkstra, Russell B. Tate, and Michel Papazian

Abstract The dragonfly and damselfly (Odonata) fauna of the oceanic islands of the Gulf of Guinea is impoverished, even compared to other Afrotropical archipelagoes, with a combined total of 22 species recorded with certainty on São Tomé, Príncipe, and Annobón. *Trithemis nigra* Longfield, 1936 from Príncipe is the only known endemic, although two reported but unidentified species may still prove to be endemic too. Most recorded species occur widely across and beyond Africa, and 27 equally widespread species are listed as potential additions. Several hypotheses for the fauna's impoverishment are briefly discussed.

Keywords Biogeography · Diversity · Gulf of Guinea · Oceanic islands · Odonata

Research History

The Odonata of the Gulf of Guinea have been poorly studied, even if the first records were provided a century ago (Martin 1908; Campion 1923). The first endemic taxon was described almost as long ago but remains the only one (Longfield 1936). Pinhey (1974) was the only specialist ever to visit, being on São Tomé for 2 weeks in April and May 1971. His review remains the main resource on all the islands' faunas, only overlooking the material from Annobón treated by Compte Sart (1962). Just four species were added to the list for the three islands combined since Pinhey's visit half a century ago, all very recently.

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Species Diversity

Twenty-two species are known from the islands, of which 19 were recorded from São Tomé, 9 from Príncipe, and 7 from Annobón (Table 14.1). The specific identity of two species, however, is uncertain. These and two other species of interest are discussed below.

***Gynacantha* sp.** — Pinhey (1974) saw a species of this genus or the similar *Heliaeschna* on São Tomé on four occasions, but these eluded capture. Two observers made sightings there since (see Table 14.1), suggesting the taxon is not rare. Both genera breed in shaded temporary pools. Adults are active at dusk, lurking in dense vegetation at daytime, making them challenging to find and catch. Pinhey (1974) remarked that "forest species of these genera on an isolated island might be expected to be distinctive." While the Comoros, Seychelles and Mascarene archipelagos indeed have endemic *Gynacantha* species, these belong to the *bispina*-group that is absent on the western side of Africa (Dijkstra 2005). Twelve species occur on the continent nearest to São Tomé, any of which might be present on the Gulf of Guinea islands (Dijkstra 2016). Indeed, a female caught there by Gérard Filippi in March 2022 probably pertains to *G. cylindrata* Karsch, 1891. That species is widespread in western and central Africa. Females are hard to separate from those of *G. vesiculata* Karsch, 1891 (ranges are similar), so confirmation is desirable.

Orthetrum brachiale (Palisot de Beauvois, 1817) — This species and *O. stemmale* (Burmeister, 1839) were confused for 140 years (Pinhey 1979). Both occur widely on the tropical African mainland, while *O. stemmale* also extends to the nearby islands of Madagascar, the Mascarenes, and Seychelles in a variety of potential but unresolved taxa (see Table 14.2). While the latter's presence in the Gulf of Guinea may thus seem likelier, both the material of Pinhey (1974, 1979) and Papazian et al. (2020) included *O. brachiale* only. Specimens in the Natural History Museum (London) and photographic records seen by the first author also agree with that species. Loureiro and Pontes (2013) reported *O. stemmale* from Príncipe without further comment, and Papazian et al. (2022) from São Tomé based on female specimens not assignable to other *Orthetrum* species found. Thus, while its presence seems very likely, confirmation with male specimens is required given the long history of taxonomic confusion.

Trithemis nigra Longfield, 1936 (Fig. 14.1) — Longfield (1936) described this as a subspecies of the Denim Dropwing *T. donaldsoni* (Calvert, 1899) based on two males, collected on Príncipe on 7 December 1932 and 1 January 1933. Pinhey (1970) raised the taxon to species level, which by morphology is nearest the Halfshade Dropwing *T. aconita* Lieftinck, 1969 and Congo Dropwing *T. congolica* Pinhey, 1970 (Damm et al. 2010). Alain Gauthier (pers. comm.) found *T. nigra* to be common in 1990. Indeed, it was found at 6 of 15 sites surveyed on the island's eastern half in 2011 (Loureiro and Pontes 2013): all streams that were partly sunny and partly shaded by forest or shrubs. The species was not seen at fully shaded or seasonal streams, nor at standing or brackish water. While the limited distribution is below thresholds for Critically Endangered on the IUCN Red List of

Table 14.1 Review of Odonata species recorded from the Gulf of Guinea Islands

Scientific name	English name	Príncipe	São Tomé	Annobón
Agriocnemis zerafica Le Roi, 1915	Sahel Wisp	Series collected 28–29 October 2019 near Santo António (Papazian et al. 2020).	Both sexes photographed on 3 January 2022 near Neves by Ernst Klimsa. A female photographed on 23 August 2005 in São Tomé town by Phil Benstead was probably this species too.	
Ceriagrion glabrum (Burmeister, 1839)	Common Citril	First reported by Martin (1908); confirmed by Loureiro and Pontes (2013), Papazian et al. (2020) and photographic records.	First reported by Campion (1923); confirmed by Pinhey (1974).	
Ischnura senegalensis (Rambur, 1842)	Tropical Bluetail	Surprisingly no records yet.	Found at several sites in October 2021 (Papazian et al. 2022) and photographed on 1 January 2022 near Neves by Ernst Klimsa.	First reported by Martin (1908); confirmed by Compte Sart (1962).
Anax ephippiger (Burmeister, 1839)	Vagrant Emperor	Surprisingly no records yet.	Not recorded since Pinhey (1974).	
Anax imperator Leach in Brewster, 1815	Blue Emperor	Surprisingly no records yet.	First recorded by Pinhey (1974); confirmed by Papazian and Filippi (2019).	First reported by Martin (1908); confirmed by Compte Sart (1962).
Gynacantha sp.	Duskhawker species		Seen by Pinhey (1974) in 1971, by Alain Gauthier in 1991, and by Russell Tate in 2020. See main text on female caught in March 2022.	
Chalcostephia flavifrons Kirby, 1889	Inspector		Both sexes photographed on 13–15 January 2022 at Praja Inhame by Ernst Klimsa.	

(continued)

Table 14.1 (continued)

Scientific name	English name	Príncipe	São Tomé	Annobón
Crocothemis erythraea (Brullé, 1832)	Broad Scarlet	Surprisingly no records yet.	First reported by Longfield (1936); confirmed by Pinhey (1974) and photographic records.	
Crocothemis sanguinolenta (Burmeister, 1839)	Little Scarlet		Not recorded since Pinhey (1974).	
Diplacodes lefebvrii (Rambur, 1842)	Black Percher	Surprisingly no records yet.	First reported by Campion (1923); confirmed by Pinhey (1974).	
Orthetrum africanum (Selys, 1887)	Elongate Skimmer	First reported by Longfield (1936); confirmed by Loureiro and Pontes (2013) and photographic records.	First recorded by Pinhey (1974); confirmed by photographic records.	
Orthetrum brachiale (Palisot de Beauvois, 1817)	Banded Skimmer	Pinhey (1974) reported *O. brachiale kalai*; confirmed as *O. brachiale* by Pinhey (1979), Loureiro and Pontes (2013), and Papazian et al. (2020).	First reported by Longfield (1936); confirmed by Pinhey (1974, 1979), Papazian et al. (2020), and photographic records.	First reported and illustrated quite accurately by Compte Sart (1962); additional record provided by Pinhey (1974).
Orthetrum julia Kirby, 1900	Julia Skimmer	First reported as *O. stemmale capense* by Longfield (1936); confirmed by Pinhey (1974) and Papazian et al. (2020).	First reported by Campion (1923) and, as *O. stemmale capense*, by Longfield (1936); confirmed by Pinhey (1974), Papazian et al. (2020), and photographic records.	
Palpopleura lucia (Drury, 1773)	Lucia Widow	First reported by Longfield (1936); confirmed by Pinhey (1974), Loureiro and Pontes (2013), Papazian et al. (2020), and photographic records.	First reported by Martin (1908), Campion (1923) and Longfield (1936); confirmed by Pinhey (1974), Papazian et al. (2020), and photographic records.	Only reported by Martin (1908).
Pantala flavescens (Fabricius, 1798)	Wandering Glider	First reported by Martin (1908); confirmed by Loureiro and Pontes (2013) and Papazian et al. (2020).	First reported by Campion (1923); confirmed by Pinhey (1974) and Papazian et al. (2020).	

Rhyothemis notata (Fabricius, 1787)	Veiled Flutterer		Male photographed on 24 January 2019 near Praia Jalé close to the island's southern tip by Anja Cervencl. Also photographed on 29 December 2021 at Praia Vanha (Papazian et al. 2022).	
Tholymis tillarga (Fabricius, 1798)	Twister	Surprisingly no records yet.	Not recorded since Pinhey (1974).	
Tramea basilaris (Palisot de Beauvois, 1817)	Keyhole Glider	Surprisingly no records yet.	Not recorded since Pinhey (1974).	Only reported by Martin (1908).
Tramea limbata (Desjardins, 1835)	Ferruginous Glider	Found at two sites in October 2021 (Papazian et al. 2022).	Surprisingly no records yet.	Only reported by Compte Sart (1962).
Trithemis nigra Longfield, 1936	Príncipe Dropwing	Described by Longfield (1936). Status studied by Loureiro and Pontes (2013).		
Zygonyx sp. near *flavicosta* (Sjöstedt, 1900)	Near Ensign Cascader			Female reported as *Pseudomacromia* sp. by Longfield (1936) was identified by Pinhey (1975) as this species.
Zygonyx torridus (Kirby, 1889)	Ringed Cascader		Female collected on 6 February 2019 at Monte Café (Papazian and Filippi 2019).	

Photographic records were taken from iNaturalist.org and Observation.org, and received directly from Ernst Klimsa

Table 14.2 Occurrence of Odonata species, that are widespread in western and central Africa, in Atlantic and Indian Ocean islands but that so far have not been recorded from the Gulf of Guinea islands (Martens et al. 2013; Van Damme et al. 2020; Dijkstra and Cohen 2021)

Scientific name	English name	CV	Com	Mad	Mas	S&A	Soc
Lestes ochraceus Selys, 1862	Ochre Spreadwing			*		*	
Lestes pallidus Rambur, 1842	Pallid Spreadwing	•					
Agriocnemis exilis Selys, 1872	Little Wisp			•	•		
Pseudagrion glaucescens Selys, 1876	Blue-green Sprite	•					
Pseudagrion sublacteum (Karsch, 1893)	Cherry-eye Sprite		•				
Anax rutherfordi McLachlan, 1883	Western Orange Emperor	•					
Anax tristis Hagen, 1867	Black Emperor	•	•	•	•		
Paragomphus genei (Selys, 1841)	Common Hooktail		•	*			•
Aethriamanta rezia Kirby, 1889	Pygmy Basker			•			
Brachythemis leucosticta (Burmeister, 1839)	Southern Banded Groundling	•		•			
Crocothemis divisa Karsch, 1898	Rock Scarlet			•			
Diplacodes luminans (Karsch, 1893)	Barbet Percher		•			•	
Olpogastra lugubris (Karsch, 1895)	Bottletail			•			
Orthetrum chrysostigma (Burmeister, 1839)	Epaulet Skimmer						•
Orthetrum icteromelas Ris, 1910	Spectacled Skimmer			*			
Orthetrum stemmale (Burmeister, 1839)	Bold Skimmer		•	•	•	*	
Orthetrum trinacria (Selys, 1841)	Long Skimmer	•	•	•		•	
Parazyxomma flavicans (Martin, 1908)	Banded Duskdarter			•			
Rhyothemis semihyalina (Desjardins, 1835)	Phantom Flutterer		•	•	•	•	•
Sympetrum fonscolombii (Selys, 1840)	Red-veined Darter	•			•		•
Tetrathemis polleni (Selys, 1869)	Black-splashed Elf			•			
Trithemis annulata (Palisot de Beauvois, 1807)	Violet Dropwing	•		*	*		
Trithemis arteriosa (Burmeister, 1839)	Red-veined Dropwing	•	•				•
Trithemis hecate Ris, 1912	Silhouette Dropwing		•	•			
Trithemis kirbyi Selys, 1891	Orange-winged Dropwing		•	*			
Urothemis assignata (Selys, 1872)	Red Basker		•	•			
Urothemis edwardsii (Selys in Lucas, 1849)	Blue Basker		•	•	•		

Taxa that differ somewhat morphologically on these islands are marked with an asterisk. *CV* Cape Verde, *Com* Comoros, *Mad* Madagascar, *Mas* Mascarenes, *S&A* Seychelles and Aldabra, *Soc* Socotra

Fig. 14.1 *Trithemis nigra* or Príncipe Dropwing, the only endemic odonate known from the islands. Photo credits: Nuno de Santos Loureiro

Threatened Species, the survey identified no threats and therefore *T. nigra* is now listed as Near Threatened (IUCN 2021).

***Zygonyx* sp. —** Species of this genus favour water with a strong current. Pinhey (1974) did not see "any *Zygonyx* near any of the waterfalls and swift-flowing streams" on São Tomé, although the well-dispersing *Z. torridus* (Kirby, 1889) was recently recorded (Papazian and Filippi 2019). Pinhey (1975) examined the unidentified female reported from Annobón by Longfield (1936), stating that "it appears to be *flavicosta*." The species *Z. flavicosta* (Sjöstedt, 1900) is widespread in western and central Africa and cannot be confused with *Z. torridus*, although other continental species are similar. The Seychelles, Comoros and Madagascar all have endemic *Zygonyx* species; thus, the presence of an endemic species on such a distant island as Annobón cannot be ruled out.

A Poor Fauna?

Considering how much suitable freshwater is present (Fig. 14.2), the 22 species known from all islands combined, and 19 from the largest and best-known island of São Tomé, seem exceptionally few. The Comoros, which geographically and ecologically are perhaps the most comparable island group, harbour 39 species in total,

Fig. 14.2 Tributary of the Rio Capitango, one of many forested streams on São Tomé. These seem perfect for endemic odonates, but none are known. Photo credits: Russell B. Tate

with 36 on the oldest and best-studied island of Mayotte. The Mascarenes and Seychelles (excluding Aldabra) are twice as far from the mainland, but have 29 and 19 confirmed species, respectively, while Mauritius and La Réunion each harbour 23 species (Dijkstra and Cohen 2021). Sixteen species have been reported from the Cape Verde islands, the only other major Afrotropical archipelago in the Atlantic Ocean (Martens et al. 2013). Although that is even fewer than in the Gulf of Guinea, those islands are also more isolated and substantially drier.

Comparing the species tallies of just a few archipelagos with very different sizes, histories, habitats, and degrees of isolation is problematic, however. Looking at the species themselves may therefore be more informative: 16 of the 22 recorded in the Gulf of Guinea are widespread across Africa, with most species' ranges including the other archipelagos mentioned (and parts of Eurasia) as well. Twenty-seven additional species are found both on the adjacent continent and on these other islands, but have yet to be found on São Tomé, Príncipe, or Annobón (Table 14.2): probably at least ten of the more widespread ones are likely present in the Gulf of Guinea islands, pushing the total species diversity over 30.

Range-restricted species, too, are unexpectedly scarce. Pinhey (1974) noted that "compared to other orders, particularly Lepidoptera, rich in species or subspecies only known from these islands, the few endemics are remarkable for their paucity." While a quarter of the Comoro, Mascarene, and Seychelles species are confined to their archipelagos (Dijkstra and Cohen 2021), *Trithemis nigra* from Príncipe is the only known endemic (Fig. 14.1). São Tomé is six times larger and twice as high but has no endemic Odonata. Socotra is larger but lies in a very dry corner of Africa (isolation is similar) and yet has similar numbers: 22 species including a single endemic (Van Damme et al. 2020). Furthermore, the mainland nearest Socotra has less than 50 species, whereas the Gulf of Guinea lies at the heart of the Afrotropics' foremost centre of odonate diversity: well over 200 species are present in the hotspot centred on the Cameroon highlands (Clausnitzer et al. 2012).

While the islands have been poorly researched, their low species numbers can probably not be ascribed only to that. The wet climate with often rainy and cloudy weather may certainly impede the activity of adult odonates and indeed of odonatologists: Pinhey (1974) found that the hot humidity made it "almost unbearable in April to scramble up the mountain after about 9 a.m." However, most widespread species are conspicuous provided it is warm enough. Sampling of five permanent forest streams in the south of São Tomé by the second author in September 2020, moreover, produced larvae of Ephemeroptera and Trichoptera, but no Odonata (Fig. 14.2) suggesting very low densities.

Perhaps the impoverishment on the islands in the Gulf of Guinea can be attributed to the same factors as the diversity on the continent around it. Odonate diversity and endemism is greatest at streams and other permanent waters, especially in areas with forest and varied relief such as in Lower Guinea (Clausnitzer et al. 2012). This is because species in stable habitats do not have to be good dispersers and can thus more easily become isolated and highly adapted to their specific environment. Species in seasonal habitats, by contrast, must be relatively tolerant and dispersive to survive (Dijkstra et al. 2014).

While very few of over 200 species found across from São Tomé, Príncipe, and Annobón may be capable of crossing over and colonising the islands, all of the less than 50 across from Socotra have to be. *Orthetrum africanum* (Selys, 1887), *Rhyothemis notata* (Fabricius, 1787), and *Gynacantha cylindrata/vesiculata* (see above) are the only species on São Tomé and Príncipe that are confined to Africa's wetter and more forested west and centre, but favour rather open or temporary habitats and thus occur widely across equatorial Africa. *Agriocnemis zerafica* Le Roi, 1915 has a similar but more northerly range, being common at seasonal habitats across the Sahel but patchy in the rainforest to the south.

The islands' only endemic fits the same pattern as those three species: the ancestors of the *basitincta*-group of species, to which *T. nigra* belongs, were inferred to prefer open standing water (Damm et al. 2010). The group first invaded flowing waters and then those with shade. The continental sister-species of *T. nigra* take an intermediate position in this transition, favouring more open and temporary sites in forests, such as flood pools near rivers. This capacity to penetrate the rainforest matrix and adapt to peripheral habitats likely allowed for the colonisation of Príncipe. This dispersal event was estimated to have occurred less than 3 million years ago (Damm et al. 2010).

Other factors may also have contributed to the poor odonate fauna in the Gulf of Guinea, such as habitat alteration by humans or volcanism, but these would seem unlikely to have impacted these insects specifically to the exclusion of other groups. The composition of the freshwater communities, however, may also be especially unsuited to Odonata. The second author noted unusually high densities of crustaceans and *Sicydium* gobies in his samples, likely caused by the absence of large fish predators. Although this is highly speculative, their abundance might in turn have led to rates of predation and/or competition that affect odonate larvae disproportionately.

Conclusions

We consider it unlikely (but not impossible) that prolonged fieldwork by a specialist may upend the current impression of a poor and unexceptional odonate fauna on São Tomé, Príncipe, and Annobón. Nonetheless, additional widespread Afrotropical species are expected, especially on Annobón, while the identities of the *Gynacantha* species on São Tomé and *Zygonyx* on Annobón remain to be clarified. Future work should focus on larvae, as sampling this life stage is less affected by wet weather, but also because their ecology might hold the key to the islands' impoverished fauna.

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Chapter 15
Diversity and Distribution of the Arthropod Vectors of the Gulf of Guinea Oceanic Islands

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Abstract The known arthropod vector species on the Gulf of Guinea islands belong to orders Diptera and Ixodida. Among the Diptera, the family Culicidae (mosquitoes) has the most species, 34 (6 endemic), Ceratopogonidae has 13 (all in the genus *Culicoides*), Tabanidae has 6, and Simuliidae has 3 (1 endemic). Ixodida has only 4 species. Most vector species and associated diseases are shared with mainland Africa. Some of these include (1) the human malaria vector *Anopheles coluzzii,* (2) yellow fever and dengue vector *Aedes aegypti,* and (3) the spotted fever group rickettsiae and Q fever vector *Amblyomma* spp. However, there is a considerable lack of information on the natural cycles of many vector-borne diseases that might

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impact local fauna, for which there may be some endemic pathogen lineages. Increased trade by air and sea should compel authorities to remain vigilant, to keep unwanted vectors and diseases at bay. Entomological diversity data remains scarce for Annobón and for the forested interior of the islands, where future sampling efforts may uncover new endemic species.

Keywords Biting midges · Diptera · Flies · Infectious diseases · Mosquitoes · Ticks

Introduction

The discipline of medical entomology originated in the late nineteenth and early twentieth centuries (Service 1978), when P. Manson and R. Ross discovered the obligatory development of specific life stages of the human pathogenic filarial, *Wuchereria bancrofti* Cobbold, 1877, and avian malaria *Plasmodium* parasite in the mosquito *Culex quinquefasciatus* Say (Ross 1911). This discipline aims at studying insects and other arthropods that affect the health of humans, domestic animals, and wildlife (hereafter called vectors). Vector biology can be subdivided into medical (emphasis on human), veterinary (domestic animals), and wildlife disciplines (Edman 2009). However, these are often intertwined, since many vectors transmit infectious agents that cause similar diseases in both humans and animals (zoonoses). A large diversity of pathogens is transmitted by hematophagous arthropods (insects or ticks), including filariae (i.e., worms), protozoa (e.g., malaria), bacteria, and viruses (e.g., dengue, yellow fever, or Zika). Of all the arthropods, the Order Diptera contains the most species that transmit pathogens to humans and wildlife, including one of the most studied families, the Culicidae (mosquitoes).

Recent mosquito surveys on Comoros (Mayotte Island: Le Goff et al. 2014), Seychelles (Le Goff et al. 2012), and Mariana Islands (Guam: Rueda et al. 2011) reveal high numbers of species but few single-island endemics. By contrast, São Tomé and Príncipe harbor six endemic mosquito species (Ramos et al. 1994; Ribeiro et al. 1998; Loiseau et al. 2019) and this high level of mosquito endemism (23%) is especially unusual considering the proximity of the islands to the mainland. In comparison, the Galapagos, Hawaii, and Canary archipelagoes do not harbor endemic mosquito species (Baez 1987; Carles-Tolra 2002; Bataille et al. 2009), while the Azores and Madeira have only one each (Ribeiro and Ramos 1999). Other Dipteran families containing disease vector species, such as Simuliidae and Ceratopogonidae, have been less studied on the Gulf of Guinea oceanic islands, probably due to their lower diversity and lesser medical importance.

In this chapter, we present an overview of the known biodiversity of arthropod vectors and their associated diseases on the Gulf of Guinea oceanic islands. We describe the microhabitats of Culicidae and Simuliidae species and propose future directions that might help in documenting and describing new vector species from the archipelago.

Diversity, Endemism, and Disease Ecology

All vector species on the Gulf of Guinea oceanic islands are Diptera or Ixodida arthropods.

Class Insecta

Order Diptera

The order Diptera is composed of two suborders, Nematocera and Brachycera (Pape et al. 2011). More than 150,000 species have been described, including numerous hematophagous insects able to transmit infectious diseases. Diptera species known as vectors in the Gulf of Guinea islands belong to five families.

Suborder Nematocera

Family Culicidae

Globally, Culicidae includes 3578 mosquito species and subspecies, in 42 genera (Walter Reed Biosystematics Unit 2001). Seven hundred and ninety-five species are known to occur in the Afrotropics (i.e., 22% of the mosquito diversity; Rueda 2008). Culicidae is one of the most studied Diptera families, both worldwide and in the Gulf of Guinea oceanic islands. Hence, for this group, we detail relevant expeditions, from the early twentieth century, which relied mostly on collecting immature stages, to more recent collections, which used both immature and adult decoy trapping.

Early Expeditions (1932–1964)

Published records dating back from the Percy Sladen and Godman Trust expeditions in 1932 and 1933 (Edwards 1934) recorded five species on São Tomé (*Anopheles gambiae* Giles, 1902, *Uranotenia micromelas* Edwards 1934, *Aedes nigricephalus* Theobald, 1901; *Culex fatigans* Wiedemann, 1828 and *Culex tamsi* Edwards, 1934) and two on Príncipe (*Aedes aegypti* Linnaeus, 1762 and *Eretmapodites chrysogaster* Graham, 1909). Two species described from material collected on this expedition, *U. micromelas* and *Cx. tamsi*, are still considered endemic to São Tomé and Príncipe. Based on samples collected during expeditions between 1952 and 1955, 15 additional species were reported for São Tomé and Príncipe (Gãndara 1956). During the program to eradicate tsetse flies on Príncipe (see section on Tabanidae), nine species of mosquito were found, four of which were new to the islands, including *Aedes (Aedimorphus)* larvae that were not identified to species (Pinhão and Mourão 1961). A few years later, an intensive survey of mosquito larvae at

14 sites on São Tomé (Mourão 1964) collected five additional species (*Uranotaenia balfouri* Theobald, 1904, *Aedes metallicus* Edwards, 1912, *Aedes circumluteolus* Theobald, 1908, *Toxorhynchites brevipalpis* Theobald, 1901 and *Culiseta fraseri* Edwards, 1914).

Further Expeditions in the Second Half of the Twentieth Century

An updated list of Príncipe Island mosquito species, based on specimens collected during an expedition in 1986, added seven species (*Ae. nigricephalus*, *Culex antennatus* Becker, 1903, *C. decens* Theobald, 1901, *C. nebulosus* Theobald, 1901, *C. quinquefasciatus* Say, 1826, *U. micromelas* and *U. principensis* da Cunha Ramos, 1993) to the seven previously recorded (Ramos et al. 1989). Then, two new species were described: *Toxorhynchites capelai* Ribeiro, 1991 (Ribeiro 1993), and *Aedes (Aedimorphus) gandarai* Ramos, Capela and Ribeiro, 1994 (Ramos et al. 1994). A few years later, the list of mosquito species increased to 14 on Príncipe and 26 on São Tomé (Ribeiro et al. 1998), including 6 São Tomé endemics, and 1 endemic to both islands (Appendix). The genus *Culex* is represented by the most species, 14, followed by *Aedes*, with 6.

On São Tomé and Príncipe Islands, the only current known vector of human malaria is *Anopheles coluzzii* Coetzee and Wilkerson 2013, previously known as *An. gambiae* M form. *An. coluzzii* is abundant in urban and village settings in coastal areas on both islands. The lower abundance and the possible absence of *An. coluzzii* inland and at elevations above 200 m (Pinto et al. 2000a, b), despite an abundance of semi-permanent pools for immature development, is likely due to much lower human population densities in these areas. After intensive indoor residual spraying campaigns, which started in 2005, the overall prevalence of malaria in children under 9 years old was reduced from 30.5% to 8.3% after the first round, and to 2.1% after the second (Tseng et al. 2008; Teklehaimanot et al. 2009). Prevalence has remained low (~1%; Chen et al. 2019), but active surveillance and mosquito control to prevent malaria outbreaks is ongoing (Lee et al. 2010). The only other *Anopheles* species present on São Tomé, but not on Príncipe, is *An. coustani* Laveran, 1900; however, its role as a secondary malaria vector is not known.

Lymphatic filariasis, a human parasitic infection, is caused by nematodes (*Wuchereria bancrofti* Cobbold, 1887, *Brugia malayi* Brug, 1927 and *B. timori* Partono, 1977), which are transmitted through the bite of infected *Ae., Cx., An.* and *Mansonia* mosquitoes (Chandy et al. 2011). The last report of the presence of *W. bancrofti* on São Tomé dates from 1956 and on Príncipe from 1958 (Fraga de Azevedo et al. 1960). The insecticide spraying that led to the eradication of *Glossina palpalis palpalis* Robineau-Desvoidy, 1830 on Príncipe (see below), probably also impacted mosquito populations, which likely led to eliminating lymphatic filariae on that island (Fraga de Azevedo et al. 1960). Further surveillance might be needed as positive serological tests for lymphatic filariasis have been reported on São Tomé in recent years (Fan et al. 2013; WHO 2019).

Recent Surveys (Within First Quarter of the Twenty-First Century)

Collections performed by the authors on São Tomé and Príncipe in 2016, 2017, and 2019 added four species to the documented diversity (*Ae. albopictus* Skuse, 1894, *Ae. tarsalis* Edwards, 1927, *U. bilineata* Theobald, 1909, and *U. connali* Edwards, 1912). These surveys were primarily focused on collecting mosquito vectors known to transmit wildlife pathogens, especially to birds. At least eight genera of mosquitoes (*Aedes*, *Aedeomyia*, *Anopheles, Culex*, *Coquillettidia*, *Culiseta*, *Mansonia,* and *Uranotaenia*) can transmit avian malaria (Valkiūnas 2004). Avian malaria has had devastating effects on the endemic bird populations of Hawaii (Fonseca et al. 2000), demonstrating the pernicious nature of introduced diseases on isolated animal populations. São Tomé and Príncipe birds are not heavily infected with *Plasmodium*, exhibiting an average prevalence of around 12% (Reis et al. 2021); however, the birds appear to be carrying *Plasmodium* lineages that originate from the mainland, particularly in lowland bird populations (Reis et al. 2021). Numerous mosquito species may be vectors of avian malaria in the Gulf of Guinea oceanic islands, but their vector competence has not yet been assessed and will be an important future research direction for monitoring the population health of the endemic avifauna.

The highly anthropophilic *Ae. albopictus* (invasive tiger mosquito), likely introduced to the Gulf of Guinea during the last 10 years, is now very widespread on both islands and is of considerable human biting nuisance (Reis et al. 2017; Loiseau et al. 2019). Along with *Ae. aegypti*, *Ae. albopictus* is considered an urban cycle vector (Kamgang et al. 2019b) of Yellow Fever, Dengue, Zika and Chikungunya viruses, which actively circulate in neighboring African mainland countries (Paupy et al. 2010; Braack et al. 2018; Kamgang et al. 2019a). Periodic outbreaks of Yellow Fever occur in neighboring mainland countries, namely in Cameroon, Gabon, and Angola (Chippaux and Chippaux 2018). One study estimated that currently there are between 51,000 and 380,000 severe cases of yellow fever annually in Africa, resulting in an estimated 19,000–180,000 deaths (Garske et al. 2014). Dengue virus strains, in the same *Flavivirus* genus as Yellow Fever virus (Daep et al. 2014), are now probably one of the most important arboviruses, since globally they infect over 100 million people annually, resulting in an estimated 500,000 severe Dengue cases (WHO 2014). A serological survey on pregnant women has actually demonstrated the circulation of this virus on the islands (Yen et al. 2016). No major outbreak of Dengue has been recorded on the islands until a recent one in São Tomé in 2022. In addition, nine resident mosquito species found in São Tomé and Príncipe (Ribeiro et al. 1998) are known as vectors of numerous other arboviruses (e.g., *Alphavirus, Flavivirus,* or *Phlebovirus*) in the Afrotropics.

Currently, both Anophelinae and Culicinae subfamilies are present in the Gulf of Guinea islands, as well as the only Culicidae genus that is endemic to Africa, *Eretmapodites* Theobald, 1901. There are 35 resident *Culicidae* species: 31 on São Tomé and 15 on Príncipe (Appendix). To our knowledge *Ae. indet* (Pinhão and Mourão 1961) has not been collected in the last 70 years, and its current presence on the islands is questionable. We have not included *An. funestus* s.l. Giles, 1900, *An. paludis* Theobald, 1901, and *An. pharoensis* Theobald, 1901 (Mesquita 1946, 1952) in the current list of species, because malaria control campaigns in the 1980s are thought to have eradicated them (Pinto et al. 2000a). The only publication on the mosquitoes of Annobón was about malaria transmission and genetic population structure of *An. coluzzii* in Equatorial Guinea (Moreno et al. 2007).

Family Simuliidae

Among the 2200 species of black flies described around the world, 214 are present in the Afrotropical region (Currie and Adler 2008), including many that transmit pathogens that affect humans (e.g., filarial disease onchocerciasis; Crosskey 1990), poultry (Alder and McCreadie 2019), and wild birds (Valkiūnas et al. 2004). Onchocerciasis (river blindness) is limited to sub-Saharan Africa and is widely known in southern Cameroon and on Bioko Island, where it is transmitted by species of the complex *Simulium damnosum* Theobald, 1903 (Post et al. 2003). Currently, this vector species does not occur on the Gulf of Guinea oceanic islands (Mustapha et al. 2004), and no cases of Onchocerciasis have been reported. The avian parasites *Leucocytozoon*, closely related to avian malaria, are present, especially in highland and forest birds of São Tomé and Príncipe (Reis et al. 2021). However, the vector competence of black fly species for *Leucocytozoon* spp. remains unknown on the islands.

Black flies were first documented at one site on São Tomé in 1988 (Grácio 1988). Extensive sampling of 71 sites on São Tomé reported the presence of two species: *Simulium (Pomeroyellum) alcocki* Pomeroy, 1922, and *S. (Anasolen) dentulosum* Roubard, 1915, the latter being the most abundant (Grácio 1999). In 1998, the São Tomé endemic *S. (Pomeroyellum) santomi* Mustapha, 2004 was added to the list (Mustapha et al. 2004). On Príncipe, only *S. dentulosum* is confirmed. No effort has been made to sample black flies on São Tomé or Príncipe during the last 20 years, and it has been suggested that they are absent from Annobón (Mustapha et al. 2004).

Family Ceratopogonidae

This family of biting midges includes 6206 species in 112 genera and has a diverse fossil record (around 300 species; Borkent and Dominiak 2020). Many species of Ceratopoginidae are important pollinators, and only four genera are known to have species that feed on blood of vertebrates, including humans (Borkent 2004): *Austroconops* Wirth and Lee, 1958, *Culicoides* Latreille, 1809, *Forcipomyia* (subgenus *Lasiohelea*) Meigen, 1818 and *Leptoconops* Skuse, 1889. *Austroconops* is the only genus that is not known to play a role in pathogen transmission, while *Culicoides* is the most important in this regard (Borkent 2004). *Culicoides* includes 1347 described species, and the assessment of this diversity has received much attention in Africa because of their status as vectors of human filarial nematodes (Agbolade et al. 2006), and of several viruses responsible for animal diseases, such as Bluetongue (Mellor 1990) and African Horse Sickness (Mellor et al. 2000; Mellor and Hamblin 2004). *Culicoides* are also known vectors of avian malaria-like parasites of the genera *Haemoproteus* (*Parahaemoproteus*) and *Leucocytozoon* (*Caulleryi*) (Valkiūnas 2004). On São Tomé, approximately 20% of the birds are infected with these parasites, with a higher prevalence in shaded plantations (Reis et al. 2021). Among the species of *Culicoides,* several can transmit *Haemoproteus*, but vector competence of *Culicoides* species remains unknown.

The first four species of *Culicoides* recorded on São Tomé were collected during the Percy Sladen and Godman Trust expeditions in the 1930s (Edwards 1934), and identified as *C. austeni* Carter, Ingram and Macfie, 1920, *C. distinctipennis* Austen, 1912, *C. citroneus* Carter, Ingram and Macfie, 1920 and *C. grahamii* Austen, 1909. A three-year study of insects in cocoa plantations identified 25 species of Ceratopogonidae, including only one *Culicoides* species: *C. imicola* Kieffer, 1913 (Wirth and Derren 1976). This fifth species recorded on the island is a known primary vector of Bluetongue and African Horse Sickness viruses, largely distributed in Africa, Asia, and Europe (Guichard et al. 2014). *C. distinctipennis*, *C. milnei* Austen, 1909 and *C. imicola* were later mentioned as present on São Tomé (Glick 1990), the latter being the sixth *Culicoides* species recorded on the island. Since the mid-1970s, there has been no evaluation of the diversity of *Culicoides* on São Tomé and Príncipe Islands, and the number of species is thus likely underestimated. There are 156 species formally described in the Afrotropical region (Labuschagne 2016), including high diversities on neighboring mainland African countries, such as Nigeria (Dipeolu 1976) and Cameroon (Callot et al. 1965; Wanji et al. 2019). Gabon is an exception since only six species have been described so far, probably due to very few studies carried out in that country (Delécolle et al. 2013; Augot et al. 2017). In 2019, nine species of *Culicoides* were found in the southeast of São Tomé, along transects from the center of an oil palm plantation to the native forest. While morphological and molecular investigations are ongoing, it is likely that seven species will be added to the records for the island (Appendix). From the four species first recorded for the island (Edwards 1934), only *C. citroneus* and *C. distinctipennis* were found recently. Surprisingly, no endemic *Culicoides* species have been found yet. Considering sampling bias in these islands, it is likely that future studies in different habitat types, especially deeper in the native forest, or in coffee and cocoa plantations, will reveal the presence of endemic *Culicoides* species. Future surveys will most certainly also increase the number of *Culicoides* species on Príncipe and Annobón, as well as clarify their ecology.

Suborder Brachycera

Family Tabanidae

Worldwide, there are currently close to 4400 species and subspecies, and 144 genera of Tabanidae described (Mullens 2019). Tabanid flies of the genera *Tabanus, Chrysops,* and *Hybomitra*, commonly known as horseflies and deerflies, are of economic, medical, and veterinary importance (Nevill et al. 1994). However, they tend to be less studied than other Dipteran families (Baldacchino et al. 2014). Tabanid flies serve as biological vectors (pathogens replicate and develop within the fly), and as mechanical vectors (pathogens are transmitted without amplification and development within the fly via contaminated blood on mouthparts) of several wildlife and livestock pathogens, such as *Trypanosoma* spp. (Nevill et al. 1994), *Babesia* spp., and *Theileria* spp. (Taioe et al. 2017), filarial nematodes, and numerous viruses and bacteria (Baldacchino et al. 2014). In forested Central Africa, tabanid flies of the genus *Chrysops* also infect humans with *Loa loa* Cobbold, 1864, which causes African eye worm (Mullens 2019). This pathogen has not been reported in São Tomé and Príncipe.

Six species in the genus *Tabanus* have been recorded on São Tomé and Príncipe: *T. biguttatus* Wiedemann, 1830; *T. congoiensis* Ricardo, 1908; *T. obscurefumatus* Surcouf, 1906; *T. taeniola*, Palisot de Beauvois, 1806; *T. principis* Bequaert, 1930 (Bequaert 1930) and *T. monocallosus* (Travassos Santos Dias 1955), the last two being endemic to the Gulf of Guinea islands. No new tabanid flies have been recorded on the archipelago in recent years.

Family Glossinidae

Glossinidae includes the single genus *Glossina* with 23 species, 6 of which are further divided into 14 subspecies, all but one found in Africa (Krinsky 2019). The genus is divided into three groups based on their ecological preferences: the savannah flies (subgenus *Morsitans*), the forest flies (subgenus *Fusca*), and the riverine flies (subgenus *Palpalis*). Species found in sub-Saharan Africa are vectors of the *Trypanosoma* parasites that cause sleeping sickness in humans (Welburn et al. 2001) and trypanosomosis in livestock (Meyer et al. 2016) and can have severe impacts on domestic cattle production (De Geier et al. 2020).

The first known introduction of the tsetse fly, *G. p. palpalis*, occurred on Príncipe Island in 1825 (Fraga de Azevedo et al. 1956). At the end of the nineteenth century and beginning of the twentieth century, it became a significant health issue for cocoa plantation workers and local inhabitants, forcing important prophylactic measures between 1911 and 1914, which included hunting for flies, swamp drainage, clearance of vegetation and slaughter of wild pigs, stray dogs, and civets (Bruto da Costa 1913). The prevalence of *Trypanosoma* dropped dramatically (Bruto da Costa 1913), and in 1914 the tsetse fly was considered eradicated in Príncipe (Figueiredo Moura da Silva 2019). In 1956, entomologists rediscovered large numbers of tsetse fly on Príncipe (Tendeiro 1956) and suggested it had been reintroduced from Bioko Island. Although no cases of trypanosomiasis were found in humans, animals or in the tsetse flies, important measures were applied again to eradicate the tsetse flies, including trapping flies, insecticide spraying, clearing of vegetation, and killing of wild pigs, monkeys, and dogs (Fraga de Azevedo et al. 1956). Eradication was effective by July 1958.

Order Siphonaptera

Two flea species, *Ctenocephalides felis* Bouché, 1935 (cat flea; Family Pulicidae) and *Tunga penetrans* Linnaeus, 1758 (chigoe flea; Family Tungidae), occur in São Tomé and Príncipe. A high percentage of dogs seem to have cat fleas infected with *Rickettsia felis*, an emerging human pathogen often causing febrile illness, while just over 3% of humans had antibodies against this bacterium (Tsai et al. 2020).

Class Arachnida

Order Ixodida

The Ixodida contains three families: Ixodidae, Argasidae, and Nuttalliellidae (Nicholson et al. 2019). The Ixodidae or hard-bodied ticks include 15 genera and 707 species, while the Argasidae or soft-bodied ticks contain about 190 species, and the Nuttalliellidae only one species. Worldwide, they are the most important disease vectors in the veterinary field and are second only to mosquitoes in public health importance (Nicholson et al. 2019). Ticks are ectoparasites that blood-feed on mammals, birds, reptiles, and amphibians, but unlike the short blood-feeding periods (at most a few minutes) of Diptera, hard-bodied ticks attach and stay on their hosts for several days. They are implicated in the transmission of numerous infectious diseases caused by pathogens, such as bacteria (e.g., *Rickettsia, Borrelia, Coxiella*; Parola et al. 2013), viruses (e.g., Crimean–Congo hemorrhagic fever virus, Tick-borne encephalitis virus; Hoogstraal 1979) and protozoa (e.g., *Babesia*; Nelder et al. 2016).

Family Ixodidae

Four species of hard-bodied ticks have been recorded through the years from São Tomé and Príncipe. *Amblyomma astrion* Dönitz, 1909 and *A. splendidum* Giebel, 1877, were collected on São Tomé, and *A. splendidum* on Príncipe (Tendeiro 1957). Subsequently, *Rhipicephalus decolaratus* (Koch, 1844) was collected on both islands (Travassos Santos Dias 1988). In the early 1980s, numerous adult cow and calf deaths on São Tomé were attributed to neurological complications, likely caused by heartwater, a tick-borne rickettsial disease of domestic and wild ruminants transmitted by *A. astrion* (Uilenberg et al. 1982). In 2016, *A. variegatum* Fabricius, 1794, was collected from cattle in the Agua Grande district on São Tomé (Hsi et al. 2020). A serological survey demonstrated the presence of Spotted fever group rickettsiae and Q fever (*Coxiella burnetti*) antibodies in people, which could explain continued reports of febrile illness in São Tomé human residents not due to malaria (Hsi et al. 2020).

Family Argasidae

To date, *Ornithodoros capensis* Neumann, 1901 is the only soft tick species reported for the islands (Travassos 1988). It is an ectoparasite of seabirds in the tropics and subtropics, and was collected in the nests of Brown Noddy *Anous stolidus* (Linnaeus, 1758), Black Noddy *A. minutus* (Boie 1844), and Sooty Tern *Onychoprion fuscatus* (Linnaeus, 1766), during an expedition to Tinhosas (small islets south of Príncipe) in 1970 (Travessos 1988). A recent census of seabird nests on these islets did not report ectoparasites (Valle et al. 2016; Bollen et al. 2018), but they may not have explicitly searched for them.

Distribution, Biology, and Habitat Specificity

In this section, we describe the habitat types and preferred environmental conditions of Culicidae and Simuliidae species, based on the observations of AJC and on the literature (Mourão 1964; Grácio 1999).

Mosquito Habitat and Distribution on São Tomé and Príncipe

Anthropophilic Mosquitoes

Mosquito species that regularly blood-feed on humans include disease vector species – *Ae. aegypti* (Fig. 15.1.1)*, Ae. albopictus* (Fig. 15.1.2)*, An. coluzzii* (Fig. 15.1.5), *Cx. quinquefasciatus,* and *Ae. circumlutelous* – and species not implicated as disease vectors – *Ae. nigricephalus* and *E. chrysogaster* (Fig. 15.1.3).

Immatures of *An. coluzzii*, vectors of malaria, are found mostly on the coast. They develop in direct contact with clear or eutrophic groundwater, in swamps, and in temporary pools, such as in roadside ditches, depressions in pathways, and between households (Fig. 15.2.1). Blood index values and low sporozoite rates in *An. coluzzii* sampled in 1997 and 1998 on São Tomé (Sousa et al. 2001) indicate that they are meso-endemic, feeding predominantly on dogs, followed by humans, and then pigs. In recent collections by AJC, *An. coluzzii* were also attracted to chicken.

Cx. quinquefasciatus (*Cx. fatigans* in Mourão 1964), a vector of filarial nematodes, is very common in urban areas. It bites humans at night inside homes, and often rests indoors or underneath houses along with *Anopheles* mosquitoes. They represent the majority of mosquitoes in the city of São Tomé (Mourão 1964). Immatures of *Cx. quinquefasciatus* are often found in very high numbers in unmaintained sewage systems and in artificial containers, such as barrels, gutters, tubs, or vats of water.

Ae. aegypti and *Ae. albopictus*, vectors of numerous viruses, primarily bite humans during the day. They have spread worldwide and become cosmopolitan

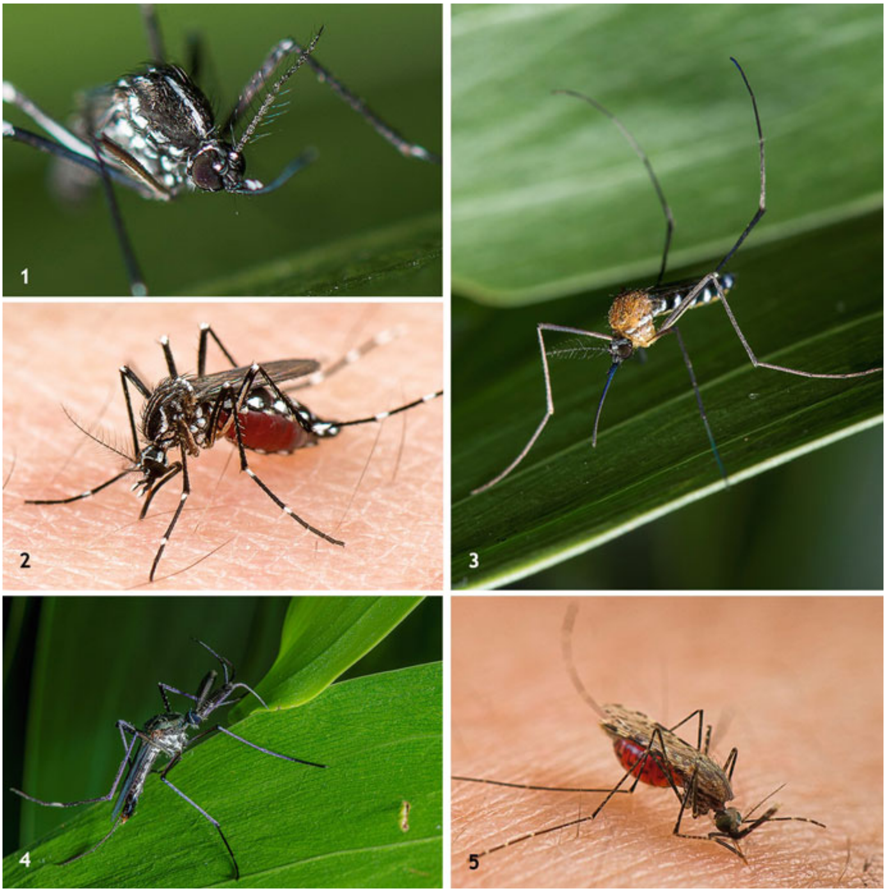

Fig. 15.1 Pictures of mosquito species: (**1**) *Aedes albopictus* (female); (**2**) *Aedes aegypti* (female); (**3**) *Eretmapodites chrysogaster* (female); (**4**) *Toxorhynchites brevipalpis* (male); (**5**) *Anopheles coluzzii* (female). Photo credits; Nil Rahola

(Paupy et al. 2009; Brown et al. 2011; Kraemer et al. 2019). Historically, they both laid eggs in tree cavities (e.g., *Erythrina* sp., *Chlorophora* sp.), but now they are considered container-breeding mosquitoes, as immatures often develop in discarded plastics, tires, and other rubbish that hold water, and in unused cisterns. Still, both species lay eggs in the abundant supply of tree cavities, as well as in fallen banana leaves, in São Tomé and Príncipe. In the past, *Ae. aegypti* was the most collected species (Mourão 1964), but its abundance seems to have decreased since *Ae. albopictus* became established in São Tomé and Príncipe (Reis et al. 2017), as in other parts of the world (Bargielowski and Lounibos 2016). The distribution of *Ae. aegypti* has now contracted into small enclaves, mostly at higher elevations on São Tomé, and is rarely collected on Príncipe.

Fig. 15.2 Examples of microhabitat of Culicidae: (**1**) Typical roadside ditch located on Príncipe with large numbers of *Anopheles coluzzii* larvae. Arrow points to fourth instar larva; (**2**) Typical slow-moving river edge on Príncipe supporting large numbers of *Uranotaenia micomelas* and *Culex decens* larvae; (**3**) Preferred daytime resting location for *Cx. cinerellus, Cx. nebulosus* and multiple *Uranotaenia* species in crab holes in road embankment in Alto Douro, São Tomé. Arrows point to *Culex* mosquitoes; (**4**) *Cx. cambournaci* larvae in water-filled *Heliconia rostrata* flower in Botanical gardens on São Tomé. Arrow points to larvae. Photo credits: Anthony Cornel

Ae. circumluteolus is localized and infrequently captured (human-biting at Mucumbli, São Tomé), and represents the only typical floodwater *Aedes* species on São Tomé, even though immatures have been found in ground pools and in artificial containers (Mourão 1964). This species is a known vector of significant arboviruses, such as Rift Valley Fever, Wesselsbron, Bunyamwera, and Pongola viruses in Africa (Braack et al. 2018).

Finally, *E. chrysogaster*, another pernicious daytime human blood-feeding mosquito, lays eggs opportunistically in trash, but mostly in natural containers, such as plant leaf axils, especially in fallen banana and palm leaves, or cocoa and coconut shells. This species is present everywhere on the islands but is not known to transmit diseases in São Tomé and Príncipe.

Opportunistic Mosquitoes

Ae. nigricephalus, an opportunistic blood feeder, bites humans during the day and does not disperse far from brackish water estuaries and mangroves, where immatures develop in crab holes. *Cx. cinerellus* Edwards, 1922 is also specialized to develop in brackish water crab holes (Hopkins 1952).

Immatures of other abundant mosquito species, which are more likely to feed on birds, and only seldom feed on humans, such as *Cx. decens, Cx. antennatus*, and *Lutzia tigripes* (de Grandpré & de Charmoy, 1901) also occur in temporary water bodies. *Cx. decens* can be abundant on São Tomé (Mourão 1964), and its larvae were frequently found in artificial containers. On Príncipe, large numbers of larvae were found along slow-moving rivers (Fig. 15.2.2).

Immatures of other species that seldom bite humans (e.g., *Ae. tarsalis, Ae. gandarai, Culex macfiei* Edwards, 1923*, Cx. nebulosus*) and nectar feeders (*Toxorhynchites capelai* and *T. brevipalpis;* Fig. 15.1.4), develop in tree holes and less so in banana or plant leaf axils. Rotting coconut fruits serve as significant sites for the development of *Cx. (Culiciomyia) nebulosus*, while adults primarily rest in crab holes (Fig. 15.2.3). Interestingly, immatures of *Cx. cambournaci* Hamon & Gandara, 1955 are often found in large numbers in the flowers of *Heliconia* species, which have been introduced from the neotropics as ornamentals (Fig. 15.2.4).

The immatures of other species including *Cx. annulioris* Theobald, 1901*, Cx. invidiosus* Theobald, 1901*, Cx. thalassius* Theobald, 1903*, Cx. tamsi, Culiseta fraseri, L. tigripes, Ur. capelai, Ur. principensis, Ur. balfouri* Theobald, 1904*, Ur. bilineata* and *Ur. connali* are typically found in river seepages, and rocky and thickly vegetated vernal pools. All these opportunistic mosquitoes are potential vectors of avian *Plasmodium.*

Black Fly Habitat and Distribution on São Tomé

Immature Simuliidae filter-feed in flowing waterways. Stream size, water velocity, and seston load are important factors that influence the distribution of black-fly species (Palmer and Craig 2000; Adler and McCreadie 2019). Interestingly, *S. alcocki* and *S. dentulosum* are not concomitant on São Tomé (Grácio 1999), *S. alcocki* is restricted to the northern interior part of the island, while *S. dentulosum* was more widespread. Their niches tend to show ecological allopatry with *S. dentulosum* found in rivers from sea level to 400 m, while *S. alcocki* occurs from 200 to 900 m above sea level. *S. alcocki* immatures tend to be restricted to the first 10 cm of the water column, whereas *S. dentulosum* are found anywhere from close to the surface to 50 cm below the surface. Finally, *S. dentulosum* seems to prefer streams or rivers with weak water flow (78 cm/s, 87% of oxygen on average), contrary to *S. alcocki* which prefers faster water flow (122 cm/s, 98% of oxygen on average; Grácio 1999). Re-sampling the same sites would be ideal to evaluate if the habitat and microhabitat specificity of these two species have changed over time. We suspect *S. alcocki* as the main vector of *Leucocytozoon* spp. in birds, since both vectors and parasites are found in greater abundance at higher elevations.

Directions for Future Disease Insect Vector Research

Sampling Effort in Diverse Habitats and Specific Vector Families

Among all expeditions and surveys that aimed to collect vectors, we discern two major sampling paucities. First, the forested interior of São Tomé, in the Obô Natural Park, and the forested south of Príncipe are poorly studied. The main reason is probably accessibility, since reaching remote native forest requires long walks and camping. While mosquitoes have been quite well sampled along the entire coast, and also in some parts of the interior of the islands, other families such as Ceratopogonidae or Tabanidae have been sampled in few sites, and do not include all habitat types found on the islands. Second, Annobón has been poorly sampled for all groups. Although the island is small (17 km^2) and more isolated, we estimate that some of its arthropod vectors are not yet described. We believe that the Gulf of Guinea oceanic islands are still full of surprises and that all three islands have the potential to hold undescribed arthropod vectors.

Surprisingly, there are no records of louse flies (family Hippoboscidae) and sand flies (family Psychodidae, subfamily Phlebotominae) on the islands. Louse flies, also known as bird flies, flat flies, or ked flies (Reeves and Lloyd 2019), are vectors of *Haemoproteus* parasites in Columbidae birds (Valkiūnas 2004), which have been detected in the blood of *Columba larvata* and *C. malherbii*, both on São Tomé and Príncipe (Loiseau et al. 2017; Reis et al. 2021). Thus, the presence of louse flies on São Tomé and Príncipe islands is highly suspected, even though no record has been published yet. Collection of louse flies can only be done on live birds, or by checking livestock coats. It is also somewhat surprising that no sand fly species have been found on any of the islands, although no surveys have specifically searched for them. Surveys should be done preferentially during the rainy season since these insects are highly seasonal, with abundance peaks during or right after rain (Munstermann 2019). *Leishmania* parasites, transmitted by sand flies, are present in Central Africa (Alvar et al. 2012) but have never been reported on the islands, supporting the hypothesis that these vectors might be absent.

New Complementary Tools to Evaluate Vector Diversity

Skilled entomologists can identify species morphologically, if they have access to updated descriptions and identification keys (Hajibabaei et al. 2007). Distinguishing characters, especially subjective ones that are used in identification keys, at the different stages (i.e., eggs, larvae, and adult specimens) are perceptively difficult for non-experts, particularly in the tropics where the diversity is often high and many species are similar. Recent developments in molecular identification techniques, coupled with reduced sequencing costs can help overcome these identification difficulties, and even reveal cryptic biodiversity. Identification of species using metabarcoding approaches on environmental DNA (eDNA) (Boerlijst et al. 2019; Krol et al. 2019) and on bulk samples (Batovska et al. 2018) is an appealing option, but it is worth noting that sequences belonging to unknown taxa are still a common problem in eDNA barcoding. Surveys of mosquito diversity using these techniques require a sound reference database, which in turn demands a considerable amount of a priori taxonomic work. This can be achieved by sequencing samples from the field and from natural history museums that have been identified by experienced entomologists.

Because dipping methods traditionally used to survey larvae may not always reflect adult diversity found with traps, determining and comparing species diversity across different types of samples (water, soil, or bulk samples) using metabarcoding might be a useful complementary approach. eDNA and bulk sample metabarcoding also show a high potential to become helpful monitoring tools to evaluate changes in relative abundance and species diversity in relation to habitat change and to detect invasive vector species in routine surveys. In addition, novel trap designs as well as visual and chemical lures to attract insects, including vector species, are always under development and may also increase surveillance and biodiversity determinations.

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Appendix

List of the arthropod vectors of the Gulf of Guinea Oceanic Islands of Príncipe (P) and São Tomé (ST).

Entomological data are almost non-existent for Annobón. Beside the record of *Anopheles coluzzii* on Annobón, and the absence of Simuliidae, we cannot state if other vector species are present or absent. Status of each species was defined as resident (R), endemic (E), introduced (I), or no data (?)

Higher Taxonomy	Subgenus/Group	Species	P	ST
ORDER DIPTERA				
Family **Culicidae**				
Anopheles Meigen, 1818	*Anopheles*	*Anopheles coustani* Laveran, 1900		R
	Cellia	*Anopheles coluzzii* (*Anopheles gambiae* M form) Coetzee & Wilkerson, 2013	R	R
Aedes Meigen, 1818	*Aedimorphus*	*Aedes nigricephalus* Theobald, 1901	R	R
		Aedes sp. indet	E	
	Catageomyia	*Aedes tarsalis* Edwards, 1927		R
	Polyleptiomyia	*Aedes gandarai* Ramos, Capela & Ribeiro, 1994		E
	Neomelaniconion	*Aedes circumluteolus* Theobald, 1908		R
	Stegomyia	*Aedes aegypti* Linnaeus, 1762	R	R
		Aedes albopictus Skuse, 1894	I	I
Culex Linnaeus 1758	*Culex*	*Culex annulioris* Theobald, 1901		R
		Culex antennatus Becker, 1903	R	R
		Culex decens Theobald, 1901	R	R
		Culex invidiosus Theobald, 1901		R
		Culex quinquefasciatus Say, 1826	R	R
		Culex tamsi Edwards, 1934		E
		Culex thalassius Theobald, 1903		R
	Culiciomyia	*Culex cambournaci* Hamon & Gãndara, 1955		E
		Culex cinerellus Edwards, 1922		R
		Culex macfiei Edwards, 1923		R
		Culex nebulosus Theobald, 1901	R	
	Eumelanomyia	*Culex inconspicuosus* Theobald, 1908	R	R
		Culex rima Theobald, 1901		R
		Culex micolo Ribeiro, Cunha Ramos & Capela, 1998		E
Culiseta Felt, 1904	*Theomyia*	*Culiseta fraseri* Edwards, 1914		R
Eretmapodites Theobald, 1901		*Eretmapodites chrysogaster* Graham, 1909	R	R
Lutzia Theobald, 1903	*Metalutzia*	*Lutzia tigripes* De Grandpré & De Charmoy, 1900	R	R
Toxorhynchites Theobald, 1901	*Afrorhynchus*	*Toxorhynchites capelai* Ribeiro, 1993		E
		Toxorhynchites brevipalpis conradti Gruenberg, 1907	R	
Uranotaenia Lynch Arribálzaga, 1891	*Pseudoficalbia*	*Uranotaenia capelai* Ramos, 1993		E
		Uranotaenia micromelas Edwards, 1934	E	E
		Uranotaenia principensis Ramos, 1993	E	
	Uranotaenia	*Uranotaenia balfouri* Theobald, 1904		R
		Uranotaenia bilineata Theobald, 1909		R
		Uranotaenia connali Edwards, 1912		R

(continued)

Higher Taxonomy	Subgenus/Group	Species	P	ST
Family **Simuliidae**				
Simulium Latreille, 1802	*Pomeroyellum*	*Simulium alcocki* Pomeroy, 1922		R
		Simulium santomi Mustapha, 2004		E
	Anasolen	*Simulium dentulosum* Roubard, 1915	R	R
Family **Ceratopogonidae**				
Culicoides Latreille, 1809	–	*Culicoides citroneus* Carter, Ingrain et Macfie, 1920	?	R
	Subgenus *Avaritia*	*Culicoides grahamii* Austen, 1909	?	R
		Culicoides imicola Kieffer, 1913	?	R
		Culicoides trifasciellus Goetghebuer, 1935	?	R
	Subgenus *Meijerehelea*	*Culicoides distinctipennis* Austen, 1912	?	R
	Subgenus *Remmia*	*Culicoides enderleini* Cornet & Brunhes, 1994	?	R
	Group Milnei	*Culicoides austeni* Carter, Ingram and Macfie, 1920	?	R
		Culicoides hortensis Khamala, 1991	?	R
		Culicoides krameri Clastrier, 1958	?	R
		Culicoides milnei Austen, 1909	?	R
		Culicoides quinquelineatus Goetghebuer, 1934	?	R
	Group Neavei	*Culicoides neavei* Austen, 1912	?	R
	Group Nigripennis	*Culicoides sp.*	?	R
Family **Tabanidae**				
Tabanus Linnaeus 1758	Group Tabanini	*Tabanus biguttatus* Wiedemann, 1830		R
		Tabanus congoiensis Ricardo, 1908		R
		Tabanus obscurefumatus Surcouf, 1906		R
		Tabanus taeniola, Palisot de Beauvois, 1806		R
		Tabanus principis Bequaert, 1930	E	
		Tabanus monocallosus Travassos Dias, 1955		E
ORDER IXODIDA				
Family **Ixodidae**				
Amblyomma Koch, 1844		*Amblyomma astrion* Dönitz, 1909		R
		Amblyomma splendidum Giebel, 1877	R	R
		Amblyomma variegatum Fabricius, 1794		R
Family **Argasidae**				
Ornithodoros Koch, 1837	Subgenus *Alectorobius*	*Ornithodoros capensis* Neumann, 1901	*	

a Found on Tinhosas Islands

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Chapter 16
Terrestrial Mollusca of the Gulf of Guinea Oceanic Islands

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Abstract The oceanic islands of the Gulf of Guinea are known for their remarkable endemic species richness, and the terrestrial Mollusca group is particularly distinctive. This chapter summarizes the exploration and diversity of this group, discussing biogeography, evolution, ecology, and conservation to identify persisting knowledge gaps. Terrestrial malacological studies in the Gulf of Guinea islands started at the end of the eighteenth century but have been intermittent. Recent systematic surveys have continued to find novelties, and the most recent revision lists 96 species, of which 62 are endemic: Príncipe has 40 terrestrial (60% single-island endemic) and

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five seashore species, São Tomé has 52 terrestrial (50% single-island endemic) and seven seashore species, Annobón has 14 terrestrial species (50% single-island endemic), 3 species are endemic to Príncipe and São Tomé, and 2 are endemic to the three islands. The islands were colonized by diverse "clades" arriving from continental Africa, which is consistent with biogeographical patterns from other taxonomic groups. However, in line with Mollusca dispersal limitations, inter-island colonization seems to be less frequent, while there are multiple cases of speciation within the same island. The land snail assemblage on São Tomé seems to be strongly structured by land-use type: endemics being associated mostly with forest and non-endemics to anthropogenically modified environments. Only 13 species have been recorded across the altitudinal range of São Tomé, suggesting altitude is also essential to determining species distribution. Habitat loss and introduced species are important threats, but so far, only the endemic *Archachatina bicarinata* has been listed as threatened. Despite recent progress, further studies are still needed to better understand this unique fauna and inform conservation strategies.

Keywords Africa · Checklist · Conservation · Endemism · Malacofauna · Taxonomy

Introduction

This chapter reviews what is known of the terrestrial Mollusca (Gastropoda) of the three oceanic islands in the Gulf of Guinea, located close to the Equator, off the Atlantic coast of central Africa: Príncipe, São Tomé (together constituting the Democratic Republic of São Tomé and Príncipe - STP), and Annobón (part of the Republic of Equatorial Guinea). Bioko (also part of Equatorial Guinea) is a continental island, and thus it has not been included. The few Mollusca living in freshwater habitats on STP (Brown 1991; Simões 1992) are not covered, whereas seashore species are briefly considered. Taxonomy and nomenclature follow a recent checklist for STP (Holyoak et al. 2020) and a similar revised list for Annobón (Appendix).

All three islands arose during the Tertiary, forming part of the extensive Cameroon Line of volcanos. The maximum age ranges from approximately 15 Ma on São Tomé and 6 Ma on Annobón to 31 Ma on Príncipe. The latter is also the only island without signs of active volcanism in the last 3 Ma (Fitton and Dunlop 1985). They all retain large proportions of rugged topography, reaching maximum altitudes of 2024 m on São Tomé, 948 m on Príncipe, and 598 m on Annobón. They are formed mainly of igneous rocks and have relatively small areas of uplifted conglomerates, sandstones, and shales. The presence of large areas of volcanic bedrock and the absence of uplifted limestone produced calcium-poor soils that limit the abundance of land snails. It is also unsurprising that fossil terrestrial Mollusca are unknown, considering the scarcity of subaerial calcareous sediments.

The islands rise from oceanic depths, and thus, unlike Bioko, they have never been joined to continental Africa. When ocean levels were lower, during some periods of the Pleistocene, the islands would have had larger land areas than at present, with maxima estimated as 144 km^2 for Annobón (now 17 km^2), 1480 km^2 for São Tomé (now 857 km^2), and 1179 km^2 for Príncipe (now 139 km^2). Nevertheless, their remoteness from the continent was not significantly reduced (Jones and Tye 2006; Norder et al. 2018) and colonization by land mollusks clearly involved long-distance overseas dispersal.

When human colonization began in the late fifteenth century, the islands were almost entirely covered by tropical rainforest, associated with hot equatorial climates and rainfall occurring throughout the year in most areas (Loboch 1962; Bredero et al. 1977). The native lowland forests are floristically distinct from montane and mist forest occurring at higher altitudes (Exell 1944). Much of the lowland forest has been replaced by cultivation, notably for sugar cane in the sixteenth century and coffee and cocoa during the nineteenth and early twentieth centuries (Exell 1944). Therefore, it is quite likely that native land mollusk species became extinct and that alien species arrived before the first thorough scientific assessments of the islands' malacofauna took place. Moreover, the islands hold a remarkable number of introduced plants (Figueiredo et al. 2011) and mammal species (Dutton 1994), partly due to being regularly visited by ships involved in the Atlantic triangular trade (Eyzaguirre 1986).

A few large land-snail shells from the islands reached Europe in the 1700s, resulting in the naming of *Atopocochlis exaratus* (Fig. 16.1.6), *Columna columna* (Müller 1774), and *Archachatina bicarinata* (Bruguiére 1792—Fig. 16.1.5). However, the first detailed study of the land Mollusca of the region was made by Rang (1831), a commander in the French navy who stayed on Príncipe for a month, allowing him to make careful descriptions of living snails and their habitats, as well as collecting specimens. Soon afterward, Morelet (e.g., 1848, 1858, 1860, 1868, 1873) named and described specimens brought back to Europe from Príncipe and São Tomé by voyagers, including Dr. Friedrich Welwitsch. Dr. Dohrn spent 6 months on Príncipe in 1865 with John Keulemans, collecting birds and snails, which he later described (Dohrn 1866a). Dohrn also named the original material of (*Apothapsia*) *thomensis* (Fig. 16.1.4) from São Tomé (Dohrn 1866b). Dohrn's slug specimens were studied by Heynemann (1868). Unfortunately, Dohrn's main collection was destroyed during the bombing of the Szczecin museum, Poland (Dance 1986).

Greeff (1882) named and described specimens collected during thorough fieldwork on both Príncipe and São Tomé in 1879–1880, including *Thyrophorella thomensis* (Fig. 16.1c) and *Pyrgina umbilicata* as new species in new genera and (*Aporachis*) *dohrni* and (*A.*) *hispida* as new species. Nobre (1886, 1891, 1894) reported on collections made on São Tomé by Adolpho Möller and capitão Castro. Francisco Newton was employed to collect on all three islands: from November 19, 1892, to early January 1893, he made the first detailed collections on Annobón, covering birds, mollusks, and more. Girard (1893a, b, 1894, 1895) named and described his land mollusk collections, including most Annobón endemics. Unfortunately, part of Girard's work on Annobón remained unpublished, including Figs. 1–11 (1894) and the newly discovered *Dendrolimax newtoni* (Ortiz de Zaráte

Fig. 16.1 Photographs of some living terrestrial Mollusca of Príncipe and São Tomé: (**1**) *Pseudoveronicella thomensis*, ca 30 mm, endemic to São Tomé; (**2**) *Pseudoveronicella forcarti*, ca 25 mm, endemic to Príncipe; (**3**) *Thyrophorella thomensis*, shell breadth ca 9 mm, endemic to São Tomé; (**4**) *Apothapsia thomensis*, shell breadth ca 12 mm, endemic to São Tomé; (**5**) *Archachatina bicarinata*, shell length ca 155 mm, endemic to Príncipe and São Tomé; (**6**) *Atopocochlis exaratus*, juvenile and adult, shell lengths ca 25 and 45 mm, endemic to São Tomé; (**7**) *Archachatina marginata*, shell length ca 105 mm, introduced on Príncipe and São Tomé; (**8**) *Limicolaria flammea*, shell length ca 22 mm, introduced on São Tomé. Photo credits: (**1**, **3**) David Holyoak, (**2**) Frazer Sinclair and Fundação Príncipe, (**4–8**) Vasco Pissarra and Forest Giants Project. Not all the species represented in the figure were photographed in their natural habitat

and Alvarez 1960) was left as a *nomen nudum*. Girard's specimens and probably many from Nobre were lost in the fire of March 1978, at the National Museum of Natural History in Lisbon (now integrated in the National Museum of Natural History and Science—MUHNAC). Crosse (1868, 1888a, b) wrote on the land mollusk faunas of STP, adding little that was really new, apart from some detailed descriptions and occasional interpretation of problems.

Germain, based at the Paris Museum, wrote a series of detailed and often well-illustrated papers on the mollusks of west and central Africa, including the Gulf of Guinea islands. He examined collections by Charles Gravier from São Tomé (Germain 1908), and by Leonardo Fea, made available by the Genoa Museum (Príncipe: Germain 1912a, b, 1915; Annobón: Germain 1916). The proportion of undescribed species he found was low compared to that in earlier accounts.

After a long gap in the publication of new work, Ortiz de Zaráte and Alvarez (1960) described the results of the Peris-Alvarez Expedition to Annobón, including several new records and the valid naming of *Dendrolimax newtoni*. Gascoigne (1994a, b) lived on São Tomé for many years, publishing several molluscan faunistic accounts, including new records, and donated specimens he collected to the Natural History Museum of London (NHMUK).

We began studying the land mollusks of the islands during a visit to São Tomé in December 2013, which resulted in a review of the taxonomy of *Rhysotina* (Holyoak and Holyoak 2016). Subsequent work included the study of *Archachatina* on São Tomé (Panisi 2017) and Príncipe (Fundação Príncipe 2019). In November and December 2018, an expedition team made large selective collections of specimens and contributed to the publication of an annotated checklist that named 13 hitherto undescribed species and 6 new genera and gave 11 other new island distributional records (Holyoak et al. 2020). An expedition team in October and November 2019 studied the distribution and habitat associations of the species occurring on São Tomé. There is ongoing work on systematics, ecology and conservation of land mollusks on both islands (Fundação Príncipe 2019; Panisi et al. 2020; Tavares 2021). Since the systematics of land Mollusca has been reviewed in detail very recently, this chapter will summarize malacological exploration and existing diversity, discussing zoogeography, evolution, ecology, and conservation to identify some of the persisting knowledge gaps.

Species Diversity

General Patterns

The list of terrestrial mollusks for the oceanic islands of the Gulf of Guinea will surely change with future research, including new records and a better understanding of species relationships and endemism. Nevertheless, a fully satisfactory taxonomy must await improved knowledge of the malacofauna of continental Africa.

Table 16.1 Numbers of species of terrestrial mollusks known to occur in the Gulf of Guinea oceanic islands (Holyoak et al. 2020—Appendix)

	Single-island endemics	Shared endemics	Native	Introduced	Total terrestrial	Seashore
Príncipe	24 (60%)	5 (13%)	9 (22%)	2 (5%)	40	5
São Tomé	26 (50%)	5 (10%)	15 (28%)	6 (12%)	52	7
Annobón	7 (50%)	2 (14%)	4 (29%)	1 (7%)	14	0
Total	57 (66%)	5 (6%)	18 (20%)	7 (8%)	87	9

Percentages were calculated excluding seashore species since these have very distinct ecology and life-histories

Currently, the malacofauna for the islands includes 9 seashore and 87 strictly land species (Appendix and Table 16.1).

Seashore species belong to Truncatellidae, Assimineidae, Ellobiidae, and Onchidiidae, and occur solely on upper levels of marine beaches. Little is known about this group in the region, but all species are assumed to be native. Only five taxa have been identified to the species level, and there are no records of seashore species from Annobón. The number of accepted species in this group will likely change with further work, especially considering that they have received little sampling effort.

Land species comprise 5 Cyclophoridae or Maizaniidae, 4 Veronicellidae, 31 Achatinidae, 1 Micractaeonidae, 16 Streptaxidae, 1 Punctidae, 1 Charopidae, 1 Succineidae, 2 Cerastidae, 2 Gastrocoptidae, 1 Truncatellinidae, 2 Valloniidae, 1 Agriolimacidae, 2 Euconulidae, 2 Helicarionidae, 14 Urocyclidae, and 1 Helicidae. All have an external shell, apart from all 4 Veronicellidae, all 3 *Dendrolimax* (Urocyclidae) and *Deroceras laeve* (Agriolimacidae). The islands hold high proportions of endemic taxa: 57 (66%) species are considered single-island endemics, and 5 (6%) shared endemics (Table 16.1). Endemic species comprise all 5 Cyclophoridae or Maizaniidae, 2 Veronicellidae (*Pseudoveronicella thomensis* from São Tomé and *P. forcarti* from Príncipe—Fig. 16.1.1–2), 23 Achatinidae, 14 Streptaxidae, 2 Gastrocoptidae, 1 Truncatellinidae, 1 Euconulidae, and 12 Urocyclidae. Compared to the African mainland taxa, endemic Achatinidae include a disproportionately high number of species with sinistral shells, namely *A. bicarinata*, all three *Columna* species and *Thyrophorella thomensis*.

No family is recognized as endemic to the islands since *Thyrophorella* was shown to be a close relative of *Pyrgina* and placed within Achatinidae, subfamily Thyrophorellinae (Fontanilla et al. 2017). Rhysotininae is still regarded as an endemic subfamily, with molecular support (Holyoak and Holyoak 2016). Currently, 14 genera are considered endemic to the islands, holding 24 species (Holyoak et al. 2020). These include distinctive taxa that are likely to be genuinely endemic, such as *Columna*, *Thyrophorella,* and *Rhysotina*, and the pairs of genera *Bocageia* and *Petriola*, and *Pyrgina* and *Thomea*. Both these pairs are distinctive, but each pair might be reduced to a single genus. Newly named genera containing only endemic species (*Aporachis*, *Apothapsia*, *Principicochlea*, *Thomithapsia,* and *Thomitrochoidea*), as well as the endemic *Sphinctostrema* (Girard 1894), and the

São Tomé endemic *Thomeomaizania*, are less likely to be truly endemic. The same may be true for near-endemic *Atopocochlis,* which currently holds only two species: *A. exaratus* endemic to São Tomé and *A. auripigmentum* endemic to Bioko (Wronski et al. 2014). On the other hand, the Príncipe endemic *Cyathopoma inexspectata* might warrant having its own genus (Holyoak et al. 2020).

Land snails and slugs include seven introduced species, five recently reported as new records for the area (Holyoak et al. 2020). Furthermore, it is unclear if the widespread *Striosubulina striatella*, originally described from Príncipe, is native or introduced on the islands. Other non-endemic species are considered native by default, but they might have been introduced before the first extensive malacological assessments of the islands.

Islands Accounts

Príncipe has 5 seashore species and 40 terrestrial species, including 1 Cyclophoridae or Maizaniidae (recently described), 3 Veronicellidae, 17 Achatinidae, 9 Streptaxidae, 1 Succinidae, 2 Cerastidae, 1 Euconulidae, and 6 Urocyclidae (Appendix). The island has 24 endemic species, plus 3 shared with São Tomé (*A. bicarinata*, *Opeas pauper,* and *Streptostele moreletiana*) and 2 shared with both São Tomé and Annobón (*O. dohrni* and *O. greeffi*). Of all endemic species, 8 (1 Cyclophoridae or Maizaniidae, 1 Veronicellidae, 3 Achatinidae, and 3 Urocyclidae) are the sole representatives of their genus on the island. Other genera are represented by multiple species: *Principitrochoidea* (Urocyclidae) has 2 island-endemic species, *Columna* and *Subulina* (both Achatinidae) have 3, *Opeas* (Achatinidae) and *Gulella* (Streptaxidae) have 4 and *Streptostele* (Streptaxidae) has 5. *Archachatina marginata* (Fig. 16.1.7) and *Laevicaulis alte* are the only confirmed introduced species, and their presence was only reported recently (Holyoak et al. 2020).

