

# 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<sup>2</sup> for Annobón (now 17 km<sup>2</sup>), 1480 km<sup>2</sup> for São Tomé (now 857 km<sup>2</sup>), and 1179 km<sup>2</sup> for Príncipe (now 139 km<sup>2</sup>). 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* (Bruguière 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) *Atopocoehlis 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). Rhysotinae 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 inexpectata* 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: *Thomeaoniaizania* (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 Urocyclidae (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 *Rhyssolina* 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 plantations). 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 *Rhyssolina* 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 (Juříčková 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 <b>Cyclophoridae</b> J.E. Gray, 1847 or <b>Maizaniidae</b> Tielecke, 1940											
<i>Afrotropis</i> Bequaert & Clench, 1936	<i>molleri</i> (Nobre, 1886)	–	E	–	NE	860–885	–	0	+	0	0
<i>Cyathopoma</i> W. & H. Blanford, 1861	<i>inexpectata</i> G. Holyoak & D. Holyoak, 2020	E	–	–	NE	216	L	1	0	0	0
<i>Maizania</i> Bourguignat, 1889	<i>furadana</i> G. Holyoak & D. Holyoak, 2020	–	E	–	NE	240	P, L, R	0	2	0	0
<i>Thomeomaizania</i> Bequaert & Clench, 1936	<i>gascoignei</i> G. Holyoak & D. Holyoak, 2020	–	E	–	NE	1300–1416	P, L	2	0	0	0
	<i>vandellii</i> (Nobre, 1886)	–	E	–	NE	96–1415	L, R, S	1	2	0	1
Family <b>Truncatellidae</b> J.E. Gray, 1840											
<i>Truncatella</i> Risso, 1826	<i>clathrus</i> R.T. Lowe, 1832	–	N	–	NE	2	L, H	0	0	0	+
	<i>rostrata</i> Gould, 1847	N	–	–	NE	–	H	0	0	0	+
Family <b>Assimineidae</b> H. Adams & A. Adams, 1856											
<i>Assiminea</i> J. Fleming, 1828	<i>sp.</i>	N	N	–	NE	–	H	0	0	0	+
Family <b>Ellobiidae</b> L. Pfeiffer, 1854											
<i>Melampus</i> Mont- fort, 1810	<i>flavus</i> (Gmelin, 1791)	N	N	–	NE	–	H	0	0	0	+
	<i>pusillus</i> (Gmelin, 1791)	N	N	–	NE	–	H	0	0	0	+
	<i>sp.</i>	–	N	–	NE	2	H	0	0	0	+
<i>Pedipes</i> A. Férussac, 1821	<i>afer</i> (Gmelin, 1791)	–	N	–	NE	–	H	0	0	0	+
	<i>sp.</i>	N	–	–	NE	2	H	0	0	0	+
Family <b>Onchidiidae</b> Rafinesque, 1815											
<i>Onchidella</i> J.E. Gray, 1850	<i>sp.</i>	–	N	–	NE	–	H	0	0	0	+
Family <b>Veronicellidae</b> J.E. Gray, 1840											
<i>Laevicaulis</i> Simroth, 1919	<i>alte</i> (A. Férussac, 1822)	I	I	–	NE	24–1159	L, S	0	+	0	1
