

AN ANNOTATED CHECKLIST OF THE EXTANT AND QUATERNARY LAND MOLLUSCS OF THE DESERTAS ISLANDS, MADEIRAN ARCHIPELAGO

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Abstract A revised and annotated checklist of the living and Quaternary land snails of the Desertas Islands, Madeiran Archipelago, is presented, incorporating recent published work and records previously unpublished. 55 species have been recorded on the Desertas, of which 36 were alive and 41 were found as Quaternary fossils. Only four species are widespread and not endemic to the Archipelago; 14 are endemic to the Desertas. 19 species are known only as Quaternary fossils from the Desertas, of which eight remain extant elsewhere in the Archipelago. Three species, *Leptaxis groviana*, *L. simia* and *Discula polymorpha*, are represented on the Desertas by more than one subspecies, although this status has not been confirmed by molecular studies. Records of a further seven species appear doubtful but are listed here.

Key words Madeiran Archipelago, Desertas Islands, land molluscs, extant, fossil.

INTRODUCTION

The Madeiran Archipelago has a rich and mostly endemic fauna of land snails that have attracted attention since the early 19th century. While Paiva (1867) and Wollaston (1878) provided early accounts of this fauna, including species known only as Pleistocene or Holocene fossils, later work has added considerably to their work both by new discoveries and taxonomic revision (Nobre, 1931; Waldén, 1983; Bank, Groh & Ripken, 2002; Seddon, 2008; Bank, 2009; Groh *et al.*, 2009). The Archipelago, consisting of Madeira itself, Porto Santo with its associated islets and the three islands of the Desertas, Chão, Deserta Grande and Bugio, holds many species or subspecies confined to one island or island group.

Within the Archipelago, the fauna of the Desertas has been the least studied, mainly due to relative inaccessibility. Further, while there are massive and well-worked fossiliferous deposits on both Madeira and Porto Santo (Goodfriend *et al.*, 1996; Cameron *et al.*, 2006), only a single fossiliferous site (on Bugio) was known until recently (Wollaston, 1878). Accounts of the Desertan

fauna were complicated by disputes between Paiva and Wollaston as to the origin and status of a number of records (Teixeira *et al.*, 2019). More recently, Cameron & Cook (1999) reported fossils from a single site on Deserta Grande, and provided a checklist of Desertan species both fossil and recent. Groh (unpublished) had also detected fossil material from Deserta Grande in 1985.

Work in the 21st century has transformed this situation. Many fossiliferous deposits have been found on Deserta Grande, and more species have been recovered from the deposits on Bugio, resulting in the discovery of new taxa (Teixeira *et al.*, 2019). Increased surveying, mainly by Isamberto Silva [I.S.] and Dinarte Teixeira [D.T.] has yielded new records of living taxa, including new species (Teixeira *et al.*, 2019; in prep.). Here, we provide a new, annotated checklist for the land mollusc fauna of the Desertas Islands incorporating these new discoveries and taxonomic revisions. It supersedes that of Cameron & Cook (1999). In compiling the list, we are aware that modern taxonomic revisions of Madeiran land mollusc genera have challenged traditional and notionally well-established nomenclature. De Mattia *et al.* (2018) and Brozzo *et al.*, 2020 provide excellent examples; there are others. Such work

has yet to be done on Desertan taxa; we have indicated where a degree of uncertainty exists.

THE DESERTAS ISLANDS

Figure 1 shows the location of the islands within the Archipelago and the islands themselves with details of places named in the text. Ilhéu Chão (ca. 0.4km²) is much the smallest of the three. It is flattened on top, with a maximum altitude of 99m. It is well vegetated. No fossiliferous deposits are known from the island. Deserta Grande (ca. 10km²) is the largest, with the highest point at Pico Pedregal (442m). While one valley, Castanheira, runs northwards, most of the island is a single ridge with remnants of summit plateaux. It is very steep-sided, and there are numerous small colluvial deposits containing

fossils along these slopes. Large areas are devoid of vegetation and heavily eroded, at least in part due to grazing pressure of rabbits (eliminated in 1996) and goats. The elimination of rabbits has resulted in some recovery of the vegetation. Bugio (ca. 3km²) is similarly very steep-sided. The two highest peaks, Amarelo (348m) and Quartos (345m) each hold a small and eroding plateau. They are separated by a knife-edge ridge. The edges of the southern Quartos plateau hold muddy fossiliferous deposits. Vegetation is similarly sparse, but it is recovering rapidly since the eradication of mice, rabbits and goats in 2010.

With the exception of the research station at Doca, Deserta Grande, the islands are uninhabited by humans, though Deserta Grande was intermittently inhabited in the past (Cameron &

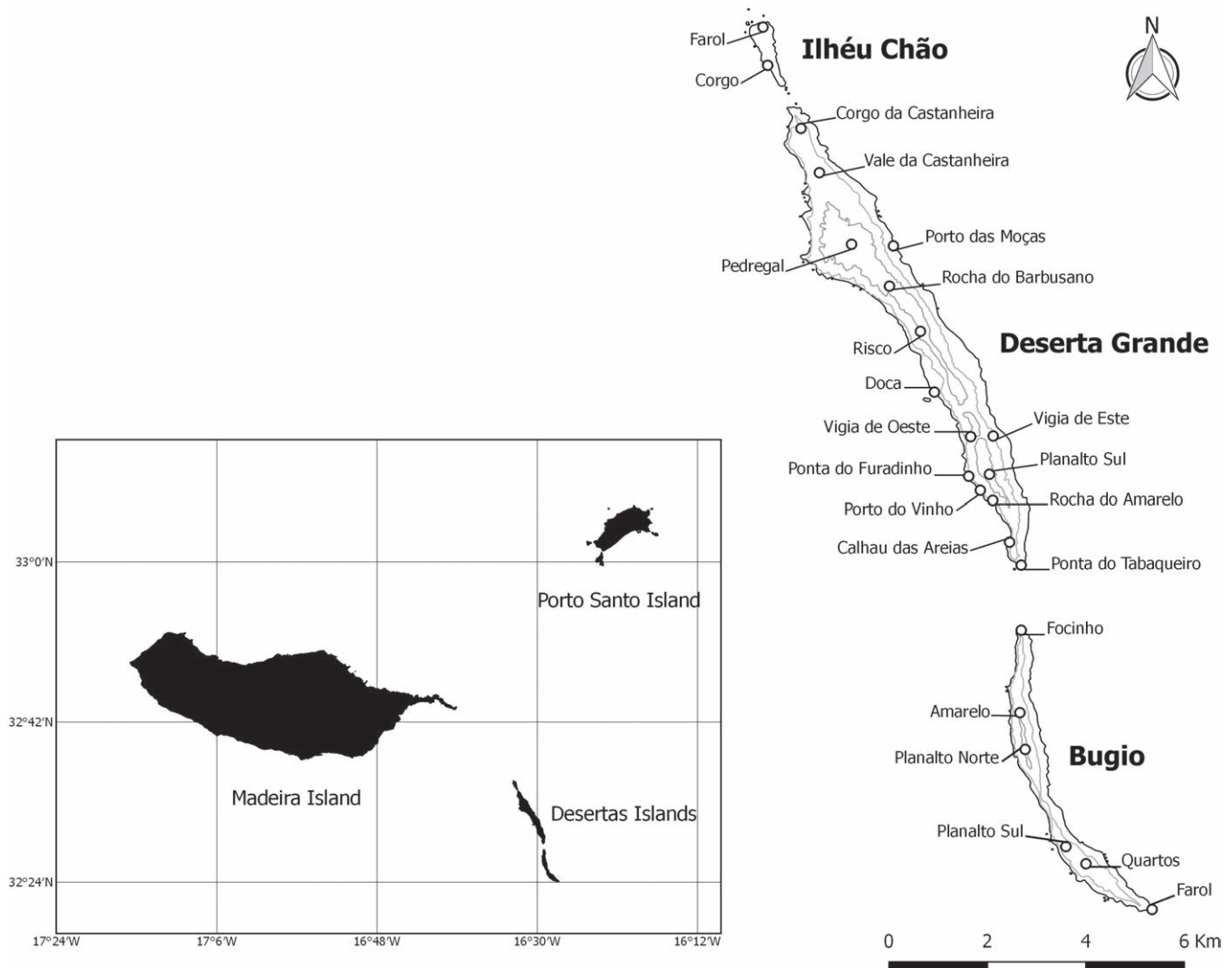


Figure 1 A map of the Desertas Islands, showing places named in the text. Further details of fossil sites are given in Teixeira *et al.*, (2019).

Cook, 1999). While the climate might be described as semi-arid, the highest parts of Deserta Grande support western bracken fern (*Pteridium aquilinum*), and in the Castanheira valley there are dense stands of the invasive bulbous canary-grass (*Phalaris aquatica*). The pre-colonisation vegetation is unknown, but is thought to have provided more cover than is present today. On Deserta Grande there are known remnants of denser cover with laurel trees, especially the species Canary Laurel (*Apollonias barbujuana*) and the Tilo or Stinkwood (*Ocotea foetens*). In the Pedregal area in the 19th century, there was a plantation of Canary Pines (*Pinus canariensis*), a reason why the longhorned beetle *Arhopalus pinetorum* (Wollaston, 1863) is reported from Deserta Grande.

CHECKLIST

Unless otherwise specified, all entries refer to species or subspecies found alive or fossil in the 21st century, mainly the product of unpublished surveys by I.S. and D.T. In a few cases, records of live snails have not been confirmed since the 19th century, but we have refrained from labeling them as extinct. Where subspecies are recognised, nomenclature follows Fauna Europaea, which relies mainly on Bank *et al.* (2002), with additions from Teixeira *et al.* (2019). The original citation of the taxon and principal later usages and synonyms are given immediately after the name accepted. We note that anatomical and molecular studies may alter their status, as many subspecies do not appear to match conventional patterns of geographical replacement. Taxa extinct (known only as fossils) on the Desertas but known living elsewhere shown *; those extinct completely shown **. A ? indicates that the record is unconfirmed and/or doubtful.