São Tomé has 7 seashore species and 52 terrestrial species, comprising 4 Cyclophoridae or Maizaniidae, 3 Veronicellidae, 21 Achatinidae, 1 Micractaeonidae, 2 Streptaxidae, 1 Punctidae, 1 Charopidae, 1 Succineidae, 2 Cerastidae, 1 Gastrocoptidae, 1 Truncatellinidae, 2 Valloniidae, 1 Agriolimacidae, 2 Euconulidae, 2 Helicarionidae, 6 Urocyclidae, and 1 Helicidae (Appendix). The island has 26 endemic species, plus 5 shared with at least one other nearby oceanic island. Of all endemic species, 16 are the sole representatives of their genus on the island (spread across 8 families). Other genera are represented by multiple species: *Thomeaonaizania* (Cyclophoridae or Maizaniidae), *Aporachis* (Achatinidae), and *Apothapsia* (Helicarionidae) have 2 island-endemic species, and *Petriola, Opeas* (both Achatinidae) and *Rhysotina* (Urocyclidae) have 3. *A. marginata* is known to have been introduced on São Tomé by the mid-twentieth century (Gascoigne 1994a), but it is now widespread (Panisi 2017) and an important source of protein for people (Carvalho et al. 2015). Recently, 5 other introduced mollusks have been reported for the island, many of which already seem to be relatively widespread, others at least locally abundant (Holyoak et al. 2020).

Annobón has the least scientifically documented malacofauna of the oceanic Gulf of Guinea islands, since it is seldom visited by researchers. It is likely that further visits will substantially increase the species list. Currently, it is known to host 14 terrestrial mollusks, comprising 4 Achatinidae, 6 Streptaxidae, 1 Succineidae, 1 Gastrocoptidae, and 2 Urocyclide (Appendix). The island has 7 endemic species, plus 2 that are shared with São Tomé and Príncipe. Of all endemic species, *Gastrocopta* (Gastrocoptidae) and *Dendrolimax* (Urocyclidae) are represented by a single species. By contrast, *Opeas* (Achatinidae) and *Sphinctostrema* (Streptaxidae) are represented by 2, and *Gulella* (Streptaxidae) by 3. *Allopeas gracile* is the only introduced species confirmed on Annobón, despite an unsubstantiated record of a large species of Achatinidae being used locally for food, which is likely to correspond to the invasive *A. marginata* (Brendan Sloan, pers. comm.).

An imbalance in the taxonomic composition between the faunas of the different islands is immediately apparent. São Tomé has very few Streptaxidae (2 species), and these are uncommon and inconspicuous elements in snail faunas on that island. By contrast, Príncipe has 9 streptaxid species, and Annobón has 6, and the family is conspicuous and common in both of those faunas. Since these streptaxids are all carnivorous, this leads to odd faunal assemblages, at least on Príncipe, where the commonest snails in ground-litter of native forests at some sites are all predators, albeit presumably eating mostly non-molluscan invertebrates. The few carnivorous land snail species on São Tomé might be partly explained by a conspicuous presence of land flatworms, which presumably originated from a single radiation (Matthias Neumann, pers. comm.). At least 3 out of the 5 recently described endemic *Othelosoma* species were seen feeding on land snails (Neumann 2016), and it is known that several species remain undescribed (Matthias Neumann, pers. comm.). Conversely, geoplanids do not seem to occur or are certainly much less conspicuous on Príncipe (Matthias Neumann, pers. comm.), which might have influenced the differences in composition of land snail faunas on the two islands. Future studies are needed to test this hypothesis.

Other taxonomic imbalance results from the presence of *Rhysotina* and *Petriola* (each genus with 3 species) only on São Tomé, whereas Príncipe alone has the genus *Principitrochoidea* (3 species). These taxonomic imbalances between islands likely result in part from in situ speciation in several of the genera as well as differing outcomes from chance colonization by ancestral species from different families present on the African mainland. Similar unbalanced patterns occur on other oceanic archipelagoes. For instance, the Canary Islands have many endemic Enidae, while the Madeiran Islands have no representatives of the family but instead have endemic radiations of Clausiliidae (lacking in Canary Islands) and numerous endemic Ferussaciidae (present only marginally in Canary Islands) (Bank et al. 2002). Chance events in early colonization and establishment success likewise appear to be the best explanations for the taxonomic imbalance of the snail faunas of those archipelagos, rather than any differences in island environments or faunas of their continental source areas.

Biogeographical Considerations

São Tomé is much larger than Príncipe, but is only marginally more species-rich, both in total numbers of species and endemics. This might be explained by the two islands having similar sizes during glaciation peaks and Príncipe being much older (Fernández-Palacios et al. 2016). Considering its small size, Annobón is also remarkably rich, especially in endemic species, which might be explained by the combination of old age and larger area during the glaciations.

Many endemic species seem to have resulted from independent colonization events, based on the observation that there are many genera represented by single island endemics. Taking into consideration that the distance between islands is similar to the distance to the continent, most dispersal events likely occurred directly from the mainland rather than between islands. This pattern of independent colonization is further supported by the distinctiveness of the faunas of each island and by the small number of "shared endemic" species. On that basis, it has been questioned if *A. bicarinata* is truly endemic to both Príncipe and São Tomé, or if it might have been introduced to one of the islands (Gascoigne 1994b; Panisi et al. 2020), especially considering that it would have been challenging for such a large snail to disperse naturally between islands. It has been reported as an important food source since the end of the nineteenth century (Moller 1894), providing a reason for intentional introduction on one of the islands, which could be clarified using molecular techniques (Panisi et al. 2020).

Large endemic land snails are usually absent or rare on oceanic islands. Although large endemic snails are prominent in the faunas of some of the largest islands such as Madagascar and Sri Lanka, those are better interpreted biogeographically as remnants of fragmented continental faunas. Among the few examples on truly oceanic islands, the large *Pseudocampylaea lowii* (A. Férussac, 1835) of Porto Santo (Madeiran Islands) is related to the considerably smaller endemic *P. portosanctana* (G.B. Sowerby I, 1824) of the same island, and both can be regarded as products of the large in situ radiation of smaller Geomitridae since the late Tertiary on the Madeiran Islands (D. Holyoak, unpublished). The massive *A. bicarinata* endemic on the Gulf of Guinea islands, by contrast, is most certainly derived from large congeneric relatives in continental Africa. Other large Achatinidae of the islands also have their apparent affinities with relatively large-shelled continental genera of the family. Thus, the overseas dispersal of large-shelled progenitors to the island species may have been enabled by the location of the Gulf of Guinea islands within an embayment of the coast of central Africa into which large rivers flow. Zoogeographers have postulated that "rafts" of floating debris have occasionally reached the islands, presumably accounting for the endemic frogs and caecilians on the islands (Measey et al. 2007). This hypothesis could also explain the colonization of the islands by large-bodied land snails, and presumably also *Pseudoveronicella* and *Dendrolimax* slugs.

Despite frequent colonization being vital to explain the origin of many endemics, there is strong evidence that others evolved from speciation in situ, namely the *Columna* and *Streptostele* species of Príncipe and the *Petriola* and *Rhysotina* of São

Tomé. Molecular studies of better-known taxa, such as birds, amphibians, and reptiles, have revealed that independent colonization events from the continent might be the dominant pattern to explain the origin of endemic species in the archipelago (Ceríaco et al. 2017; Valente et al. 2020). Nevertheless, radiations across islands also occur (Melo et al. 2011; Bell et al. 2015) and as more molecular studies become available, our understanding of the dominant patterns may change.

Habitat Associations

Recent surveys carried out on Príncipe and São Tomé have enhanced our understanding of the terrestrial Mollusca and their habitats (Appendix). These surveys consisted of a series of observations in a range of diverse molluscan habitats (Fundação Príncipe 2019; Holyoak et al. 2020) and an additional stratified survey across three different regions and four land-use types on São Tomé (Tavares 2021). No recent surveys have taken place on Annobón, and the data available on the terrestrial Mollusca of this island consists of a few records with scant information on the habitat of each species.

On São Tomé, the presence and abundance of 33 non-seashore species were analyzed across four land-use categories (Tavares 2021), reflecting a gradient of increasing forest degradation: native forest, secondary forest, shade plantations, and non-forested areas. Non-forested areas have lower local species richness (alpha diversity) than shade plantation and secondary forest, while native forests have intermediate values. However, due to lower distinctiveness between sites (beta diversity), shade plantations have the lowest overall species richness (Appendix). Secondary forest and shade plantation show a higher average abundance than native forest and non-forested areas. According to the general patterns of richness and abundance, endemic species tend to be associated with forests, while non-endemics tend to be associated with degraded areas.

Most species on São Tomé occur in more than one land-use type. Only the endemic *O. pauper*, the native *Pseudopeas crossei*, and the introduced *Limicolaria flammea* (Fig. 16.1.8) and *L. alte* were found exclusively in non-forested areas. Twenty-one species were found only in forested areas, 18 of which were only in forests (i.e., not in shade plantantions). Ten of them occur both in secondary or native forest, half of these being endemic, all achatinids: *A. bicarinata*, both *Aporachis* species, *P. umbilicata* and *Thomea newtoni*. Five species were recorded only in secondary forest: *Gastrocopta nobrei*, *Truncatellina thomensis*, *Pupisoma dioscoricola*, *Afroditropis molleri* and *Maizania furadana*. Two species were recorded exclusively in native forest, both single-island endemics: *Nothapalus solitarius* and *Thomeomaizania gascoignei*. Thirteen species were recorded in all the four land-use types, including two introduced species, *A. marginata* and *Deroceras laeve*, and eight endemic species: all three *Petriola* species, both *Apothapsia* species, *Dendrolimax greeffi* and all three *Rhysotina* species. Most of these are widespread and abundant across habitats, as with *Apothapsia thomensis*, which is probably the most common land snail in wooded habitats on the island, and the introduced *A. marginata*, which is widespread across degraded habitats and very abundant in shade plantations and secondary forest (Panisi 2017).

Concerning altitude, 13 species were recorded across a wide altitudinal range (Appendix), from lowland (below 800 m a.s.l) to mist forests (above 1400 m a.s.l., Exell 1944). Nine species were found exclusively in lowland, 8 exclusively in montane regions (between 800 and 1400 m a.s.l.), 15 in both lowland and montane regions, and 3 in montane and mist forests. Introduced species occur mainly at lower altitudes, while endemic species richness persists across all altitudes. Thirty-seven species occur in the lowlands, including 5 introduced and 23 endemic (62% endemic). In montane regions, 39 species were recorded, including 4 introduced and 25 endemic (64%). Mist forests hold 16 species, the lowest species richness, but they have only one introduced species, *Deroceras laeve*, and 13 endemics, the highest proportion across altitudinal zones (81%).

São Tomé land snails and slugs are associated with a variety of strata (Appendix). Most species live mainly on or near the ground, namely on leaf-litter, among tree buttress roots, beneath fallen wood, under rocks, or on shell debris. Live snails often congregate on anvils of the São Tomé Thrush *Turdus olivaceofuscus* (Jones and Tye 2006), searching for calcium (Holyoak et al. 2020). Few species are found on leaves, exceptions include *A. thomensis*, *P. thomensis,* and *A. exaratus*. Some species are found in waterfall spray-zones, such as the endemic *A. hispida,* both *Pupisoma* species and other small native species.

On Príncipe, recent mollusk sampling has been less extensive and less systematic than on São Tomé, including ca 30 locations selected ad hoc across a range of habitat types (Fundação Príncipe 2019; Holyoak et al. 2020). Surveys between 2012 and 2020 have confirmed the continued presence of 30 out of the 40 non-seashore species known from Príncipe. Additional attention has been given to *A. bicarinata*, with over 100 records made between 2018 and 2020, and an ongoing monitoring and ecological study on both islands (Fauna & Flora International and Fundação Príncipe 2019; Fundação Príncipe 2019; Panisi et al. 2020).

Although the sampling effort is more limited on Príncipe, some patterns of habitat association appear broadly similar to those described for São Tomé. Sites at the transition between forested land-use types seem to hold high species richness, and non-native species seem to prefer disturbed areas, while the endemics prefer forests. At higher altitudes, species richness is low, but the proportion of endemics is high. This includes the recently described *Principicochlea tenuitesta*, which is known only from the vicinities of the highest point of the island, Pico Príncipe (Fundação Príncipe 2019; Holyoak et al. 2020).

Most species documented on Príncipe were found within leaf litter on the ground. Tree canopies were not sampled, although fallen shells have been collected from the ground. Sieving of leaf litter was only attempted for a small subset of sampling locations but revealed distinct species and may yield interesting further novelties (Holyoak et al. 2020). Live specimens, particularly those of *Gulella crystallum*, are often apparent in shell debris at Blue-breasted Kingfisher *Halcyon malimbica* anvils and empty *A. bicarinata* shells. Several species were conspicuous on understorey foliage, especially in some higher altitude sites where the endemic *P. forcati* and *P. tenuitesta* are locally abundant (Appendix).

The low densities of forest-floor snail faunas recorded on both islands, and especially on Príncipe, deserve future studies but might be linked to calcium shortages in the topsoil and leaf litter (Juřičková et al. 2008). This would explain the high concentrations of land snails at the anvil sites of the São Tomé Thrush and Blue-breasted Kingfisher.

Conservation

Habitat loss and introduced species seem to be key threats to native land snails and slugs on the oceanic islands of the Gulf of Guinea, as is the case for most animal taxa on oceanic islands (IUCN 2020), and notably for island snail species (Chiba and Cowie 2016). Habitat loss on these islands is strongly linked to agricultural expansion and intensification, including horticulture and forest gardens to supply the local markets, and export cash crops, such as cocoa, oil palm, and coffee. Additional factors linked to habitat loss include increased use of fire, logging, mining, infrastructure development to support urban and tourism expansion, livestock and expanding silviculture, with products such as oil palm wine and medicinal plants (Oyono et al. 2014).

The effect of introduced species on the native malacofauna of these islands is less well understood, but the introduction of many mammal (Dutton 1994) and plant species (Figueiredo et al. 2011) might have detrimental impacts on the general grounds that they affect ecosystem functioning. For instance, feral pigs and cows feed on understorey plants and revolve the soil, disturbing key forest habitat for some native land snail and slug species that evolved in the absence of large terrestrial animals. Introduced species might also have direct effects through predation or competition (Panisi 2017). Most introduced mollusks seem to avoid forests, where most native species occur. It is nevertheless hard to assess the effect of introduced mollusks, since it might be minimal if they have distinct habitats (Tavares 2021—Appendix), or not so minimal if they are excluding native species from the more degraded ecosystems. The fast expansion of the introduced *A. marginata* seems to be linked to the decline of *A. bicarinata*, through a process that remains poorly understood but might involve direct competition and introduced diseases (Panisi and de Lima 2022). Additionally, *A. bicarinata* is the only native land snail species that might be affected by overexploitation, as it is collected for food and traditional medicine. Despite a steep population decline on both islands (Dallimer and Melo 2010; Panisi 2017), overexploitation continues to be an issue due to the higher commercial value of each snail individual when compared to the widespread and abundant *A. marginata*, but it is currently more recognized by people than the endemic species (Panisi et al. 2022a).

The malacofauna might also be affected by pollution, given the widespread use of pesticides to prevent malaria. Agricultural chemicals might also be a problem in São Tomé, but less so in Príncipe, where the import of agricultural chemicals is limited (Ministry of Public Works, Infrastructure, Natural Resources and Environment 2019). Finally, climate change is also a potential threat, especially as many of the endemic mollusk species have restricted altitudinal ranges and specific habitat associations (Holyoak et al. 2020—Appendix).

Considering that at least some of these threats might affect whole populations, either quickly in the near future or more pervasively in the longer term, many of the mollusks endemic to Príncipe, São Tomé, and Annobón might go extinct due to anthropogenic factors, even if specific conservation measures are implemented. This has been the case in many other oceanic islands across the globe (Chiba and Cowie 2016), and notably in the Pacific (Lydeard et al. 2004). Therefore, it is vital that we act quickly to protect these species. Protecting the remaining native forest and additional vital habitats for native fauna is the single most important measure to secure the future of these species. In this regard, all three islands have significant proportions of their territory dedicated to biodiversity conservation (UNEP-WCMC and IUCN 2020), which are predicted to expand soon (BirdLife 2019), even though enforcement of existing protected areas remains weak (Lima et al. 2017). Additionally, it is also vital to improve our understanding of more pervasive threats, such as invasive species and climate change, and our knowledge of the ecology of native mollusk species, which will be key to design species-specific conservation measures.

Despite the remarkable number of endemic species, many remain notoriously scarce in collections (Holyoak et al. 2020; Tavares 2021), and *A.bicarinata* is the only endemic species listed as threatened for the islands (IUCN 2020). It is currently classified as Vulnerable, although an updated assessment might result in uplisting to Endangered (Panisi et al. 2022b). *T. thomensis*, *P. umbilicata,* and *T. newtoni* have also been assessed but were all classified as Data Deficient (IUCN 2020). All these species were assessed in 1996, and an update is certainly in order, considering that recent surveys have greatly improved our knowledge on the taxonomy, ecology, and threats to these species. Even if most species are to remain "Data Deficient," the information available to support classification has greatly improved, which might improve recognition of the importance of the malacofauna of these islands, and help identify the species that are at greater risk of extinction.

Concluding Remarks

Recent surveys (Holyoak et al. 2020) have added 13 newly described species, 6 microgastropods and 6 introduced species to the STP list of terrestrial mollusks. They have also enabled confirmation of old records, such as the continued presence of *Gulella joubini* on Príncipe, which was hitherto known only from its 1912 holotype. Five of the recently named species are known from unique specimens. Two undescribed forms that will be new to Príncipe require the collection of complete adult specimens. Based on these considerations, future research will undoubtedly yield novelties and should focus on overlooked parts of the indigenous fauna, namely microgastropods, Annobón, and undersampled regions and habitats, especially those that are less accessible.

Almost all taxonomy on the land Mollusca of the oceanic islands of the Gulf of Guinea is based on conventional comparative studies of shell form, sometimes supplemented by genital anatomy. As a result, problems of species identification and delimitation have been frequent. Some persist due to insufficient information on nominal species from the African continent, where mollusk collections are often even sparser than from these islands. DNA sequence data are often valuable to elucidate molluscan phylogenies. For instance, genetic data have led to the inclusion of the formerly recognized family Subulinidae in the broadly defined Achatinidae (Fontanilla et al. 2017). However, DNA sequencing has not yet been widely used on species from tropical Africa, where it would surely help clarify the phylogenetic and biogeographical relationships of this rich and complex malacofauna.

Future research should also focus on the ecology of endemic species, which will be vital to support conservation initiatives. The ongoing decline and current scarcity of charismatic big species, such as *A. bicarinata* on São Tomé and Príncipe and the genus *Columna* on Príncipe are starting to be recognized as conservation priorities. For example, *A. bicarinata* has been widely used as a flagship for the protection of the unique malacofauna of São Tomé and Príncipe, and even for the conservation of their endemic-rich forests (Panisi et al. 2020; Panisi et al. 2022b). Still, information on many other endemic species remains scant. The unique malacofauna of Príncipe, São Tomé, and Annobón has been little studied for decades, but we hope that recent findings will promote a new wave of curiosity about this exceptional diversity and that it is translated into practical measures for the protection of the endemic species and their habitats.

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Appendix

Checklist of terrestrial and seashore Mollusca species recorded from the Gulf of Guinea oceanic islands

Higher Taxonomy	*Species*	P	ST	A	IUCN	Altitude (m)	Strata	NF	SF	SP	NN
Family **Cyclophoridae** J.E. Gray, 1847 or **Maizaniidae** Tielecke, 1940											
Afroditropis Bequaert & Clench, 1936	*molleri* (Nobre, 1886)	–	E	–	NE	860–885	–	0	+	0	0
Cyathopoma W. & H. Blanford, 1861	*inexspectata* G. Holyoak & D. Holyoak, 2020	E	–	–	NE	216	L	1	0	0	0
Maizania Bourguignat, 1889	*furadana* G. Holyoak & D. Holyoak, 2020	–	E	–	NE	240	P, L, R	0	2	0	0
Thomeomaizania Bequaert & Clench, 1936	*gascoignei* G. Holyoak & D. Holyoak, 2020	–	E	–	NE	1300–1416	P, L	2	0	0	0
	vandellii (Nobre, 1886)	–	E	–	NE	96–1415	L, R, S	1	2	0	1
Family **Truncatellidae** J.E. Gray, 1840											
Truncatella Risso, 1826	*clathrus* R.T. Lowe, 1832	–	N	–	NE	2	L, H	0	0	0	+
	rostrata Gould, 1847	N	–	–	NE	–	H	0	0	0	+
Family **Assimineidae** H. Adams & A. Adams, 1856											
Assiminea J. Fleming, 1828	*sp.*	N	N	–	NE	–	H	0	0	0	+
Family **Ellobiidae** L. Pfeiffer, 1854											
Melampus Montfort, 1810	*flavus* (Gmelin, 1791)	N	N	–	NE	–	H	0	0	0	+
	pusillus (Gmelin, 1791)	N	N	–	NE	–	H	0	0	0	+
	sp.	–	N	–	NE	2	H	0	0	0	+
Pedipes A. Férussac, 1821	*afer* (Gmelin, 1791)	–	N	–	NE	–	H	0	0	0	+
	sp.	N	–	–	NE	2	H	0	0	0	+
Family **Onchidiidae** Rafinesque, 1815											
Onchidella J.E. Gray, 1850	*sp.*	–	N	–	NE	–	H	0	0	0	+
Family **Veronicellidae** J.E. Gray, 1840											
Laevicaulis Simroth, 1919	*alte* (A. Férussac, 1822)	I	I	–	NE	24–1159	L, S	0	+	0	1
Pseudoveronicella Germain, 1908	*forcarti* D. Holyoak, G. Holyoak & F. Sinclair, 2020	E	–	–	NE	353–906	P	2	0	0	0
	liberiana (Gould, 1850)	N	N	–	NE	22–1028	P, L, R, S	0	1	4	2

(continued)

Higher Taxonomy	*Species*	P	ST	A	IUCN	Altitude (m)	Strata	NF	SF	SP	NN
	thomensis (Girard, 1893)	–	E	–	NE	160–1418	P, L, W	1	3	1	0
Family **Achatinidae** Swainson, 1840											
Archachatina Albers, 1850	*bicarinata* (Bruguière, 1792)	E	E	–	VU	43–1266	L, W, R	2	1	0	0
	marginata (Swainson, 1821)	I	I	–	NE	6–1327	L, W, R, S	3	5	5	3
Atopocochlis Crosse & Fischer, 1888	*exaratus* (O.F. Müller, 1774)	–	E	–	NE	101–928	P	+	1	1	0
Columna Perry, 1811	*columna* (O.F. Müller, 1774)	E	–	–	NE	255–386	–	1	0	0	0
	hainesi L. Pfeiffer, 1856	E	–	–	NE	–	–	–	–	–	–
	leai Tryon, 1866	E	–	–	NE	58	–	0	0	+	0
Lignus J.E. Gray, 1834	*alabaster* (Rang, 1831)	E	–	–	NE	24–386	P	+	+	+	0
Limicolaria Schumacher, 1817	*flammea* (O.F. Müller, 1774)	–	I	–	NE	69–500	L, R, S	0	0	0	1
Ischnoglessula Pilsbry, 1919	*fuscidula* (Morelet, 1858)	N	N	–	NE	–	–	–	–	–	–
Striosubulina Thiele, 1933	*striatella* (Rang, 1831)	N	N	N	NE	6–1490	L, W, R, S	2	5	5	5
Subulina Beck, 1837	*feai* Germain, 1912	E	–	–	NE	–	–	–	–	–	–
	moreleti Girard, 1893	E	–	–	NE	194–860	–	+	+	0	0
	newtoni Girard, 1893	E	–	–	NE	281–860	–	+	0	0	0
Cecilioides A. Férussac, 1814	sp.	–	N	–	NE	–	–	–	–	–	–
Aporachis D. Holyoak, 2020	*dohrni* (Greeff, 1882)	–	E	–	NE	959–1490	P, L, R	2	1	0	0
	hispida (Greeff, 1882)	–	E	–	NE	885–1416	R, F	+	1	0	0
Bocageia Girard, 1893	*lotophaga* (Morelet, 1848)	E	–	–	NE	–	–	–	–	–	–
Nothapalus von Martens, 1897	*solitarius* G. Holyoak & D. Holyoak, 2020	–	E	–	NE	1300	–	+	0	0	0
Petriola Dall, 1905	*clavus* (L. Pfeiffer, 1864)	–	E	–	NE	124–1490	L, W, R, S	5	4	3	2
	marmorea (Reeve, 1850)	–	E	–	NE	160–1490	L, W, R, S	3	4	3	1
	monticola (Morelet, 1866)	–	E	–	NE	236–1477	L, R, S	3	3	1	1
Pyrgina Greeff, 1882	*umbilicata* Greeff, 1882	–	E	–	DD	160–1418	L, W, R	3	3	0	0

(continued)

Higher Taxonomy	*Species*	P	ST	A	IUCN	Altitude (m)	Strata	NF	SF	SP	NN
Thomea Girard, 1893	*newtoni* Girard, 1893	–	E	–	DD	181–1418	L	1	+	0	0
Allopeas H. B. Baker, 1935	*gracile* (T. Hutton, 1834)	–	–	I	NE	–	–	–	–	–	–
Opeas Albers, 1850	*dohrni* (Girard, 1893)	E	E	E	NE	–	–	–	–	–	–
	greeffi (Girard, 1893)	E	E	E	NE	240	–	+	0	0	0
	hannense (Rang, 1831)	–	N	–	NE	12–678	R	0	+	0	1
	pauper (Dohrn, 1866)	E	E	–	NE	74	R	0	0	0	1
	subpauper Germain, 1912	E	–	–	NE	–	–	–	–	–	–
Pseudopeas S. Putzeys, 1899	*crossei* (Girard, 1893)	N	N	–	NE	240–1114	–	+	0	0	+
Thyrophorella Girard, 1895	*thomensis* Greeff, 1882	–	E	–	DD	323–1490	P, L, S	3	1	0	1
Family **Micractaeonidae** Schileyko, 1999											
Micractaeon Verdcourt, 1993	*koptawelilense* (Germain, 1934)	–	N	–	NE	885–1290	L, R, F	+	2	0	0
Family **Streptaxidae** Gray, 1860											
Gulella L. Pfeiffer, 1856	*azeitonae* D. Holyoak, G. Holyoak & F. Sinclair, 2020	E	–	–	NE	194	–	0	+	0	0
	crystallum (Morelet, 1848)	E	–	–	NE	51–860	–	+	+	+	0
	girardi (Kobelt, 1904)	–	–	E	NE	–	–	–	–	–	–
	insularis (Girard, 1894)	–	–	E	NE	–	–	–	–	–	–
	joubini (Germain, 1912)	E	–	–	NE	353–372	–	+	0	0	0
	nemoralis (Germain, 1915)	–	–	E	NE	–	–	–	–	–	–
	sorghum (Morelet, 1848)	E	–	–	NE	–	–	–	–	–	–
Sphinctostrema Girard, 1894	*annobonensis* (Girard, 1894)	–	–	E	NE	–	–	–	–	–	–
	bocagei (Girard, 1894)	–	–	E	NE	–	–	–	–	–	–
Streptostele Dohrn, 1866	*abbreviata* D. Holyoak, G. Holyoak & F. Sinclair, 2020	E	–	–	NE	414		+	0	0	0
	fastigiata (Morelet, 1848)	E	–	–	NE	24–860	L	2	2	2	0
	folini (Morelet, 1858)	E	–	–	NE	24–194	L	2	2	2	0
	truncata Germain, 1915	–	–	N	NE	–	–	–	–	–	–
Streptostele (?) Dohrn, 1866	*feai* Germain, 1912	E	–	–	NE	–	–	–	–	–	–

(continued)

Higher Taxonomy	*Species*	P	ST	A	IUCN	Altitude (m)	Strata	NF	SF	SP	NN
	moreletiana (Dohrn, 1866)	E	E	–	NE	–	–	–	–	–	–
Tomostele Ancey, 1885	*musaecola* (Morelet, 1860)	–	I	–	NE	74–181	R	0	+	0	1
Family **Punctidae** Morse, 1864											
Punctum Morse, 1864	*camerunense* de Winter, 2017	–	N	–	NE	1254–1292	–	+	+	0	0
Family **Charopidae** Hutton, 1884											
Trachycystis Pilsbry, 1893	*iredalei* Preston, 1912	–	N	–	NE	1257–1288	–	+	+	0	0
Family **Succineidae** Beck, 1837											
Quickia Odhner, 1950	*concisa* (Morelet, 1848)	N	N	N	NE	6–678	P, L	0	+	1	1
Family **Cerastidae** Wenz, 1923											
Gittenedouardia Bank & Menkhorst, 2008	*burnayi* (Dohrn, 1866)	N	N	–	NE	5–398	P	+	+	1	0
	eminula (Morelet, 1848)	N	N	–	NE	24–1477	P, L	1	1	1	1
Family **Gastrocoptidae** Pilsbry, 1918											
Gastrocopta Wollaston, 1878	*annobonensis* (Girard, 1894)	–	–	E	NE	–	–	–	–	–	–
	nobrei (Girard, 1893)	–	E	–	NE	6–126	L, W	0	+	0	0
Family **Truncatellinidae** Steenberg, 1925											
Truncatellina R.T. Lowe, 1852	*thomensis* D. Holyoak & G. Holyoak, 2020	–	E	–	NE	1254–1292	–	0	+	0	0
Family **Valloniidae** Morse, 1864											
Pupisoma Stoliczka, 1873	*dioscoricola* (C.B. Adams, 1845)	–	N	–	NE	197–1292	R, F	0	+	0	0
	harpula (Reinhardt, 1886)	–	N	–	NE	885–1292	R, F	+	+	0	0
Family **Agriolimacidae** H.Wagner, 1935											
Deroceras Rafinesque, 1820	*laeve* (O.F. Müller, 1774)	–	I	–	LC	254–1402	P, L, R, S	1	1	1	2
Family **Euconulidae** H.B. Baker, 1928											
Afroconulus Van Mol & van Bruggen, 1971	*roseus* D. Holyoak & G. Holyoak, 2020	–	E	–	NE	530–1353	P	0	1	0	1
Afropunctum F. Haas, 1934	*seminium* (Morelet, 1873)	N	N	–	NE	236–1400	P, R, F	2	2	0	0
Family **Helicarionidae** Bourguignat, 1877											
Apothapsia D. Holyoak & G. Holyoak, 2020	*moreleti* (Germain, 1915)	–	E	–	NE	22–1244	P, L	1	1	1	1
	thomensis (Dohrn, 1866)	–	E	–	NE	6–1402	P, L, W, R	5	5	5	4
Family **Urocyclidae** Simroth, 1889											
Dendrolimax Heynemann, 1868	*greeffi* Simroth, 1889	–	E	–	NE	22–1343	P, L	+	1	1	1

(continued)

Higher Taxonomy	*Species*	P	ST	A	IUCN	Altitude (m)	Strata	NF	SF	SP	NN
	heynemanni Heynemann, 1868	E	–	–	NE	220–498	P	+	0	0	0
	newtoni A. Ortiz de Zaráte & Alvarez, 1960	–	–	E	NE	–	–	–	–	–	–
Rhysotina Ancey, 1887	*hepatizon* (Gould, 1845)	–	E	–	NE	153–1477	L, W, R, S	4	3	2	2
	sublaevis G. Holyoak & D. Holyoak, 2016	–	E	–	NE	22–1199	L, R	1	3	3	2
	welwitschi (Morelet, 1866)	–	E	–	NE	54–1323	L, W, R, S	3	3	3	3
Africarion Godwin-Austen, 1883	*dumeticola* (Dohrn, 1866)	E?	–	–	NE	–	P	–	–	–	–
Principicochlea D. Holyoak & G. Holyoak, 2020	*tenuitesta* D. Holyoak, G. Holyoak & F. Sinclair, 2020	E	–	–	NE	860	P	+	0	0	0
Principitrochoidea D. Holyoak & G. Holyoak, 2020	*aglypta* (Dohrn, 1866)	E	–	–	NE	193–344	L	+	+	0	0
	convexa G. Holyoak, D. Holyoak & F. Sinclair, 2020	E	–	–	NE	24–375	P	+	+	0	+
	folini (Morelet, 1848)	N	–	–	NE	24–216	L	+	+	0	+
Thomithapsia D. Holyoak & G. Holyoak, 2020	*bomsucessica* G. Holyoak & D. Holyoak, 2020	–	E	–	NE	418–1300	L, W	+	1	0	+
Thomitrochoidea D. Holyoak & G. Holyoak, 2020	*trindadensis* D. Holyoak & G. Holyoak, 2020	–	E	–	NE	22–900	P	+	1	1	0
Trochozonites Pfeffer, 1883	*adansoniae* (Morelet, 1848)	–	–	N	NE	–	–	–	–	–	–
Family **Helicidae** Rafinesque, 1815											
Cornu Born, 1778	*aspersum* (O.F. Müller, 1774)	–	I	–	LC	821–1150	P	0	0	1	2

Species are listed as endemic (E), presumed autochthonous or native non-endemics (N) or introduced (I) in the island (s) where they occur: Príncipe (P), São Tome (ST), and Annobón (A). See taxonomic comments in Holyoak et al. (2020). Global conservation status is reported according to the IUCN Red List of Threatened Species: Not Evaluated (NE), Data Deficient (DD), Vulnerable (VU), or Least Concern (LC). When available, habitat associations are provided, namely: altitudinal ranges, strata where live specimens were collected [Live plant (P); Plant litter (L); Dead wood (W); Rocks (R); Bare soil (S); Seashore (H); Waterfall spray-zone (F)], and relative abundance [Uncertain (+); No records (0); Rare (1); Not common, but locally abundant (2); Common (3); Abundant (4); Very abundant (5)] for each land-use category [Native forest (NF); Secondary forest (SF); Shade plantation (SP); Non-forested areas (NN)]

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Chapter 17
The Fishes of the Gulf of Guinea Oceanic Islands

Luis M. da Costa, Hugulay Albuquerque Maia, and Armando J. Almeida

Abstract This chapter reviews the current knowledge of the marine (including deep-sea species) and freshwater fishes of the Gulf of Guinea oceanic islands. Some biogeographic and conservation considerations are also presented. A total of 1045 species are likely present in the region, including 107 Elasmobranchii (37 confirmed, 65 potential, and 5 erroneous), one confirmed Holocephali, and 937 Actinopteri species (515 confirmed, 385 potential, 32 erroneous, and 5 questionable). Most of the coastal species are shared with the surrounding African continental shelf, while several species are amphi-Atlantic (present in both sides of the Atlantic Ocean), and some species have sister-species in the western Atlantic. A total of 15 species are endemic to the region, and 2 are introduced. Further studies are still needed to better understand the ichthyofauna of the Gulf of Guinea oceanic islands and help policymakers better define conservation and protection plans.

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Introduction

The Gulf of Guinea Oceanic Islands (GGOI), Príncipe, São Tomé, and Annobón, are oceanic islands located in the Tropical Eastern Atlantic. The GGOI are part of the Cameroon Volcanic Line, an intraplate basalt in the ocean-continent boundary region, ranging over 1600 km (Burke 2001; Elsheikh et al. 2014; Belay et al. 2019). All three GGOI are ideally located for fish diversity: close enough to the African continent to host typical shelf region fish species, but also with a narrow platform separated by seas with over 1500 m depth that provide coastal habitat to several fishes. In addition, several currents contribute to coastal upwelling (Bakun 1978; Djakouré et al. 2017) and biological productivity (Binet 1997; Ukwe et al. 2006) for highly migratory offshore and deep-sea fish species. The GGOI are at the crossroads of three major currents: one incoming (from west to east), the Guinea Current (GC), and two outgoing (from east to west), the South Equatorial Current (SEC) and the Gabon-Congo Undercurrent (Djakouré et al. 2014). The GC, sourcing from the combination of the North Equatorial Countercurrent and the Canary Current, flows east along the western coast of Africa (from Sierra Leone to Nigeria) with slight seasonal flow variations in direction and velocity, salinity, and sea-surface temperature (Richardson and Reverdin 1987; Odekunle and Eludoyin 2008; Djakouré et al. 2014, 2017). The northern part of the SEC borders the GC and flows westward. The Equatorial Undercurrent (EUC) also flows eastward below the SEC (Djakouré et al. 2014; Herbert et al. 2016; Houndegnonto et al. 2021; see also Ceríaco et al. 2022a). A Guinea Undercurrent (GUC) is also present, flowing eastward, in deeper water along the coast. The GGOI are influenced by all these currents in the "southern alternance region," dominated by strong seasonal contrasts and with influxes of equatorial upwelling (Le Lœuff and Cosel 1998). Water salinity, temperature, and turbidity are also influenced by major freshwater river discharges (Congo and Niger basins) and resulting plumes (Alory et al. 2021; Houndegnonto et al. 2021; Ceríaco et al. 2022a). The combination of these characteristics, along with the upwelling and high biological productivity, contribute to the occurrence of a spectacular fish diversity.

The marine ichthyofauna of the Gulf of Guinea, including the continental shelf, continental islands (Bioko), and oceanic islands, presents a remarkable level of endemism (approximately 20%), but many species are still poorly known and studied (Jones 1994). The endemism of reef fish species reaches about 65% in some of these areas, indicating their high degree of isolation (Jones 1994). By contrast, only three freshwater fish species (all non-indigenous) are recorded for the islands of Príncipe, São Tomé, and Annobón, all showing tolerance to salinity and capable of dispersal among the oceanic islands (Jones 1994). The GGOI are part of the Guinea Current Large Marine Ecosystem (GCLME), extending from Guinea Bissau to Angola (to the northern seasonal limit of the Benguela Current) and covering 16 countries' Exclusive Economic Zones (Ukwe et al. 2006). Because of its bathymetry, chemistry, hydrography, and trophodynamics, the GCLME is among the most productive coastal and offshore waters in the world with rich fishery resources, an important reservoir of marine biological diversity, and excellent potential for tourism (Ukwe et al. 2003).

Most of the fish species recorded from the GGOI are also present in other parts of the Gulf of Guinea, with few species endemic to the islands, and several species with amphi-Atlantic or circum-global distributions. As of 2019, a total of 268 coastal fish species have been recorded in the GGOI (see "Species Diversity" section) with about 12% of the species (28) reported as endemic to the Gulf of Guinea, and a few of these only observed in São Tomé and Príncipe, such as *Clepticus africanus* Heiser, Moura and Robertson, 2000, and *Scorpaena annobonae* Eschmeyer, 1969 (Wirtz et al. 2007; Wirtz 2017). This low level of endemism is likely a consequence of the vagility of marine fishes as zooplankton and the proximity of the islands to the African continent (Krakstad et al. 2010).

The current chapter presents a brief overview of the marine and freshwater ecosystems present in the GGOI, the current knowledge of marine and freshwater fish species, biogeography and evolution, and finally conservation. An updated taxonomic checklist of marine (coastal, offshore, and deep-water) and freshwater species is presented, with revised inventories for coastal and reef fish species.

Brief History of Ichthyology Research

In 1871, the Portuguese naturalist Félix António Brito Capello (1828–1879) published the first list of fishes accessioned at the Lisbon Museum collection. This list, in three parts, includes specimens from the Portuguese islands of Madeira and Azores, and from its overseas territories, including São Tomé and Príncipe (Capello 1871a, b, 1872). After his death, António Roberto Pereira Guimarães (?–1889?) continued Capello's analysis of the material housed at the Lisbon Museum and published two additional papers on the topic (Guimarães 1882, 1884). Later, the Portuguese zoologist Balthazar Osório (1855–1926) presented the first list focusing on fish species from São Tomé and Príncipe, mostly based on the specimens collected by the Portuguese naturalists Adolfo Möller (1842–1920) and Francisco Newton (1864–1909) (Osório 1891, 1892, 1893, 1894, 1895a, 1898, 1906), and from Annobón (Osório 1895b), with several descriptions of species and original information. After a gap of about five decades, Frade (1955) and Frade and Correia da Costa (1956, 1957) reported new records based on pelagic fisheries species (see also Almeida and Alves 2019). Later, from 1961 to 1987, several international scientific expeditions provided complementary information (Arnoult et al. 1966; Bayer et al. 1966; Blanc et al. 1968; Iwamoto 1970; see Afonso et al. 1999 and Ceríaco et al. 2022b for a detailed bibliography), with rare studies reporting new records (Thys van den Audenaerde and Tortonese 1974). Only during the late twentieth and early twenty-first centuries, several publications focused on São Tomé or Príncipe and published new species description and records (e.g., Afonso et al. 1999; Wirtz et al. 2007; Rocha et al. 2012; Almeida and Alves 2017, 2019; Iwamoto and Wirtz 2018). Complementarily, several reports and guides estimating species occurrence around the Gulf of Guinea Islands were published by FAO and others (e.g., Allen 1985; Carpenter and De Angelis 2016a–c; Almeida and Biscoito 2019; Sutton et al. 2020).

Marine and Freshwater Ecosystems

A marine ecosystem can be defined as the geographic area (of any size), comprised of communities of organisms and their environment, where biological and energy interactions are greater within than with adjacent ecosystems (Zhao and Costello 2020). This biological system is characterized by two factors: the biotic (e.g., plants, animals, microbes) and abiotic (e.g., sunlight, oxygen, dissolved nutrients, depth, temperature). These components influence the dynamics of natural communities at different spatial scales, from global to local. Marine ecosystems of the GGOI are underwater equivalent of tropical forests. Both natural systems are complex and three-dimensional. Furthermore, they have an impressive variety of habitats from the intertidal zone to the abyssal region (Laborel 1974).

The three oceanic islands (Príncipe, São Tomé, and Annobón) that make up this system have different geological ages and the steep underwater relief results in a relatively small, shallow platform (Cowburn 2018; Maia et al. 2018a). The underwater areas of the island seascapes are mainly dominated by volcanic rocky reefs with limited coral growth (Laborel 1974; Quimbayo et al. 2019). Ecological studies carried out in recent years have described a variety of marine habitats. For example, on Príncipe Island, Cowburn (2018) mapped four subtidal habitats and four coastal habitats along the island. In addition, a recent study investigated the role of four different reef microhabitats in shaping biological interactions of fishes (Canterle et al. 2020). Regarding São Tomé Island, the scenario is very similar to that of Príncipe. Maia et al. (2018a) characterized reef environments on this island based on the composition of the benthic community and found a diversity of habitats between the ranges of 10–30 m deep, including a new habitat in the deep reef north of the island (Morais and Maia 2017).

Major Aquatic Ecosystems in the Gulf of Guinea Oceanic Islands

Estuaries (Fig. 17.1, 1): An estuary is a coastal zone sheltered from extreme weather where oceans meet rivers, and nutrients and salts from the ocean mix with those from the river (Cameron and Pritchard 1963). As a result, estuaries are among the most

Fig. 17.1 Gulf of Guinea oceanic island aquatic ecosystems: (**1**) Estuary; (**2**) Mangrove forest; (**3–5**) Coral reefs; (**6**) Coral reefs and seagrass; (**7**) Open and deep-sea ocean; (**8**) River. Photo credits: (**1**, **6–8**) Hugulay Albuquerque Maia, (**2**) Luis MP Ceríaco, (**3–5**) Luiz Rocha

productive places on Earth and support many life forms. Because they are located where rivers join the ocean, estuaries have traditionally supported many human communities and activities like fishing, shipping, and transportation. Some of the larger rivers flowing from the islands form brackish lagoons, usually bounded at the seaward edge by sand banks that only submerge during the highest tides (Cowburn 2018). These lagoons appear to be an important habitat for some resident fish species (e.g., *Periophthalmus barbarus* (Linnaeus, 1766)) and a nursery area for reef fish species (e.g., *Lutjanus agennes* Bleeker, 1863; *Caranx hippos* (Linnaeus, 1766)), crustaceans, molluscs, and other marine life, probably due to the concentration of nutrients in these areas.

Mangrove Forests (Fig. 17.1, 2): Mangroves are considered blue carbon ecosystems because they are more efficient at absorbing and storing large amounts of carbon compared to terrestrial ecosystems (Mcleod et al. 2011). Until 2010 this habitat was mentioned in the literature as present only on the island of São Tomé (Spalding et al. 2010) but more recently, small extensions on Príncipe Island have been identified. Haroun et al. (2018) provided updated information about the flora and fauna, and environmental, conservation and management issues related to mangroves present along the coasts of these islands.

Coral Reefs (Fig. 17.1, 3–6): Despite crystal-clear waters and optimum temperature for coral development, the GGOI do not present a homogeneous matrix of coral reefs, but instead exhibit more complex microhabitats spread in their rocky and biogenic reefs (Maia et al. 2018a). These habitats are composed of some key benthic organisms, including epilithic algal matrix, calcareous algae, coralline algae (that form small ~5 cm diameter globular structures over mobile substrates), macroalgae, hard corals, sponges, zoanthids and gorgonians (Laborel 1974; Maia et al. 2018a). Rocky reefs and solid shores occur where the volcanic basalt bedrock is exposed (Cowburn 2018). The seagrass *Halodule wrightii* Ascherson, 1868 was found along the coast of São Tomé and Príncipe Islands (Alexandre et al. 2017). No data are available for Annobón Island.

Open and Deep-Sea Ocean (Fig. 17.1, 7): Open ocean ecosystems vary widely as the depth of the ocean changes. At the surface of the ocean (the euphotic zone), the ecosystem receives plenty of light and oxygen and thus is fairly warm and supports many photosynthetic organisms. Many of the organisms that we associate with marine ecosystems, such as whales, dolphins, cephalopods, and sharks, live in the open ocean. As the depth of the ocean increases, it gets darker, colder, and less oxygen is available. Organisms living in deep-sea ecosystems within the dysphotic and aphotic zones have unusual adaptations that help them survive in these challenging environments. Some organisms have extremely large mouths that allow them to catch whatever nutrients fall from shallower ocean depths. Others get their energy via the chemosynthesis of chemicals from hydrothermal vents. Although the underwater geomorphology of the GGOI is known, it is thought that they harbor some of the least known tropical reefs in the world. Underwater forests in mesophotic reefs are known from the northwest of São Tomé Island (Morais and Maia 2017) that are dominated by black corals between 30 and 50 m depth.

Streams and Rivers (Fig. 17.1, 8): The hydrographic structure of the GGOI is radial, from the central mountains to the shore, resulting in numerous streams and small rivers (up to 27 km length) (e.g., in São Tomé: Ió Grande, Caué, Mussacavu, Quija, Rio do Ouro, Contador; in Príncipe: Rio Papagaio; in Annobón: A Bobo; see

Ceríaco et al. 2022a) or crater-lakes (e.g., in São Tomé: Lagoa Amélia; in Annobón: Lago A Pot). The river network is well distributed around the islands, entering the sea by creating small estuarine habitats (12 mangroves in São Tomé and 3 in Príncipe) or small waterfalls or cascades. Several small inland lagoons are also distributed over the islands. These habitats host the fishes *Eleotris vittata* Duméril, 1861, *Sicydium bustamantei* Greeff, 1884, and *Aplocheilichthys spilauchen* (Duméril, 1861). Several aquatic invertebrates also inhabit freshwater habitats, including GGOI endemics such as the snail *Neritina manoeli* (Dohrn, 1866), or the crabs *Potamonautes principe* Cumberlidge, Clark and Baillie, 2002, *Potamonautes saotome* Cumberlidge and Daniels, 2018, and *Potamonautes margaritarius* (Milne-Edwards, 1869) (Cumberlidge et al. 2002; Allen et al. 2011; Cumberlidge and Daniels 2018).

Species Diversity

To compile an updated taxonomic checklist of the marine (coastal, offshore, and deep-water) and freshwater fish species occurring in the GGOI, we reviewed the bibliography. This included historical and recent inventories and taxonomic studies (Osório 1891, 1892, 1893, 1894, 1895a, b, 1898, 1906, 1917; Fowler 1936a, b; Frade 1955; Frade and Correia da Costa 1956, 1957; Arnoult et al. 1966; Bayer et al. 1966; Blanc et al. 1968; Thys van den Audenaerde and Tortonese 1974; Afonso et al. 1999; Pezold et al. 2006; Fricke 2007; Wirtz et al. 2007; Kovačić and Schliewen 2008; Schliewen and Kovačić 2008; Rocha et al. 2012; Félix et al. 2016; Reiner and Wirtz 2016; Vasco-Rodrigues et al. 2016; Wirtz and Iwamoto 2016; Almeida and Alves 2017, 2019; Fricke and Wirtz 2017; Tuya et al. 2017; Wirtz 2017; Iwamoto and Wirtz 2018) as well as general reports and species revisions on the ichthyofauna of the eastern Atlantic Ocean (Compagno 1984a, b, 2001; Allen 1985; Nakamura 1985; Whitehead 1985; Whitehead et al. 1988; Carpenter and Allen 1989; Heemstra and Randall 1993; Nakamura and Parin 1993; Nielsen et al. 1999; Krakstad et al. 2010; Ebert 2015; Carpenter and De Angelis 2016a–c; Last et al. 2016; Vasco-Rodrigues et al. 2018; Parenti and Randall 2020; Sutton et al. 2020). These later sources allowed us to include deep-sea fishes (mostly Holocephali and Elasmobranchii) and large pelagic species that likely occur in waters around the GGOI.

In addition, we also compiled a list of species that may occur in the waters of the GGOI, based on known occurrences in the Gulf of Guinea. Therefore, we searched for voucher records in databases listing international natural history museum specimens (e.g., FishNet2 2021; Froese and Pauly 2021; GBIF 2021; iDigBio 2021; OBIS 2021) or other published references. Classification, authority and date follow Fricke et al. (2021), and family arrangement follows Van der Laan et al. (2014). We also list several questionable and erroneous records, which were verified by us against specimens in natural history museum collections or published data. Common names are mostly those adopted by the Food and Agricultural Organization of the

United Nations (Carpenter and De Angelis 2016a–c), FishBase (Froese and Pauly 2021) or provided by the original species descriptions.

The compiled full list contains 1045 species (Appendix). Of these, 553 species are confirmed to occur in the GGOI, including 515 Actinopteri distributed in 39 orders (141 families), 37 Elasmobranchii in six orders (17 families), and one Holocephali. The 450 potentially occurring species consist of 385 Actinopteri (30 orders, 109 families) and 65 Elasmobranchii (10 orders, 28 families). Additionally, 32 Actinopteri and five Elasmobranchii previously reported for these islands are here considered as erroneous and five records of Actinopteri are questionable.

Focusing exclusively on the 553 confirmed species, Elasmobranchii (elasmobranchs: sharks, rays, skates, and wedgefishes) accounts for 6.7% (37 species) of the diversity, Holocephali (chimaeras) for 0.2% (one species), and Actinopteri (Actinopterygians: bony or ray-finned fishes) for 93.1% (515 species). A total of 46 orders and 159 families were recorded, with the richest families being Gobiidae (25 species), Carangidae (23), Serranidae (22), Stomiidae (19), and Myctophidae (18—Table 17.1).

Elasmobranchii

Among the Elasmobranchii, 37 species of sharks and batoid fishes (wedgefishes and rays) are confirmed to occur in the GGOI. Sharks, belonging to three orders (Carcharhiniformes, Lamniformes, Orectolobiformes), account for 45.9% (17 species), while rays, belonging to two orders (Myliobatiformes, Torpediniformes), account for 51.4% (19 species) of Elasmobranchii diversity. Wedgefishes, order Rhinopristiformes are represented by a single species (2.7%). The most speciose orders are Myliobatiformes, with 17 species (46%), followed by Carcharhiniformes with 12 species (32.4%). A total of 17 families are listed, with Carcharhinidae, Dasyatidae, and Mobulidae presenting the highest number of species, with 21.6% (8), 18.9% (7), and 10.8% (4), respectively.

The first record of African wedgefish, *Rhynchobatus luebberti* Ehrenbaum, 1915, for São Tomé (Reiner and Wirtz 2016) deserves a special highlight. This species is Critically Endangered (CR—Kyne and Jabado 2019), and has a limited Eastern Tropical Atlantic range distribution, from Mauritania to Congo (Carpenter and De Angelis 2016a). The Scalloped hammerhead shark, *Sphyrna lewini* (Griffith and Smith, 1834), and Sand tiger shark, *Carcharias taurus* Rafinesque, 1810, records from the GGOI (with the exception of Annobón) are also noteworthy as both species are also assessed as CR (Rigby et al. 2021). The iconic Whale shark, *Rhincodon typus* Smith, 1828, assessed as Endangered (EN—Pierce and Norman 2016), was observed in 2015 around São Tomé and the Gulf of Guinea (Vasco-Rodrigues et al. 2016). The species presents a circumtropical distribution with high suitability habitat in the eastern Atlantic (around Gabon, Congo, and Equatorial Guinea) (Sequeira et al. 2014). Recently, a shark specimen captured by locals had several features attributable to Tiger shark, *Galeocerdo cuvier* (Péron and Lesueur, 1822), a Near

Table 17.1 Classification and diversity of the confirmed Gulf of Guinea oceanic islands fish fauna. Taxonomic arrangement follows Van der Laan et al. (2014)

Class	Order	Families	Genera	Species
Elasmobranchii	Orectolobiformes	2	2	2
	Lamniformes	3	3	3
	Carcharhiniformes	4	8	12
	Torpediniformes	1	2	2
	Rhinopristiformes	1	1	1
	Myliobatiformes	6	11	17
Holocephali	Chimaeriformes	1	1	1
Actinopteri	Elopiformes	2	2	3
	Albuliformes	1	1	1
	Notacanthiformes	1	2	3
	Anguilliformes	11	34	43
	Saccopharyngiformes	1	1	1
	Clupeiformes	2	4	6
	Alepocephaliformes	2	3	3
	Siluriformes	1	1	1
	Argentiniformes	4	8	8
	Stomiiformes	4	25	41
	Aulopiformes	8	12	15
	Myctophiformes	1	13	18
	Lampriformes	1	1	1
	Zeiformes	1	1	1
	Stylephoriformes	1	1	1
	Gadiformes	5	8	11
	Polymixiiformes	1	1	1
	Beryciformes	3	5	5
	Holocentriformes	1	3	3
	Ophidiiformes	3	9	9
	Scombriformes	8	23	26
	Syngnathiformes	6	10	11
	Kurtiformes	1	3	4
	Gobiiformes	3	20	31
	Carangiformes	13	36	62
	Cichliformes	1	1	1
	Atheriniformes	1	1	1
	Cyprinodontiformes	1	1	1
	Beloniformes	3	12	18
	Mugiliformes	1	3	5
	Gobiesociformes	1	2	2
	Blenniiformes	2	6	8
	Acanthuriformes	7	11	12
	Lophiiformes	4	7	10
	Tetraodontiformes	5	12	24

(continued)

Table 17.1 (continued)

Class	Order	Families	Genera	Species
	Centrarchiformes	2	2	5
	Acropomatiformes	3	3	4
	Perciformes *sedis mutabilis*	12	39	69
	Perciformes	13	31	50

Threatened species (NT—Ferreira and Simpfendorfer 2019). Despite the low resolution of the available image (see Fig. 17.2, 1), this is the first observation confirming the occurrence of this species around São Tomé, but the species had already been reported from Príncipe (Carpenter and de Angelis 2016a). In a recent study, Bernard et al. (2021) confirmed that Tiger shark populations from the Atlantic Ocean are genetically distinct from the Indo-Pacific Ocean populations showing that these long-distance dispersing populations are not interbreeding.

Holocephali

The sole Holocephali (Chimaeriformes, Rhinochimaeridae), the Sicklefin Chimaera, *Neoharriotta pinnata* (Schnakenbeck, 1931), accounts for 0.2% of the confirmed species in the region and is considered a Near Threatened species. The Sicklefin Chimaera is known in the eastern Atlantic Ocean off the west African coast from Western Sahara to Namibia, including the Gulf of Guinea islands. The species is found at the edge of the shelf in depths ranging from 200 to 600 m (Carpenter and De Angelis 2016a).

Actinopteri

The Actinopteri is the most diverse fish class, with 515 confirmed species for the GGOI. A total of 141 families were recorded, with Gobiidae being the richest with 4.8% of the species (25), followed by Carangidae with 4.5% (23), Serranidae with 4.3% (22), Stomiidae with 3.7% (19), Myctophidae with 3.5% (18), Sparidae with 2.9% (15), and Haemulidae, Muraenidae, and Ophichthidae with 2.1% (11) each. All 132 remaining families are represented by fewer than ten species and account for the remaining 70% of the species. To be as exhaustive as possible, the current checklist integrates potential deep-sea and large migrant pelagic fish species based on several guides and reports. Due to the deep water around all three GGOI, several species (e.g., *Opisthoproctus soleatus* Vaillant, 1888; *Scopelosaurus argenteus* (Maul, 1954)) were collected by offshore scientific surveys or accidentally by industrial fishing vessels. In addition, several deep-sea fish species are already reported in the

Fig. 17.2 Gulf of Guinea oceanic island fishes: (**1**) Tiger Shark *Galeocerdo cuvier* (Péron and Lesueur, 1822); (**2**) Atlantic Mudskipper *Periophthalmus barbarus* (Linnaeus, 1766); (**3**) São Tomé Clingfish *Apletodon wirtzi* Fricke, 2007; (**4**) Island Cowfish (juvenile) *Acanthostracion notacanthus* (Bleeker, 1863); (**5**) Small Goby *Bathygobius burtoni* (O'Shaughnessy, 1875); (**6**) Small Goby *Gobius* aff. *rubropunctatus* Delais, 1951; (**7**) Margintail *Paraconger caudilimbatus* (Poey, 1867); (**8**) African Speckled Scorpionfish *Scorpaenodes africanus* Pfaff, 1933. Photo credits: (**1**) Ivete Carneiro, (**2**) Luis MP Ceríaco, (**3–8**) João Luiz Gasparini

literature for the GGOI (e.g., *Cyclothone* spp., *Ichthyococcus ovatus* (Cocco, 1838), *Vinciguerria nimbaria* (Jordan and Williams, 1895)).

The Actinopteri fishes present a high variety of shapes, distributions, and behaviors. The extraordinary and unusual looking Atlantic mudskipper, *P. barbarus*, occurring along the West African coast, from Morocco to Angola and several offshore islands, is also present in the GGOI (Fig. 17.2, 2). Of special interest are: the São Tomé clingfish, *Apletodon wirtzi* Fricke, 2007, endemic to the GGOI and currently only known from its type locality, Bombom Islet, north of Príncipe Island

(Fricke 2007; Fig. 17.2, 3); the Island cowfish, *Acanthostracion notacanthus* (Bleeker, 1863), which has a restricted distribution around several islands (São Tomé, Príncipe, Saint Helena, Ascension, and Azores) and two African coastal locations (Ghana and Angola) (Fig. 17.2, 4); one small goby, *Bathygobius burtoni* (O'Shaughnessy, 1875), an Endangered species and Gulf of Guinea endemic (Ghana to Cameroon, Bioko Island), which is confirmed from São Tomé and Príncipe islands (Carpenter et al. 2015—Fig. 17.2, 5); another small goby, *Gobius* aff. *rubropunctatus* Delais, 1951, from São Tomé and Príncipe islands that is a putative undescribed species (Wirtz et al. 2007—Fig. 17.2, 6); the Margintail, *Paraconger caudilimbatus* (Poey, 1867), an amphi-Atlantic species, only reported from São Tomé Island in the eastern Atlantic (Wirtz et al. 2007—Fig. 17.2, 7); and the African speckled scorpionfish, *Scorpaenodes africanus* Pfaff, 1933, with a fragmented distribution including Senegal, São Tomé, and Annobón (Eschmeyer 1969—Fig. 17.2, 8).

The American whitespotted filefish, *Cantherhines macrocerus* (Hollard, 1853), a typical western Atlantic species, also occurs in the eastern Atlantic Ocean. The species is suspected to have been transported to the Gulf of Guinea by oil platforms coming from Brazil or the Caribbean (Herrero-Barrencua et al. 2019). Nonetheless, natural dispersal observed in a western Atlantic congener (*Cantherhines pullus* (Ranzani, 1842)) into the Gulf of Guinea (Afonso et al. 1999) suggests a similar scenario for *C. macrocerus* is possible (Herrero-Barrencua et al. 2019). Two introduced freshwater species have been reported for the islands: the Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852), in São Tomé (Félix et al. 2016), and the Banded lampeye, *A. spilauchen*, in Príncipe (Cravo 2021). Both introduction dates are not determined, but the Mozambique tilapia is already widespread throughout the island (Félix et al. 2016).

Compared to the most recent studies regarding the fishes of the GGOI (Wirtz 2017; Iwamoto and Wirtz 2018), the present work includes several unique and new records: Cichlidae—*O. mossambicus*, introduced species; Exocoetidae—*Hirundichthys affinis* (Günther, 1866), new record for São Tomé; Gempylidae—*Nealotus tripes* Johnson, 1865; Monacanthidae—*C. macrocerus*; Polymixiidae—*Polymixia nobilis* Lowe, 1836; Serranidae—*Anthias cyprinoides* (Katayama & Amaoka, 1986), *Serranus accraensis* (Norman, 1931), *Serranus drewesi* Iwamoto, 2018, *Serranus heterurus* (Cadenat, 1937); Sparidae—*Spicara melanurus* (Valenciennes, 1830); and Stomiidae—*Bathophilus nigerrimus* Giglioli, 1882 (Krakstad et al. 2010; Félix et al. 2016; Almeida and Alves 2017, 2019; Iwamoto and Wirtz 2018; Vasco-Rodrigues et al. 2018; Herrero-Barrencua et al. 2019; Parenti and Randall 2020; Cravo 2021). *Gobioides* cf. *africanus* (Giltay, 1935), Gobiidae, reported by Cravo (2021) needs confirmation.

Biogeography and Evolution of Fishes in Gulf of Guinea Oceanic Islands

Oceanic island ecosystems in the Tropical Eastern Atlantic (TEA) include the Cape Verde archipelago and the islands of the Gulf of Guinea: Príncipe, São Tomé, and Annobón (Floeter et al. 2008). Despite its relatively old age, São Tomé has low marine endemism (e.g., 3% for fishes; Hachich et al. 2015) due to high oceanographic connectivity to the African coast (Wirtz 2003; Floeter et al. 2008). On the other hand, the regional endemism level of the TEA is high (30%; Floeter et al. 2008), a phenomenon presumably due to the geographic isolation of the TEA from the other Atlantic reef areas (e.g., ~3500 km from the Brazil and ~8696 km from the Caribbean; Floeter et al. 2008), as well as a history of recurrent isolation and connectivity with the Indo-Pacific at an evolutionary timescale (Cowman et al. 2017). Indeed, several species show a trans-Atlantic distribution (amphi-Atlantic) with most of the species belonging to families of pelagic-spawners with long pelagic larval durations (e.g., Muraenidae, Serranidae), but also smaller-sized genera (e.g., *Abudefduf taurus*; Müller and Troschel, 1848) and *Centropyge aurantonotus* Burgess, 1974—Floeter et al. 2008). Entire families are composed of amphi-Atlantic species (e.g., Diodontidae, Holocentridae, Priacanthidae, Synodontidae). In addition to the Benguela Current that limits the movements of tropical species from the Indian Ocean, cold waters from the northeastern Atlantic also limit the geographic range of tropical species (Floeter et al. 2008; Almada et al. 2013). Thus, the TEA and the southwestern Indian Ocean only share about 15 species (e.g., *Lithognathus mormyrus* (Linnaeus, 1758) and *Gnatholepis thompsoni* Jordan, 1904) or genera (e.g., *Prionurus* and *Plectorhynchus*—Rocha et al. 2005; Wirtz et al. 2007; Floeter et al. 2008).

Since the waters of the Gulf of Guinea have received limited scientific attention, with Annobón the least studied area of the GGOI (Osório 1895b; Blanc et al. 1968), the marine organisms desperately require further study (Floeter et al. 2008). Recent works dealing with the biogeography and evolution of some reef fish families include representatives from this region, as in the case of the genus *Clepticus* (Labridae). This recent study revealed that *C. africanus*, an endemic species from the Gulf of Guinea, is genetically closer to *Clepticus brasiliensis* Heiser, Moura and Robertson, 2000, from the Brazilian coast, than to the Caribbean *Clepticus parrae* (Bloch and Schneider, 1801) (Beldade et al. 2009). The biogeographic affinities of other endemics in the archipelago are largely unknown.

With 268 coastal fish species in the GGOI, the diversity is high when compared to other Atlantic islands (e.g., 140 coastal fish species from Saint Helena, 170 species from Azores, or 226 species from Madeira—Table 17.2). This is mostly due to the location of the GGOI, closer to the African shelf and surrounded by a vortex created by all the currents crossing the area. However, the total number is low when compared to the Cape Verde (325 costal fish species) and Canary (330) islands, probably a sampling artifact due to the dearth of surveys around the GGOI.

Table 17.2 Coastal fish species richness, number of endemics and % endemism of Atlantic islands

Islands	Coastal fish species			References
	Total	N° endemics	% Endemism	
Ascension	173	11	10.2	Wirtz et al. (2014)
Cape Verde	325	19	8.4	Wirtz et al. (2013); Freitas et al. (2018)
Saint Helena	140	10	12.3	Brown et al. (2019)
Saint Peter and Saint Paul's archipelago	117	5	7.7	Vaske et al. (2008)
Madeira	226	0	0	Wirtz et al. (2008)
Canary	330	NA	NA	Brito et al. (2002)
Azores	170	NA	NA	Santos et al. (1997); Afonso et al. (2013)
São Tomé and Príncipe	268	7	3.0	Wirtz et al. (2007); Wirtz (2017)

Marine fish species are moving, and tropicalization is one of the observed processes in some eastern Atlantic islands where several TEA species are expanding their ranges (e.g., *Muraena melanotis* (Kaup, 1859), *Holacanthus africanus* Cadenat, 1951, and *Cirrhitus atlanticus* Osório, 1893—Brito et al. 2005; Falcón et al. 2018). We also highlight the occurrence of *Epinephelus fasciatus* (Forsskål, 1775), an Indo-Pacific species, potentially introduced by ballast water or in association with oil platforms (Brito et al. 2005; Falcón et al. 2018). Rocha et al. (2005) and confirmed recent connections in several taxa during warm interglacial periods (Peeters et al. 2004), such as the genus *Gnatholepis* that invaded the Atlantic from the Indian Ocean. Currently, the Agulhas Current in extreme conditions can force any tropical invaders from the Indian Ocean to move to the Atlantic Ocean through the 'Agulhas leakage' that forms water rings at the Agulhas retroflection (Lutjeharms and Van Ballegooyen 1988; Gordon 2003; Lutjeharms 2006; Beal et al. 2011). Invading fish species are likely moving with these rings through the Western Atlantic and South-central Atlantic before ending up in the TEA, rather than moving north with the Benguela Current, which is probably more lethal to tropical fish species (Rocha et al. 2005).

Some fish species have highly skewed distributions, with 84 genera occurring in the eastern Atlantic, but not in the western Atlantic (e.g., *Thorogobius*, *Wheelerigobius*—Floeter et al. 2008; Cowman et al. 2017). Other genera are amphi-Atlantic, but much more diverse in the eastern Atlantic (e.g., *Diplodus*, *Scartella*—Cowman et al. 2017) or with sister-species in the western Atlantic (e.g., *Hypleurochilus aequipinnis* (Günther, 1861)—Wirtz et al. 2007). Finally, several eastern Atlantic genera occur in the Indo-Pacific, but are not present in the western Atlantic (e.g., *Coris*, *Lethrinus*—Cowman et al. 2017). Cowman et al. (2017) observed that the Gulf of Guinea fish species assemblages are distinctive within the east Atlantic cluster (Cape Verde, Gulf of Guinea West, and Sahelian Upwelling).

Conservation

The GGOI, together with Cape Verde, have been considered important global hotspots for marine conservation (Roberts et al. 2002), with high levels of endemism (~30%, Floeter et al. 2008). Several factors likely contribute to this designation including:

1. The geographic location and connectivity with tropical western Atlantic via the Equatorial Counter Current (Wirtz et al. 2007; Floeter et al. 2008; Herrero-Barrencua et al. 2019).
2. The moderate isolation from the Continental slope (Floeter et al. 2008; Hachich et al. 2015; Cowman et al. 2017; Quimbayo et al. 2019).
3. The Benguela Current working as a shield and limiting Indian Ocean tropical fish species from moving northward (Floeter et al. 2008).
4. The northeastern Atlantic cold waters limiting the northern range of tropical fish species (Floeter et al. 2008; Almada et al. 2013).
5. The lowest fish biomass and highest density in reef assemblage (Quimbayo et al. 2019).

With 27 fish species reported, plus two uncertain identifications (*Gobioides* cf. *africanus* and *Citharus* cf. *linguatula* (Linnaeus, 1758)—Cravo 2021), mangroves and seagrasses are also essential habitats to the fish diversity by providing fisheries production (Félix et al. 2016; Alexandre et al. 2017; Cravo 2021).

Globally, mangroves are highly impacted by deforestation for onshore aquaculture (for fish and shellfish production), agriculture, and urban development (FAO 2007; Friess et al. 2019; Goldberg et al. 2020). With at least 35% of world area lost, mangroves, or inter-tidal forest communities, are one of the major tropical environments threatened by agriculture, overharvesting, changing hydrology, pollution, and coastal erosion (Valiela et al. 2001). Otero-Ferrer et al. (2020) emphasized that at the island scale, the protection of fish assemblages needs to consider the interconnected habitat network by including the seascapes boundaries where fundamental ecological functions might also occur. The GGOI exhibit lower biomass despite higher primary productivity, an unexpected observation likely caused by intense fishing activities (Maia et al. 2018a; Quimbayo et al. 2019).

In 2000, Annobón Island and the surrounding waters were designated as a Marine Nature Reserve at National level, limiting fishing to traditional subsistence practices and scientific research (UNEP-WCMC and IUCN 2021). In 2006, the São Tomé Obô and Príncipe Obô Natural Parks were established, covering 262 km^2 and 45 km^2 in the respectively islands (UNEP-WCMC and IUCN 2021). The natural park in São Tomé covers three out of 12 mangroves, including Malanza, by far the largest of such ecosystems in the GGOI (Afonso 2019). The natural park in Príncipe included a marine portion on the southwestern coast. Since 2012, the Ramsar site of Tinhosas islets (covering Tinhosa Grande, Tinhosa Pequena and Tinhosinha, south of Príncipe) and the island of Príncipe are a UNESCO World Biosphere Reserve (UNEP-WCMC and IUCN 2021).

Regarding fishing activities, Equatorial Guinea and São Tomé and Príncipe are part of the Fishery Committee for the Eastern Central Atlantic (CECAF) with the purpose of promoting the sustainable utilization of all living marine resources within the delimited area by proper management and development of the fisheries and fishing operations. Fisheries catches include small-scale artisanal, subsistence (fishing operations in remote communities with no access to market to supplement family needs, and portion taken home for consumption from artisanal catch), and foreign industrial (dominated by fleets from the European Union, Japan, Taiwan, and China) catches (Belhabib 2015; Maia et al. 2018b). Nevertheless, only limited data from fisheries surveys are reported (Belhabib 2015). Increasing numbers of fishers, destructive blast fishing practices, and pollution from industrial fishing vessels (oil-spills) are the main causes of negative fish catch changes over time (Maia et al. 2018b). The low biomass of medium and large fish species reflects the long-term fishing pressure on São Tomé Island, as does deeper reef habitats having higher species richness, abundance, and biomass (Maia et al. 2018a).

Within Elasmobranchii, 27 (73%) out of 37 species are considered threatened (Vulnerable—VU, Endangered—EN or Critically Endangered—CR) and one species (2.7%) is Data Deficient (DD), following IUCN categories (Appendix). Few countries impose catch limits and overfishing is a main threat to oceanic sharks, as are the loss and degradation of habitat and climate change (Pacoureau et al. 2021). Regarding Actinopteri, 19 (3.7%) out of 515 species are considered threatened (VU or EN) and 47 species (9.1%) are DD. Fifteen species are reported as endemic to the GGOI, of which seven are Gobiidae (small species with limited dispersive abilities) and four are freshwater/brackish species (Appendix). Annobón Island is the least studied of the GGOI with very few scientific surveys (Osório 1895b; Blanc et al. 1968). Nevertheless, and as expected, about 75% of its ichthyofauna is shared with the African coast. From the remaining species, some are endemic to Annobón Island (*S. annobonae*), only present around the GGOI (*Eleotris annobonensis* Blanc, Cadenat and Stauch, 1968), common to other islands system (*Rypticus saponaceus* (Bloch and Schneider, 1801)), or amphi-Atlantic (*Uroconger syringinus* Ginsburg, 1954). Therefore, the establishment of a network of Marine Protected Area in the GGOI is fundamental to reduce further negative impacts on the reef by commercial fisheries and to secure their sustainability.

Concluding Remarks

The present checklist includes coastal, deep-sea, pelagic marine and freshwater fish species. Nevertheless, further surveys are still needed. These future surveys and research projects should combine traditional and new approaches (e.g., environmental DNA) to understand and highlight the occurrence of discrete (pelagic) species, but also to better define the distribution of endemic species around all three GGOI. Annobón Island should be a region of primary focus because it is the least studied. Moreover, the creation of one or more Marine Protected Areas in co-management with fisheries will be fundamental to protect the unique GGOI fish biodiversity hotspot, not only for the endemic species, but also to maintain sustainable fisheries.