<i>Pseudoveronicella</i> Germain, 1908	<i>forcarti</i> D. Holyoak, G. Holyoak & F. Sinclair, 2020	E	–	–	NE	353–906	P	2	0	0	0
	<i>liberiana</i> (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
	<i>thomensis</i> (Girard, 1893)	–	E	–	NE	160–1418	P, L, W	1	3	1	0
Family <b>Achatinidae</b> Swainson, 1840											
<i>Archachatina</i> Albers, 1850	<i>bicarinata</i> (Bruguière, 1792)	E	E	–	VU	43–1266	L, W, R	2	1	0	0
	<i>marginata</i> (Swainson, 1821)	I	I	–	NE	6–1327	L, W, R, S	3	5	5	3
<i>Atopocochlis</i> Crosse & Fischer, 1888	<i>exaratus</i> (O.F. Müller, 1774)	–	E	–	NE	101–928	P	+	1	1	0
<i>Columna</i> Perry, 1811	<i>columna</i> (O.F. Müller, 1774)	E	–	–	NE	255–386	–	1	0	0	0
	<i>hainesi</i> L. Pfeiffer, 1856	E	–	–	NE	–	–	–	–	–	–
	<i>leai</i> Tryon, 1866	E	–	–	NE	58	–	0	0	+	0
<i>Lignus</i> J.E. Gray, 1834	<i>alabaster</i> (Rang, 1831)	E	–	–	NE	24–386	P	+	+	+	0
<i>Limicolaria</i> Schumacher, 1817	<i>flammea</i> (O.F. Müller, 1774)	–	I	–	NE	69–500	L, R, S	0	0	0	1
<i>Ischnoglessula</i> Pilsbry, 1919	<i>fuscidula</i> (Morelet, 1858)	N	N	–	NE	–	–	–	–	–	–
<i>Striosubulina</i> Thiele, 1933	<i>striatella</i> (Rang, 1831)	N	N	N	NE	6–1490	L, W, R, S	2	5	5	5
<i>Subulina</i> Beck, 1837	<i>feai</i> Germain, 1912	E	–	–	NE	–	–	–	–	–	–
	<i>moreleti</i> Girard, 1893	E	–	–	NE	194–860	–	+	+	0	0
	<i>newtoni</i> Girard, 1893	E	–	–	NE	281–860	–	+	0	0	0
<i>Cecilioides</i> A. Férussac, 1814	sp.	–	N	–	NE	–	–	–	–	–	–
<i>Aporachis</i> D. Holyoak, 2020	<i>dohrni</i> (Greeff, 1882)	–	E	–	NE	959–1490	P, L, R	2	1	0	0
	<i>hispidata</i> (Greeff, 1882)	–	E	–	NE	885–1416	R, F	+	1	0	0
<i>Bocageia</i> Girard, 1893	<i>lotophaga</i> (Morelet, 1848)	E	–	–	NE	–	–	–	–	–	–
<i>Nothapalus</i> von Martens, 1897	<i>solitarius</i> G. Holyoak & D. Holyoak, 2020	–	E	–	NE	1300	–	+	0	0	0
<i>Petriola</i> Dall, 1905	<i>clavus</i> (L. Pfeiffer, 1864)	–	E	–	NE	124–1490	L, W, R, S	5	4	3	2
	<i>marmorea</i> (Reeve, 1850)	–	E	–	NE	160–1490	L, W, R, S	3	4	3	1
	<i>monticola</i> (Morelet, 1866)	–	E	–	NE	236–1477	L, R, S	3	3	1	1
<i>Pyrgina</i> Greeff, 1882	<i>umbilicata</i> Greeff, 1882	–	E	–	DD	160–1418	L, W, R	3	3	0	0

(continued)



<i>Higher Taxonomy</i>	<i>Species</i>	P	ST	A	IUCN	Altitude (m)	Strata	NF	SF	SP	NN
<i>Thomea</i> Girard, 1893	<i>newtoni</i> Girard, 1893	–	E	–	DD	181–1418	L	1	+	0	0
<i>Allopeas</i> H. B. Baker, 1935	<i>gracile</i> (T. Hutton, 1834)	–	–	I	NE	–	–	–	–	–	–
<i>Opeas</i> Albers, 1850	<i>dohrni</i> (Girard, 1893)	E	E	E	NE	–	–	–	–	–	–
	<i>greeffi</i> (Girard, 1893)	E	E	E	NE	240	–	+	0	0	0
	<i>hannense</i> (Rang, 1831)	–	N	–	NE	12–678	R	0	+	0	1
	<i>pauper</i> (Dohrn, 1866)	E	E	–	NE	74	R	0	0	0	1