Class Gastropoda Cuvier, 1795
 Subclass Caenogastropoda Cox, 1960
 Order Architaenioglossa Haller, 1890
 Superfamily Cyclophoroidae J. E. Gray, 1847
 Family Craspedopomatidae Kobelt & Möllendorff, 1898

Genus *Craspedopoma* L. Pfeiffer, 1847

Craspedopoma mucronatum (Menke, 1830)

Valvata mucronata Menke, 1830, *Cyclostoma lucidum* R. T. Lowe, 1831, *Craspedopoma lucidum* – L. Pfeiffer, 1847, ? *Paludina conoidea* Küster, 1852, *Cyclostoma lucidum* var. α *polita* R. T. Lowe, 1860, *Cyclostoma lucidum* var. β *rustica* R. T. Lowe, 1860, *Craspedopoma mucronatum* – Waldén, 1983.

Extant species, endemic to Madeira – from where it is also known as a fossil – and the Desertas. Reported as fossil *lucidum* from Bugio (Wollaston, 1878), and recently as alive from Deserta Grande (Risco, Rocha do Barbusano and Furadinho, leg. D.T., I.S.). Fossil from Deserta Grande and Bugio (Teixeira *et al.*, in prep.). These are the first records, alive or fossil, from Deserta Grande.

Subclass Heterobranchia Burmeister, 1837
 Superorder Eupulmonata Haszprunar & Huber, 1990

Order Stylommatophora A. Schmidt, 1855
 Suborder Helicina Rafinesque, 1815
 Superfamily Pupilloidea W. Turton, 1831

Family Lauriidae Steenberg, 1925

Genus *Lauria* J. E. Gray, 1840

Subgenus *Lauria* s. str.

Lauria (Lauria) cylindracea (da Costa, 1778)

Turbo cylindraceus da Costa, 1778, *Pupa umbilicata* Draparnaud, 1801, *Pupa anconostoma* R. T. Lowe, 1831, *Pupa anconostoma* var. α *gyrata* R. T. Lowe, 1831, *Pupa anconostoma* var. β *curta* R. T. Lowe, 1831, *Pupa umbilicata anconostoma* – Wollaston, 1878, *Lauria (Lauria) cylindracea* – Bank *et al.*, 2002.

This species is widely distributed around the Mediterranean, Western Europe, parts of Africa and on Macaronesia (Bruggen, van, 1991). There are early records (mid 19th century) from both Deserta Grande (Lowe) and Bugio (Paiva), and it is listed from both islands as *Pupa umbilicata anconostoma* R. T. Lowe, 1831 by Wollaston (1878). It has never been found since on either island, nor as a fossil. The records may represent adventitious and short-lived introductions.

Genus *Leiostyla* R. T. Lowe, 1852

Pending revision of this genus, we have not allocated species to subgenera.

*****Leiostyla castanheiraensis* Groh & Pokryszko, 2019**

Endemic. Fossil from a single site on Deserta Grande (Teixeira *et al.*, 2019).

*****Leiostyla cooki* Cameron & Pokryszko, 2019**

Endemic. Fossil from a single site on Deserta Grande (Teixeira *et al.*, 2019).

*****Leiostyla desertaensis* Pokryszko & Teixeira, 2019**

Endemic. Fossil from Deserta Grande and Bugio (Teixeira *et al.*, 2019).

***Leiostyla macilenta* (R. T. Lowe, 1852)**

Pupa [*Leiostyla*] *macilenta* R. T. Lowe, 1852, *Lauria recta macilenta* – Pilsbry, 1923, *Leiostyla recta macilenta* – Waldén, 1983, *Leiostyla macilenta* – Cameron & Cook, 1999, *Leiostyla (Leiostyla) recta macilenta* – Bank *et al.*, 2002.

Wollaston (1878) accepted the species rank, while most later authors regarded it as a subspecies of *L. recta* (Waldén, 1983, Bank *et al.*, 2002), which is endemic to Madeira. Endemic to the Desertas. Live from Chão (leg. B. Pokryszko and I.S.), Deserta Grande and Bugio (Cameron & Cook, 1999, Teixeira *et al.*, in prep.). A single aberrant specimen from Deserta Grande, possibly fossil, may be related.

*****Leiostyla simulans* Pokryszko & Groh, 2019**

Endemic. Fossil from Deserta Grande and Bugio (Teixeira *et al.*, 2019).

***Leiostyla millegrana* (R. T. Lowe, 1852)**

Pupa [*Leiostyla*] *millegrana* R. T. Lowe, 1852, *Leiostyla (Craticula) millegrana* – Bank *et al.*, 2002.

Extant species, endemic to Madeira and the Desertas from where it is also known as a fossil. Alive from Chão, Deserta Grande and Bugio (Cameron & Cook, 1999, Teixeira *et al.*, in prep.), fossil from Deserta Grande and Bugio (Teixeira *et al.*, 2019). First record for Chão.

Family Valloniidae Morse, 1864

Subfamily Valloniinae Morse, 1864

Genus *Vallonia* Risso, 1826

***Vallonia pulchella* (O. F. Müller, 1774)**

Helix pulchella O. F. Müller, 1774, *Helix [Glaphyra] pulchella* – Paiva, 1867, *Helix [Vallonia] pulchella* – Wollaston, 1878, *Vallonia pulchella* – Bank *et al.*, 2002.

This globally distributed species was introduced to the Madeiran archipelago in historical times, where it is known from Madeira and Porto Santo. Paiva (1867) reported it as rare on Bugio, and it has not been found there since. It has recently been found fresh in Vale da Castanheira, Deserta Grande (leg. I.S), the first record for the island.

Family Truncatellinidae Steenberg, 1925

Genus *Truncatellina* R. T. Lowe, 1852

****Truncatellina linearis* (R. T. Lowe, 1852)**

Pupa [*Truncatellina*] *linearis* – R. T. Lowe, 1852

Extant species, endemic to Madeira from where it is also known as a fossil from the Quaternary deposits of the Ponta de São Lourenço. Fossil from Deserta Grande and Bugio (Teixeira *et al.*, in prep.). First record for the Desertas.

*****Truncatellina prainhana* Hutterer & Groh, 1993**

Fossil species, described from the Quaternary deposits of the Ponta de São Lourenço, Madeira (Hutterer & Groh, 1993). Fossil from Deserta Grande (Teixeira *et al.*, in prep.). First record for the Desertas.

Family Vertiginidae Fitzinger, 1833

Subfamily Nesopupinae Steenberg, 1925

Genus *Staurodon* R. T. Lowe, 1852

****Staurodon seminulum* (R. T. Lowe, 1852)**

Pupa [*Staurodon*] *seminulum* R. T. Lowe, 1852, *Staurodon seminulum* – Bank *et al.*, 2002, *Staurodon saxicola* – Seddon, 2008.

Extant species, endemic to Madeira and Porto Santo, from where it is also known as a fossil from Quaternary deposits. Bank *et al.* (2002) pointed out that the valid name to be used is *S. seminulum*

(R. T. Lowe, 1852), even though the synonymous name *Pupa saxicola*, described in the same work has page preference (Seddon, 2008); this name is preoccupied by *Pupa saxicola* Moquin-Tandon, 1843. Fossil from Bugio (Teixeira *et al.*, in prep.). First record for the Desertas, from which no live specimens have been recorded.

Superfamily Clausilioidea J. E. Gray, 1855

Family Clausiliidae J. E. Gray, 1855

Genus *Boettgeria* Heynemann, 1863

Subgenus *Boettgeria* s. str.

***Boettgeria (Boettgeria) jensi* Neubert & Groh, 1998**

Extant species, endemic to the major Desertas Islands. Recorded alive from Deserta Grande and Bugio (Neubert & Groh, 1998) and also known as fossils from the latter (Wollaston, 1878) under *Clausilia deltostoma* (R. T. Lowe, 1831) and from Deserta Grande (Teixeira *et al.*, in prep.).

***Boettgeria (Boettgeria) deltostoma crebristriata* (R. T. Lowe, 1855)**

Clausilia deltostoma var. β *crebristriata* R. T. Lowe, 1855, *Boettgeria deltostoma crebristriata* – Groh & Hemmen, 1986.

This subspecies was described as a form from Madeira and the Desertas. Groh & Hemmen (1986) restricted the locus typicus to the Desertas to exclude confusion with other narrowly ribbed forms of the species. Live records from Chão (leg. D.T., I.S.) and Deserta Grande. No fossil records, so possibly introduced by man in historical times.

Suborder Achatinina

Superfamily Achatinoidea Swainson, 1840

Family Ferussaciidae Bourguignat, 1883

Genus *Cecilioides* A. Férussac, 1814

***Cecilioides major* (Paiva, 1867)**

Achatina [Acicula] acicula var. β *major* Paiva, 1867.

Cecilioides veneta – Seddon, 2008 (non *Achatina veneta* Strobel, 1855 which is figured in Seddon's pl. 7, fig. C).

Known from the Madeira mainland (Ponta de São Lourenço alive) it has also been found live at Vale da Castanheira, Deserta Grande (leg. D.T.), and fossil in the north of Deserta Grande (leg. Gerber, Groh & Hemmen 1985; Teixeira *et al.*, 2019). Seddon (2008) erroneously referred this larger species to a south European species, *C. veneta* (Strobel, 1855) and consequently also wrongly synonymised *C. nyctelia* var. *maderensis* Pilsbry, 1908, but the fossil record proves that we have to deal with an autochthonous species to the Madeiran archipelago.

***Cecilioides* cf. *nyctelia* (Bourguignat, 1856)**

Helix [Cochlicopa] acicula [in part] – R. T. Lowe, 1831 (non *Buccinum acicula* O. F. Müller, 1774), *Glandina [Cionella] acicula* [in part] – Albers, 1854 (non *Buccinum acicula* O. F. Müller, 1774), *Achatina acicula* [in part] – R. T. Lowe, 1855 (non *Buccinum acicula* O. F. Müller, 1774), *Caecilianella nyctelia* Bourguignat, 1856 [replacement-name for *Glandina acicula* sensu Albers, 1854], *Achatina [Acicula] acicula* var. α *gracilis* Paiva, 1867, *Achatina [Acicula] acicula* [in part] – Wollaston, 1878 (non *Buccinum acicula* O. F. Müller, 1774), *Cecilioides (Cecilioides) nyctelia* – Waldén, 1983, *Cecilioides (Cecilioides) acicula* [in part] – Bank *et al.*, 2002 (non *Buccinum acicula* O. F. Müller, 1774), *Cecilioides acicula* [in part] – Seddon, 2008 (non *Buccinum acicula* O. F. Müller, 1774).