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Appendix

Checklist of marine and freshwater fish species reported from the Gulf of Guinea Oceanic Islands: Príncipe (P), São Tomé (S), Annobón (A). A complete checklist including confirmed, potential, erroneous and questionable marine and freshwater fish species reported from the Gulf of Guinea Oceanic Islands, together with common names, voucher numbers of museum specimens, and additional notes is available at [https://doi.org/10.1007/978-3-031-06153-0_17]

X, present; I, introduced; #, museum voucher specimen(s); E, endemic. IUCN Red List category: not evaluated (NE), data deficient (DD), least concern (LC), near threatened (NT), vulnerable (VU), endangered (EN), and critically endangered (CR). Taxa arranged according to Van der Laan et al. (2014). References: (1) Collette and Nauen (1983); (2) Allen (1985); (3) Nakamura (1985); (4) Whitehead (1985); (5) Whitehead et al. (1988); (6) Carpenter and Allen (1989); (7) Cohen et al. (1990); (8) Heemstra and Randall (1993); (9) Nakamura and Parin (1993); (10) Compagno (1984a); (11) Compagno (1984b); (12) Afonso et al. (1999); (13) Nielsen et al. (1999); (14) Compagno (2001); (15) Kotlyar (2004); (16) Pezold et al. (2006); (17) Fricke (2007); (18) Wirtz et al. (2007); (19) Kovačić and Schliewen (2008); (20) Krakstad et al. (2010); (21) Kotlyar 2011; (22) Schliewen (2011); (23) Rocha et al. (2012); (24) Ebert (2015); (25) Carpenter and De Angelis (2016a); (26) Carpenter and De Angelis (2016b); (27) Carpenter and De Angelis (2016c); (28) Félix et al. (2016); (29) Last et al. (2016); (30) Reiner and Wirtz (2016); (31) Vasco-Rodrigues et al. (2016); (32) Wirtz and Iwamoto (2016); (33) Almeida and Alves (2017); (34) Fricke and Wirtz (2017); (35) Tuya et al. (2017); (36) Wirtz (2017); (37) Yokota and Carvalho (2017); (38) Haroun et al. (2018); (39) Iwamoto and Wirtz (2018); (40) Vasco-Rodrigues et al. (2018); (41) Almeida and Biscoito (2019); (42) Almeida and Alves (2019); (43) Herrero-Barrencua et al. (2019); (44) Reiner (2019); (45) Parenti and Randall (2020); (46) Sutton et al. (2020); (47) Cravo (2021)

Higher taxonomy	Species	P	S	A	IUCN	Reference
Class Elasmobranchii						
Order Orectolobiformes						
Family **Rhincodontidae**	*Rhincodon typus* Smith, 1828	?	X	?	EN	25, 31, 40
Family **Ginglymostomatidae**	*Ginglymostoma cirratum* (Bonnaterre, 1788)	?	X	?	VU	10, 12, 18
Order Lamniformes						
Family **Carchariidae**	*Carcharias taurus* Rafinesque, 1810	X	X	?	CR	14
Family **Pseudocarchariidae**	*Pseudocarcharias kamoharai* (Matsubara, 1936)	X	X	?	LC	14, 24
Family **Lamnidae**	*Isurus oxyrinchus* Rafinesque, 1810	X	X	X	EN	14, 25
Order Carcharhiniformes						
Family **Scyliorhinidae**	*Scyliorhinus cervigoni* Maurin and Bonnet, 1970	X	?	?	DD	25
Family **Hemigaleidae**	*Paragaleus pectoralis* (Garman, 1906)	X	X	X	EN	11, 25
Family **Carcharhinidae**	*Carcharhinus brevipinna* (Müller and Henle, 1839)	X	X	X	VU	25
	Carcharhinus falciformis (Bibron in Müller and Henle, 1839)	#	#	X	VU	11, 25
	Carcharhinus galapagensis (Snodgrass and Heller, 1905)	?	X	?	LC	11, 12, 18, 25
	Carcharhinus limbatus (Valenciennes in Müller and Henle, 1839)	?	#	?	VU	11, 25
	Galeocerdo cuvier (Péron and Lesueur, 1822)	X	X	?	NT	25
	Negaprion brevirostris (Poey, 1868)	X	?	?	VU	11, 25
	Prionace glauca (Linnaeus, 1758)	X	X	X	NT	11, 12, 18, 25
	Rhizoprionodon acutus (Rüppell, 1837)	X	X	X	VU	11, 12, 18, 25
Family **Sphyrnidae**	*Sphyrna lewini* (Griffith and Smith, 1834)	?	X	?	CR	12
	Sphyrna zygaena (Linnaeus, 1758)	X	?	?	VU	11, 25
Order Torpediniformes						
Family **Torpedinidae**	*Tetronarce nobiliana* (Bonaparte, 1835)	?	X	?	LC	12, 25, 29
	Torpedo torpedo (Linnaeus, 1758)	?	X	?	VU	12, 25, 29
Order Rhinopristiformes						
Family **Rhinidae**	*Rhynchobatus luebberti* Ehrenbaum, 1915	?	X	?	CR	30
Order Myliobatiformes						
Family **Zanobatidae**	*Zanobatus schoenleinii* (Müller and Henle, 1841)	X	X	X	VU	25, 29
Family **Dasyatidae**	*Bathytoshia lata* (Garman, 1880)	X	X	?	VU	29
	Dasyatis marmorata (Steindachner, 1892)	X	X	X	NT	25

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
	Dasyatis pastinaca (Linnaeus, 1758)	X	X	?	VU	40
	Fontitrygon margarita (Günther, 1870)	X	X	X	VU	25, 29
	Fontitrygon margaritella (Compagno and Roberts, 1984)	X	X	X	NT	25, 29
	Pteroplatytrygon violacea (Bonaparte, 1832)	X	X	X	LC	25, 29
	Taeniurops grabatus (Geoffroy Saint-Hilaire, 1817)	X	X	X	NT	18, 25, 29
Family **Gymnuridae**	*Gymnura altavela* (Linnaeus, 1758)	X	X	X	EN	25, 29
	Gymnura sereti Yokota and Carvalho, 2017	?	#	?	EN	37
Family **Aetobatidae**	*Aetobatus narinari* (Euphrasen, 1790)	X	X	X	EN	25, 29
Family **Myliobatidae**	*Aetomylaeus bovinus* (Geoffroy Saint-Hilaire, 1817)	X	X	X	CR	25
	Myliobatis aquila (Linnaeus, 1758)	X	X	X	CR	25, 29
Family **Mobulidae**	*Mobula birostris* (Walbaum, 1792)	X	X	X	EN	25, 29
	Mobula hypostoma (Bancroft, 1831)	X	X	X	EN	25, 29
	Mobula tarapacana (Philippi, 1892)	?	X	?	EN	31, 40
	Mobula thurstoni (Lloyd, 1908)	?	X	?	EN	31, 40
Class Chondrichthyes | subclass Holocephali						
Order Chimaeriformes						
Family **Rhinochimaeridae**	*Neoharriotta pinnata* (Schnakenbeck, 1931)	X	X	X	NT	25
Class Actinopterygii | subclass Actinopteri						
Order Elopiformes						
Family **Elopidae**	*Elops lacerta* Valenciennes, 1847	X	X	X	LC	26
	Elops senegalensis Regan, 1909	?	#	?	DD	12, 26, 28
Family **Megalopidae**	*Megalops atlanticus* Valenciennes, 1847	X	#	X	VU	26, 28, 47
Order Albuliformes						
Family **Albulidae**	*Albula goreensis* Valenciennes, 1847	?	#	?	NE	18, 42
Order Notacanthiformes						
Family **Halosauridae**	*Aldrovandia oleosa* Sulak, 1977	X	X	X	LC	26
	Halosaurus attenuatus Garman, 1899	#	X	X	LC	26
	Halosaurus ovenii Johnson, 1864	X	X	X	LC	26
Order Anguilliformes						
Family **Heterenchelyidae**	*Panturichthys longus* (Ehrenbaum, 1915)	E	E	E	LC	26
	Pythonichthys macrurus (Regan, 1912)	X	X	X	NE	26

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
	Pythonichthys microphthalmus (Regan, 1912)	X	X	X	NE	26
Family **Chlopsidae**	*Chlopsis olokun* (Robins and Robins, 1966)	X	X	X	LC	26
Family **Myrocongridae**	*Myroconger compressus* Günther, 1870	X	#	?	DD	26, 42
Family **Muraenidae**	*Anarchias longicauda* (Peters, 1877)	X	X	X	LC	26
	Anarchias similis (Lea, 1913)	?	?	#	LC	26
	Channomuraena vittata (Richardson, 1845)	?	X	X	LC	12, 26, 40
	Echidna peli (Kaup, 1856)	#	X	#	LC	18, 26, 40
	Enchelycore nigricans (Bonnaterre, 1788)	?	X	#	LC	12, 26, 40
	Gymnothorax afer Bloch, 1795	X	X	X	LC	12, 26
	Gymnothorax mareei Poll, 1953	#	X	X	LC	12, 26
	Gymnothorax vicinus (Castelnau, 1855)	X	X	#	LC	26, 40
	Muraena melanotis (Kaup, 1859)	#	X	#	LC	12, 20, 25, 35, 40
	Muraena robusta Osório, 1911	X	X	X	LC	12, 26, 40
	Uropterygius wheeleri Blache, 1967	X	X	X	LC	26, 31
Family **Synaphobranchidae**	*Histiobranchus bathybius* (Günther, 1877)	#	?	?	DD	26
Family **Ophichthidae**	*Brachysomophis atlanticus* Blache and Saldanha, 1972	#	?	?	LC	26
	Callechelys guineensis (Osório, 1893)	?	X	?	LC	26, 30
	Dalophis boulengeri (Blache, Cadenat and Stauch, 1970)	#	?	?	LC	18, 26
	Dalophis cephalopeltis (Bleeker, 1863)	?	#	?	LC	26, 28
	Echelus myrus (Linnaeus, 1758)	?	X	?	LC	20
	Myrichthys pardalis (Valenciennes, 1839)	X	#	X	LC	12, 26, 35, 40
	Myrophis plumbeus (Cope, 1871)	#	?	?	LC	26
	Ophichthus ophis (Linnaeus, 1758)	?	X	?	LC	20, 26
	Ophichthus rufus (Rafinesque, 1810)	#	?	?	LC	18
	Ophisurus serpens (Linnaeus, 1758)	X	X	X	LC	26
	Pisodonophis semicinctus (Richardson, 1848)	?	X	?	LC	
Family **Congridae**	*Ariosoma balearicum* (Delaroche, 1809)	X	#	#	LC	26
	Bathycongrus bertini (Poll, 1953)	X	X	X	LC	26
	Bathyuroconger vicinus (Vaillant, 1888)	X	X	X	LC	26
	Heteroconger longissimus Günther, 1870	X	X	?	LC	18, 35
	Paraconger caudilimbatus (Poey, 1867)	?	X	?	LC	18
	Paraconger notialis Kanazawa, 1961	X	X	X	LC	26

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
	Uroconger syringinus Ginsburg, 1954	X	#	#	LC	26
	Xenomystax congroides Smith and Kanazawa, 1989	X	X	X	LC	26
Family **Muraenesocidae**	*Cynoponticus ferox* Costa, 1846	X	X	X	LC	26
Family **Nemichthyidae**	*Avocettina infans* (Günther, 1878)	X	#	X	LC	46
	Nemichthys curvirostris (Strömman, 1896)	?	X	?	LC	20, 26
	Nemichthys scolopaceus Richardson, 1848	?	#	?	LC	26, 46
Family **Serrivomeridae**	*Serrivomer beanii* Gill and Ryder, 1883	?	#	?	LC	26, 46
Family **Nettastomatidae**	*Hoplunnis punctata* Regan, 1915	X	#	X	LC	26
	Nettastoma melanura Rafinesque, 1810	X	X	X	LC	26
Order Saccopharyngiformes						
Family **Eurypharyngidae**	*Eurypharynx pelecanoides* Vaillant, 1882	?	#	?	LC	26, 46
Order Clupeiformes						
Family **Clupeidae**	*Ethmalosa fimbriata* (Bowdich, 1825)	?	#	?	LC	18, 47
	Pellonula vorax Günther, 1868	?	?	#	LC	26
	Sardinella aurita Valenciennes, 1847	?	#	?	LC	12, 20, 42
	Sardinella maderensis (Lowe, 1838)	?	#	?	VU	20, 42
	Sardinella rouxi (Poll, 1953)	#	#	?	DD	4, 18, 42
Family **Engraulidae**	*Engraulis encrasicolus* (Linnaeus, 1758)	X	X	X	LC	5, 26
Order Alepocephaliformes						
Family **Alepocephalidae**	*Photostylus pycnopterus* Beebe, 1933	?	#	?	LC	26, 46
Family **Platytroctidae**	*Holtbyrnia macrops* Maul, 1957	X	X	X	LC	26
	Searsia koefoedi Parr, 1937	#	?	?	LC	46
Order Siluriformes						
Family **Ariidae**	*Carlarius parkii* (Günther, 1864)	X	#	X	LC	26
Order Argentiniformes						
Family **Argentinidae**	*Glossanodon polli* Cohen, 1958	?	#	?	LC	26
Family **Microstomatidae**	*Microstoma microstoma* (Risso, 1810)	?	#	?	LC	26, 46
	Xenophthalmichthys danae Regan, 1925	?	#	?	LC	26, 46
Family **Bathylagidae**	*Bathylagichthys greyae* (Cohen, 1958)	?	#	?	LC	46
	Bathylagoides argyrogaster (Norman, 1930)	?	#	#	LC	26, 46
Family **Opisthoproctidae**	*Monacoa grimaldii* (Zugmayer, 1911)	?	#	?	LC	26, 46

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
	Opisthoproctus soleatus Vaillant, 1888	#	#	?	LC	26, 46
	*Winteria telescop*a Brauer, 1901	?	#	?	LC	26, 46
Order Stomiiformes						
Family **Gonostomatidae**	*Bonapartia pedaliota* Goode and Bean, 1896	#	#	?	LC	26, 46
	Cyclothone acclinidens Garman, 1899	?	#	#	LC	26
	Cyclothone braueri Jespersen and Tåning, 1926	?	#	#	LC	26
	Cyclothone livida Brauer, 1902	?	#	#	LC	26, 46
	Cyclothone microdon (Günther, 1878)	?	#	#	LC	26
	Diplophos taenia Günther, 1873	?	#	?	LC	26
	Gonostoma atlanticum Norman, 1930	?	#	?	LC	26, 46
	Manducus maderensis (Johnson, 1890)	#	?	?	DD	26, 46
	Sigmops elongatus (Günther, 1878)	#	#	?	LC	26, 46
Family **Sternoptychidae**	*Argyropelecus affinis* Garman, 1899	#	#	#	LC	26, 46
	Argyropelecus gigas Norman, 1930	?	#	#	LC	26, 46
	Argyropelecus olfersii (Cuvier, 1829)	?	#	?	LC	46
	Argyropelecus sladeni Regan, 1908	?	#	?	LC	26, 46
	Maurolicus muelleri (Gmelin, 1789)	#	#	?	LC	46
	Polyipnus polli Schultz, 1961	?	#	?	LC	26, 46
	Sternoptyx diaphana Hermann, 1781	#	#	#	LC	26, 46
	Sternoptyx pseudobscura Baird, 1971	?	#	?	LC	26, 46
	Valenciennellus tripunctulatus (Esmark, 1871)	?	#	#	LC	26, 46
Family **Phosichthyidae**	*Ichthyococcus ovatus* (Cocco, 1838)	#	?	?	LC	26, 46
	Pollichthys mauli (Poll, 1953)	?	#	#	LC	26, 46
	Vinciguerria attenuata (Cocco, 1838)	?	?	#	LC	26
	Vinciguerria nimbaria (Jordan and Williams, 1895)	#	#	#	LC	26, 46
Family **Stomiidae**	*Aristostomias grimaldii* Zugmayer, 1913	#	?	?	LC	26, 46
	Aristostomias xenostoma Regan and Trewavas, 1930	?	#	?	LC	26, 46
	Astronesthes caulophorus Regan and Trewavas, 1929	?	#	?	LC	26, 46
	Astronesthes niger Richardson, 1845	?	#	?	LC	26
	Astronesthes richardsoni (Poey, 1852)	?	#	?	LC	26, 46

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
	Borostomias elucens (Brauer, 1906)	?	#	?	LC	26, 46
	Chauliodus sloani Bloch and Schneider, 1801	#	#	#	LC	26, 46
	Eustomias melanonema Regan and Trewavas, 1930	?	#	?	LC	26, 46
	Eustomias monoclonoides Clarke, 1999	?	#	?	LC	26, 46
	Eustomias monoclonus Regan and Trewavas, 1930	?	?	#	LC	26
	Leptostomias gracilis Regan and Trewavas, 1930	#	?	?	LC	46
	Malacosteus niger Ayres, 1848	?	#	?	LC	26, 46
	Neonesthes capensis (Gilchrist and von Bonde, 1924)	?	#	?	LC	26, 46
	Pachystomias microdon (Günther, 1878)	?	#	?	LC	26, 46
	Photostomias atrox (Alcock, 1890)	?	#	?	LC	26, 46
	Photostomias guernei Collett, 1889	?	#	#	LC	26, 46
	Stomias affinis Günther, 1887	?	#	?	LC	26, 46
	Stomias boa (Risso, 1810)	?	#	?	LC	26
	Stomias longibarbatus (Brauer, 1902)	?	#	?	LC	26, 46
Order Aulopiformes						
Family **Aulopidae**	*Aulopus cadenati* Poll, 1953	X	X	X	LC	26
Family **Ipnopidae**	*Bathypterois phenax* Parr, 1928	#	?	?	LC	26
Family **Scopelarchidae**	*Scopelarchoides danae* Johnson, 1974	#	#	?	LC	26, 46
	Scopelarchus analis (Brauer, 1902)	?	#	?	LC	26, 46
	Scopelarchus michaelsarsi Koefoed, 1955	?	#	?	LC	26, 46
Family **Notosudidae**	*Scopelosaurus argenteus* (Maul, 1954)	#	?	?	LC	26, 46
	Scopelosaurus lepidus (Krefft and Maul, 1955)	?	#	?	LC	26, 46
	Scopelosaurus smithii Bean, 1925	#	#	?	LC	26, 46
Family **Synodontidae**	*Saurida brasiliensis* Norman, 1935		Err		LC	
	Saurida parri Norman, 1935	?	#	?	LC	20
	Synodus intermedius (Spix and Agassiz, 1829)		Err		LC	12, 18
	Synodus synodus (Linnaeus, 1758)	#	#	?	LC	12, 26, 40, 42
	Trachinocephalus myops (Forster, 1801)	#	#	X	LC	12, 20, 26
Family **Paralepididae**	*Lestrolepis intermedia* (Poey, 1868)	#	#	?	LC	26, 46
	Paralepis elongata (Brauer, 1906)	?	#	?	LC	26, 46

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
Family **Evermannellidae**	*Odontostomops normalops* (Parr, 1928)	?	#	?	LC	26, 46
Family **Omosudidae**	*Omosudis lowii* Günther, 1887	?	#	?	LC	26, 46
Order Myctophiformes						
Family **Myctophidae**	*Benthosema suborbitale* (Gilbert, 1913)	#	#	#	LC	26, 46
	Bolinichthys photothorax (Parr, 1928)	?	#	?	LC	26, 46
	Centrobranchus nigroocellatus (Günther, 1873)	?	#	?	LC	
	Ceratoscopelus warmingii (Lütken, 1892)	?	#	?	LC	
	Dasyscopelus asper (Richardson, 1845)	?	#	#	LC	26, 46
	Diaphus holti Tåning, 1918	?	#	?	LC	26
	Diaphus luetkeni (Brauer, 1904)	?	#	?	LC	26, 46
	Diaphus vanhoeffeni (Brauer, 1906)	?	#	?	LC	26, 46
	Diogenichthys atlanticus (Tåning, 1928)	?	#	#	LC	26, 46
	Hygophum macrochir (Günther, 1864)	?	#	?	LC	26
	Hygophum reinhardtii (Lütken, 1892)	?	#	?	LC	26, 46
	Lampanyctus alatus Goode and Bean, 1896	?	#	?	LC	26, 46
	Lampanyctus isaacsi Wisner, 1974	?	#	?	LC	26
	Lepidophanes guentheri (Goode and Bean, 1896)	?	#	?	LC	26, 46
	Lobianchia dofleini (Zugmayer, 1911)	?	#	?	LC	26, 46
	Myctophum affine (Lütken, 1892)	?	#	#	LC	26, 46
	Myctophum nitidulum Garman, 1899	?	#	?	LC	26, 46
	Notolychnus valdiviae (Brauer, 1904)	?	#	#	LC	26, 46
Order Lampriformes						
Family **Lophotidae**	*Eumecichthys fiski* (Günther, 1890)	?	#	?	LC	20, 26, 46
Order Polymixiiformes						
Family **Polymixiidae**	*Polymixia nobilis* Lowe, 1836	?	#	?	LC	33, 42
Order Zeiformes						
Family **Zeidae**	*Zeus faber* Linnaeus, 1758	#	?	?	DD	20
Order Stylephoriformes						
Family **Stylephoridae**	*Stylephorus chordatus* Shaw, 1791	#	#	?	LC	26, 46

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
Order Gadiformes						
Family **Bregmacerotidae**	*Bregmaceros atlanticus* Goode and Bean, 1886	?	#	?	LC	26, 46
Family **Melanonidae**	*Melanonus zugmayeri* Norman, 1930	?	#	#	LC	26, 46
Family **Moridae**	*Gadella imberbis* (Vaillant, 1888)	X	#	X	LC	20, 26
	Laemonema laureysi Poll, 1953	X	X	X	LC	7, 26
	Physiculus cyanostrophus Anderson and Tweddle, 2002	?	#	?	LC	20
	Physiculus huloti Poll, 1953	?	#	?	LC	26
Family **Bathygadidae**	*Bathygadus macrops* Goode and Bean, 1885	X	X	X	LC	7, 26
	Bathygadus melanobranchus Vaillant, 1888	X	X	X	LC	7, 26
Family **Macrouridae**	*Coelorinchus geronimo* Marshall and Iwamoto, 1973	X	X	X	LC	26
	Malacocephalus laevis (Lowe, 1843)	X	X	X	LC	7, 26
	Malacocephalus occidentalis Goode and Bean, 1885	X	X	X	LC	7, 26
Order Beryciformes						
Family **Berycidae**	*Beryx decadactylus* Cuvier, 1829	?	X	?	LC	31, 40
Family **Melamphaidae**	*Melamphaes eulepis* Ebeling, 1962	?	#	?	LC	15, 46
	Poromitra megalops (Lütken, 1878)	?	X	?	DD	15, 26
	Scopelogadus mizolepis (Günther, 1878)	?	#	?	LC	15, 26, 46
Family **Cetomimidae**	*Cetostoma regani* Zugmayer, 1914	?	#	?	DD	
Order Holocentriformes						
Family **Holocentridae**	*Holocentrus adscensionis* (Osbeck, 1765)	#	#	#	LC	12, 26, 35, 40, 42
	Myripristis jacobus Cuvier, 1829	#	#	#	LC	12, 26, 35, 40, 42
	Sargocentron hastatum (Cuvier, 1829)	X	#	#	LC	12, 35, 40
Order Ophidiiformes						
Family **Ophidiidae**	*Acanthonus armatus* Günther, 1878	#	?	?	LC	26
	Bassozetus normalis Gill, 1883	#	?	?	LC	13, 26
	Brotula barbata (Bloch and Schneider, 1801)	X	X	X	LC	13, 20, 26
	Ophidion saldanhai Matallanas and Brito, 1999	?	#	?	DD	
	Spectrunculus grandis (Günther, 1877)	?	?	#	LC	13, 26
Family **Carapidae**	*Carapus acus* (Brünnich, 1768)	#	#	?	LC	20, 26
	Echiodon dentatus (Cuvier, 1829)	?	#	?	LC	26
Family **Bythitidae**	*Grammonus longhursti* (Cohen, 1964)	?	#	?	LC	13, 18, 26

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
	Parabrotula plagiophthalma Zugmayer, 1911	?	#	?	LC	27
Order Scombriformes						
Family **Nomeidae**	*Cubiceps pauciradiatus* Günther, 1872	#	#	?	LC	20, 27, 46
	Nomeus gronovii (Gmelin, 1789)	#	X	?	LC	27
Family **Ariommatidae**	*Ariomma bondi* Fowler, 1930	#	?	?	LC	20
Family **Pomatomidae**	*Pomatomus saltatrix* (Linnaeus, 1766)	X	X	X	VU	27, 40
Family **Chiasmodontidae**	*Chiasmodon niger* Johnson, 1864	?	#	?	LC	27, 46
	Kali kerberti (Weber, 1913)	?	#	?	LC	27
	Pseudoscopelus altipinnis Parr, 1933	?	#	?	LC	27, 46
Family **Scombridae**	*Acanthocybium solandri* (Cuvier, 1832)	?	X	?	LC	1, 12, 27, 40
	Auxis thazard (Lacépède, 1800)	?	#	?	LC	1, 12, 27, 40
	Euthynnus alletteratus (Rafinesque, 1810)	#	#	X	LC	1, 12, 20, 40
	Katsuwonus pelamis (Linnaeus, 1758)	?	X	?	LC	1, 12, 27, 35, 40
	Sarda sarda (Bloch, 1793)	X	#	X	LC	1, 27
	Scomber colias Gmelin, 1789	?	#	?	LC	42
	Scomberomorus tritor (Cuvier, 1832)	X	#	X	LC	1, 12, 27, 42
	Thunnus albacares (Bonnaterre, 1788)	?	X	?	NT	1, 12, 27
	Thunnus obesus (Lowe, 1839)	?	X	?	VU	1, 12, 27, 40, 46
Family **Caristiidae**	*Paracaristius aquilus* Stevenson and Kenaley, 2011	#	?	?	LC	46
	Paracaristius nudarcus Stevenson and Kenaley, 2011	?	#	?	DD	27, 46
	Platyberyx andriashevi (Kukuev, Parin and Trunov, 2012)	#	?	?	DD	27, 46
	Platyberyx opalescens Zugmayer, 1911	#	#	#	LC	46
Family **Bramidae**	*Taractichthys longipinnis* (Lowe, 1843)	?	#	?	LC	27, 46
Family **Gempylidae**	*Gempylus serpens* Cuvier, 1829	#	?	#	LC	9, 27
	Nealotus tripes Johnson, 1865	#	#	?	LC	9, 27, 42, 46
	Nesiarchus nasutus Johnson, 1862	#	#	?	LC	9, 20, 27, 46
	Promethichthys prometheus (Cuvier, 1832)	X	#	#	LC	9, 20, 27, 46
	Ruvettus pretiosus Cocco, 1833	X	X	X	LC	9, 27
Order Syngnathiformes						
Family **Dactylopteridae**	*Dactylopterus volitans* (Linnaeus, 1758)	#	#	X	LC	12, 20, 25, 40
Family **Mullidae**	*Mulloidichthys martinicus* (Cuvier, 1829)	?	X	?	LC	12, 27, 35, 40
	Pseudupeneus prayensis (Cuvier, 1829)	X	#	#	VU	12, 20, 27, 35, 40, 42
Family **Callionymidae**	*Callionymus bairdi* Jordan, 1888	X	#	X	LC	18, 27

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
	Synchiropus phaeton (Günther, 1861)	X	X	X	LC	27
Family **Aulostomidae**	*Aulostomus strigosus* Wheeler, 1955	X	#	X	LC	12, 20, 25, 40
Family **Fistulariidae**	*Fistularia petimba* Lacépède, 1803	#	#	X	LC	20
	Fistularia tabacaria Linnaeus, 1758	X	#	X	LC	12, 26, 40
Family **Syngnathidae**	*Enneacampus kaupi* (Bleeker, 1863)	?	X	?	LC	36
	Hippocampus algiricus Kaup, 1856	#	#	?	VU	18, 40
	Microphis aculeatus (Kaup, 1856)	#	#	?	DD	18, 28, 47
Order Kurtiformes						
Family **Apogonidae**	*Apogon imberbis* (Linnaeus, 1758)	#	#	#	LC	12, 18, 27, 35, 40
	Apogon pseudomaculatus Longley, 1932	?	#	?	LC	18, 35, 40
	Paroncheilus affinis (Poey, 1875)	X	#	X	LC	18, 27, 35
	Phaeoptyx pigmentaria (Poey, 1860)	X	X	#	LC	18, 27, 40
Order Gobiiformes						
Family **Eleotridae**	*Bostrychus africanus* (Steindachner, 1879)	X	#	X	LC	22, 27, 28
	Dormitator lebretonis (Steindachner, 1870)	X	X	X	LC	
	Eleotris annobonensis Blanc, Cadenat and Stauch, 1968	E#	E#	E#	DD	18, 27, 28
	Eleotris feai Thys van den Audenaerde and Tortonese, 1974	?	?	#	NE	
	Eleotris vittata Duméril, 1861	#	#	X	LC	27
Family **Gobiidae**	*Awaous bustamantei* (Greeff, 1882)	?	E#	E	VU	22, 28
	Awaous lateristriga (Duméril, 1861)	X	#	X	LC	22, 27, 28, 42
	Bathygobius burtoni (O'Shaughnessy, 1875)	#	#	?	EN	12, 22, 27, 28, 40
	Bathygobius casamancus (Rochebrune, 1880)	X	X	#	LC	22, 27
	Bathygobius soporator (Valenciennes, 1837)	#	#	#	LC	22, 27
	Corcyrogobius lubbocki Miller, 1988	X	#	#	VU	18, 22, 27
	Ctenogobius lepturus (Pfaff, 1933)	X	X	X	LC	22, 27, 30
	Didogobius amicuscaridis Schliewen and Kovačić, 2008	E	E#	?	VU	18, 22, 27
	Gnatholepis thompsoni Jordan, 1904	?	#	?	LC	12, 40
	Gobioides africanus (Giltay, 1935)	X	X	X	LC	22, 27
	Gobioides sagitta (Günther, 1862)	X	X	X	LC	22, 27
	Gobionellus occidentalis (Boulenger, 1909)	X	X	X	LC	22, 27

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Higher taxonomy	Species	P	S	A	IUCN	Reference
	Gobius aff. rubropunctatus Delais, 1951	#	#	?	LC	18, 22
	Gobius senegambiensis Metzelaar, 1919	X	X	X	LC	22, 27
	Gorogobius nigricinctus (Delais, 1951)	X	#	#	LC	18
	Gorogobius stevcici Kovačić and Schliewen, 2008	?	E#	?	VU	18, 19, 22, 27, 40
	Nematogobius brachynemus Pfaff, 1933	#	#	#	LC	18
	Nematogobius maindroni (Sauvage, 1880)	#	#	X	LC	18, 22, 27
	Porogobius schlegelii (Günther, 1861)	X	#	X	LC	22, 27, 28, 47
	Sicydium brevifile Ogilvie-Grant, 1884	E#	E#	E#	LC	16, 18, 22, 27
	Sicydium bustamantei Greeff, 1884	E#	E#	E#	DD	16, 18, 22, 27
	Thorogobius laureatus Sauberer, Iwamoto and Ahnelt, 2018	?	E#	?	NE	
	Wheelerigobius maltzani (Steindachner, 1881)	X	#	#	LC	18, 22, 27, 40
	Wheelerigobius wirtzi Miller, 1988	E#	E#	?	LC	12, 18, 22, 40
	Yongeichthys thomasi (Boulenger, 1916)	?	X	?	LC	22
Family **Oxudercidae**	*Periophthalmus barbarus* (Linnaeus, 1766)	#	#	X	LC	27, 28, 47
Order Carangiformes						
Family **Sphyraenidae**	*Sphyraena afra* Peters, 1844	X	X	X	LC	27
	Sphyraena barracuda (Edwards, 1771)	X	X	X	LC	12, 27, 35, 40
	Sphyraena guachancho Cuvier, 1829	X	#	X	LC	18, 20, 27
	Sphyraena sphyraena (Linnaeus, 1758)	X	#	X	LC	12, 20, 27, 42
Family **Polynemidae**	*Galeoides decadactylus* (Bloch, 1795)	#	#	#	NT	12, 20, 27, 28, 42
	Pentanemus quinquarius (Linnaeus, 1758)	X	X	X	VU	27
	Polydactylus quadrifilis (Cuvier, 1829)	X	X	X	LC	27
Family **Psettodidae**	*Psettodes belcheri* Bennett, 1831	X	?	?	DD	20
Family **Citharidae**	*Citharus linguatula* (Linnaeus, 1758)	?	#	?	LC	20
Family **Cyclopsettidae**	*Syacium guineense* (Bleeker, 1862)	X	X	X	LC	20, 27
Family **Bothidae**	*Arnoglossus imperialis* (Rafinesque, 1810)	X	#	X	LC	20, 27
	Arnoglossus sp. Bleeker, 1862	?	#	?	-	
	Bothus guibei Stauch, 1966	?	#	#	DD	12, 20, 27, 42
	Bothus lunatus (Linnaeus, 1758)	?	X	?	LC	12, 27, 40
	Bothus podas (Delaroche, 1809)	?	#	#	LC	20, 27
	Chascanopsetta lugubris Alcock, 1894	?	#	?	DD	44

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Higher taxonomy	Species	P	S	A	IUCN	Reference
	Monolene microstoma Cadenat, 1937	X	X	X	LC	27
Family **Paralichthyidae**	*Citharichthys stampflii* (Steindachner, 1894)	?	#	?	LC	44
Family **Soleidae**	*Dagetichthys lusitanicus* (de Brito Capello, 1868)	X	X	X	DD	27
	Dicologlossa cuneata (Moreau, 1881)	?	#	?	LC	18
	Heteromycteris proboscideus (Chabanaud, 1925)	X	#	X	DD	27
	Microchirus boscanion (Chabanaud, 1926)	X	X	X	DD	27
	Microchirus frechkopi Chabanaud, 1952	?	#	?	DD	20
	Microchirus hexophthalmus (Bennett, 1831)	?	#	?	LC	20
	Microchirus wittei Chabanaud, 1950	X	#	X	LC	27
	Pegusa lascaris (Risso, 1810)	X	#	X	LC	27
	Pegusa triophthalma (Bleeker, 1863)	X	X	X	DD	27
Family **Cynoglossidae**	*Cynoglossus browni* Chabanaud, 1949	?	#	?	DD	44
	Cynoglossus cadenati Chabanaud, 1947	#	?	?	DD	
	Cynoglossus canariensis Steindachner, 1882	?	#	?	NT	44
	Cynoglossus monodi Chabanaud, 1949	?	#	?	NT	18
	Cynoglossus senegalensis (Kaup, 1858)	?	#	?	NT	12
Family **Istiophoridae**	*Istiophorus albicans* (Latreille, 1804)	?	X	?	NE	3, 12, 40
	Istiophorus platypterus (Shaw, 1792)	?	#	?	LC	27
	Makaira nigricans Lacépède, 1802	?	X	?	VU	3, 31, 40
Family **Carangidae**	*Alectis alexandrina* (Geoffroy Saint-Hilaire, 1817)	X	X	X	LC	1, 27, 35
	Alectis ciliaris (Bloch, 1787)	X	X	X	LC	27
	Caranx bartholomaei Cuvier, 1833	X	X	?	LC	18, 20, 40
	Caranx crysos (Mitchill, 1815)	X	#	#	LC	12, 20, 40, 42
	Caranx fischeri Smith-Vaniz and Carpenter, 2007	X	#	X	LC	18
	Caranx hippos (Linnaeus, 1766)	X	#	X	LC	12, 18, 35, 40
	Caranx latus Agassiz, 1831	#	#	X	LC	18, 27, 40
	Caranx lugubris Poey, 1860	X	X	?	LC	18, 27, 40
	Caranx rhonchus Geoffroy Saint-Hilaire, 1817	?	X	?	LC	
	Chloroscombrus chrysurus (Linnaeus, 1766)	X	#	X	LC	27
	Decapterus macarellus (Cuvier, 1833)	X	#	X	LC	12, 20, 27, 42
	Decapterus punctatus (Cuvier, 1829)	X	#	X	LC	12, 20, 27, 40

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
	Elagatis bipinnulata (Quoy and Gaimard, 1825)	X	#	X	LC	12, 27, 35, 40, 42
	Hemicaranx bicolor (Günther, 1860)	X	X	X	LC	27
	Lichia amia (Linnaeus, 1758)	X	X	X	LC	27
	Pseudocaranx dentex (Bloch and Schneider, 1801)	X	X	X	LC	27
	Selar crumenophthalmus (Bloch, 1793)	X	#	#	LC	12, 20, 42
	Selene dorsalis (Gill, 1863)	X	#	X	LC	12, 20, 27, 42
	Seriola carpenteri Mather, 1971	X	X	X	LC	20, 27
	Seriola rivoliana Valenciennes, 1833	X	X	?	LC	18, 20, 27, 40
	Trachinotus goreensis Cuvier, 1832	?	X	?	LC	
	Trachinotus ovatus (Linnaeus, 1758)	X	#	#	LC	12, 27, 35, 42
	Uraspis secunda (Poey, 1860)	X	X	X	LC	12, 20, 27
Family **Echeneidae**	*Echeneis naucrates* Linnaeus, 1758	X	X	?	LC	27, 40
	Remora brachyptera (Lowe, 1839)	#	X	?	LC	12, 27
	Remora remora (Linnaeus, 1758)	?	#	?	LC	27
Family **Coryphaenidae**	*Coryphaena equiselis* Linnaeus, 1758	?	X	?	LC	12, 27
	Coryphaena hippurus Linnaeus, 1758	?	#	?	LC	31, 40
Order Cichliformes						
Family **Cichlidae**	*Oreochromis mossambicus* (Peters, 1852)	?	I	?	LC	28
Order Atheriniformes						
Family **Atherinidae**	*Atherina lopeziana* Rossignol and Blache, 1961	X	X	X	DD	26
Order Cyprinodontiformes						
Family **Procatopodidae**	*Aplocheilichthys spilauchen* (Duméril, 1861)	I	?	?	LC	47
Order Beloniformes						
Family **Belonidae**	*Ablennes hians* (Valenciennes, 1846)	X	X	X	LC	12, 26
	Platybelone argalus (Lesueur, 1821)	X	X	X	LC	26
	Platybelone argalus annobonensis Collette and Parin, 1970	X	X	X	LC	12, 18
	Strongylura senegalensis (Valenciennes, 1846)	X	X	X	LC	26
	Tylosurus acus rafale Collette and Parin, 1970	X	#	X	LC	12, 42
	Tylosurus crocodilus (Péron and Lesueur, 1821)	#	#	X	LC	12, 26

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
Family **Hemiramphidae**	*Hemiramphus balao* Lesueur, 1821	X	#	#	LC	12, 26, 42
	Hemiramphus brasiliensis (Linnaeus, 1758)	X	X	X	LC	26
	Hyporhamphus picarti (Valenciennes, 1847)	X	X	X	LC	26
Family **Exocoetidae**	*Cheilopogon cyanopterus* (Valenciennes, 1847)	X	#	#	LC	20, 26
	Cheilopogon melanurus (Valenciennes, 1847)	?	X	?	LC	12
	Cheilopogon milleri (Gibbs and Staiger, 1970)	#	X	X	LC	26
	Cheilopogon pinnatibarbatus (Bennett, 1831)	X	X	X	LC	
	Exocoetus obtusirostris Günther, 1866	?	#	?	LC	
	Exocoetus volitans Linnaeus, 1758	#	X	?	LC	
	Fodiator acutus (Valenciennes, 1847)	?	X	?	LC	
	Hirundichthys affinis (Günther, 1866)	X	#	#	LC	20, 26
	Prognichthys gibbifrons (Valenciennes, 1847)	X	#	X	LC	

Order Mugiliformes

Family **Mugilidae**	*Chelon dumerili* (Steindachner, 1870)	?	X	?	DD	
	Chelon richardsonii (Smith, 1846)	?	X	?	NE	30
	Mugil cephalus Linnaeus, 1758	X	X	X	LC	26
	Mugil curema Valenciennes, 1836	#	#	?	LC	18, 42, 47
	Parachelon grandisquamis (Valenciennes, 1836)	?	#	?	DD	18, 26, 28, 47

Order Gobiesociformes

Family **Gobiesocidae**	*Apletodon wirtzi* Fricke, 2007	E#	E#	?	LC	17, 18, 27, 40
	Lecanogaster gorgoniphila Fricke and Wirtz, 2017	?	E#	?	NE	34

Order Bleniiformes

Family **Labrisomidae**	*Labrisomus nuchipinnis* (Quoy and Gaimard, 1824)	#	#	#	LC	12, 27
Family **Blenniidae**	*Entomacrodus cadenati* Springer, 1967	?	X	#	LC	12, 27
	Hypleurochilus aequipinnis (Günther, 1861)	?	X	#	LC	12, 40
	Hypleurochilus langi (Fowler, 1923)	?	?	X	LC	27
	Hypleurochilus pseudoaequipinnis Bath, 1994	#	#	?	LC	18
	Microlipophrys velifer (Norman, 1935)	?	#	?	LC	12, 40
	Ophioblennius atlanticus (Valenciennes, 1836)	#	#	#	LC	12, 40
	Scartella cristata (Linnaeus, 1758)	?	#	#	LC	12

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
Order Acanthuriformes						
Family **Lobotidae**	*Lobotes surinamensis* (Bloch, 1790)	?	#	?	LC	12, 27
Family **Pomacanthidae**	*Centropyge aurantonotus* Burgess, 1974	?	#	?	LC	18, 40
	Holacanthus africanus Cadenat, 1951	#	X	?	LC	12, 27, 40
Family **Drepaneidae**	*Drepane africana* Osório, 1892	X	X	?	LC	12, 18, 20, 27, 42
Family **Chaetodontidae**	*Chaetodon hoefleri* Steindachner, 1881	?	#	#	LC	20, 27
	Chaetodon robustus Günther, 1860	?	#	?	LC	12, 18, 40, 42
	Prognathodes marcellae (Poll, 1950)	?	#	?	LC	18, 20, 27, 40
Family **Ephippidae**	*Chaetodipterus lippei* Steindachner, 1895	?	X	?	LC	30
	Ephippus goreensis Cuvier, 1831	?	X	?	LC	12, 20, 27, 40
Family **Acanthuridae**	*Acanthurus monroviae* Steindachner, 1876	X	X	#	LC	12, 18, 20, 27, 35
	Prionurus biafraensis (Blache and Rossignol, 1962)	E	E#	E	LC	12, 18, 27, 35
Family **Antigoniidae**	*Antigonia capros* Lowe, 1843	?	#	?	LC	27
Order Lophiiformes						
Family **Antennariidae**	*Antennarius multiocellatus* (Valenciennes, 1837)	?	#	?	LC	18
	Antennarius pardalis (Valenciennes, 1837)	#	#	?	LC	18, 20, 26
	Antennarius striatus (Shaw, 1794)	?	#	?	LC	26
	Histrio histrio (Linnaeus, 1758)	?	#	?	LC	26
Family **Oneirodidae**	*Lophodolos acanthognathus* Regan, 1925	?	#	?	LC	26
	Oneirodes anisacanthus (Regan, 1925)	?	#	?	DD	26
	Oneirodes carlsbergi (Regan and Trewavas, 1932)	?	#	?	LC	26
Family **Ceratiidae**	*Ceratias uranoscopus* Murray, 1877	?	#	?	LC	26, 46
	Cryptopsaras couesii Gill, 1883	?	#	?	LC	20
Family **Linophrynidae**	*Linophryne arborifera* Regan, 1925	?	#	?	LC	26
Order Tetraodontiformes						
Family **Diodontidae**	*Chilomycterus mauretanicus* (Le Danois, 1954)	#	X	X	LC	20, 27
	Chilomycterus reticulatus (Linnaeus, 1758)	?	X	#	LC	12, 40
	Diodon holocanthus Linnaeus, 1758	#	X	#	LC	12, 20
	Diodon hystrix Linnaeus, 1758	?	X	?	LC	12

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
Family **Tetraodontidae**	*Canthigaster rostrata* (Bloch, 1786)		Err #		LC	20
	Canthigaster supramacula Moura and Castro, 2002	#	#	?	LC	18, 35, 40
	Lagocephalus laevigatus (Linnaeus, 1766)	X	#	X	LC	12, 20, 27
	Lagocephalus lagocephalus (Linnaeus, 1758)	X	X	#	LC	20, 27
	Sphoeroides marmoratus (Lowe, 1838)	X	X	X	LC	12, 27, 35, 40
	Sphoeroides pachygaster (Müller and Troschel, 1848)	#	X	X	LC	20, 27
Family **Ostraciidae**	*Acanthostracion guineense* (Bleeker, 1865)	X	X	X	LC	20, 27
	Acanthostracion notacanthus (Bleeker, 1863)	#	X	?	DD	1, 39
Family **Monacanthidae**	*Aluterus heudelotii* Hollard, 1855	#	X	?	LC	30
	Aluterus monoceros (Linnaeus, 1758)	X	X	X	LC	20
	Aluterus schoepfii (Walbaum, 1792)	X	X	X	LC	27
	Aluterus scriptus (Osbeck, 1765)	X	#	X	LC	12, 27, 35, 40
	Cantherhines macrocerus (Hollard, 1853)	X	?	?	LC	43
	Cantherhines pullus (Ranzani, 1842)	X	X	#	LC	12, 27, 35, 40
	Stephanolepis hispida (Linnaeus, 1766)	#	X	#	LC	
Family **Balistidae**	*Balistes capriscus* Gmelin, 1789	#	#	#	VU	12, 20, 27, 35, 40
	Balistes punctatus Gmelin, 1789	#	#	X	VU	12, 20, 27, 35, 40
	Balistes vetula Linnaeus, 1758	X	X	X	NT	27
	Canthidermis maculata (Bloch, 1786)	X	#	X	LC	27
	Canthidermis sufflamen (Mitchill, 1815)	X	X	?	LC	12, 35, 40
	Melichthys niger (Bloch, 1786)	X	X	X	LC	27, 35, 40
Order Centrarchiformes						
Family **Kyphosidae**	*Kyphosus bigibbus* Lacépède, 1801	X	X	X	LC	27
	Kyphosus incisor (Cuvier, 1831)	X	#	X	NE	12, 28
	Kyphosus sectatrix (Linnaeus, 1758)	?	#	?	LC	42
	Kyphosus vaigiensis (Quoy and Gaimard, 1825)	X	X	X	LC	
Family **Cirrhitidae**	*Cirrhitus atlanticus* Osório, 1893	#	#	X	LC	12, 27, 35, 40
Order Acropomatiformes						
Family **Synagropidae**	*Synagrops bellus* (Goode and Bean, 1896)	?	#	?	LC	20
Family **Epigonidae**	*Epigonus constanciae* (Giglioli, 1880)	?	#	?	LC	18
	Epigonus denticulatus Dieuzeide, 1950	?	#	?	LC	
Family **Howellidae**	*Howella sherborni* (Norman, 1930)	#	#	?	NE	46

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
Order Perciformes *sedis mutabilis*						
Family **Serranidae**	*Alphestes afer* (Bloch, 1793)	?	X	?	LC	18, 27, 36, 40, 45
	Anthias anthias (Linnaeus, 1758)	#	#	X	LC	12, 20
	Anthias cyprinoides (Katayama and Amaoka, 1986)	?	?	X	DD	45
	Cephalopholis nigri (Günther, 1859)	#	#	?	LC	8, 12, 27, 35, 40, 42
	Cephalopholis taeniops (Valenciennes, 1828)	#	#	#	LC	8, 12, 27, 35, 40, 42, 45
	Epinephelus adscensionis (Osbeck, 1765)	#	#	#	LC	12, 40, 42, 45
	Epinephelus aeneus (Geoffroy Saint-Hilaire, 1817)	X	X	X	NT	12, 20, 27, 35
	Epinephelus costae (Steindachner, 1878)	X	X	X	DD	27
	Epinephelus goreensis (Valenciennes, 1830)	X	#	X	NT	12, 20, 27, 40
	Epinephelus marginatus (Lowe, 1834)	?	#	?	VU	27, 42
	Hyporthodus haifensis (Ben-Tuvia, 1953)	X	X	X	LC	27
	Liopropoma emanueli Wirtz and Schliewen, 2012	?	X	?	NE	31, 40
	Liopropoma n.sp.	X	X	?	-	18
	Paranthias furcifer (Valenciennes, 1828)	#	#	#	LC	8, 12, 20, 27, 40, 42
	Pseudogramma guineensis (Norman, 1935)	X	#	#	LC	18, 27, 45
	Rypticus saponaceus (Bloch and Schneider, 1801)	X	#	#	LC	12, 18, 20, 27, 35, 40, 42
	Rypticus subbifrenatus Gill, 1861	#	X	#	LC	18, 27, 45
	Serranus accraensis (Norman, 1931)	X	#	?	LC	20, 39, 45
	Serranus cabrilla (Linnaeus, 1758)	#	#	?	LC	27, 39, 42
	Serranus drewesi Iwamoto, 2018	?	E#	?	DD	39, 45
	Serranus heterurus (Cadenat, 1937)	?	#	#	LC	39, 45
	Serranus pulcher Wirtz and Iwamoto, 2016	E#	E#	?	LC	18, 32, 40, 45
Family **Priacanthidae**	*Heteropriacanthus cruentatus* (Lacépède, 1801)	X	X	#	LC	12, 35, 40
	Priacanthus arenatus Cuvier, 1829	#	#	X	LC	20
	Branchiostegus semifasciatus (Norman, 1931)	?	X	?	LC	12
Family **Emmelichthyidae**	*Erythrocles monodi* Poll and Cadenat, 1954	?	#	?	LC	12, 42
Family **Lutjanidae**	*Apsilus fuscus* Valenciennes, 1830	X	#	X	LC	2, 12, 20, 27, 40
	Lutjanus agennes Bleeker, 1863	X	#	X	DD	27, 28, 40, 47
	Lutjanus dentatus (Duméril, 1861)	#	#	X	DD	2, 27, 40, 42
	Lutjanus endecacanthus Bleeker, 1863	#	#	X	DD	2, 18, 27, 28, 42

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
	Lutjanus fulgens (Valenciennes, 1830)	X	#	X	LC	2, 12, 20, 27, 40, 42
	Lutjanus goreensis (Valenciennes, 1830)	#	#	X	DD	12, 20, 27, 28, 40, 47
	Lutjanus griseus (Linnaeus, 1758)	?	?	#	LC	
Family **Gerreidae**	*Eucinostomus melanopterus* (Bleeker, 1863)	X	#	#	LC	12, 27, 28, 42, 47
	Gerres nigri Günther, 1859	X	X	X	LC	27
Family **Haemulidae**	*Brachydeuterus auritus* (Valenciennes, 1832)	X	#	X	NT	18, 20, 27
	Parakuhlia macrophthalmus (Osório, 1893)	X	#	X	DD	12, 27, 40
	Parapristipoma humile (Bowdich, 1825)	X	X	X	LC	27
	Parapristipoma octolineatum (Valenciennes, 1833)	X	X	X	LC	27
	Plectorhinchus macrolepis (Boulenger, 1899)	X	#	X	LC	27, 28
	Plectorhinchus mediterraneus (Guichenot, 1850)	X	X	X	LC	27
	Pomadasys incisus (Bowdich, 1825)	X	#	#	LC	20, 27, 40, 42
	Pomadasys jubelini (Cuvier, 1830)	X	#	X	LC	28
	Pomadasys perotaei (Cuvier, 1830)	?	X	#	LC	
	Pomadasys rogerii (Cuvier, 1830)	X	#	X	LC	12, 20
	Pomadasys suillus (Valenciennes, 1833)	#	X	?	NE	
Family **Sparidae**	*Boops boops* (Linnaeus, 1758)	X	#	X	LC	12, 20, 27, 35, 40, 42
	Dentex canariensis Steindachner, 1881		Err		LC	20
	Dentex congoensis Poll, 1954	#	#	X	LC	12, 20, 27, 42
	Dentex gibbosus (Rafinesque, 1810)	X	X	X	LC	27
	Dentex macrophthalmus (Bloch, 1791)	X	X	X	LC	27
	Lithognathus mormyrus (Linnaeus, 1758)	X	X	X	LC	27
	Oblada melanura (Linnaeus, 1758)	X	X	X	LC	27, 35
	Pagellus bellottii Steindachner, 1882	X	#	X	LC	12, 20, 27, 42
	Pagrus africanus Akazaki, 1962	X	X	X	LC	27
	Pagrus auriga Valenciennes, 1843	X	X	X	LC	27
	Pagrus caeruleostictus (Valenciennes, 1830)	X	#	X	LC	12, 20, 27, 42
	Pagrus pagrus (Linnaeus, 1758)	?	X	?	LC	
	Spicara alta (Osório, 1917)	X	X	X	LC	27
	Spicara melanurus (Valenciennes, 1830)	X	X	X	LC	27, 40
	Spicara nigricauda (Norman, 1931)	X	#	?	LC	12

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
	Spondyliosoma cantharus (Linnaeus, 1758)	X	X	X	LC	27
Family **Lethrinidae**	*Lethrinus atlanticus* Valenciennes, 1830	#	#	#	LC	6, 12, 20, 27, 40, 42
Family **Sciaenidae**	*Pseudotolithus senegalensis* (Valenciennes, 1833)	?	#	?	EN	18, 20
	Pseudotolithus senegallus (Cuvier, 1830)	?	#	?	VU	18, 42
	Umbrina canariensis Valenciennes, 1843	?	X	#	LC	20
	Umbrina cirrosa (Linnaeus, 1758)	?	X	?	VU	18
Family **Monodactylidae**	*Monodactylus sebae* (Cuvier, 1829)	X	#	X	LC	18, 27, 28
Family **Cepolidae**	*Cepola pauciradiata* Cadenat, 1950	X	#	X	DD	27
Order Perciformes						
Family **Pomacentridae**	*Abudefduf hoefleri* (Steindachner, 1881)	X	#	?	DD	27, 35, 40, 42
	Abudefduf saxatilis (Linnaeus, 1758)	X	#	X	LC	12, 27, 35, 40, 42
	Abudefduf taurus (Müller and Troschel, 1848)	?	#	#	LC	18
	Azurina multilineata (Guichenot, 1853)	#	X	?	LC	12, 27, 35, 40
	Chromis cadenati Whitley, 1951	?	X	?	LC	31, 40
	Chromis limbata (Valenciennes, 1833)	?	X	?	LC	31, 40
	Microspathodon frontatus Emery, 1970	X	#	#	LC	12, 27, 35, 40, 42
	Stegastes imbricatus Jenyns, 1840	#	#	#	LC	12
Family **Labridae**	*Acantholabrus palloni* (Risso, 1810)	X	X	X	LC	18, 27
	Bodianus pulchellus (Poey, 1860)	?	#	?	LC	12, 18, 40, 42
	Bodianus speciosus (Bowdich, 1825)	X	X	X	DD	12, 20
	Clepticus africanus Heiser, Moura and Robertson, 2000	?	E#	?	DD	18, 35
	Coris atlantica Günther, 1862	X	X	?	LC	12, 35, 40
	Doratonotus megalepis Günther, 1862	X	X	?	LC	27
	Thalassoma newtoni (Osório, 1891)	X	#	?	LC	18, 27
	Xyrichtys novacula (Linnaeus, 1758)	#	#	X	LC	12, 20, 27, 35, 40
	Xyrichtys sanctaehelenae (Günther, 1868)	?	#	?	LC	18
Family **Scaridae**	*Nicholsina collettei* Schultz, 1968	X	X	X	LC	18, 27
	Nicholsina usta (Valenciennes, 1840)	?	#	?	LC	18
	Scarus hoefleri (Steindachner, 1881)	#	#	X	LC	12, 27, 35, 40
	Sparisoma choati Rocha, Brito and Robertson, 2012	X	#	X	NE	18, 23, 27, 35

(continued)

Higher taxonomy	Species	P	S	A	IUCN	Reference
Family **Ammodytidae**	*Gymnammodytes capensis* (Barnard, 1927)	?	X	?	LC	
Family **Trachinidae**	*Trachinus armatus* Bleeker, 1861	X	#	?	LC	20
	Trachinus lineolatus Fischer, 1885	?	X	?	LC	26
	Trachinus radiatus Cuvier, 1829	X	?	?	LC	20
Family **Uranoscopidae**	*Uranoscopus albesca* Regan, 1915	X	X	X	LC	27
	Uranoscopus cadenati Poll, 1959	X	X	X	LC	27
	Uranoscopus polli Cadenat, 1951	#	X	X	LC	12, 20, 27
Family **Bembropidae**	*Bembrops greyae* Poll, 1959	?	#	?	LC	27, 44
Family **Sebastidae**	*Helicolenus dactylopterus* (Delaroche, 1809)	X	X	X	LC	26
Family **Setarchidae**	*Ectreposebastes imus* Garman, 1899	X	X	#	LC	26
	Setarches guentheri Johnson, 1862	X	X	X	LC	26
Family **Scorpaenidae**	*Pontinus accraensis* Norman, 1935	X	#	X	LC	18, 26
	Pontinus kuhlii (Bowdich, 1825)	?	#	?	DD	12, 26
	Scorpaena angolensis Norman, 1935	X	X	X	LC	26
	Scorpaena annobonae Eschmeyer, 1969	?	?	#	DD	
	Scorpaena elongata Cadenat, 1943	X	X	X	LC	26
	Scorpaena laevis Troschel, 1866	X	#	#	LC	12, 20, 26
	Scorpaena normani Cadenat, 1943	X	X	X	LC	26
	Scorpaena stephanica Cadenat, 1943	X	X	X	LC	26
	Scorpaenodes africanus Pfaff, 1933	?	#	#	DD	18, 26
Family **Triglidae**	*Chelidonichthys gabonensis* (Poll and Roux, 1955)	?	#	?	LC	20
	Chelidonichthys lastoviza (Bonnaterre, 1788)	X	?	?	LC	20
	Lepidotrigla cadmani Regan, 1915	#	#	X	LC	26
	Lepidotrigla carolae Richards, 1968	X	#	X	LC	20, 26
Family **Peristediidae**	*Peristedion cataphractum* (Linnaeus, 1758)	X	X	X	LC	26
Family **Platycephalidae**	*Solitas gruveli* (Pellegrin, 1905)	X	#	X	LC	20, 26

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Chapter 18
The Amphibians of the Gulf of Guinea Oceanic Islands

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Abstract This chapter reviews the diversity, evolutionary relationships, ecology, and conservation of the Gulf of Guinea oceanic islands' endemic caecilian and anuran fauna. A total of nine amphibian species (representing five families) are known from São Tomé and Príncipe islands, all of which are endemic. No amphibians have been reported from Annobón. Taxonomic research on this group of animals began in the second half of the nineteenth century with subsequent refinement following the advent of molecular techniques. The presence of several amphibians from distinct evolutionary lineages is unexpected for oceanic islands and has motivated several biogeographic studies to reconstruct the evolutionary histories of these enigmatic species. Yet, the continental source for many of the islands' amphibians remains unknown. The amphibians of São Tomé and Príncipe also exhibit intriguing phenotypic diversity for addressing long-standing hypotheses in evolutionary biology, including body size evolution and gigantism on islands, intraspecific variation and interspecific divergence in coloration, and reproductive and dietary niche partitioning. Recent studies have confirmed the presence of the fungal pathogen *Batrachochytrium dendrobatidis* in amphibian communities on both São Tomé and Príncipe, but it is unclear whether this pathogen is negatively impacting local populations. Most of the Gulf of Guinea oceanic island endemic amphibians are incredibly abundant and widespread, occurring in primary forest, secondary forest, and agricultural habitats across the islands. Three anuran species

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(*Hyperolius thomensis, Leptopelis palmatus, Ptychadena newtoni*) have more limited distributions and/or more specialized ecologies; consequently, additional land-use change poses a threat to the long-term persistence of these taxa.

Keywords Anura · Gymnophiona · Hybridization · Endemism · Taxonomy · Conservation

Introduction

Island faunas have inspired evolutionary biologists for centuries, and the enigmatic history of insular amphibians is particularly captivating. Amphibians are considered poor dispersers across saltwater barriers and are thus naturally absent from most oceanic islands (Darwin 1859; Vitt and Caldwell 2014). Yet overseas dispersal and in situ diversification have contributed to the accumulation of a surprisingly diverse amphibian fauna in the Gulf of Guinea oceanic islands, which are located 250–300 km from the western coast of Central Africa. The presence of a combined nine amphibian species on São Tomé and Príncipe islands, all of which are endemic, presents an intriguing biogeographic anomaly within which to explore the potential pathways and timing of overseas dispersal events. In addition, some lineages have further diversified within and between islands in the archipelago, presenting the opportunity to investigate the tempo and mechanisms underlying in situ diversification. This chapter presents an updated taxonomic overview of the amphibians on São Tomé and Príncipe islands (no amphibians occur on Annobón), highlighting the biogeographic patterns, organismal biology, and conservation threats for each species. The amphibian fauna of Bioko Island, a land-bridge island that is part of the Gulf of Guinea archipelago, is entirely distinct from that of the oceanic islands in the archipelago (see Sánchez-Vialas et al. 2020). We also provide a brief history of the research on amphibians in the archipelago and highlight important avenues for future work.

History of Amphibian Research

The history of amphibian research in the Gulf of Guinea oceanic islands is closely linked to the history of reptile research, as most authors have worked with both groups. Ceríaco et al. (2022) provide a comprehensive summary of the herpetological surveys and studies carried out on the islands. Hence, we focus on the primarily amphibian-focused studies and refer to Ceríaco et al. (2022) for more general studies.

The first herpetological studies in the Gulf of Guinea oceanic islands were based on opportunistic collections by European medical staff and colonial officers who visited or worked in the region. The first published record of an amphibian from São Tomé dates to 1868, when the German zoologist Wilhelm C. H. Peters (1815–1883) described the Príncipe Giant Tree Frog *Hylambates* (currently *Leptopelis*) *palmatus* based on three female specimens (holotype ZMB 6067) collected by German explorer Heinrich Wolfgang Ludwig Dhorn (1838–1913) on Príncipe (Peters 1868). In 1870, Peters described the Príncipe Puddle Frog *Arthroleptis dispar* (later transferred to *Phrynobatrachus* by Laurent 1941) based on a single specimen from Príncipe (holotype ZMB 6133; Peters 1870), also collected by Dhorn. In 1873, the Portuguese zoologist José Vicente Barboza du Bocage (1823–1907), director of the National Museum of Lisbon (also known as Museu Bocage, now Museu Nacional de História Natural e da Ciência, Lisbon, Portugal; MUHNAC), described the São Tomé caecilian *Siphonops* (currently *Schistometopum*) *thomense* based on two preserved specimens donated to the museum by Pedro Carlos de Aguiar Craveiro Lopes (1834–?), Portuguese governor of São Tomé and Príncipe at the time (Bocage 1873). In 1874, Peters described *Siphonops brevirostris* based on a single specimen with imprecise locality information ("Westküste Afrikas [Guinea]") that he acquired from an animal dealer (Peters 1874). The type locality for *S. brevirostris* has since been restricted to Ilhéu das Rolas (Gorham 1962), but the justification for this restriction is doubtful (Nussbaum and Pfrender 1998). This specimen is extant at the Museum für Naturkunde (Berlin, Germany; ZMB) and Nussbaum and Pfrender (1998) indicate the holotype is ZMB 4911 rather than ZMB 4711 as reported in the description. In his major revision of caecilians, Peters subsequently placed both *S. thomense* and *S. brevirostris* in the primarily neotropical genus *Dermophis* based on a combination of shared morphological features (Peters 1879). Upon examining specimens of *S. thomense*, Peters later determined that his *S. brevirostris* was the same as Bocage's *S. thomense* (Peters 1880), and this synonymy continues to be recognized by most authors. Finally, Parker (1941) placed the species in the genus *Schistometopum* where it remains today.

The German zoologist Richard Greeff (1829–1892) explored São Tomé and Ilhéu das Rolas (a small islet ~2 km off the southern tip of São Tomé) from 1879 to 1880 and provided one of the first reports of its herpetofauna (Greeff 1884a). Greeff was particularly interested in São Tomé caecilians and published a brief study on their biology (Greeff 1884b). Greeff's specimens are still extant in the collections of the Museum für Naturkunde (Berlin, Germany; ZMB), Zoologische Staatssammlung München (München, Germany; ZSM), and Zoologisches Museum Hamburg (Hamburg, Germany; ZMH).

In 1885, the Botanical Gardens of the University of Coimbra sent their chief gardener Adolfo Frederico Möller (1842–1920) to São Tomé to explore and collect natural history specimens for the Botanical Gardens and the university museum. Most of the zoological specimens collected by Möller were sent to the University of Coimbra (now part of the Museu da Ciência da Universidade de Coimbra; Coimbra, Portugal; MCUC) and Vieira (1886) published a brief inventory of these specimens. Almost all of this material was examined and identified by José Vicente Barbosa du Bocage and is still extant in the collections of MCUC (Themido 1941; LMPC pers. obs.). Some amphibian and reptile specimens, however, were likely sent by Möller to the Russian zoologist Jacques von Bedriaga (1854–1906) who was a scholar at the University of Coimbra. Bedriaga published a thorough revision of the amphibians and reptiles of São Tomé (Bedriaga 1892), where he described Moller's Reed Frog, *Rappia* (currently *Hyperolius*) *molleri*, endemic to São Tomé (Bedriaga 1892). There are no further records of the specimens sent by Möller to Bedriaga, and they are presumably lost; however, one syntype of *H. molleri* is extant at the Natural History Museum (London, UK; NHMUK).

Also in 1885, Francisco Xavier Oakley de Aguiar Newton (1864–1909) was hired by the Museu Bocage to conduct zoological surveys in the Gulf of Guinea. From 1885 to 1895, Newton explored all the Gulf of Guinea islands, as well as Benin, and his specimens were ultimately deposited in the Museu Bocage. The amphibians were studied by Barbosa du Bocage and based on this collection, he described the São Tomé Giant Reed frog *Hyperolius thomensis* and Newton's Grassland frog *Rana* (currently *Ptychadena*) *newtoni,* both from São Tomé (Bocage 1886). Unfortunately, the entirety of Newton's collections was lost in the fire that destroyed the Museu Bocage in 1978.

The Italian explorer Leonardo Fea (1852–1903) explored the four principal islands of the Gulf of Guinea from 1901 to 1902 under the sponsorship of the Museo Civico di Storia Naturale of Genoa (currently known as Museo Civico di Storia Naturale "Giacomo Doria;" Genoa, Italy; MSNG). Fea's collections were initially studied by George Albert Boulenger (1858–1937; Boulenger 1906) and are still extant in the MSNG with a small subset in the Natural History Museum of London (NHMUK). Based on material Fea collected on Príncipe, Boulenger (1906) described *Phrynobatrachus feae*, which was later placed in synonymy with *P. dispar* by Schätti and Loumont (1992).

During the 1950s and 1960s, the Portuguese Zoology Center of the Overseas Research Committee (Centro de Zoologia da Junta de Investigações do Ultramar; Lisbon, Portugal; CZL) conducted zoological surveys on São Tomé and Príncipe. Several herpetological specimens were collected by different researchers associated with the colonial enterprise over the course of multiple scientific surveys. The material collected during these surveys was studied by the Portuguese herpetologist Sara Maria Bárbara Marques Manaças (1896–?), resulting in two publications (Manaças 1958, 1973). Most of the specimens were housed in the collections of the Instituto de Investigação Científica Tropical (Lisbon, Portugal; IICT), but in 2016 they were incorporated into the MUHNAC collections.

Throughout the 1960s and 1970s, several authors used existing specimens in various collections for taxonomic revisions of different genera. For instance, the Swiss herpetologist Jean-Luc Perret (b. 1925) reviewed the taxonomic position and status of São Tomé and Príncipe anurans (Perret 1962, 1966, 1973, 1976, 1988). Perret placed both reed frog species in a new genus *Nesionixalus* based on several shared morphological features (Perret 1976); however, subsequent morphological and genetic analyses have found strong support for both species belonging to the genus *Hyperolius* (Drewes 1984; Drewes and Wilkinson 2004; Portik et al. 2019). The North American herpetologist Edward Harrison Taylor (1889–1978) described *Schistometopum ephele* based on material collected from São Tomé by the Leonardo Fea Expedition and deposited in the MSNG (MSNG 8773; Taylor 1965).

Following the independence of São Tomé and Príncipe from Portugal in 1975, several teams undertook expeditions to the islands to document biodiversity. In 1984 a team from the zoology and anthropology department of the Faculty of Sciences of the University of Lisbon and the Museu Bocage, Lisbon, Portugal, led by Luis Mendes (b. 1946), conducted a 1-month zoological expedition to São Tomé (Mendes et al. 1988). Although the expedition did not have a dedicated herpetologist, some amphibian specimens were collected, and these are extant in MUHNAC collections.

Ronald Nussbaum (b. 1942) from the University of Michigan and Michael Pfrender (b. 1960) visited the islands of São Tomé and Príncipe in 1988 and placed *S. ephele* in synonymy with *S. thomense* (Nussbaum and Pfrender 1998). The specimens they collected are in the University of Michigan Museum of Zoology (Ann Arbor, United States of America; UMMZ). From 1989 to 1991, expeditions to São Tomé and Príncipe led by Catherine Loumont (b. 1942), Tillman Nill (dates unknown) Jakob Fahr (dates unknown) and Jan Haft (b. 1967), resulted in reviews of the herpetofauna of these islands, including important natural history data on amphibians (Loumont 1992; Schätti and Loumont 1992; Fahr 1993; Haft and Franzen 1996). Some of these specimens are housed in the ZMB and the collections of the Musée d'Histoire Naturelle de la Ville de Genéve, Switzerland (MHNG).

The beginning of the twenty-first century marked a new period for the study of the amphibians of the Gulf of Guinea oceanic islands. Robert C. Drewes (b. 1942), herpetology curator of the California Academy of Sciences (San Francisco, United States of America; CAS), and his team have made 12 expeditions to the islands since 2001. The amphibian collections resulting from these expeditions are deposited at CAS and are currently the largest in the world (Table 18.1). Drewes and his colleagues have published several studies, including the description of the São Tomé Puddle Frog, *Phrynobatrachus leveleve* (Uyeda et al. 2007), taxonomic reviews and updates (Drewes and Stoelting 2004; Drewes and Wilkinson 2004), biogeographic history (Measey et al. 2007), and population genetics (Stoelting et al. 2014). During this same period, John Measey (b. 1968) and colleagues conducted evolutionary, ecological, and biomechanics studies of the São Tomé caecilian, making important contributions to our understanding of these secretive animals (Delêtre and Measey 2004; Measey and Herrel 2006; Measey and Van Dongen 2006; Wollenberg and Measey 2009; Herrel and Measey 2010, 2012). More recently, Rayna C. Bell (b. 1985), herpetology curator of the CAS, has contributed studies on the biogeographic and evolutionary history of *Hyperolius* (Bell et al. 2015a, b, 2017), hybridization of *H. molleri* and *H. thomensis* on São Tomé (Bell et al. 2015b; Bell and Irian 2019), the description of *H. drewesi*, endemic to Príncipe, and the evolutionary history of the São Tomé caecilians (O'Connell et al. 2021). As the type material of *H. thomensis* was lost in the 1978 fire at the Museu Bocage in Lisbon, Portugal (Drewes and Wilkinson 2004), and the original type localities of *H. thomensis* and *H. molleri* were vague and may have included individuals with hybrid ancestry, Bell (2016) designated neotypes for both *H. thomensis* and *H. molleri*. Bell participated in several expeditions led by Drewes, and most of the specimens are at CAS with a smaller subset at the Smithsonian Institution's National

Table 18.1 Natural history institutions housing type specimens and significant collections of amphibians from the Gulf of Guinea oceanic islands. Total number of specimen records includes tadpole lots and clutches of eggs. Acronyms follow Sabaj (2020)

Collection	São Tomé	Príncipe	Type specimens	Total
CAS—California Academy of Sciences, San Francisco, California, USA	793	320	4	1113
UMMZ—University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA	757	16	–	773
MHNG—Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland	583	39	–	622
MSNG—*Museo* Civico di Storia Naturale "Giacomo Doria," Genova, Italy	68	55	22	123
MUHNAC/IICT—Museu Nacional de História Natural e da Ciência/Instituto de Investigação Científica Tropical, Lisbon, Portugal	68	43	–	111
NHMUK—Natural History Museum, London, UK	60	13	2	75
USNM—National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, USA	29	35	–	64
NMP-P6V—National Museum in Prague, Prague, Czech Republic	19	–	–	19
ZMB—Museum für Naturkunde, Berlin, Germany	17	3	3	20
FMNH—Field Museum of Natural History, Chicago, Illinois, USA	14	–	–	14
ZSM—Zoologische Staatssammlung München, München	8	–	–	8
MCUC—Museu da Ciência da Universidade de Coimbra, Coimbra, Portugal	7	–	–	7
ZMH—Zoologisches Museum Hamburg, Hamburg, Germany	4	–	–	4

Museum of Natural History (Washington DC, United States of America; USNM). Since 2013, a team from MUHNAC led by Luis M. P. Ceríaco (b. 1987) completed four herpetological surveys in São Tomé and Príncipe. A few amphibian specimens were collected and are now housed in MUHNAC.

Diversity and Endemism

Although the islands of São Tomé and Príncipe have never been physically connected to the African continent, they host a remarkable nine endemic species of amphibians, each of which is restricted to just one of the islands (Table 18.2, Fig. 18.1). We provide a brief summary of the taxonomic status of each species, its biogeographic history (when known), and notes on distribution, ecology, and behavior.

Table 18.2 List of amphibians from Príncipe and São Tomé islands (no amphibians are known from Annobón)

Higher taxonomy	Species/subspecies	P	ST	IUCN
Order Gymnophiona				
Family **Dermophiidae**				
Schistometopum Parker 1941	*Schistometopum thomense* (Bocage 1873)		E	LC
	Schistometopum ephele (Taylor 1965)		E	
Order Anura				
Family **Arthroleptidae**				
Leptopelis Günther 1859 "1858"	*Leptopelis palmatus* (Peters 1868)	E		EN
Family **Hyperoliidae**				
Hyperolius Rapp, 1842	*Hyperolius drewesi* Bell 2016	E		
	Hyperolius molleri (Bedriaga 1892)		E	LC
	Hyperolius thomensis Bocage 1886		E	EN
Family **Phrynobatrachidae**				
Phrynobatrachus Günther, 1862	*Phrynobatrachus dispar* (Peters, 1870)	E		LC
	Phrynobatrachus leveleve Uyeda, Drewes & Zimkus 2007		E	LC
Family **Ptychadenidae**				
Ptychadena Boulenger 1917	*Ptychadena newtoni* (Bocage 1886)		E	EN

E, endemic. IUCN Red List Categories (IUCN 2021): LC, least concern; VU, vulnerable; EN, Endangered

Gymnophiona

Caecilian diversity in the Gulf of Guinea oceanic islands includes two endemic species (family Dermophiidae) that are distributed across São Tomé Island, even though caecilians were reported from Príncipe Island in error (Taylor 1968). The presence of these enigmatic and secretive amphibians on an oceanic island is especially captivating given their presumed low vagility and dispersal potential (Taylor 1968). Caecilians are not the only fossorial vertebrates that have reached the archipelago, however, as there are also several endemic fossorial squamates on both São Tomé and Príncipe (Ceríaco et al. 2022). This high level of endemic diversity among vertebrates with low dispersal potential provides strong support for the overseas rafting hypothesis proposed by Measey et al. (2007) and described in further detail in Melo et al. (2022).

Family Dermophiidae

The São Tomé caecilian *S. thomense* was initially described by Bocage (1873), and though he did not observe the species in life, he noted the two preserved specimens were uniform light yellow and olive in coloration, respectively. Unfortunately, a fire

Fig. 18.1 Gulf of Guinea oceanic island amphibians: (**1**) São Tomé caecilians, *Schistometopum thomense* (top) and *Schistometopum ephele* (bottom), from São Tomé Island; (**2**) Príncipe Giant Tree Frog, *Leptopelis palmatus*, from Príncipe Island; (**3**) Drewes' Reed Frog, *Hyperolius drewesi*, from Príncipe Island; (**4**) Moller's Reed Frog, *Hyperolius molleri*, from São Tomé Island; (**5**) São Tomé Giant Reed Frog, *Hyperolius thomensis*, from São Tomé Island; (**6**) Leveleve Puddle Frog, *Phrynobatrachus leveleve*, from São Tomé Island; (**7**) Príncipe Puddle Frog, *Phrynobatrachus dispar*, from Príncipe Island; (**8**) Newton's Grass Frog, *Ptychadena newtoni*, from São Tomé Island. Photo credits: Andrew Stanbridge

at the Lisbon Museum in 1978 destroyed this material and reports of a possible extant syntype at the Berlin Museum (ZMB 8738) are doubtful because the size of the specimen does not match Bocage's description (Nussbaum and Pfrender 1998). Several decades later, Taylor described *S. ephele* and recognized *S. ephele* as distinct from *S. thomense* based on its smaller, pointier head and prominent brown flecking pattern (Taylor 1965). The provenance of this material is reported as "Agua Izé, 400–700 m, Ilha São Thomé," a locality that is likely between Agua Izé (a coastal community on the eastern side of the island) and the community of Java that is directly inland of Agua Izé at ~600 m elevation (pers comm G. Doria, MSNG). In the description, Taylor also noted that two other individuals under this number were uniform yellow (unflecked) and thus referred to *S. thomense*. Nussbaum and Pfrender (1998) quantified coloration, morphometric, and meristic variation of *Schistometopum* specimens collected from ten sites across São Tomé (including Ilhéu das Rolas). Although they found strong separation in a multivariate comparison of northern and southern populations, Nussbaum and Pfrender (1998) interpreted this variation as a phenotypic cline in a widespread species, placing *S. ephele* in synonymy with *S. thomense*. Stoelting et al. (2014) revisited this hypothesis with mtDNA (16s and ND4) sequence data and sampling from more than 20 sites across the island. These authors found deep genetic divergence between lineages that they proposed may correspond to *S. thomense* and *S. ephele*; however, the distributions of these mtDNA lineages overlapped in the center of the island. Consequently, Stoelting et al. (2014) proposed that the lineages diverged in allopatry but refrained from making taxonomic recommendations solely based on these maternally inherited loci. A more recent study examining genome-wide variation found strong support for distinct lineages corresponding to *S. thomense* and *S. ephele*, and inferred a history of divergence in allopatry with a narrow hybrid zone where the ranges presently overlap in the center of São Tomé Island (O'Connell et al. 2021). Based on this evolutionary history, and the revised interpretation of the apparent phenotypic cline in the Nussbaum and Pfrender (1998) study, O'Connell et al. (2021) removed *S. ephele* from synonymy with *S. thomense*.

The only other species in the genus *Schistometopum* is the East African *S. gregorii*, which presents an intriguing biogeographic scenario for the island endemic species (Wilkinson et al. 2003; San Mauro et al. 2014). Depending on the method and/or mutation rate used, estimates for divergence between *S. thomense* and *S. gregorii* based on mtDNA loci range from 0.6 to 3.2 Myr (Loader et al. 2007), indicating that dispersal to São Tomé occurred relatively recently in the islands' 13 Myr history. Using genome-wide markers, divergence between *S. thomense* and *S. ephele* on São Tomé was estimated at 281–326 kya with secondary contact between the lineages occurring ~100 kya (O'Connell et al. 2021), highlighting that São Tomé is accumulating endemic diversity via both overseas dispersal and in situ diversification even in the more recent period of its long geologic history. On São Tomé, caecilians occur in a wide variety of habitats ranging from sea level to over 1400 m elevation, including agricultural fields, modified landscapes, and the ~2 km^2 islet Ilhéu das Rolas (Bocage 1886; Loumont 1992; Fahr 1993; Haft and Franzen 1996; Nussbaum and Pfrender 1998; Drewes and Stoelting 2004; Measey and Van

Dongen 2006; Stoelting et al. 2014). Due to this broad distribution and high abundance (estimated density 0.3 per m^2; Measey 2006), caecilians are well known to São Toméans, who refer to them as “Cobra-bobô” (i.e., yellow snake).