	<i>subpauper</i> Germain, 1912	E	–	–	NE	–	–	–	–	–	–
<i>Pseudopeas</i> S. Putzeys, 1899	<i>croseii</i> (Girard, 1893)	N	N	–	NE	240–1114	–	+	0	0	+
<i>Thyrophorella</i> Girard, 1895	<i>thomensis</i> Greeff, 1882	–	E	–	DD	323–1490	P, L, S	3	1	0	1
Family <b>Micractaeonidae</b> Schileyko, 1999											
<i>Micractaeon</i> Verdcourt, 1993	<i>koptawelilense</i> (Germain, 1934)	–	N	–	NE	885–1290	L, R, F	+	2	0	0
Family <b>Streptaxidae</b> Gray, 1860											
<i>Gulella</i> L. Pfeiffer, 1856	<i>azeionae</i> D. Holyoak, G. Holyoak & F. Sinclair, 2020	E	–	–	NE	194	–	0	+	0	0
	<i>crystallum</i> (Morelet, 1848)	E	–	–	NE	51–860	–	+	+	+	0
	<i>girardi</i> (Kobelt, 1904)	–	–	E	NE	–	–	–	–	–	–
	<i>insularis</i> (Girard, 1894)	–	–	E	NE	–	–	–	–	–	–
	<i>joubini</i> (Germain, 1912)	E	–	–	NE	353–372	–	+	0	0	0
	<i>nemoralis</i> (Germain, 1915)	–	–	E	NE	–	–	–	–	–	–
	<i>sorghum</i> (Morelet, 1848)	E	–	–	NE	–	–	–	–	–	–
<i>Sphinctostrema</i> Girard, 1894	<i>annobonensis</i> (Girard, 1894)	–	–	E	NE	–	–	–	–	–	–
	<i>bocagei</i> (Girard, 1894)	–	–	E	NE	–	–	–	–	–	–
<i>Streptostele</i> Dohrn, 1866	<i>abbreviata</i> D. Holyoak, G. Holyoak & F. Sinclair, 2020	E	–	–	NE	414	–	+	0	0	0
	<i>fastigiata</i> (Morelet, 1848)	E	–	–	NE	24–860	L	2	2	2	0
	<i>folini</i> (Morelet, 1858)	E	–	–	NE	24–194	L	2	2	2	0
	<i>truncata</i> Germain, 1915	–	–	N	NE	–	–	–	–	–	–
<i>Streptostele</i> (?) Dohrn, 1866	<i>feai</i> Germain, 1912	E	–	–	NE	–	–	–	–	–	–

(continued)

<i>Higher Taxonomy</i>	<i>Species</i>	P	ST	A	IUCN	Altitude (m)	Strata	NF	SF	SP	NN
	<i>moreletiana</i> (Dohrn, 1866)	E	E	–	NE	–	–	–	–	–	–
Tomosteles Ancy, 1885	<i>musaeicola</i> (Morelet, 1860)	–	I	–	NE	74–181	R	0	+	0	1
Family <b>Punctidae</b> Morse, 1864											
<i>Punctum</i> Morse, 1864	<i>camerunense</i> de Winter, 2017	–	N	–	NE	1254–1292	–	+	+	0	0
Family <b>Charopidae</b> Hutton, 1884											
<i>Trachycystis</i> Pilsbry, 1893	<i>iredalei</i> Preston, 1912	–	N	–	NE	1257–1288	–	+	+	0	0
Family <b>Succineidae</b> Beck, 1837											
<i>Quickia</i> Odhner, 1950	<i>concisa</i> (Morelet, 1848)	N	N	N	NE	6–678	P, L	0	+	1	1
Family <b>Cerastidae</b> Wenz, 1923											
<i>Gittenouardia</i> Bank & Menkhorst, 2008	<i>burmayi</i> (Dohrn, 1866)	N	N	–	NE	5–398	P	+	+	1	0
	<i>eminula</i> (Morelet, 1848)	N	N	–	NE	24–1477	P, L	1	1	1	1
Family <b>Gastrocoptidae</b> Pilsbry, 1918											
<i>Gastrocopta</i> Wolleston, 1878	<i>annobonensis</i> (Girard, 1894)	–	–	E	NE	–	–	–	–	–	–
	<i>nobrei</i> (Girard, 1893)	–	E	–	NE	6–126	L, W	0	+	0	0
Family <b>Truncatellinidae</b> Steenberg, 1925											