Recorded live from Deserta Grande (Wollaston) and Bugio (Paiva) in the 1860s under the name *C. acicula* (see Wollaston, 1878). At present, it is not clear if we are dealing with introduced European *C. acicula* itself, or with a species possibly endemic to the Madeiran archipelago which was, referring to a figure of Albers (1854), named *nyctelia* by Bourguignat in 1856. If there is a second *Cecilioides* on the Desertas, it is more probable that it is autochthonous. Modern records are needed and missing.

Genus *Amphorella* R. T. Lowe, 1852

Subgenus *Amphorella* s. str.

In listing *Amphorella* species below, we draw attention to the lack of any modern revision of this genus, in which conchological characters, the only ones used, need quantitative assessment and the support of molecular systematics.

***Amphorella* (incert. sed.) cf. *gracilis* (R. T. Lowe, 1831)**

Helix [*Cochlicopa*] *gracilis* R. T. Lowe, 1831, *Achatina* [*Ferussacia*] *gracilis* var. γ *vitrea* R. T. Lowe, 1855 (non *Achatina vitrea* Webb & Berthelot, 1833), *Achatina* [*Cionella*] *gracilis* var. β *vitrea* – Paiva, 1867, *Lovea* [*Fusillus*] *gracilis* – Wollaston, 1878, *Amphorella gracilis* – Bank *et al.*, 2002.

Amphorella gracilis (R. T. Lowe, 1831) was originally described from Porto Santo but was subsequently found alive on both Deserta Grande and Bugio (Wollaston, 1878). It has recently been recorded alive only on Bugio (Seddon *et al.*, 2017). While it appears that the name *gracilis* should be restricted to the form var. γ *vitrea* R. T. Lowe, 1855 (see above), it is not yet determined if the Desertan and Porto Santan forms are truly conspecific. It is not known as fossil on the Desertas.

***Amphorella* (*Amphorella*) *hypselia* (Pilsbry, 1909)**

Achatina [*Acicula*] *producta* R. T. Lowe, 1852 (non *Achatina producta* Reuss, 1849), *Achatina* [*Cionella*] *tornatellina* var. ϵ Paiva, 1867, *Lovea* [*Amphorella*] *producta* – Wollaston, 1878, *Ferussacia hypselia* Pilsbry, 1909 [replacement name for *Achatina producta* R. T. Lowe, 1852], *Amphorella* (*Amphorella*) *hypselia* – Bank *et al.*, 2002.

Extant endemic to Bugio from where it was reported by Wollaston (1878) under the name *Lovea producta* (Lowe, 1852), a preoccupied name, and confirmed alive by Cameron & Cook (1999). This species is not known as a fossil.

****Amphorella* (*Amphorella*) *intermedia* (Wollaston, 1878)**

? *Achatina* [*Cionella*] *tornatellina* var. β major Paiva, 1867, *Lovea* [*Amphorella*] *tornatellina* var. γ *intermedia* Wollaston, 1878, *Amphorella* (*Amphorella*) *intermedia* – Bank *et al.*, 2002.

This enigmatic species, apparently recorded alive on Porto Santo, is certainly known from the Desertas only from Deserta Grande, where it is recorded as live only by Wollaston (1878) and more recently as a fossil (Teixeira *et al.*, in prep.). A record from Bugio, accepted by Wollaston, derives from Paiva (1867). It is not clear that this represents presently recognised *A. intermedia*, as Paiva distinguishes it from *A. tornatellina* var. δ subvar. 2 that he records from Pico Branco on

Porto Santo, the type locality for the species. It is thus uncertain to what Paiva's var. β major refers, and the report of fossil *A. intermedia* on Bugio given in Bank *et al.*, (2002), accepting Wollaston's synonymy, might not stand.

? *Amphorella* (*Amphorella*) *melampoides* (Lowe, 1831)

Helix [*Cochlicopa*] *melampoides* R. T. Lowe, 1831, ?*Achatina* [*Amphorella*] *tornatellina* var. γ *maxima* Paiva, 1867.

Paiva (1867) reported a form, *Achatina tornatellina* var. γ *maxima* as alive, but rare on Bugio. The dimensions given match those of *Amphorella melampoides*. Neither Wollaston (1878) nor Seddon (2008) recognise it as an inhabitant of the Desertas, and there are no subsequent finds. The species is otherwise known both alive and fossil only from Porto Santo and its islets (Bank *et al.*, 2002).

***Amphorella* (*Amphorella*) cf. *mitriformis* (R. T. Lowe, 1852)**

Achatina [*Amphorella*] *mitriformis* R. T. Lowe, 1852, *Lovea* [*Amphorella*] *mitriformis* – Wollaston, 1878.

This extant species is recorded from all the larger islands of the Madeiran archipelago. Reported alive from all three Desertas and fossil from Bugio by Wollaston (1878), it is recently reported living on Chão and Deserta Grande only, but additionally for the first time as a fossil from the latter (Teixeira *et al.*, in prep.). Bank *et al.* (2002) do not include the record from Porto Santo, a single shell reported by Lowe and examined by Wollaston (1878), nor those from the Desertas, despite Wollaston's remark that it is widespread on all three. It cannot be taken for granted that the Desertan forms are conspecific with those of Madeira; Wollaston (1878) notes some difference in appearance.

Superfamily Punctoidea Morse, 1864

Family Punctidae Morse, 1864

Subfamily Laominae Suter, 1913

Genus *Paralaoma* Iredale, 1930

***Paraloma servilis* (Shuttleworth, 1852)**

Helix [*Helicella*] *pusilla* R. T. Lowe, 1831 (non *Helix pusilla* Vallot, 1801, nec *Helix pusilla* Fleming,

1828), *Helix servilis* Shuttleworth, 1852, *Patula* [*Acanthinula*] *pusilla* – Wollaston, 1878, *Punctum* (*Toltecia*) *pusillum* – Waldén, 1983, *Paralaoma caputspinulae* – Cameron & Cook, 1999, *Paralaoma servilis* – Bank *et al.*, 2002.

World-wide spread neozoon (Gittenberger *et al.*, 2020), found already in the 1820s on Madeira (Lowe, 1831) and the 1860's "not uncommonly" by Lowe & Wollaston on Deserta Grande (Wollaston, 1878). Recently recorded alive at Doca, Deserta Grande, by Cameron & Cook (1999) under *Paralaoma caputspinulae* (Reeve, 1852). This is the only recent record.

Superfamily Gastrodontoidea Tryon, 1866

Family Pristilomatidae T. Cockerell, 1891

Genus *Vitrea* Fitzinger, 1833

Vitrea contracta (Westerlund, 1871)

Helix crystallina – R. T. Lowe, 1831 (non O. F. Müller, 1774), *Helix crystallina* – Paiva, 1867 (non O. F. Müller, 1774), *Zonites contracta* Westerlund, 1871, *Hyalina* [*Cristallina*] *crystallina* – Wollaston, 1878 (non O. F. Müller, 1774), *Vitrea* (*Vitrea*) *contracta* – Waldén, 1983.

This widely distributed European species has been frequently recorded on Madeira since the 1820s (Lowe, 1831) under the name *Helix crystallina*. Recorded once on Deserta Grande by Cameron & Cook (1999), and reported from *graminosis* (grassy) sites on Bugio by Paiva (1867). The latter record has not been confirmed.

Family Gastrodontidae Tryon, 1866

Genus *Atlantica* Ancey, 1887

Atlantica calathoides (R. T. Lowe, 1863)

Helix [*Euromphala*] *calathoides* R. T. Lowe, 1852, *Discus* (*Atlantica*) *guerinianus calathoides* – Waldén, 1983, Bank *et al.*, 2002.

This extant species, endemic to the Desertas, has sometimes been treated as a subspecies of *Discus* (*Atlantica*) *guerinianus* (R. T. Lowe, 1863), endemic to Madeira, despite conchological differences noted by Wollaston (1878). Following Cameron *et al.* (2013), the genus is now placed in the family Gastrodontidae. Reported as possibly alive on Deserta Grande and as a fossil on Bugio

by Wollaston (1878), and recently confirmed alive on Deserta Grande at Risco, Rocha do Amarelo and Porto das Moças (leg. D.T., I.S.). Living populations are small, isolated and at-risk (Teixeira, 2017). Confirmed fossils are known from Deserta Grande and Bugio (Teixeira *et al.*, in prep.), but it has not been found alive on Bugio.

Genus *Janulus* R. T. Lowe, 1852

Janulus bifrons (R. T. Lowe, 1831)

Helix [*Helicella*] *bifrons* R. T. Lowe, 1831, *Patula* [*Janulus*] *bifrons* – Wollaston, 1878, *Janulus bifrons* – Waldén, 1983.

Extant species, endemic to Madeira, from where it is also known as a fossil from the Quaternary beds of Caniçal, and to the Desertas, where it is known alive from Deserta Grande (many recent finds) and Bugio (Wollaston, 1878; Cook unpublished, 1970) and recently also found on Chão (leg. D.T.). Fossil from Deserta Grande (first record Teixeira *et al.*, in prep.) and Bugio (Wollaston, 1878).

Family Oxychilidae Hesse 1927 (1879)

Subfamily Oxychilinae Hesse 1927 (1879)

Genus *Oxychilus* Fitzinger, 1833

Subgenus *Oxychilus* s. str.

? *Oxychilus* (*Oxychilus*) *cellarius* (O. F. Müller, 1774)

Helix cellaria O. F. Müller, 1774, *Helix* [*Hyalina*] *cellaria* – Paiva, 1867, *Hyalina* [*Lucilla*] *cellaria* – Wollaston, 1878.

This originally western European species is now found in many parts of the world. It is known from both Madeira and Porto Santo. Once reported under the name *Helix* [*Hyalina*] *cellaria* as being rare on Bugio by Paiva (1867), it has not been found since and it seems doubtful if the species ever lived on the Desertas.

Family Vitrinidae Fitzinger, 1833

Subfamily Plutoniinae T. Cockerell, 1893

Genus *Plutonia* Morelet, 1864

Subgenus *Madeirovitrina* Groh & Hemmen, 1986

****Plutonia (Madeirovitrina) crassa* (Groh & Hemmen, 1986)**

Described as an endemic fossil from the Quaternary beds of the Ponta de São Lourenço and possibly still alive in a tiny region in the northeast of Madeira, it is for the first time recorded fossil from Deserta Grande (Teixeira *et al.*, in prep.).