At collection sites with harder, mineral soils, animals may be found under leaf litter or rotten logs, whereas at sites with softer soils, including agricultural fields, animals are found within the soil (Haft 1992; Haft and Franzen 1996; Delêtre and Measey 2004). Likewise, in drier habitats, caecilians occur deeper in the soil (Nussbaum and Pfrender 1998) whereas, after heavy rains and in the evening, they can be observed moving aboveground (Fahr 1993; Haft and Franzen 1996). Correspondingly, laboratory studies quantifying the behavior and biomechanics of burrowing in São Tomé caecilians indicated that they did not construct tunnels in soils with high compaction and that even intermediate levels of soil compaction can deter or prevent burrowing (Ducey et al. 1993). In addition, in laboratory settings, caecilians opted to use existing tunnels rather than construct new ones (Ducey et al. 1993). These behaviors are consistent with the more terminal mouth position of São Tomé caecilians relative to the subterminal (countersunk lower jaw) mouths of caecilians that are dedicated burrowers (Sherratt et al. 2014). Like all caecilians, São Tomé caecilians show skin-vertebral independence and use internal and whole-body concertina locomotion while burrowing or moving through narrow tunnels (Herrel and Measey 2010). When moving across high friction substrates (i.e., a moist towel) São Tomé caecilians switch to lateral undulating locomotion (Herrel and Measey 2010). An extensive survey of caecilian body size variation across São Tomé found that individuals at higher elevation sites (where soil temperatures are cooler) were longer and heavier than individuals at lower elevations (Measey and Van Dongen 2006). This trend has been noted in many endothermic vertebrates with the explanation that larger body sizes result in lower heat loss via larger surface-area-to-volume ratios (Bergmann 1847); however, the potential mechanisms to explain this pattern in an ectotherm are less clear.

São Tomé caecilians are sexually dimorphic in head size (but not in body size), which could indicate ecological divergence between the sexes (e.g., differences in diet; Nussbaum and Pfrender 1998) or antagonistic behaviors among males (Delêtre and Measey 2004). Delêtre and Measey (2004) tested this first hypothesis with a diet study of males, females, and juveniles from both natural forest and agricultural sites. Earthworms (including epigeic [surface-active] and endogeic [deeper soil-dwelling] species) accounted for over 98% of identified prey items, with the remaining contents comprising centipedes, ants, mites, and unidentified larvae (Delêtre and Measey 2004). Counter to expectations, the authors did not find significant differences in prey mass or prey size between the sexes (though prey size did correlate with gape diameter among females), suggesting that larger head size in males is not related to capturing larger prey. A subsequent study of caecilian diets reexamined the Delêtre and Measey (2004) earthworm morphospecies dataset and found that adults fed on both epigeic and endogeic earthworms in equal proportions, whereas juveniles appeared to only feed on endogeic species (Jones et al. 2006). Future research investigating the extent of dietary specialization in São Tomé caecilians (across habitats and throughout the year) as well as potential ontogenetic shifts in diet will provide important insight into the role caecilians play in mediating population dynamics of soil ecosystem engineers (earthworms, termites and ants) and soil ecology more broadly (Lavelle et al. 1997; Jones et al. 2006).

Observations in captivity suggest that São Tomé caecilians are predominantly nocturnal, sit-and-wait predators, extending their heads beyond their burrows and waiting for prey to come within reach (Haft and Franzen 1996; Hofer 1998). To our knowledge, predation behaviors in field settings have not yet been documented in the scientific literature; however, in laboratory settings São Tomé caecilians feeding on earthworms exerted strong bite forces and used long-axis body rotations to subdue and shred their prey (Measey and Herrel 2006; Herrel and Measey 2012). Laboratory measurements of resting metabolism and aerobic capacity of São Tomé caecilians indicated they have very low resting metabolic rates with a high capacity for aerobic metabolism that is consistent with a largely sedentary, sit-and-wait predatory lifestyle (Smits and Flanagin 1994). The same study also revealed surprisingly high cutaneous gas exchange in caecilians despite their thickened skin, suggesting that cutaneous respiration is likely sufficient to support resting metabolic rates (Smits and Flanagin 1994).

Based on the current understanding of reproductive biology in caecilians, all species have internal fertilization via an intromittent organ formed by an eversible portion of the male's cloaca (the phallodaeum) that may vary in shape and ornamentation among species (Gower and Wilkinson 2002). The phallodaeum of São Tomé caecilians is quite similar to that of *S. gregorii* from Tanzania, but Tanzanian and Kenyan *S. gregorii* differ from one another, and these populations have previously been hypothesized to be distinct species (Taylor 1968; Gower and Wilkinson 2002). A better understanding of intraspecific and interspecific variation in phallodaeum morphology would provide deeper insights as to the potential significance of this trait in reproductive isolation. Several authors have noted bite marks on the heads of male and female São Tomé caecilians from both field-caught and laboratory individuals (e.g., Nussbaum and Pfrender 1998; Teodecki et al. 1998). Biting among conspecific males in territorial disputes and males biting females during copulation have been proposed as alternative hypotheses for larger head size in males (Delêtre and Measey 2004). The role of biting in communication and/or sexual selection in São Tomé caecilians would be a compelling future avenue of behavioral research in these curious organisms.

Viviparity has evolved independently in several lineages of caecilians, including the family Dermophiidae, which are all viviparous (Gower et al. 2008; San Mauro et al. 2014). Observations of São Tomé caecilians in captivity suggest clutch sizes typically range from 2 to 7 young that are fully formed at birth with no signs of gill scars (Nussbaum and Pfrender 1998). The energetic demands of reproduction are likely high as young caecilians are born at up to 50% the length of their mothers (Wake 1977; Nussbaum and Pfrender 1998), and females reproduce biennially (Teodecki et al. 1998). In addition, developing fetuses have specialized dentition with which to scrape the epithelium of the oviduct and stimulate the secretion of nutrient-rich "uterine milk" from their mothers during gestation (Parker 1956; Parker and Dunn 1964; Wake 1977). Captive-born young reached adult size after 2 years

(Haft and Franzen 1996), and the adult coloration and pattern were present at birth (Nussbaum and Pfrender 1998). It is tempting to consider that the prominent yellow coloration of São Tomé caecilians may be aposematic, and a study of yellow coloration across all caecilians indicates that this conspicuous coloration has evolved multiple times in species that are surface-active (Wollenberg and Measey 2009). Anecdotal evidence suggests São Tomé caecilians are distasteful (Hofer 1998; Teodecki et al. 1998); however, their chemical defenses have not yet been characterized. Likewise, the dominant predators of São Tomé caecilians are also unknown; consequently, much additional foundational research is needed to understand whether this yellow coloration is cryptic or aposematic. While a role in intraspecific communication and/or sexual selection is also a possible explanation for this bright coloration, São Tomé caecilians likely have poor eyesight (Mohun et al. 2010) and like all caecilians are considered to rely primarily on olfactory cues to sense their environments (Himstedt and Simon 1995).

Anura

Anuran diversity in the Gulf of Guinea oceanic islands includes seven endemic species from four families: Arthroleptidae, Hyperoliidae, Phrynobatrachidae, and Ptychadenidae (Table 18.2).

Family Arthroleptidae

The Príncipe Giant Tree Frog *Leptopelis palmatus* has historically been confused with another large-bodied species from continental Africa, *L. rufus*, with several authors placing *L. rufus* in synonymy with *L. palmatus* (Anderson 1909; Parker 1936; Witte 1941; Perret 1962). Throughout this period of nearly a century of taxonomic confusion, *L. palmatus* was reported from Cameroon, Equatorial Guinea (including Bioko Island), Gabon, and Nigeria (Boulenger 1882; Mocquard 1902; Boulenger 1906; Nieden 1910; Ahl 1931; Schiøtz 1963; Mertens 1965). Perret (1973) resurrected *L. rufus* after comparing a large series of males and females with the sole female holotype of *L. palmatus* available for study and clarified that *L. palmatus* was an insular species. Upon this close examination, Perret (1973) confirmed that the two species differed in tympanum size and several additional morphological features, concluding that the two species may not even be closely related. Male specimens were finally collected and formally described following an expedition to the islands in 2002 (Drewes and Stoelting 2004). Loumont (1992) characterized the karyotype of this species, reporting 24 chromosomes.

The phylogenetic relationships within the African genus *Leptopelis* are poorly understood, and consequently, the biogeographic history of *L. palmatus* remains unclear. Previous studies have hypothesized that *L. palmatus* is closely related to a group of large-bodied species in West and Central Africa (*L. macrotis, L. millsoni,* and *L. rufus*) based on a combination of mtDNA and morphological data (Idris 2004). A more recent mtDNA phylogeny with expanded taxonomic sampling does not support this relationship (Jaynes et al. 2021), and a more robust phylogenetic inference is sorely needed. The distribution of *L. palmatus* ranges from sea level to over 600 m elevation on Príncipe, primarily in forested habitats (Loumont 1992; Drewes and Stoelting 2004). Males and females can be observed at night perched one meter or higher off the ground on branches or leaves, especially near small flowing streams (Loumont 1992; Drewes and Stoelting 2004; RCB and LAS pers. obs). By contrast, large females have been encountered on or near the ground both in the evening and during the day (Drewes and Stoelting 2004; RCB and LAS pers obs). Although males lack vocal sacs (Drewes and Stoelting 2004), they produce advertisement calls at breeding sites (characterized in Jaynes et al. 2021). Both male and female dorsal coloration is variable, ranging from dark green/black with or without small white spots to bright green and even bright yellow (Manaças 1958; Loumont 1992; Drewes and Stoelting 2004; Jaynes et al. 2021). It does not appear that this variation is sexually dimorphic or related to ontogeny, as has been described in many species of the African genus *Hyperolius* (Schiøtz 1967; Portik et al. 2019). Manaças (1958) reported Orthoptera (crickets), Blattodea (cockroaches and termites), and Coleoptera (beetles) in the stomach contents of specimens they examined.

Sexual size dimorphism is quite pronounced in *L. palmatus,* with male snout–vent length less than half that of females (Drewes and Stoelting 2004). In addition, the largest measured female was 110 mm snout–vent length (Loumont 1992), which remains the largest reported size of any female specimen in the entire genus *Leptopelis* by more than 20 mm (Channing and Rödel 2019). Despite these large adult body sizes, post-metamorphic individuals are quite small (10–11 mm; Drewes and Stoelting 2004). This combination of extreme sexual size dimorphism and exceptionally large body size in females may indicate selection for increased fecundity (e.g., Darwin 1874). Unfortunately, the reproductive biology of *L. palmatus* is entirely unknown. Other species in the genus *Leptopelis* bury their eggs in humid soil from which larvae hatch and complete their development within streams or ponds (Portik and Blackburn 2016). One species, *L. brevirostris*, is thought to reproduce by direct development because females produce large eggs that are buried far from water (Perret 1966; Amiet and Schiøtz 1974; Schiøtz 1999). Documenting this important aspect of its biology will be critical to understanding the habitats *L. palmatus* relies upon throughout its lifecycle.

Family Hyperoliidae

Three species of reed frogs in the genus *Hyperolius* are endemic to the islands of São Tomé and Príncipe: the São Tomé Giant Reed Frog *Hyperolius thomensis* and Moller's Reed Frog *H. molleri* (both endemic to São Tomé), and *H. drewesi* (endemic to Príncipe). Prior to the recognition of *H. drewesi* as a distinct species, *H. molleri* was reported from both São Tomé and Príncipe islands (Loumont 1992;

Fahr 1993; Drewes and Wilkinson 2004). Loumont (1992) characterized the karyotypes of *H. thomensis* and *H. molleri* (*sensu stricto*), reporting 24 chromosomes.

Phylogenetic analyses indicate that the three island species form a monophyletic group and are part of the *H. cinnamomeoventris* species complex (Drewes and Wilkinson 2004; Schick et al. 2010; Bell et al. 2015a, 2017; Portik et al. 2019). Within the *H. cinnamomeoventris* species complex, the island endemics are most closely related to *H. olivaceus*, a species distributed throughout the Lower Guinean forests of Gabon and the Republic of Congo (Bell et al. 2017). The distribution of *H. olivaceus* encompasses the Ogooué River and the mouth of the Congo River, suggesting that either river drainage could have served as a source for a vegetation raft that ferried reed frogs to the archipelago. Divergence time estimates indicate the island endemics and *H. olivaceus* shared a most recent common ancestor in the Late-Miocene to Pliocene (Bell et al. 2015a, 2017; Portik et al. 2019). The island endemics, however, shared a most recent common ancestor within the last 1.7–0.5 Ma, with divergence between *H. molleri* and *H. drewesi* estimated at 1.1 Ma to 270 ka (Bell et al. 2015a). As with the São Tomé caecilians, the timing of colonization and in situ diversification of the reed frogs are quite recent in the islands' long geological histories. The pattern of divergence among the three species is consistent with a single dispersal event to the islands and suggests that reed frogs first colonized São Tomé Island, diversified in situ, and then dispersed to Príncipe Island (Bell et al. 2015a, b). The pattern of lower genetic diversity in *H. drewesi* relative to *H. molleri* is also consistent with this colonization history (Bell et al. 2015b). Although it appears that dispersal between São Tomé and Príncipe occurred at some point in the past, analyses of mtDNA and genome-wide variation indicated that gene flow between the islands is not ongoing (Bell et al. 2015b).

H. thomensis inhabits closed-canopy, primary forest habitats from 300 to 1300 m elevation, which are primarily on the wetter southern half of São Tomé (Loumont 1992; Drewes and Stoelting 2004; Gilbert and Bell 2018; Bell and Irian 2019). By contrast, *H. molleri* occurs in a wide range of habitats across the island from sea level to ~1400 m elevation, including swampy areas in the drier habitats on the northern side of São Tomé, agricultural areas, secondary and primary forests (Loumont 1992; Fahr 1993; Bell et al. 2015b; Gilbert and Bell 2018; Bell and Irian 2019). *H. drewesi* is ecologically similar to *H. molleri*, occurring in a wide range of habitats across Príncipe Island from sea level to ~600 m elevation (Loumont 1992; Drewes and Stoelting 2004; Bell 2016). Observations in the field and in captivity suggest that all three species are primarily nocturnal (Fahr 1993); however, like most anurans, these species are primarily observed during their reproductive periods, and thus less is known about their activities during other times of day or throughout the rest of the year.

The forest specialist *H. thomensis* differs from the other two species in its reproductive biology. First, males of *H. thomensis* produce advertisement calls from high up in the canopy (from 1 to >5 m), whereas males of *H. molleri* and *H. drewesi* call from perches 30–200 cm above ground on leaves and thin branches overhanging slow-moving streams and pools of standing water (Fahr 1993; Gilbert and Bell 2018). Furthermore, the abundance of individuals at breeding sites varies between species, with only a single to several *H. thomensis* calling at a given site versus upwards of 50 individuals of *H. molleri* congregating along a 15 m long stretch of stream (Fahr 1993; Gilbert and Bell 2018). These differences in calling site and breeding aggregation size may be associated with the specialized microhabitats *H. thomensis* select to deposit their eggs. While *H. molleri* and *H. drewesi* deposit their egg masses on leaves overhanging water (Fahr 1993; Drewes and Stoelting 2004; Bell 2016), which is the typical reproductive mode for *Hyperolius* (Portik and Blackburn 2016), *H. thomensis* deposit their eggs on the walls of water-filled cavities in trees, rotting logs, and bamboo (Drewes and Stoelting 2004; Gilbert and Bell 2018). These specialized breeding microhabitats are the only standing water available for anuran reproduction in some landscapes and may provide shelter to vulnerable eggs and larvae from potential predators (Drewes and Stoelting 2004; Lehtinen et al. 2004); however, they also present some unique challenges (lower dissolved oxygen, lower nutrient availability; Guimarães-Souza et al. 2006; Ferreira et al. 2019). Large egg size (2–2.5 mm; Perret 1976) and small clutch size in *H. thomensis* (20–40; Drewes and Stoelting 2004) relative to most species of *Hyperolius* (Channing and Rödel 2019) may be adaptations to the specialized reproduction in this species.

All three *Hyperolius* endemic to São Tomé and Príncipe are sexually dimorphic in size, with females displaying larger body sizes than males (Bell 2016; Bell and Irian 2019). The forest specialist *H. thomensis* is also substantially larger than *H. molleri, H. drewesi,* and *H. olivaceus* and is among the largest of the ~150 described species in the genus (Portik et al. 2020). The selective mechanisms underlying body size evolution in *Hyperolius* and in anurans more broadly are still poorly understood (Womack and Bell 2020); consequently, investigating ecological differences among these closely related species may provide some important insights. For instance, although both *H. thomensis* and *H. molleri* are insectivorous (Perret 1976), they may consume different sizes or types of prey, as demonstrated in other sympatric reed frog species that differ in body size (Luiselli et al. 2004). Males of all three species possess dorsal epidermal asperities (fine projections from the skin; Perret 1988), which are pigmented in *H. thomensis* and *H. molleri* but not in *H. drewesi* (Bell 2016). The potential functions of these sexually dimorphic features, which are also present in several continental species of *Hyperolius*, are poorly understood. Although the island reed frogs do not exhibit sexual dichromatism, as exhibited by a large proportion of the genus *Hyperolius* (Portik et al. 2019), *H. molleri* and *H. drewesi* exhibit differences in juvenile and adult coloration (Schiøtz 1967) with metamorphic and juvenile individuals of both species displaying light brown coloration with thin, white dorsolateral lines (Loumont 1992; Fahr 1993; Bell 2016). In addition, *H. thomensis* exhibit bright orange and black ventral coloration that is often associated with aposematism and chemical defense in amphibians (e.g., Kang et al. 2017), but this hypothesis has not yet been tested in *H. thomensis*. A handful of colorful *Hyperolius* from Cameroon was screened for defensive alkaloids, and none were found (Portik et al. 2015). Similar to *L. palmatus*, *H. thomensis* also exhibit extensive variation in dorsal coloration ranging from dark or bright green to turquoise to golden with dark spots, whereas both *H. molleri* and *H. drewesi* are consistently bright green (RCB and LAS pers. obs).

Despite differences in body size, coloration, and breeding biology, *H. thomensis* and *H. molleri* hybridize where their ranges are sympatric (Bell et al. 2015b). Males of the two species produce advertisement calls that differ in dominant frequency, and these differences are strongly correlated with body size (Gilbert and Bell 2018). Correspondingly, hybrid males are intermediate in body size and produce advertisement calls with intermediate peak frequencies (Gilbert and Bell 2018). Variation in both size and ventral coloration among hybrid frogs overlaps with that of *H. molleri* (Bell and Irian 2019); consequently, hybrids cannot reliably be identified without genetic analysis. Several sites with high proportions of hybrid individuals are at the boundary of primary forest and agricultural development, where breeding frogs congregate around artificial bodies of water (e.g., cisterns; Bell and Irian 2019). Hybrids can also be found at the crater lake Lagoa Amélia, which is within 1 km of the forest edge (Bell and Irian 2019). Although adult *H. thomensis* can be found in anthropogenically modified habitats and reproduce at these sites (Strauss et al. 2018), these environments may be population sinks if larvae and juveniles experience lower survival than in forested sites. In addition, the geographic extent of hybridization between *H. thomensis* and *H. molleri* across the island is unknown as are the potential consequences of hybridization, both of which warrant further attention.

Family Phrynobatrachidae

Two species of puddle frogs in the genus *Phrynobatrachus* are endemic to São Tomé and Príncipe: *P. dispar* on Príncipe and *P. leveleve* on São Tomé and Ilhéu das Rolas. Prior to the recognition of *P. dispar* and *P. leveleve* as a distinct species, *P. dispar* was reported from both Príncipe and São Tomé (including Ilhéu das Rolas; Boulenger 1906; Loumont 1992; Fahr 1993; Drewes and Stoelting 2004). Loumont (1992) characterized the karyotypes of *Phrynobatrachus* on both São Tomé and Príncipe, reporting 16 chromosomes.

Unlike the island endemic reed frogs, phylogenetic analyses of the genus *Phrynobatrachus* indicate that divergence between *P. dispar* on Príncipe and *P. leveleve* on São Tomé is not recent (Uyeda et al. 2007; Zimkus et al. 2010). Genetic divergence at mtDNA (cytochrome b) between the two is ~19% (Uyeda et al. 2007), and the island endemics form a monophyletic group with *P. mababiensis* (Zimkus et al. 2010), a southern African species that ranges from Angola to Tanzania and Mozambique (Channing and Rödel 2019). This pattern suggests that *Phrynobatrachus* may have colonized the archipelago twice, though estimates of continental species diversity and phylogenetic relationships in this genus are still in a state of flux. Genetic diversity within species on each island (based on mtDNA) is quite low, further supporting the existence of only a single species on each island and Schätti and Loumont's (1992) proposed synonymy of Boulenger's *P. feae* (Uyeda et al. 2007).

Puddle frogs are abundant and widespread on both islands (and on Ilhéu das Rolas), occurring from sea level to ~1400 m on São Tomé and from sea level to ~950 m on Príncipe in primary forest, secondary forest, agricultural fields and residential areas (Loumont 1992; Fahr 1993; Drewes and Stoelting 2004; Uyeda et al. 2007). They can be found perched low to the ground in grasses or shrubs, in crevices, and on the ground, especially near small bodies of water (Loumont 1992; Fahr 1993). Like many species of *Phrynobatrachus*, *P. dispar* and *P. leveleve* are active during the day and at night but are most often encountered at twilight (Fahr 1993). Both species use a wide range of water bodies for reproduction, including small temporary puddles at higher elevations (Fahr 1993), which *P. leveleve* sometimes share with *Ptychadena newtoni* (Drewes and Stoelting 2004). On Príncipe, *P. dispar* shares breeding sites with *H. drewesi* and heterospecific amplexus between the species has been observed (Bell and Scheinberg 2016). Relatively small clutch size (15–30 eggs) and rapid larval development (14–20 days) suggest the puddle frogs' reproductive biology is well suited for breeding in ephemeral puddles, which may enable *P. dispar* and *P. leveleve* to occupy higher elevations than the other island endemic anurans (Fahr 1993). Male advertisement calls have been described, however, these studies were conducted prior to two species being recognized, and the calls likely correspond only to *P. leveleve* (Loumont 1992; Fahr 1993). Likewise, Fahr (1993) reports that adults in captivity live up to 2 years, but it is not clear whether these observations correspond to *P. dispar* or to *P. leveleve* or both.

Like many frogs, *P. dispar* and *P. leveleve* exhibit sexual size dimorphism with females being slightly larger than males (Uyeda et al. 2007). These diminutive frogs fall within the typical size range of *Phrynobatrachus* on the continent (Channing and Rödel 2019); however, similar to the São Tomé caecilians, patterns of intraspecific body size variation on each island are consistent with Bergmann's Rule with larger individuals occupying higher elevations (Uyeda et al. 2007). Males of both species have dorsal epidermal asperities, and these are also present in females of *P. dispar* but apparently absent in female *P. leveleve* (Uyeda et al. 2007). Both species are also highly variable in coloration but are generally of various shades and patterns of brown (Uyeda et al. 2007).

Family Ptychadenidae

Newton's Grassland Frog *P. newtoni* is endemic to São Tomé, but like many of the Gulf of Guinea amphibians, this species has a convoluted taxonomic history. First, *P. newtoni* was placed in synonymy of *P. oxyrhynchus* by Andersson (1937), and then in synonymy of *P. mascareniensis* by Guibé and Lamotte (1957). Perret (1976) removed *P. newtoni* from synonymy with *P. mascareniensis* and noted that although the species resembled *P. oxyrhynchus*, it was likely unique given the high level of endemism on the Gulf of Guinea islands. A phylogenetic study of mitochondrial DNA indicated that *P. newtoni* was indeed unique and that it was part of the *P. mascareniensis* species complex (Measey et al. 2007). Loumont (1992) characterized the karyotype of *P. newtoni,* reporting 24 chromosomes.

The *P. mascareniensis* complex consists of a dozen named and candidate taxa with a distribution that covers much of continental Africa, Madagascar, the Seychelles, and the Mascarenes (Zimkus et al. 2017). Within the *P. mascareniensis* species complex, *P. newtoni* appears to be most closely related to the Nile Grass frog, *P. nilotica*, which occurs along the Nile Basin and into eastern Africa (Zimkus et al. 2017). This relationship is somewhat surprising considering that lineages within the *P. mascareniensis* complex occur throughout West and Central Africa, and are much more proximate to the Gulf of Guinea. Previous authors have interpreted this pattern as evidence for rafting along the Congo River drainage as a dispersal route to the islands (Measey et al. 2007). Divergence time estimates suggest *P. newtoni* and *P. nilotica* shared a most recent common ancestor in the Mid- to Late-Miocene (Zimkus et al. 2017); however, a more robust phylogeny of the *P. mascareniensis* species complex will provide a better understanding of the evolutionary history of *P. newtoni*.

On São Tomé, *P. newtoni* occurs in lower elevation habitats (sea level to ~600 m) including plains, agricultural fields, and around human-built structures (Loumont 1992; Fahr 1993; Drewes and Stoelting 2004). Most of the remaining habitat at these lower elevations is heavily impacted by human activities, and thus while *P. newtoni* appears to be somewhat resilient to these landscape changes, there is some concern that very little of its original habitat remains (Fahr 1993; Drewes and Stoelting 2004). Not much is known of the biology of *P. newtoni*. Throughout its distribution, *P. newtoni* occurs with both *H. molleri* and *P. leveleve,* and the three species may use the same temporary water bodies for reproduction (Fahr 1993; Drewes and Stoelting 2004). As with most anurans, this species is sexually size-dimorphic and is the largest species in the genus *Ptychadena* with females reaching up to 76 mm snout–vent length (Loumont 1992; Channing and Rödel 2019). Its advertisement call is described (Loumont 1992; Fahr 1993) and it is mostly a nocturnal species but can be found during the day if it is raining (Fahr 1993). Like most *Ptychadena*, *P. newtoni* is primarily a ground-dwelling species and is a very accomplished jumper (Fahr 1993). As documented in *P. mascareniensis* on Madagascar (Tolojanahary et al. 2011), the diet of *P. newtoni* likely consists primarily of arthropods.

Conservation

Most of the Gulf of Guinea oceanic island endemic amphibians are incredibly abundant and widespread, occurring in primary forest, secondary forest, and agricultural habitats across the islands (e.g., *S. ephele, S. thomense, H. molleri, H. drewesi, P. dispar, P. leveleve*). By contrast, *H. thomensis*, *L. palmatus* and *P. newtoni* appear to have more specialized habitat requirements, and these habitats are under considerable anthropogenic pressure. Consequently, these species are considered Endangered according to the most recent IUCN assessments (Table 18.2; IUCN 2021). In the case of *H. thomensis* and *L. palmatus*, these species appear to prefer closed-canopy forest habitats and have more specialized reproduction; thus, they may be more susceptible to deforestation. For *H. thomensis* in particular, deforestation may directly limit the availability of suitable breeding sites as cavities that collect water typically occur in large mature trees. Furthermore, if deforestation is associated with hybridization between *H. thomensis* and *H. molleri* (as suggested in Bell and Irian 2019), the rarer *H. thomensis* may be at risk of extinction by hybridization (Rhymer and Simberloff 1996). In the case of *P. newtoni*, although this species occurs around the São Tomé capital and other heavily modified landscapes (e.g., the Agripalma oil palm plantation), very little of its original habitat remains unchanged and the impacts of land use on recruitment and adult survival are unknown. Although the São Tomé caecilian also appears quite resilient to land-use change, reports that it may be extirpated from the heavily developed Ilhéu das Rolas are concerning (Loumont 1992).

The amphibian chytrid fungal pathogen, *Batrachochytrium dendrobatidis* (Bd), is implicated in the declines and extinctions of amphibians across the globe (Scheele et al. 2019). Although the pathogen has been documented in many species across the Afrotropics, our understanding of how this pathogen impacts Afrotropical anuran diversity lags far behind that of other regions (Zimkus et al. 2020). Surveys of freshly sampled and historical specimens confirmed that the pathogen is present on both São Tomé and Príncipe (Hydeman et al. 2013, 2017). The earliest infections date from the oldest specimens screened to date (2001), indicating that the pathogen has been present on the islands for at least 20 years (Hydeman et al. 2017). All of the endemic species have tested positive for Bd (including the caecilians), and genomic sequencing of the positive samples indicates that the more virulent Bd-GPL strain occurs on the islands (Byrne et al. 2019). No symptomatic individuals have been reported; however, we recommend careful monitoring of this emergent pathogen.

Future Research

The biogeographic history of the amphibian fauna of the Gulf of Guinea oceanic islands is emerging as our understanding of evolutionary relationships within African genera continues to improve. Robust phylogenies of *Leptopelis* and *Phrynobatrachus*, and better resolution within the *Ptychadena mascareniensis* species complex, will fill important gaps in our understanding of how and when representatives of these genera reached the islands. The ecology and behavior of all the island species are incompletely understood, including basic aspects of reproductive biology (e.g., *L. palmatus*) and dependence on particular habitats (e.g., *P. newtoni*, *H. thomensis*), which are likely important considerations for effective conservation management. Like most vertebrates, São Tomé and Príncipe's amphibians also serve as hosts for many parasites, including the fungal pathogen Bd and a recently described nematode (*Meteterakis saotomensis*; Junker et al. 2015), but the diversity of this microfauna and potential impacts on the amphibian hosts are poorly known. For instance, a recent study identified cryptic infection of *P. leveleve* (misidentified as *P. dispar* in the study) tadpoles by Perkinsea protists (Chambouvet et al. 2015) that have caused mass mortality events in the United States (Davis et al. 2007). Further studies investigating the prevalence of this parasite in the tadpoles of the other endemics and whether it is associated with tadpole mortality are sorely needed. Beyond these more practical avenues for future research, the amphibians of São Tomé and Príncipe also exhibit intriguing phenotypic diversity for addressing long-standing hypotheses in evolutionary biology, including body size evolution and gigantism on islands (e.g., *H. thomensis*, *L. palmatus*, *P. newtoni*), intraspecific variation and interspecific divergence in coloration, and reproductive and dietary niche partitioning.

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Chapter 19
The Terrestrial Reptiles of the Gulf of Guinea Oceanic Islands

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Abstract This chapter reviews current knowledge on the diversity of terrestrial reptiles in the Gulf of Guinea oceanic islands and provides a brief history of research on this group of animals. A total of 29 species of terrestrial reptiles (representing 14 genera and seven families) are resident on the Gulf of Guinea oceanic islands, of which 22 species are endemic. Taxonomic work on these animals began in the second half of the nineteenth century, with more recent updates following the advent of molecular techniques and more comprehensive sampling. Although nearly complete, the taxonomic inventory of the Gulf of Guinea oceanic island terrestrial

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reptiles is still ongoing, and further studies on the natural history, ecology, and conservation of these animals are urgently needed.

Keywords Conservation · Endemism · Herpetofauna · Introduced species · Taxonomy

Introduction

Across the world, islands harbor a rich diversity of reptile species, many of them endemic. In contrast to other groups of non-volant terrestrial vertebrates such as small mammals and amphibians, reptiles are successful dispersers across marine barriers due to their ecology and physiology, which enable them to endure long-distance rafting events (Vitt and Caldwell 2004). Some island reptiles, such as the Galapagos tortoises and marine iguanas, rank amongst the most iconic species in the world. These species are especially famous for providing Charles Darwin (1809–1882) with the inspiration for his theory of evolution by natural selection. Island reptiles have since become important models for the study of evolution and adaptation in insular environments. For instance, the anoles (Squamata: Dactyloidea) of the West Indies and lacertids (Squamata: Lacertidae) of the Mediterranean islands are now classic systems for evolutionary and ecological studies (e.g., Corti et al. 2006; Losos 2009). In the eastern Atlantic, reptiles of the Madeira, Cabo Verde and the Gulf of Guinea oceanic archipelagos have been the subject of phylogenetic and biogeographic studies (e.g., Jesus et al. 2003, 2005a–c, 2006, 2007, 2009; Vasconcelos et al. 2010), recent descriptions of cryptic diversity (e.g., Miller et al. 2012; Ceríaco 2015; Ceríaco et al. 2016, 2017, 2021a; Soares et al. 2018), as well as ecological studies (e.g., Lopes et al. 2019).

With approximately 30 species and exceptional endemism, the Gulf of Guinea archipelago is a hotspot for reptile diversity, especially when considering the small land area of the islands. Here we present an updated taxonomic overview of the terrestrial reptiles of these islands and surrounding islets, highlighting diversity, endemism, biogeographic patterns and conservation. Marine turtles are the only non-terrestrial reptiles occurring in these islands and are covered in Ferreira-Airaud et al. (2022). We also provide a brief history of the research on reptiles in the archipelago and highlight important avenues for future work.

History of Reptile Research

The first record of a reptile from the Gulf of Guinea oceanic islands was the description of *Mocoa* (currently *Panaspis*) *africana* by Gray (1845). There are no data regarding the collector or precise locality of collection, but the type locality has since been restricted to Príncipe Island (Soares et al. 2018). Some decades later, the curator of the Zoological Museum of Berlin, Wilhelm Peters (1815–1883), described *Typhlops* (*Ophthamidion*) [currently *Afrotyphlops*] *elegans* based on specimens collected by the German explorer Heinrich Wolfgang Ludwig Dhorn (1838–1913) on Príncipe (Peters 1868). Subsequently, the German zoologist Richard Greeff (1829–1892) explored São Tomé and Rolas islet from 1879 to 1880 and provided one of the first reports of their herpetofauna (Greeff 1884). Based on specimens collected by Greeff, two species of reptile were described: *Scalabotes* (now *Lygodactylus*) *thomensis* by Peters (1881) and *Hemidactylus greeffii* by Bocage (1886a). Some of Greeff's specimens are still extant in the collections of the Museum für Naturkunde Berlin (ZMB) and Zoologisches Museum Hamburg (ZMH).

Following Greeff's surveys, two Portuguese museums funded expeditions to the Gulf of Guinea oceanic islands. In 1885, the Botanical Gardens of the University of Coimbra sent their chief gardener Adolfo Frederico Möller (1842–1920) to São Tomé to explore and collect natural history specimens for the Botanical Gardens and the university museum. Most of the zoological specimens collected by Möller were sent to the Zoological Museum of the University of Coimbra (ZMUC, now part of the Museu da Ciência da Universidade de Coimbra—MCUC), and a brief inventory of these specimens was published by Vieira (1886). Almost all of this material was examined and identified by the Portuguese zoologist José Vicente Barbosa du Bocage (1823–1907) and is still extant in the collections of MCUC (Themido 1941; LMPC pers. obs.). Some amphibian and reptile specimens, however, were likely sent by Möller to the Russian zoologist Jacques von Bedriaga (1854–1906) who was a correspondent scholar with the University of Coimbra. Bedriaga published a thorough revision of the amphibians and reptiles of São Tomé and described a new subspecies of gecko, *Hemidactylus mabouia* var. *molleri* (currently a synonym of *H. longicephalus*, see below), in honor of Adolfo Möller and provided a detailed description of a specimen of *Dendroaspis jamesonii* from the island (Bedriaga 1892, 1893a–c). Bedriaga's publications triggered criticism from Bocage (1892a–c, 1893), who cast doubts on the identity of *Hemidactylus mabouia* var. *molleri* (Bocage 1892a) and the *Dendroaspis* (Bocage 1892c). These disagreements have since been addressed in Ceríaco and Marques (2012) and Ceríaco et al. (2018). There are no further records of the specimens sent by Möller to Bedriaga and they are presumably lost.

Also in 1885, Francisco Xavier Oakley de Aguiar Newton (1864–1909), commonly known as Francisco Newton, was hired by the National Museum of Lisbon to conduct zoological surveys in the Gulf of Guinea. From 1885 to 1895, Newton explored all the Gulf of Guinea islands, as well as Benin, and his specimens were ultimately deposited in the Zoological Section of the National Museum of Lisbon. This material was studied by Barbosa du Bocage, director of the museum, and Júlio Guilherme Bethencourt Ferreira (1866–1948), Bocage's pupil. Based on Newton's collections Bocage described four species of reptile from the Gulf of Guinea oceanic islands: *Feylinia polylepis*, *Mabuia* [= currently *Trachylepis*] *ozorii*, *Typhlops* [= currently *Letheobia*] *newtoni*, and *Philothamnus girardi*. Also based on these collections, Bocage provided important revisionary works on the fauna of these islands (Bocage 1886a–c, 1873, 1887, 1890, 1892a–c, 1893, 1895, 1903, 1905), and Ferreira (1897) described *Hemidactylus newtoni* from Annobón. The entirety of Newton's collections was unfortunately lost in the fire that destroyed the Museu Bocage, Lisbon, in 1978.

Following Newton's steps, the Italian explorer Leonardo Fea (1852–1903) explored the four principal islands of the Gulf of Guinea from 1901 to 1902 under the sponsorship of the Museo Civico di Storia Naturale of Genoa, Italy (currently known as Museo Civico di Storia Naturale "Giacomo Doria;" MSNG). Fea's collections, which are still extant in the MSNG with a small subset in the Natural History Museum of London (BMNH), were initially studied by George Albert Boulenger (1858–1937). Based on these collections, Boulenger (1906) described four new taxa: *Hemidactylus aporus* from Annobón, *Typhlops* [currently *Letheobia*] *feae* from São Tomé, *Boodon* [=*Boaedon*] *bedriagae*, from both São Tomé and Príncipe, and *Gastropyxis* [currently *Hapsidophrys*] *principis* from Príncipe. Some of these specimens were revisited by Lilia Capocaccia in a revision of certain snake genera (Capocaccia 1961a) and the type catalog of the MSNG (Capocaccia 1961b).

A small collection of reptiles from São Tomé and Príncipe, collected by Henri Navel (1878–1963) in 1920, was subsequently studied by the French herpetologist Fernand Angel (1881–1950), who described *Typhlops naveli* (currently considered as a junior synonym of *Letheobia newtoni*; fide Roux-Estève 1974) from Príncipe (Angel 1920). An additional contribution to the knowledge of São Tomé snakes was provided by the curator of the American Museum of Natural History, Charles M. Bogert (1908–1992), who used specimens collected by the Portuguese explorer José G. Correia (1881–1954) to review the identity of the São Tomé Jitas (*Boaedon*; Bogert 1940).

During the 1950s and 1960s the Portuguese Centro de Zoologia da Junta de Investigações do Ultramar (CZL) conducted zoological surveys on São Tomé and Príncipe. The first mission, conducted by the Portuguese zoologist Fernando Frade Viegas da Costa (1898–1983; commonly referred to simply as Fernando Frade), lasted from September 10 to December 26, 1954. Between 1966 and 1967, several herpetological specimens were collected by different researchers associated with the colonial enterprise over the course of multiple scientific surveys. The material collected during these surveys was studied by the Portuguese herpetologist Sara Maria Bárbara Marques Manaças (1896–death date unknown), resulting in two publications (Manaças 1958, 1973). Most of the specimens were housed in the collections of the Instituto de Investigação Científica Tropical (IICT), in Lisbon, Portugal, but in 2016 they were incorporated into the collections of the Museu Nacional de História Natural e da Ciência (MUHNAC), of the University of Lisbon, Lisbon, Portugal. A total of 157 reptile specimens from these expeditions are still extant in these collections (Ceríaco and Marques 2018; Ceríaco et al. 2021b).

Throughout the 1960s and 1970s, several authors used existing specimens in various collections for taxonomic revisions of different genera, resulting in important contributions to the knowledge of the Gulf of Guinea oceanic islands taxa. For instance, the French herpetologist Georges Pasteur (1930–2015) used specimens of the Fea collections in the BMNH to revise the *Lygodactylus* of these islands (Pasteur 1962), leading to the description of two subspecies of *L. thomensis*: *L. thomensis delicatus* from Príncipe, and *L. thomensis wermuthi* from Annobón. The Swiss herpetologist Jean-Luc Perret (1925–) used specimens from the CZL and Fea collections in the BMNH for his major revision of the genus *Panaspis* (Perret 1972). Subsequently, the Romanian herpetologist Ion Eduard Fuhn (1916–1987) used specimens from Fea collections housed in the BMNH to describe *Panaspis annobonensis* from Annobón and review the *Panaspis* of São Tomé and Príncipe, at the time both considered *P. africana* (Fuhn 1972).

Following the independence of Equatorial Guinea (from Spain in 1968) and São Tomé and Príncipe (from Portugal in 1975), several teams undertook expeditions to the islands to further expand knowledge on their herpetological diversity. In 1984 a team from the zoology and anthropology department of the Faculty of Sciences of the University of Lisbon and the Museu Nacional de História Natural (Museu Bocage), Lisbon, led by Luis Mendes (1946–), conducted a 1 month (June 13 to July 7) zoological expedition to São Tomé (Mendes et al. 1988). Although the expedition did not have a dedicated herpetologist, some reptile specimens were collected, and these are still extant in MUHNAC collections (Ceríaco and Marques 2019).

Ronald Nussbaum (1942–) from the University of Michigan and Michael Prfender (1960–) visited the islands of São Tomé and Príncipe in June and July of 1988. While mainly focused on the study of amphibians, especially the São Tomé endemic caecilian *Schistometopum thomense* (Bocage, 1873), Nussbaum and Pfrender also collected several reptile specimens, of which 333 are still in the collections of the University of Michigan Museum of Zoology (UMMZ; see University of Michigan Museum of Zoology 2020). These specimens have not been included in any publication or study, although they represent the third largest reptile collection from São Tomé and Príncipe in any museum and are an important source of data on the geographical distributions of many species. From 1989 to 1991 expeditions to São Tomé and Príncipe led by Catherine Loumont (1942–), Tillman Nill (date of birth unknown), Jakob Fahr (1966–) and Jan Haft (1967–), resulted in reviews of the herpetofauna of these islands (Schätti and Loumont 1992; Nill 1993; Haft 1993). Some of these specimens are housed in the ZMB and the collections of the Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland (Andreas Schmitz pers. comm.)

A major contribution to our understanding of the herpetofauna of the three oceanic islands of the Gulf of Guinea was provided by José Jesus (1967–) from the University of Madeira, Funchal, Portugal, who dedicated part of his Ph.D. thesis to study the phylogeny and phylogeography of the islands' reptiles, providing molecular data for many of the taxa. Jesus and his team visited Príncipe, São Tomé and Annobón in the summer of 2002, and based on the specimens and tissues collected, provided the first molecular phylogenetic and phylogeographic context for the species of the genus *Trachylepis* (Jesus et al. 2005a, b), *Hemidactylus* (Jesus et al. 2005c), *Lygodactylus* (Jesus et al. 2006), *Panaspis* (Jesus et al. 2007) and *Philothamnus* (Jesus et al. 2009) occurring in these islands. Jesus et al. (2003) also provided an updated checklist of the reptiles of Annobón, in which they noted the first records of Tropical House Gecko, *Hemidactylus mabouia*, and the invasive Flowerpot snake, *Indotyphlops braminus* on the island. The specimens collected by Jesus and his team were primarily deposited in the collections of the University of Madeira, with smaller subsets in MUHNAC and the California Academy of Sciences (CAS), San Francisco.

Table 19.1 Main natural history institutions housing reptile specimens from the Gulf of Guinea oceanic islands. Acronyms follow Sabaj (2020)

Collection	São Tomé	Príncipe	Annobón	Type specimens	Total
CAS: California Academy of Sciences, San Francisco, United States of America	228	219	8	24	455
MUHNAC/IICT: Museu Nacional de História Natural e da Ciência/Instituto de Investigação Científica Tropical, Lisbon, Portugal	108	239	14	26	361
UMMZ: University of Michigan Museum of Zoology, Ann Arbor, United States of America	122	210	–	–	332
MHNG: Muséum d'Histoire naturelle de la Ville de Genève, Geneva, Switzerland	136	–	–	7	136
MSNG: Museo Civico di Storia Naturale 'Giacomo Doria', Genova, Italy	43	49	9	5	101
MHNCUP: Museu de História Natural e da Ciência da Universidade do Porto, Porto, Portugal	22	18	–	–	40
MNHN: Muséum National d'Histoire Naturelle, Paris, France	13	5		–	18
NHM: Natural History Museum, London, United Kingdom	2	6	7	3	15[a]
ZMH: Zoologisches Museum Hamburg, Hamburg, Germany	8	1	1	1	10
SNM: Natural History Museum of Denmark, Copenhagen, Denmark	10	–	–	–	10
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, United States of America	1	4	1	–	6

[a] Probably more

At about the same time, in 2001, the CAS led by herpetology curator Robert "Bob" C. Drewes (1942–), began what would become known as the CAS Gulf of Guinea Expeditions. This project, which has made a total of 12 expeditions to the islands as of 2020, is still ongoing and has been one of the most comprehensive efforts to study the biodiversity of São Tomé and Príncipe islands since Francisco Newton's expedition in the nineteenth century. Due to Drewes' herpetological background, the project has always had a strong emphasis on the study of the amphibians and reptiles of these islands (see Bell et al. 2022). The reptile collections resulting from these expeditions are currently the largest in the world (Table 19.1), with a total of 449 specimens (Scheinberg and Fong 2019). One important taxonomic contribution from these expeditions was the description of the Príncipe Gecko, *Hemidactylus principensis* Miller, Sellas and Drewes, 2012, the first endemic reptile described from the Gulf of Guinea oceanic islands since 1972 (Miller et al. 2012).

Finally, since 2013, a team from MUHNAC led by Luis M. P. Ceríaco (1987–) started herpetological surveys in São Tomé and Príncipe. A total of four expeditions (two in 2013, one in 2015, one in 2016) to Príncipe and São Tomé islands, as well as to Tinhosa Grande islet, were conducted by the team, which resulted in the collection of 155 reptile specimens, currently housed in MUHNAC collections (Ceríaco and Marques 2019). Combined with the specimens collected by Mendes et al. (1988) and those originally from IICT (Ceríaco and Marques 2018), MUHNAC collections hold a total of 354 specimens of São Tomé and Príncipe reptiles and are the second largest in the world. Building on the knowledge amassed through newly collected specimens, the available Portuguese and North American collections, as well as the molecular baseline provided by the Jesus et al. studies, Ceríaco and team have contributed to the taxonomic revision of most of the reptile groups occurring on the islands. This led to the description of: three species of skinks of the genus *Trachylepis* (Ceríaco 2015; Ceríaco et al. 2016)—*Trachyelpis adamastor* Ceríaco, 2015, *Trachylepis thomensis* Ceríaco, Marques and Bauer, 2016, and *Trachylepis principensis* Ceríaco, Marques and Bauer, 2016, endemic to Tinhosa Grande islet, São Tomé, and Príncipe, respectively; a new species of Cobra (Ceríaco et al. 2017)—*Naja* (*Boulengerina*) *peroescobari* Ceríaco, Marques, Schmitz and Bauer, 2017; a new species of the genus *Panaspis*, endemic to São Tomé (Soares et al. 2018)—*Panaspis thomensis* Ceríaco, Soares, Marques et al., 2018; and a new species of lamprophid snake of the genus *Boaedon* (Ceríaco et al. 2021a)—*Boaedon mendesi* Ceríaco, Arellano, Jadin et al., 2021. In 2018 Ceríaco's team moved to the Museu de História Natural e da Ciência of the University of Porto (MHNCUP) and new field work has been carried out since then.

Diversity and Endemism

At present, a total of 29 reptile species have been reported as resident from the oceanic islands of the Gulf of Guinea (Table 19.2). Of these, 22 are endemic to one or two islands, three are presumed invasive/introduced species, and one corresponds to questionable records of a putative species of mamba. An additional species is considered vagrant to São Tomé. We discuss the taxonomic status and biology of each species in more detail below.

Crocodilians

There are currently no established crocodilian populations inhabiting the Gulf of Guinea oceanic islands. Historical records dating back to the first decades of Portuguese presence suggest that a species of *Crocodylus* occurred on São Tomé. A report from the Portuguese navigator Gonçalo Pires (birth and death dates unknown), transcribed by Valentim Fernandes (ca. 1450–1519) and subsequently

Table 19.2 List of terrestrial reptiles from Príncipe (P), São Tomé (ST) and Annobón (A) islands

Higher taxonomy	Species/subspecies	P	ST	A	IUCN
Order Crocodylia					
Family **Crocodylidae**					
Crocodylus Laurenti, 1768	*Crocodylus niloticus* Laurenti, 1768		V		
Order Testudines					
Family **Pelomedusidae**					
Pelusios Wagler, 1830	*Pelusios castaneus* (Schweigger, 1812)	X	X		LC
Order Squamata					
Family **Gekkonidae**					
Hemidactylus Goldfuss, 1820	*Hemidactylus aporus* Boulenger, 1906			E?	DD
	Hemidactylus greeffii Bocage, 1886		E		NT
	Hemidactylus mabouia (Moreau de Jonnés, 1818)	I	I	I	LC
	Hemidactylus longicephalus Bocage, 1873	I	I		LC
	Hemidactylus principensis Miller, Sellas and Drewes, 2012	E			NT
	Hemidactylus newtoni Ferreira, 1897			E	DD
Lygodactylus Gray, 1864	*Lygodactylus delicatus* Pasteur, 1962	E			LC
	Lygodactylus thomensis (Peters, 1881)		E		LC
	Lygodactylus wermuthi Pasteur, 1962			E	LC
Family **Scincidae**					
Feylinia Gray, 1845	*Feylinia polylepis* Bocage, 1887	E			LC
Panaspis Cope, 1868	*Panaspis africana* (Gray, 1845)	E			LC
	Panaspis thomensis Ceríaco et al. 2016		E		LC
	Panaspis annobonensis (Fuhn, 1972)			E	DD
Trachylepys Fitzinger, 1843	*Trachylepis adamastor* Ceríaco, 2015	E			LC[a]
	Trachylepis affinis (Gray, 1838)	X			LC
	Trachylepis thomensis Ceríaco, Marques and Bauer, 2016		E		LC
	Trachylepis ozorii (Bocage, 1893)			E	LC
Family **Typhlopidae**					
Afrotyphlops Broadley and Wallach, 2009	*Afrotyphlops elegans* (Peters, 1868)	E			LC
Letheobia Cope, 1869	*Letheobia newtoni* (Bocage, 1890)	E	E		DD
	Letheobia feae (Boulenger, 1906)	E	E		DD
Indotyphlops Hedges, Marion, Lipp, Marin and Vidal, 2014	*Indotyphlops braminus* (Daudin, 1803)			I	LC
Family **Lamprophiidae**					
Boaedon Duméril, Bibron and Duméril, 1854	*Boaedon bedriagae* Boulenger, 1906		E		LC
	Boaedon mendesi Ceríaco et al. 2021	E			NE

(continued)

Table 19.2 (continued)

Higher taxonomy	Species/subspecies	P	ST	A	IUCN
Family **Colubridae**					
Philothamnus Smith, 1847	*Philothamnus thomensis* Bocage, 1882		E		LC
	Philothamnus girardi Bocage, 1893			E	LC
Hapsidophrys Fischer, 1856	*Hapsidophrys principis* (Boulenger, 1906)	E			LC
Family **Elapidae**					
Naja Laurenti, 1768	*Naja* (*Boulengerina*) *peroescobari* Ceríaco, Marques, Schmitz and Bauer, 2017		E		EN
Dendroaspis Schlegel, 1848	*Dendroaspis* cf. *jamesoni* (Trail, 1843)		?		LC

Status in each island: E, endemic; I, introduced; V, vagrant; X, resident; ?, uncertain. IUCN Red List Categories: DD, data deficient; LC, least concern; NE, not evaluated; NT, near threatened; EN, endangered

[a] As *T. principensis*

published by several authors (Henriques 1917; Baião 1940; Ceríaco et al. 2018) mentions the following:

> There were many lizards of about twelve cubits [approximately 540 cm], but now there are few. They eat men and women, cows and bulls and all types of animals. These lizards don't exit the water, as their tails stay always inside freshwater, and any animal that he captures he takes into the water and in the water he kills it, and it rears up on his tail achieving the size of a man. The current captain, Fernã do Mello, has a very big and fearful lizard contained in a pond, and above this pond he mounted a scaffold to allow its observation. This lizard used to move from the river to the pond several times a month. And he caused a lot of damage to the men and animals, and 1 day, a small and despicable man who observed the lizard for some time, once he found it in the pond and with his hoe he cut the lizard's limbs and closed the pond so he couldn't ever escape and went to tell this to the captain.
>
> [LMP Ceríaco's translation from the archaic Portuguese original]

In a subsequent passage of the text, the authors refer to the "*very big lizards, that now fear the men*." [author's translation from the archaic Portuguese original]. Due to the perceived danger that the São Tomé crocodiles posed to the Portuguese settlers, it is fair to assume that the population was completely extirpated. As no archeological remains of these animals are known, the taxonomic identity of this historical São Tomé crocodilian cannot be determined but is likely that they were either an insular population of *Crocodylus niloticus* Laurenti, 1768, or *C. suchus* Geoffroy Saint-Hilaire, 1807.

However, the presence of crocodiles in the islands may be more common than the available data suggest. In early April 2021, a live crocodile appeared on Roça Colónia Açoreana beach, in the southeastern part of São Tomé Island (Fig. 19.1, 1). Other records of a large lizard seen in the Angra Toldo region, and said to be a crocodile, had previously surfaced on social media, but these records have never been confirmed. The animal from Colónia Açoreana was a female *Crocodylus*

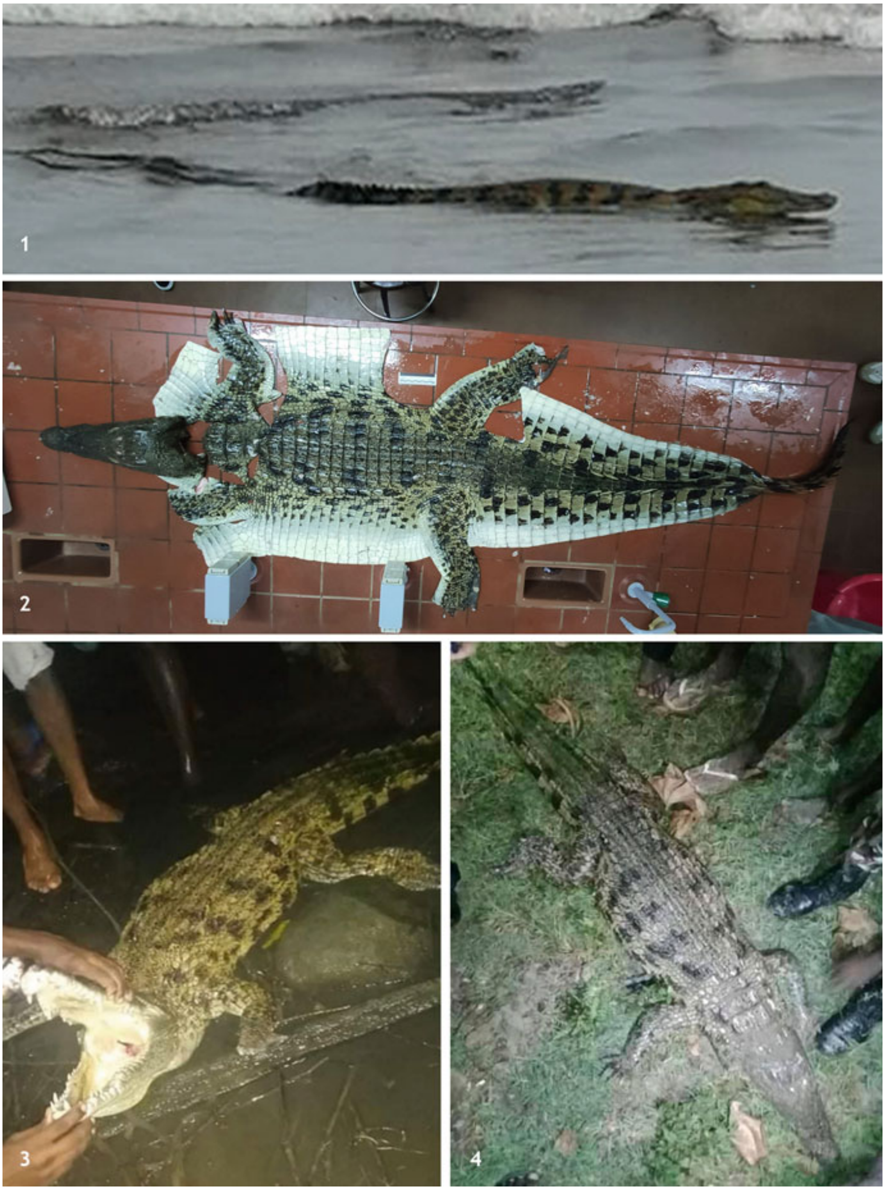

Fig. 19.1 Crocodile from Colónia Açoreana beach, São Tomé Island: (**1**) Live photo of the animal on 4 April 2021; (**2**) Skin of the specimen in the biology laboratory of the Portuguese School of São Tomé; (**3**, **4**) Specimen after being shot. Photo credits: (**1**) Maria Branco, (**2**) Luis M. P. Ceríaco, (**3**, **4**) Unknown

niloticus, of approximately two meters total length, which was observed and photographed for several weeks on the beach. Due to the safety concerns it presented, the animal was killed by the authorities at the end of the month (Fig. 19.1, 3–4). The specimen's head and skin were prepared by two of the authors (LMPC and MPM) and deposited in the biology laboratory of the Portuguese School of São Tomé and Príncipe (Fig. 19.1, 2). Molecular studies are underway to identify the source population of the animal in continental Africa. At about the same time of the appearance of the crocodile in Colónia Açoreana, two Angolan fishermen in a castaway boat that had drifted from the Angolan coast near the mouth of Congo River were rescued near São Tomé by the local authorities. The Gulf of Guinea sea currents and the considerable flow of the Congo River at that time due to heavy rains on the continent may help to explain both of these arrivals.

Terrapins

Family Pelomedusidae

Only one species of terrapin occurs in the Gulf of Guinea oceanic islands, the West Africa mud turtle, *Pelusios castaneus* (Schweigger, 1812) (Fig. 19.2, 1). The species has mostly been recorded from São Tomé, where it is locally known as "Bencú" and is used by Santomeans in the local gastronomy. Recent sightings in Príncipe suggest that the species also occurs on the island, but currently, there are still no available specimens in public collections to permit a clearer and detailed assessment of its taxonomic status. The species has a considerable distribution through West and Central Africa, extending from Senegal to northern Angola (Bour et al. 2016; Rhodin et al. 2017). Fritz et al. (2010) presented evidence from three mitochondrial and three nuclear loci that the population from São Tomé is closely related to populations from Ivory Coast and represents a recent colonization. A subsequent study by Kindler et al. (2016) using the same loci but with additional geographic sampling uncovered several geographically distinct clades across the distribution of *P. castaneus*, with the São Tomé population nested within a West African clade along with specimens from Ivory Coast and Nigeria. Despite not being a common species, *P. castaneus* has been reported from the island since the 1880s (Greeff 1884; Bocage 1886a, 1889) and was more recently found in Oque d'el Rei, Água Grande District (February 2013, specimens deposited in the collections of MUHNAC). Data on the distribution, abundance, ecology, and natural history of this species in São Tomé are still very limited, although it is expected that the species inhabits rivers, streams and temporary water bodies as it does throughout its range in continental Africa (Bour et al. 2016). As the phylogenetic studies indicate, a possible human-mediated introduction of *P. castaneus* to São Tomé cannot be rejected, but further research is needed to clarify the evolutionary history of this population.

Fig. 19.2 Gulf of Guinea oceanic island reptiles: (**1**) West African mud turtle, *Pelusios castaneus*, from São Tomé Island; (**2**) Príncipe Gecko, *Hemidactylus principensis*, from Príncipe Island; (**3**) Manyscale Feylinia, *Feylinia polylepis*, from Príncipe Island; (**4**) Adamastor Skink, *Trachylepis thomensis*, from São Tomé Island; (**5**) Elegant Worm Snake, locally known as Cobra-bobô, *Afrotyphlops elegans*, from Príncipe Island; (**6**) Mendes' House Snake, locally known as Jita, *Boaedon mendesi*, from Príncipe Island; (**7**) Príncipe Emerald Snake, locally known as Suá-suá, *Hapsidophrys principis*, from Príncipe Island; (**8**) São Tomé Cobra, locally known as Cobra-preta, *Naja peroescobari*, from São Tomé Island. Photo credits: (**1**–**8**) Luis M. P. Ceríaco

Squamata

Squamate diversity in the Gulf of Guinea oceanic islands includes 28 species from two families of lizards—Gekkonidae, Scincidae—and four families of snakes—Typholpidae, Lamprophiidae, Colubridae and Elapidae. All species are endemic to the islands, except for one native skink (family Scincidae), two introduced geckos (family Gekkonidae), one introduced snake (family Typholopidae), and one gecko (family Gekkonidae) and one snake (family Elapidae) that are based on doubtful or problematic records that require further investigation.

Family Gekkonidae

The geckos of the Gulf of Guinea oceanic islands belong to two different genera: the Dwarf Geckos of the genus *Lygodactylus* Gray, 1864, and the Tropical House Geckos of the genus *Hemidactylus* Goldfuss, 1820. Each island is represented by its own endemic form of *Lygodactylus*: the Príncipe Dwarf Gecko, *L. delicatus* Pasteur, 1962, the São Tomé Dwarf Gecko, *L. thomensis* (Peters, 1881), and the Annobón Dwarf Gecko, *L. wermuthi* Pasteur, 1962. Following the initial description of *L. thomensis* by Peters (1881), several authors considered the populations on all three islands as conspecific (e.g., Bocage 1886a, 1892b, 1893, 1903, 1905; Boulenger 1885, 1906; Sternfeld 1917; Loveridge 1947). Pasteur (1962) reviewed the group and described *delicatus* and *wermuthi* as subspecies of *thomensis* based on morphological and coloration differences. With the exception of Manaças (1958), subsequent authors followed the Pasteur (1962) taxonomy (Schätti and Loumont 1992; Haft 1993). Jesus et al. (2006) were the first to provide molecular data for these island taxa and found the level of divergence in 12S and 16S mitochondrial genes was within the level of divergence observed between other species within the genus. With this combination of phenotypic and genetic distinctiveness, and their allopatric distributions, Ceríaco et al. (2018) considered each island population as a valid species. Data on the distribution, abundance, ecology, and natural history of the three species are limited. *Lygodactylus thomensis* and *L. delicatus* are commonly observed in human settlements, especially on walls, fences and other structures (Manaças 1958, LMPC pers. obs.); however, Jesus et al. (2003) noted that *L. wermuthi* has only been found in forested areas. Manaças (1958) recorded specimens of flies (Diptera) in the stomach contents of *L. delicatus*.

The taxonomy of the genus *Hemidactylus* is considerably more complex. A total of six species are currently recorded for the islands. Four of these are endemic to the islands: the Príncipe Gecko, *Hemidactylus principensis* Miller, Sellas and Drewes, 2012, endemic to Príncipe and Tinhosa Grande islet (Fig. 19.2, 2); Greeff's Gecko, *H. greeffii* Bocage, 1866, endemic to São Tomé and Rolas islet; Newton's Gecko, *H. newtoni* Ferreira, 1897, endemic to Annobón; and the Annobón Gecko, *H. aporus* Boulenger, 1906. The remaining two species are most likely human introductions—the Long-Headed Tropical Gecko, *H. longicephalus*, Bocage, 1873, occurring on

São Tomé and Príncipe, the Tropical House Gecko, *H. mabouia* (Moreau de Jonnès, 1818), occurring on all three islands and Rolas.

Príncipe and São Tomé islands, as well as the surrounding islets of Tinhosa Grande and Rolas, respectively, host an endemic lineage of the genus *Hemidactylus* comprising *H. principensis* and *H. greeffii* (Bauer et al. 2010; Miller et al. 2012; Ceríaco et al. 2020a). These two species exhibit a clear synapomorphic character that differentiates them from all other African species of *Hemidactylus*: the absence of the terminal phalanx and claw of the first digit (thumb) of the manus (Bocage 1886a, 1905; Boulenger 1906; Loveridge 1947; Haft 1993; Miller et al. 2012). Both species are members of the African-Atlantic clade, a group mainly comprising Angolan and Western African species that are closely related to Brazilian species such as *H. brasilianus* Amaral, 1935 (Ceríaco et al. 2020a). While *H. greeffii* was described in the 1880s by Bocage (1886a), *H. principensis* was only recently described by Miller et al. (2012) on the basis of genetic divergence and several morphological differences, including iris coloration and body size. The unidentified *Hemidactylus* from Tinhosa Grande reported by Ceríaco (2015) was shown, through the use of molecular data, to be conspecific with *H. principensis* from Príncipe Island (Ceríaco et al. 2020b). The known distribution of both species is very limited (Greeff 1884; Bocage 1886a, 1905; Boulenger 1906; Manaças 1958; Schätti and Loumont 1992; Haft 1993; Miller et al. 2012). Both species appear to be less abundant in more developed areas and preferring less disturbed habitats (LMPC pers. obs.); however, they are able to colonize and thrive in both forested and more xeric areas, as in the case of the Tinhosa Grande islet population.

The Annobón endemics, *H. newtoni* and *H. aporus*, have a more convoluted taxonomic history. *H. newtoni* was described by Ferreira (1897) based on a series of seven specimens collected by Francisco Newton in 1893: one adult male, five adult females and one juvenile. These same specimens were previously examined by Bocage (1893), who tentatively identified them as *H. mabouia*, noting, however, that they differed from *H. mabouia* in being "smaller and having relatively larger and closer dorsal tubercles." Ferreira (1897) considered the dorsal patterns of transverse "W" shaped markings extending from the neck to the insertion of the tail, the number and disposition of the dorsal tubercles, and the "very long and flattened digits, with strong claws and enlarged proximally, with larger and more numerous number of subdigital lamellae [7–8 in the first finger, 11–12 in the fourth toe]" as diagnostic characters for *H. newtoni*. Bocage (1903) provided a French translation of the original Ferreira (1897) description in Portuguese. Surprisingly, neither Ferreira (1897) nor Bocage (1903) provided data on the number of preanal or femoral pores of the male specimen. Loveridge (1947) interpreted this omission as a complete lack of preanal or femoral pores in the male syntype, which would thus resemble the other putative endemic species, *H. aporus* (see below). Loveridge noted that "if correctly counted, the greater number of subdigital scansors of *H. newtoni*, approaching those of *H. echinus* O'Shaughnessy, 1875, afford good grounds for separation." The type series of *H. newtoni* was lost in the fire that destroyed the collections of Museu Bocage (Lisbon) in 1978. Jesus collected new material in the early 2000s and provided the first molecular data for *H. newtoni*

(Jesus et al. 2005c), noting that it was sister to "an individual from an undescribed form from São Tomé," recently identified as *H. longicephalus* by LMPC (pers. obs.). Further studies are needed to better understand the phylogenetic placement of *H. newtoni* among its African congeners and begin to understand its evolutionary history, as well as its natural history, distribution and ecology.

The second Annobón endemic, *H. aporus,* was described by Boulenger (1906) based on several specimens, including males and females, collected by Fea. According to the author, the species is very similar to *H. bocagii* [=*H. longicephalus*], but differs by having the dorsal tubercles "larger, closer together, forming 16–20 more regular longitudinal series" and lacking precloacal or femoral pores in males (present in *H. longicephalus*; see Ceríaco et al. 2020a, b). The species differs from *H. newtoni* in the number of subdigital lamellae ("5 lamellae under the inner digit, 7 under the third and fourth" in *H. aporus* fide Boulenger (1906) versus "7–8 in the first finger, 11–12 in the fourth toe" in *H. newtoni* fide Ferreira (1897)). Loveridge (1947) considered the species valid, noting that the absence of pores in the males distinguishes *aporus* from all other West African species with the exception of sympatric *H. newtoni* [if this is indeed true], from which it differs in "possessing fewer subdigital scansors, 7 (instead of 11–12) under the fourth toe, and 16–20 (instead of irregularly disposed) dorsal tubercles." The species has not been collected since its original description over a century ago, and our current knowledge is limited to the very brief, original description (Meiri et al. 2017). The type series is still extant in the Museo Civico di Storia Naturale "Giacomo Doria," Genoa, Italy (Giulliano Doria pers. comm.). While the available evidence supports the identity of *H. newtoni* as a valid species, the status of *H. aporus* requires further research.

The presence of *Hemidactylus longicephalus*, a coastal species endemic to western Angola and southwestern Democratic Republic of the Congo, was first noted in São Tomé when Bedriaga (1892) misidentified the specimens at his disposal as a new subspecies of *H. mabouia*, which he named as *H. mabouia* var. *molleri*. The convoluted history of this putative taxon was briefly discussed by Ceríaco and Marques (2012) and Ceríaco et al. (2018). Ceríaco et al. (2020a) definitively synonymized *molleri* with *longicephalus*, a hypothesis already put forward by Loveridge (1947). In addition to the records from São Tomé provided by Bedriaga (1892), Bocage (1903; as *H. bocagii*, a junior synonym of *longicephalus*) and Manaças (1958) provided records from Príncipe, and Carranza and Arnold (2006) and Ceríaco et al. (2020a) provided additional records of the species for São Tomé. Jesus et al. (2005c) noted the presence of a putative new species of *Hemidactylus* from São Tomé, which was later confirmed to be conspecific with *longicephalus* (LMPC pers. obs.) Both morphological and molecular data provided by Ceríaco et al. (2020a), unambiguously identify the São Tomé and Príncipe populations as conspecific with the Angolan form. Consequently, the authors concluded that the species naturally colonized the islands relatively recently or were introduced to the islands through human activities, as São Tomé, Príncipe and Angola were Portuguese colonies, and the islands were an important stopover for ships departing from Angola to the Americas and Europe (Ceríaco et al. 2020a). Due to the limited number of collected specimens, not much is known about the ecology and distribution of this species on the islands, but in Angola, it tends to be found in coastal lowland areas or in human settlements (Ceríaco et al. 2020a).

Finally, *H. mabouia* is one of the most widespread and ubiquitous species of gecko in the world, native to Central and Western Africa but introduced to North, Central and South America, as well as the Caribbean (Kraus 2009; Agarwal et al. 2021). There are historical and modern records of this species on the three islands (e.g., Greeff 1884; Bocage 1886c, 1889, 1892a, 1905; Vieira 1886; Bedriaga 1892; Boulenger 1906; Manaças 1958, 1973; Schätti and Loumont 1992; Haft 1993; Hofer 2002; Jesus et al. 2003, 2005c; Miller et al. 2012; Ceríaco et al. 2018, 2020a). Jesus et al. (2005c) and Ceríaco et al. (2020a) provided molecular evidence indicating that the Gulf of Guinea oceanic islands populations are almost indistinguishable from the continental populations of the species, suggesting a recent arrival/introduction to the archipelago. The species is very common in human settlements and is often observed on houses and other buildings at night.

Family Scincidae

The skinks occurring on the Gulf of Guinea oceanic islands belong to three different genera: the feylinias of the genus *Feylinia* Gray, 1845, leaf-litter skinks (also known as snake-eyed skinks) of the genus *Panaspis* Cope, 1868, and the common skinks of the genus *Trachylepis* Fitzinger, 1843. The fossorial and limbless Many-scaled Feylinia, *Feylinia polylepis* Bocage, 1887 is endemic to Príncipe (Fig. 19.2, 3). Described by Bocage (1887) as a subspecies of *Feylinia currori* Gray, 1845, the species has been recorded on the island by several authors (Bocage 1903; Boulenger 1906; Angel 1920; Manaças 1958, 1973; Brygoo and Roux-Estève 1983; Hofer 2002; Ceríaco et al. 2018; Soares et al. 2018). Due to its secretive lifestyle, this species is still poorly known in terms of its ecology, natural history, and phylogenetic position, although, as noted by Brygoo and Roux-Estève (1983), its taxonomic validity is unquestionable. The species is morphologically most similar to *Feylinia currori*, but the lack of molecular data for most of the representatives of the genus limits any attempt to understand its phylogenetic placement. The feylinia is very common and is found under leaf-litter, logs, or rocks.

The taxonomic history of leaf-litter skinks, genus *Panaspis*, of the Gulf of Guinea oceanic islands is quite complex. All authors who have dealt with this species during the nineteenth and the first half of the twentieth century considered that populations on the three islands were conspecific (e.g., Greeff 1884; Bocage 1886a, 1889, 1903, 1905; Bedriaga 1892; Boulenger 1906; Manaças 1958), bearing the specific epithet *africana* (or *aftricanum*, depending on the genus they were placed in by the different authors—see Soares et al. 2018). The species was originally described as *Mocoa africana* by Gray (1845). Although Gray (1845) did not provide a precise type locality, the type specimen is unambiguously identifiable as originating from Príncipe (Soares et al. 2018). Subsequently, Fuhn (1972) revised the Gulf of Guinea *Panaspis*, leading to the description of the Annobón population as *P. africana* *annobonensis*. Perret (1973) considered *annobonensis* as a full species, a decision that would later be supported using molecular data (three mitochondrial and one nuclear locus) by Jesus et al. (2007) and Medina et al. (2016). A more recent taxonomic revision by Soares et al. (2018) led to the description of a third species—*Panaspis thomensis* Ceríaco, Soares, Marques et al., 2018, endemic to São Tomé. The three species form a clade within the genus *Panaspis* along with *P. cabindae* (Bocage, 1866) from Angola (Medina et al. 2016; Soares et al. 2018). *Panaspis africana*, *P. annobonensis,* and *P. thomensis* are some of the most conspicuous reptiles on their respective islands. They are typically encountered in forested areas in leaf-litter, and even in gardens in more urban areas (Jesus et al. 2003; Soares et al. 2018).

Similar to the Leaf-litter skinks, the common skinks of the genus *Trachylepis* are also among the most conspicuous lizards on these islands. Four species occur in the Gulf of Guinea oceanic islands: *Trachylepis adamastor* Ceríaco, 2015, endemic to Príncipe and Tinhosa Grande islet; *T. thomensis* Ceríaco, Marques and Bauer, 2016, endemic to São Tomé and surrounding islets (Fig. 19.2, 4); *T. ozorii* (Bocage, 1893), endemic to Annobón; and *T. affinis* (Gray, 1838) on Príncipe. Originally described in the late nineteenth century by Bocage (1893), the taxonomy and nomenclatural history of *T. ozorii* have always been stable (see Ceríaco et al. 2016). Based on mitochondrial sequence data, Jesus et al. (2005a) concluded that *T. ozorii* was not closely related to any of the Gulf of Guinea oceanic island *Trachylepis*. This result was confirmed by Ceríaco et al. (2016) and Weinell et al. (2019), the latter demonstrating that *T. ozorii* is sister to the Western African species *Trachylepis polytropis* (Boulenger, 1903) and represents a distinct dispersal event to the archipelago. Jesus et al. (2003) noted that the species was widespread across the island, but was not usually found in wet or shaded areas.

The taxonomy of *T. adamastor* and *T. thomensis* is somewhat more muddled than that of the Annobón congener. For a long time, both the Príncipe and São Tomé populations were considered conspecific to the *T. maculilabris* (Gray, 1845) species complex (see Ceríaco et al. 2016), a widespread species in West and Central Africa, long known to harbor cryptic diversity (Mausfeld-Lafdhiya et al. 2004). Jesus et al. (2005a) were the first to show, based on molecular data (three mitochondrial loci), that the populations from Príncipe and São Tomé were not conspecific. As a first step to clarify the taxonomy of the group, Ceríaco (2015) described *T. adamastor* from Tinhosa Grand islet. The available specimens had been preserved in formalin, and therefore, no molecular data were available for comparison with the other island populations. Consequently, the species was described solely based on its striking size and coloration differences relative to the other island's specimens. Ceríaco et al. (2016) later described two additional species based on a combination of morphological and genetic data: *T. principensis* from Príncipe and *T. thomensis* from São Tomé. In a species-level phylogeny of the genus, Weinell et al. (2019) confirmed the distinctiveness of the Príncipe and São Tomé populations and noted that the species were not each other's closest relatives—the Príncipe lineage (incorrectly labeled by Weinell et al. (2019) as *T. thomensis*) is sister to *T. maculilabris*, while the São Tomé population (incorrectly labeled by Weinell et al. (2019) as *T. principensis*) is sister to the Indian Ocean endemic *Trachylepis comorensis* (Peters, 1854), which occurs in Comoros, Madagascar and coastal Mozambique. Both Ceríaco et al. (2016) and Weinell et al. (2019) lacked molecular data for *T. adamastor* and were unable to assess its taxonomic position in the context of a molecular phylogeny. Ceríaco et al. (2020b) provided the first molecular data for *T. adamastor*, showing that it is actually conspecific to *T. principensis*, rendering *T. principensis* as a junior synonym of *T. adamastor*. *Trachylepis thomensis* is commonly found in forested areas and in human settlements, showing an almost exclusively terrestrial lifestyle. By contrast, *T. adamastor* is more abundant in less populated areas, ranging from forested habitats to the open, rocky habitats of the Tinhosa Grande islet. *Trachylepis adamastor* is commonly found basking on trees (Ceríaco et al. 2016). More recently the population size and diet of the Tinhosa Grande population of *T. adamastor* was reviewed by Sousa et al. (2022).