<i>Truncatellina</i> R.T. Lowe, 1852	<i>thomensis</i> D. Holyoak & G. Holyoak, 2020	–	E	–	NE	1254–1292	–	0	+	0	0
Family <b>Vallonidae</b> Morse, 1864											
<i>Pupisoma</i> Stoliczka, 1873	<i>dioscoricola</i> (C.B. Adams, 1845)	–	N	–	NE	197–1292	R, F	0	+	0	0
	<i>harpula</i> (Reinhardt, 1886)	–	N	–	NE	885–1292	R, F	+	+	0	0
Family <b>Agriolimacidae</b> H.Wagner, 1935											
<i>Deroceras</i> Rafinesque, 1820	<i>laeve</i> (O.F. Müller, 1774)	–	I	–	LC	254–1402	P, L, R, S	1	1	1	2
Family <b>Euconulidae</b> H.B. Baker, 1928											
<i>Afroconulus</i> Van Mol & van Bruggen, 1971	<i>roseus</i> D. Holyoak & G. Holyoak, 2020	–	E	–	NE	530–1353	P	0	1	0	1
<i>Afropunctum</i> F. Haas, 1934	<i>seminium</i> (Morelet, 1873)	N	N	–	NE	236–1400	P, R, F	2	2	0	0
Family <b>Helicarionidae</b> Bourguignat, 1877											
<i>Apothapsia</i> D. Holyoak & G. Holyoak, 2020	<i>moreleti</i> (Germain, 1915)	–	E	–	NE	22–1244	P, L	1	1	1	1
	<i>thomensis</i> (Dohrn, 1866)	–	E	–	NE	6–1402	P, L, W, R	5	5	5	4
Family <b>Urocyclidae</b> Simroth, 1889											
<i>Dendrolimax</i> Heynemann, 1868	<i>greeffi</i> 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
	<i>heyneimanni</i> Heyneimann, 1868	E	–	–	NE	220–498	P	+	0	0	0
	<i>newtoni</i> A. Ortiz de Zarate & Alvarez, 1960	–	–	E	NE	–	–	–	–	–	–
<i>Rhysotina</i> Ancey, 1887	<i>hepatizon</i> (Gould, 1845)	–	E	–	NE	153–1477	L, W, R, S	4	3	2	2
	<i>sublaevis</i> G. Holyoak & D. Holyoak, 2016	–	E	–	NE	22–1199	L, R	1	3	3	2
	<i>welwitschi</i> (Morelet, 1866)	–	E	–	NE	54–1323	L, W, R, S	3	3	3	3
<i>Africarion</i> Godwin-Austen, 1883	<i>dumeticola</i> (Dohrn, 1866)	E?	–	–	NE	–	P	–	–	–	–
<i>Principicochlea</i> D. Holyoak & G. Holyoak, 2020	<i>tenuitesta</i> D. Holyoak, G. Holyoak & F. Sinclair, 2020	E	–	–	NE	860	P	+	0	0	0
<i>Principitrochoidea</i> D. Holyoak & G. Holyoak, 2020	<i>aglypta</i> (Dohrn, 1866)	E	–	–	NE	193–344	L	+	+	0	0
	<i>convexa</i> G. Holyoak, D. Holyoak & F. Sinclair, 2020	E	–	–	NE	24–375	P	+	+	0	+
	<i>folini</i> (Morelet, 1848)	N	–	–	NE	24–216	L	+	+	0	+
<i>Thomithapsia</i> D. Holyoak & G. Holyoak, 2020	<i>bomsucessica</i> G. Holyoak & D. Holyoak, 2020	–	E	–	NE	418–1300	L, W	+	1	0	+
<i>Thomitrochoidea</i> D. Holyoak & G. Holyoak, 2020	<i>trinidadensis</i> D. Holyoak & G. Holyoak, 2020	–	E	–	NE	22–900	P	+	1	1	0
<i>Trochozonites</i> Pfeffer, 1883	<i>adansoniae</i> (Morelet, 1848)	–	–	N	NE	–	–	–	–	–	–
<b>Family Helicidae Rafinesque, 1815</b>											
<i>Cornu</i> Born, 1778	<i>aspersum</i> (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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