Superfamily Helicoidea Rafinesque, 1815

Family Geomitridae C. Boettger, 1909

Subfamily Geomitrinae C. Boettger, 1909

Tribe Cochlicellini Schileyko, 1991

Genus *Cochlicella* A. Férussac, 1821

? *Cochlicella acuta* (O. F. Müller, 1774)

Helix acuta O. F. Müller, 1774, *Bulimus* [*Cochlicellus*] *ventrosus* (non *Bulimus ventrosus* A. Férussac, 1820, nec *Bulimus ventricosus* Draparnaud, 1801 [= *Cochlicella (Prietocella) barbara* (Linnaeus, 1758)]) – Paiva, 1879.

This originally European species is known from Madeira and Porto Santo. Once reported under the name *Bulimus* [*Cochlicellus*] *ventricosus* as being rare on Bugio by Paiva (1867) it seems doubtful if the species ever lived on the Desertas.

Tribe Geomitriini C. Boettger, 1909

Genus *Helicomela* R. T. Lowe, 1855

Helicomela was previously regarded as a subgenus of *Caseolus*, but *Caseolus* has been shown after genetical analysis to be polyphyletic (Brozzo *et al.*, 2020).

*****Helicomela bowdichiana* (A. Férussac, 1832)**

Helix [*Helicogena*] *bowdichiana* A. Férussac, 1832, *Helix bowdichiana* – R. T. Lowe, 1855, *Caseolus (Helicomela) bowdichianus* – Mandahl-Barth, 1950.

The fossil species *H. bowdichianus*, frequent on Porto Santo and at the Ponta de São Lourenço on Madeira, was recently found on Deserta Grande (Teixeira *et al.*, 2019), a first record for the Desertas group.

***Helicomela punctulata avellana* (R. T. Lowe, 1855)**

Helix [*Helicomela*] *punctulata* var. β *avellana* R. T. Lowe, 1855, *Helix* [*Plebecula*] *punctulata* var. α *avellana* – Paiva, 1867, *Caseolus (Helicomela) punctulatus avellanus* – Mandahl-Barth, 1950, *Caseolus (Caseolus) punctulatus avellanus* – Bank *et al.*, 2002.

The status of this subspecies of *H. punctulatus*, which has its nominate subspecies living on Porto Santo, requires further anatomical and genetical work. It may merit species rank. Described alive from Bugio, from where it was also reported as a fossil (Wollaston, 1878) its occurrence has recently been confirmed. Additionally, it has also been found both alive on Deserta Grande (Rocha do Amarelo, leg. D.T., I.S.) and also as a fossil (Teixeira *et al.*, in prep.).

Genus *Caseolus* R. T. Lowe, 1852

Subgenus *Caseolus* s. str.

****Caseolus (Caseolus?) galeatus* (R. T. Lowe, 1862)**

Helix calva var. γ *galeata* R. T. Lowe, 1862, *Helix* [*Lemniscia*] *galeata* – Wollaston, 1878, *Lemniscia calva galeata* – Mandahl-Barth, 1950, *Lemniscia galeata* – Waldén, 1983, *Caseolus (Caseolus?) calvus galeatus* – Bank *et al.*, 2002.

We follow Seddon (2008) in seeing this as a valid species, not a subspecies of *C. calvus* (R. T. Lowe, 1831). Being an extant species endemic to the northeast Madeira mainland, it is here for the first time recorded as a fossil only from Deserta Grande (Teixeira *et al.*, in prep.). The relationship to *Lemniscia*, represented by *L. michaudi* (Deshayes, 1839) on Porto Santo, is doubtful, as Brozzo *et al.* (2020) find *Lemniscia* closely related to the genera *Hystericella*, *Callina* and *Wollastonaria* rather than *Caseolus*. The relationship to *Caseolus* has, however, yet to be confirmed by anatomical and genetical research.

***Caseolus (Caseolus) abjectus nesiotus* (Wollaston, 1878)**

Helix [*Caseolus*] *abjecta* var. γ *nesiotus* Wollaston, 1878, *Caseolus (Caseolus) abjectus nesiotus* – Mandahl-Barth, 1950.

Extant endemic subspecies, found on Deserta Grande and Bugio. The nominate subspecies, *C. abjectus abjectus* lives on Porto Santo. Live records from Bugio (Wollaston, 1878) and Deserta Grande (Paiva, 1867) have been confirmed in recent times (Cameron & Cook, 1999, IFCN 2020). First fossil records from Deserta Grande only, but not Bugio (Teixeira *et al.*, in prep.). The status of this subspecies of *C. abjectus* (R. T. Lowe, 1831) requires further anatomical and genetical work, an elevation to species rank seems probable.

***Caseolus (Caseolus?) pittae* (Paiva, 1866)**

Helix Pittae Paiva, 1866, *Helix [Actinella] Pittae* – Paiva, 1867, not *Helix [Discula] polymorpha* var δ Pittae – Wollaston, 1878 (see under *Actinella fecundaerrata*), *Caseolus (Caseolus?) innominatus pittae* – Bank *et al.*, 2002.

Endemic to and possibly alive on Bugio (Paiva 1866, 1867). There are no records subsequent to the original discovery, but existence is proven by type material in the collection of the MNHN Paris. See discussion in Teixeira *et al.* (2019) dealing with the confusion with *Actinella fecundaerrata* Groh & Cameron, 2019. The taxon was ignored by Mandahl-Barth (1950), Waldén (1983) and Seddon (2008).

? *Caseolus (Caseolus) innominatus compactus* (R. T. Lowe, 1831)

Caseolus innomimatus J. E. Gray, 1825, *Helix [Helicella] compacta* R. T. Lowe, 1831, *Caseolus (Caseolus) compactus compactus* – Mandahl-Barth, 1950, *Caseolus (Caseolus) innominatus compactus* – Bank *et al.*, 2002.

The occurrence of this extant subspecies, otherwise restricted to the Ponta de São Lourenço on Madeira, was recorded by Paiva (1867) from Bugio. It has not been found subsequently and the record seems doubtful. Other subspecies of *Caseolus innominatus* (J. E. Gray, 1825) are recorded from Porto Santo.

Subgenus *Leptostictea* Mandahl-Barth, 1950

? *Caseolus (Leptostictea) leptostictus* (R. T. Lowe, 1831)

Helix [Helicella] leptosticta R. T. Lowe, 1831, *Helix [Ocenebrina] leptosticta* – Paiva, 1867, *Caseolus (Leptostictea) leptostictus* – Mandahl-Barth, 1950,

Caseolus (Leptostictea) leptostictus leptostictus – Bank *et al.*, 2002.

There is only one report of this otherwise Madeiran species from Bugio (Paiva, 1867). All later finds of specimens on the Desertas Islands assigned to this subgenus are *C. micromphalus* (see below).

***Caseolus (Leptostictea) micromphalus* (R. T. Lowe, 1852)**

Helix [Placentula] micromphala R. T. Lowe, 1852, *Caseolus (Leptostictea) micromphalus* – Mandahl-Barth, 1950, *Caseolus (Leptostictea) leptostictus micromphalus* – Bank *et al.*, 2002, *Caseolus micromphalus* – Seddon, 2008.

An extant endemic species of the Desertas, it was reported alive from Chão, Deserta Grande and Bugio and from the latter also as a fossil by Wollaston (1878). This was confirmed in recent times (Cameron & Cook, 1999; leg. D.T., IFCN, 2020); the fossil record from Deserta Grande is new (Teixeira *et al.*, in prep.). Bank *et al.* (2002) treat it as a subspecies of *C. leptostictus* (R. T. Lowe, 1831).

Genus *Disculella* Pilsbry, 1895

? *Disculella spirulina* (T. Cockerell, 1921)

Helix [Placentula] spirorbis R. T. Lowe, 1852 (non *Helix spirorbis* Linnaeus, 1758), *Helix [Ocenebrina] spirorbis* – Paiva, 1867, *Geomitra (Disculella) spirulina* T. Cockerell, 1921, *Ochthebrina spirorbis* – Mandahl-Barth, 1950, *Disculella spirulina* – Waldén, 1983.

The occurrence of this extant species, endemic to the west of Madeira itself, was only mentioned once by Paiva (1867) under the name *Helix spirorbis* from Bugio, but this record seems to be doubtful.

Genus *Actinella* R. T. Lowe, 1852

Subgenus *Actinella* s. str.

***Actinella (Actinella) actinophora* (R. T. Lowe, 1831)**

Helix [Helicogena] actinophora R. T. Lowe, 1831, *Helix [Gonostoma] actinophora* – Wollaston, 1878, *Actinella (Actinella) actinophora* – Mandahl-Barth, 1950, *Actinella (Actinella) actinophora actinophora* – Waldén, 1983.

This species is an extant endemic of the Madeira mainland and Deserta Grande. From Madeira it is also known as a fossil from the Quaternary beds of Caniçal (Wollaston, 1878). Fossil findings on Bugio (Wollaston, 1878) referring to that species concern the fossil taxon *A. descendens* (see below); Wollaston also records that Paiva obtained living specimens from Bugio, but it cannot be excluded that these refer to *A. descendens* (see below). *A. actinophora* was rediscovered live at Risco and Rocha do Barbusano on Deserta Grande (leg. D.T., I.S., IFCN 2020). Fossils were first found recently on Deserta Grande (Teixeira et al., 2019 and in prep.).

*****Actinella (Actinella) descendens* (Wollaston, 1878)**

Helix [Gonostoma] actinophora var. β descendens Wollaston, 1878, *Actinella (Actinella) actinophora descendens* – Waldén, 1983.

A fossil species (excluding the undetermined live record from Bugio, see above), endemic to the Desertas. Described from Bugio as a variation of *A. actinophora* (Wollaston, 1878), and later seen as a subspecies of *A. actinophora*. It has been recently recorded as a fossil on Deserta Grande and Bugio. Morphometrics and co-occurrence with fossil *A. actinophora* establish its status as a species (Teixeira et al., 2019).

****Actinella (Actinella) arcinella* (R. T. Lowe, 1855)**

Helix [Rimula] arcinella R. T. Lowe, 1855, *Actinella (Faustella) arcinella* – Mandahl-Barth, 1950, *Actinella (Actinella) arcinella arcinella* – Waldén, 1983, *Actinella (Actinella) arcinella* – Bank et al., 2002.

An endemic fossil species, described from the Quaternary beds of Caniçal (Lowe, 1855) and later also detected on Deserta Grande (Bank et al., 2002), where it has also been recorded recently. It is now also recorded for the first time from Bugio, albeit from a single specimen (Teixeira et al., in prep.).