The presence of *T. affinis*, a complex of species occurring from Senegal to Angola, on São Tomé and Príncipe has been interpreted differently by several authors. In particular, Fischer (1886) described *Euprepes cupreus* from São Tomé, and this taxon is currently considered a junior synonym of *T. affinis* (Ceríaco et al. 2016, 2018). To date, Fischer's (1886) record remains the only available record of this species on São Tomé. By contrast, several authors reported the species from Príncipe under a variety of names—*Mabuya raddoni* (Angel 1920; Manaças 1958, Hofer 2002), *Mabuya blanlingii* [sic] (Manaças 1958) and *Mabuya/Trachylepis affinis* (Hallermann 1998; Jesus et al. 2005a; Ceríaco et al. 2016, 2018). These are all currently synonyms of *T. affinis*, according to Ceríaco et al. (2016), based on the molecular similarity between Principe and other continental populations. The species likely represents a recent arrival to the island, and further data are needed to assess if a São Tomé population is extant. In Príncipe, the species is mostly found in the vicinity of human settlements, especially around Santo António city.

Family Typhlopidae

Considering the diminutive size and isolation of the Gulf of Guinea oceanic islands, the diversity of typhlopid snakes is remarkable. At least four species from three different genera—*Afrotyphlops* Broadley and Wallach, 2009, *Letheobia* Cope, 1868, and *Indotyphlops* Hedges, Marion, Lipp, Marin and Vidal, 2014—occur on the islands. The genus *Afrotyphlops* is represented by the Príncipe endemic *Afrotyphlops elegans* (Peters, 1868), locally known as "Cobra-bobô" (Fig. 19.2, 5), which is the same name used on São Tomé to refer to the endemic caecilians of the genus *Schistometopum* Parker, 1941 (Bell et al. 2022). Not much is known about the ecology of this fossorial species, however, in multi-locus and morphological phylogenetic analyses of typhlopid snakes, Kornilios et al. (2013) and Hedges et al. (2014) showed that it is closely related to the Central African *Afrotyphlops angolensis* (Bocage, 1866).

Two species of *Letheobia* are currently recognized and both occur on Príncipe and São Tomé: *Letheobia newtoni* (Bocage, 1890) and *Letheobia feae* (Boulenger, 1906). Both species were originally described from São Tomé (Bocage 1890; Boulenger 1906), and recent molecular data indicate the species are distinct and form a monophyletic group with *Letheobia simoni* (Boettger, 1879) and *L. episcopus* (Frazen and Wallach, 2002), from Israel and Turkey, respectively (Kornilios et al. 2013; Hedges et al. 2014). This intriguing biogeographic pattern may be an artifact of our current poor knowledge of the taxonomic diversity and distribution of the species of genus *Letheobia*. Two other forms were described from Príncipe: Boulenger (1906) described *Typhlops* [=*Letheobia*] *principis* and Angel (1920) described *Typhlops* [=*Letheobia*] *naveli*. Both of these species were later synonymized with *L. feae* and *L. newtoni,* respectively, by Roux-Estève (1974). No molecular data exist for the Príncipe populations, and thus their taxonomic relationships with the São Tomé forms have not been fully ascertained. Given the patterns of speciation in the archipelago and the morphological conservatism of these snakes, the possibility that the Príncipe forms represent valid species should be investigated. Due to their mostly fossorial lifestyles, almost nothing is known about the ecology and distribution of either species.

Finally, Jesus et al. (2003) reported the presence of *Indotyphlops* (as *Ramphotyphlops*) *braminus* (Daudin, 1802) on Annobón. These small, fossorial snakes are an invasive species originally from Southern Asia and have been introduced to islands across the globe (Wallach 2009).

Family Lamprophiidae

Two species of lamprophid snakes occur in the Gulf of Guinea oceanic islands: *Boaedon bedriagae* Boulenger, 1906, endemic to São Tomé, and *B. mendesi*, endemic to Príncipe (Fig. 19.2, 6). The two taxa were considered conspecific by most authors over the last century but were recently split into distinct species by Ceríaco et al. (2021a). The species are sister taxa and are closely related to the southern African *B. capensis* Duméril, Bibron & Duméril, 1854 species complex, contrary to the historical assignment to either the *Boaedon lineatus* Duméril, Bibron & Duméril, 1854 or *Boaedon fuliginosus* (Boie, 1827) species complexes from Western and Central Africa (Ceríaco et al. 2021a). Locally known as “Jita,” these species rank amongst the most well-known species on the islands, where the locals recognize them as harmless. Both species are quite common and are often found in both pristine habitats and agricultural areas (Ceríaco et al. 2021a). Both species can be observed perched in trees or in vegetation and are often observed at reed frog (*Hyperolius* spp.) breeding sites, suggesting anurans may be an important part of their diet (RCB, LMPC pers. obs.).

Family Colubridae

The colubrids of the Gulf of Guinea oceanic islands belong to two different genera: the arboreal emerald snakes, genus *Hapsidophrys* Fischer, 1856, represented by the Príncipe endemic *Hapsidophrys principis* (Boulenger, 1906), locally known as Suá-suá (Fig. 19.2, 7), and the arboreal green snakes of the genus *Philothamnus* (Smith, 1847), represented by the São Tomé endemic, *Philothamnus thomensis* Bocage, 1882, also locally known as Suá-suá, and the Annobón endemic *Philothamnus girardi* Bocage, 1893.

The Príncipe Suá-suá, *H. principis* was described in the early twentieth century by Boulenger (1906), although older records exist from the late nineteenth century, as *Gastropyxis* (= *Hapsidophrys*) *smaragdina* (Bocage 1887, 1903). The species is relatively poorly studied, but Jesus et al. (2009) provided a phylogeny based on two mtDNA loci supporting *H. principis* as a distinct evolutionary lineage sister to *H. smaragdina* from Gabon. *Hapsidophrys principis* is an arboreal species, mostly found in forested areas (LMPC pers. obs.).

Regarding the two species of *Philothamnus*, recent molecular revisions by Engelbrecht et al. (2019) provided some insights regarding their taxonomic validity and placement within the genus. With a molecular dataset of three mtDNA and two nuDNA loci, Engelbrecht et al. (2019) found that the island species form a strongly supported clade with West-Central African congener *P. dorsalis* (Bocage, 1866). Species delimitation analyses with this same dataset found moderate support for *P. thomensis* as a distinct evolutionary lineage but no support for *P. girardi* as a distinct lineage (Engelbrecht et al. 2019). Given the geographic isolation of *P. girardi* on Annobón, morphological differences noted by Bocage (1893), and the relatively modest molecular dataset and geographic sampling in Engelbrecht et al. (2019), we conservatively maintain *P. girardi* as a valid species. *Philothamnus thomensis* is considered a forest specialist but can also be found in shade-plantation habitats and gardens (RCB, pers. obs.), while Jesus et al. (2003) noted that *P. girardi* is widespread on Annobón, mainly in large open spaces with shrubs and grasses, outside of the main village.

Family Elapidae

Only one species of elapid snake is confirmed for the Gulf of Guinea oceanic islands: the São Tomé endemic *Naja* (*Boulengerina*) *peroescobari* Ceríaco, Marques, Schmitz and Bauer, 2017, locally known as "Cobra-preta" (Fig. 19.2, 8). It is the only venomous species of snake in the Gulf of Guinea oceanic islands, and human fatalities can occur even if rare (Ceríaco et al. 2017). As a large and conspicuous snake, it was one of the first reported species of reptiles for São Tomé. The species was historically identified as *Naja melanoleuca* Matschie, 1893, a widely distributed Central African species (Ceríaco et al. 2016). Until recently, it was assumed that Portuguese settlers introduced Cobra-preta to control rodent pests that afflicted agricultural crops. However, historical, morphological and molecular evidence reject this hypothesis (Ceríaco et al. 2017; Wüster et al. 2018) and instead indicate that the Cobra-preta is distinct from *N. melanoleuca* and is endemic to São Tomé. The Cobra-preta is classified as Endangered by the International Union for the Conservation of Nature (IUCN 2021), and is the only threatened terrestrial reptile from the Gulf of Guinea oceanic islands. The Cobra-preta is mostly seen in forested and shady habitats across the southern half of the island and is apparently absent in the northeast regions. It is commonly seen basking on roads during the day (Ceríaco et al. 2017). The invasive Least weasel, *Mustela nivalis* Linnaeus, 1766, and Black rat, *Rattus rattus* Linnaeus, 1758, have been reported as prey items of the species (Ceríaco et al. 2017).

There are unconfirmed records of a second species of elapid snake on São Tomé: a green Mamba of the genus *Dendroaspis*. The evidence regarding the presence of this snake on São Tomé was summarized in Ceríaco et al. (2018). Three experienced herpetologists reported a species of mamba from the island: *Dendroaspis jamesoni* by Jan (1857, 1858, 1859, 1863), Jan and Sordelli (1870) and Fischer (1856, 1885) and *Dendroaspis angusticeps* by Bedriaga (1893a). Fischer (1856) even provided a drawing of the specimen from "Insel St. Thomé (West-Africa)" (Fig. 19.3). Unfortunately, none of the specimens examined by the three different authors is still extant. The specimen examined by Jan (1857, 1858, 1859, 1863) was destroyed during the Allied bombing of Milan, Italy, during the World War II. Fischer's (1885) specimen likely suffered the same fate when the ZMH collections were damaged during WWII. The specimens sent by Adolfo Möller to Bedriaga and used by the latter to describe his specimen of *Dendroaspis angusticeps* (Bedriaga 1893a) are also currently unaccounted for. Lacking the original specimens and without any recent record of the species, there are significant doubts regarding these accounts, and several authors have recognized this mystery (Schätti and Loumont 1992; Nill 1993; Ceríaco et al. 2018). Either the historical records are simply cases of mistaken identity and/or poor locality data, or there is an elusive species of green Mamba on São Tomé that has evaded researchers for more than a century.

Conservation

Although no studies have yet been conducted to specifically assess the threats faced by the reptiles of the Gulf of Guinea oceanic islands, it is likely that these are similar to the threats faced by their continental African counterparts. Habitat degradation and destruction caused by land-use change, climate change, non-native species, and direct persecution (especially in the case of snakes) can have seriously detrimental effects on local populations of reptiles. Given their abundance and mostly generalist ecology, as well protected habitats in the Obô Natural Parks on São Tomé and Príncipe, most species of reptiles from the Gulf of Guinea oceanic islands are not currently considered threatened (IUCN 2021; Table 19.2). The endemic geckos *H. greeffii* and *H. principensis*, however, are considered Near Threatened, and

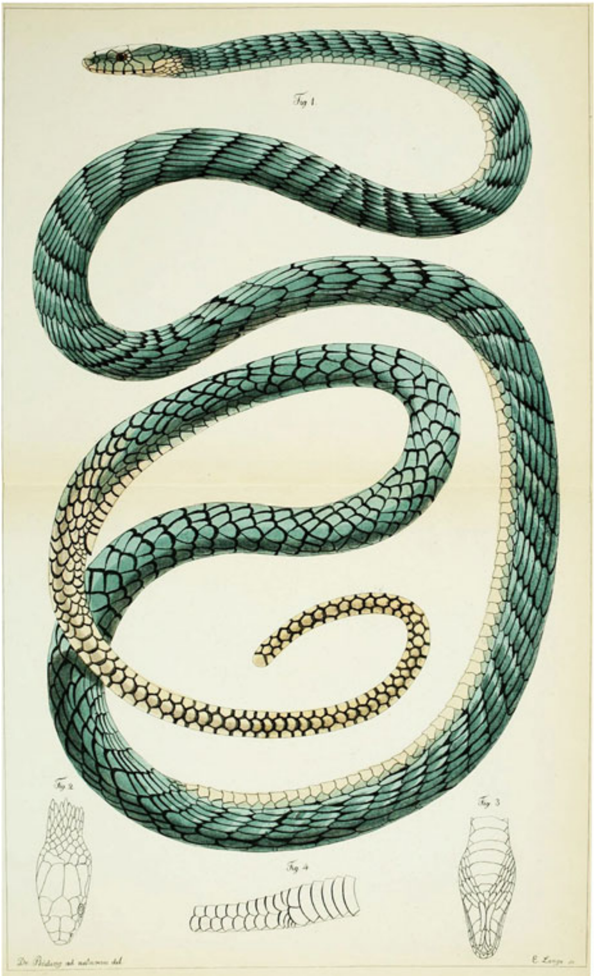

Fig. 19.3 Fischer's (1856) plate of "*Dendroaspis Jamesonii* Schlegel" from "Insel St. Thomé (West-Africa)"

their apparently low abundance and the potential for competition with introduced congeners *H. mabouia* and *H. longicephalus* may have negative impacts on their populations. Many species, including *Hemidactylus aporus*, *H. newtoni*, *Panaspis annobonensis*, *Letheobia newtoni* and *L. feae* are classified as Data Deficient due to insufficient population and distribution data and lingering taxonomic uncertainty. Currently, only *Naja* (*Boulengerina*) *peroescobari* is considered threatened, as Endangered. This classification is due to its endemic status and threats associated with both direct persecution and indirect death by car traffic. More detailed studies are needed to uncover potential risks caused by land-use change, one of the main and more prevalent threats to reptiles of the Gulf of Guinea oceanic islands, as well as local strategies to mitigate persecution, especially in the case of the Cobra-preta.

In recent years several reports on social media have depicted non-native species occurring on São Tomé Island. For instance, a dead specimen of an adult Orton's Boa Constrictor (*Boa constrictor ortonii* Cope, 1877), a subspecies endemic to Peru, South America, was found in the vicinity of São Tomé airport in August 2018. These animals are not easily transported by accident, and its presence on the island is likely due to intentional importation. Boas are listed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and thus importation to the country should be registered. Consulting the CITES Trade Database (UNEP–WCMC and CITES 2021), there are no records of any live specimen of reptile being legally imported to the country since 1975. Thus, illegal trade may be operational in the country, which could constitute a major threat to the native biodiversity. In March 2020, an adult female of agama, *Agama* sp. was found basking on the walls of a building in downtown Santo António city, Príncipe. The specimen was collected and euthanized and deposited at the facilities of Príncipe Trust Foundation in Santo António (Frazer Sinclair, pers. comm.). The specimen was collected at a construction site with raw materials imported from the African mainland, suggesting this individual was a stowaway. To our knowledge, no other specimens have been observed on the island. Some species of the genus *Agama* are usually human commensals and have already been introduced to the Cape Verde islands (Vasconcelos et al. 2014). Research is underway to identify the source population of this sole agama female specimen.

Future Research

Despite over a century of research, the taxonomy and diversity of terrestrial reptiles from the Gulf of Guinea oceanic islands are still incompletely documented. Taxonomic revisionary studies are sorely needed for some groups (as noted above), and the presence of the São Tomé Green Mamba remains an intriguing mystery. In addition, the biogeographic history of most lineages is poorly understood in part because the taxonomy of continental species is still in flux. Other than some anecdotal data presented in taxonomic reviews (e.g., Ceríaco et al. 2016, 2017), there are few studies focused on the ecology, natural history, and conservation of species. Furthermore, in contrast to the comprehensive assessments that have been conducted for other groups, notably birds (Melo et al. 2022), no studies exist on the impacts of invasive species or land use for terrestrial reptiles (Soares et al. 2022). Another important topic that needs further attention is the venom composition, medical significance and social impact of *N. peroescobari* snakebite. Finally, Pacheco et al. (2020) report considerable *Haemocystidium* parasite diversity in reptiles, and although this study did not include samples from any Gulf of Guinea oceanic islands taxa, the topic presents an exciting opportunity to investigate parasite-host interactions in an insular community.

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Chapter 20
The Sea Turtles of São Tomé and Príncipe: Diversity, Distribution, and Conservation Status

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Abstract The unique islands of São Tomé and Príncipe harbor five of the seven existent sea turtle species, and offer optimal conditions for these threatened species both on the beaches and on the foraging sites at sea. These populations might have been exploited since the sixteenth century and are still being harvested. In the past decade, our knowledge of these populations has greatly improved, highlighting their regional and global importance. Several conservation initiatives have also prioritized their protection. This chapter reviews our knowledge on the diversity, distribution, and conservation status of sea turtles in São Tomé and Príncipe, providing a brief history of conservation actions from the past 20 years and presenting ongoing research and conservation initiatives.

Keywords *Caretta caretta* · *Chelonia mydas* · Conservation · *Dermochelys coriacea* · *Eretmochelys imbricata* · *Lepidochelys olivacea*

Introduction

Sea turtles have been traveling the oceans for millions of years and with an incredible resilience have survived to the present day. This is probably why they are much appreciated and arouse so much interest in the general public and scientists, alike. Turtles belong to the most ancient line of living reptiles, first appearing more than

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200 million years ago, in the late Triassic. But it was probably around some 110 million years ago, in the Jurassic, during the reign of dinosaurs, that turtles entered the sea and shared the ocean with several other air-breathing reptiles, such as ichthyosaurus and plesiosaurus. While the end of the Cretaceous was the scene of the mass extinction of large reptiles that dominated the earth, sea turtle lineages persisted until the present day (Lutz and Musick 1997; Motani 2009).

These large marine reptiles are well adapted to life in the ocean, performing vast migrations between foraging and nesting areas that can be thousands of kilometers apart, and inhabiting a variety of neritic and pelagic habitats of tropical and subtropical waters globally (Carr 1982). The oceanic islands of the Gulf of Guinea, particularly São Tomé and Príncipe, harbor important breeding and foraging grounds for sea turtles. Sea turtle nesting grounds on Annobón, the smallest island in the Gulf of Guinea, are limited with only a few suitable beaches available, although important foraging grounds might exist (Castroviejo et al. 1994; Fretey 2001).

It was only in the 1990s that the presence of five sea turtle species in São Tomé and Príncipe was confirmed (Fig. 20.1): the Green Turtle *Chelonia mydas* (Linnaeus, 1758), the Olive Ridley Turtle *Lepidochelys olivacea* (Eschscholtz, 1829), the Hawksbill Turtle *Eretmochelys imbricata* (Linnaeus, 1766), the Leatherback Turtle *Dermochelys coriacea* (Vandelli, 1761), and the Loggerhead Turtle *Caretta caretta* (Linnaeus, 1758). Research in the past decade has greatly improved our knowledge of these populations, highlighting their regional and global importance. Simultaneously, there have also been significant efforts towards their protection. Since data regarding sea turtles in Annobón is scarce and that there are no conservation initiatives targeting these species on that island, this chapter will focus on Príncipe and São Tomé.

History of Sea Turtle Conservation in São Tomé and Príncipe

The first references to sea turtles in São Tomé and Príncipe date back to 1883. At this time, sea turtles were described as being common and were exploited by local communities, with carapaces used in the manufacture of jewelry and other ornamental items (Greeff 1884; Bocage 1903). The first sea turtle surveys of the Atlantic coast of Africa started as early as 1957 (Carr 2002), but it was only between 1985 and 1994 that the first attempts were made to describe the status of sea turtles in São Tomé and Príncipe (Stuart and Adams 1990; Schneider 1992; Atkinson et al. 1994; Castroviejo et al. 1994; Graff 1996).

Between 1994 and 1996, a more comprehensive survey was initiated on São Tomé Island thanks to a collaboration between ECOFAC (European Commission Program for the Conservation and Sustainable Use of Forest Ecosystems in Central Africa) and the U. S. Peace Corps. This survey confirmed the sea turtle species occurring in São Tomé and Príncipe, identified the main nesting beaches, assessed the impact of harvesting by the local communities (Graff 1996) and resulted in the baseline information being used to implement a monitoring and protection program

Fig. 20.1 Sea turtles of the Gulf of Guinea islands: (**1**) Female Green Turtle *Chelonia mydas*; (**2**) Green Turtle hatchlings; (**3**) Female Leatherback Turtle *Dermochelys coriacea*; (**4**) Leatherback Turtle hatchlings; (**5**) Female Olive Ridley Turtle *Lepidochelys olivacea*; (**6**) Juvenile Hawksbill Turtle *Eretmochelys imbricata*; (**7**) Male Loggerhead Turtle *Caretta caretta*; (**8**) Mating Green Turtles. Photo credits: (**1**) Maria Branco | Programa Tatô, (**2**, **4**, **7**) Ana Besugo, (**3**) Ivana Tacikova, (**5**) Joana Meneses, (**6**) Victor Jimenez | Programa Tatô, (**8**) Lara Baptista | Fundação Príncipe

on the main nesting beaches (Graff 1996; Rosseel 1997). This project gave rise to Programa Tatô (*Tatô* refers to the Olive Ridley Turtle in the local language) in 1998. Led by ECOFAC until 2001, it included the monitoring of the main nesting beaches, training of local community members as beach rangers and the construction of hatcheries (Dontaine and Neves 1999; Fretey and Dontaine 2001; Formia et al. 2003). In 2002, MARAPA (Mar, Ambiente e Pesca Artesanal), a national NGO created in 1999, took responsibility for Programa Tatô's conservation activities. This program survived until 2008 under the jurisdiction of the Central Africa Protected Areas Network (RAPAC) in partnership with the regional network PROTOMAC (Protection Tortues Marines Afrique Centrale), when it suddenly collapsed. Since then, several groups have kept sea turtle conservation efforts going on both islands.

In Príncipe, the Center for the Biodiversity Conservation of Príncipe Island (CBioP), an international research center under the responsibility of the University of Algarve's CCMar—Ocean Sciences Center in Portugal and the Regional Government of Príncipe, started Programa Sada (*Sada* refers to the Hawksbill Turtle in the local language) in 2009. The program aims to ensure sea turtle protection and conservation actions in partnership with the regional government and local communities of Príncipe, and focuses on the populations of the Critically Endangered Hawksbill Turtle. In 2010, the Government of the Autonomous Region of Príncipe approved the creation of the Sea Turtle Commission (*Comissão Tartaruga Marinha*) by the Natural Park of Príncipe, with the main goal of promoting and reinforcing sea turtle protection and their sustainable use on Príncipe.

In 2012, the Natural Park of Príncipe joined efforts with Here Be Dragons Príncipe (HBD, a tourism investment company established in 2010 for the sustainable development of Príncipe Island) and the Association for the Research, Protection, and Conservation of Sea Turtles in Lusophone Countries (ATM, a Portuguese NGO) to develop a comprehensive sea turtle monitoring and protection program on Príncipe Island. After two extremely successful seasons in Príncipe, ATM in 2014 combined efforts with the NGO MARAPA on São Tomé and their partnership reinitiated Programa Tatô. This resulted in the growth of Programa Tatô's team. In 2018, Programa Tatô was no longer just a MARAPA project. The coordination team, with the support and encouragement of its technical and financial partners, decided to give more autonomy and sustainability to this program and created an International NGO, Association Programa Tatô—the original name, which was well known to all local communities, national authorities, civil society as well as international partners, was preserved.

Meanwhile, on Príncipe, with the transition of ATM to São Tomé Island in 2014, Protetuga Project was created and managed by Fundação Príncipe (FP), a national NGO, established to support environmental and social actions by the HBD group with funding from the South African private-investor and businessman Mark Shuttleworth. At the end of 2016, due to budget cuts from the main donor, FP started to work with its regional, national, and international partners to become independent. Today, FP is independent and has a strategic plan focused on the conservation of biodiversity and the social and economic development of the communities on the island, with more than 15 different donors and projects directed at marine and terrestrial conservation.

Regarding Annobón, although classified as a Nature Reserve since 2000, there is no information or knowledge of any sea turtle conservation efforts on the island.

Species and Status

The modern marine turtles are placed in two families and are the only living members of what had been a large and diverse fauna: the family Dermochelyidae, which consists of a single species, the Leatherback Turtle, and the family Cheloniidae, which comprises six species of hard-shelled sea turtles: the Loggerhead Turtle, the Green Turtle, the Hawksbill Turtle, the Olive Ridley Turtle, the Kemp's Ridley Turtle *Lepidochelys kempii* Garman 1880, and the Flatback Turtle *Natator depressus* (Garman, 1880).

Five of the seven modern species are found in São Tomé and Príncipe, all of which are listed as threatened (IUCN 2021): the Olive Ridley, the Leatherback and the Loggerhead Turtles as Vulnerable, the Green Turtle as Endangered), and the Hawksbill Turtle as Critically Endangered. All of these five species nest on the beaches of the islands, except for the Loggerhead, which is occasionally found at sea (unpublished data). The Green Turtle is the most common sea turtle in the archipelago, nesting on virtually all sandy beaches of both islands (unpublished data). This nesting population exhibits relatively high levels of genetic diversity and distinctiveness, representing an important genetic pool in the region (Hancock 2019). The Olive Ridley Turtle is the second most numerous species on São Tomé, while only sporadic nesting occurs on Príncipe (unpublished data). These islands harbor one of the last remaining Hawksbill Turtle nesting aggregations in the region, which have a unique genetic haplotype and low genetic variability (Monzón-Argüello et al. 2011) and are one of the 11 most threatened sea turtle populations in the world (Wallace et al. 2011), emphasizing the high degree of isolation and vulnerability of this population. The Leatherback Turtle is the least abundant nesting species in the archipelago (unpublished data).

Distribution and Habitat

São Tomé and Príncipe are unique islands with clear warm oceanic waters surrounded by shallow rocky reefs sparsely colonized by hard and soft corals, vast beds of rhodoliths, and great diversity of macroalgae and seagrass meadows, which are more common in São Tomé. Coastlines change from an extensive shallow shelf and low wave exposure in the northern coasts to short and deeper shores more exposed to waves in the southern coasts of both islands. Freshwater enters the sea from small streams and rivers, forming small estuarine habitats in a few areas with mangroves bordering some of the river mouths (Bollen 2017; Cowburn 2018; Airaud et al. 2020; Ferreira-Airaud et al. 2021).

São Tomé has a diversity of beaches ranging from golden yellow sand to dark gray sandy or rocky stretches and varying between 0.17 and 2.11 km in length. Coastal vegetation is shaped by a wide range of precipitation and relatively homogeneous temperature (daily average of 27 °C): coastal meadows and a savanna-type ecosystem can be found on the northern coast, where rainfall is less than 700 mm a year, while in the south yearly rainfalls over 7000 mm feed luscious rainforests (Ceríaco et al. 2022; Dauby et al. 2022). Mangroves can be found on sheltered coasts along this gradient. Príncipe displays a luxurious green wilderness with a magnificent topography of volcanic landscapes. The forest is omnipresent and, in most places, falls directly into the ocean from high cliffs with several narrow beaches up to 1.4 km in length ranging from white, golden to black sand or rocky stretches.

This exceptional environment offers optimal conditions for colonization by sea turtles, both on the nesting beaches and on foraging sites at sea.

Nesting Beaches

Sea turtle nesting occurs on almost all the sandy beaches of both islands that offer suitable conditions for nesting, even though distribution and density vary between species. The nesting season on both islands coincides with the rainy season, which runs from October to May, providing suitable conditions for nesting and incubation.

In São Tomé, nesting occurs on the northern, eastern, and southern coasts (Fig. 20.2). The northern and eastern coastal areas host large human settlements, whereas the southern (particularly southwestern) beaches are relatively remote. The lack, or very low prevalence, of nesting on the western coast of São Tomé is likely due to the rocky beaches characterizing this stretch of coast.

In Príncipe, nesting occurs mainly on the northern and southeastern beaches (Fig. 20.3). Most of the southern beaches are particularly remote with almost no human settlements.

In Annobón, nesting is limited due to the availability of only a few suitable beaches (Castroviejo et al. 1994), this oceanic island.

Green Turtle The Green Turtle is the most common species in the archipelago. Its nesting has been confirmed on virtually all sandy beaches of both islands, ranging from 49 to 1177 nests per year on São Tomé and from 287 to 2050 nests per year on Príncipe (from data collected by our team between 2014 and 2020). Data collected since 2014 confirm what was observed during the initial surveys in the 1990s, namely that Green turtles on São Tomé nest mainly in the south, with Praia Jalé being the preferred beach (70% of the total nesting by the species), followed by Praia Grande, both in the region of Porto Alegre, in the Caué district (Fig. 20.2a). This area is characterized by high rainfall, dense tree cover, beaches with steeper slopes and high wave exposure. On Príncipe, green turtles nest mainly in Praia Grande do Norte

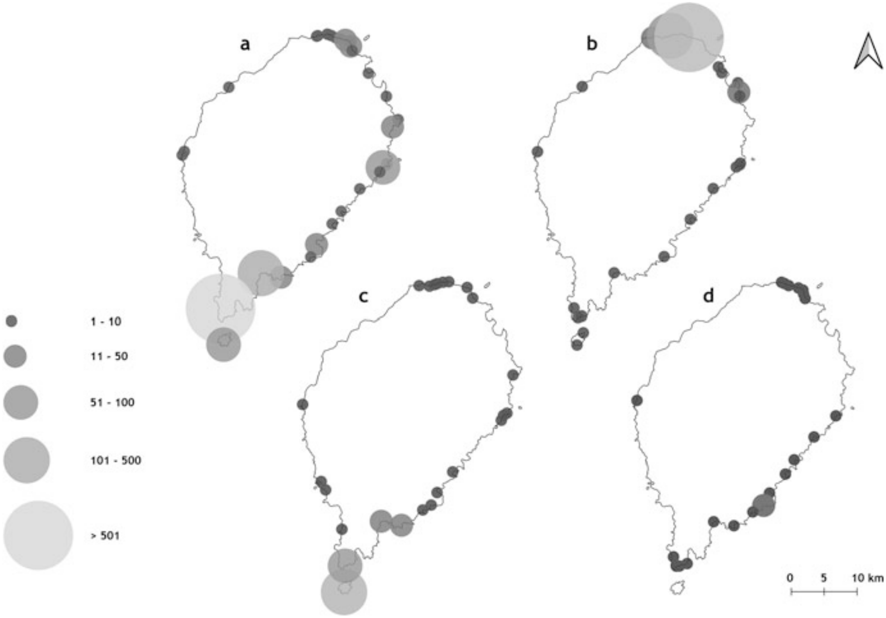

Fig. 20.2 Distribution of the average number of nests per species in São Tomé, from 2017 to 2020: (**a**) Green Turtle *Chelonia mydas*; (**b**) Olive Ridley Turtle *Lepidochelys olivacea*; (**c**) Hawksbill Turtle *Eretmochelys imbricata*; and (**d**) Leatherback Turtle *Dermochelys coriacea*

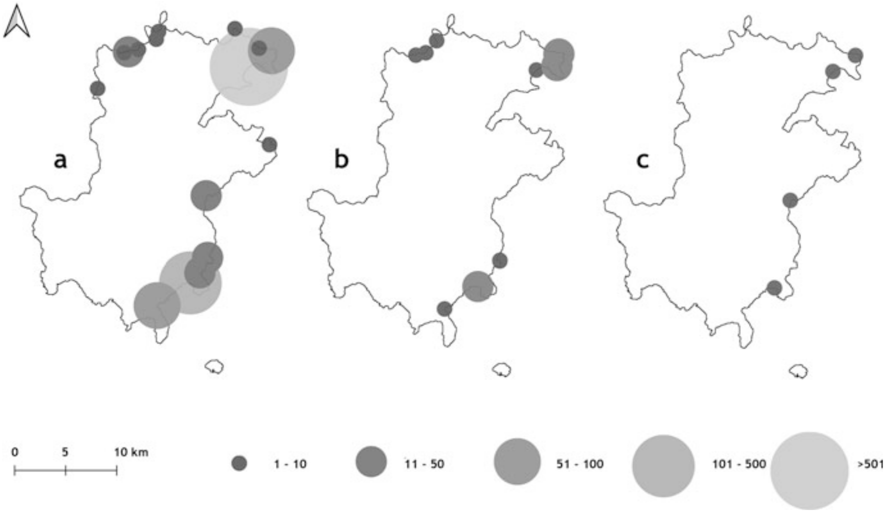

Fig. 20.3 Distribution of the average number of nests per species in Príncipe, from 2017 to 2020: (**a**) Green Turtle *Chelonia mydas*; (**b**) Hawksbill Turtle *Eretmochelys imbricata*; and (**c**) Leatherback Turtle *Dermochelys coriacea*

in the northern part of the island and in Praia Infante in the south (Fig. 20.3a). Green turtle nesting occurs year-round (except June), with a nesting peak in December and January.

Olive Ridley Turtle Major nesting grounds of Olive Ridley Turtles in West Africa are in Angola and Gabon (Metcalfe et al. 2015; Morais and Tiwari 2022). Nevertheless, this is the second most numerous species on São Tomé, ranging from 326 to 683 nests per year between 2014 and 2020 (unpublished data). On Príncipe only two nesting observations were recorded on Praia Macaco in 2012, and on Praia Grande do Norte in 2018. This species nests year-round (except June), with a nesting peak in November and December. Olive Ridley Turtles seem to prefer the northern area of São Tomé from Praia Juventude to Praia das Conchas, adjacent to the fishing communities of Micoló, Fernão Dias, and Morro Peixe, where 90% of the nesting occurs (Fig. 20.2b). This area is characterized by lower rainfall, gentle sloping beaches, an extensive shallow shelf and low wave exposure shores. The northern part of São Tomé is also notable for the presence of seagrass meadows, an ecologically valuable marine habitat and feeding grounds for the Green Turtle.

Hawksbill Turtle The Hawksbill Turtle is the most threatened turtle species on São Tomé and Príncipe and, nowadays, its distribution is less extensive due to the indiscriminate harvesting for its meat and shell (Fretey et al. 2000). Nevertheless, the number of nests appears to be increasing slightly, ranging from 13 to 246 nests per year on São Tomé and from 43 to 118 nests per year on Príncipe (unpublished data collected between 2014 and 2020). Most of its nesting (60%) on São Tomé occurs on Rolas Islet, south of São Tomé, highlighting the importance of this islet as a priority site for the conservation of this Critically Endangered species (Fig. 20.2c). On Príncipe, the preferred beaches are Praia Infante in the south and Praia Grande do Norte in the north (Fig. 20.3b). Hawksbill nesting occurs from August to April with a nesting peak in December and January. Like Green Turtles, Hawksbill Turtles seem to prefer beaches characterized by dense tree cover, steeper slopes, high wave exposure and high rainfall.

Leatherback Turtle One of the major nesting grounds for Leatherback Turtles is in Gabon, approximately 300 km from São Tomé and Príncipe, with as many as 36,185–126,480 nests, and 5865–20,499 breeding females per year (Witt et al. 2009). In São Tomé and Príncipe, it is the least abundant nesting species with 15–155 nests per year in São Tomé and 3–44 nests per year in Príncipe, (unpublished data collected between 2014 and 2020). Nesting occurs from September to March with a nesting peak in December. Although this species has a more heterogeneous distribution, there is a certain preference for the southeastern beaches on São Tomé (Fig. 20.2d) and the northern and eastern beaches on Príncipe (Fig. 20.3c).

Loggerhead Turtle Extensive surveys in the eastern Atlantic suggest that the only significant nesting aggregation is in Cabo Verde (Fretey 2001; Ehrhart et al. 2003; Marco et al. 2012). Historically, in São Tomé and Príncipe there have been only a couple of observations of Loggerhead Turtle nesting on São Tomé, but there is no evidence that this species has ever nested frequently on the islands (Fretey 2001).

Since 2014, only one nesting event (82 cm CCL—curved carapace length) has been registered on São Tomé, in January 2017 at Praia Inhame in the south of the island (Porto Alegre region; our data). In addition to these isolated events, Loggerhead Turtles are occasionally observed at sea (our data).

Foraging Grounds

After hatchlings emerge from the nest and make it safely to the sea, they swim in a frenzy to reach the open ocean. The "lost years" characterize this lesser-known period when young sea turtles stay away from coastal areas until they become juveniles. Foraging habitats vary among species (Musick and Limpus 1997). All species occurring in São Tomé and Príncipe are found foraging year-round in coastal waters.

Green Turtle Local fishermen have indicated several foraging or aggregation sites of Green Turtles around both Príncipe and São Tomé, which have been confirmed through in-water surveys developed by the sea turtle conservation programs (our data). Both islands host two distinct immature groups of foraging green turtles: small immature, likely to have recruited recently from the oceanic to the neritic zone, and larger immatures that explore the local resources for extended periods.

On São Tomé, Green Turtle immatures hand-captured at sea since 2014 during Programa Tatô in-water surveys ranged from 34 to 45 cm CCL (Curve Carapace Length; Hancock et al. 2018), which is consistent with historical records from the 1990s of small immatures ranging from 33 to 45 cm CCL (Fretey and Dontaine 2001). This is within the expected size range at recruitment for post-pelagic turtles of this species (Musick and Limpus 1997) but slightly smaller than other locations in the Atlantic (Reisser et al. 2013) and Pacific (Arthur et al. 2008).

Small immature Green Turtles are more commonly found in a foraging ground identified in the south of São Tomé; it is possible that the rocky substrate of southern São Tomé is well suited for omnivores because it is rich in macroalgae and benthic invertebrates and provides more resting or hiding sites for the smallest individuals than the exposed seagrass beds located in the north foraging ground. Large immatures range from 45 to 75 cm CCL, since the minimum size observed in nesting females on São Tomé ranges between 72 and 75 cm CCL. These large immatures are more often found feeding upon green algae and seagrasses in the northern foraging ground, where there are large seagrass meadows.

On Príncipe, the recruitment size for small immatures is lower than on São Tomé, with the smallest individual observed having 28 cm CCL; large immatures on Príncipe have a maximum CCL over 70 cm. Individuals are observed, mainly in rocky reefs covered with macroalgae all around Príncipe, but to date the main green turtle foraging grounds on Príncipe have not been identified. Analysis of stomach contents of stranded immature green turtles revealed that these animals feed on several algae species present on rocky reefs around the island. Transmitters with cameras placed on adult females nesting in Praia Grande do Norte, north of Príncipe, in 2018, confirmed that these females feed on algae during the inter-nesting period in the bays near the nesting beach.

These foraging sites clearly indicate that these islands are important recruitment and development habitats for immature Green Turtles in the region, and that after reaching maturity, adults move to other foraging sites in the region. Ongoing satellite telemetry studies will refine our understanding of adult foraging grounds and migration routes.

Olive Ridley Turtle Globally, Olive Ridley Turtles may use a wide range of foraging habitats, primarily neritic in relatively shallow benthic waters or sometimes in major estuaries as recorded in Australia (Whiting et al. 2007), Oman (Rees et al. 2012), French Guiana (Plot et al. 2015), and Brazil (Santos et al. 2019). They are also known to feed in oceanic deep waters, as seen in Costa Rica (Plotkin 2010), India (Ram et al. 2009), Gabon and Angola (Maxwell et al. 2011).

The foraging behavior of Olive Ridley Turtles in São Tomé and Príncipe is largely unknown, with only a few observations in the past few years during in-water surveys. However, recent incidental fishery bycatch records, beach strandings, and fishermen testimonials revealed that the coastal waters of both islands may host important foraging areas for both adults and immatures throughout the year. Small immatures were observed on a few occasions at both islands. The smallest were registered in 2014 on São Tomé with a CCL of 20 cm, and in 2015 on Príncipe with a CCL of 18.8 cm; others individuals within the same size range have been observed since then. According to a local fisherman, they can be seen feeding on eggs of flying fish (*Exocoetus* spp.) that breed on the southwest coast of São Tomé from June to August.

Hawksbill Turtle As with Green Turtles, shallow waters of both islands host year-round Hawksbill Turtle foraging aggregations of small and large immatures, and of mature males and females in rocky reef and coralline algae (rhodolith) habitats. On São Tomé, the main foraging grounds are in the south, at Rolas Islet, and on the northwest coast, adjacent to Neves and Santa Catarina. On Príncipe, most of the rocky reefs are used by the species, where it can find a variety of suitable food items, such as rhodoliths and macroalgae, hard and soft corals and other invertebrates.

While immature Hawksbill Turtles found in shallow waters are assumed to be residents for certain periods, ongoing satellite telemetry studies on nesting females have revealed that most of the adults migate from nesting to foraging grounds, adults may.

On São Tomé, the smallest Hawksbill Turtle hand-captured at sea was 30 cm CCL, while the minimum size observed for nesting females was 55 cm CCL on São Tomé.

On Príncipe, the smallest immature had 26.5 cm CCL (Ferreira et al. 2018).

Leatherback Turtle Leatherbacks are the most pelagic sea turtle species, spending much of their life in the open sea, but foraging over continental shelves where environmental conditions favor the presence of gelatinous zooplankton, their favorite prey (Dodge et al. 2014).

In São Tomé and Príncipe there are no recent records of Leatherbacks foraging in the coastal waters, besides sightings and bycatch by local fishermen during the nesting season. Older records mention three immatures in Príncipe, ranging from 17 to 21 cm CCL, and a of 14 cm CCL one on São Tomé (Fretey et al. 1999). However, since there are no recent records of small immatures, these are thought to be occasional, even though there has been no concerted effort to record immatures of this species.

Loggerhead Turtle In São Tomé and Príncipe, sporadic observations at sea of adult loggerheads have been recorded over the years during in-water surveys (Ferreira et al. 2015), from local fishermen and in incidental fishery bycatch reports. The most recent record was in 2020, when one was captured with two adult Olive Ridley Turtles, in a bottom gill net around the coast of Príncipe.

Main Threats for the Survival of Sea Turtles

Sea turtles were once very abundant, but today all seven sea turtle species are threatened at a global scale (IUCN 2021). Unquestionably, human interference throughout the past centuries is the cause of their decline (Lutcavage et al. 1997). Today most of the threats affecting sea turtles in the oceanic islands of the Gulf of Guinea are not exclusive to this part of the world, although cumulative impacts make their conservation particularly challenging.

Historical records reveal that sea turtles were once abundant in São Tomé and Príncipe (Matos 1916) and might have been heavily exploited for their meat and shells since the sixteenth century, when São Tomé and Príncipe were first inhabited (Greeff 1884; Parsons 1962; Parsons 1972). The Portuguese transported hundreds of sea turtles on caravels to feed their crews (Fretey et al. 2000; Loureiro and Torrão 2008) and carapaces and scales were delivered to royal and noble families that collected tortoiseshell jewelry and art objects (Orey 1995). Parsons (1962) indicated that a tortoiseshell industry existed on the islands and supported a domestic trade. Later on, there was also a trading network with Angola, where tortoiseshell products were made into souvenirs (Brongersma 1982; Stuart and Adams 1990; Carr and Carr 1991). The Convention on International Trade in Endangered Species (CITES) came into effect in 1975, to protect plant and animal species from unsustainable levels of international commercial trade, but it was only ratified by São Tomé and Príncipe in 2001 (de Lima et al. 2022). Angola ratified CITES only in 2013, and local artisans of São Tomé and Príncipe report that the occasional clandestine trading of turtle shells still persists.

In the 1990s, 43 artisans working with turtle scutes, known as “tartarugueiros,” were identified (35 in São Tomé and 8 in Príncipe), and an inventory of the scutes and manufactured objects that they possessed weighed 225 kg and 45 kg, respectively, for an estimated value of around 30,000 Euros (Fretey et al. 2000). In 2002/2003, with funds from European Union, all stocks of scutes and manufactured objects were bought from the artisans and donated to the National Museum of São Tomé and Príncipe, and recently destroyed. Until this period, the use of the Hawksbill Turtle shell for the manufacture of handicrafts and jewelry was the greatest driver of the indiscriminate harvest and decline of this species. Today it is still common to find turtle jewelry being sold in some shops in São Tomé, mostly to uninformed tourists.

In the 1990s, almost every sea turtle found at the beach or sea was killed for its meat or shell (Fretey 1998), and despite many conservation efforts over the past few decades, turtles are still killed for their meat and eggs in São Tomé and Príncipe. At sea, adult sea turtles were indiscriminately captured using hooks, harpoons, and gillnets set in front of the main nesting beaches (Castroviejo et al. 1994). Fresh or salted turtle meat was until very recently part of certain traditional menus in São Tomé and Príncipe, and the shell was very often used in the preparation of these dishes as well as for traditional medicinal or as an aphrodisiac (Fretey 1998). However, the use of these animals in traditional ceremonies is not as common as in other West African countries (Barbosa and Regalla 2016). Up until 2016, it was still possible to buy sea turtle meat in the local markets. The most expensive was Green Turtle meat, which sold for 50–100 dobras (2–4 euros) for approximately 300 g, while the least expensive was the Olive Ridley, which sold for around 300 dobras (12 euros) per turtle. Although these practices have decreased drastically in both islands, they still represent a threat to sea turtles in some communities. Finally, a variety of domestic animals and natural predators, including crabs, rats, dogs, and pigs, also depredate sea turtle eggs and hatchlings. Approximately 60% of the sea turtle nests in São Tomé must be transferred to protected hatcheries to prevent nest predation.

In addition to direct exploitation, sea turtles are affected by several indirect threats in São Tomé and Príncipe. Commercial fisheries (many from east Asian countries) operating in the Gulf of Guinea are thought to incidentally capture many sea turtles, mainly Olive Ridley and Leatherback Turtles (Huang 2015). Small-scale fishing activity in both São Tomé and Príncipe represents a major source of income for coastal communities who have few economic resources and opportunities, and the unintentional take in a major threat to sea turtles, particularly longline (vertical and horizontal), demersal gillnet, surface driftnet and purse seine (pers. obs.). However, little is known about the impacts of these artisanal fisheries on sea turtles and other marine resources in São Tomé and Príncipe. The Gulf of Guinea is also the focus of extensive and rapidly increasing oil exploitation activities. Vast oil reserves have been discovered in the last decade, in areas that host important sea turtle habitats. Drilling activities by large international oil corporations, associated with pollution and habitat destruction, are threats that have been increasing and are expected to continue increasing in the region, soon expanding to São Tomé and Príncipe (de Lima et al. 2022).

With a human population estimated to have just surpassed the 200,000 mark, and to be growing at 1.5% each year (Central Intelligence Agency 2021), construction around São Tomé is increasing fast, namely for the tourism sector. The increase in tourism will bring, along with its benefits, some environmental challenges, such as the increase in disturbance of nesting beaches, the need of sand for construction, and the increase in artificial lights by the coast. Despite a national ban of sand mining activities on beaches since 1999 (Decreto-Lei n°35/99) and recently updated (Law n.°9/2020, from 22 of September), sand continues to be extracted, namely from sea turtle nesting beaches, where the effects of sand removal is accelerating erosion, causing the disappearance of several nesting beaches, and exacerbating the consequences of sea level rise due to climate change.

Around urban areas on both islands, most sewage is discharged untreated into the sea. The most extreme national example may be seen in São Tomé city, where the Água Grande river regularly pumps a combination of untreated sewage and petrochemical waste (from the city's electric generators) directly into the sea at Ana Chaves Bay. In Príncipe, dead stranded turtles found on the beach have been analyzed by Fundação Príncipe to understand whether there is a relationship with the increased presence of waste in the sea and these events. Preliminary analyses show that young and adult turtles (mostly Green Turtles) feed on various solid residues, mostly plastic. In addition to the increasingly presence of this type of waste in the intestinal tract of these animals, it is common to see immature Green Turtles with fibropapillomatosis, a disease that results in the production of tumors, both external and internal, which are benign but may obstruct crucial functions, such as swimming, feeding, sight, and buoyancy, and may lead to death (Herbst 1994). A strong link between this disease and the environmental health of the coastal habitats is already known (Santos et al. 2010; Santos et al. 2011). The first records of this disease in turtles in Príncipe date from 2009 (Loureiro and Matos 2009). Turtles are also particularly vulnerable to a variety of environmental conditions, such as higher water temperature, pollutants, and marine biotoxins, all of which can weaken their immune functions, making them more susceptible to a wide range of pathogens. Sea turtles are often considered sentinels of ecosystem health and in fact, it has been suggested that fibropapillomatosis could serve as an effective tool to monitor ecosystem health in near-shore marine habitats (Aguirre and Lutz 2004).

Conservation

Since the initiation of conservation activities in the country in 1998, one of the first strategies was to work with the government to implement a National Law to protect these threatened species in São Tomé and Príncipe. In 2001, the first draft of the decree was proposed to the national government, but it was only in 2014 that the national law protecting sea turtles and criminalizing the consumptive use of sea turtles and their by-products was adopted in São Tomé and Príncipe (Decreto-Lei n° 8/2014). Remarkably, 5 years before the national law was officialized, the regional government of Príncipe, which has administrative autonomy, implemented a law to protect sea turtles on the island (Decreto-Lei n° 03/2009), which may have encouraged the national government to take action. However, as in many developing nations around the world, enforcement of environmental laws is still challenging, since relevant institutions often lack the technical capability and means to effectively implement the legislation. Since the adoption of the sea turtle national law in 2014, there have been virtually no penalties or sanctions against sea turtle hunters or traders in São Tomé. As for Príncipe, only two cases were penalized with the payment of a fine and some other cases were included in the social assistance program. In this social assistance program, violators of the sea turtle protection law are required to perform social services for the regional government and for the Fundação Príncipe sea turtle conservation program, including a mandatory participation in awareness-raising activities in their own community. This initiative has been an opportunity to involve and promote a change in the mentality of those who violate the law protecting sea turtles.

Before the creation of these domestic laws, São Tomé and Príncipe ratified several international conventions that support in-situ conservation actions (de Lima et al. 2022). The Convention on Biological Diversity (CBD) was ratified in 1999, followed by the Convention on the Conservation of Migratory Species of Wild Animals and CITES in 2001, and by the Abidjan Convention (United Nations Environment Program) in 2002. Although these laws were approved and several conventions were ratified, legal protection of sea turtles does not automatically translate into realistic changes felt on a daily basis. In fact, one of the biggest challenges to sea turtle conservation in developing countries, such as São Tomé and Príncipe, is changing the habits of coastal communities for whom sea turtles are an important source of subsistence and income and are essential for survival. So, as with many other conservation programs worldwide (e.g., Marcovaldi et al. 2005), a consistent and long-lasting conservation program that integrates and generates direct and indirect socio-economic benefits for local communities is essential to prevent sea turtle extinction.

Today, Programa Tatô in São Tomé, and Fundação Príncipe in Príncipe are the key drivers of sea turtle conservation and research in the country. Both conservation programs are based on the key principle that the participation and engagement of local communities are essential for a successful conservation program. On São Tomé, more than 80 people are involved in the conservation activities of Programa Tatô (90% of whom are nationals) and include members from the local communities, young professionals, and 51 rangers responsible for monitoring and protecting foraging grounds and 77 out of the 107 breeding beaches. On Príncipe, Fundação Príncipe, has a team of around 62 people (91% of whom are nationals) developing marine and terrestrial conservation projects, including 32 rangers, who monitor and protect foraging grounds and 36 out of the 50 beaches.

On São Tomé, Programa Tatô initiated a conversion process in 2016, to identify and develop alternative livelihoods for the women who were trading sea turtle products at the main national market, giving rise to a productive group of 17 women willing to transition towards a new livelihood, independent of the sale of sea turtle meat and eggs. Currently, these women produce handicrafts, including school uniforms, reusable masks, and menstrual pads. The program includes continuous follow-up, ensuring the consolidation of this group and their economic sustainability, thus promoting a long-term behavioral change and the recovery of sea turtle populations in São Tomé and Príncipe (Vieira et al. 2017).

We note, however, that the monitoring of beaches and foraging grounds and the direct involvement of a small percentage of the country's inhabitants is not enough to improve the conservation status of sea turtles. Besides direct employment by creating new jobs for research, internships, ecotourism guides and production of handicrafts, both organizations also develop active and innovative environmental education and public awareness campaigns. In São Tomé, these campaigns were developed after a study to estimate the prevalence of consumption, preference, and availability of sea turtle meat and eggs, and make use of trusted influencers and communication channels. This study helped develop a structured and rigorous approach using behavioral insights to guide behavior change efforts (Veríssimo et al. 2020; Thomas-Walters et al. 2020). Communication, education, and awareness proved to be fundamental strategies not only because they create a better relationship and trust between conservation organizations and communities, but also because they contribute to the development of environmental awareness about the ecological and socio-economic value of sea turtles and about the benefits of their conservation. Awareness efforts involve a variety of initiatives, including educational school programs, sports activities, theater, radio and TV programs and soap operas, beach and ocean clean-ups, and fishing sector awareness activities, among others.

Considering the challenges that sea turtle conservation faces nowadays, both Programa Tatô and Fundação Príncipe have adopted an integrated approach, which is essential to improve the protection and sustainable management of key sea turtle habitats, while developing a community-based marine conservation program that combines research, ecological monitoring, protection of critical sites, environmental education, advocacy, community-based ecotourism, reconversion of former poachers and traders, and development of alternative livelihoods. Thus, these programs have been addressing the diverse and complex challenges of sea turtle conservation, increasing our knowledge of all the sea turtle species that occur on and around both islands, and improving the relationship between sea turtles and diverse stakeholders from small-scale fishing communities to national politicians. Although human threats are still a reality, levels of sea turtle harvest have decreased considerably, and the number of sea turtles recorded on the nesting beaches appears to be increasing (Thomas-Walters et al. 2020). Today sea turtle conservation in São Tomé and Príncipe has an increasing and wider public appreciation, support, and understanding, which provide an opportunity for local stewardship, changing attitudes towards sea turtles and other living marine resources, and preparing future generation to be more aware of environmental topics.

Although research is underway on both islands to better understand the reproductive ecology, spatial and temporal movements, the foraging grounds, and the impacts of anthropogenic threats, it is essential to increase our scientific knowledge for adequate and effective sea turtle conservation guidance, so that critical habitats may be protected using evidence-based conservation priorities and strategies. Major challenges for the future include obtaining resources to maintain the levels of operation developed to date, to continue to support and improve the self-sufficiency of former sea turtle hunters and traders, and to promote greater self-sufficiency of both conservation programs. Nevertheless, the commitment of Programa Tatô and Fundação Príncipe will remain focused on the coastal communities, who are the true motivation for and the main component of any marine conservation program.

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Chapter 21
The Avifauna of the Gulf of Guinea Oceanic Islands

Martim Melo, Peter J. Jones, and Ricardo F. de Lima

Abstract Although birds have always been one of the best-known taxa on the Gulf of Guinea oceanic islands, our understanding of their ecology and evolution has increased substantially in the last two decades. Intensive field-based surveys have allowed the first detailed island-wide distribution maps for most species and a much better grasp of habitat associations, highlighting the importance of native forests for many of the endemic birds. Molecular data have provided important insights into evolutionary history, leading to an extensive revision of the taxonomy of the islands' endemic avifauna. Most speciation events are much more recent than the age of the islands, indicating a high species turn-over that is likely explained by the islands' history of intense volcanic activity and their moderate distances to the mainland. These islands have the highest accumulation of endemic bird species for small oceanic islands: at least 29 endemic species occur in three islands with a total area of just over 1000 km^2. This may be explained by their particular geographic location: offshore from a species-rich continent at distances that allowed the colonization and evolution in isolation of many distinct lineages. All these contributions are now

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being used to ensure bird conservation, through updated species conservation status and species action plans for the most threatened species, and also to promote the conservation of the native forests on which most of the endemic birds depend.

Keywords Biodiversity · Birds · Conservation · Endemism · Radiation · Speciation

Birds are one of the animal groups with which people are most familiar. This is especially true in the oceanic islands of the Gulf of Guinea where the avifauna has a prominent position in popular culture. The islands' birds have also been a preferential target of scientific investigation since the colonial period, in part due to the exceptionally high number of endemic species. This richness has played an important role in bringing global attention to the unique biota of these islands. The state of ornithological knowledge on these islands was summarized at the start of the present century (Jones and Tye 2006), but since then a wealth of new information has been gathered by an increasing number of studies. Here we provide an updated overview of the diversity, ecology, and evolution of this remarkable avifauna.

We follow the taxonomy and nomenclature of Clements et al. (2021), which is identical to the most recent checklist of the birds of the region (de Lima and Melo 2021). Taxonomic authorities are presented in the checklist (Appendix).

History of Ornithological Research

The avifauna of the Gulf of Guinea islands was little known before the nineteenth century. These relatively isolated oceanic islands were logistically difficult to access, with rugged, inhospitable interiors, so that progress was slow and sporadic, with decades-long gaps between collections. By the end of the nineteenth century, the avifauna was well documented, although important collections made at various times in the twentieth century further contributed to recognizing the importance of the islands' unusually high endemism. Throughout this period, it became clear that several endemic taxa were extremely rare and their forest habitats vulnerable to development, prompting conservation concerns in recent decades. Easier access to the islands and better logistical support have made it possible to run longer-term research and conservation projects, and the advent of modern molecular phylogenetics has enabled significant insights into the evolutionary history of the endemic bird community.

Apart from a few specimens collected earlier, the avifauna remained little known until the 1840s, when the islands were used as a base for the British Expedition to the River Niger. Expedition members collected several new species on São Tomé and Annobón but visited Príncipe only briefly and did not collect any birds there (Allen and Thomson 1848). Considerable confusion surrounded the provenance and identity of these specimens, however, due in part to the repeated loading and unloading of cargoes between ships and between islands. Other misidentifications resulted simply because African bird taxonomy was then in its infancy.

The most important early collections on Príncipe and São Tomé were made between 1847 and 1850 for the museums of Hamburg and Bremen by Carl Weiss, most of whose specimens were described in Hamburg by Gustav Hartlaub (1850, 1857), but confusion surrounded many Príncipe specimens that were wrongly ascribed to the African continent. These confusions were eventually resolved with the help of Heinrich Dohrn and John Gerrard Keulemans, whose collections on Príncipe between April and September 1865 were complemented by the field notes of Keulemans that proved to be a valuable source of information (Dohrn 1866; Keulemans 1866).

In 1885, Adolpho Frederico Moller obtained some birds from São Tomé while collecting plants for the Coimbra Botanic Gardens (Vieira 1887). Between 1885 and 1895, Francisco Newton assembled a comprehensive collection from all three islands for the Lisbon Museum, which were described in a long series of papers by José du Bocage (Bocage 1867, 1879, 1887a, b, 1888a–c, 1889a–c, 1891, 1893a, b, 1903, 1904). Newton was also a keen observer whose descriptions of behavior and ecology were partially published by Bocage as ancillary information. However, the original letters that Newton wrote to Bocage to accompany his specimens and almost all the specimens themselves were destroyed in the disastrous 1978 fire in the Museu Bocage in Lisbon. By the end of the nineteenth century, most landbird species had been described but an important collection was made for the museum at Genoa by Leonardo Fea between 1899 and 1901 (Salvadori 1903a–c).

Two significant collections were made in the early decades of the twentieth century. Boyd Alexander visited the main islands in 1909 collecting for the British Museum (Bannerman 1914, 1915a, b) and José Correia and his wife Virginia collected on Príncipe and São Tomé for the American Museum of Natural History in 1928–29 (Correia 1928–29; Amadon 1953). Both Alexander and the Correias kept extensive field notes on the distribution and status of the endemic bird species they collected at a time when agricultural exploitation of the islands was at its peak and some species had evidently become very rare. Correia's valuable and entertaining diary (1928–29) remains unpublished, but his collection allowed Amadon (1953) to produce an important synthesis on the avian zoogeography of the Gulf of Guinea islands.

The next ornithological survey of Príncipe and São Tomé took place in 1949, when an Oxford University team published the first detailed field notes for most of the endemic birds (Snow 1950). Annobón has always been difficult to access because of its remoteness, so there was an even longer gap between Alexander's 1909 expedition and subsequent visits by Aurélio Basilio in 1955 (Basilio 1957) and Hilary Fry in 1959 (Fry 1961).

A Portuguese scientific mission to Príncipe and São Tomé in 1954 collected birds and assessed the status of those that might require protection under colonial law (Frade 1958, 1959; Frade and Santos 1977). René de Naurois visited the islands several times in 1963 and 1970–73, publishing extensively on the ecology and systematics of most indigenous species, including all the endemic birds (Naurois

1972a, b, 1973a, b, 1975a, b, 1979, 1980, 1981, 1982, 1983a, b, 1984a–d, 1985, 1987a–c, 1988a–c; Naurois and Castro Antunes 1973; Naurois and Wolters 1975). He also wrote the first book to deal exclusively with the birds of all three oceanic Gulf of Guinea islands (Naurois 1994).

In June 1983, ornithologists from the Dresden Museum visited São Tomé (Günther and Feiler 1985) and again in March-April 1991, the second time as part of a multi-disciplinary expedition (Nadler 1993). Annobón belatedly received further attention with visits by Mike Harrison (1990) and Jaime Pérez del Val (2001). In 1996–97 an expedition by the University of the Azores conducted the first detailed study dedicated to seabirds (Monteiro et al. 1997).

The Red Data Book for African birds considered seven endemic bird species of these islands to be threatened (Collar and Stuart 1985), highlighting the fact that four single-island endemics on São Tomé had not been seen for over 50 years and were possibly extinct. This publication prompted conservation initiatives by the International Union for Conservation of Nature (IUCN—Jones and Tye 1988; Burlison and Jones 1988) and by the European Union. The latter acted mostly through ECOFAC, a program sponsored by the European Union promoting the conservation and sustainable use of forest ecosystems in Central Africa (Anon. 1994) that published the first field guide to the birds of São Tomé and Príncipe (Christy and Clarke 1998). Increased attention led to the rediscovery of all four "missing" bird species: São Tomé Short-tail *Motacilla bocagii* in 1987 (Eccles 1988), Sao Tome Ibis *Bostrychia bocagei*, Newton's Fiscal *Lanius newtoni* in 1990 (Atkinson et al. 1994), and São Tomé Grosbeak *Crithagra concolor* in 1991, more than a century after it had last been seen (Sergeant et al. 1992). On Príncipe, the rare endemic Príncipe Thrush *Turdus xanthorhynchus* was rediscovered in 1996, after more than 50 years (Christy and Gascoigne 1996).

The number of ornithological studies has greatly increased since the turn of the twenty-first century, leading to numerous taxonomic changes and a much better understanding of this unique avifauna (Jones and Tye 2006; Melo 2007; de Lima and Melo 2021). However, there is still much to be discovered as exemplified by the existence of the Príncipe Scops-Owl, which was only confirmed in 2016, 90 years after Correia collected information from local people on its putative occurrence (Verbelen et al. 2016).

Species Diversity and Distribution

General Patterns

According to the latest assessment (de Lima and Melo 2021), the avifauna of the oceanic islands of the Gulf of Guinea comprises 146 confirmed species (Appendix). These include 66 resident species, which contain a remarkably high number of endemics: 29 (44%) species and 16 (24%) subspecies (Table 21.1). Seventeen species (26%) are possibly non-native, six are breeding migrant species (all of

Table 21.1 Numbers of bird species known from the Gulf of Guinea oceanic islands (de Lima and Melo 2021: Appendix). Percentages of endemics and possibly non-native species were calculated for the number of residents. One endemic species, the Príncipe Seedeater *Crithagra rufobrunnea*, has three endemic subspecies, which were not added to the tally of endemic subspecies

	Residents					Non-resident	
Island	Total	Single-island endemics	Shared endemics	Endemic subspecies	Possibly non-native	Breeding seabirds	Non-breeding migrants
Príncipe	32	8 (25%)	3 (9%)	9 (28%)	5 (16%)	5	3
São Tomé	50	17 (34%)	3 (6%)	7 (14%)	17 (34%)	3	4
Annobón	11	1 (9%)	1 (9%)	3 (27%)	3 (27%)	4	1
TOTAL	66	26 (39%)	3 (5%)	16 (24%)	17 (26%)	6	4

which are seabirds), four are regular non-breeding migrants, and 62 are vagrants. Eight species are of uncertain status, including five that may breed in the archipelago and three that have been recorded on the islands in the past. Additionally, the occurrence of 51 species remains unconfirmed, being based solely on uncorroborated observations (de Lima and Melo 2021).

The most outstanding feature of the resident bird assemblage is the high level of endemism (Fig. 21.1). Almost all endemic species are single-island endemics, except for the Sao Tome Pigeon *Columba malherbii*, which occurs on all three islands, and the Sao Tome Spinetail *Zoonavena thomensis* and Príncipe Seedeater *Crithagra rufobrunnea*, both of which occur on Príncipe and São Tomé (Table 21.2). Endemic subspecies are also mostly restricted to a single island with two exceptions. The Little Swift *Apus affinis bannermani* occurs on Príncipe and São Tomé and is also considered the taxon present on the neighboring land-bridge island Bioko. Likewise, the African Emerald Cuckoo *Chrysococcyx cupreus insularum* is considered the taxon present on all three oceanic islands in the archipelago (Table 21.3, Box 21.1). Another defining feature is the unusually high phylogenetic diversity of these oceanic islands, with resident birds representing 28 families (Appendix).

Non-endemic native resident species include a large proportion of aquatic species, including three Ardeidae, one Phalacrocoracidae, and one Rallidae. They also include single representatives of Accipitridae, Psittacidae, Sturnidae, Nectariniidae, and Estrildidae. Possibly non-native species include five Ploceidae, three Phasianidae, three Estrildidae, two Columbidae, and single representatives of Apodidae, Psittacidae, Viduidae, and Fringillidae.

Breeding migrants include six seabird species: four Laridae, one Phaethontidae, and one Sulidae. Apart from the White-tailed Tropicbird *Phaethon lepturus*, which can breed in tree cavities and cliffs on the main islands, these species breed on bare offshore islets, such as Boné de Jóquei, Tinhosas (both near Príncipe), Sete Pedras, Rolas (both near São Tomé) and Tortuga (near Annobón). There are surprisingly few regular non-breeding migrants: three coastal waders (Scolopacidae) and the Barn Swallow *Hirundo rustica* (Hirundinidae). This contrasts with the large number of occasional migrants, comprising 62 species belonging to 27 families (Appendix),

Fig. 21.1 Some of the endemic birds of the oceanic islands of the Gulf of Guinea, including four Critically Endangered species (**1–4**), an undescribed species that was only confirmed for the first time in 2016 (**8**), two giants (**3**, **7**) and a dwarf (**1**), and two phenotypically "aberrant" species (**5**, **6**): (**1**) São Tomé Ibis *Bostrychia bocagei*; (**2**) Newton's Fiscal *Lanius newtoni*; (**3**) São Tomé Grosbeak *Crithagra concolor*; (**4**) Príncipe Thrush *Turdus xanthorhynchus*; (**5**) Dohrn's Thrush-Babbler *Sylvia dohrni*; (**6**) São Tomé Short-tail *Motacilla bocagii*; (**7**) São Tomé Sunbird *Dreptes thomensis*; (**8**) Príncipe Scops-Owl *Otus* sp. nov. Photo credits: (**1**, **2**, **4**, **5**) Lars Petersson, (**3**, **8**) Martim Melo, (**6**, **7**) Paul van Giersbergen

Table 21.2 Endemic bird species of the Gulf of Guinea oceanic islands: Príncipe (P), São Tomé (ST), and Annobón (A), with their respective IUCN Red List category (IUCN 2021). Taxonomy and nomenclature follow Clements et al. (2021)

Species	Common name	P	ST	A	IUCN
Order Columbiformes					
Family **Columbidae**					
Columba thomensis	Maroon Pigeon		•		EN
Columba malherbii	São Tomé Pigeon	•	•	•	NT
Treron sanctithomae	São Tomé Green-Pigeon		•		EN
Order Caprimulgiformes					
Family **Apodidae**					
Zoonavena thomensis	São Tomé Spinetail	•	•		LC
Order Pelecaniformes					
Family **Threskiornithidae**					
Bostrychia bocagei	São Tomé Ibis		•		CR
Order Strigiformes					
Family **Strigidae**					
Otus sp. nov.	Príncipe Scops-Owl	•			NE[a]
Otus hartlaubi	São Tomé Scops-Owl		•		VU
Order Passeriformes					
Family **Oriolidae**					
Oriolus crassirostris	São Tomé Oriole		•		VU
Family **Monarchidae**					
Terpsiphone atrochalybeia	São Tomé Paradise-Flycatcher		•		LC
Family **Laniidae**					
Lanius newtoni	Newton's Fiscal		•		CR
Family **Cisticolidae**					
Prinia molleri	São Tomé Prinia		•		LC
Family **Sylviidae**					
Sylvia dohrni	Dohrn's Thrush-Babbler	•			LC
Family **Zosteropidae**					
Zosterops ficedulinus	Príncipe White-eye	•			EN
Zosterops griseovirescens	Annobón White-eye			•	VU
Zosterops feae	São Tomé White-eye		•		NT
Zosterops lugubris	Black-capped Speirops		•		LC
Zosterops leucophaeus	Príncipe Speirops	•			LC
Family **Sturnidae**					
Lamprotornis ornatus	Príncipe Starling	•			LC
Family **Turdidae**					
Turdus xanthorhynchus	Príncipe Thrush	•			CR
Turdus olivaceofuscus	São Tomé Thrush		•		LC
Family **Nectariniidae**					
Anabathmis hartlaubii	Príncipe Sunbird	•			LC
Anabathmis newtonii	Newton's Sunbird		•		LC
Dreptes thomensis	São Tomé Sunbird		•		VU

(continued)

Table 21.2 (continued)

Species	Common name	P	ST	A	IUCN
Family **Ploceidae**					
Ploceus princeps	Príncipe Golden-Weaver	•			NT
Ploceus grandis	Giant Weaver		•		VU
Ploceus sanctithomae	São Tomé Weaver		•		VU
Familiy **Motacillidae**					
Motacilla bocagii	São Tomé Short-tail		•		VU
Familiy **Fringillidae**					
Crithagra rufobrunnea[b]	Príncipe Seedeater	•	•		LC
Crithagra concolor	São Tomé Grosbeak		•		CR

IUCN Red List categories: LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered; NE, not evaluated

[a] Recently discovered and still being described. Field data suggest it might classify as CR (Freitas 2019)

[b] *Crithagra rufobrunnea* is represented by three endemic subspecies (Table 21.3)

mostly shorebirds and passerines, whose number will continue to grow as currently uncorroborated records are confirmed. These patterns reinforce the hypothesis that migrants, whether Afrotropical or Palearctic, do not regularly cross the open sea of the Gulf of Guinea (Jones and Tye 2006).

Island Accounts

Príncipe has 88 confirmed species (Table 21.1, Appendix), including 32 resident species, of which 8 are single-island endemics and 3 are shared endemics with the neighboring islands (Tables 21.1 and 21.2). Príncipe also holds 9 (28%) endemic subspecies from species occurring on the mainland, together with two endemic subspecies of the endemic Príncipe Seedeater (Table 21.2). Five species (16%) are possibly non-native: two Columbidae, two Estrildidae, and one Apodidae. Príncipe, and especially its surrounding islets, holds breeding colonies of all seabird species that reproduce in the oceanic islands of the Gulf of Guinea, except Bridled Tern *Onychoprion anaethetus*. Tinhosas islets are remarkable for their seabird colonies, which hold around 200,000 breeding pairs of Sooty Tern *O. fuscatus*, accounting for 1% of the global population of this species and meeting the criteria for Important Bird Area (Valle et al. 2016). Both Tinhosas and Boné de Jóquei also hold important but declining breeding colonies of Brown Booby *Sula leucogaster*.

São Tomé has 96 confirmed species (Table 21.1, Appendix), including 50 resident species, of which 17 (34%) are single-island endemics and 3 (6%) are endemics shared with the nearby islands (Tables 21.1 and 21.2). This island also holds seven (14%) endemic subspecies of species that occur in continental Africa, together with one endemic subspecies of the endemic Príncipe Seedeater (Tables 21.1 and 21.3). Seventeen species (34%) are possibly non-native: five Ploceidae, three Estrildidae,

Table 21.3 Endemic bird subspecies of the Gulf of Guinea oceanic islands: Príncipe (P), São Tomé (ST), and Annobón (A). Taxonomy and nomenclature follow Clements et al. (2021); taxonomic authorities given in Appendix. Notes link to taxonomic comments in Box 21.1

Species	Common name	P	ST	A	Notes
Order Galliformes					
Family **Phasianidae**					
Coturnix delegorguei histrionica	Harlequin Quail		•		1
Order Columbiformes					
Family **Columbidae**					
Columba larvata principalis	Lemon Dove	•			2
Columba larvata simplex			•		2
Treron calvus virescens	African Green-Pigeon	•			3
Order Cuculiformes					
Family **Cuculidae**					
Chrysococcyx cupreus insularum	Emerald Cuckoo	•	•	•	4
Order Caprimulgiformes					
Family **Apodidae**					
Apus affinis bannermani	Little Swift	•	•		5
Order Pelecaniformes					
Family **Threskiornithidae**					
Bostrychia olivacea rothschildi	Olive Ibis	•			6
Order Strigiformes					
Family **Tytonidae**					
Tyto alba thomensis	Barn Owl		•		7
Family **Strigidae**					
Otus senegalensis feae	African Scops-Owl			•	8
Order Coraciiformes					
Family **Alcedinidae**					
Corythornis cristatus thomensis	Malachite Kingfisher		•		9
Corythornis cristatus nais		•			9
Halcyon malimbica dryas	Blue-breasted Kingfisher	•			10
Order Psittaciformes					
Family **Psittacidae**					
Psittacus erithacus princeps	Gray Parrot	•			11
Order Passeriformes					
Family **Dicruridae**					
Dicrurus modestus modestus	Velvet-mantled Drongo	•			12
Family **Monarchidae**					
Terpsiphone rufiventer smithii	Black-headed Paradise-Flycatcher			•	13
Family **Sturnidae**					
Onychognathus fulgidus fulgidus	Chestnut-winged Starling		•		14
Familiy **Fringillidae**[a]					
Crithagra rufobrunnea rufobrunnea	Príncipe Seedeater	•			

(continued)

Table 21.3 (continued)

Species	Common name	P	ST	A	Notes
Crithagra rufobrunnea thomensis			•		
Crithagra rufobrunnea fradei		•[b]			

[a] *Crithagra rufobrunnea* is an endemic species of Príncipe and São Tomé
[b] Endemic to the 3 ha islet of Boné de Jóquei, c. 3 km off Príncipe

two Phasianidae, two Columbidae, two Psittacidae, and single representatives of Apodidae, Viduidae, and Fringillidae. São Tomé and its surrounding islets, notably Sete Pedras and Rolas, hold breeding colonies of three seabird species: Brown Noddy *Anous stolidus*, White-tailed Tropicbird, and Brown Booby.

Annobón has 30 confirmed species (Table 21.1, Appendix), including 11 resident species, of which one is a single-island endemic and one is an endemic shared with São Tomé and Príncipe (Tables 21.1 and 21.2). It has three endemic subspecies, two of which are treated as full species by some authors (Table 21.3, Box 21.1), three native non-endemic species (Cuculidae, Rallidae, and Ardeidae), and three possibly non-native species (two phasianids and one estrildid). Seabird colonies include Brown Noddy, Black Noddy *Anous minutus*, Bridled Tern, and White-tailed Tropicbird.

Box 21.1: Comments on Taxonomic Uncertainties

The numbers link to the species in Table 21.3. Taxonomic authorities given in Appendix

1. *Coturnix delegorguei histrionica*. Endemic subspecies from São Tomé whose validity should be re-appraised combining multiple lines of evidence, including molecular data.
2. The systematic position of the Lemon Dove has never been satisfactorily resolved. Currently treated as *Columba larvata*, it was, for a long time, placed in its own genus, *Aplopelia*. Its current placement within *Columba* remains uncertain (Pereira 2013): it groups together with the Bronze-naped Pigeon superspecies (*C. malherbii*, *C. delegorguei*, *C. iriditorques*) within a larger clade encompassing the Old-World *Columba* and most *Streptopelia* species, but the exact affinities with these two genera remain unresolved. The plumage of *Columba larvata* provides little phylogenetic information as it varies widely, both between and within populations, and it may also change with age (Amadon 1953; Serle 1959). As such, it is imperative to conduct a full taxonomic revision supported by extensive molecular sampling (Baptista et al. 2020), where many of the current arrangements are unlikely to prevail. The subspecies from São Tomé have been treated by some authorities as a distinct species, but evidence supporting it is anecdotal (Baptista et al. 2020). Molecular

(continued)

Box 21.1 (continued)

evidence for the São Tomé and Príncipe populations detected large differentiation in mitochondrial haplotypes, suggesting at least two colonization events from the mainland (Pereira and Melo, unpublished results). The same data also showed that these populations are closely related to those from southern Cameroon but very distinct from those from Malawi (up to 3.2 my divergence), suggesting that there may be multiple distinct species on the mainland. No molecular data are available for the Annobón population, which is currently placed under *C. l. inornata*, occurring from Sierra Leone to Gabon.

3. *Treron calvus* has 15 recognized subspecies, many of which might not be valid (Hoyo et al. 2020). Molecular data placed the endemic Príncipe subspecies, *T. c. virescens*, together with birds from Bioko, currently treated as an endemic subspecies, *T. c. poensis*, and revealed two cases (in 14) of mitochondrial introgression from *T. sanctithomae*, endemic from São Tomé, into the Príncipe population (Pereira 2013).
4. *Chrysococcyx cupreus insularum*. Endemic subspecies of the three Gulf of Guinea oceanic islands, although most authorities treat or recommend treating *C. cupreus* as a monotypic species (HBW and BirdLife International 2020; Clements et al. 2021; Gill et al. 2021).
5. *Apus affinis bannermani* is a subspecies considered to be restricted to the Gulf of Guinea islands of Príncipe, São Tomé, and Bioko (Clements et al. 2021; Gill et al. 2021)—so not strictly speaking an endemic of the oceanic islands. The validity of this subspecies should be re-appraised as it has been considered indistinguishable from the neighboring mainland population (Amadon 1953).
6. *Bostrychia olivacea rothschildi.* Molecular studies on museum specimens are required to determine if this extinct endemic subspecies from Príncipe is valid, and whether it was more closely related to the São Tomé *B. bocagei* or to the mainland species *B. olivacea*.
7. *Tyto alba thomensis*. Recent molecular evidence suggested that this phenotypically distinct taxon, restricted to São Tomé, may constitute a separate species (Uva et al. 2018; Alves 2019).
8. *Otus senegalensis feae*. A recent assessment, using multiple lines of evidence but no molecular data, considered the scops-owl from Annobón as a valid endemic species, *Otus feae* (Collar and Boesman 2020). Both molecular data and phenotypic data (Freitas 2019) place it well within the intra-specific variation of *Otus senegalensis*, which indicates a recent colonization. The Annobón population is now very likely isolated from *O. senegalensis*, which is absent from the neighboring mainland. A deep phylogeographic study of *O. senegalensis* sensu lato is needed to understand its evolutionary history and clarify the taxonomic status of the

(continued)

Box 21.1 (continued)

Annobón population. In any case, several authorities already recognize it as a valid endemic species (e.g., HBW and BirdLife International 2020; Gill et al. 2021).

9. *Corythornis cristatus thomensis* and *Corythornis cristatus nais* are endemic subspecies from São Tomé and from Príncipe, respectively. Genetically they fall well within the nominate subspecies: mitochondrial divergences from samples from Malawi were only 0.3% for *C. c. thomensis* and 0.9% for *C. c. nais*, and divergence between the two island lineages is 0.8% (Melo and Fuchs 2008). The two subspecies have phenotypic differences: *C. c. nais* being intermediate between *C. cristatus* and *C. leucogaster*, while *C. c. thomensis* has darker plumage than mainland birds, especially the juveniles (Christy and Clarke 1998). It is possible that these populations represent recent and distinct colonization events that are now evolving in isolation. They are treated as separate endemic species by BirdLife International (HBW and BirdLife International 2020).
10. *Halcyon malimbica dryas*. Endemic subspecies from Príncipe, whose likely validity should nevertheless be confirmed using multiple lines of evidence, including molecular data.
11. *Psittacus erithacus princeps*. Mitochondrial data inferred a relatively simple, albeit curious, history for the gray parrots from Príncipe (Melo and O'Ryan 2007), which created the only real taxonomic conundrum for the avifauna of the Gulf of Guinea oceanic islands. This population is the result of two colonization events: one that occurred up to 1.4 mya and a contemporary one. The first colonization came from the mainland stock that evolved into *P. timneh*, whereas the recent colonization came from *P. erithacus*. We cannot exclude that the latter was an accidental introduction linked to the Portuguese trade of this species from Angola to Europe, which used to be done by boats that made a stopover in Príncipe (Melo and O'Ryan 2007). Most of the Príncipe birds (75%) have the Príncipe mitochondrial lineage, even though morphologically they are closer to *P. erithacus*. We still do not know the overall impact on the genome of the mixing of the two lineages. The International Ornithological Council opted to use the genetic evidence to treat the Príncipe population as a subspecies of *P. timneh* (Gill et al. 2021), while other authorities have kept the original treatment (HBW and BirdLife International 2020; Clements et al. 2021). We consider this to be an open issue that can only be sorted out with an extensive genetic investigation.
12. *Dicrurus modestus modestus*. The drongo present on Príncipe has been treated for a long time as an endemic species, although its taxonomic status was always considered unclear (Jones and Tye 2006). A recent

(continued)

Box 21.1 (continued)

molecular study on the *D. adsimilis* complex returned a new taxonomic arrangement for the group, in which the Príncipe population is conspecific with the populations occurring in the forests of the Lower Congo Forest Block, despite clear differences in bill and tail size (Fuchs et al. 2018).

13. *Terpsiphone rufiventer smithii*. The population of *T. rufiventer* from Annobón was, until recently, often treated as a separate species, and still is by some authors (Gill et al. 2021). As it is unlikely that there is regular gene flow with the neighboring mainland populations, this population is likely on an independent evolutionary trajectory.
14. *Onychognathus fulgidus fulgidus*. The nominate subspecies of this large forest starling was described from São Tomé, to which it is endemic. The birds on São Tomé are larger, more robust, and more vocal than those occurring on the African mainland (Amadon 1953; Christy and Clarke 1998), warranting molecular research to determine if it may constitute a distinct species.

Habitat Associations

The aquatic avifauna of the islands is species-poor but occupies a wide variety of ecological niches (Lima et al. 2021). Regularly breeding seabirds include two noddies, two terns, one tropicbird, and one booby, all of which breed in different sets of offshore islets (Monteiro et al. 1997; Jones and Tye 2006—Appendix), where they have distinct nesting microhabitats (Leventis and Olmos 2009; Valle et al. 2016; Bollen et al. 2018). The White-tailed Tropicbird also breeds on cliffs and trees on the main islands, and a putatively distinct form of the Band-rumped Storm-Petrel *Hydrobates castro* is thought to breed within burrows on the ground in São Tomé's native forests (Flood et al. 2019). The resident Black Kite *Milvus migrans parasitus* is also commonly found foraging at sea. Other resident aquatic bird species include predominantly coastal species that also occur along larger rivers, such as Western Reef-Heron *Egretta gularis* and Long-tailed Cormorant *Microcarbo africanus*. Predominantly freshwater species also occur along the coast and in brackish waters, such as Common Moorhen *Gallinula chloropus* and Striated Heron *Butorides striata*. The islands receive remarkably few non-breeding aquatic species as regular visitors, most of which occur on the coast or along the lower reaches of rivers and streams. The lagoons on the northern coast of São Tomé and the bay of Santo António on Príncipe are the main localities where vagrant aquatic birds have been recorded (Jones and Tye 2006; de Lima et al. 2021).

Until the 1990s, assessments of the distributions and habitat associations of the terrestrial birds of the oceanic islands of the Gulf of Guinea were mostly based on non-systematic observations (Jones and Tye 2006) and focused on understanding the links between endemic species and land-use types to evaluate conservation status (Jones and Tye 1988; Atkinson et al. 1991; Peet and Atkinson 1994). Knowledge greatly improved following systematic surveys on both Príncipe (Baillie 2001; Dallimer and King 2008; Dallimer et al. 2012; Fundação Príncipe 2019) and São Tomé (Dallimer et al. 2009; de Lima et al. 2013, 2014; Soares 2017; Soares et al. 2020). These studies have shown that native species, including endemics, dominate the avifauna across the islands, while non-natives tend to be restricted to degraded environments, such as plantations and notably, to non-forested areas. A few of the endemics are more sensitive to anthropogenic influence and are currently restricted to the best-preserved forests. The Giant Weaver *Ploceus grandis* on São Tomé and the Príncipe Golden-Weaver *P. princeps* seem to be the only endemic species that are clearly more abundant outside forests, even though the Sao Tome Pigeon, the Sao Tome White-eye *Zosterops feae* and a few of the endemic subspecies are also frequently encountered outside native forest. As in other tropical forests (e.g., Newbold et al. 2013), species sensitive to forest degradation tend to be larger, and insectivorous or frugivorous, while non-natives are mostly small and granivorous. Other environmental factors are often correlated with land use, making it hard to disentangle their effect on bird assemblages but, overall, the highest proportions of endemics are found in remote steep areas at higher altitudes and with higher rainfall. Annobón is seldom visited by ornithologists, and thus the ecology of its avifauna remains the most incompletely documented (Sloan 2017).

Several studies have focused on the habitat associations of the islands' Critically Endangered species: Sao Tome Ibis (Margarido 2015; de Lima et al. 2017), Newton's Fiscal (Maia and Alberto 2009; Lewis et al. 2018), Príncipe Thrush (Dallimer et al. 2010; Rebelo 2021), and Sao Tome Grosbeak (Solé et al. 2012), as well as the Príncipe Scops-Owl, which has also been proposed to qualify as Critically Endangered (Freitas 2019). Other studies have addressed the habitat associations of the Gray Parrot *Psittacus erithacus* on Príncipe (Valle et al. 2017), the Annobón population of the African Scops-Owl *Otus senegalensis feae* (Rodriguez-Prieto et al. 2014), the distinctive São Tomé subspecies of Barn Owl *Tyto alba thomensis* (Alves 2019), and the endemic pigeons of São Tomé (Carvalho et al. 2014). In addition to providing an understanding of distribution and ecology, these studies have also helped in estimating population sizes (i.e., Azevedo 2015) and informing conservation strategies (BirdLife International 2014a, b; Fundação Príncipe et al. 2021).

The Endemic Birds

How Many Endemics?

Endemism in the oceanic islands of the Gulf of Guinea is restricted to resident landbirds (Jones and Tye 2006; de Lima and Melo 2021), although the still undescribed local population of the Band-rumped Storm-Petrel may represent an exception (Flood et al. 2019). Out of the 66 resident landbird species of the three islands, 17 are possibly non-native (de Lima and Melo 2021), and of the remaining 49 confirmed extant natives, 90% are endemic at the species or subspecies level (Tables 21.2, 21.3, and 21.4, Appendix). The exact number of endemic species varies according to different authorities (Hoyo 2020), with the most recent assessments recognizing 32 (HBW and BirdLife International 2021), 31 (Gill et al. 2021), and 29 species (Clements et al. 2021; de Lima and Melo 2021). These discrepancies

Table 21.4 Divergence time estimates, in million years (Ma), between endemic birds of the oceanic islands of the Gulf of Guinea and their closest mainland relative(s); square brackets indicate clades. These estimates are illustrative only as they were derived from different markers and used different rates and estimation methods. When available, 95% confidence intervals are shown. Note that the ages of the oldest known sub-aerial rocks are 31 Ma for Príncipe, 15 Ma for São Tomé and 6 Ma for Annobón (Ceríaco et al. 2022)

Island taxa	Mainland sister taxa	Divergence time (Ma)	Reference
Columba thomensis	*Columba arquatrix*	1.5 (1.0–2.1)	Pereira (2013)
Columba malherbii	[*Columba iriditorques* | *C. delegorguei*]	1.3 (0.6–2.1)	Pereira (2013)
Treron sanctithomae	*Treron calvus*	2.0 (1.9–2.6)	Pereira (2013)
Tyto alba thomensis	all other taxa under *Tyto alba*	c. 1.8	Uva et al. (2018)
Otus sp. nov	[*Otus hartlaubi* | *O. senegalensis*]	0.9 (0.7–1.1)	Melo et al. (unpublished data)
Otus hartlaubi	*Otus senegalensis*	0.8 (0.6–1.0)	Melo et al. (unpublished data)
Oriolus crassirostris	*Oriolus brachyrhynchus laetior*[a]	c. 1.7[b]	Jønsson et al. (2019)
Terpsiphone atrochalybeia	*Terpsiphone corvina* or *T. mutata comorensis*	c. 1.4[c]	Bristol et al. (2013)
Lanius newtoni	*Lanius mackinnoni*	2.1 (0.9–3.7)	Fuchs et al. (2011)
Sylvia dohrni	[*Sylvia abyssinica* | *S. atriceps* | *S. galinieri* | *S. nigricapillus*]	c. 8.1[d]	Cai et al. (2019)
Zosterops ficedulinus	Large clade including mainland taxa and the Indian Ocean *maderaspatanus* clade	0.9 (0.7–1.1)	Melo and O'Ryan (2007)
Zosterops griseovirescens			
Zosterops feae			
Zosterops lugubris			
Zosterops leucophaeus			
Turdus xanthorhynchus	*Turdus pelios*	c. 4[e]	Batista et al. (2020)
Turdus olivaceofuscus		c. 5[f]	Melo et al. (2010)
Ploceus sanctithomae	[*Ploceus bicolor – Anaplectes* (= *Ploceus*) *rubriceps*]	c. 1.2–1.4[g]	De Silva et al. (2019)
Ploceus grandis	*Ploceus weynsi*	c. 1.6–1.8[h]	De Silva et al. (2019)
Motacilla bocagii	[*Motacilla clara* | *M. capensis*]	3.3 (2.2–4.6)	Alström et al. (2015)
Crithagra rufobrunnea	*Crithagra striolata* and other African taxa	1.7 (1.0–2.3)[i]	Melo et al. (2017)

(continued)

Table 21.4 (continued)

Island taxa	Mainland sister taxa	Divergence time (Ma)	Reference
Crithagra concolor	[*C. citrinelloides* | *C. mozambica* | *C. leucopygia*]	0.6 (0.4–0.8)[j]	Melo et al. (2017)

[a] Genetic divergence from other *O. brachyrhynchus* taxa, and sister species relationship with *O. crassirostris*, may warrant treatment as separate species *O. laetior* (Jønsson et al. 2019)

[b] Divergence time estimate read from chronogram (Supplementary Fig. S4: Jønsson et al. 2019)

[c] Divergence time estimate read from chronogram (Fig. 3: Bristol et al. 2013)

[d] Divergence time estimate read from chronogram (Fig. 3a: Cai et al. 2019)

[e] Divergence time estimated from large scale genomic data and fossil calibrations

[f] Divergence time estimated from cytochrome *b* data using Weir and Schluter's (2008) rate. Estimates from ND2 and ND3 using Lerner's et al. (2011) rates returned estimates of c. 2 mya (not shown)

[g] Divergence time estimated from uncorrected pairwise distances estimated from partial COI sequences (298 and 100 bp) from De Silva et al. (2019) using Weir and Schluter's (2008) rate

[h] Divergence time estimated from uncorrected pairwise distances estimated from partial sequences of ND2 (543 bp) and COI (298 bp) from De Silva et al. (2019) using Weir and Schluter's (2008) rate

[i] Divergence time estimated from cytochrome *b* data using Weir and Schluter's (2008) rate

[j] Divergence time estimated from mitochondrial (ND2, ND3) and nuclear (GAPDH, MYO2, ODC) DNA using Lerner's et al. (2011) rates. These very recent estimates may be driven by the behavior of the ND2 in recent times (i.e., closer to the tips of the trees)

are restricted to recent speciation events, in which some authors treat sister taxa as species, while others treat them as subspecies (Box 21.1). Such divergent taxonomic treatments are to be expected considering that speciation is a continuous process, and authorities agree that there is a total of 45 distinct evolutionary lineages (endemic species and subspecies, including the Príncipe Scops-Owl). Here we follow a conservative approach, where recent divergence events are treated as subspecies until further evidence emerges, resulting in a total of 29 endemic species (Tables 21.1 and 21.2) and 16 endemic subspecies (Tables 21.1 and 21.3). Additionally, the endemic Príncipe Seedeater has diverged into three single-island endemic subspecies: the nominate restricted to Príncipe, another to Boné de Jóquei (islet c. 3 km offshore from Príncipe), and the third to São Tomé (Table 21.3), a taxonomic arrangement supported by molecular data (Melo 2007).

Bird Endemism of the Gulf of Guinea Oceanic Islands in Perspective

Although confined to a land area of just over 1000 km^2, the 29 endemic species of Príncipe, São Tomé, and Annobón represent 60% of the endemic bird species of the vast Guinean Forests of West Africa biodiversity hotspot (area: 621,705 km^2; IUCN 2015). It is not surprising for oceanic islands to be centers of endemism, but it is still instructive to compare the bird endemism levels of the Gulf of Guinea islands with those found elsewhere. The Galapagos have 22 endemic landbirds in 13 islands

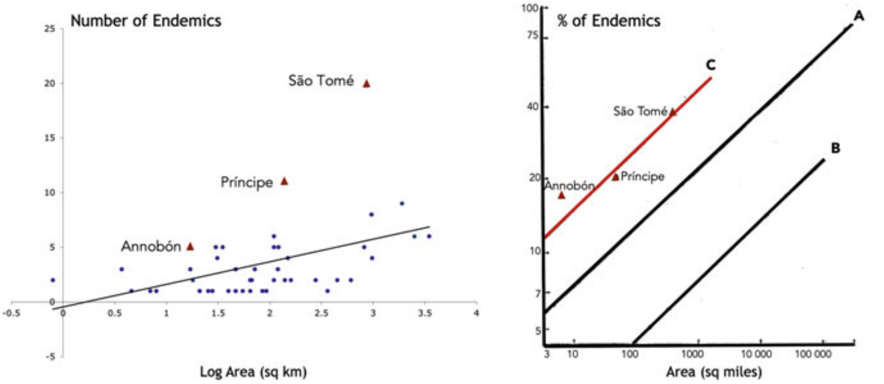

Fig. 21.2 The number of endemic bird species in the oceanic islands of the Gulf of Guinea has no equivalent worldwide. Left—number of endemic bird species in relation to island area for all the small oceanic islands of the world that have at least one endemic species; data from Coyne and Price (2000). Right—adaptation of Figure 1 from Mayr's (1965) global analysis of species turnover on islands (percentage of bird endemism in relation to island area), where three island categories were defined: A—solitary, well-isolated islands; B—single islands near continents or large archipelagos; C—islands in the Gulf of Guinea. In both cases, the Gulf of Guinea islands follow a distinct trajectory, characterized by a much higher number of endemics than expected from their area alone

totaling some 8000 km^2, whereas the six largest Hawaiian Islands have 30 extant endemic species and 19 documented extinct endemics in over 16,000 km^2 (Stattersfield et al. 1998). The high level of bird endemism within the relatively restricted area of the Gulf of Guinea oceanic islands has no parallel, with the islands following a very distinct trajectory to the global pattern (Mayr 1965; Fig. 21.2). In a survey of the 45 small islands ($<$10,000 km^2) that have at least one endemic species, the mean number of endemic species is 2 and the mode is a single species (Coyne and Price 2000). By comparison, São Tomé, 857 km^2, has 17 single-island endemic species and Príncipe, 139 km^2, has eight, plus three additional shared endemic species. A recent worldwide analysis of bird communities on oceanic islands further identified Príncipe and São Tomé as the only group of islands where the number of species, colonizations, and within-archipelago speciation all exceeded the predictions of the global model (Valente et al. 2020).

Why So Many Endemic Birds?

The 29 endemic species of the oceanic islands of the Gulf of Guinea belong to 20 distinct evolutionary lineages from 16 families. This means that the current diversity of the endemics required at least 20 independent colonization events from the mainland. Hence, the impressive level of bird endemism is spread across independent phylogenetic lineages rather than being concentrated within species-rich genera from just a few colonizations, such as in the well-known adaptive radiations that have occurred in other archipelagos. In the Galapagos, six colonizations gave rise to the 22 extant endemic species, dominated by the radiation of Darwin's finches (Grant and Grant 2008), and in the Hawaiian archipelago, six colonizations diversified into more than 40 endemic species, dominated by the Hawaiian honeycreepers (Pratt 2005). The factor underlying these distinct patterns is geography. These two archipelagos are much farther from the mainland than the Gulf of Guinea oceanic islands. The oceanic islands of the Gulf of Guinea constitute an 'intermediate island system' (Melo 2007; Ricklefs and Bermingham 2007), whose biogeographical characteristics lie between very isolated and virtually independent systems, and those so close to the mainland that their diversity patterns are determined mostly by ecological factors. In addition, the diverse and species-rich ecosystems of West Africa and the Congo Basin to the north and east, respectively, provide ample sources for potential colonization to the Gulf of Guinea oceanic islands. This "surrounding landmass proportion" is not only very large, but it consists mostly of habitats that are similar to those of the islands themselves—the two most important parameters associated with an increased likelihood of successful colonization (Weigelt and Kreft 2013).

The linear arrangement of the Gulf of Guinea islands and the relatively large distances between them, which are similar to their distances from the African continent, appear to have favored independent colonizations from the mainland relative to dispersal between islands. Colonization by so many mainland species is expected to increase inter-specific competition, reducing the chances for adaptive radiation (Schluter 2000; Ricklefs and Bermingham 2007). Nevertheless, white-eyes (Zosteropidae) represent a five-species radiation in these islands (Melo et al. 2011—Box 21.2). Other instances of inter-island dispersal events leading to speciation include the Giant and Príncipe Golden weavers (Valente et al. 2020), and the Príncipe Sunbird *Anabathmis hartlaubi* and the Sao Tome Sunbird *Dreptes thomensis* (Rauri Bowie, unpublished data: sister species relationship supported by mitochondrial and nuclear markers.; MM and Luís Valente, unpublished data: sister species relationship supported by mitochondrial sequence data). Inter-island dispersal has also resulted in the differentiation of the Príncipe Seedeater into three subspecies (Jones and Tye 2006; Melo 2007). The distinct species of green-pigeons (Pereira 2013), scops-owls (Freitas 2019), thrushes (Melo et al. 2010), and *Crithagra* canaries (Melo et al. 2017) present on different islands may have been derived either from independent colonizations from the African continent or from inter-island dispersal. The same applies to the island subspecies of the Lemon Dove *Columba larvata* (Pereira 2013), and the Malachite Kingfisher (Melo and Fuchs 2008).

Although the proximity to a species-rich continent does increase the chances of successful colonizations, it also increases the probability that gene flow between island and mainland populations is maintained at levels that will prevent population divergence and eventual speciation. Hence, the most likely reason that the oceanic islands of the Gulf of Guinea support the highest concentration of endemic birds worldwide is their unique geographic location: they are close enough to the African continent to be colonized by a diverse array of species, but far enough to allow successful immigrants to evolve in isolation.

In summary, bird speciation in the oceanic islands of the Gulf of Guinea has in most cases occurred by independent divergence in allopatry (allospeciation: Mayr and Diamond 2001), when an immigrant population from the mainland reached one island and evolved there in isolation. This is the overwhelmingly dominant route for bird speciation on islands (Ricklefs and Bermingham 2007; Valente et al. 2020) and for birds in general (Price 2008). In addition, molecular data have now revealed previously unrecognized radiations on the islands, most remarkably among the white-eyes (Box 21.2). Although comprising only five species, this radiation may be the third largest globally for birds inhabiting small oceanic islands, and further stands out by having the fastest speciation rates recorded in birds and one of the highest in vertebrates (Appendix 5 in Melo et al. 2011).

Box 21.2: The Radiation of the White-Eyes (Zosteropidae) of the Oceanic Islands of the Gulf of Guinea

The spectacular radiations of the Hawaiian honeycreepers (Pratt 2005) and of the Galapagos finches (Grant and Grant 2008) could mislead us into believing that radiations are a common diversification process for birds on small oceanic islands—when they are in fact a very rare exception (Valente et al. 2020). The next largest oceanic island bird radiation worldwide is found in the Gulf of Guinea, where the five white-eyes species descend from a single ancestor that reached the islands within the last 0.7–1.1 my (Melo et al. 2011). Although modest in size, the white eye radiation boasts one of the fastest rates of speciation ever documented in vertebrates (Melo et al. 2011).

The radiation itself is a textbook example of the "archipelago radiation model" developed originally for island birds (Lack 1947; Grant 2001; Petren et al. 2005), which is also in agreement with current views of the speciation process (Rundle and Nosil 2005; Nosil 2012), where inter-specific competition is the engine of phenotypic diversification (numbers refer to photos below):

(I) Descendants of the original colonization (6: mainland relative), island-hop and diverge in isolation (1, 3, 5).

(II) Presumably because they occupy similar habitats, phenotypic changes are not pronounced—as illustrated by the Príncipe and São Tomé white-eyes (1, 3), which are indistinguishable in the field (Hering et al. 2018).

(III) Inter-island dispersal events bring diverging populations together, setting the stage for inter-specific competition.

(IV) The pressure of resource competition is felt more strongly in the outnumbered new arrivals. These undergo the most phenotypic change and at very fast rates. The most aberrant species of the group (2, 4) represent the most recent speciation events: they may have diverged from one another less than 0.3 mya and from a typical white-eye less than 0.5

(continued)

Box 21.2 (continued)

mya—a timeframe typical of intra-specific but not inter-specific divergence in birds (Melo et al. 2011). This process of asymmetric divergence driven by resource competition has been predicted by theory (Doebeli and Dieckmann 2000) and is now empirically supported by the radiation of Darwin's finches (Petren et al. 2005) and of the Gulf of Guinea white-eyes.

(**1**) Príncipe White-eye *Zosterops ficedulinus*. (**2**) Príncipe Speirops *Z. leucophaeus*. (**3**) São Tomé White-eye *Z. feae*. (**4**) Black-capped Speirops *Z. lugubris* (São Tomé). (**5**) Annobón White-eye *Zosterops griseovirescens*. (**6**) Northern Yellow White-eye *Z. senegalensis*, the closest mainland relative with the typical white-eye phenotype. Photo credits: (**1**–**4**) Lars Petersson, (**5**) Martim Melo, (**6**) Jake Selby

Systematics of the Endemic Birds: New Insights from Molecular Data

The taxonomy and systematics of the endemic birds of the Gulf of Guinea were mostly addressed by Amadon (1953) and Naurois (1994) and later summarized by Jones and Tye (2006). Evolutionary inferences were still then dependent on phenotypic data, and particularly on morphological traits, which are often adaptive and can quickly lose their phylogenetic signal. This issue is particularly problematic in birds (Bock 1967; Hafner et al. 1984) and on oceanic islands, where both rapid phenotypic evolution (Millien 2006; Melo et al. 2011; Garcia-Porta et al. 2016; Sendell-Price et al. 2020) and phenotypic convergence (Fleischer et al. 2008; Covas 2016; Benítez-López et al. 2021) are common. Molecular phylogenies are expected to constitute better hypotheses of evolutionary history than phenotype-based phylogenies, as they use genetic markers that are mostly independent from phenotypic traits, and not under direct selection (Bromham et al. 2002; Davies and Savolainen 2006).

The most important insight brought by molecular phylogenies was that most bird speciation events in the Gulf of Guinea islands are recent, having occurred since the late Pliocene (2.5 Ma—Table 21.4). The exceptions so far are the Príncipe and São Tomé thrushes and the Sao Tome Short-tail, which may have speciated in the mid-Pliocene (c. 3.5–4.0 Ma), and Dohrn's Thrush-Babbler *Sylvia dohrni*, which may date back to the Miocene (c. 8 Ma—Table 21.4). Even without estimates of speciation times for some of the endemics, it is safe to conclude that the present species are all much more recent than the emergence of the islands they inhabit, which range from 31 to 6 Ma (Ceríaco et al. 2022). This pattern indicates that the oceanic islands of the Gulf of Guinea constitute a speciation center rather than a stable refuge for species that went extinct on the mainland. The absence of old species is nevertheless surprising and could be due to the recent and intense volcanic history of the islands (Lee et al. 1994; Barfod and Fitton 2014; Ceríaco et al. 2022). The patterns of genetic variation of the lizard *Trachylepis thomensis* within São Tomé have been linked to the impact of volcanic activity, with the extent of this variation being much lower than expected from the age of the island (Jesus et al. 2005). Likewise, volcanic activity on São Tomé has been linked to the evolutionary history of two sister caecilian lineages—*Schistometopum ephele* and *S. thomense* (O'Connell et al. 2021). In the absence of (sub)fossil evidence, it is not known if cycles of sea-level rise during post-glacial periods may have caused extinctions (Jones and Tye 2006; Ceríaco et al. 2022). Príncipe is likely to have been the most affected, having lost almost 90% of its land area as recently as 12,000 years ago (Norder et al. 2018). Likewise, during glacial periods Annobón was eight times larger, whereas the size of São Tomé did not change greatly. In any case, the relatively small sizes of the islands and their proximity to the mainland might make them susceptible to more rapid species turnover, which may further help explain the young age of most endemic bird species.

The main taxonomic consequence of the fast rates of phenotypic divergence inferred from molecular phylogenies is that all the endemic genera have been found invalid. This includes the Dohrn's Thrush-Babbler and the Sao Tome Short-tail, formerly placed in the monotypic genera *Horizorhinus* and *Amaurocichla*, respectively, whose peculiar traits obscured to which families they belonged (i.e., classified as *incertae sedis*). Dohrn's Thrush-Babbler, from Príncipe, is sister to a clade including the African Hill Babbler *Sylvia abyssinica*, an Afromontane forest species present also in the neighboring land-bridge island Bioko and Mount Cameroon (Voelker et al. 2009). In the case of the Sao Tome Short-tail, several of its traits, such as nine primaries (albeit a vestigial tenth primary is present) and ten rectrices with a protruding shaft, led to the suggestion that it could share an ancestor with the South-American Furnariidae (Naurois 1982). In actuality, it represents a recent speciation event from continental Africa, derived from the same ancestor as the Mountain Wagtail *Motacilla clara*, with which it shares the ecological niche of forest streams, and the Cape Wagtail *M. capensis* (Alström et al. 2015). The São Tomé Grosbeak, a *Crithagra* canary (Fringillidae) sister to the co-occurring Príncipe Seedeater (Moreau 1962; Melo et al. 2017), was originally placed in the monotypic genus *Neospiza*, and was often classified as a weaver (Ploceidae) (e.g., Bocage 1888b—he later placed it in Fringillidae: Bocage 1904; Sclater 1924; Bannerman 1953; Moreau 1962). The Sao Tome Weaver *Ploceus sanctithomae*, formerly in the endemic monotypic genus *Thomasophantes* (Amadon 1953; Moreau 1960; Naurois 1994), is now considered sister to the clade including the Forest Weaver *Ploceus bicolor* and the Red-headed Weaver *Anaplectes rubriceps* (*Anaplectes* being invalid as well; De Silva et al. 2019). The Sao Tome Sunbird is currently still classified under the only remaining endemic genus, *Dreptes*, which is known to be invalid, since the species is sister to the Príncipe Sunbird (genus *Anabathmis*) (Rauri Bowie, pers comm.; MM and Luís Valente, unpublished data). Finally, the genus *Speirops*, endemic to the Gulf of Guinea, is also no longer considered valid (Melo et al. 2011). It used to group four species of "aberrant" white-eyes (Zosteropidae): Black-capped Speirops *Zosterops lugubris* (São Tomé), Príncipe Speirops *Z. leucophaeus*, Bioko Speirops *Z. brunneus*, and Cameroon Speirops *Z. melanocephalus* (Mount Cameroon). However, molecular data show that the four species are not monophyletic and that the "aberrant" characters are the result of fast phenotypic divergence. On the oceanic islands, aberrant species represent the most recent speciation events (Box 21.2; Melo et al. 2011), rather than being derived from the oldest colonizations as previously assumed (Amadon 1953; Moreau 1957).

Conservation

The importance of the islands for conservation was first noted when the southwestern forests of São Tomé were identified as the second most important for bird conservation in Africa (Collar and Stuart 1988). As a result, an IUCN-funded mission surveyed plants and vertebrates of São Tomé and Príncipe confirming the high endemism and the global importance of the biological diversity of the oceanic islands (Jones and Tye 1988; Jones et al. 1991; Jones 1994). For birds, each of the oceanic islands is listed by BirdLife International as an independent Endemic Bird Area (Stattersfield et al. 1998; BirdLife International 2021a). More recently, the moist lowland forests of Príncipe, São Tomé, and Annobón were identified as the third most important in the world for the conservation of forest birds (Buchanan et al. 2011), and the endemic birds were the main factor for the protected areas of São Tomé and Príncipe combined to be considered globally as the 17th most important protected area for the conservation of threatened species (Le Saout et al. 2013).

Some of the endemic birds were already extremely rare early in the twentieth century and remain at high risk, but only the Príncipe subspecies of the Olive Ibis *Bostrychia olivacea rothschildi* became extinct (de Lima and Melo 2021). The most recent assessment listed 14 threatened bird taxa for the islands (IUCN 2021): five Critically Endangered, including the Annobón Scops-Owl *Otus feae*—which we treat as a subspecies of *O. senegalensis* following Clements et al. (2021); four Endangered, including the Gray Parrot, which is common on Príncipe and the only non-endemic threatened bird on the islands (Valle et al. 2021); and five Vulnerable (Tables 21.2 and 21.3).

The number of threatened taxa has increased since 2000, when only nine were listed: three Critically Endangered (the Annobón Scops-Owl and the Príncipe Thrush were not recognized as species by IUCN), none Endangered (the Maroon Pigeon *Columba thomensis* was Vulnerable, the Príncipe and São Tomé white-eyes were treated as conspecific and Vulnerable, and the Sao Tome Green-Pigeon *Treron sanctithomae* and the Gray Parrot were Least Concern), and six were Vulnerable (including the Principe and Sao Tome white-eyes treated as the same taxon). Most of these changes have been due to improved knowledge and not necessarily to a deterioration of the situation of the species, despite indications that conditions might be worsening for several taxa (IUCN 2021). The conservation status of each bird species is reviewed every year (BirdLife International 2021b) and thus further changes are expected. Other taxa await assessment, namely all endemic subspecies and putative new species, many of which are likely to be threatened. These include the Boné de Jóquei Islet subspecies of the Principe Seedeater *Crithagra rufobrunnea fradei*, which has a highly restricted range (Melo 2007), the elusive Gulf of Guinea Band-rumped Storm-Petrel (Flood et al. 2019), and the Príncipe Scops-Owl, which is still being described but will likely classify as Critically Endangered (Freitas 2019).

Habitat loss, overexploitation, and introduced species are key threats to native birds both globally (IUCN 2021) and in the Gulf of Guinea. Given the habitat associations described in the previous section, forest loss and degradation are the main threats to the birds on these islands (e.g., Dallimer et al. 2012; Soares et al. 2020). Most of this habitat loss can be attributed to agricultural expansion and intensification (Oyono et al. 2014), both to supply the local markets (notably horticulture) and to produce export cash crops (e.g., cocoa, palm oil, and coffee). Logging, fire, mining, infrastructure development, urban and tourism expansion, livestock, and silviculture (e.g., oil palm wine and medicinal plants) also contribute to habitat loss. To halt ongoing habitat loss, it is vital to ensure the effective implementation of existing protected areas, and their possible expansion, since some important forests are not yet formally protected (BirdLife International 2020; de Lima et al. 2022). Furthermore, environmentally friendly practices should be promoted in extractive and agricultural activities to ensure that complex vegetation structures are not lost and that introduced species are kept under control (de Lima et al. 2014; Carvalho 2015).

Most bird species are hunted, but the effects of direct exploitation are more noticeable on larger species (de Lima et al. 2013), such as the Sao Tome Ibis (Sampaio et al. 2016; de Lima et al. 2017), pigeons (Palmeirim et al. 2013; Carvalho 2015; Fundação Príncipe 2019) and the Brown Booby (Bollen et al. 2018). The diffuse nature of hunting coupled with the rugged terrain makes it extremely difficult to enforce existing laws that regulate this activity (Albuquerque and Carvalho 2015a, b; de Lima et al. 2022). Given that bird hunting is mostly a cultural, commercial, and recreational activity that contributes little to protein intake, diverting hunting efforts to instead control populations of introduced mammals could have a dual positive effect on bird conservation (Carvalho 2015).

Introduced bird species are thought to be strongly associated with land-use intensification, having little or no impact on the native avifauna (Soares et al. 2020). On the other hand, the effects of introduced mammals (Dutton 1994) and plants (Figueiredo et al. 2011) have long been identified as potential threats, even though their impacts remain poorly understood (BirdLife International 2014a, b; Fundação Príncipe et al. 2021). Feral pigs and cows feed on understory plants and turn over the soil, disturbing key forest habitats that evolved in the absence of large terrestrial mammals. Rats *Rattus* sp. and Mona Monkeys *Cercopithecus mona* are likely to have direct effects through nest predation (Guedes et al. 2021). Introduced mammal and plant species also have the potential to change forest structure in the long term, namely through the disruption of seed dispersal and other processes linked to forest regeneration (Heleno et al. 2021).

Other factors, such as pollution and climate change have also been identified as potential threats to the endemic-rich avifauna of these islands (IUCN 2021). For example, the intensive use of insecticides was claimed to be responsible for a severe population crash of the Sao Tome Paradise Flycatcher *Terpsiphone atrochalybeia* in the 1970s (Naurois 1984a).

Because most threats to biodiversity act synergistically and often occur as a result of habitat loss, protecting the remaining native forest is the single most important measure to secure the future of these species (de Lima 2012). Fortunately, all the islands have significant proportions of their territory already dedicated to biodiversity conservation (UNEP-WCMC and IUCN 2021), and the protected area network is soon expected to expand to cover additional important habitats (BirdLife

International 2020; de Lima et al. 2022). However, weak enforcement of environmental legislation remains a major concern (de Lima et al. 2017). Improving our knowledge of species ecology and of pervasive threats, such as hunting, invasive species, and climate change, will also be key to designing effective species-specific conservation measures. In this regard, conservation priorities in São Tomé and Príncipe have been identified through extended discussions, both for protected areas (Albuquerque and Carvalho 2015a, b) and for all Critically Endangered bird species (BirdLife International 2014a, b; Fundação Príncipe et al. 2021). Despite not being entirely fulfilled, these have been extremely useful in guiding conservation action, and continued revision will be essential. The success of ongoing conservation efforts ultimately relies on engaging the inhabitants of the islands, a process that is still in its infancy (de Lima et al. 2022). In this regard, birds are also being used to raise awareness locally and globally for the value of the unique biodiversity of the islands (e.g., Rebelo 2021; Ayres et al. 2022).

Concluding Remarks

The oceanic islands of the Gulf of Guinea constitute an outstanding example of an intermediate island system for birds, whose geographical location and rich rainforests maximize the accumulation of bird endemism. As such, they offer a valuable suite of phylogenetically independent replicates for testing hypotheses about evolutionary processes in speciation and adaptation. Knowledge gaps persist regarding Annobón and the status of some species, including potential undescribed endemics, past extinctions, and the origins of putative non-native species. Birds are still the best-known taxon in the archipelago, however, making them ideal exemplars that can guide future work on other groups. Our knowledge of environmental constraints and the history of human occupation of these islands also make them excellent models for understanding ecological processes and testing conservation strategies that can be used in a wider context, for instance in other small forested islands.

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Appendix

Checklist of bird species on the oceanic islands of the Gulf of Guinea, excluding vagrant and unconfirmed species (de Lima and Melo 2021). Islands: P, Príncipe; S, São Tomé; A, Annobón. Status: E, endemic species; I, probably non-native; R, native non-endemic resident; S, endemic subspecies; X, extinct; B, breeding migrant; M, non-breeding migrant; ?, uncertain. Subspecies are only identified when they are endemic. Taxonomy and nomenclature follow Clements et al. (2021)

Higher taxonomy	Species/subspecies	P	S	A
Order Galliformes				
Family **Numididae**				
Numida Linnaeus, 1764	*N. meleagris* (Linnaeus, 1758)		I	I
Family **Phasianidae**				
Coturnix Garsault, 1764	*C. delegorguei histrionica* (Hartlaub, 1849)		S	
Pternistis Wagler, 1832	*P. afer* (Müller, PLS, 1776)		I	
Gallus Brisson, 1760	*G. gallus* (Linnaeus, 1758)			I
Order Columbiformes				
Family **Columbidae**				
Columba Linnaeus, 1758	*C. livia* Gmelin, 1789	I	I	
	C. thomensis Bocage, 1888		E	
	C. malherbii Verreaux & Verreaux, 1851	E	E	E
	C. larvata inornata (Reichenow, 1892)			S
	C. l. principalis (Hartlaub, 1866)	E		
	C. l. simplex (Hartlaub, 1849)		E	
Streptopelia Bonaparte, 1855	*S. senegalensis* (Linnaeus, 1766)	I	I	
Treron Vieillot, 1816	*T. sanctithomae* (Gmelin, 1789)		E	
	T. calvus virescens Amadon, 1953	S		
Order Cuculiformes				
Family **Cuculidae**				
Chrysococcyx Boie, F., 1826	*C. cupreus insularum* Moreau & Chapin, 1951	S	S	S
Order Caprimulgiformes				
Family **Apodidae**				
Zoonavena Mathews, 1918	*Zoonavena thomensis* (Hartert, 1900)	E	E	
Apus Scopoli, 1777	*A. affinis bannermani* Hartert, 1928	S	S	
Cypsiurus Lesson, R., 1843	*C. parvus* (Lichtenstein, 1823)	I	I	
Order Gruiformes				
Family **Rallidae**				
Paragallinula Sangster, Garcia-R & Trewick, 2015	*P. angulata* (Sundevall, 1851)	?	?	

(continued)

Higher taxonomy	Species/subspecies	P	S	A
Gallinula Brisson, 1760	*G. chloropus* (Linnaeus, 1758)	R	R	R
Order Charadriiformes				
Family **Scolopacidae**				
Numenius Brisson, 1760	*N. phaeopus* (Linnaeus, 1758)	M	M	M
Actitis Illiger, 1811	*A. hypoleucos* (Linnaeus, 1758)	M	M	
Tringa Linnaeus, 1758	*T. nebularia* (Gunnerus, 1767)	M	M	
Family **Laridae**				
Anous Stephens, 1826	*A. stolidus* (Linnaeus, 1758)	B	B	B
	A. minutus Boie, F., 1844	B	?	B
Onychoprion Wagler, 1832	*O. fuscatus* (Linnaeus, 1766)	B	?	?
	O. anaethetus (Scopoli, 1786)	?	?	B
Order Phaethontiformes				
Family **Phaethontidae**				
Phaethon Linnaeus, 1758	*P. lepturus* Daudin, 1802	B	B	B
	P. aethereus Linnaeus, 1758	?		
Order Procellariiformes				
Family **Oceanitidae**				
Hydrobates Boie, F., 1822	*H.* cf. *castro* (Harcourt, 1851)		?	
Order Suliformes				
Family **Sulidae**				
Sula Brisson, 1760	*S. leucogaster* (Boddaert, 1783)	B	B	?
Family **Phalacrocoracidae**				
Microcarbo Bonaparte, 1856	*Microcarbo africanus* (Gmelin, J. F., 1789)		R	
Order Pelecaniformes				
Family **Ardeidae**				
Egretta T. Forster, 1817	*E. gularis* (Bosc, 1792)	R	R	R
Bubulcus Bonaparte, 1855	*B. ibis* (Linnaeus, 1758)	R	R	
Butorides Blyth, 1852	*B. striata* (Linnaeus, 1758)	R	R	
Family **Threskiornithidae**				
Bostrychia G. R. Gray, 1847	*B. olivacea rothschildi* (Bannerman, 1919)	X		
	B. bocagei Chapin, 1923		E	
Order Accipitriformes				
Family **Accipitridae**				
Milvus Lacépède, 1799	*M. migrans* (Boddaert, 1783)	R	R	
Order Strigiformes				
Family **Tytonidae**				
Tyto Billberg, 1828	*T. alba thomensis* (Hartlaub, 1852)		S	
Family **Strigidae**				
Otus Pennant, 1769	*O. hartlaubi* (Giebel, 1849)		E	
	O. senegalensis feae (Salvadori, 1903)			S
	Otus sp. nov.	E		

(continued)

Higher taxonomy	Species/subspecies	P	S	A
Order Coraciiformes				
Family **Alcedinidae**				
Corythornis Kaup, 1848	*C. cristatus thomensis* (Salvadori, 1902)		S	
	C. cristatus nais (Kaup, 1848)	S		
Halcyon Swainson, 1821	*H. malimbica dryas* Hartlaub, 1854	S		
Ceryle F. Boie, 1828	*C. rudis* (Linnaeus, 1758)	?		
Order Psittaciformes				
Family **Psittaculidae**				
Agapornis Selby, 1836	*A. pullarius* (Linnaeus, 1758)		I	
Family **Psittacidae**				
Psittacus Linnaeus, 1758	*P. erithacus princeps* Alexander, 1909	S	I	
Order Passeriformes				
Family **Oriolidae**				
Oriolus Linnaeus, 1766	*O. crassirostris* Hartlaub, 1857		E	
Family **Dicruridae**				
Dicrurus Vieillot, 1816	*D. modestus modestus* Hartlaub, 1849	S		
Family **Monarchidae**				
Terpsiphone Gloger, 1827	*T. atrochalybeia* (Thomson, 1842)		E	
	T. rufiventer smithii (Fraser, 1843)			S
Family **Laniidae**				
Lanius Linnaeus, 1758	*L. newtoni* Bocage, 1891		E	
Family **Cisticolidae**				
Prinia Horsfield, 1821	*P. molleri* Bocage, 1887		E	
Family **Hirundinidae**				
Hirundo Linnaeus, 1758	*H. rustica* (Linnaeus, 1758)		M	
Family **Sylvidae**				
Sylvia Scopoli, 1769	*S. dohrni* (Hartlaub, 1866)	E		
Family **Zosteropidae**				
Zosterops Vigors & Horsfield, 1827	*Z. ficedulinus* Hartlaub, 1866	E		
	Z. griseovirescens Bocage, 1893			E
	Z. feae Salvadori, 1901		E	
	Z. lugubris (Hartlaub, 1848)		E	
	Z. leucophaeus (Hartlaub, 1857)	E		
Family **Sturnidae**				
Onychognathus Hartlaub, 1849	*O. fulgidus fulgidus* (Hartlaub, 1849)		S	
Lamprotornis Temminck, 1820	*L. splendidus* (Vieillot, 1822)	R		
	L. ornatus (Daudin, 1800)	E		
Family **Turdidae**				
Turdus Linnaeus, 1758	*T. xanthorhynchus* Salvadori, 1901	E		
	T. olivaceofuscus Hartlaub, 1852		E	

(continued)

Higher taxonomy	Species/subspecies	P	S	A
Family **Nectariniidae**				
Anabathmis Reichenow, 1905	*A. hartlaubii* (Hartlaub, 1857)	E		
	A. newtonii (Bocage, 1887)		E	
Dreptes Illiger, 1811	*D. thomensis* (Bocage, 1889)		E	
Cyanomitra Reichenbach, 1853	*C. olivacea* (Smith, 1840)	R		
Family **Ploceidae**				
Ploceus Cuvier, 1816	*P. princeps* (Bonaparte, 1851)	E		
	P. velatus Vieillot, 1819		I	
	P. cucullatus (Müller, 1766)		I	
	P. grandis (G. R. Gray, 1844)		E	
	P. sanctithomae (Hartlaub, 1848)		E	
Quelea Reichenbach, 1850	*Q. erythrops* (Hartlaub, 1848)		?	
Euplectes Swainson, 1829	*E. hordeaceus* (Linnaeus, 1758)		I	
	E. aureus (Gmelin, 1789)		I	
	E. albonotatus (Cassin, 1848)		I	
Family **Estrildidae**				
Nigrita Strickland, 1843	*N. bicolor* (Hartlaub, 1844)	R		
Estrilda Swainson, 1827	*E. astrild* (Linnaeus, 1758)	I	I	
Uraeginthus Cabanis, 1851	*U. angolensis* (Linnaeus, 1758)		I	
Spermestes Swainson, 1837	*S. cucullata* (Swainson, 1837)	I	I	I
Family **Viduidae**				
Vidua Cuvier, 1816	*V. macroura* (Pallas, 1764)		I	
Family **Motacillidae**				
Motacilla Linnaeus, 1758	*Motacilla bocagii* (Sharpe, 1892)		E	
Family **Fringillidae**				
Crithagra Swainson, 1827	*C. mozambica* (Müller, 1776)		I	
	C. rufobrunnea[a] (Gray, 1862)	E		
	C. concolor (Bocage, 1888)		E	

[a] *C. rufobrunnea* is represented by three endemic subspecies (Table 21.3)

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Chapter 22
Current Knowledge and Conservation of the Wild Mammals of the Gulf of Guinea Oceanic Islands

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Abstract Oceanic islands are usually difficult for mammals to colonize; consequently, the native mammal fauna is typically species-poor, often consisting of just a few species of bats. The oceanic islands of the Gulf of Guinea are no exception to this pattern. Still, the known mammal richness is relatively high for the small size of the islands. Out of a total of 13 native species, including 11 bats and 2 shrews, at least 7 species and 3 subspecies are single-island endemics. In addition to native species, at least 6 other wild mammals have been introduced to the islands purposely or accidentally by humans. Some of these are among the world's most notorious invasive species and cause damage to native species, ecosystems, and humans. Predation by exotic species can threaten native island mammals, which are especially sensitive due to their small populations and limited ranges. These impacts are likely worsened by other threats, such as forest degradation and climate change, and a general lack of knowledge about the natural history of most species also hampers the implementation of conservation measures. Therefore, fostering further research on the endemic-rich mammal fauna of these islands is vital to ensure their persistence.

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Introduction

Large expanses of ocean are often extreme barriers to mammal dispersal, and even some bat species are known to be reluctant to fly over open bodies of water (Castella et al. 2000). Therefore, it is not surprising that oceanic islands typically host a small number of native mammals, usually only a few species of bats (Whittaker and Fernández-Palacios 2007). How non-flying mammals overcome this obstacle to naturally reach oceanic islands is a controversial topic. The most frequent explanation, natural rafting, makes assumptions that sometimes seem impossible to meet, particularly in the case of small animals with high metabolic rates and freshwater requirements (Ali and Vences 2019; Mazza et al. 2019). In addition, as humans colonized oceanic islands, they usually brought with them a large number of mammal species, which often came to exceed the number of native mammals (Tennyson 2010). As a result of this process, humans have caused the extinction of several mammals native to oceanic islands and also biotic homogenization (Longman et al. 2018).

The oceanic islands of the Gulf of Guinea are an excellent example of these processes of natural and human-mediated colonization. Considering the small size of the islands, they host a surprisingly large number of mammal species. Of the 19 known wild species (Appendix), 13 are native and, of these, at least 7 species and 3 subspecies are single-island endemics. Most endemic and native species are bats (Juste and Ibáñez 1994a; Rainho et al. 2010), but there are also two endemic shrews (Bocage 1887; Ceríaco et al. 2015). Their presence on oceanic islands at such a long distance from the mainland is still puzzling (Heim de Balsac and Hutterer 1982; Ceríaco et al. 2015). Even with the potential ability to use torpor in situations of food scarcity (McKechnie and Mzilikazi 2011), shrews would have had substantial limitations to obtain freshwater during the long dispersal trip to the islands. Furthermore, the number of reproducing individuals reaching the islands would be expected to be far too small to sustain a viable population.

The remaining six species of mammals were introduced by humans (Dutton 1994), either purposely or accidentally. Two of these, the house mouse *Mus musculus* Linnaeus 1758 and the ship rat *Rattus rattus* (Linnaeus, 1758), are among the 100 worst invasive species globally, due to the impacts they cause on ecosystems when they are introduced (Lowe et al. 2000). Thus, their abundance on the Gulf of Guinea islands is concerning for the native flora and fauna. Although there are also domestic and feral mammals on these islands, such as dogs, cats, pigs, goats, cows, horses, and others that might have arrived at the islands more recently, these species will not be addressed in detail in this chapter.

Knowledge is the basis of conservation, and this chapter aims to compile the information available to date on the species of wild mammals that occur on the islands of Príncipe, São Tomé, and Annobón. Threats to endemic and native species and knowledge gaps will also be discussed.

A Brief History of Mammal Research

Records of the presence of mammals on the oceanic islands of the Gulf of Guinea date to the first manuscripts of the first Portuguese travelers to these islands. An example of this is the excerpt presented by Sousa (1888) of a manuscript entitled "*Da viagem de dom Francisco d'Almeyda primeiro visorey da Índia*" [The journey of Dom Francisco d'Almeyda, India's first viceroy] dated ca. 1505. In this text, it is mentioned that "*n'esta ilha ha gatos d'algalia que criam que fugiram aos armadores que trouxerom da terra firme*" [on this island there are breeding civets that fled from the shipowners who brought them from the mainland] confirming the presence of the African civet *Civettictis civetta* (Schreber, 1776) in São Tomé already at the beginning of the sixteenth century.

More systematic surveys of mammals began much later. During the nineteenth century, Richard Greeff visited São Tomé and Rolas Islet between 1879 and 1880. Although this expedition did not focus on mammals, it confirmed the presence of two bat species *Cynonycteris stramineus*—currently *Eidolon helvum* (Kerr, 1792)—and *Phyllorhina caffra*—currently *Hipposideros ruber* (Noack, 1893). Greeff also confirmed the presence of the least weasel *Mustela nivalis* Linnaeus 1766 in São Tomé, based on a specimen found in the digestive tract of a cobra-preta *Naja* (*Boulengerina*) *peroescobari* Ceríaco et al. 2017 (Greeff 1884; Bocage 1905). These observations were further confirmed by A. F. Nogueira who also listed monkeys, bats, civets, weasels, and many rats in São Tomé (Nogueira 1885). In 1885, a botanical survey of São Tomé led by Adolpho F. Möller was commissioned by the Botanical Gardens of the University of Coimbra. Although focusing on botanical matters, some animal specimens were also collected. A list published by L. Vieira (1886) included mona monkey *Cercopithecus mona* (Schreber, 1774), *Viverra civetta* (currently *C. civetta*), *Cynonycteris stramineus* (currently *E. helvum*), *Phyllorhina caffra* (currently *H. ruber*), *Mus ducomanus* (currently *Rattus norvegicus* (Berkenhout, 1769)), *Mus rattus* (currently *Rattus rattus*), and *Mus musculus*.

Between 1885 and 1895, Francisco Newton was hired by the National Museum of Lisbon to conduct a zoological survey in the Gulf of Guinea. This survey included all the Gulf of Guinea islands, being the first known zoological survey in Annobón (Peris 1961). The mammal specimens were studied by J. V. Barbosa du Bocage, at the time director and curator of Zoology at the National Museum of Lisbon, resulting in several papers describing new species for the islands (see Bocage 1905). Such was the case of the São Tomé shrew *Crocidura thomensis* (Bocage, 1887), Newton's long-fingered bat *Miniopterus newtoni* Bocage 1889, the São Tomé horseshoe bat *Phyllorhina (Commersoni) thomensis* (currently *Macronycteris thomensis* (Bocage, 1891)) and the São Tomé collared fruit bat *Cynonycteris brachycephala* (currently *Myonycteris brachycephala* (Bocage, 1889)).

In 1954, a scientific expedition to São Tomé was undertaken by researchers from the Centro de Zoologia da Junta de Investigação do Ultramar. A report lists the bat specimens collected during this expedition (Lopes and Crawford-Cabral 1992), deposited in the collection of the Portuguese Institute of Scientific and Tropical Research. In 1955, Father Aurelio Basilio remained in Annobón for 3 months, reporting the presence of *R. norvegicus* for the first time on this island (Peris 1961).

During the 1970s, the French zoologist Henri Heim de Balsac took advantage of the presence of Father René de Naurois on the islands and asked him to collect pellets of Barn owl *Tyto alba* (Scopoli, 1769) during his ornithological surveys. Heim de Balsac believed that this would be an easy way to identify the spectrum of micromammals present on the island. Despite the high number of pellets collected, the diet of the barn owl proved to be composed essentially of ship rats *R. rattus*, and other than those, only one bird and one house mouse were found. Further efforts were made, and finally, some shrews were captured in São Tomé by R. Naurois, and in Príncipe by R. Naurois and Daniel Nunez, confirming the presence of *Crocidura thomensis* in São Tomé and identifying the species present in Príncipe as *C. poensis* (Fraser, 1843) (Heim de Balsac and Hutterer 1982). This mammal family was further reviewed by John Dutton and Jan Haft, based on the results of three expeditions, two German and one British, that visited São Tomé between 1989 and 1991 (Atkinson et al. 1994; Dutton and Haft 1996).

During the early 1990s, bats were the focus of Spanish investigators who started working in this region. This team made a massive contribution to the knowledge of this group, publishing several papers focusing on bat taxonomy (Juste and Ibáñez 1992, 1993b; Juste et al. 2007), morphology, and genetics (Juste and Ibáñez 1993a; Juste et al. 1996, 2000) and even echolocation (Guillén et al. 2001). They also described one new species, the São Tomé free-tailed bat *Chaerephon tomensis* (Juste and Ibáñez, 1993) and discovered the presence of an undescribed pipistrelle of the genus *Pseudoromicia* Monadjem et al. 2020 in Príncipe (Juste and Ibáñez 1993c, 1994a).

During the first decade of the twentieth century, bats were again the focus of research on the islands. In 2002, a study of the abundance of *E. helvum* in Príncipe was carried out by a team of English researchers (Dallimer et al. 2006). In 2010, a team from the University of Lisbon studied the status and distribution of bats on São Tomé (Rainho et al. 2010), adding a new species for São Tomé, the tricolored mouse-eared bat *Myotis* cf. *tricolor* (Temminck, 1832). In 2012, Peel and colleagues published a study on the persistence of several viruses on the isolated population of *E. helvum* in Annobón (Peel et al. 2012).

Among the studies published recently, it is worth highlighting the reviews on the species of *Crocidura* in São Tomé (de Lima et al. 2016) and Príncipe (Ceríaco et al. 2015), the latter describing the shrew of Príncipe as *Crocidura fingui* Ceríaco et al. 2015, and demonstrating that it is endemic to the island. Ecological studies have also included information on the mammals of the oceanic islands of the Gulf of Guinea; for example, studies on the hunting of wild species in São Tomé (Carvalho et al.

2015a, b; Hayman and Peel 2016), and the study of seed dispersal networks on this island (Mendes 2017; Coelho 2018; Heleno et al. 2021). Studies of broader geographical scope also addressed some mammal species from the Gulf of Guinea islands. This is the case of the work by Peel and colleagues (e.g., Shi et al. 2014; Peel et al. 2016, 2017), who studied ecology, traits, genetics, and possible zoonosis associated with *E. helvum,* and hypothesized on colonization and movements of this species between the islands. Rodrigues and colleagues (2017) have investigated the origin and process of invasion of the least weasel on the Atlantic islands, including São Tomé. Finally, a recent expedition was carried out in 2019 by a team from the University of Lisbon on the bats of Príncipe Island (JMP and ST, pers. obs). Their main results are included in the following sections of this chapter.

Current State of Knowledge

Order Primates

Family Cercopithecidae

Only one species of non-human primate occurs on the islands. The mona monkey was introduced in São Tomé and Príncipe 150–500 years ago (Glenn and Bensen 2013). The reason for its introduction is not fully known, but it is possible that it was used as food by enslaved plantation workers or, more likely, sailors and slavers kept them as pets (Denham and Denham 1987). The mona monkey was also introduced on the Caribbean island of Grenada, with animals originating from São Tomé and Príncipe (Glenn and Bensen 2013). No reference was found to the historical or contemporary presence of monkeys in Annobón.

The mona monkey is a forest species native to West Africa. Once common across its native range, it has become rare and even extirpated in some areas due to habitat loss and over-hunting by humans (Goodwin et al. 2020). Where it is still common, its densities vary between 15 and 49 ind/km^2 (Glenn et al. 2014). It is common on the islands, with estimates of 19 ind/km^2 in São Tomé and 21 ind/km^2 in Príncipe (Glenn 1998; Glenn et al. 2014), even though it is also hunted for human consumption on both islands (Carvalho et al. 2015a). The mona monkey is considered a generalist because it uses various types of forest, has a very diverse diet, and has been successful in colonizing forests outside its native range (Glenn et al. 2014). In Príncipe, this species seems to be particularly abundant in the transition zones between the forest and the agricultural areas where food is plentiful (JMP pers. obs. and Filipa Soares pers. comm.). It mainly feeds on fruits and arthropods but also eats leaves, flowers, small lizards, and bird eggs and chicks (Glennet al. 2014). Mona monkeys are among the introduced species that may affect the seed dispersal networks on São Tomé because they favor plant species with large fruits and seeds (Heleno et al. 2021). They are often regarded as agricultural pests. Dutton (1994) mentioned that they can impact forest regeneration, and Carvalho et al. (2015a) suggested that monkeys can potentially become significant predators of small vertebrates, particularly of endemic birds that have low resilience and small populations. Their predation of bird nests has recently been confirmed (Guedes et al. 2021), but further work is required to determine the impacts on bird populations.

Order Rodentia

Family Muridae

São Tomé and Príncipe support populations of all three introduced murid rodents in Africa: the ship rat, the brown rat, and the house mouse. Both the house mouse and the brown rat occur and are abundant also on Annobón (Bocage 1893; Peris 1961; Jones and Tye 2005; Fry 2008; Martim Melo pers. comm.).

These commensal species may have reached the islands as stowaways in boats arriving from Europe. The ship rat and the house mouse are likely to have been accidentally introduced with the arrival of Portuguese ships to the islands during the fifteenth century. According to Dutton (1994), the brown rat only reached the islands during the eighteenth century, when it became abundant in the ports of western Europe (Atkinson 1985).

Given their invasive character, even in mainland Africa (Denys et al. 2009; Dalecky et al. 2015), these three species are likely to occur across the three islands and to be most abundant in anthropogenically-modified environments. Atkinson (1994) confirmed the presence of all three rodents around villages in São Tomé and referred to the occurrence of rats at the margins of the primary forest and in the secondary forest along the Quija River. They also highlighted the capture of several young brown rats in Lagoa Amélia and Morro Esperança (Atkinson et al. 1994). A recent pilot study was performed in São Tomé, confirming the presence and high abundance of ship rats throughout the island, while recording only one brown rat in the capital city (Ward-Francis et al. 2017). Ship rats seem to be abundant in Príncipe (Fundação Príncipe 2019, Martim Melo pers. comm.), where the presence of brown rats has recently been confirmed in the south of the island (JMP and ST pers. obs.). These species can also be a problem to the human inhabitants of the islands. For instance, in 2004, the farmers of Annobón faced huge crop damages caused by an overabundance of rats on the island (Martim Melo pers. comm.).

Other Species

In 2019, a non-identified rodent was observed and photographed at Lagoa Amélia on São Tomé island (Fig. 22.1, 1; Leonel Viegas and Francisco Alamô pers. comm.). The overall external morphology of the observed individual (reddish fur, long snout, black dorsal stripe, long tail) suggests it may belong to the sub-Saharan genus

Fig. 22.1 Some of the poorly known mammal species of the islands of the Gulf of Guinea: (**1**) Small rodent probably belonging to the genus *Dendromus*; (**2**) *Hypsignathus monstrosus*; (**3**) *Myotis* cf. *tricolor*; (**4**) *Pseudoromicia* sp., a novel species occurring in Príncipe; (**5**) *Crocidura thomensis*; (**6**) *Myonycteris brachycephala*; (**7**) *Miniopterus newtoni*; (**8**) *Civettictis civetta*. Photo credits: (**1**) Leonel Viegas, (**3**, **7**) Ana Rainho, (**4**) Jorge Palmeirim and Sólveig Thorsteinsdóttir, (**5**) Ricardo de Lima, (**6**) Javier Juste, (**2**, **8**) unknown photographer

Dendromus Smith, 1829 (Family Nesomydae). This is a tentative identification, by no means conclusive, particularly taking into consideration the confusion that still prevails in the field of African rodent taxonomy and the frequent lack of external morphological characters separating taxa (Monadjem et al. 2015). Further research is necessary to clarify the identity, distribution, and natural history of this species.

Order Eulipotyphla

Family Soricidae

Two species of shrew are known to occur on the oceanic islands of the Gulf of Guinea: the São Tomé white-toothed shrew *Crocidura thomensis* (Fig. 22.1, 5) endemic to São Tomé, and the Príncipe White-Toothed Shrew *Crocidura fingui* endemic to Príncipe (Heim de Balsac and Hutterer 1982; Dutton and Haft 1996; Ceríaco et al. 2015; de Lima et al. 2016). No shrews have been found on Annobón (Heim de Balsac and Hutterer 1982).

Crocidura thomensis was described by Bocage (1887) based on a specimen captured by Francisco Newton in 1886 at Roça Minho. A few years later, it was also captured by Newton and António Lobo de Almada Negreiros at Santa Maria and another unknown location (Bocage 1905). By the end of the twentieth century, the species had been recorded from fewer than ten locations (Dutton and Haft 1996). Recent data suggest, however, that it may not be as rare as initially suspected. Without directed sampling effort, this species was recorded 23 times in 15 new locations in recent years (de Lima et al. 2016). It seems to be widely distributed, occurring from near sea level to high mountainous areas (Fig. 22.2), inhabiting humid areas across a variety of habitats ranging from mist forests to lowland plantations (Dutton and Haft 1996; de Lima et al. 2016). The use of humid habitats may result from the higher availability of arthropod prey (Dutton and Haft 1996; de Lima et al. 2016). *Crocidura thomensis* is listed as Endangered in the IUCN Red List of Threatened Species (Kennerley 2016). This status is due to its reduced extent of occurrence and the continuing decline in the extent and quality of the available habitat. Other possible threats are predation by introduced species, use of pesticides, and agricultural intensification (Dutton and Haft 1996; de Lima et al. 2016). If confirmed, the dependence on humid habitats may make this species vulnerable to climate change (de Lima et al. 2016).

The taxonomic status of the shrew species occurring in Príncipe has undergone several changes since its first records. It was first identified as *C. thomensis* by Bocage (1887) based on a specimen captured by F. Newton at Oquê Nazareth in 1894. A century later, Heim de Balsac and Hutterer (1982) identified the species as *C. poensis*, a species also occurring in West Africa, based on 12 new specimens (plus 4 young) captured on the island by R. de Naurois and Daniel Nunez. Four other individuals were captured in 2013 (Ceríaco et al. 2015). The morphological and molecular analysis of these latter specimens led Ceríaco et al. (2015) to conclude that

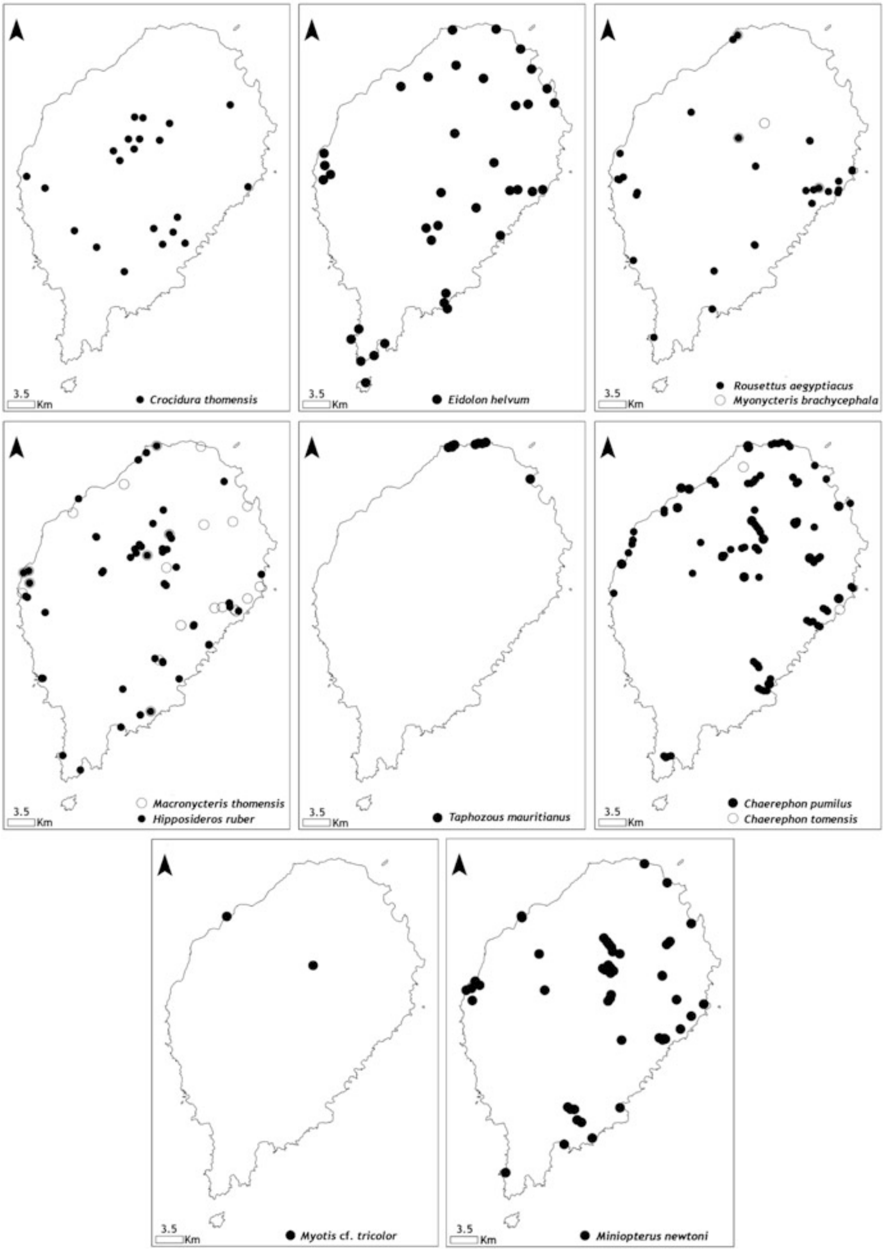

Fig. 22.2 Locations where different wild mammal species were recorded on the island of São Tomé. Sources: Lopes and Crawford-Cabral (1992), Juste and Ibáñez (1994a), Rainho et al. (2010), de Lima et al. (2016), Peel et al. (2017), and ACR (2020)

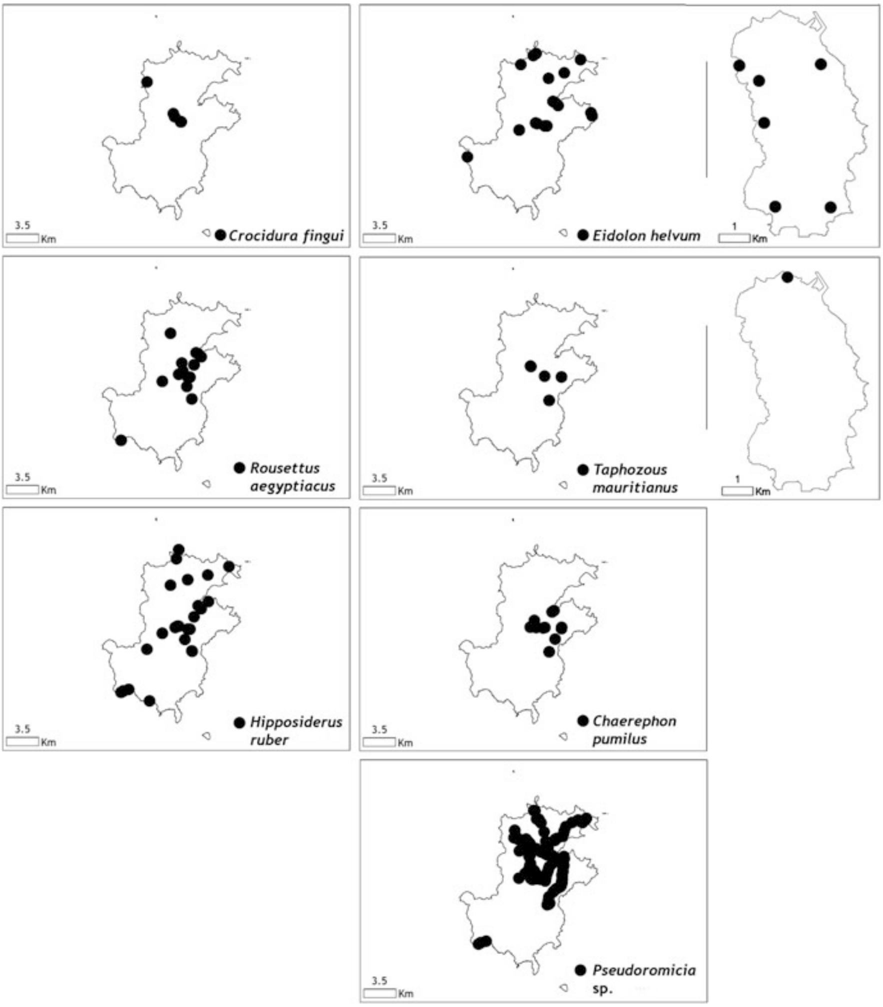

Fig. 22.3 Locations where different wild mammal species were recorded on the islands of Príncipe and Annobón. Sources: Lopes and Crawford-Cabral (1992), Juste and Ibáñez (1994a), Ceríaco et al. (2015), Peel et al. (2017), ACR (2020), Juste (2020), and JMP and ST (pers. obs.)

this is indeed a distinct species, endemic to Príncipe, that they named *C. fingui*. Based on molecular clock estimates, this island endemic diverged from the Central-East African lineage of *C. poensis* ~1.0–1.2 Ma (Nicolas et al. 2019). The distribution of *C. fingui* has not been studied, but so far, it has only been recorded in the northern part of the island (Fig. 22.3). It seems to be versatile in terms of habitat, occurring both near human settlements and in forest (Ceríaco et al. 2015). Due to the lack of knowledge about the distribution of this species, its ecological requirements, and potential threats, it is listed as Data Deficient in the IUCN Red List of Threatened Species (Ceríaco et al. 2019).

Order Chiroptera

Family Pteropodidae

Three species of fruit bats occur in the oceanic islands of the Gulf of Guinea. In 2019, photos of a fourth species, a male hammer-headed bat *Hypsignathus monstrosus* H. Allen, 1862, allegedly captured in the town of São Tomé, appeared on social media (Fig. 22.1, 2). Since we have not been able to collect more information, we refrain from commenting on this observation.

The conspicuous and noisy African straw-colored fruit bat, *Eidolon helvum*, is the largest bat and probably one of the most abundant native mammals on the islands. Dallimer et al. (2006) estimated the density of this species on Príncipe at between 82 and 111 ind/km^2. Peel et al. (2017) produced a slightly higher estimate for Príncipe at between 156 and 159 ind/km^2 and estimated a density between 94 and 176 ind/km^2 for Annobón. All estimates show that this species reaches densities similar to those found in mainland Africa (Dallimer et al. 2006). *Eidolon helvum* is commonly seen flying with slow strokes high above the canopy in forests, plantations, and even city gardens and orchards, foraging on native and planted fruits (all authors, pers. obs.).

Eidolon helvum is migratory on the African mainland, where it is considered monotypic despite its broad distribution (O'Toole 2019). Conversely, all three island populations are considered non-migratory (Juste et al. 2000; Peel et al. 2016, 2017). The populations of *E. helvum* from São Tomé, Príncipe, and Annobón show genetic differentiation in a clear geographic pattern (Peel et al. 2013). Genetic and demographic analyses provide evidence that *E. helvum* of Príncipe and São Tomé are broadly part of the same genetic population cluster, though dispersal between the islands is rare (Juste et al. 2000; Peel et al. 2013). By contrast, the Annobón population is recognized as a taxonomically distinct entity (*E. helvum annobonense* Juste et al. 2000). It exhibits island dwarfism, with individuals being significantly smaller than those of the other two islands (Juste et al. 2000; Peel et al. 2016, 2017).

Despite its high density on the Gulf of Guinea islands, *E. helvum* was classified as Vulnerable on São Tomé because of its reduced range and habitat degradation (Rainho et al. 2010). Moreover, it is hunted in large numbers on São Tomé (Carvalho et al. 2015b; Hayman and Peel 2016; Peel et al. 2017) and on Príncipe (Hayman and Peel 2016, JMP and ST pers. obs.). Hayman and Peel (2016) quantified the effects of hunting on the demographic structure of the population on São Tomé but did not find detrimental impacts on Príncipe. Increased hunting pressure may result in the unsustainable exploitation of this species, a problem compounded by the frequent disturbance of its colonies (Rainho et al. 2010; Peel et al. 2017). Globally, *E. helvum* is Near Threatened on the IUCN Red List due to a significant decline of its population and over-harvesting, making this species close to qualifying for Vulnerable status (Cooper-Bohannon et al. 2020).