*****Actinella (Actinella) fecundaerrata* Groh & Cameron, 2019**

Helix senilis var. γ pusilla R. T. Lowe, 1855 (non *Helix pusilla* Vallot, 1801), *Helix [Discula] polymorpha* var. δ Pittae – Wollaston, 1878, not in part,

Discula (Discula) polymorpha poromphala – sensu Bank et al., 2002.

An endemic fossil species found only on Bugio, from where it was described as *Helix senilis* var. γ pusilla by Lowe in 1855 and later misreported by Wollaston (1878) under the name *Helix polymorpha* var. δ pitta. For the differences from the true *Helix pitta* Paiva, 1866 see the discussion in Teixeira et al. (2019).

***Actinella (Actinella) laciniosa* (R. T. Lowe, 1852)**

Helix [Irus] laciniosa R. T. Lowe, 1852, *Actinella (Actinella) laciniosa* – Mandahl-Barth, 1950.

An extant endemic species of Chão, where it was found in 1848 by Leacock (Wollaston, 1878), and the extreme north of Deserta Grande (Lowe, 1852). From both islands, it has been confirmed recently by D.T. in 2012 (IFCN, 2020). Not known as a fossil.

****Actinella (Actinella) lentiginosa* (R. T. Lowe, 1831)**

Helix [Helicella] lentiginosa R. T. Lowe, 1831, *Helix [Actinella] lentiginosa* – Wollaston, 1878.

Fossil material from near Doca, Deserta Grande, has been assigned to *A. lentiginosa* (Fig. 2c; living specimen from Madeira, Fig. 2d), where it constitutes the first record for the Desertas (Teixeira et al., in prep.). It is living on Madeira, where two subspecies, *A. lentiginosa lentiginosa* (R. T. Lowe, 1831) and *A. lentiginosa stellaris* (R. T. Lowe 1852) are recognised (Bank et al., 2002). The Desertan specimens cannot be assigned with certainty to either, and their status requires review.

? *Actinella (Actinella) arcta* (R. T. Lowe, 1831)

Helix [Helicodonta] arcta R. T. Lowe, 1831, *Helix [Actinella] arcta* – Paiva, 1867, *Actinella (Actinella) arcta* – Mandahl-Barth, 1950.

A. arcta was recorded extant on Bugio by Paiva (1867). There are no subsequent records, extant or fossil, from that island and this record must be regarded as doubtful. Living *A. arcta* from Madeira is shown in Fig. 2b.

***Actinella (Actinella) sp. aff. arcta* (R. T. Lowe, 1831)**

Living specimens of an *Actinella* species have been found on Deserta Grande at Tabaqueiro

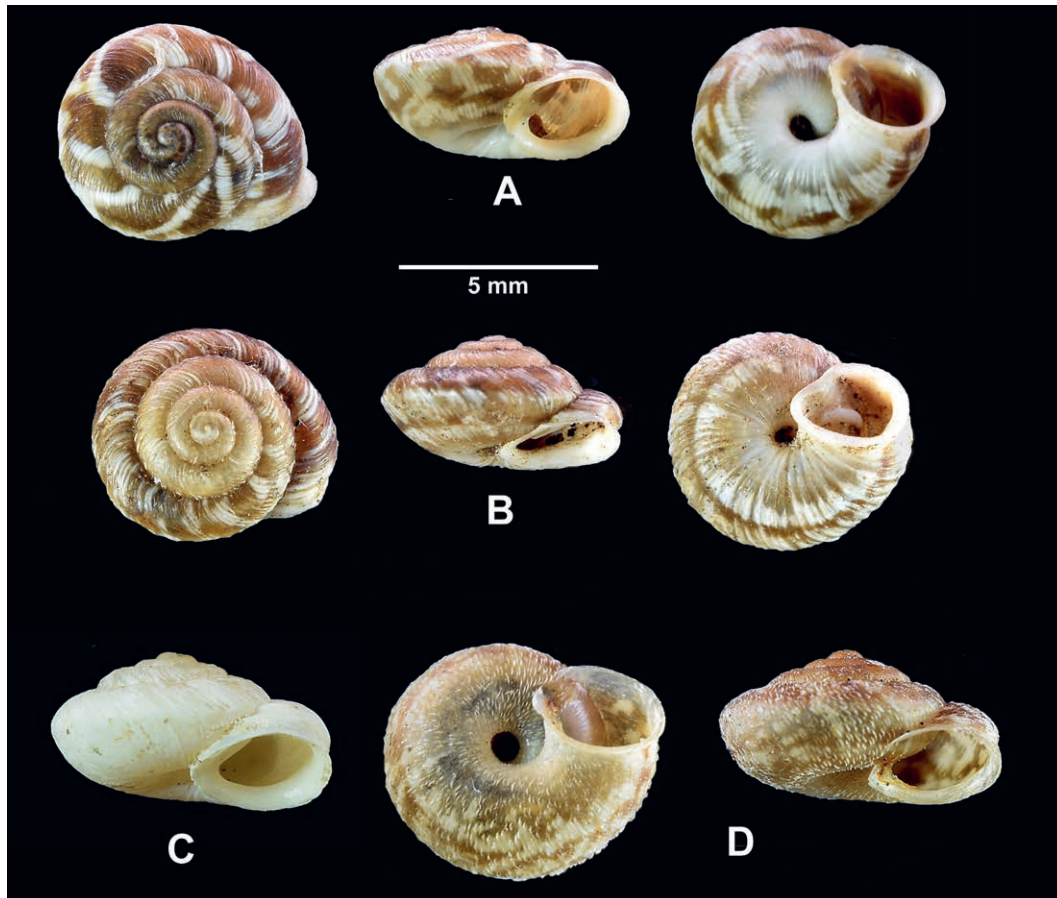


Figure 2 *Actinella* species from the Desertas Islands. **A:** fresh *Actinella* aff. *arcta* from Deserta Grande (leg. IS); **B:** fresh *A. arcta* from Madeira (leg. RADC); **C:** fossil *A. lentiginosa* from Deserta Grande: Teixeira *et al.* (in prep.); **D:** fresh *A. lentiginosa* from Madeira (leg. RADC).

(Fig. 2a), Furna dos Lobos and Calhau das Areias (leg. I.S.). These lack the internal callosity in the shell mouth of *A. arcta*. They also have an umbilicus resembling that of *A. lentiginosa*, but in shell sculpture and sharp-shouldered appearance of the periphery, they resemble *A. arcta*. Molecular and anatomical studies are needed to relate these to living material from Madeira.

Genus *Plebecula* R. T. Lowe, 1852

Plebecula, formerly a subgenus of *Actinella*, has been shown after genetical analysis to be an isolated clade of the polyphyletic *Actinella* (Brozzo *et al.*, 2018).

Plebecula nitidiuscula (G. B. Sowerby I, 1824)

Helix nitidiuscula G. B. Sowerby I, 1824, *Helix* [*Plebecula*] *vulgata* R. T. Lowe, 1852, *Helix* [*Plebecula*] *vulgata* var. α major Paiva, 1867 (in part), *Helix* [*Plebecula*] *vulgata* var. δ pulchra

Paiva, 1867 (in part), *Actinella* (*Plebecula*) *nitidiuscula nitidiuscula* – Mandahl-Barth, 1950.

This extant species is an endemic, living on Madeira and on Deserta Grande (Paiva, 1867 as var. major in part) and Bugio (Paiva, 1867 as var. pulchra) from where it was mentioned by Wollaston (1878) under the name *Helix vulgata* (R. T. Lowe, 1852). It is now found alive on both Deserta Grande and Bugio and Teixeira *et al.* (2019) report the first fossil records from Deserta Grande only. What Wollaston (1878) names *Helix nitidiuscula* from Porto Santo is in fact *Plebecula littorinella*, endemic to that island. We note that although the name *nitidiuscula* has been accepted as the correct one for this Madeiran and Desertan species (Mandahl-Barth, 1950; Bank *et al.*, 2002; Seddon, 2008), the locus typicus is uncertain.

***Plebecula saxipotens* (Wollaston, 1878)

Helix [*Plebecula*] *vulgata* var. ϵ saxipotens Wollaston, 1878, *Helix* [*Plebecula*] *vulgata* var. δ

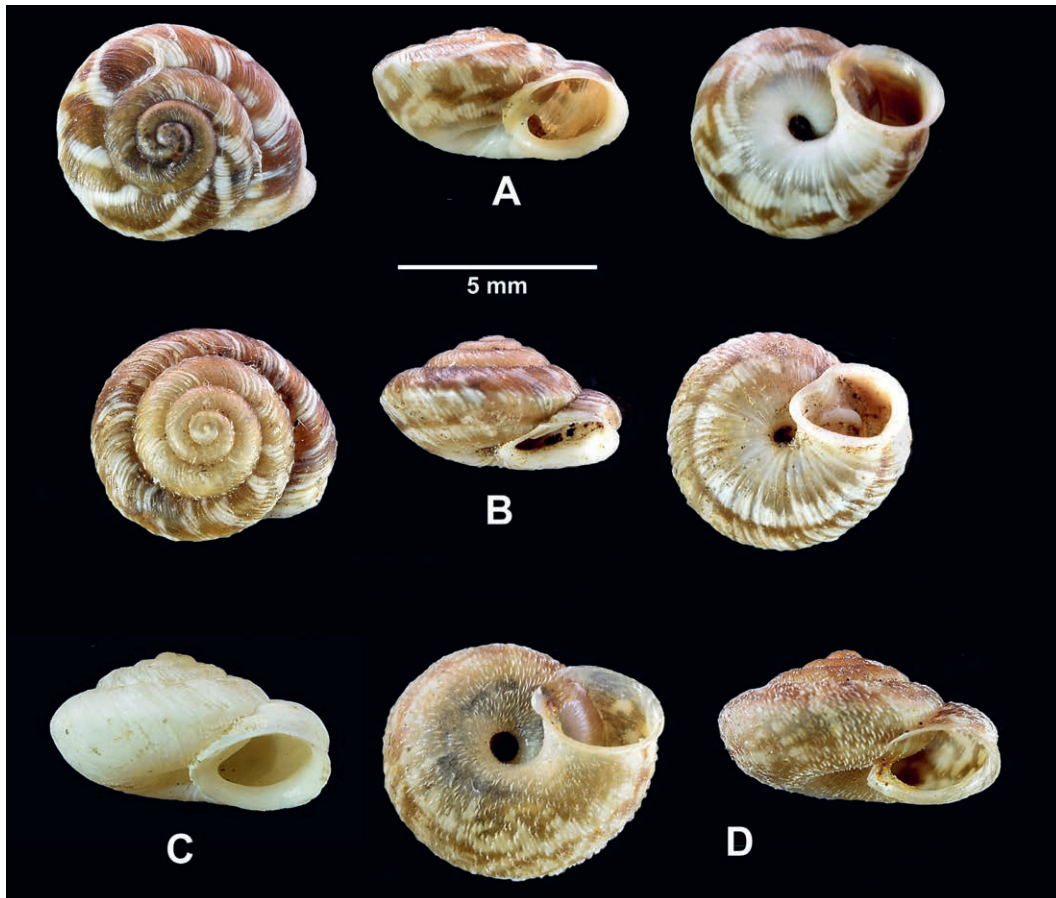


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(Fig. 2a), Furna dos Lobos and Calhau das Areias (leg. I.S.). These lack the internal callosity in the shell mouth of *A. arcta*. They also have an umbilicus resembling that of *A. lentiginosa*, but in shell sculpture and sharp-shouldered appearance of the periphery, they resemble *A. arcta*. Molecular and anatomical studies are needed to relate these to living material from Madeira.

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Plebecula nitidiuscula (G. B. Sowerby I, 1824)

Helix nitidiuscula G. B. Sowerby I, 1824, *Helix* [*Plebecula*] *vulgata* R. T. Lowe, 1852, *Helix* [*Plebecula*] *vulgata* var. α major Paiva, 1867 (in part), *Helix* [*Plebecula*] *vulgata* var. δ pulchra

Paiva, 1867 (in part), *Actinella* (*Plebecula*) *nitidiuscula nitidiuscula* – Mandahl-Barth, 1950.

This extant species is an endemic, living on Madeira and on Deserta Grande (Paiva, 1867 as var. major in part) and Bugio (Paiva, 1867 as var. pulchra) from where it was mentioned by Wollaston (1878) under the name *Helix vulgata* (R. T. Lowe, 1852). It is now found alive on both Deserta Grande and Bugio and Teixeira *et al.* (2019) report the first fossil records from Deserta Grande only. What Wollaston (1878) names *Helix nitidiuscula* from Porto Santo is in fact *Plebecula littorinella*, endemic to that island. We note that although the name *nitidiuscula* has been accepted as the correct one for this Madeiran and Desertan species (Mandahl-Barth, 1950; Bank *et al.*, 2002; Seddon, 2008), the locus typicus is uncertain.

***Plebecula saxipotens* (Wollaston, 1878)

Helix [*Plebecula*] *vulgata* var. ϵ saxipotens Wollaston, 1878, *Helix* [*Plebecula*] *vulgata* var. δ

pulchra Paiva, 1867 (in part), *Actinella* (*Plebecula*) *nitidiuscula saxipotens* – Mandahl-Barth, 1950.

A fossil species described by Wollaston (1878) from Bugio under the name *Helix vulgata* var. ϵ saxipotens. It is present as a fossil on both Deserta Grande and Bugio (Teixeira *et al.*, 2019), and its status is confirmed by co-existence in some deposits with *P. nitidiuscula*. It was first recorded as a fossil on Deserta Grande by Cameron & Cook (1999) and has been found in other sites since (Teixeira *et al.*, 2019). It is not known alive.

Plebecula anaglyptica (Reeve, 1852)

Helix anaglyptica Reeve, 1852, *Helix* [*Plebecula*] *vulgata* var. α major Paiva, 1867 (in part), *Helix* [*Plebecula*] *vulgata* var. β [sic! pro α] deserticola Wollaston, 1878, *Actinella* (*Plebecula*) *anaglyptica* – Mandahl-Barth, 1950.

An extant endemic species of the island of Chão only, from where it was named by Paiva (1867) *Helix vulgata* var. α major and by Wollaston (1878) var. β deserticola. Nevertheless, it was described by Reeve 36 years earlier. Cameron & Cook (1999) recorded it from Chão under *A. nitidiuscula*. It remains living there (IFCN, 2020).

Genus *Geomitra* Swainson, 1840

Geomitra coronula (R. T. Lowe, 1852)

Helix [*Coronaria*] *coronula* R. T. Lowe, 1852, *Helix* [*Octephila*] *coronula* – Paiva, 1867 (in part), *Helix* [*Coronaria*] *coronula* – Wollaston, 1878, *Geomitra* (*Geomitra*) *coronula* – Mandahl-Barth, 1950, *Craspedaria* (*Coronaria*) *coronula* – Bank *et al.*, 2002, *Geomitra coronula* – Seddon, 2008.

An extant and fossil endemic species of both southern Desertas islands. Whilst it was described as a fossil by R. T. Lowe in 1852 and thought by Wollaston (1878) to be restricted to Bugio alone, recent finding of living specimens on Deserta Grande (Pedregal, leg. D.T., I.S.), where it is rare (Teixeira *et al.*, 2018a), make it probable that Moniz (in Paiva, 1867) found it alive there and that Paiva did not mix it up with the following species. This is the first documented living record from Deserta Grande where it also was detected at several fossil sites, as also on Bugio, where it has not been found alive (Teixeira *et al.*, 2019).

Geomitra grabhami (Wollaston, 1878)

Helix [*Octephila*] *coronula* – Paiva, 1867 (in part), *Helix* [*Coronaria*] *Grabhami* Wollaston, 1878,

Geomitra (*Geomitra*) *grabhami* – Mandahl-Barth, 1950, *Craspedaria* (*Coronaria*) *grabhami* – Bank *et al.*, 2002, *Geomitra grabhami* – Seddon, 2008.

An extant endemic species of the north of Deserta Grande where Moniz first detected it in the 1860s (Paiva, 1867). It still lives on Deserta Grande (Fajã Grande, leg. D.T., I.S.), where it is rare (Teixeira *et al.*, 2018b) and is also now known as fossils from the north end of the island (leg. Gerber, Groh & Hemmen, 1985; Cameron & Cook, 1999; Teixeira *et al.*, 2019).

? *Geomitra* (*Geomitra*) *tiarella* (Webb & Berthelot, 1833)

Helix tiarella Webb & Berthelot, 1833, *Helix* [*Coronaria*] *tiarella* Wollaston, 1878, *Geomitra* (*Geomitra*) *tiarella* – Mandahl-Barth, 1950, *Craspedaria* (*Coronaria*) *tiarella* – Bank *et al.*, 2002, *Geomitra tiarella* – Seddon, 2008.

Wollaston (1878) regarded this species as endemic to Madeira itself, where closely related populations still live – in shrinking numbers – as rock-dwellers in the north of the island in coastal areas, but it is abundant as a fossil in the Quaternary beds of the Ponta São Lourenço. The indication by Bank *et al.* (2002) that it also occurs on Deserta Grande as a fossil seems unlikely. We have no good evidence for the existence of *G. tiarella* in the Desertas.

***Geomitra* (*Geomitra*) sp. indet. juv. (n. sp.?)

This fossil species, of which only juveniles are known (Fig. 3b), is endemic to Deserta Grande and probably closely related to a yet undescribed species that lives in the south of Madeira mainland (Fig. 3a) (Teixeira *et al.*, 2019; in prep.).

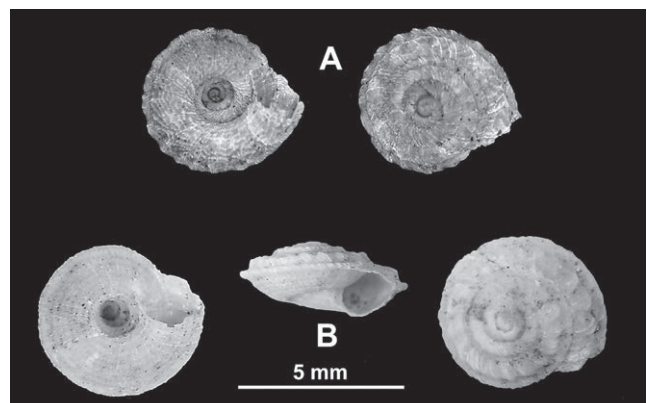


Figure 3 Undetermined *Geomitra* species. **A:** fresh from SW Madeira (leg. KG); **B:** fossil from Deserta Grande (site 3 of Teixeira *et al.*, 2019).

Genus *Discula* R. T. Lowe, 1852**Subgenus *Discula* s. str.*****Discula (Discula) cameroni* Pokryszko, Groh & Teixeira, 2019**

Endemic. First detected as fossils on Deserta Grande (Teixeira *et al.*, 2019) and subsequently living at the southern end of Deserta Grande (Planalto Sul and Rocha do Amarelo, leg. D.T., IFCN 2020), and at the northern end of Bugio (leg. & coll. I.S.) (Teixeira *et al.*, in prep.).

***Discula (Discula) tetrica* (R. T. Lowe, 1862)**

Helix tetrica R. T. Lowe, 1852, *Helix [Discula] tetrica* – Wollaston, 1878, *Discula (Discula) tetrica* – Mandahl-Barth, 1950.

Endemic. Live and fossil on Bugio only (Wollaston, 1878), but also found both fresh and fossil recently (leg. I.S.) (Teixeira *et al.*, in prep.).

***Discula (Discula) polymorpha* (R. T. Lowe, 1831)**

Helix [Helicella] polymorpha R. T. Lowe, 1831, *Helix [Discula] polymorpha* – Wollaston, 1878.

There are many described subspecies of this very variable species (Bank *et al.*, 2002), found on both Madeira and the Desertas. While it is clear that many do not represent clearly defined and geographically replacing taxa, those listed below have been recorded on the Desertas. Patterns of distribution suggest a degree of convergent evolution or phenotypic plasticity among them. Molecular analysis of forms from all three islands is needed to establish relationships.

***Discula (Discula) polymorpha minor* Mandahl-Barth, 1950**

Discula (Discula) polymorpha minor – Waldén, 1983, *Discula (Discula) polymorpha poromphala* – Bank *et al.*, 2002. Note remarks on *Actinella (Actinella) fecundaerrata* above.

A form of *D. polymorpha* described from Chão by Mandahl-Barth (1950) which closely resembles *D. polymorpha poromphala* (see below), to which it appears to be assigned by Wollaston (1878). H. W. Waldén (unpublished) regarded it as endemic to Chão, while the very similar form found in the northern part of Deserta Grande he assigned to *D. polymorpha poromphala*. Recent studies (D.T. unpublished) suggest that there is

a single form common to Chão and the north of Deserta Grande as far as Pedregal.