The Egyptian rousette, *Rousettus aegyptiacus* (Geoffroy, 1810), is found on Príncipe and São Tomé islands (Figs. 22.2 and 22.3). The genus *Rousettus* Gray 1821 is unique among Old World fruit bats for its echolocation capacity (Holland et al. 2004; Table 22.1), allowing roosting in total darkness in caves and buildings. The populations on Príncipe and São Tomé are clearly differentiated morphologically and genetically from other African forms and recognized as endemic at subspecies rank (Juste and Ibáñez 1993b). These two subspecies represent classic examples of island dwarfism in the case of *R. aegyptiacus princeps* Juste and Ibáñez 1993 on Príncipe and gigantism by *R. aegyptiacus tomensis* Juste and Ibáñez 1993 on São Tomé (Juste and Ibáñez 1993b; Juste et al. 1996). Still, both forms share features (like their massive dentition) that point to a common evolutionary history (Juste and Ibáñez 1993b). *Rousettus aegyptiacus* is a cave-dwelling species that forages in multiple habitats on the islands, feeding on native and cultivated fruits (Rainho et al. 2010). On São Tomé, it was observed sharing a roost with *H. ruber* and *M. newtoni* in a large marine cave (Rainho et al. 2010). On Príncipe, a small colony was found roosting in a cliff in Pico Papagaio (Juste 1990). *Rousettus a. tomensis* is listed as Vulnerable because of its small range and projected habitat degradation (Rainho et al. 2010). Although harvested for human consumption, it remains relatively common on both Príncipe and São Tomé (Rainho et al. 2010; JMP and ST pers. obs). However, an increase in harvesting, aggravated by the disturbance of the colonies in their roosts, may become a threat (Rainho et al. 2010).

A third fruit bat species, the São Tomé collared fruit bat *Myonycteris brachycephala* (Fig. 22.1, 6) is only found on São Tomé (Fig. 22.2). This endemic species is unique in having lost a lower incisor, hence displaying the only asymmetrical dental formula known in any mammal (Juste and Ibáñez 1993a). It is very elusive, and despite netting efforts, it is only known from two localities beyond the type locality (Cascata, São Tomé), both in a rugged landscape, one (Morro Palmira) in montane forest and the other (Belavista) in lowland cocoa plantations (Juste and Ibáñez 1994a). It is considered Endangered (Juste 2016).

Family Hipposideridae

The family Hipposideridae comprises many insectivorous species spread throughout the Old World tropics, all featuring a highly complex leaf-nose. The oceanic islands of the Gulf of Guinea host two species: *Hipposideros ruber* and *Macronycteris thomensis*. The latter is endemic to São Tomé and was described by Bocage (1891) based on specimens from Ribeira Peixe and Roça Saudade. It is a large microbat (forearm (FA) ~85 mm, weight ~56 g) and is part of a group of leaf-nosed bat species that were recently moved from the genus *Hipposideros* to *Macronycteris* (Foley et al. 2017). Very little is known about the biology of this species; however, it is presumably somewhat similar to that of *M. gigas* (Wagner, 1845), a close relative present on Bioko (Juste and Ibáñez 1994a) and the adjacent mainland (Happold

Table 22.1 Characteristics of the echolocation calls of different bat species present in São Tomé

Species	F_{min} (kHz)	F_{max} (kHz)	F_{maxE} (kHz)	Duration (ms)	Interval (ms)	*N*
Rousettus aegyptiacus	9.3 ± 2.4	110.5 ± 48.0	–	0.33 ± 0.12	122.5 ± 28.7	8
	4.1–11.9	44.0–150.0		0.2–0.5	81.7–165.0	
Hipposideros ruber	139.7 ± 0.2	141.5 ± 0.4	140.9 ± 0.3	5.9 ± 0.2	14.1 ± 4.2	6
	139.3–139.8	140.8–141.9	140.4–141.1	5.7–6.1	10.4–22.1	
Macronycteris thomensis	66.0 ± 0.8	68.0 ± 1.0	67.2 ± 0.4	20.7 ± 4.0	66.8 ± 17.4	10
	64.3–66.8	66.8–70.2	66.4–68.0	15.6–28.6	43.2–106.4	
Myotis cf. tricolor	39.3 ± 2.0	117.3 ± 3.3	78.4 ± 2.1	1.84 ± 0.1	82.7 ± 16.2	5
	36.6–41.6	112.0–120.8	76.4–81.8	1.74–1.92	58.4–102.6	
Miniopterus newtoni	50.3 ± 1.3	101.7 ± 16.7	55.9 ± 2.7	4.8 ± 2.1	61.4 ± 23.6	14
	47.8–52.2	69.6–119.0	53.2–61.0	2.3–7.8	31.8–105.7	
Taphozous mauritianus	24.2 ± 0.7	31.9 ± 0.6	28.3 ± 0.2	14.8 ± 1.7	77.4 ± 6.4	5
	23.4–25.2	31.4–32.5	28.1–28.4	12.8–16.8	70.7–86.4	
Chaerephon pumilus	24.9 ± 2.7	36.0 ± 8.7	28.4 ± 2.3	13.6 ± 3.0	258.4 ± 156.5	32
	19.8–29.4	24.7–51.5	23.4–31.5	8.1–18.6	62.8–472.0	
Chaerephon sp.	21.0 ± 1.1	23.0 ± 1.1	22.1 ± 1.0	16.3 ± 1.7	350.7 ± 97.2	26
	19.0–22.4	20.4–25.5	19.9–24.1	12.7–19.9	137.0–558.5	

Values indicate mean, standard deviation and range of observed values. F_{min}, minimum pulse frequency; F_{max}, maximum pulse frequency; F_{maxE}, maximum energy frequency. Note that the values indicated for *Chaerephon* sp. may refer to *Chaerephon pumilus* or another species of the same genus (e.g., *Ch. tomensis*)
Adapted from Rainho et al. (2010)

2013a; Foley et al. 2017). *Macronycteris thomensis* looks like a dwarf form of *M. gigas*. A colony of several hundred individuals was found in an underground roost, and a single individual was observed roosting under the leaves of a palm tree. It is common throughout the island but much less so than *H. ruber* (Rainho et al. 2010).

Hipposideros ruber is a small leaf-nosed bat (FA ~50 mm, weight ~11 g) with two very distinct color forms: dull brown and orange. The species is part of a species complex present across much of Africa (Patterson et al. 2019) and is common throughout Príncipe and São Tomé. On both islands, the species is mostly associated with primary and secondary forests, but it is also present in other ecosystems. On São Tomé, it seems to be somewhat less common in the dryer northeast of the island than in the well-forested and humid center and south (Rainho et al. 2010). It uses a wide variety of roost types and has been found in caves and abandoned buildings on Príncipe (JMP and ST pers. obs.). On São Tomé, in addition to these types of roosts, it uses artificial tunnels (Rainho et al. 2010). On the mainland, it is known to also roost in tree hollows (Happold 2013b) and likely does so on the islands as well. *Hipposideros ruber* has very broad wings and highly maneuverable flight, capable of foraging by hawking and gleaning in cluttered forest habitats (Happold 2013b). Both foraging behaviors have been observed on the islands. Its diet has not been studied on São Tomé or Príncipe, but on the mainland, it feeds on a variety of insects, including beetles, moths, dipterans, and isopterans (Happold 2013b). An unusual feature of the population of *H. ruber* on São Tomé is its daytime flying habits. Although most of its activity takes place during the night, it is common to find this bat flying and foraging in the forest during the day (Russo et al. 2011). São Tomé and Príncipe populations produce constant frequency (CF) calls that are typical for the family and include two harmonics, where the second and higher-pitched one is the information carrier (Guillén et al. 2001). The resting frequency is the same as that reported for bats from the mainland and averaged 136.6 and 136.1 kHz for females and 139.7 and 136.7 kHz for males on São Tomé and Príncipe, respectively (Guillén et al. 2001). Although *H. ruber* is classified as Least Concern globally (Monadjem et al. 2017), it was considered Near Threatened in São Tomé due to the probable decline in the number of individuals and colonies resulting from the reduction of roost availability (Rainho et al. 2010).

Family Emballonuridae

The Mauritian Tomb bat *Taphozous mauritianus* (Geoffroy Saint-Hilarie, 1818) is the only emballonurid species known to be present on the Gulf of Guinea oceanic islands. This species, originally described from the island of Mauritius, is quite common across sub-Saharan Africa (Bonaccorso 2019). As an open-space forager, *T. mauritianus* is quite good at colonizing islands (Bonaccorso 2019). In mainland Africa, its diet consists of aerial insects such as Lepidoptera, Isoptera, and Coleoptera (Dengis 1996 and references therein). It typically roosts at the base of the crown of leaves in coconut trees. It was found at several sites along the northern coast of São Tomé (Fig. 22.2) and is presumably common across other coastal areas of the island (Juste and Ibáñez 1994a). It has not been collected on Príncipe, but its presence there has recently been confirmed acoustically (JMP and ST pers. obs.; Fig. 22.3) Finally, *T. mauritianus* seems to be very rare on Annobón (Fig. 22.3), where a single specimen was found dead and is now housed at the Estación Biológica de Doñana (EBD-CSIC) collections in Seville (Juste 2020). In São Tomé, it was classified as Endangered, given its reduced area of occupancy, the number of known locations, and projected decline in habitat quality (Rainho et al. 2010).

Family Molossidae

Two species of molossids occur on the islands and both are insectivorous, the São Tomé free-tailed bat *Chaerephon tomensis* endemic to São Tomé (Juste and Ibáñez 1993c), and the little free-tailed bat *Chaerephon pumilus* (Cretzschmar, 1826), which is found on both São Tomé and Príncipe (JMP and ST pers. obs.). The latter is an abundant habitat generalist, widely distributed across Africa and the islands around the continent and is currently classified as Least Concern (Bouchard 1998; Mickleburgh et al. 2019). By contrast, *C. tomensis* is classified as Endangered, reflecting its small extent of occurrence and likely decreasing population trend as a result of habitat loss associated with coastal development and land conversion for agricultural use, and possibly competition with its much more abundant congener (Monadjem et al. 2019).

During recent island-wide surveys, Rainho et al. (2010) captured several dozen individuals of *C. pumilus* on São Tomé, in shade cocoa plantations, coconut groves and at roosts (Fig. 22.2). On Príncipe, JMP and ST (pers. obs.) captured it at a roost in the roof of a house near Porto Real and recorded its calls at several locations in the NE of the island (Fig. 22.3). By contrast, *C. tomensis* seems to be so rare that recent extensive trapping efforts have failed to document it. The only records to date are the type series of three specimens captured in two lowland localities, in a coastal lagoon at Praia das Conchas in the drier northern area of São Tomé and at the mouth of a river in cocoa plantations in Água Izé (Juste and Ibáñez 1993c). Acoustic sampling further confirmed the ubiquitous presence of *C. pumilus* on São Tomé (Table 22.1). In addition, these data revealed that *Chaerephon* emits vocalizations that fall into two distinct groups that differ in a number of call characteristics (Table 22.1). The first can unequivocally be assigned to *C. pumilus* (FmaxE $\approx$ 28 kHz), while the second group (FmaxE $\approx$ 22 kHz) could potentially correspond to *C. tomensis* (Rainho et al. 2010), thus offering a glimmer of hope that this species still occurs on the island.

Family Vespertilionidae

In São Tomé and Príncipe, this large family of insectivorous bats is represented by one species on each island. On São Tomé, recent surveys led to the detection of a species of mouse-eared bat, *Myotis* Kaup, 1829 (Rainho et al. 2010). While its general morphology suggests the species is a tricolored mouse-eared bat (Fig. 22.1, 3), *M.* cf. *tricolor*, genetic and morphological comparisons, as well as its echolocation calls (Table 22.1), indicate differentiation from mainland specimens (authors' unpublished data). An integrative taxonomic assessment is underway to establish its phylogenetic placement with respect to other Afrotropical *Myotis*. Rainho et al. (2010) captured several individuals in a single roost in a coastal cave at Ponta Figo, south of Neves, comprised of several dozen individuals of *M.* cf. *tricolor* and several thousand *M. newtoni* (described below). No other roosts of the species were found, the species has not been captured elsewhere on the island, and has merely been recorded acoustically at one other location (Bom Sucesso, Fig. 22.2) attesting to its overall rarity (Rainho et al. 2010).

The island of Príncipe is home to a very small pipistrelle bat that is considered an endemic form for the island (Fig. 22.1, 4). Although first reported over 30 years ago (Juste 1990; Juste and Ibáñez 1994b), its formal description is still pending, and its phylogenetic placement in one of the most entangled African bat groups requires clarification. Its general dark brown morphology, baculum characteristics, and genetic comparisons indicate that the pipistrelle belongs to the *Neoromicia* group (JJ pers. obs.) and possibly to the recently described genus *Pseudoromicia* (Monadjem et al. 2020). The species is abundant and ecologically eclectic, having been captured or recorded in urban, agricultural, and forest areas (JMP and ST pers. obs.). As is the case for other bat species, the distribution map suggests that the species is more common in the northern part of Príncipe (Fig. 22.3), but this is mostly a result of biased sampling due to difficulty accessing the southern part of the island.

Family Miniopteridae

Only one species of this family occurs on the Gulf of Guinea oceanic islands, *Miniopterus newtoni*. It has only been recorded on São Tomé (Fig. 22.2), and was first reported for the island and described as a new species by Bocage (1889, 1903). The original material used by Bocage was lost in a fire in Lisbon, and Juste and Ibáñez (1992) provided a neotype from Santa Catarina. These authors distinguished the species morphologically from the mainland western (*occidentalis*) and eastern (*minor*) little *Miniopterus* forms, all considered subspecies of *M. minor* Peters, 1867. A subsequent genetic assessment confirmed the specific rank of this endemic (Juste et al. 2007). The species seems relatively common across São Tomé (Juste and Ibáñez 1994a; Rainho et al. 2010) and was found in modified habitats (e.g., foraging around streetlamps in urban areas) as well as in primary lowland forests, from sea level up to 1300 m in Morro Palmira (Juste 1990). It appears to roost strictly in caves, water mines, and tunnels. It can form colonies of thousands of individuals, often with other species. *Miniopterus newtoni* emits low duty cycle frequency-modulated echolocation calls with maximum energy of around 56 kHz (Table 22.1). It was locally considered Near Threatened due to a probable decline in the number of individuals and locations because of the destruction and/or disturbance of underground roosts (Rainho et al. 2010). However, it is listed as Data Deficient in the IUCN Red List (Juste 2019).

Order Carnivora

Family Mustelidae

One of the wild carnivores present on São Tomé is the least weasel (Bocage 1895; Dutton 1994). To the best of our knowledge, this species was not reported for Príncipe or Annobón. Although the Portuguese were most likely responsible for the introduction of the least weasel on São Tomé, genetic analyses by Rodrigues et al. (2017) revealed that the animals that occur on this island do not appear to be closely related to mainland Portugal populations. Instead, they are identical to those from the Azores (a Portuguese volcanic archipelago in the mid-Atlantic), which, in turn, are thought to have been introduced from the Balearic Islands in the Mediterranean. Morphological similarity between individuals of São Tomé and the Azores had already been highlighted by Bocage (1895), and Barrett-Hamilton (1904) mentioned that the animals of São Tomé might have been imported from the Azores.

There is little information about the abundance and distribution of the least weasel on São Tomé and Príncipe. Atkinson et al. (1994) observed weasels both at Fernão Dias and Ribeira Peixe. The least weasel feeds mainly on rodents, both in its native and introduced range, but can also consume birds and their eggs, small reptiles, and invertebrates, particularly if the rodent population declines or if an easy predation opportunity arises (Sheffield and King 1994 and references therein; King et al. 2001). According to Dutton (1994), the abundance of rodents on the islands may reduce the impact of weasels on other animal groups. However, shrews are frequently part of the weasel's diet and the endemic shrews might thus be vulnerable to its presence (Sheffield and King 1994).

Family Viverridae

The African civet (Fig. 22.1, 8) is endemic to sub-Saharan Africa, occurring between latitudes 15° N and around 29° S (Ray 2013). It is naturally present on Zanzibar but absent from other offshore African islands (Ray 2013). It is likely that the Portuguese introduced the African civet to both São Tomé and Príncipe (Bocage 1905; Dutton 1994; Fundação Príncipe 2019), not only for the control of rodents but also for the exploitation of its musk (Frade 1958). No reference was found to the presence of this species on Annobón.

The African civet is a solitary, silent species that is active only at night. Thus it is not easy to observe, and information on its distribution and abundance is scarce. Atkinson et al. (1994) observed a fresh civet hole in a secondary forest between Santo António and São Miguel, and JJ (pers. obs.) recorded this species near São Tomé and at Cantagalo, Monte Belo, Monte Café, and Praia das Conchas in the early 1990s. During the last decade, the species has been observed across São Tomé, from the savannas in Morro Peixe to Monte Café and Monte Carmo, and from the road to the native forest (Ricardo de Lima pers. comm.). In Príncipe, it was camera-trapped at Morro Leste (Fundação Príncipe 2019). In mainland Africa, this species does not usually dwell in primary forests, but will use this habitat if accessible by logging roads (Ray and Sunquist 2001). African civets are omnivorous and opportunistic, feeding mainly on fruit, arthropods, mammals, and, less frequently, on birds and reptiles (Ray 2013 and references therein). The African civet is not a good climber or digger (Ray 2013), so tree-dwelling species should be relatively safe from civet predation (Dutton 1994). The potential impact on native ground-dwelling fauna is not known.

Conservation

The long-term isolation of Príncipe, São Tomé, and Annobón allowed the differentiation of insular populations, resulting in a very high level of endemism and an exceptional mammal conservation value. The taxonomy of these mammals is still in flux but of the 13 native species currently recognized, 7–9 are endemic species, and 3–4 are endemic subspecies, with no endemism shared between islands (Appendix). Most of these native and endemic species are bats (Appendix), though Príncipe and São Tomé each have an endemic species of shrew, and São Tomé may have a yet undescribed rodent. All the remaining mammals were introduced by humans.

Little is known about the threats faced by these species, although they should all be considered somewhat fragile due to their very small ranges (Le Breton et al. 2019). In particular, further deforestation and forest degradation would likely result in a potentially threatening situation for several mammal species. All the endemics likely evolved in humid forest, and several species show some level of association to this habitat (e.g., *Ch. tomensis*, *E. helvum annobonense* and *H. ruber*). Although much of the forest on the three islands has, at some point in the past, been converted to plantation agriculture or profoundly altered, there are still areas of relatively undisturbed habitat in rugged parts of the islands (Jones and Tye 2005; de Lima et al. 2022). The remaining primary forest is mostly in protected areas and, along with complementary areas of secondary forest, is likely to provide suitable habitat to maintain populations of all native mammals. The area of native forest on Annobón is very small, but the only mammal that is endemic to this island, the subspecies *E. helvum annobonense*, also uses secondary habitats (JJ pers. obs.).

Hunting of *E. helvum* and *R. aegyptiacus* for food is common on São Tomé (Carvalho et al. 2015b; Peel et al. 2017) and on Príncipe (Peel et al. 2017; JMP and ST pers. obs.). Still, both species remain quite numerous, presumably because these frugivorous species take advantage of the increase in fruit resources due to agriculture. The endemic *M. brachycephala*, however, is quite rare and it may be caught in traps set up to capture the two more abundant species, so hunting is a potentially significant threat to this species.

Some carnivorous mammals, both wild and domestic, have been introduced in São Tomé, all of which are also widespread in Príncipe, except for the least weasel. Although the impact of these species on the native wildlife has not yet been studied, they are all known to consume small mammals, so they are potential predators of the native shrews. Rats prey on smaller mammals and may thus also prey on both shrew species and potentially bats (Racey and Entwistle 2003).

Because so little is known about the real impact of the various potential threats to native mammals on these islands, it is not possible to formulate very specific conservation recommendations. However, it is evident that the protection of forest is essential. The expansion of conservation management to areas of well-preserved secondary forest and increased surveillance and enforcement are necessary to ensure the continuity of the forests on the islands and all the biodiversity they sustain. Integrated management actions directed at the control of exotic predators are also urgently needed, within the forest but also in anthropogenic systems (Courchamp et al. 2003). Alien invasions are recognized as a significant cause of species endangerment and extinction, and the rodents present on the islands are among the most damaging invasive alien species (Lowe et al. 2000). Their devastating effects on natural systems, particularly on islands, and impacts on human activities and health have been thoroughly documented around the globe (Dutton 1994; Drake and Hunt 2009; Harris 2009; Russell et al. 2017).

In the case of bats, cave-dwelling species are always of particular concern, because the availability of suitable underground roosts is limited and the concentration of bats in these roosts exposes them to additional risks. Five cave-dwelling bat species are known to occur on São Tomé, two of which have populations also on Príncipe. It is thus essential to take measures to ensure that these roosts are adequately identified and protected. The importance of each roost should be evaluated, using criteria based on the number of individuals and number of species using the site and their conservation status. High-ranking roosts should be identified, regularly monitored, and human access physically limited if necessary (Rainho et al. 2010). Frugivorous bat species are considered pests by many farmers because they consume planted fruits. In extreme damage and food-loss situations, the use of wildlife-friendly exclusion nets to protect individual trees or fruits may be licensed and supported (Tollington et al. 2019). However, this conflict should be managed with care and in partnership with farmers.

Educational outreach about the value of biodiversity is needed to provide citizens with a better understanding of the importance of their local mammal species. In the case of bats, for instance, highlighting their importance in seed dispersal and in the control of insects that are agricultural pests as well as vectors of diseases. Finally, it is important to highlight the need to carry out more research on which to base the conservation of the endemic-rich mammalian fauna of the islands.

Challenges and Future Research

Although recent efforts have advanced our understanding of the mammal fauna and in particular the bat fauna of São Tomé and Príncipe (Rainho et al. 2010), the preceding sections clearly highlight that our knowledge is fragmented, and important gaps remain to be addressed in future research. Detailed taxonomic assessments that integrate multiple lines of evidence based on craniometric, morphological, genetic, and (for bats) acoustic data are needed to resolve the identity and taxonomic relationships of several species, specifically *M.* cf. *tricolor* in São Tomé, *Pseudoromicia* sp. in Príncipe and of the putative *Dendromus* species recently discovered in São Tomé.

At least 7 of the 19 wild mammal species occur only on one of the Gulf of Guinea islands, including 3 Endangered and 2 Data Deficient species (Appendix). The long-term conservation of this large number of single-island endemics, such as the bats *Ch. tomensis* and *M. brachycephala* or the shrews *C. fingui* and *Cr. thomensis,* constitutes a fundamental challenge. In this regard, further detailed surveys of the islands are needed, to gather reliable data to assess the ecology, distribution, threats, and current status of populations. In particular, Annobón should be targeted since it has not been surveyed for decades. Ideally, such surveys should be conducted at regular intervals to be able to monitor population trends (Meyer et al. 2010) and to trigger appropriate management interventions if needed. Such detailed surveys are also urgently needed to fill important knowledge gaps concerning basic biology and ecological requirements—information that is scant or lacking for many species (e.g., *Ch. tomensis*, *M. thomensis*, *M. newtoni*). Finally, further field surveys are needed to assess the population status of the invasive species, particularly the murid rodents, and to quantify their impact on the Gulf of Guinea island ecosystems.

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Appendix

List of the wild terrestrial mammals of the Gulf of Guinea oceanic islands. Occurrence status per island: E, endemic; R, resident; I, introduced; ?, uncertain. IUCN Red List category: NE, not evaluated; DD, data deficient; LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered

Higher taxonomy	Species/subspecies	P	ST	A	IUCN
Order Primates					
Family **Cercopithecidae**					
Cercopithecus Linnaeus, 1758	*Cercopithecus mona* (Schreber, 1775)	I	I		NT
Order Rodentia					
Family **Muridae**					
Mus Linnaeus, 1758	*Mus musculus* Linnaeus, 1758	I	I	I	LC
Rattus Fischer, 1803	*Rattus rattus* (Linnaeus, 1758)	I	I	?	LC
	Rattus norvegicus (Berkenhout, 1769)	I	I	I	LC
Order Eulipotyphla					
Family **Soricidae**					
Crocidura Wagler, 1832	*Crocidura fingui* Ceríaco et al 2015	E			DD
	Crocidura thomensis (Bocage, 1887)		E		EN
Order Chiroptera					
Family **Pteropodidae**					
Eidolon Rafinesque, 1815	*Eidolon helvum* (Kerr, 1792)	R	R		NT
	E. helvum annobonense Juste et al., 2000			E	
Rousettus Gray, 1821	*Rousettus aegyptiacus* (É. Geoffroy, 1810)				NT
	R. aegyptiacus tomensis Juste and Ibáñez, 1993		E		
	R. aegyptiacus princeps Juste and Ibáñez, 1993	E			
Myonycteris Matschie, 1899	*Myonycteris brachycephala* (Bocage, 1889)		E		EN
Family **Hipposideridae**					
Macronycteris Gray, 1866	*Macronycteris thomensis* (Bocage, 1891)		E		LC
Hipposideros Gray, 1831	*Hipposideros ruber* (Noack, 1893)	R	R		LC
Family **Emballonuridae**					
Taphozous É. Geoffroy, 1818	*Taphozous mauritianus* É. Geoffroy, 1818	R	R	R	LC

(continued)

Higher taxonomy	Species/subspecies	P	ST	A	IUCN
Family **Molossidae**					
Chaerephon Dobson, 1874	*Chaerephon pumilus* (Cretzschmar, 1826)	R	R		LC
	Chaerephon tomensis (Juste and Ibáñez, 1993)		E		EN
Family **Vespertilionidae**					
Myotis Kaup, 1829	*Myotis cf. tricolor* (Temminck, 1832)		R		
Pseudoromicia Monadjem et al., 2020	*Pseudoromicia sp.*	E			NE
Family **Miniopteridae**					
Miniopterus Bonaparte, 1837	*Miniopterus newtonii* Bocage, 1889		E		DD
Order Carnivora					
Family **Mustelidae**					
Mustela Linnaeus, 1758	*Mustela nivalis* Linnaeus, 1766		I		LC
Family **Viverridae**					
Civettictis Pocock, 1915	*Civettictis civetta* (Schreber, 1776)	I	I		LC

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Chapter 23
Cetaceans of São Tomé and Príncipe

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Abstract The Gulf of Guinea is a marine biodiversity hotspot, but cetacean fauna in these waters is poorly studied and our knowledge is documented mostly from opportunistic (sightings and strandings) and whaling data. This chapter presents a short review of historical whaling in the Gulf of Guinea and an update of cetacean biodiversity in the waters of São Tomé and Príncipe. Observations since 2002 have confirmed the presence of 12 species of cetaceans, 5 of them new to the region (Striped Dolphin, Rough-toothed Dolphin, Risso's Dolphin, Pygmy Killer Whale, and Dwarf Sperm Whale). The archipelago seems to be an important area for cetaceans, with some species (Bottlenose Dolphin and Pantropical Spotted Dolphin) being present throughout the year. The volcanic origin of the archipelago produces great depths very close to the coast, which may favor the approach of pelagic species

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like Sperm Whales, Killer Whales, and Short-finned Pilot Whales. Bays and shallow waters may also serve as protection or rest areas for particular groups, like mother and calf pairs of Humpback Whales. Major anthropogenic threats to cetaceans in São Tomé and Príncipe include habitat degradation due to overfishing, fisheries interactions, possibly some occasionally directed takes and, more recently, oil and gas prospecting. Consistent and dedicated research to inform national legislation, together with increasing environmental awareness and local engagement, would help to identify effective cetacean conservation strategies in the archipelago.

Keywords Conservation · Dolphins · Gulf of Guinea · Whales · Whaling

Introduction

Top predators, such as cetaceans, are known to seek and associate with predictable regions of high biological activity ("hotspots"). Oceanic islands are topographic features that result in localized upwellings, eddies, and convergence zones, which in turn may cause enhanced primary productivities that promote biomass accumulation and congregate biodiversity in their vicinity (Doty and Oguri 1956; Caldeira et al. 2002; Palacios 2002).

The Gulf of Guinea is a globally important region that hosts high concentrations of rare, range-restricted, and threatened marine species, such as sea turtles, elasmobranchs, and marine mammals (Weir 2010; Lucifora et al. 2011; Selig et al. 2014; Polidoro et al. 2017) and is considered a marine biodiversity hotspot (Roberts et al. 2002). The waters of the Gulf of Guinea support key life-history stages for several cetacean species (Jefferson et al. 1997; Weir 2010, 2011). However, the cetacean fauna along the west coast of Africa, as well as of the oceanic islands of the Gulf of Guinea, is incompletely described and, despite historical information and verbal descriptions of great diversity, there is relatively little scientific information about the ecology of species from this group occurring in the region (Hoyt 2005; Weir 2010).

The nation of São Tomé and Príncipe is composed of two main islands and several small islands and islets. Due to their volcanic origin, the islands display high relief and the littoral surrounding fringe is very narrow with depths of around 200 m close to the shore (Afonso et al. 1999). The country has an Exclusive Economic Zone (EEZ) of almost 165,000 km^2, and a strong dependence on fishing; however, knowledge related to its marine fauna is limited, and only a few studies have been conducted in recent years (e.g., Afonso et al. 1999; Maia et al. 2018; Hancock et al. 2019; Quimbayo et al. 2019).

This chapter provides a brief summary of historical whaling activity in the Gulf of Guinea region, an updated review of the occurrence of cetaceans in the waters of São Tomé and Príncipe (no studies available for Annobón), and a brief history of cetacean research in the archipelago. It also identifies priorities for future research and conservation of cetaceans in the region.

Cetacean Occurrences Based on Historical Whaling Data

Background on Historical Whaling in the Gulf of Guinea

Early written references to cetaceans in the Gulf of Guinea include observations of "*big fishes such as porpoises*" (Dias 1934 in Brito 2009) and "*many whales, large and small, that it is a wonderful thing to say*" (Anonymous 1812). As with other Atlantic islands and the coast of the African mainland, cetaceans stranded on the shore were probably used by local people and settlers, who consumed the meat and transformed blubber into fuel (Brito et al. 2017; Vieira 2020).

By the second half of the eighteenth century, the Governor of São Tomé and Príncipe reported the presence of English vessels hunting whales around Cap Lopez (Gabon) and Fernando Po (Bioko) Island (Ferreira 1773). Those operations followed "American whaling" techniques, which included the persecution of animals from open boats and hand harpooning (Macy 1835; Townsend 1935). Humpback Whales *Megaptera novaeangliae* (Borowski, 1781) were one of the main targets along equatorial West Africa, due to their seasonal migratory movements, preference for coastal waters during migration and breeding, and slower swimming speed compared with other baleen whales (Townsend 1935; Tønnessen and Johnsen 1982). The combination of these factors made this species an easy target for coastal whaling globally during the nineteenth century (Reeves and Smith 2006), including in the waters of São Tomé and Príncipe, for instance during the voyage of the Vessel Admiral Blake. The Vessel arrived at São Tomé on June 22, 1869, and anchored on Príncipe Island on June 24, 1869. The crew went on "bay whaling" until the end of August hunting humpback cow and calf pairs (Anonymous 1869–70).

Starting in the mid-1800s, whaling became dramatically more effective due to several innovations, including explosive harpoons and modern steam-driven whaling boats (Tønnessen and Johnsen 1982; Clapham and Baker 2002). This allowed the capture of previously unattainable fast-swimming species, especially *Balaenoptera* whales including Blue Whale *Balaenoptera musculus* (Linnaeus, 1758), Sei Whale *Balaenoptera borealis* (Lesson, 1828), Bryde's whale *Balaenoptera edeni* (Anderson, 1879), and Fin Whale *Balaenoptera physalus* (Linnaeus, 1758).

In the early twentieth century, engine-powered Norwegian floating factories (moored near shore or working in the open sea) accompanied by fleets of catcher boats with deck-mounted harpoons began operations in the Gulf of Guinea. During this time whaling went through periods of expansion and crisis (Rocha et al. 2015). Despite the breaks in whaling activity resulting from World Wars I and II, after years of intense captures, the following seasons were significantly less successful. Pelagic and coastal whaling operations were conducted from Cap Lopez (Gabon) in 1912 and took place in 1912–1914, 1922–1926, 1930, 1934–1937, 1949–1952, and 1959. Whaling operations took place mostly between the end of June and November, with a peak in July/August (Budker and Collingon 1952), corresponding to the breeding period of Humpback Whales, the main target of the catch. Bryde's, Sei, Sperm

Physeter macrocephalus (Linnaeus, 1758) and Fin whales were also taken (Budker 1953; Tønnessen and Johnsen 1982). During the whaling seasons, high fluctuation of total catches, with a substantial decline not only in numbers but in the mean length of the individuals caught indicated the depletion of the Humpback Whale stock (Budker and Collignon 1952; Budker 1953).

In the late 1960s, overexploitation was notorious, and almost every whale stock was depleted or had already collapsed. The International Whaling Commission (IWC), an intergovernmental organization established in 1946 to provide conservation of whale stocks and management of the whaling industry, began to impose restrictions on whale catches. Restrictions for Blue and Humpback whales were imposed in the 1960s, Sei and Fin whales in the 1970s, and in 1986 the moratorium went into effect with zero catch quota for both pelagic and coastal whaling (Clapham and Baker 2002). In the 1970s, illegal captures, mostly of Bryde's and Sei whales, continued by the catcher/factory vessel Run/Sierra in the Gulf of Guinea (Tønnessen and Johnsen 1982; Best 2001).

In addition to commercial whaling, an aboriginal whaling operation in Annobón has been reported since the late nineteenth century (Doce 1932, 1951; Aguilar 1985), and with recent evidence of continuing until today (Collins et al. 2019; Fielding and Barrientos 2021). The Annobonese retained the skills and practices of hunting whales from their experience on foreign whaling vessels, and the activity was integrated into local culture. Small rowing boats with two rowers and one harpooner were used in July and August, targeting coastal Humpback Whales, mainly calves (Aguilar 1985). However, the status of this hunt is uncertain and more information is needed.

Industrial Whaling in São Tomé and Príncipe

First attempts to promote modern whaling in São Tomé using a factory-ship and catchers date to the 1930s (Henriques 2016) but not much is known from that period. From 1945, the company *Grémio dos Armadores da Pesca da Baleia* of Lisbon, regulated the activity in mainland Portuguese waters and overseas (Henriques 2016).

There are some references on whaling operations off São Tomé and Príncipe in the 1940s. Tenreiro (1961) mentioned that local fishermen and Norwegian companies established on São Tomé hunted Sperm Whales and sharks. He notes that 1946 was an excellent year when they caught 100 cetaceans, which generated 1079 tons of oil, produced in the factory in the town of Neves (Fig. 23.1, 1). In 1951, a decree granted a Norwegian company the right to hunt whales in the archipelago for a period of 10 years, with one of several conditions being the distribution of whale meat to the local population (Henriques 2016). The operation was supported by the modern factory in Praia Rosema (Neves), in the northeast of São Tomé Island (Figueiredo 1960; Henriques 2016). Among the workforce were local people, Portuguese, and foreigners (Boletim Semanal 1951). The factory operated between July and October of 1951, processing an average of seven animals per day, with a

Fig. 23.1 Whaling industry on São Tomé: (**1**) Whaling factory at Praia Rosema (Neves, São Tomé; Tenreiro 1961); (**2–5**) Remains of the whaling factory in 2005. Photo credits: (**2–5**) Inês Carvalho

total of 714 animals: 336 Bryde's Whales, 323 Humpback Whales, 53 Sperm Whales, and 2 Fin Whales (Figueiredo 1960).

The Humpback Whales killed in the waters of São Tome and Príncipe belong to the Gabon stock that by 1951 the IWC had already identified as being depleted.

Nevertheless, at the time, Portugal was not a member of the IWC (joining only in 2002) and despite the criticism, whaling was allowed in STP waters (Budker and Collignon 1952). However, with increasing international criticism, the competition with French enterprises in the Gulf waters, and the low number of captures, the factory closed in that same year (Budker and Collignon 1952; Henriques 2016). Its remains are still part of the São Tomé seascape (Figs. 23.1, 2–5).

Historical Catches of Cetaceans in the Gulf of Guinea Region

Whaling data provides valuable information on species identification, distribution, migration, life history, and population status of whale stocks around the world (e.g., Townsend 1935; Josephson et al. 2008; Gregr 2011; Smith et al. 2012). To gather information on the occurrence and distribution of cetacean species in the eastern Gulf of Guinea area during the whaling period, two databases were used. The first was the American Offshore Whaling Logbook database (Lund et al. 2021), which includes information from 1381 logbooks from American offshore whaling voyages (1784–1920) extracted from original whaling logbooks from three different sources: Matthew Maury (1850s), Townsend (1930s), and the Census of Marine Life project (Barnard et al. 2002). The second database was the IWC compilation of worldwide whale catches since 1900 (Allison 2016a, b). The IWC data is continually updated (Allison and Smith 2004) and consequently, the total number of catches reported has changed over time (e.g., Findlay 2000; Best 2001; Weir 2010). Whaling records and species identifications were accepted as published, despite the likely misidentification between Sei Whale and Bryde's Whale in the whaling statistics (Best 2001). Prior to 1960, whalers could not reliably distinguish between the two species (Best 2001; Weir 2010). This led to records of "Sei Whales" along the coast of West Africa likely being misidentified Bryde's Whales; thus, records of the two species were merged. Since several cetacean catches are represented by the same geographic positions, the data were separated into two seasons for better visualization (Fig. 23.2): June to October, representing the breeding season for Humpback Whales; and November to May.

Humpback Whale was the main target species of whaling in the Gulf of Guinea region with more than 10,000 animals captured mostly near the coast of Gabon and around Príncipe Island between June and October (Fig. 23.2, top). Bryde's/Sei Whales were caught throughout the year, mainly off the southern coast of Gabon, the offshore waters off the west coast of São Tome, and between the islands of São Tomé and Annobón (Fig. 23.2). Sperm and Fin Whale catches were more infrequent and spread in offshore waters across the entire region, while catches of other cetacean species were rare (Fig. 23.2).

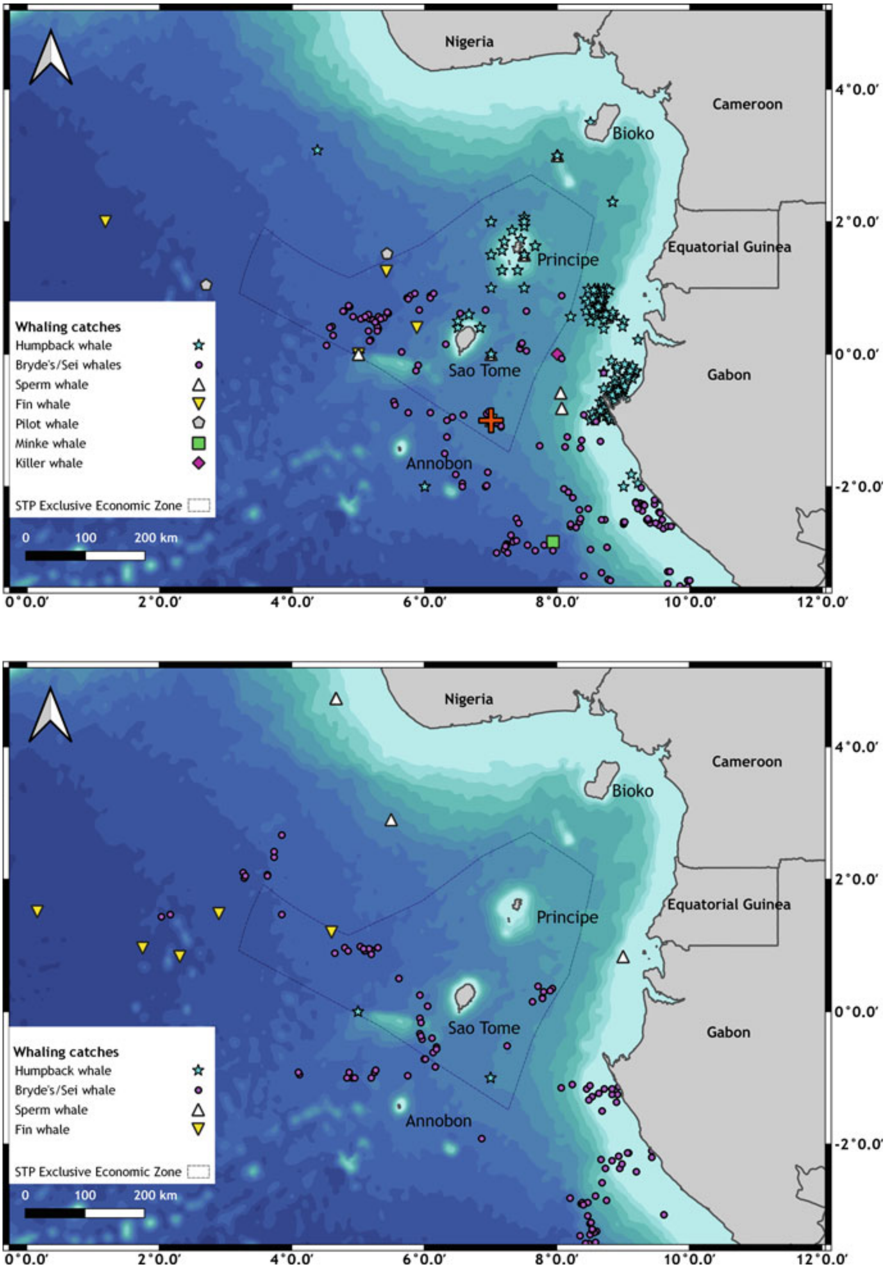

Fig. 23.2 Distribution of whale catch positions around the Gulf of Guinea Islands. Data from American Offshore Whaling Logbook database (https://whalinghistory.org/av/logs/aowl/) and IWC database (Allison et al 2016b), representing N = 11845 catches (10553 Humpback whales; 1010 Bryde's/Sei whales; 261 Sperm whales; 15 Fin whales; 2 Pilot whales; 1 Blue whale; 1 Right whale

Recent Data from Fieldwork on São Tomé and Príncipe

There is limited information about the spatial and temporal patterns of the distribution and abundance of cetaceans in the Gulf of Guinea, and most of the available information is based on whaling data (e.g., Townsend 1935; Budker and Collignon 1952), reports on strandings, by-catch data, and some dedicated cetacean research (e.g., Walsh et al. 2001; Van Waerebeek et al. 2009; Segniagbeto and Van Waerebeek 2010; Weir et al. 2010; Weir 2011; Sohou et al. 2013; Rosenbaum et al. 2014; Escalle et al. 2015; De Boer et al. 2016; Collins et al. 2019; Trew et al. 2019).

In 2002, the first field study dedicated to cetaceans of São Tomé Island started with the objective of collecting baseline data on the occurrence of cetaceans in these waters. The fieldwork of this project was based at Rolas Islet, and the boat surveys in 2002 and 2003 were conducted in the south region of São Tomé. Data on occurrence, movements, seasonality, and behavior (including acoustic behavior) of several species were collected and analyzed (Picanço et al. 2009). In 2004, a PhD focusing on the population structure of the Humpback Whale on the West African coast was initiated, in collaboration with the Wildlife Conservation Society and the American Museum of Natural History. Fieldwork was conducted between 2004 and 2006 in São Tomé waters to collect data on the occurrence, distribution, behavior, and genetics of humpback whales (Carvalho et al. 2011, 2014; Carvalho 2012; Kershaw et al. 2017). In 2012, a partnership between the NGOs MARAPA (São Tomé) and Associação para as Ciências do Mar (APCM; Portugal) started the project "*Operação Tunhã*." The aim of the project was to establish a program to collect systematic baseline data on cetaceans in São Tomé, to assess the local capacity to develop a sustainable whale watching activity, and at the same time to raise awareness among stakeholders on local cetacean conservation.

In Príncipe Island, data collection about cetaceans has been more limited. Some sighting and stranding records have been collected intermittently over the years by Fundação Príncipe (Vanessa Schmitt pers. comm.). In 2020, between August and November, a field survey was carried out in the archipelago's waters to collect visual and acoustic data on cetaceans, for the South Atlantic Cetacean project by the Edmaktub Association (Sesani et al. 2020).

Fig. 23.2 (continued) (*Eubalaena australis* Desmoulins, 1822); 1 Minke whales; 1 Killer whale). Top map-whaling catches between June-October, Bottom map-whaling catches between November-May. The symbol ○ (on top map in red) represents the records without specific geographic coordinates provided by IWC. Blue, Right and several Humpback whale catches were recorded with this point, which indicates that they were caught in the area but there was no specific location

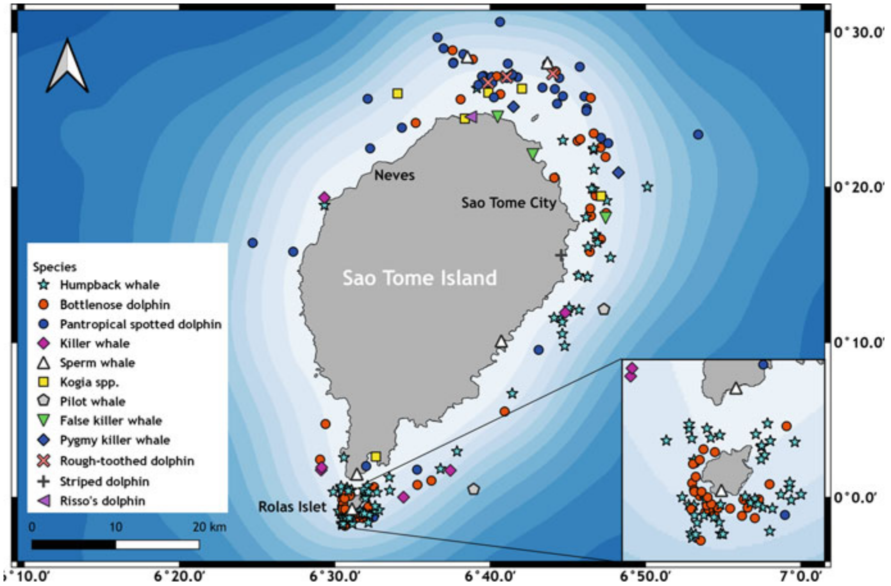

Fig. 23.3 Cetacean sightings and strandings in São Tomé Island recorded from 2002 to 2006 and from 2012 to 2015 ($N = 215$; Picanço et al. 2009; Carvalho et al. 2014; Collins et al. 2019; Associação para as Ciências do Mar, Portugal unpublished data)

Cetacean Species Recorded in São Tomé and Príncipe Waters

To date, the presence of 12 cetacean species has been confirmed (Fig. 23.3, Appendix), based on data collected by the authors during 2002–2006 and 2012–2015 around São Tomé Island. Five of those species were only confirmed recently by the authors: Striped Dolphin *Stenella coeruleoalba* (Meyen, 1833), Rough-toothed Dolphin *Steno bredanensis* (Lesson, 1828), Risso's Dolphin *Grampus griseus* (G. Cuvier, 1812), Pygmy Killer Whale *Feresa attenuata* (Gray, 1874), and Dwarf Sperm Whale *Kogia sima* (Owen, 1866).

Megaptera novaeangliae Humpback Whales (Fig. 23.4, 1) in the Southern Hemisphere migrate between summer feeding areas in the nutrient-rich waters of the Southern Ocean and winter breeding areas in tropical waters (Townsend 1935). The Gulf of Guinea region is known as a breeding area for the Humpback Whale B stock (IWC 2001). Catch histories and recent genetic data suggest that this stock may be sub-structured (Findlay 2000; Carvalho et al. 2014) with some temporal and spatial segregation; Humpback Whales use two different migration corridors and different feeding areas, in South Africa and Antarctica (Barendse et al. 2011; Rosenbaum et al. 2014; Carvalho et al. 2014). Between 2002 and 2014, 74 sightings of Humpback Whales were collected around São Tomé waters (Carvalho et al. 2011; APCM unpublished data). In 2020, 63 sightings were collected mostly around Príncipe Island (Sesani et al. 2020). The sightings were collected between July and late

Fig. 23.4 Cetacean species photographed in São Tomé waters: (**1**) Humpback Whale; (**2**) Bottlenose Dolphin; (**3**) Pantropical Spotted Dolphin; (**4**) Rough-toothed Dolphin; (**5**) Killer Whale; (**6**) Pygmy Killer Whale; (**7**) Short-finned Pilot Whale; (**8**) Sperm Whale. Photo credits: (**1**) Maria Pimentel, (**2**, **5**, **7**) Inês Carvalho, (**3**) Cristina Picanço, (**4**, **6**, **8**) Bastien Loloum

November. São Tomé appears to be used primarily by mother/calf pairs, as a calving, nursing, and resting area. This is suggested by the high frequency of observed groups with a calf present (more than 70%) and long occupancy of several weeks in the area by these groups (Carvalho et al. 2011; Sesani et al. 2020). Female Humpback Whales with calves prefer shallow waters (Ersts and Rosenbaum 2003), being sighted mostly around Rolas Islet (sometimes very close to the shore), near São Tomé city (northeast), and around Príncipe Island (Picanço et al. 2009; Carvalho et al. 2011; Sesani et al. 2020).

Physeter macrocephalus The Sperm Whale (Fig. 23.4, 8) is a cosmopolitan species but shows differential sex-and age-related distributions. Females and immature individuals inhabit primarily warm waters in tropical to subtropical areas (Whitehead 2002). As males get older, they disperse from these warmer areas to higher latitudes (Whitehead 2002). There are three stranding records of Sperm Whales in São Tomé (2002, 2010 and 2013; Fig. 23.4) and one in Príncipe in 2014 (Collins et al. 2019). Two sightings of single animals were recorded off the north coast of São Tomé Island, one reported in 2005, at 1500 m depth (Picanço et al. 2009), and another one in 2013 at 980 m depth (APCM unpublished data). These records suggest the occurrence of the expected "nursery groups," as young calves were recorded from strandings and immature animals and adults were recorded from sightings. Sesani et al. (2020) described a sighting of two individuals in 2020, 80 km off the east coast of São Tomé Island at 2500 m depth, with no information on age and sex.

***Kogia* spp.** Two *Kogia* species are currently recognized: the Dwarf Sperm Whale (*Kogia sima*) and the Pygmy Sperm Whale *Kogia breviceps* (de Blainville, 1838) (Rice 1998). Both occur in deep temperate and tropical waters worldwide, with overlapping distributions, and they are very difficult to distinguish. The Dwarf Sperm Whale is smaller and has a more prominent dorsal fin, whereas the Pygmy Sperm Whale is slightly larger and has a smaller and rounded dorsal fin. There were two confirmed records of the Dwarf Sperm Whale off São Tomé, one sighting in February 2012, off the northwest coast, at around 150 m depth, and one a by-catch record in the southern region in February of 2014 (APCM unpublished data). Four additional sightings of *Kogia* spp. were recorded off the north region of São Tomé Island, two in March and April of 2012 and two in January of 2014 (APCM unpublished data), but the species could not be fully confirmed.

***Orcinus orca* (Linnaeus, 1758)** The Killer Whale (Fig. 23.4, 5) is distributed across oceans (Rice 1998), but reports are less common in tropical waters (Weir et al. 2010). Six sightings were reported around São Tomé (Picanço et al. 2009; Weir et al. 2010): one in November, four in December, and one in January. Four of the six sightings occurred around Rolas Islet, in the south, and the remaining on the east and northwest coasts (Fig. 23.4). Four sightings occurred in shelf edge habitat (270–790 m), one in shallow waters (55 m) and another one in deep-water (1200 m; Weir et al. 2010). The average group size was estimated at six animals and included adults and calves. Weir et al. (2010) photo-identified 13 animals. Two animals were first photo-identified together in 2002, and then in 2004; one of these individuals was also photographed in 2003. The four sightings during December 2002 were the result of repeated encounters on successive dates with a single group of Killer Whales. A predation event was observed off São Tomé during January 2003, when an adult–calf pair of killer whales was observed feeding on an Ocean Sunfish *Mola mola* (Linnaeus, 1758) at the surface (Weir et al. 2010). Repeated sightings of the same group of killer whales around São Tomé suggested the regular use of that area (at least seasonally) by a particular group of animals. In 2020, there were two recorded sightings off western São Tomé, one individual in October and two individuals in November (Sesani et al. 2020). The three individuals were photo-identified, but there was no cross-checking with photographs from previous years.

Steno bredanensis The Rough-toothed Dolphin (Fig. 23.4, 4) inhabits primarily warm oceanic waters worldwide (Rice 1998). Four sightings of this species were recorded, off the north coast of São Tomé Island, in August and September of 2012 and within the 200 m bathymetry. Three of the sightings comprised average groups of eight individuals, all adults. The fourth sighting was a larger group of around 20 adults and juveniles sighted together with a group of 8–10 Pygmy Killer Whales, at around 2 km from the coast and depths under 100 m (APCM unpublished data). In October of 2008, there was one offshore sighting of a group of 35 individuals, west of São Tomé at 3271 m depth (Weir 2011).

Grampus griseus The Risso's Dolphin inhabits temperate and tropical waters worldwide and generally prefers deeper offshore waters, especially close to the continental shelf edge and slope (Jefferson et al. 2008). One individual was stranded on the north coast of São Tomé (Fig. 23.3) in February 2015 (Collins et al. 2019).

***Pseudorca crassidens* (Owen, 1846)** The False Killer Whale inhabits primarily tropical to subtropical waters, and sometimes also occurs in warm temperate waters (Rice 1998). The first record of this species was a sighting of 6–8 adult animals engaged in feeding activities (some animals had fish in their mouths) off the north coast of São Tomé Island in April 2012 (APCM unpublished data). The two subsequent records, in 2013 and 2014, came from strandings in the same coastal region (Collins et al. 2019). The most recent sightings were recorded in 2020, one south of Rolas Islet (on São Tomé) and another on the southwestern coast of Príncipe (Sesani et al. 2020). The estimated group size of these sightings was 30 and 20 individuals, respectively. The group observed off Príncipe was composed of adults and calves (Sesani et al. 2020). All the sightings of this species were within the 250 m bathymetry.

Feresa attenuata The Pygmy Killer Whale (Fig. 23.4, 6) occurs mainly in deep warm tropical waters (Rice 1998). Off the north of São Tomé Island, two groups of eight (in August) and 12 animals (in December) were recorded in 2012 (APCM unpublished data). The eight Pygmy Killer Whales were sighted together with rough-toothed dolphins at less than 100 m depth. The other 12 animals were sighted around 450 m deep.

***Globicephala macrorhynchus* (Gray, 1846)** There are two species of pilot whales: the Short-finned Pilot Whale (Fig. 23.4, 7), which is mostly found in tropical waters, and the Long-finned Pilot Whale, *Globicephala melas* (Traill, 1809), which inhabits colder waters. Picanço et al. (2009) reported a sighting in January 2003 of around 20 pilot whales as Long-finned Pilot Whales, mixed with Bottlenose Dolphins, off the southeast coast of São Tomé, over the shelf edge (975 m). During this sighting, eleven individuals were identified by photographs of the dorsal fins. The second sighting of pilot whales was recorded in February 2012, a group of eight Short-finned Pilot whales, including calves, traveling off the east coast of São Tomé (APCM *unpubl.* data). Photographs confirmed that both sightings refer to Short-finned Pilot Whales and that the most conspicuous individual identified in 2003 was re-sighted after 9 years, suggesting long-term site fidelity that could also apply to other individuals of the group.

***Stenella attenuata* (Gray, 1846)** The Pantropical Spotted Dolphin (Fig. 23.4, 3) occurs in tropical and subtropical waters (Rice 1998). This species is one of the most frequently observed cetaceans in São Tomé, and it is present throughout the year. Since 2002, a total of 37 sightings have been recorded off São Tomé Island; 14 sightings recorded by Picanço et al. (2009) and 23 afterward. Most sightings were recorded over the slope (400–2000 m) to the north of São Tomé (APCM unpublished data). More recently, this species was also recorded around Príncipe, with five sightings (Sesani et al. 2020). The Pantropical Spotted Dolphin can form large groups, ranging from a few animals to several hundred animals. The majority of the sightings were groups of more than 100 animals. In 2012, one animal died from by-catch in the south of São Tomé (Collins et al. 2019).

Stenella coeruleoalba The Striped Dolphin is a mostly oceanic species and occurs in deep warm temperate, subtropical, and tropical waters worldwide (Rice 1998). There was a single record of one stranded individual in March 2012, off the east coast of São Tomé (Collins et al. 2019).

***Tursiops truncatus* (Montagu, 1821)** The Common Bottlenose Dolphin (Fig. 23.4, 2) is a cosmopolitan species with a worldwide distribution in tropical and temperate regions (Rice 1998). It is the most commonly sighted small cetacean species around São Tomé and occurs regularly throughout the year (Pereira et al. 2013). The average group size for this species was estimated at 45 individuals. Calves and juveniles were sighted regularly with adults. Pereira et al. (2013) photo-identified 140 individuals during sightings from 2002 to 2006 and 2012 around São Tomé. The sightings occurred mainly around Rolas Islet and to the northeast of São Tomé (adjacent to São Tomé city), sometimes very close to shore. Most sightings around São Tomé were recorded below the 200 m bathymetry. Some of the individuals identified showed a degree of site fidelity (Pereira et al. 2013). Eight individuals recorded from 2002 to 2006 were resighted in 2012, and one of them was sighted in every survey year. On several occasions, Bottlenose Dolphins were sighted in mixed groups with other species, such as Sperm Whales (on two occasions), Pantropical Spotted Dolphins, and Short-finned Pilot Whales. In 2020, there were five sightings of this species along the northeastern coast of São Tomé, around the 250 m bathymetric, but none around Príncipe (Sesani et al. 2020).

Threats, Conservation Needs, and Future Research

The Gulf of Guinea is one of the 18 global hotspots for marine biodiversity conservation (Roberts et al. 2002). Globally, it is also one of the fastest developing marine regions, and a highly productive ecosystem, that includes some of the most productive coastal and offshore fisheries (Aryeetey 2002). This region also has substantial oil and gas reserves. Marine species are therefore subject to a range of pressures, such as incidental capture (by-catch) in fisheries, overfishing of their prey, direct catch (meat and other products), as well as habitat loss and pollution, namely linked to intense deep-water oil and gas exploration (Weir and Pierce 2013; Escalle et al. 2015). The expansion of offshore hydrocarbon extraction activity has been a concern for the populations using the waters of central Africa and the eastern Gulf of Guinea (Findlay et al. 2006). Seismic surveys use high-amplitude sound sources, that can have negative impacts on acoustically-sensitive animals such as cetaceans, which can result in changes in habitat use, including spatial avoidance (Weir 2008; Kavanagh et al. 2019), and behavioral changes (Cerchio et al. 2014; Dunlop et al. 2017). In recent years, several seismic surveys have been conducted in the EEZ of São Tomé and Príncipe for future oil exploration (e.g., Anonymous 2018). Although there was no assessment of the impact seismic surveying had on cetaceans in the area, it is most likely that such extended surveys resulted in some degree of responses by the animals.

In São Tomé and Príncipe, fishing provides more than 80% of the animal protein consumed by the population (Maia et al. 2018). From 1955 to 2010, the number of artisanal fishers in the archipelago increased by about 116%, from 1127 to 2428 (Maia et al. 2018). Moreover, catches by national semi-industrial fishing and foreign industrial fishing (by the European Union, Japan, and China) have continued to increase during recent decades (Carneiro 2011; EU 2019), despite a reduced capacity for monitoring, control, and surveillance by national authorities (Belhabib 2015). Maia et al. (2018) suggested a potential decline in the catch trends (mainly coastal) in São Tomé and Príncipe’s artisanal fisheries. Declining catches and increasing fishing efforts can lead fishermen to expand their fishing grounds further offshore, use destructive fishing practices (such as explosives and grenades), use illegal gillnets, and sometimes target different species (Santos 2017). Most sightings of cetaceans in northern and southern São Tomé coincide with areas of intense artisanal fisheries. Episodes of cetacean by-catch (Collins et al. 2019) and direct hunting of cetaceans (APCM unpublished data) have been described in recent years. Fishermen themselves recognize that the problem of overexploitation of marine resources should be addressed through the creation of marine reserves (Maia et al. 2018). So far, São Tomé and Príncipe has not created any marine protected areas (MPAs), but presently efforts are being made by local and international NGOs together with the government to propose a network of co-managed coastal MPAs (de Lima et al. 2022). Well-managed MPAs have been reported to lead to increases in marine biodiversity, abundance, and biomass (Ballantine 2014; Grorud-Colvert et al. 2021), benefit fisheries (Harrison et al. 2012), and improve the local economy.

In 2018, at the 67th IWC meeting, several countries from the Gulf of Guinea (São Tomé and Príncipe included) voted, along with whaling nations, to re-establish appropriate catch limits for some stocks/species, and voted against the proposal to create a Whale Sanctuary in the South Atlantic (IWC 2018). Cetaceans in the waters of São Tomé and Príncipe have no specific legal protection, although there are laws regarding general aspects of environmental protection (Brito et al. 2010; Decree-Law N° 11/1999—Fauna and Flora conservation and protected areas; Decree-Law N° 6/2014—Marine turtles protection and Decree-Law N° 22/XI/5^{a}/2021—new fisheries law mentions the creation of protected areas for cetaceans in important regions for migration and/or feeding). There is a clear need for action at national and regional levels to quantify the impact of human activities (especially by-catch and direct take) and to implement legislation and measures for the protection of cetaceans.

Cetacean research in the Gulf of Guinea has focused mostly around São Tomé waters and in coastal areas, with some research on Príncipe and none at all on Annobón. Broadening the survey area to include the islands of Príncipe and Annobón, and covering a wider temporal window, may provide important information on the level of population structure, habitat use, and seasonal dynamics of several cetacean species. In addition, extending the survey area to offshore waters will provide new information on the more oceanic species (Bryde's and Sperm Whales, for example) that are present in other regions of the Gulf of Guinea, and are expected to occur around the archipelago. Establishing the year-round monitoring of species composition, distribution, and abundance as well as identifying critical habitats for cetacean survival and its overlap with human activities (specially by-catch and direct takes) should be a priority for future research. This is especially important since whale catches and recent sightings indicate that the region may be important for several cetacean species (Picanço et al. 2009; Carvalho et al. 2011). For the implementation of long-term population monitoring, it will be essential to promote greater conservation efforts by involving local biologists and NGO technicians in training programs that include species identification, photography techniques, and collection of samples from stranded animals. Moreover, it is crucial to engage with the local population and fisheries communities by developing conservation campaigns and targeting different stakeholders. By allying consistent research and local awareness it will be possible to better understand and protect the cetaceans of this region.

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Appendix

Cetacean species confirmed for São Tomé and Príncipe. IUCN conservation status (IUCN 2021): data deficient (DD); least concern (LC); near threatened (NT); vulnerable (VU)

Higher taxonomy	Species	English name	IUCN
Family **Balaenopteridae**			
Megaptera Gray, 1846	*Megaptera novaeangliae* (Borowski, 1781)	Humpback Whale	LC
Family **Physeteridae**			
Physeter Linnaeus, 1758	*Physeter macrocephalus* (Linnaeus, 1758)	Sperm Whale	VU
Family **Kogiidae**			
Kogia Gray, 1846	*Kogia sima* (Owen, 1866)	Dwarf Sperm Whale	LC
Family **Delphinidae**			
Orcinus Fitzinger, 1860	*Orcinus orca* (Linnaeus, 1758)	Killer Whale	DD
Steno Gray, 1846	*Steno bredanensis* (Lesson, 1828)	Rough-toothed Dolphin	LC
Grampus Gray, 1828	*Grampus griseus* (Cuvier, 1812)	Risso’s Dolphin	LC
Pseudorca Reinhardt, 1862	*Pseudorca crassidens* (Owen, 1846)	False Killer Whale	NT
Feresa Gray, 1870	*Feresa attenuata* (Gray, 1874)	Pygmy Killer Whale	LC
Globicephala Lesson, 1828	*Globicephala macrorhynchus* (Gray, 1846)	Short-finned Pilot Whale	LC
Tursiops Gervais, 1855	*Tursiops truncatus* (Montagu, 1821)	Common Bottlenose Dolphin	LC
Stenella Gray, 1866	*Stenella attenuata* (Gray, 1846)	Pantropical Spotted Dolphin	LC
	Stenella coeruleoalba (Meyen, 1833)	Striped Dolphin	LC

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Chapter 24
Biodiversity Conservation in the Gulf of Guinea Oceanic Islands: Recent Progress, Ongoing Challenges, and Future Directions

Ricardo F. de Lima, Jean-Baptiste Deffontaines, Luísa Madruga, Estrela Matilde, Ana Nuno, and Sara Vieira

Abstract The biodiversity of the oceanic islands of the Gulf of Guinea is valued internationally for its uniqueness and locally for its contribution to human welfare, but it is under growing anthropogenic pressure. We provide an overview of recent progress, ongoing challenges, and future directions for terrestrial and marine conservation. The islands were colonized in the late fifteenth century and have since relied heavily on international markets. Nevertheless, the livelihoods of many islanders depend directly on local natural resources, and growing human populations

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and economies are intensifying the use of these resources, including timber, land, and fisheries. Here we summarize conservation initiatives on the islands, including pivotal projects and achievements, as well as the rise of civil society and governmental engagement. We also review species and site-based conservation priorities and highlight the need for continuous updating based on ongoing research. Engagement in conservation has increased steadily in recent decades but not fast enough to counteract the growth of anthropogenic pressure on biodiversity. Fostering capacity building, environmental awareness, and research is thus urgent to ensure a thriving future for the islands, able to reconcile economic development and biodiversity conservation.

Keywords Endemics · Nature–human interactions · Prioritization · Protected areas · Research · Threatened species

Introduction

The oceanic islands of the Gulf of Guinea (Príncipe, São Tomé, and Annobón) are widely recognized as global priorities for biodiversity conservation. Considering their small size, they have exceptionally high numbers of endemic and threatened species (Jones 1994). They are part of the "Guinean Forests of West Africa" biodiversity hotspot (Myers et al. 2000) and of the "Cameroon-Guinea" Centre of Plant Diversity (WWF and IUCN 1994). These islands also retain a high proportion of natural vegetation cover (WWF 2019) compared to other oceanic islands (e.g., Norder et al. 2020), having relatively large extents of well-preserved native vegetation across lowland, montane, and mist forests (Exell 1944). Among the islands, mist forests are exclusive to São Tomé and hold especially high numbers of endemic and threatened plant species (Dauby et al. 2022; Stévart et al. 2022). Being mountainous, the islands function as ecological and evolutionary refugia, offering a wide variety of stable environments whose climates are buffered by the ocean (Ceríaco et al. 2022a). Príncipe and São Tomé also have a few mangrove areas, which despite their small size provide important ecosystem services (Afonso et al. 2021; Cravo 2021). The islands are situated within one of the 18 global hotspots for marine conservation (Roberts et al. 2002) and the most important marine biodiversity hotspot of the "West African Coast" (Polidoro et al. 2017), which connects the eastern and western Atlantic marine faunas (Wirtz et al. 2007). Their marine environments include areas that are key for the life cycles of seabirds, marine megafauna (cetaceans, sea turtles, rays, and sharks), and large, commercially valuable, pelagic, migratory fish species.

Here, we provide an overview of terrestrial and marine conservation in the oceanic islands of the Gulf of Guinea. We start by describing the links between biodiversity and livelihoods on the islands, focusing on the direct dependence of people on natural resources, and on their unsustainable use, to understand current threats to biodiversity. Then, we provide a brief history of conservation initiatives on the islands, summarizing the history of conservation movements and providing an overview of species conservation statuses and of sites prioritized for conservation.

Finally, we highlight important lessons and ongoing challenges to define priorities for the future of conservation on these unique islands.

People and Biodiversity: Close Together on Small Islands

The oceanic islands of the Gulf of Guinea are thought to have been uninhabited until Portuguese sailors reached São Tomé on 21 December 1471, Príncipe on 17 January 1472, and Annobón on 1 January 1473 (Seibert 2016). European colonization of the islands started during the fifteenth century and focused on the slave trade and on exploiting cash crops, such as sugar cane, coffee, and cocoa (Eyzaguirre 1986). The peoples of the islands thus derive mostly from a mixture of African and European settlers (Hagemeijer and Rocha 2019; Almeida et al. 2021). The relatively recent colonization and economic reliance on intensive agriculture are reflected in the somewhat superficial connection to local nature when compared to other African cultures, and instead bear stronger similarity with other colonial-based cultures, such as those of many Caribbean islands (Eyzaguirre 1986). A connection with nature is nevertheless embedded in the traditions of islanders, namely in the cuisine (Gonçalves et al. 2014), medicine (Roseira 1984; Madureira et al. 2008), beliefs, and worldviews (Valverde 2000).

The human population is unevenly split between islands: Príncipe is 139 km^2 and has 8778 inhabitants (65/km^2), São Tomé is 857 km^2 and has 201,462 inhabitants (235/km^2—INESTP 2019), and Annobón is 17 km^2 and has 5314 inhabitants (313/km^2—INEGE 2018). The rugged terrain of the islands has meant that, up until today, most people live by the coast (Norder et al. 2020), benefiting from resources provided by both the ocean and the forest (e.g., Torres 2005; Pereira 2021). In addition, human activities are concentrated in the drier and flatter coasts in the north of the islands, whereas the mountainous south and center are still dominated by rainforest (Jones and Tye 2006). These contrasting landscapes provide ecosystem services that are key for human wellbeing in the islands, and that islanders recognize as essential: forests are important for pure air, water, foraged foods, medicinal plants, and tourism, while plantations are key for agriculture, livestock, and fruits (BirdLife International 2021a).

The economy of Annobón is mostly focused on services and relies on national income resulting from oil revenues (INEGE 2018), while that of Príncipe and São Tomé is heavily dependent on foreign aid and on export crops (INESTP 2019). All islands are heavily reliant on imports, even though internal markets and the subsistence of most islanders are strongly based on agriculture and other activities on the primary sector. Fisheries (Dias 2013), fuelwood and charcoal (Nuno 2021), and timber (do Espírito et al. 2020) are essential to meet basic needs, and thus natural resources are viewed as a primary source of protein, energy, and shelter that also create diverse job opportunities. Some natural resources might play a small role in subsistence overall, such as hunting (Carvalho et al. 2015a) and medicinal plants (Madureira et al. 2008), but their significance should not be overlooked, even if it is predominantly cultural. Economic and cultural importance ascribed to introduced species, some of which are invasive, also has relevant implications for conservation. For instance, the West African giant land snail, *Archachatina marginata* (Swainson, 1821), is an important source of protein and income, particularly among vulnerable social groups (Pereira 2021). More broadly, there is also a greater awareness of the economic benefits and uses of introduced species than of the endemic-rich native biodiversity, which might hinder willingness to adopt conservation measures (Carvalho et al. 2015b; Panisi et al. 2022).

Having an economy largely based on cash crops has been, and still is, the defining factor for the extent and severity of anthropogenic impacts on the environment. Historically, deforestation and other key components of human impacts on the islands have been decoupled from population size (Norder et al. 2020). This is because human populations on the islands are heavily reliant on external markets, producing agricultural goods to export and then importing much of what is consumed on the islands (Eyzaguirre 1986). Nevertheless, both the economy and the human population have been rapidly growing in recent times. These increases are most notable in São Tomé, which has rapidly been growing since the 2000s (Muñoz-Torrent et al. 2022) when malaria infections were greatly reduced (Lee et al. 2010). The impacts of this growth are noticeable in the depletion of many natural resources (Fig. 24.1), including timber (do Espírito et al. 2020), land conversion to agriculture (de Lima 2012; Soares 2017), quarry species (Carvalho 2015), and fisheries (Belhabib 2015; Maia et al. 2018; Nuno et al. 2021). The underlying effects of less direct anthropogenic impacts, such as introduced species and climate change remain largely unstudied (but see Brito 2013; Heleno et al. 2022).

Major threats to the conservation of terrestrial biodiversity identified by local stakeholders include tree logging, land-use changes derived mostly from agricultural pressure, hunting and collection of threatened and endemic species, invasive introduced species, and the development of macroprojects (BirdLife International 2019). These threats strongly coincide with those that had already been identified for the islands (Jones et al. 1991; Oyono et al. 2014; Ndang'ang'a et al. 2014a, b), and largely match the most salient factors threatening species globally: habitat loss and degradation; overexploitation; invasive species; pollution, and global climate change (Vié et al. 2009).

Less is known about threats in marine environments. The overexploitation of fisheries is certainly relevant: the Marine Trophic Index in São Tomé and Príncipe scored 14.5 in a 0–100 range (Wendling et al. 2020), indicating that species higher in the food web might have been fished out and that fishing is now targeting lower trophic levels. Fisheries in São Tomé and Príncipe consist of small-scale activities focused on the territorial sea, and of European-dominated industrial fleets that extract most of the volume of fish removed from the Exclusive Economic Zone (Porriños 2021). The evaluation of fish stocks and the control of fishing have been almost inexistent, even though fishing agreements with the European Union represent 40% of the non-fiscal revenues of the country and are meant to promote sustainable fishing (FAO 2019). Increased pressure on marine resources is leading to the use of destructive practices that maximize catch in the short-term, but that

Fig. 24.1 Examples of threats to the endemic-rich biodiversity of the oceanic islands of the Gulf of Guinea: (**1**) Fire and agriculture shape the landscape in the driest portions of northern São Tomé; (**2**, **3**) Small plots of horticulture around Bom Sucesso threaten the endemic-rich montane forests of São Tomé, encroaching on São Tomé Obô Natural Park; (**4**) Illegal selective logging is widespread on São Tomé; (**5**) Several introduced species, such as the Mona Monkey *Cercopithecus mona* (Schreber, 1774) threaten ecosystem function; (**6**) Charcoal production is widespread but particularly intensive in the drier north of São Tomé; (**7**) Hunting threatens several endemic birds, such as the Endangered Sao Tome green-pigeon *Treron sanctithomae* (Gmelin, 1789); (**8**) Longline fishing (baited hooks linked to short lines attached to a long main line) is a damaging practice that destroys the ocean floor and results in bycatch and discarded fishing gear. Photo credits: (**1–3**, **6**) Jean-Baptiste Deffontaines, (**4**, **5**) Ricardo F. de Lima, (**7**) Ricardo Rocha, (**8**) Luísa Madruga

threaten biodiversity, the livelihoods of coastal communities, and food security on the islands in the long term. The exploration of mineral resources in the oceans is increasingly a threat since large deposits of petroleum were found offshore in the 1990s. These are yet to be extracted but are already boosting the economy of the island (Frynas et al. 2003). Finally, there is also evidence that the waters around Annobón have been used to dump large quantities of toxic waste and that these activities have affected its marine life (Wood 2004).

Conservation Initiatives

Early in the twentieth century, several authors expressed concerns about the environmental implications of deforestation linked to the expansion of cocoa plantations on the islands, mentioning several actions to ensure the future of remaining forests, such as the protection of mountaintops (e.g., Campos 1908; Henriques 1917). These might be the first conservation safeguards known to take place on the islands. However, the collapse of the economy based on export crops (Eyzaguirre 1986), the focus of colonial scientific research on agricultural production, the poor local capacity and, later on, political instability linked to the post-independence period (Cruz 2014) meant that, for many decades biodiversity research was fairly limited (Ceríaco et al. 2022b). Only in the late 1980s, the first initiatives based on modern principles of conservation (Soulé 1985) started taking shape, following a few successful expeditions to the islands (Jones and Tye 1988; Jones et al. 1991; Atkinson et al. 1991).

In 1993, a workshop took place in Jersey (United Kingdom), bringing together several scientists to assess knowledge on the biodiversity of the Gulf of Guinea islands (including Bioko) and define priorities for future research and conservation action (Juste and Fa 1994). The Gulf of Guinea Conservation Group emerged from this meeting and was the umbrella under which many scientists visited the islands over the next two decades, in great part thanks to the efforts of Angus Gascoigne, who resided in São Tomé and facilitated links to local institutions (Melo 2012).