***Discula (Discula) polymorpha nebulata* (R. T. Lowe, 1855)**

Helix [Discula] senilis (non *Helix senilis* Morelet, 1851) var. α *nebulata* R. T. Lowe, 1855, *Helix [Discula] salebrosa* R. T. Lowe, 1862, *Helix [Discula] polymorpha* var. β . *salebrosa* – Wollaston, 1878, *Discula (Discula) polymorpha senilis* – Mandahl-Barth, 1950, *Discula (Discula) polymorpha salebrosa* – Waldén, 1983, *Discula (Discula) polymorpha nebulata* – Bank *et al.*, 2002.

Found both living and fossil on Deserta Grande (Teixeira *et al.*, 2019). Wollaston (1878), under var. β . *salebrosa*, records it live from Madeira and all three Desertas, and as fossil from both Madeira and Bugio. While Madeiran records need reassessment, our surveys have found it only on Deserta Grande. All specimens of *D. polymorpha* recently found both living and fossil from Bugio have been assigned to *D. p. poromphala* (below).

***Discula (Discula) polymorpha poromphala* (R. T. Lowe, 1852)**

Helix [Discula] poromphala R. T. Lowe, 1855, *Discula (Discula) polymorpha poromphala* – Mandahl-Barth, 1950, Waldén, 1983, *Discula (Discula) polymorpha pusilla* – Waldén, 1983 (non *Helix senilis* var. γ *pusilla* R. T. Lowe, 1855=*Actinella (Actinella) fecundaerrata* Groh & Cameron, 2019).

Endemic to the Desertas. While it has been recorded recently both as a fossil and alive on Bugio (Teixeira *et al.*, 2019), it is not known as a fossil from Deserta Grande. Wollaston (1878) records it alive from all three Deserta Islands. H.W. Waldén (unpublished), as stated above under *D. polymorpha minor*, assigned the form from the north of Deserta Grande to this subspecies, while D.T. (unpublished) regarded these as the same as those on Chão. It is clear that the systematics of these taxa is unresolved.

***Discula (Discula) polymorpha docaensis* Teixeira & Groh, 2019**

Endemic to Deserta Grande, where it has been found both living (leg. R. A. D. Cameron and L. M. Cook) and fossil (Teixeira *et al.*, 2019) only in the vicinity of Doca. This subspecies is both highly distinctive and geographically localised.

***Discula (Discula) lyelliana* (R. T. Lowe, 1852)**

Helix [*Tectula*] *lyelliana* R. T. Lowe, 1852, *Helix* [*Tectula*] *Bulwerii* var β Albers, 1854, *Helix* [*Tectula*] *lyelliana* var. β *gigas* Wollaston, 1878, *Discula (Discula) lyelliana* – Mandahl-Barth, 1950, *Discula (Discula) lyelliana gigas* – Mandahl-Barth, 1950.

Endemic. Both alive (Risco, leg. D.T. & I.S.) and fossil (Teixeira *et al.*, in prep.) on Deserta Grande. Fossil on Bugio, west side of south plateau at 210m (leg. & coll. I.S. 20.8.2008). This is the first record for Bugio.

Subgenus *Mandahlia* Forcart, 1965****Discula (Mandahlia) tectiformis ludovici* (Albers, 1854)**

Helix [*Crenea*] *Ludovici* Albers, 1854, *Discula (Tectula) tectiformis ludovici* – Mandahl-Barth, 1950, *Discula (Mandahlia) tectiformis ludovici* – Waldén, 1983.

Known as a fossil from a single site on Deserta Grande, above Doca (South) at 60m (leg. & coll. I.S. 9.8.2008). This extinct subspecies was previously known only from Porto Santo (Bank *et al.*, 2002), where there is a living subspecies *D. tectiformis tectiformis* (G. B. Sowerby I, 1824). First record for the Desertas.

Genus *Steenbergia* Mandahl-Barth, 1950

The genus *Steenbergia* was separated on anatomical characters by Mandahl-Barth (1950) from a closely related monospecific genus usually known as *Heterostoma* Hartmann, 1843, a name that is unfortunately preoccupied by an older homonym proposed by De Filippi (1837) for a platyhelminth. Genital anatomy, however, does not correlate well with shell morphology, and is complicated by the occurrence, sometimes synonymically, of hemiphallics (Craze & Lace, 2000). While there may be a close relationship between *Steenbergia/Heterostoma* and *Spirorbula* (Brozzo *et al.*, 2018), it seems that all taxa previously referred to as *Heterostoma* should be referred to as *Steenbergia*.

Steenbergia desertae* (Mandahl-Barth, 1950)**Steenbergia duplex desertae* Mandahl-Barth, 1950**

Known alive from all three Desertas, and as fossils from Deserta Grande and Bugio (Teixeira *et*

al., in prep.). The status of described species of *Steenbergia* requires clarification; there may be a complex of forms attributable to *S. paupercula* (R. T. Lowe, 1831). Bank *et al.* (2002) treat it as a species of *Heterostoma*, Seddon (2008) figures it as a form of *Steenbergia paupercula*.

Genus *Spirorbula* R. T. Lowe, 1852****Spirorbula squalida* (R. T. Lowe, 1852)**

Helix [*Irus*] *squalida* R. T. Lowe, 1852, *Spirorbula squalida* – Mandahl-Barth, 1950.

Known only as fossil from Deserta Grande. (Teixeira *et al.*, in prep.), but also living on Madeira (Seddon, 2008).

? *Spirorbula* sp. indet. (n.sp.?)**

A single, damaged and fossil specimen from the north of Deserta Grande appears not to match *S. squalida* (Teixeira *et al.*, 2019).

Genus *Leptaxis* R. T. Lowe, 1852**Subgenus *Leptaxis* s. str.*****Leptaxis (Leptaxis) simia* (A. Férussac, 1832)**

As with *Discula polymorpha* (see above), this species has a number of designated subspecies. The fossil material is frequently fragmented, making allocation among these doubtful. Three such subspecies are recorded for the Desertas.

***Leptaxis (Leptaxis) simia advenoides* (Paiva, 1867)**

Helix [*Leptaxis*] *erubescens* var. γ *advenoides* Paiva, 1867, *Leptaxis (Leptaxis) erubescens advenoides* – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Leptaxis) simia advenoides* – Bank *et al.*, 2002.

Originally described as a fossil from the Ponta de São Lourenço (Paiva, 1867: 14), it is also recorded extant on Chão (Wollaston, 1878). While also recorded from the north of Deserta Grande by Mandahl-Barth (1950), recent finds of *L. simia* from the northern two-thirds of Deserta Grande refer to *L. simia simia* (leg. D.T.). Bank *et al.* (2002) state that it is only fossil on Madeira and living on Ilhéu Chão, whilst Seddon (2008) restricts the subspecies to Ilhéu Chão alone.

***Leptaxis (Leptaxis) simia hyaena* (R. T. Lowe, 1852)**

Helix [*Leptaxis*] *hyaena* R. T. Lowe, 1852, *Helix* [*Leptaxis*] *erubescens* var. β Paiva, 1867, *Helix* [*Leptaxis*] *erubescens* var. δ *hyaena* – Wollaston, 1878, *Leptaxis (Leptaxis) erubescens hyaena* – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Leptaxis) simia hyaena* – Bank *et al.*, 2002.

Known both alive and fossil from Bugio (Teixeira *et al.*, in prep.) and alive from the southern part of Deserta Grande, where early records (Paiva, 1867; Wollaston, 1878) have recently been confirmed (leg. D.T., I.S., IFCN 2020).

***Leptaxis (Leptaxis) simia simia* (A. Férussac, 1832)**

Helix (Helicogena) simia A. Férussac, 1832, *Helix [Helicogena] erubescens* R. T. Lowe, 1831 (non *Helix erubescens* Solander, 1786), *Helix [Leptaxis] erubescens* var. β [normalis] Wollaston, 1878, *Leptaxis (Leptaxis) erubescens erubescens* – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Leptaxis) simia simia* – Bank *et al.*, 2002.

Native to Madeira and Deserta Grande where it is known both alive and fossil (Teixeira *et al.*, in prep.). Fossils from Deserta Grande are placed here with caution. Introduced to São Miguel and Terceira in the Azorean islands (Bank *et al.*, 2002).

*****Leptaxis (Leptaxis) furva grandissima*
T. Cockerell, 1922**

Leptaxis furva var. *grandissima* T. Cockerell, 1922

Found at one site at the north end of Deserta Grande, represented by one empty shell of uncertain age (Teixeira *et al.*, 2019). This taxon was also recorded as fossil from Madeira (Cockerell, 1922), and originates most probably from the Ponta de São Lourenço. This is the only evidence for the occurrence of *L. furva* (R. T. Lowe, 1831) s. lat. on the Desertas; it is extant on Madeira.

*****Leptaxis (Leptaxis) isambertoii* Teixeira & Cameron, 2019**

Endemic to Deserta Grande, known only as fossils (leg. & coll. I.S.) (Teixeira *et al.*, 2019). Clearly closely related to *L. furva*.

Subgenus *Cryptaxis* R. T. Lowe, 1855***Leptaxis (Cryptaxis) groviana* (A. Férussac, 1832)**

Helix (Helicogena) groviana A. Férussac, 1832, *Helix [Helicogena] undata* R. T. Lowe, 1831 (non *Helix undata* Gmelin, 1791).

As with *Discula polymorpha*, the status of forms within this species requires clarification. Only one subspecies, *L. groviana groviana* (see below) is recognised on Madeira itself, while a variety of forms are recognised on the Desertas Islands. With the exception of *Leptaxis groviana antiqua* (see below), there is clinal variation along the island chain and the division into subspecies is somewhat arbitrary. With the exception of the following two subspecies, the others are listed as they occur from north to south.

***Leptaxis (Cryptaxis) groviana groviana* (A. Férussac, 1832)**

Leptaxis (Cryptaxis) undata undata – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Cryptaxis) groviana groviana* – Bank *et al.*, 2002.

Endemic to Madeira, where it is widespread, but with a single population from the Castanheira valley, Deserta Grande. This is a suspected introduction from Madeira, with evidence of hybridisation with *L. groviana vulcania* or *L. groviana vulcania* var. β *desertae*, see discussion in Teixeira *et al.* (2019), and below.