Also, in 1993, the European Commission started funding the ECOFAC program, aiming to promote the conservation and sustainable use of forest ecosystems in central Africa (Table 24.1). Besides promoting numerous studies, ECOFAC was fundamental to many of the conservation efforts that have since taken place in São Tomé and Príncipe (Fig. 24.2), such as the establishment of terrestrial protected areas and other environmental legislation, the creation of the Bom Sucesso Botanical Garden and São Tomé and Príncipe National Herbarium (STPH; NYBG 2021), and the training of many islanders and foreigners that still work toward conservation on the islands. The Global Environment Facility has been another key source of funding for conservation on the islands over the last two decades (Table 24.1). More recently, other sources of funding, such as the Critical Ecosystem Partnership Fund (CEPF 2021) or the Rufford Small Grants for Nature Conservation (The Rufford Foundation 2021) have allowed smaller projects to develop important

Table 24.1 Key conservation projects in São Tomé and Príncipe. The details of equivalent programs that have focused on Annobón are not known

Project	Period	Funding	Implementation	Description	Source
ECOFAC.1—Support the creation of the Obô Natural Park	1992–1997	783 k€ + Technical Assistance (European Commission)	AGRECO + CIRAD Forêt	Preparatory work for the designation of a protected area; research program—inventory & management-oriented, and evaluation of the area.	Muriel Vives (pers. comm.)
ECOFAC.2—Establish the management structure of the Obô Natural Park	1997–2001	645 k€ + Technical Assistance (European Commission)	AGRECO + BDPA-SCETAGRI + SECA + CIRAD Forêt + FFI	Protected Area Management Plan & Management Structure, including research & ecological monitoring, and institutional support to the forest	Muriel Vives (pers. comm.)
Programa Tatô	1998–ongoing	Currently c. 250 k€/year (USFWS + Oceanário de Lisboa + Tusk Conservation + FFEM + private sector)	Associação Programa Tatô + MARAPA (1998–2002: ECOFAC; 2002–2017: MARAPA)	Sea turtle conservation program in São Tomé Island	Betânia Ferreira-Airaud (pers. comm.); Associação Programa Tatô (2021)
GEF-2—Biodiversity Strategy, Action Plan and First National Report and Clearing House Mechanism	2000–2005	163 k$ (through The World Bank)	Department for the Environment	Enable the Government of São Tomé and Príncipe to develop a biodiversity strategy in compliance with CBD and to identify priority actions for biodiversity conservation and management	GEF (2021)
ECOFAC.3—Development of tourist activities and support for the promotion of sites	2001–2005	600 k€ + Technical Assistance (European Commission) + 250 k€ (AFD)	AGRECO + SECA + CIRAD Forêt	Development of ecotourism activities. Support to the Obô Natural Park. Botanical Garden. Scientific research for the conservation of marine turtles, gray parrots. Conservation measures to limit charcoal, sand extraction, etc.	Muriel Vives (pers. comm.)

(continued)

Table 24.1 (continued)

Project	Period	Funding	Implementation	Description	Source
ECOFAC.4—São Tomé and Príncipe Obô Natural parks	2007–2010	595 k€ (European Commission)	BRL Ingenieurie + GFA Consulting Group + DFS	Natural Parks (São Tomé Obô natural Park, Príncipe Natural Park), and respective buffer zones management	David Bruguière (pers. comm.)
GEF-5—Integrated ecosystem approach to biodiversity mainstreaming and conservation in the Buffer Zones	2011–2017	2.4 M$ (through IFAD)	Directorate of Environment + Directorate of Agriculture and Rural Development	Rehabilitate degraded ecosystems in STP to provide ecosystem services and habitat for endemic species of flora and fauna of global importance	GEF (2021)
ECOFAC.5—Strengthen eco-tourism around São Tomé Obô Natural Park	2012–2015	200 k€ (European Commission)	ONG Alisei + MARAPA	Strengthen the co-management of the conservation systems of the Obô Natural Park and its periphery, particularly around the Malanza and Jalé mangroves	Bastien Loloum (pers. comm.)
Protetuga	2015–ongoing	Currently c. 150 k€ / year (OAK Foundation, Kosmos, HBD, Rufford, USFWS, YWPF, CEPF)	Fundação Príncipe	Sea turtle conservation program in Príncipe Island	Estrela Matilde (pers. comm.); Fundação Príncipe (2021a)
Omali Vida Nón 1—Improving Marine Biodiversity and Livelihood of coastal communities in Príncipe	2016–2019	295 k£ (Darwin Initiative)	University of Exeter + Fundação Príncipe	Improved food security, increased gender equality, and poverty reduction in coastal communities in Príncipe, through a social-ecological approach to enhance marine resource management and diversify livelihood opportunities	Darwin Initiative (2021); Fundação Príncipe (2021d)

Kike da Mungu 1—Sustainable co-management of fisheries in the south of São Tomé Island	2017–2020	581 k€ (European Union + Instituto Camões)	Oikos + MARAPA	Contribute to sustainable fisheries, conservation of marine biodiversity, and food security for the Santomean population	Oikos and MARAPA (2021)
ECOFAC.6—São Tomé and Príncipe Obô Natural Parks	2018–2022	2 M€ (European Commission)	BirdLife International + Oikos + RSPB + SPEA+ Plataforma de Turismo Responsável e Sustentável	Natural Parks (São Tomé Obô natural Park, Príncipe Natural Park), and respective buffer zones, through landscape approaches	EC (2021); ECOFAC6 (2021)
Blue Action Fund—Establishing a network of marine protected areas across São Tomé and Príncipe through a co-management approach	2018–2023	2.59 M€ (Blue Action Fund + Arcadia Fund)	Fauna & Flora International + Oikos + Fundação Príncipe + MARAPA	Support the designation of the first co-managed Marine Protected Areas across São Tomé and Príncipe	BAF (2018); Fundação Príncipe (2021d); Oikos and MARAPA (2021)
Taking action for Príncipe's threatened trees	2019–2022	104 K£ (Global Trees Campaign)	Missouri Botanical Garden, Herbarium of Université Libre de Bruxelles, University of Coimbra, FFI, Fundação Príncipe, Institut de Recherche pour le Développement	Generate data and build local capacity for research and conservation through field surveys, monitoring and threat assessment for three threatened tree species	Estrela Matilde (pers. comm.)
Action for sustainable landscape management in São Tomé and Príncipe	2021–2024	2.32 M€ (European Union)	Oikos + BirdLife International + Zatona-ADIL	Improve the use of natural resources through integrated landscape management, for sustainable access to food, wealth, and the preservation of the Obô Natural Park and São Tomé High Conservation Value forests	EU (2021)

(continued)

Table 24.1 (continued)

Project	Period	Funding	Implementation	Description	Source
GEF-6—Enhancing Biodiversity Conservation and Sustainable Land and Natural Resource Management	2021–2025	4.28 M$ (through UNDP)	General Directorate for the Environment	Safeguard globally significant terrestrial biodiversity and ecosystems services by strengthening national capacities and frameworks for biodiversity and natural resource management (. . .)	GEF (2021)
GEF-7—Improving biodiversity mainstreaming in the agro-forestry and fishery sectors in São Tomé and Príncipe	Concept approved	3.55 M$ (through IFAD)	Ministry of Agriculture, Fisheries, and Rural Development	Mainstream biodiversity conservation (. . .) to minimize the negative impacts of the agro-forestry and fishery sector development while enhancing the contribution of ecosystem services to livelihoods in São Tomé and Príncipe	GEF (2021)

Fig. 24.2 Examples of conservation initiatives that have been taking place in the oceanic islands of the Gulf of Guinea: (**1**) Sign marking the boundary of the São Tomé Obô Natural Park; (**2**) Small trees being distributed in a school in the buffer zone of the São Tomé Obô Natural Park; (**3**) An Obô guardian surveying the forests of São Tomé; (**4**) The orchidarium at the Bom Sucesso Botanical Garden in São Tomé; (**5**) Sea turtle hatcheries are used to protect nests at risk from feral animal predation, poaching and beach erosion in São Tomé and Príncipe; (**6**) Inspection of illegal logging activities in a forest in Príncipe; (**7**) Freshwater macroinvertebrates surveys in Rio Papagaio, Príncipe; (**8**) Young parabotanist surveying tree diversity in Príncipe. Photo credits: (**1**) Ricardo F. de Lima, (**2**) Raphaela Nazaré, (**3**, **4**, **6**) Jean-Baptiste Deffontaines, (**5**) Maria Branco, (**7**, **8**) Vasco Pissarra | Fundação Príncipe

complementary tools for conservation. Previous phases of ECOFAC have also covered Equatorial Guinea, where it coincided with the EU-funded project of Conservation and Rational Use of Forest Ecosystems (Conservación y Utilización Racional de los Ecosistemas Forestales—CUREF 1996–2001), aiming to describe ecosystems, to promote sustainable use of natural resources, and to create a network of protected areas (García and Eneme 1997, Angela Formia *pers. comm.*). However, it is unclear how these have contributed to creating the Annobón Nature Reserve or any other conservation initiative on the island.

Since 2016, there has been a noticeable and much needed increased investment in coastal and marine conservation, focusing on sustainable fisheries through engagement with coastal fishing communities (Table 24.1), namely through the *Omali vida nón* project in Príncipe (Nuno 2019; FFI et al. 2021; Fundação Príncipe 2021d), and the *Kike da mungu* project in São Tomé (Oikos and MARAPA 2021). Building on these, since late 2018, Fauna & Flora International, in close collaboration with the government authorities, has partnered with Fundação Príncipe, Oikos, and MARAPA to establish a network of co-managed marine protected areas across São Tomé and Príncipe (BAF 2018). There have been significant efforts for the conservation of sea turtles on both of these islands (Associação Programa Tatô 2021; Fundação Príncipe 2021a; Ferreira-Airaud et al. 2022). There has also been some research on cetaceans in São Tomé (MARAPA 2021b), and in June 2021 a project has been approved to study the little known but highly threatened shark populations of São Tomé and Príncipe (NGANDU 2021).

Parallel to increased funding, civil society awareness toward conservation has also greatly increased over the past few decades, which is clearly reflected in the number and impact of local environmental non-governmental organizations (Ayres et al. 2022). MARAPA has been active in marine conservation initiatives for São Tomé Island, promoting sustainable fisheries and environmental education since its creation in 1999 (MARAPA 2021a). Associação Monte Pico emerged in 2006 from a group of Santomeans trained by ECOFAC; it has been working for sustainable ecotourism and rurality, and supporting scientific research and the management of protected areas (Associação Monte Pico 2021). Founded in 2015, Fundação Príncipe focuses on marine and terrestrial biodiversity conservation and the socio-economic development of Príncipe Island, in close partnership with regional authorities and communities (Fundação Príncipe 2021b). Since 2017, Rede.Bio has brought together seven environmental NGOs from São Tomé and Príncipe to promote integrated and sustainable development based on the protection and valorization of the natural heritage of the country, namely by reinforcing the participation of civil society in environmental governance (Rede.Bio 2021). Most recently, on October 16, 2020, the Gulf of Guinea Biodiversity Center had its inaugural meeting, bringing together national and international scientists and conservationists in an initiative that aims to facilitate research, education, and conservation of the unique diversity of the plants and animals of the islands (GGBC 2021).

Several international environmental organizations have also increased their presence in São Tomé and Príncipe. BirdLife International has had a long-term interest in these islands and has been increasing its presence especially since 2012, working with park authorities and other governmental institutions, and with communities to promote research, conservation, and empowerment. In 2018, BirdLife opened an office in country (BirdLife International 2021d). Fauna & Flora International has been working closely with Fundação Príncipe since its inception in 2015, to build conservation capacity, conduct research, raise environmental awareness, and diversify the livelihoods of communities on Príncipe (FFI 2021). Oikos—Cooperação e Desenvolvimento has had a growing presence in São Tomé and Príncipe since 2015, working toward the rational use of natural resources and enhanced livelihood in communities (Oikos 2021). In 2018, the international NGO Associação Programa Tatô was created to continue the work on marine conservation focusing on sea turtles that had been initiated by ECOFAC and MARAPA on São Tomé (Associação Programa Tatô 2021).

Little is known about conservation initiatives on Annobón, besides a few small conservation projects led by the national NGO Amigos de Natureleza y Desarollo de Guinea Ecuatorial (ANDEGE).

Over the last few decades, the São Tomé and Príncipe and Equatorial Guinea governments have also shown a strong national and international commitment to developing policies aiming to ensure the conservation of biodiversity (Appendix). In São Tomé and Príncipe, environmental responsibilities are split between the General Directorate for the Environment (part of the Ministry of Infrastructures, Natural Resources and Environment), the Fisheries Directorate, and the Forest and Biodiversity Directorate (both part of the Ministry for Agriculture, Fisheries and Rural Development). Príncipe is an autonomous region that has its own Regional Government, where environmental responsibilities are also split but following a distinct organization. This complex administrative structure, which often changes when a new government takes power, hinders progress and post-project sustainability of conservation initiatives. In Equatorial Guinea, the National Institute for Forestry Development and Protected Areas Management (INDEFOR-AP) from the Ministry of Agriculture and Forests has developed a national network of protected areas and is responsible for environmental and wildlife conservation but little is known about the local government structure in the province of Annobón.

Threatened Species

The oceanic islands of the Gulf of Guinea hold several hundred endemic species, a number that will certainly increase as new endemics are still being described every year, even among the best-known taxonomic groups (de Lima 2016). Many of the endemic species are at risk of extinction and only terrestrial vertebrate species have been thoroughly evaluated (IUCN 2021). Out of 67 endemic species of terrestrial vertebrates, 58 have been assessed, and 18 are threatened. These include 11 birds (Melo et al. 2022), three mammals (Rainho et al. 2022), one reptile (Ceríaco et al. 2022c), and three amphibians (Bell et al. 2022). Of these species, four are Critically Endangered, ten are Endangered, and four are Vulnerable. Among terrestrial vertebrates, there are also seven Data Deficient, seven Near Threatened, and nine species that are not recognized or have not been assessed. Finally, both Príncipe and São Tomé have populations of the non-endemic Endangered Gray Parrot *Erithacus psittacus* Linnaeus, 1758.

Scientific research in coastal and marine environments is still scarce and mostly dedicated to studies of ichthyofauna. Fishes are the only non-terrestrial vertebrate group with endemic species (but see Flood et al. 2019). Out of 15 endemic species (Costa et al. 2022), only eight have been assessed (IUCN 2021): three Vulnerable and five Data Deficient. There are also large numbers of non-endemic fish species that are threatened including 6 Critically Endangered (all cartilaginous fishes), 15 Endangered (only two bony fishes), and 28 Vulnerable species (of which 16 are bony fishes). Additionally, 58 species are Data Deficient (all bony fishes) and nine are Near Threatened (including three cartilaginous fishes). The remaining threatened marine vertebrates are the Critically Endangered Hawksbill Turtle *Eretmochelys imbricata* (Linnaeus, 1766), the Endangered Green Turtle *Chelonia mydas* (Linnaeus, 1758), the Vulnerable Sperm Whale *Physeter macrocephalus* Linnaeus, 1758, and three Vulnerable sea turtle species (Ferreira-Airaud et al. 2022). Additionally, there are also the Data Deficient Killer Whale *Orcinus orca* (Linnaeus, 1758), the Near Threatened False Killer Whale *Pseudorca crassidens* (Owen, 1846), and ten Least Concern cetacean species (Carvalho et al. 2022).

Very few endemic terrestrial invertebrates have been assessed by the IUCN: four mollusks, two crabs, one butterfly, and one dragonfly species, of which half are Data Deficient, two Near Threatened, one Least Concern, and only the Vulnerable Búzio-d'Obô *Archachatina bicarinata* (Bruguiere, 1792) is classified as threatened. Among the endemic marine invertebrates, only 23 species of mollusks have been assessed, all of which are Data Deficient, apart from the Vulnerable *Haliotis geigeri* Owen, 2014.

Among plants, 272 species have been assessed (IUCN 2021) out of a total that should exceed 1700 species (Garcia et al. 2022; Stévart et al. 2022). Out of almost 200 endemic plant species, only 49 have been assessed. These include two Extinct, two Critically Endangered, 14 Endangered, 22 Vulnerable, and 7 Near Threatened. Additionally, there are seven Endangered, 11 Vulnerable, 6 Near Threatened, and 1 Data Deficient plant species that are not endemic. Considering ongoing work, especially focusing on describing and red-listing seed plant species (Fundação Príncipe et al. 2021), it is evident that these numbers will greatly increase soon (Stévart et al. 2022). The situation is even more dire when it comes to fungi, a group for which Red List evaluations are scarce, with none of the species of the oceanic islands of the Gulf of Guinea assessed so far (Desjardin and Perry 2022).

In 2004, amphibians, mammals, and birds were fully assessed for the first time (IUCN 2021). At that point, there were 38 recognized endemic species in these taxonomic groups, of which there were 14 threatened species (five Critically Endangered, three Endangered, and six Vulnerable), compared to the current 17 threatened species (four Critically Endangered, nine Endangered, and four Vulnerable) out of 45 recognized endemics. These trends reflect mostly an improvement of knowledge, showing that even among some of the best-studied groups there have been major changes not only in the Red List status but also in taxonomy. The high numbers of species that are still being described, that have not yet been assessed, or that remain Data Deficient attest to the urgent need for future work in the region. There has been an attempt to list species at the national level in São Tomé and Príncipe (Gascoigne 1995), but in recent years all assessments have been directly linked to the IUCN Red List because most species of interest are endemic, and therefore national assessments are also global.

In addition to the IUCN Red List, there are other tools to define priorities for species conservation. The EDGE of Existence is an example that combines the IUCN Red List status with the amount of unique evolutionary history represented by species of terrestrial vertebrates, cartilaginous fishes, and corals (EDGE 2021). This program has identified 31 species on the islands, including 16 cartilaginous fishes, one amphibian, three sea turtles, one cetacean, and ten birds as high priority. The Critically Endangered Dwarf Olive Ibis *Bostrychia bocagei* (Chapin, 1923), and the Endangered Newton's Grassland Frog *Ptychadena newtoni* (Bocage, 1886) ranked the highest among terrestrial species, while the Critically Endangered Hawksbill Turtle and the Endangered Whale Shark *Rhincodon typus* Smith, 1828 ranked the highest in the ocean.

After identifying priority species for conservation, it is also essential to define strategies for conservation action. In these islands, so far only the Critically Endangered birds (Ndang'ang'a et al. 2014a, b—currently under review, Fundação Príncipe 2021c) and the Vulnerable Búzio-d'Obô (Panisi et al. 2020) have Species Action Plans dedicated to defining priority activities for conservation, further highlighting the long road ahead toward defining conservation priorities and implementing effective conservation action.

Site-Based Conservation

Several assessments have identified areas of global conservation relevance in the oceanic islands of the Gulf of Guinea (Fig. 24.3). The islands include three Alliance for Zero Extinction sites: "Príncipe Forests" (5712 ha), "Sao Tome Uplands" (28,660 ha), and "São Tomé Lowland Forests" (21,833 ha—AZE 2019). These largely coincide with Key Biodiversity Areas ("Príncipe Forests": 5708 ha; "São Tomé Montane and Cloud-forests": 4839 ha; and "São Tomé Lowland Forests": 21,832 ha—currently under review), of which there are five more on the islands: "Annobón" (2891 ha), "Tinhosas Islands" (18 ha), "São Tomé Northern Savannas" (526 ha), "Parque Natural Obô de São Tomé e Zona Tampão" (45,132 ha), and "Zona Ecológica dos Mangais do Rio Malanza" (231 ha—BirdLife International 2021c). The Tinhosas are a Ramsar site, due to their important seabird colony, as is the whole island of Annobón and surrounding waters (230 km^2), mostly due to the threatened species and ecological assemblages it supports (Ramsar 2021). As part of the "Congolian Coastal Forests," the "São Tomé, Príncipe and Annobón moist lowland forests" (WWF 2019) are listed as Critical or Endangered Terrestrial

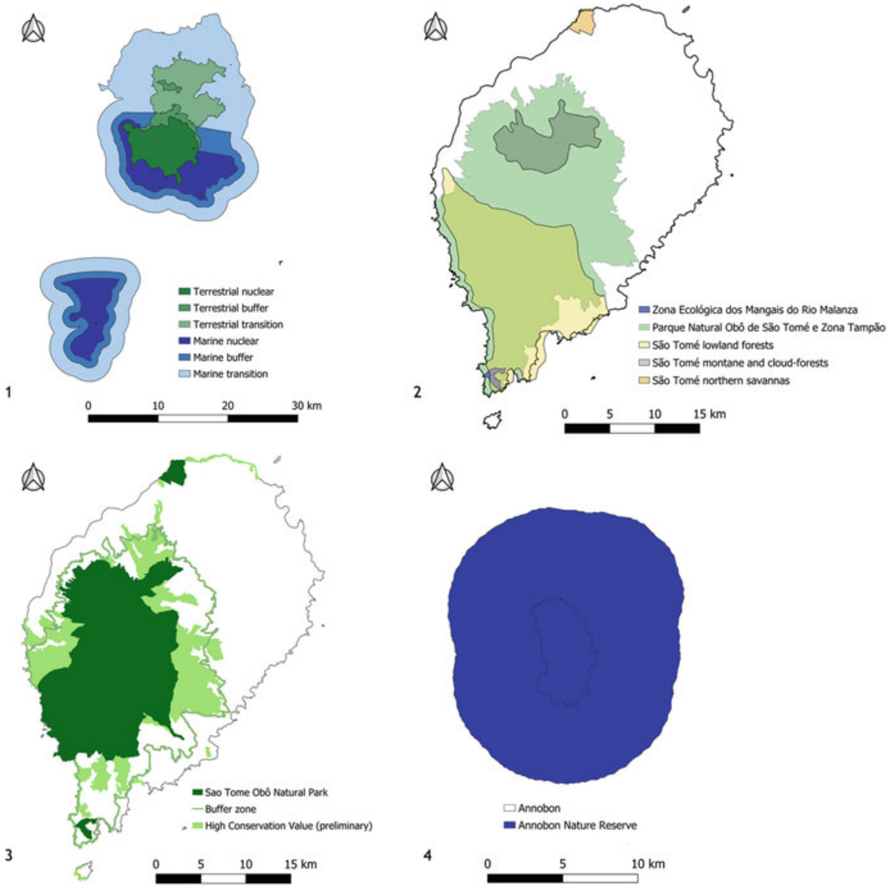

Fig. 24.3 Map of sites prioritized for conservation in the oceanic islands of the Gulf of Guinea: (**1**) Príncipe Biosphere Reserve (UNESCO 2021); (**2**) São Tomé Key Biodiversity Areas (BirdLife International 2021c); (**3**) São Tomé Obô Natural Park, buffer zone and preliminary High Conservation Value areas (BirdLife International et al. 2020; UNEP-WCMC and IUCN 2021); (**4**) Annobón Nature Reserve (UNEP-WCMC and IUCN 2021). The nuclear terrestrial area of the Príncipe Biosphere Reserve corresponds to the Príncipe Natural Park, and the buffer corresponds to the buffer of the Natural Park. To the southwest of Príncipe Island, the marine protected areas demarcated around the Tinhosas Islets are a Ramsar site and a Key Biodiversity Area. The boundaries of the São Tomé lowland forests Key Biodiversity Area are not aligned with the contour of the island and will be revised in the ongoing national reassessment of Key Biodiversity Areas

Ecoregions of the World (Olson and Dinerstein 2002) and have been identified among the most important ecoregion for the conservation of forest-dependent birds worldwide (Buchanan et al. 2011). Due to the unique assemblage of bird species, each of the main islands is a separate Endemic Bird Area, and they rank on the three highest priority categories of this assessment: São Tomé is critical, Príncipe is urgent, and Annobón is high (Stattersfield et al. 1998; BirdLife International

2021b). Since 2012, Príncipe has been recognized as a UNESCO Biosphere Reserve that includes the Tinhosas, all other islets around the main island, and 576 km^2 of surrounding marine environment (UNESCO 2021).

As a result of its rich and productive marine life, the region has three Ecologically or Biologically Significant Marine Areas: "Tinhosas Islands," "Lagoa Azul and Praia das Conchas," and the "Equatorial Tuna Production Zone" (CBD 2021).

At the national level, each island has one protected area: the Annobón Natural Reserve, created in 2000 includes the whole island and surrounding marine environments (230 km^2), the São Tomé Obô Natural Park (252 km^2), and the Príncipe Obô Natural Park (45 km^2), both created in 2006, the latter also including a strip of coastal ecosystems (Fig. 24.3, Appendix—UNEP-WCMC and IUCN 2021). The last two cover the wettest and most rugged portions of each island, where the best-preserved forests remain and are critical for the survival of many endemic species, especially the most threatened (e.g., de Lima et al. 2017; Soares 2017; Fundação Príncipe 2019; Soares et al. 2022). Taken together, they were assessed as the 32nd most important protected area in the world for the conservation of mammals, birds, and amphibians, the 17th if only threatened species are considered, and the 2nd *ex aequo* if only threatened bird species are counted (Le Saout et al. 2013). Unfortunately, despite having management plans (Albuquerque and Carvalho 2015a–d—currently under review) and receiving significant funding (Table 24.1), the effective implementation and success of both parks is lacking, largely due to a lack of stable and reliable sources of funding (BirdLife International 2019). A sustainable finance plan for protected areas and biodiversity is currently assessing best-revenue options, while several initiatives are already promoting implementation (Natural Strategies 2021). In São Tomé and Príncipe, the first efforts to create marine protected areas are only now taking place (Table 24.1—FFI et al. 2021).

There have been several national initiatives in recent years aimed at identifying additional areas that are relevant for conservation, beyond the strict concept of protected areas (Fig. 24.3). The laws that created both Obô Natural Parks (Appendix) envisaged the existence of a buffer zone, which would extend at least 250 m around the park boundaries, whenever possible, to work as a transition zone that would minimize the impact of human activities in the core protection area. These buffer zones are widely recognized and have received international funding (Table 24.1), but their boundaries and regulations were never clearly defined, and seem to have limited success at minimizing human impacts (Ward-Francis et al. 2017). Since 2018, BirdLife International has been leading the identification of High Conservation Values areas in São Tomé terrestrial and coastal ecosystems (BirdLife International et al. 2020), an initiative that is now being extended to Príncipe (D'Avis 2022). Since 2016, the Ministry of Infrastructures, Environment and Natural Resources of São Tomé and Príncipe, funded by the African Development Fund (Table 24.1) has been working on a national land planning initiative, which has identified large extents around the protected areas on each island as Conservation Areas (MIRNASTP 2021).

These initiatives should be continuously revised, since current knowledge on the distribution of biodiversity is still limited (Dauby et al. 2022; Soares et al. 2022). Ideally, these should be mostly based on the prioritization of ecosystem types to ensure that the best-preserved and most unique components of biodiversity are maintained. So far, the typification of ecosystems on the islands is not yet well established (Dauby et al. 2022). Areas at higher altitudes harbor endemic-rich and threatened ecosystems, even though biased sampling has limited our understanding of patterns along the altitudinal gradient (Stévart et al. 2022). The characterization and distribution of spatially restricted ecosystems, such as wetlands and coastal or rupicolous forests, constitutes a particularly pertinent challenge, since these hold specific plant associations (Diniz and Matos 2002; Dauby et al. 2022) and have unique ecologies that ensure key ecosystem services (e.g., Afonso et al. 2021) and thus deserve targeted conservation action. The peculiar palustrine system of Lagoa Amélia in São Tomé is one such example, holding several species that have highly restricted ranges (e.g., Stévart and Oliveira 2000) and the source of the springs that feed all main rivers in the north of the island. In this regard, the newly developed IUCN Red List for Ecosystems (Keith et al. 2015) might prove an invaluable tool.

Concluding Remarks

Príncipe, São Tomé, and Annobón are widely recognized as global priorities for biodiversity conservation, mostly due to their extraordinary number of endemic species. The value of their biodiversity is also promptly acknowledged by the islanders for the valuable services they provide and is engrained in the local culture. Nevertheless, the fast-growing population and economy, heavily reliant on the exploitation of natural resources, are threatening the long-term persistence of this precious natural heritage. Knowledge, awareness, attitudes, and investment in the conservation of the endemic-rich biodiversity of the islands have improved in recent decades but not fast enough to counteract the growth of anthropogenic pressure on natural resources. Remoteness and insularity, a colonial past and conflicting land tenure structures since independence, inadequate legal frameworks, weak institutional capacity to monitor and enforce laws, social inequity, and poor governance, all contribute to the environmental deregulation that threatens the biodiversity of the islands. While natural resources, like forests and fisheries are state-controlled in theory, high rates of non-compliance mean that these are de facto open access.

Although our knowledge of the biodiversity of the islands is still very incomplete, key priorities for conservation are mostly clear and should be the focus of future conservation activities. The exceptions are marine environments and Annobón, where biodiversity remains particularly understudied. Current knowledge must be used to expand the network of protected areas in marine and terrestrial environments, and to ensure effective protection of the best-preserved and keystone ecosystems.

Likewise, management mechanisms that enhance the role of biodiversity for development, for instance through ecotourism, sustainable extraction of forest products, or payment for ecosystem services should be implemented. More broadly, biodiversity-friendly practices and alternative livelihoods should be mainstreamed into the economic and social development of communities to reduce pressure on natural resources by maintaining diverse agroforests, promoting sustainable levels of resource exploitation (e.g., fisheries, hunting, or timber logging), or even enhancing the biodiversity value of sites through business-based restoration mechanisms. More specific activities might also be necessary and highly beneficial for sensitive species or ecosystems, as is the case of restoring degraded wetlands, protecting sea turtle breeding sites, controlling invasive species, or even promoting conservation ex situ of highly threatened species.

There have also been an increasing number of initiatives aiming to improve environmental awareness on the islands (Ayres et al. 2022), which is vital to boost public support and locally-led initiatives, ultimately contributing toward more robust conservation. In addition, making biodiversity information more accessible (e.g., GBIF 2021) will strengthen local capacity and engagement in conservation. All these actions would benefit from continued research, but enough is already known to make biodiversity conservation a political priority and to improve conservation management.

The success of conservation on the islands will ultimately rely on public support, therefore it is pivotal to continue listening, informing, training, and engaging island inhabitants and institutions, to ensure that conservation projects are inclusive. Much has already been done in this regard, and conservation initiatives are increasingly moving toward integrating local needs and sensibilities, particularly through enhanced investment in in-country leadership for successful conservation. Nevertheless, there is still a difficult road ahead, as it is not always straightforward to balance biodiversity conservation with human needs to find truly sustainable development models. Reaching economic development and conservation goals must center on empowerment and equity, while considering trade-offs in a transparent and participatory approach. Only by promoting the involvement of diverse stakeholders working toward a shared vision, and through the co-development of integrative strategies, will we be able to ensure a thriving future for the unique biodiversity and human inhabitants of the islands.

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Appendix: International Agreements and National Legislation and Strategies Relevant to Biodiversity Conservation

International agreements adhered to by the Democratic Republic of São Tomé and Príncipe (STP) and the Republic of Equatorial Guinea (EG):

- Framework Convention on Climate Change (1992 – STP; 2000 – EG)
- Convention on International Trade in Endangered Species of Wild Fauna and Flora (1992 – EG; 2001 – STP)
- Convention to Combat Desertification (1994 – EG; 1995 – STP)
- Convention on Biological Diversity (1995 – EG; 1998 – STP)
- Kyoto Protocol (2000 – EG; 2008 – STP)
- Bonn Convention on the Conservation of Migratory Species of Wild Animals (2001 – STP; 2010 – EG)
- Ramsar Convention on Wetlands of International Importance Especially as Waterfowl Habitat (2003 – EG; 2006 – STP)
- Convention concerning the Protection of the World Cultural and Natural Heritage (2006 – STP; 2010 – EG)
- Agreement on Port State Measures to Prevent, Deter and Eliminate Illegal, Unreported and Unregulated Fishing (2016—STP)
- Nagoya Protocol on Access and Benefit Sharing (2017 – STP)

Biodiversity conservation legislation—STP (Carvalho and Baía 2012):

- Law 10/99 – Basic Law for the Environment
- Law 11/99—Conservation of Fauna, Flora and Protected Areas
- Decree-Law 37/99—Environmental Impact Assessment Process
- Law 5/01—Forests
- Law 9/11—Fisheries and Fishery Resources (currently under revision)
- Law 6/06—São Tomé Obô Natural Park
- Law 7/06—Príncipe Obô Natural Park
- Regional Decree 3/09—Protection and Conservation of Sea Turtles
- Decree Law 6/14—Capture and commercialization of sea turtles and their products
- Decree Law 1/16—Hunting regulation

Biodiversity conservation legislation—EG (Osono et al. 2015):

- Law 8/88—Wild Fauna, Hunting, and Protected Areas
- Law 1/97—Forest Use and Management
- Law 1/00—Taxation on timber exports
- Law 4/00—Protected Areas
- Law 7/03—Environment
- Law 10/03—Fishing
- Law 3/07—Water and Coasts
- Law 4/09—Land tenure

- Decree Law 130/04—Fishing
- Decree Law 171/05—Biodiversity Conservation National Strategy and Action Plan
- Decree Law 172/05—Trade of wild threatened species of flora and fauna
- Decree Law 173/05—Environmental inspection
- Decree Law 61/07—Timber exportation
- Decree Law 72/07—Primate hunting, selling, consumption, and ownership
- Decree 60/02—National Institute for Forest Development and Management of the National Protected Area Network

National strategies for biodiversity conservation—STP:

- National Environmental Plan for Sustainable Development (RDSTP 1998)
- Strategic Plan for Tourism Development (UNDP 2001)
- National Forest Development Plan (Salgueiro and Carvalho 2001; Carvalho et al. 2017)
- National Action Plan for Climate Change Adaptation (NAPA 2006)
- Fisheries Master Plan (MAPDRSTP 2010)
- Strategy and National Action Plan for Developing the Sector of Non-Timber Forest Products (Bonfim et al. 2016)
- Multisectoral Investment Plan to Integrate Climate Change Resilience and the Risk of Catastrophes in Coastal Management (Carrasco et al. 2017)
- National Land Use Plan (MIRNASTP 2021)
- Sustainable Development Plan for the Autonomous Region of Príncipe: Príncipe 2030 (UNDP 2019)
- National Plan for Forest and Landscape Restoration (António et al. 2021)

National strategies for biodiversity conservation—EG (Osono et al. 2015):

- 2020 National Plan for Economic and Social Development
- National Plan for Environmental Management
- Biodiversity Conservation National Strategy and Action Plan
- National Land Use Plan
- National Protected Area Network
- National Forest Policy Plan
- National Climate Change Adaptation Plan
- National Action Plan for Coastal and Marine Ecosystems
- National Hydrological Plan
- National Education Plan

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Chapter 25

Environmental Education in São Tomé and Príncipe: The Challenges of Owning a Unique Biodiversity

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Abstract The islands of São Tomé and Príncipe host extraordinary biodiversity that evolved over millions of years without human presence. In the fifteenth century, the colonization of the islands created a society of migrants, associated with extensive land-use change and generally low knowledge and stewardship of autochthonous biodiversity. Formal education became widely accessible after the country's independence but the curriculum has never been aligned with the natural heritage of the islands. Informal environmental education started in the 1990s alongside the pioneer conservation initiatives involving the scientific community. In the last decade, these efforts have multiplied, in line with the need to engage and involve local actors to promote stewardship and ensure the success of conservation efforts. Some changes were made recently at a formal level with the inclusion of environmental education

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curricula and new manuals. In addition, several initiatives and improvements are being developed in the private education sector. However, limited access to resources for educators reduces motivation and capacity to implement longer-term improvements. Most environmental education activities are still promoted by NGOs and mainly focus on endemic or threatened species and target school-age audiences. Other initiatives focusing on specific demographic groups have provided interesting results but are more intermittent and their impacts have largely not yet been evaluated. Improving formal assessments for current and future projects to assess impacts and refine future approaches will be essential moving forward. In addition, ensuring the involvement of local actors, coordination between different initiatives, and the use of diversified approaches will ensure that environmental education engages the widest possible audiences.

Keywords Civil society · Environmental education curriculum · Formal education · Gulf of Guinea · Informal education · Oceanic islands

Brief Historical Background of Environmental Education in São Tomé and Príncipe

How the Landscape and History Shaped Environmental Education

Príncipe, São Tomé, and Annobón are remote oceanic islands with a unique and understudied biodiversity, which evolved over millions of years without human interaction. We were unable to find information about local perspectives on environmental education for Annobón and thus, here we will solely focus on São Tomé and Príncipe.

When the Portuguese discovered São Tomé and Príncipe in 1470, the islands were uninhabited. The human population of the islands was mostly brought from other parts of Africa, and, to a lesser extent, from Europe, in two main colonization periods. The first was associated with the slave trade and the second with contracted labor for the coffee and cocoa plantations (Seibert 2015). The islands have a history of extensive plantation agriculture that is closely related to the degradation of vast areas of forest in São Tomé and Príncipe and possibly with the extinction of endemic species before they were formally described to science. Early scientific studies to describe the biodiversity of São Tomé and Príncipe were conducted by European naturalists during the nineteenth and early twentieth centuries (Ceríaco et al. 2022).

The natural ecosystems of the islands, nowadays recognized for the uniqueness of their species, were poorly known and of little use for the newly established human population. The local plants and animals were unfamiliar and few edible plants and animals from the native forest were known or used (e.g., Seibert 2015). Thus, land-use change was promoted with the introduction of species and the conversion of the native ecosystems to agricultural land with introduced plants and animals that could be exploited. Some of the native ecosystems endured, due to their remoteness and difficulty of access, and the biodiversity within remained largely unknown to most people living on the islands.

Santomeans had limited access to primary education before independence and opportunities were divided between a nearly-formal setting in the plantations, which provided basic education to the workers' children, and an informal setting called "bush school" ("escola do mato"), which took place in villages without any official context or support (Amado 2018). Secondary school only appeared in the mid twentieth century, first with a private status and later open to the wider public, but still restricted to just one school. Education was fully structured according to the norms of the hierarchical and centralized colonial administrative model. It was designed to impose civilizational standards and the European culture on students, disregarding and discriminating against the "sons of the land" and their culture (Amado 2021).

From Independence to Strategic Environmental Education Options

After centuries of colonialism, São Tomé and Príncipe achieved independence on July 12, 1975, inheriting an educational system marked by low literacy, only one post-primary school, and the absence of professional education (Barreto 2012). During the first phase of the post-independence period, called "First Republic" (also known as "Single Party Period"), from 1975 to 1990, the government made education a priority with mass literacy one of its main objectives (Cardoso 2004). In the year of independence, the illiteracy rate was 80%. Fifteen years later, it fell to 30% (MECF 2012). Today, São Tomé and Príncipe report that 92.8% (2018) of the population over 15 years old is literate, representing the best index among African countries in which Portuguese is the official language (UNESCO 2021). Despite important progress, illiteracy remains a problem, especially in some areas of the country, such as the southern and northern regions of São Tomé Island, affecting mostly the female portion of the rural population. The Santomean government has set the goal of eradicating illiteracy by 2022 (MECF 2012).

The democratic reforms and the opening of the country in the late 1980s marked the start of the "Second Republic" ("Multiparty Democracy"), bringing important interventions with the aim to establish a better framework for education. The institution of democracy gradually created opportunities for the national curriculum to become more open to incorporate the pedagogical innovations and guidelines coming from international organizations such as UNESCO, UNICEF, and UNDP (MEC 2002). In 1986, an educational reform began in the country with support from the Calouste Gulbenkian Foundation (Portugal) and the World Bank, focusing on the production and editing of textbooks for the first 6 years of basic education. However, the program never reached its final objectives, and only a few manuals were produced. These manuals were used for over 20 years without being updated (Meia-Onça 2013).

The country has always been concerned with the quality of its educational system (Cotrim 2019). All the reforms sought to accompany changes in Santomean society and keep pace with the rest of the world, but the educational system was not ready for the new challenges facing the country (Cardoso 2004). The Basic Law of the Education System (Law 2/2003) introduced only two significant changes: an increase in compulsory schooling from 4 to 6 years and the inclusion of the 12th grade (MECJD 2006). Despite many attempts to develop a national curriculum adapted to the context and needs of the country, it was not until the last decade that the sciences received more attention. Today the curriculum is still insufficiently adapted to its audience and fails to reflect the natural heritage of the islands.

Nevertheless, the environmental education needs of the country were widely recognized and highlighted by the scientific and conservation communities, with strong and significant efforts starting in the 1990s. In 1992, São Tomé and Príncipe received assistance from the EU's European Development Fund in support of the Forestry Commission's efforts to prevent harvesting in primary forests and to promote efforts to educate the public about forest conservation. Under the ECOFAC Programme, an EU-funded regional program for the conservation and rational use of forest ecosystems in Central Africa, this work is still ongoing on the islands and lead to the establishment of the protected areas network of São Tomé and Príncipe. This network covers roughly one-third of the islands and culminated with the creation of two Natural Parks in 2006 (Lima et al. 2022). Meanwhile, an Action Statement on biodiversity conservation in the four Gulf of Guinea islands arose from a workshop held in 1993. This document reviewed the state of the main habitats on all the islands, current threats, and existing institutions and management actions taken so far (Juste and Fa 1994). This work led to the formation of an international group of scientists and a special issue of the journal *Biodiversity and Conservation* (vol 3, 1994). These events were key for synthesizing biodiversity knowledge and conservation actions for the islands, and also for igniting local actions to engage Santomeans in protecting their natural heritage.

The first environmental education activities emerged with ECOFAC around sea turtles (with Programa Tatô, still active as an independent NGO since 2018) and gray parrots. These were some of the better-known species at the time, highly pressured by the capture of individuals and eggs for food, trade, and crafts (AGRECO – SECA – CIRAD 2005). As the scientific knowledge of other groups and species increased and diversified, the need to involve the local population in environmental initiatives grew and has been a strong driver for most of the ongoing programs. The islands' potential for ecotourism has also been an important driver for the expansion of environmental outreach activities to reach the whole population and foreign visitors.

The Current State of Environmental Education in São Tomé and Príncipe

Formal Education: Environmental Education in Public and Private Schools

The public school system on São Tomé and Príncipe had the subject of Environmental Education (EE) formally introduced in 2010, but only to the eighth grade curriculum (Barreto 2012). Most private schools use EE in their lessons, formally or informally, linked to their internal curricula or to international curricula, such as the EE benchmarks provided by the Portuguese Ministry of Education.

Public Schools

Before 2010, environmental education content could be found in the Natural Science manuals but was not considered a priority. With the educational reform in the country, teachers of basic education inserted themes related to environmental education, namely on how to protect the environment from pollution or on how to conserve the fauna and flora, through the subjects of “Physical and Social Environment” for classes from the first cycle. Classes from the second cycle worked by the “Student Manual” in the science module, in which information and /or small themes were adjusted to include environmental education.

In 2010, the NGO MARAPA (Mar, Ambiente e Pesca Artesanal), CTA (Centro Técnico de Cooperação Agrícola e Rural), and ACP-EU (African, Caribbean and Pacific Group of States-European Union) sponsored the publication of the manual “Ecologia, Ambiente e Educação Ambiental em São Tomé e Príncipe” (“Ecology, Environment and Environmental Education in São Tomé and Príncipe”) to be used by teachers of the fifth and sixth grade (Carvalho et al. 2010). The manual includes simple environmental education modules together with different practical activities and teaching tools to be used by teachers of all subjects. Teachers from across the country were trained but there was no formal assessment of the program’s efficacy or impact. The manual was then used to support the elaboration of the EE curriculum for the eighth grade (under Projeto Escola+) when, after 2010, EE as a subject was inserted as part of a separate enrichment to the curriculum. Three different areas were introduced in high schools in both São Tomé and Príncipe: “Environmental Education” was introduced to eighth grade students, incorporating group work and other interactive activities to the lectures; “Health Education” to the seventh grade; and “Civic Training” for ninth graders.

The curriculum content was developed by a select group of secondary school teachers under the supervision of the Secondary Education Directorate. The educators from Projeto Escola+, coordinated by the Instituto Marquês de Valle Flôr, supported by several European partnerships, and approved by the Ministry of

Education and Culture, made the school manuals available along with a series of structured training events held to promote the development of key stakeholders in the second cycle educational network (Barreto 2012). After publication, the manual was made available for teachers to use in the classroom, along with regular training offered on how to integrate the manual into the environmental education curriculum by the First Cycle Board. The curriculum was not widely adopted by teachers but achieved greater use on the island of São Tomé and was included sporadically in classes on Príncipe.

In 2014, following the inclusion of environmental education in the school curriculum, along with a dedicated teacher's manual, actions were focused on the eighth grade students. This resulted in the production of a new EE student manual (Eloy et al. 2014). This material was intended to alert and prepare young people to the worsening environmental situation in the country, and to the need to promote sustainable economic development while preserving the islands' biodiversity. Due to various limitations after its publication, very few people knew about the existence of this material, including teachers and students in São Tomé and Príncipe.

Private Schools

Based on a sample ($n = 5$) of private schools (pre-k to 12 grade) interviewed in São Tomé in 2020 and 2021, environmental education (EE) is part of the curriculum but it is not adapted to the context of the islands and does not use examples of the local biodiversity and habitats. Four schools used the curriculum published by the Portuguese Ministry of Education: Referencial de Educação Ambiental para a Sustentabilidade (Environmental Education Benchmark for Sustainability). Some schools teach about the history and geography of São Tomé and Príncipe first and then proceed with the Portuguese curriculum. Only one school incorporated a few EE topics related to the islands with the support of local NGOs. Príncipe recently opened its first private pre-k school on the island. The school integrates EE activities such as Earth Day, but EE is not yet connected to a formal curriculum.

The EE topics taught by the private schools depend on how closely they follow the Portuguese benchmarks, covering preschool to secondary level, to develop lessons and activities that aim to contribute directly to the personal and social development of their students. The ninth grade of a particular school we interviewed added "environmental sustainability," which incorporates first-hand experiences. For instance, in one of their modules students go into the field to test water quality, using knowledge acquired in the classroom to interpret their results and reach conclusions.

Another school took a step further and incorporated EE (using a mix of both Santomean and Portuguese concepts) into their mission statement, consequently linking all their curricular activities toward raising children's awareness about the importance of protecting and appreciating the natural world. Children as early as

12 months old have exposure to activities both in and outside of the classroom, with the purpose of promoting values and actions that can later result in the development of environmental stewardship in São Tomé and Príncipe. This particular school uses beach cleanup as its "beacon activity" to introduce the issue of trash pollution, which chronically impacts the islands' local beaches and city centers. Their aim is to reinforce the notion that children can be an important part of the solution and they also play an active role in teaching behavioral changes to family members and civil society.

Informal Education: Past and Ongoing Efforts

The basis for informal environmental education in São Tomé and Príncipe has been built upon the recent scientific work on the species-rich and under-explored biodiversity of the islands. A project by Veríssimo et al. (2012) aimed to understand the knowledge and attitudes of key stakeholders toward biodiversity, sustainability, and natural resource management, revealed that there is still the need to improve engagement and communication with local actors. International institutions and researchers need to invest time and resources to develop effective ways to better communicate their scientific findings through environmental education. Nevertheless, major efforts on EE have been made to raise awareness about the conservation of these unique islands over the past 23 years, with several national and international projects being held in the country that reach local residents and tourists alike (Table 25.1).

The lack of a centralized database to track records of early EE programs in São Tomé and Príncipe makes it difficult to assemble a complete assessment of the diversity of the project aims, target populations (TP), and outputs, but there has clearly been increased investment in long-term projects over the last decade (Fig. 25.1). Based on four "one-off" and 11 currently "ongoing" informal EE projects, five take place on both islands, five exclusively in São Tomé, and five exclusively in Príncipe, although collaborations are frequent between organizations from both islands. The establishment of a larger number of NGOs in the country contributed to the increase in longevity of the programs, funding, and creation of training and employment opportunities for members of the civil society. The main topic covered is biodiversity conservation, especially focusing on the valorization of threatened species and ecosystems. Projects address a wide range of taxa and ecosystems, although some focus on a specific taxon (e.g., marine turtles, bees, and terrestrial mollusks) or topics (e.g., recycling and illegal hunting). Twelve projects target schools and local communities, but the target audience can be project specific, depending on the main aims (e.g., fishermen and fishmongers for marine ecosystem conservation or hunters for terrestrial ecosystem conservation).

Table 25.1 Summary of environmental education projects in São Tomé (ST), Príncipe (P) and both in São Tomé and Príncipe (STP)

Projects	Period	Place	Main theme	Target population	Methodology
Arribada Club: Arribada initiative | Fundação Príncipe	2017 – present	P	STEM | biodiversity | endemic species | conservation technology | conservation | protection	Primary school	After-school program | lecture | multimedia communication | hands-on activity
BirdLife International Partners Programme: RSPB | SPEA	2015–2017 | (under ECOFAC 6 as of 2018)	ST	Biodiversity | endemic species | conservation not hunting | protection	Hunter	Outreach | training | hands-on activity
Bumbu D'Iê: Terrestrial Conservation Programme | Fundação Príncipe	2016–2019	P	Bees | biodiversity | ecology | conservation | protection | sustainable business practices | income-generating activity	Primary school | community | general public | NGO agent	Product development and distribution | outreach | lecture | training | workshop | multimedia communication | field trip | hands-on activity
ECOFAC 4: PNOST | Zuntabawê	March–June 2010	STP	Biodiversity | endemic species | conservation | ownership	Community | community leader | NGO agent | Nat'l park staff	Outreach | training | multimedia communication | hands-on activity
ECOFAC 6 (Obô Ôvyô Campaign): BirdLife International | Oikos	2018 – present	STP	Biodiversity | endemic species | conservation | protection | sustainable business practices | effective land management | protected areas | National Parks | natural heritage | ecotourism	Hunter | primary school | community | community leader | general public | eco guide	Outreach | training | workshop | multimedia communication | field trip | hands-on activity
Environmental Education Manual: MARAPA | CTA | ACP-EU	August 2010–June 2011	STP	Biodiversity | ecology | conservation | environmental education principles & didactic tools	Teacher | community | NGO agent | nature Club	Product development and distribution | training | meeting | hands-on activity
Forest Giants: Alisei Onlus NGO | FCUL	2018 – present	ST	Terrestrial mollusks | biodiversity | endemic species | conservation | protection | ecology | snail husbandry	Teacher | primary school | community | general public | NGO agent | eco guide	Outreach | lecture | training | workshop | meeting | multimedia communication | field trip | hands-on activity
		STP			

<table>
<tr><td>Gulf of Guinea: California Academy of Sciences</td><td>2010 – present</td><td></td><td>Biodiversity | endemic species | conservation | protection | ownership | stewardship</td><td>Teacher | primary school | community | general public</td><td>Product development and distribution | outreach | training | workshop | multimedia communication | hands-on activity</td></tr>
<tr><td>Missão Dimix Association</td><td>2017 – present</td><td>ST</td><td>Arts | biodiversity | marine life | conservation | protection | stewardship</td><td>Primary school | secondary school</td><td>After-school program | lecture | multimedia communication | exhibition | field trip | hands-on activity</td></tr>
<tr><td>Omali Vida Nón 1 & 2: University of Exeter, UK | FP | DRAPP | DGP | Principe Island UNESCO Biosphere Reserve | FFI | Oikos | MARAPA</td><td>Phase 1
July 2016–March 2019
Phase 2
2018 – present</td><td>P
STP</td><td>Phase 1 | better Management of Marine Resources | sustainable practices
Phase 2 | creation of marine protected areas | conservation | protection</td><td>Fisherman | fishmonger | community</td><td>Outreach | multimedia communication</td></tr>
<tr><td>Príncipe Thrush: Terrestrial Conservation Programme | Fundação Príncipe</td><td>2018 – present</td><td>P</td><td>Principe thrush | ecology | population size & distribution | conservation | protection</td><td>Primary school | community | general public | NGO agent</td><td>Outreach | lecture | multimedia communication | hands-on activity</td></tr>
<tr><td>Programa Tatô: ECOFAC (1998–2002); MARAPA (2002–2018); Associação Programa Tatô (2018 – present)</td><td>1998 – present</td><td>ST</td><td>Sea turtles | conservation | protection | biodiversity | marine life | ownership | stewardship | income-generating activities</td><td>Fisherman | fishmonger | kindergarten | primary school | secondary school | community | general public | eco guides | tourists | NGO agents | government</td><td>Product development and distribution | outreach | lecture | workshop | training | meetings | multimedia communication | exhibition | guided Tours | museum interpretive activities | field trip | theater play production | museum | hands-on activity |</td></tr>
<tr><td>Protetuga: Fundação Príncipe</td><td>2015 – present</td><td>P</td><td>Sea turtles | biodiversity | marine life | conservation | protection | ownership | stewardship | income-generating activity</td><td>Kindergarten | primary school | secondary school | community | general public | NGO agent | eco guide | tourist | government</td><td>Outreach | lecture | training | meeting | multimedia communication | guided Tours | museum interpretative activity | museum | field trip | hands-on activity</td></tr>
</table>

(continued)

Table 25.1 (continued)

Projects	Period	Place	Main theme	Target population	Methodology
RaizArte: BLI support	2019 – present	ST	Performing arts | biodiversity | endemic species | ecology | nature themes | conservation | protection | ownership | stewardship	Secondary school | general public	After-school program | lecture | training | multimedia communication | theater play production | hands-on activity
Water & Recycling: Fundação Príncipe	2013–2015	P	Plastic bottle recycling | reusable water bottle | water filling station | waste management | stewardship	Primary school | community | general public | tourist	Outreach | hands-on activity

ACP-EU: African, Caribbean and Pacific Group of States-European Union – BLI: BirdLife International, UK – CTA: Technical Centre for Agriculture and Rural Cooperation, European Union – DGP: Direcção Geral das Pescas, STP – DRAPP: Direcção Regional da Agricultura, Pesca e Pecuária, STP – FCUL: Faculdade de Ciências da Universidade de Lisboa, Portugal – FFI: Fauna & Flora International, UK – FP: Fundação Príncipe, STP – MARAPA: Mar, Ambiente e Pesca Artesanal, STP – PNOST: Parque Natural Obo de São Tomé – RSPB: Royal Society for the Protection of Birds, UK – SPEA: Sociedade Portuguesa para o Estudo das Aves, Portugal

Approaches to Informal Environmental Education

Outreach in primary public schools is the preferred method used by the informal EE programs, possibly due to the fact that primary school students have very little exposure to environmental sciences. Informal EE projects are addressing some of the existing gaps by using a variety of hands-on methodologies and approaches within or outside the classroom. In 2011, the California Academy of Sciences pioneered a large-scale education effort based on scientific research to raise awareness about the islands' unique biodiversity in both São Tomé and Príncipe (Drewes 2012). The Gulf of Guinea Project uses a unique approach for content assimilation, following the same cohort of students from third to fifth grades, aiming to promote knowledge and stewardship about biodiversity in students' own "backyard." The project distributes to each student and their teachers captivating take-home educational materials after every lesson (Fig. 25.1 (6)), using the main message: "Only Here! São Tomé and Príncipe, Our Special Islands, and Nowhere else in the World!"

The opportunities for meaningful learning outside of the classroom in the public school system are almost non-existent on the islands and 20% of the EE projects are organized as after-school programs to address this limitation. The Protetuga Project in Príncipe, for example, incorporates their turtle conservation program through the Zero Capture campaign into the school calendar, creating the unique opportunity to organize field trips to their Kaxí Tetuga Museum at Praia Grande, where students visit a biodiversity museum and participate in the release of turtle hatchlings into the ocean amongst other educational activities (Fig. 25.1 (7)). The Arribada Club, in Príncipe, introduces primary school students to computers and conservation technology, such as GPS trackers and audio recording devices (Fig. 25.1 (1)). The Forest Giants Project creates debates with students and rural communities to raise awareness about biodiversity conservation, using the story of the rapid decline of the threatened Obô Giant Snail *Archachatina bicarinata* and provides hands-on teaching and training opportunities for learning about local species and for interacting with the Obô Giant Snail at the Botanical Garden of Bom Sucesso, São Tomé (Fig. 25.1 (5)). Other projects create awareness using visual or performing arts. Missão Dimix Association organizes student art exhibitions made with recycled materials showcasing their focus on marine life conservation, in addition to their regular after-school programs and camps. RaizArte works with teenagers on playwriting, stage design, and performing art techniques using biodiversity, conservation, and other nature-related themes (e.g., the Se o Obô Falasse theater play addresses species conservation in São Tomé and Príncipe; Fig. 25.1 (8)). *Programa Tatô* develops an array of educational printed materials, such as the story book *A viagem da visitante mais antiga de São Tomé e Príncipe* (The journey of the oldest visitor of São Tomé and Príncipe), the activity book *Livro de atividades para os dias de chuva* (Activity book for rainy days), and an annual booklet *Ngê di Omali* (Sea people), which is distributed to primary schools with a different theme every year.

The peer teaching and learning experiences, along with facilitated themed discussions and activities, can create paths to promote a sense of ownership and

Fig. 25.1 Examples of environmental education projects in São Tomé and Príncipe: (**1**) Arribada Club Project computer science class, Príncipe; (**2**) ECOFAC 4 "Net of Life" activity in Claudino Faro rural community, São Tomé; (**3**) ECOFAC-6 plant nursery activity with students at Diogo Vaz primary school, São Tomé; (**4**) Bumbu D'Iê classroom program about bee conservation, Príncipe; (**5**) Forest Giants Project lesson to primary school students about terrestrial biodiversity conservation and the decline of the Obô Giant Snail Archachatina bicarinata, São Tomé; (**6**) Gulf of Guinea Project primary school outreach program "Our Special Birds" about the endemic species of birds from São Tomé and Príncipe, São Tomé; (**7**) Protetuga Project hatchling release activity with school

valorization of the natural resources. Projects that work with specific audiences (e.g., fishermen, fishmongers, hunters, loggers, National Park staff, school teachers, and students that live in the vicinity of protected areas) used "train the trainer" methods to capacitate community leaders to conduct training sessions with their own communities using a variety of hands-on activities and facilitation tools (e.g., photo montage, films, role play, games, sports championships, cooking competitions, fairs). This method is proven to be efficient to raise environmental awareness and well accepted among communities. In a pilot study in the scope of ECOFAC 4 (Fig. 25.1 (2)), focusing on communities around São Tomé Obô Natural Park, the "train the trainer" method was shown to be a potentially strong tool to develop and promote increased knowledge toward endemic biodiversity and nature conservation. In 2018, the ECOFAC 6 project investment is working in the buffer zones of the natural parks of both São Tomé and Príncipe, developing training to promote sustainable use of natural resources for income-generating activities, imperative to generate real results toward the conservation and valorization of natural heritage, biodiversity, and ecosystems (Fig. 25.1 (3)).

The Omali Vida Nón project works with the government and coastal communities to create a network of marine protected areas across both islands through a co-management approach. It aims to create awareness and promote the adoption of alternative sustainable methods as a way of balancing human impact with the subsistence living of the communities. Likewise, to promote sustainable honey practices, the Bumbu D'Iê project provided training to beekeepers for an alternative model of honey production that does not involve bee-burning in the forest, combined with EE hands-on activities (Fig. 25.1 (4)).

Multimedia communication is used by nine of the projects to reach wider and more diverse audiences, which is frequently amplified by content productions on TV, radio, and social media. Even some of the most rural parts of the islands have radios and television sets (plugged-in to generators) available at home or at the local kiosk. Community members tend to congregate in such venues, to socialize and watch TV or listen to the radio at the end of the workday, in the evenings, and especially over the weekends. The Programa Tatô, for example, uses local media celebrities on educational radio soap operas on São Tomé to raise awareness about their sea turtle conservation program. Fauna and Flora International (2019) concluded that the use of posters and radio was an efficient and cost-effective method to reach and engage large numbers of people. The report cautioned, however, that a high level of engagement does not necessarily translate into effective dissemination of the underlying message.

Fig. 25.1 (continued) children at Praia Grande, Príncipe; (**8**) RaizArte "Se o Ôbo Falasse" play written, directed, and performed by high school students, São Tomé. Photo credits: (**1**, **4**, **7**) Fundação Príncipe, (**2**) Mariana Carvalho, (**3**) Raphaela Nazaré, (**5**) Vasco Pissarra, (**6**) Andrew Stanbridge, (**8**) BirdLife International

Evaluation of Projects

Evaluation is a very important tool to determine what works well and what could be improved; however, only six of the EE projects (40%) have an evaluation tool in place. This makes it difficult to measure the real impact of the programs, which may compromise reporting to stakeholders and limit funding opportunities relative to projects that use quantitative data to assess impact.

EE projects that use evaluation tools commonly use questionnaires with adults, and drawings, games, or simple question-answer sheets with children, to evaluate knowledge gain and understanding of the concepts being taught. Oral interviews are commonly used to obtain direct feedback from stakeholders such as governmental authorities, teachers, school administrators, and students. ECOFAC 6 is the first project to use a more comprehensive method of evaluation, defining project indicators (e.g., days of training vs. number of people trained, number of people trained in green economy and entrepreneurship, number of followers on social media, number of students involved in awareness activities, and percentage of people with correct understanding of basic environmental concepts) to determine success. Programa Tatô has made big strides toward evaluating the impact of their conservation marketing campaign *Tataluga – Mém di Omali* on the consumption of sea turtle meat and eggs in São Tomé (Thomas-Walters et al. 2020).

A recent study on the use of children's drawings to evaluate the impacts of environmental education activities (Sinclair 2020), carried out by researchers at the University of Exeter (UK) in partnership with the Protetuga project by Fundação Príncipe, provided useful insights to inform efforts for sea turtle conservation on the island. The study demonstrated that using drawings as a tool for assessing levels of knowledge about the biodiversity of Príncipe and evaluating change in children's knowledge over time can be useful to inform interventions, is highly engaging, and has low-cost implementation on-the-ground. This assessment method demonstrated that Protetuga's EE activities over 4 years resulted in increased knowledge of conservation issues and solutions among children.

These findings are particularly promising, as they validate some of the progress undertaken through informal education efforts in the past years and provide valuable guidance for future monitoring and recognition of the EE projects.

Challenges and Lessons Learned

One of the biggest challenges concerning formal education in the public system is the fact that EE is only part of the eighth grade curriculum, and not present in any other grade. Thus, much of EE falls under informal education, which is not offered systematically and is not connected to formal education. Furthermore, teachers are not motivated to embrace EE in and outside the classroom, due to the lack of a support system, namely proper training and resources to promote extracurricular activities. Such challenges become a serious roadblock toward making any substantial advances.

More than 60% of the local teachers from first to sixth grade have no formal educational training (MECCC 2016), and the required qualifications for filling teacher vacancies in primary and secondary education in the country are low. For example, it is possible for someone who has just finished high school to start teaching eighth grade students. This is the result of a fast-growing society built on a job market with very limited options for young people entering the workforce or pursuing a university degree. The University of São Tomé was formally founded only in 2014, after many years of existence as several different independent educational institutions. Other international universities, like the University of Évora or the Lusíada University (both from Portugal), have a branch on São Tomé, offering higher education courses. However, the tuition is typically far beyond the financial means of the target demographic, contributing to the scarcity of professionals with formal academic training. Individuals that obtain a college degree in another country rarely return to São Tomé and Príncipe due to the low salaries and scarce job opportunities. In some cases, teachers also hold appointments in other governmental departments and teaching is a second job, which means that their availability and engagement in the teaching role may be low. Institutions like the World Bank occasionally finance and provide teacher-training opportunities led by the local government in partnership with different Portuguese institutions, or private sectors. However, these opportunities are rare and generally cover small groups or a small percentage of teachers in the country.

For Príncipe residents, the conditions are even more challenging, as only recently (2012/2013) was it made possible for students to finish high school on the island. Up to a few years ago, students from Príncipe had to attend high school in São Tomé, resulting in a high percentage of youths without a high school degree. On the other hand, even with the governmental "isolation allowance" (financial incentive), Príncipe still struggles to find teachers willing to move to the island due to the high cost of living and isolation.

In March of 2021, we interviewed 10 primary and secondary school teachers from Príncipe and six from São Tomé, all working in the public system, to learn about their perception regarding their job experience satisfaction and knowledge about local biodiversity. The results showed that 56% have chosen this profession because they enjoy teaching and 37% due to a lack of options. When asked about the availability of opportunities and the kind of limitations they are confronted with regarding career advancement, they shared their concerns about the limitations imposed on career advancement, which are linked to the lack of the schools' basic needs (e.g., electricity, water, sewage, and nutritious meals), and the absence of a recognition system for different teaching categories, with salary compensation dependent on the amount of training. Teachers interviewed in São Tomé did not receive any specific training on local biodiversity or environmental issues, but in Príncipe only one said that he had not received some type of training, either through other teachers, universities, or NGOs. Only one teacher in Príncipe and one in São Tomé stated that before becoming a teacher they did not have any knowledge about the importance of biodiversity and other issues related to the protection of the environment in São Tomé and Príncipe. All teachers we interviewed recognize the importance of the environmental issues on the islands and emphasize the role of biodiversity in maintaining the health of ecosystems.

As in the public school system, opportunities for private school teacher training on EE adapted specifically to the local context are very rare. Only one of the private schools we interviewed invested time and resources to keep their teachers connected to the subject by either bringing professionals from different areas of environmental sciences or organizing field trips to different NGOs. Overall, the support system to either train teachers, or to facilitate access to EE materials pertaining to the local fauna and flora is underdeveloped, but it exists. Willing teachers can work with informal environmental educators, biologists, technicians or NGOs to complement and explore different local EE topics.

Various EE projects have observed that the schools in the capital of São Tomé have higher student and teacher engagement during program delivery than in rural areas. Schools situated in very remote areas not only have lower engagement but also have difficulty in understanding basic concepts and the overall message of the content. It is also in these rural communities that children most often have to support their household with domestic tasks, making it very hard for them to be available for activities outside the school period. In addition, conditions in rural schools such as an excessive number of students per classroom, no electricity, and malnutrition, can make learning more difficult. The socio-economic situation on the islands clearly reflects the degree of knowledge and understanding of the communities about the importance of their unique biodiversity. It is extremely difficult to convey nature conservation messages when the basic needs of the local communities are not met.

A recent study was conducted with 361 students from both rural and urban primary schools in São Tomé to assess children's knowledge of local biodiversity (Panisi et al. 2022). It showed that students' wildlife knowledge improved among the male student population of impoverished rural schools, and that threatened endemic species were less often recognized than non-native species. Students in São Tomé preferred to protect species according to their attractiveness or profitability (e.g., species that can be eaten or sold). These findings reveal existing disparities in children's knowledge about biodiversity among genders, economic backgrounds, and reasons to protect wildlife. A lack of targeted and well-planned EE actions can result in the progressive extinction of knowledge about the unique fauna and flora of the island by the younger generation, especially in more urbanized areas (Soga et al. 2018).

Despite the fact that different generations have the opportunity to experience EE through programs and activities, in many cases, ownership or follow-up is still missing. This could be the result of poor planning (e.g., time constraints, budget, personnel), type of language used (e.g., low involvement of local educators to ensure educational tools are locally adapted), and insufficient long-term engagement to create continuity. The very few existing published reports from past efforts are not comprehensive enough to prevent repeating the same errors, which may deter further development of EE in the country. Until today, the majority of EE actions happening on São Tomé and Príncipe have been conducted informally and under the responsibility and leadership of international NGOs, with engagement of local civil society. In recent years, EE has been growing and progressively led by national organizations, with several recognized Santomean educators who keep their engagement with the dissemination of conservation messages throughout the years in different projects and in their own communities and networks.

During 2020, the COVID-19 pandemic was a global challenge, and education was one of the sectors that suffered the most. In the majority of developed countries, the online system was a solution to keep children and youth engaged, while in non-developed countries, where access to electricity and the internet is limited, this global crisis resulted in a complete stop of the education process. The limits to social gatherings and the lack of virtual platforms also impaired projects working with communities or other target groups. Consequently, all formal and informal EE programs and activities also came to a halt in both São Tomé and Príncipe. In 2021, the EE activities (formal and informal) are slowly starting as schools are back in session and meeting restrictions are starting to be lifted.

Looking into the Future

There are many political, economic, and social challenges on São Tomé and Príncipe that directly impact the general quality of the education system. Consequently, the subject of EE, including the focus on the importance of the islands' local biodiversity, is less of a priority to the country. In today's world, issues related to the environment and education are more relevant than ever. Scientific knowledge of the endemic and unique biodiversity of the islands has significantly increased in the last few decades, and the national policies are starting to see biodiversity as a development tool through tourism. Príncipe has been at the forefront of creating a model for sustainable development, with the island being recognized as a UNESCO Biosphere Reserve in 2012 and the development of the Plan for Sustainable Development "Príncipe 2030." São Tomé seems eager to follow these steps with work being done to achieve UNESCO Biosphere Reserve status as well. However, this fragile and recent understanding of the importance of the local biodiversity is not yet evident in the education system. Without the support and leadership of non-governmental national and international organizations, the local knowledge of the environmental relevance of São Tomé and Príncipe would be still precarious.

Teachers' feedback indicated that a national education reform paired with a dedicated budget is imperative to increase and sustain the investment on training local teachers, improving schools' basic conditions, and promoting the inclusion of EE in all grades of the public system. EE has to be seen as a priority, and integrating children with an environmental agenda is an investment in creating future adults engaged with the conservation of the country's natural resources. In parallel with the integration of the EE curriculum in all grades of public education, the private education system should enhance the use of their resources, and dedicate a budget to strengthen the efforts made to promote more EE activities. Integration of local partners and stakeholders and the use of materials with messages and content tailored to the local reality are also key elements to the future of EE on the islands.

Going forward, it is highly recommended that all organizations promoting EE (public, private, informal) in the country monitor and evaluate their activities, and commit to share their results to ensure the growth and advancement of EE on São Tomé and Príncipe. The development of an evaluation protocol to be used nationally could be of great benefit to accomplish such an important task. Additionally, a potential development of an online database of EE initiatives in the country could serve as an important learning tool for anyone planning or currently working in the country, and promote exchanges with other regions or educators. There are few meaningful opportunities for teachers, students, and civil society to engage and network with local and international professionals in the field of EE, as most of the communication and materials are done in languages other than Portuguese. In the last decade, the islands have hosted several events related to environmental education in Lusophone countries. These conferences and meetings, although limited in time, represent opportunities to exchange and develop ideas, establish collaborations and keep people inspired and motivated by EE.

It is evident that there is an urgent need to create a strong and well-defined joint strategy with local governmental support between public, private, formal, and informal educational institutions, to ensure a successful integration of EE on São Tomé and Príncipe, and to generate positive, long-lasting results on the islands' biodiversity conservation. Education is the most effective way to achieve greater public support and establish solid goals to preserve the fragile and threatened biodiversity of these islands. This is urgent to ensure the future of both people and biodiversity. Past EE efforts left a legacy in transmitting knowledge, motivating and training people, and developing valuable materials that are currently addressing critical environmental issues. Present and future EE efforts will inspire and engage the next generation of national leaders to take a more critical and active role in shaping the future of the unique biodiversity of the Gulf of Guinea oceanic islands.

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Chapter 26
A Thriving Future for the Gulf of Guinea Oceanic Islands

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Abstract The oceanic islands of the Gulf of Guinea hold extraordinary levels of endemism across many taxonomic groups. Biodiversity surveys are still uncovering species new to science, and much work remains to be done on the evolution, ecology, and conservation of this unique biological heritage. The next 10 years will be crucial to find and implement development strategies that can respond to the needs of the islands' inhabitants while sustaining the biodiversity and

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ecosystem functions on which they depend. We outline seven priority areas that need to be addressed on the path for a thriving future for both people and biodiversity.

Keywords Biodiversity databases · Capacity · Exploration · Natural history collections · Outreach · Small islands developing states · Sustainable development

Earth's islands collectively hold the greatest concentration of biodiversity that exists on our planet. Although islands have long served as important models for understanding the ecology and evolution of biodiversity, islands have also been recognized as epicenters of extinction with approximately 75% of all recent bird, reptile, amphibian, and mammal extinctions occurring on islands. Much of the remaining global island diversity is threatened, with up to 85% of remaining reptile, amphibian, and mammal species, along with nearly half of island birds, at risk of extinction today. Similar figures are expected for other taxonomic groups, for which global assessments are currently missing. This biodiversity crisis is particularly notable on tropical oceanic islands, where species evolved in stable and isolated conditions and are especially vulnerable to the fast pace of ongoing environmental change. As extinctions multiply, island ecosystems begin to crumble and further cascades of species extinction will follow. As a result, the human inhabitants who depend on these ecosystems will lose their livelihoods and ways of life. At the same time, because island ecosystems are relatively simple, they also offer an opportunity to understand how to stop this crisis, and to alter the course of our relationship with biodiversity.

This edited volume provides an important summary of over 200 years of biological research on the oceanic islands of the Gulf of Guinea, highlighting the archipelago's extraordinary endemism across the tree of life. Much of this diversity is still being formally described to science, and the conservation status of most endemic species has not yet been formally assessed. Likewise, our understanding of species natural history, interactions among species, and characteristics of the islands' diverse ecosystems is still woefully incomplete. Importantly, these gaps in knowledge hinder our ability to halt biodiversity loss on the islands and to secure a thriving future for the islands' human inhabitants. In support of the United Nations Small Island Developing States commitment to reach sustainable development, the following activities should be a top priority for the oceanic islands of the Gulf of Guinea over the next 10 years:

- *Field surveys and taxonomic research that target specific taxonomic and geographic gaps in knowledge*. Key knowledge gaps are discussed in more detail in each of the taxonomic chapters, but we also note that for some branches of the tree of life, the current state of knowledge for the oceanic islands of the Gulf of Guinea is so sparse that we could not provide a chapter and/or checklist for that particular group. This includes algae, lichens, and several groups of terrestrial (e.g., annelids, bees, flies) and aquatic invertebrates (e.g., crustaceans, corals, echinoderms, sponges). For much of the archipelago's biodiversity, this work will

also necessitate a better understanding of regional species diversity and evolutionary relationships. Molecular techniques will continue to prove an invaluable tool for advancing taxonomy and systematics in these lesser known groups.
- *Mobilizing existing natural history collections and their data to democratize knowledge and expedite biodiversity research.* Biodiversity surveys over the last two centuries have resulted in extensive natural history collections that document the diversity and distribution of the archipelago's terrestrial and aquatic ecosystems. Most of these collections are housed in Europe and the USA, and many have not yet been curated, georeferenced, digitized, and made available to the local or global research community. This critical work must continue and take advantage of the growing availability and accessibility of online platforms for collections data.
- *Integrating data from targeted field surveys and existing collections to map species distributions.* The distributions of most species in the oceanic islands of the Gulf of Guinea are unknown, which limits our inference of species richness and endemism across the islands' ecosystems. Existing natural history collections already hold much of this information, and future surveys should be designed to fill conspicuous gaps in knowledge. These spatial data can be combined with maps of current protected areas and estimates of future climate and land-use change to inform sustainable development and conservation planning that centers biodiversity resilience.
- *Promoting the islands as models for ecological studies*. Biodiversity is dynamic and relies on complex interactions at multiple levels of organization that are challenging to study. As the species and ecosystems of the Gulf of Guinea oceanic islands become more completely documented, hypothesis-driven studies to promote a deeper understanding of their ecology are becoming possible. Although few such studies have been conducted, it is already clear that the islands are valuable mesocosms to test and develop advanced ecological theories, including population dynamics, community ecology, species interactions, ecosystem resilience, and the impact of human activities on biodiversity.
- *Bolstering local taxonomic expertise and resources for biological research.* An increasing number of Santomean and Equatoguinean researchers are contributing to biodiversity science, but this community is still small and largely under resourced. Local institutions, including universities, herbaria, botanical gardens, and libraries, need an influx of funding and training to support the growth in taxonomic expertise and leadership that is essential for islanders to direct the next phase of biodiversity research and environmental stewardship.
- *Augmenting resources for island residents of all ages to learn about their local biodiversity.* Effective biodiversity conservation requires a well-informed and engaged local community. Currently, science literacy in the Gulf of Guinea oceanic islands is limited and formal curricula do not feature the islands' unique biological heritage. Developing widely available, accessible references and environmental learning opportunities for those with less scientific training will be vital to stimulate environmental stewardship and to recruit more local naturalists. These resources can also serve to advertise the islands as a destination for

sustainable tourism. The contents of this book can serve as a baseline reference for updating school and university science curricula to focus on local biodiversity, ecosystems, and environmental stewardship. Likewise, this book can serve as a reference for developing taxon-focused field guides with illustrations, distribution maps, natural history accounts, identification keys, and interactive tools. Finally, featuring local biodiversity in community spaces through art, music, and theatrical performances can further extend the reach of biodiversity knowledge and stewardship.

The next 10 years will be critical to set the stage for biodiversity conservation and sustainable development in the oceanic islands of the Gulf of Guinea. Building on a foundation of more than two centuries of biodiversity science, robust commitments from local leadership, and strong cross-sector partnerships, this unique archipelago is well situated to change course from cascades of species extinction towards a thriving future for biodiversity. Most powerfully of all, the islands can teach us how to assess and support healthy ecosystem function and scale these approaches to Earth's larger systems.