*****Leptaxis (Cryptaxis) groviana antiqua*
Cameron & Teixeira, 2019**

Endemic to Deserta Grande, known only as fossils (Teixeira *et al.*, 2019). This subspecies is clearly distinct from all living forms on conchological grounds.

***Leptaxis (Cryptaxis) groviana vulcania* (R. T. Lowe, 1852)**

Helix [Leptaxis] vulcania R. T. Lowe, 1852, *Helix [Cryptaxis] vulcania* – Wollaston, 1878, *Helix [Cryptaxis] vulcania* var. β *desertae* – Wollaston, 1878, *Leptaxis (Cryptaxis) undata vulcania* – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Cryptaxis) groviana vulcania* – Bank *et al.*, 2002.

A Desertan endemic, found living and abundant, but not certainly as a fossil on Chão and

the northern two-thirds of Deserta Grande. Fossil records listed in Cameron & Cook (1999) were based on fragments; they cannot be distinguished from *L. groviana antiqua*. Wollaston (1878) described what appears to be clinal variation, with those from Deserta Grande labelled as var. β desertae being slightly larger. There is indeed a cline within Deserta Grande, with more southerly populations being larger (Teixeira *et al.*, 2019). The status of var. β desertae from Deserta Grande remains to be determined.

***Leptaxis (Cryptaxis) groviana leonina* (R. T. Lowe, 1852)**

Helix [*Leptaxis*] *leonina* R. T. Lowe, 1852, *Helix* [*Cryptaxis*] *leonina* – Wollaston, 1878, *Helix* [*Cryptaxis*] *leonina* var. α *intermedia* Wollaston, 1878, *Leptaxis (Cryptaxis) undata leonina* – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Cryptaxis) groviana leonina* – Bank *et al.*, 2002.

Desertan endemic recorded both alive and fossil from Bugio (Teixeira *et al.*, 2019 and coll. I.S.) and alive only from the southern end of Deserta Grande (Wollaston, 1878; and coll. D.T.). Wollaston (1878) suggested clinal variation on Deserta Grande with *L. g. vulcania* and named those that appeared to be intermediate as var. α *intermedia*.

Family Helicidae Rafinesque, 1815

Subfamily Helicinae Rafinesque, 1815

Tribe Otalini G. Pfeffer, 1930

Genus *Idiomela* T. Cockerell, 1921

***Idiomela subplicata* (G. B. Sowerby I, 1824)**

Helix subplicata G. B. Sowerby I, 1824, *Helix (Idiomela) subplicata* – Mandahl-Barth, 1950, *Idiomela subplicata* – Hemmen & Groh, 1984.

Previously thought to be a Porto Santan endemic, living at present only on the Ilhéu de Baixo, but widespread as a fossil on Porto Santo and Ferro and Baixo islets. Recently found alive on Bugio, in the southeast slope at Planalto Sul (leg. I.S., 2019). Not present in the fossil records (Teixeira *et al.*, in prep.), it may represent an adventitious introduction. First record for the Desertas.

DISCUSSION

At the time the last annotated checklist of Desertan snails was produced (Cameron & Cook, 1999), the only certainly known fossil material came from the mid 19th century records from Bugio (Wollaston, 1878), and from a limited sample from the northern extremity of Deserta Grande (Cameron & Cook, 1999). Excluding dubious records and allowing for changes in taxonomic status, 27 living species-level taxa were known from the Desertas, plus a further three known only as fossils. Some of the living species had not been seen since the 19th century. That list made no attempt to distinguish subspecies.

The list presented here reflects the discovery of many fossiliferous deposits on Deserta Grande and more intensive sampling of the deposits on Bugio (Teixeira *et al.*, 2019). It also reflects a significant increase in the sampling of living species. Further, the eradication or reduction of introduced mammalian grazers and predators such as rabbits and mice has resulted in some habitat recovery (Bell, 2001; SPNM, 2005; IFCN, 2020). While the status of many subspecies is unclear, we have listed those from the Desertas that appear to be endemic. Some appear not to conform to the typical requirements of distinct, non-overlapping ranges, while others might prove to be regarded as species when modern molecular approaches are used.

In the list presented here, we regard the records of six species, *Oxychilus cellarius*, *Cochlicella acuta*, *Caseolus innominatus*, *Disculella spirulina*, *Geomitra tiarella* and *Actinella arcta* as unsubstantiated, although the last of these may be represented by a closely related taxon. A further putative species, *Amphorella melampoides*, not recorded as such, is also excluded. Without these, and allowing for a few cases of ambiguity, there are 55 species-level taxa recorded from the Desertas. Of these, four are widespread species; a further 28 are known alive or fossil elsewhere in the archipelago, and 23 appear to be endemic to the Desertas. These counts of species underestimate the degree of specifically Desertan endemism, as *Leptaxis groviana*, *Leptaxis simia* and *Discula polymorpha* are represented on the Desertas by more than one endemic subspecies, while the subspecies of *Caseolus abjectus* and *Helicomela punctulata* are also endemic to the Desertas.

36 species have been recorded alive. 14 of these have not been recorded as fossils. Of these, four are widespread species probably introduced to the archipelago, two are confined, or nearly so, to Chão, and one, *Caseolus pittae*, has not been found since its initial discovery in the 19th century.

Among the 41 species recorded as fossils, 19 have not been found alive on the Desertas. Of these, eight are known alive elsewhere in the Madeiran Archipelago; eight are apparently extinct Desertan endemics and three are known only as fossils in any part of the Archipelago. Thus, it would appear that 48% of the known fossil fauna has become extinct on the Desertas, and 31% have disappeared completely. This contrasts with a total of 21 species known as fossils in 1999, of which only four (19%) had never been found alive. Even allowing for some revision as modern taxonomic techniques are applied, the scale of local extinction is far greater than previously thought. Further analysis of these fossil faunas is in preparation (Teixeira *et al.*, in prep.). Molecular and anatomical studies in progress will determine relationships and status of living taxa more precisely.

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REFERENCES

- ALBERS JC 1854 Malacographia Maderensis sive enumeratio molluscorum quae in insulis Madaerae et Portus Sancti aut vive extant aut fossilis reperiuntur. 94 pp, 17 pls. Berolini
- BANK RA 2009 Systematic list of the Recent terrestrial gastropods of the Madeiran archipelago. *Conchylia* 40(3/4): 61–64.
- BANK RA, GROH K & RIPKEN TH EJ 2002 Catalogue and bibliography of the non-marine Mollusca of Macaronesia. Pp. 89–235, 13 pp. explanations to 13 pls in: Falkner, M., Groh, K., & Speight, M.C.D (Eds) *Collectanea Malacologica, Festschrift für Gerhard Falkner*. Hackenheim & München: ConchBooks & Verlag der Friedrich-Held-Gesellschaft.
- BELL BD 2001. Removal of rabbits from Deserta Grande Island, Madeira Archipelago. *Arquipelago. Life and Marine Sciences. Supplement 2 (Part B)*: 117–119. Ponta Delgada. ISSN 0873–4704.
- BOURGUIGNAT JR 1856 Aménités Malacologiques. § L. Du genre *Caecilianella*. *Revue et Magasin de Zoologie* (2)8(9): 430, pl. 12, figs 21–22.
- BROZZO A, HARL J, DE MATTIA W, TEIXEIRA D, WALTHER F, GROH K, PALL-GERGELY B, GLAUBRECHT M, HAUSDORF B & NEIBER MT 2020 Molecular phylogeny and trait evolution of Madeiran land snails: radiation of the Geomitriini (Stylommatophora: Helicoidea: Geomitridae) *Cladistics* 36: 594–616.
- BRUGGEN AC VAN 1991 *Pupa tabularis* Melvill & Ponsonby, 1893, a new synonym of *Lauria cylindracea* (Da Costa, 1787) (Gastropoda Pulmonata: Pupillidae). *Basteria* 55: 21–24.
- CAMERON RAD & COOK LM 1999 Land snail faunas of the Deserta Islands, Madeiran Archipelago, past and present. *Journal of Conchology* 36: 1–15.
- CAMERON RAD, COOK LM, GOODFRIEND GA & SEDDON MB 2006 Fossil land snail faunas of Porto Santo, Madeiran Archipelago: change and stasis in Pleistocene to recent times. *Malacologia* 49: 25–60.
- COCKERELL TDA 1922 The helicoid genus *Leptaxis* Lowe. *Nautilus* 35: 101–103.
- CRAZE PG & LACE LA 2000 Spatial ecology, habitat and speciation in the Porto Santan land snail genus *Heterostoma* (Helicidae). *Biological Journal of the Linnean Society* 71: 665–676.
- DE FILIPPI F 1837 Descrizione di nuovi entozoi trovati in alcuni molluschi d'acqua dolce. *Biblioteca italiana: o sia Giornale di letteratura, scienze ed arti* 87: 333–340.

- GITTENBERGER, E, BUDHA, PB & BANK, RA (2020): Amazing *Paralaoma servilis* (Gastropoda, Pulmonata, Punctidae) in Nepal. *Basteria* **84** (1–3): 76–82.
- GOODFRIEND GA, CAMERON RAD, COOK LM, COURTY MA, FEDEROFF N, KAUFMAN A, LIVETT E & TALLIS J 1996 Quaternary eolianite sequence of Madeira: stratigraphy, chronology and palaeoenvironmental interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **120**: 195–234.
- GROH K & HEMMEN J 1986 Zur Kenntnis der Vitrinidenes Madeira Archipels (Pulmonata: Vitrinidae). *Archiv für Molluskenkunde* **116**: 1–39.
- GROH K, RÄHLE W, KITTEL K, HEMMEN J & BANK RM 2009 Corrections and additions to Mary B. Seddon's "The landsnails of Madeira. An illustrated compendium of the landsnails and slugs of the Madeiran archipelago" (2008). *Conchylia* **40**(3/4): 2–25.
- HUTTERER R & GROH K 1993 [for 1991] A review of Macaronesian *Truncatellina* (Gastropoda: Vertiginidae) with descriptions of four new species. *Bocagiana* **151**: 1–19.
- IFCN 2020 Final report of the LIFE Recover Natura project (LIFE12/NAT/PT/000195), Secretaria Regional do Ambiente, Recursos Naturais e Alterações Climáticas, Funchal.
- LOWE RT 1852 Brief diagnostic notices of new Madeiran land shells. *Annals and Magazine of Natural History* (2) **9** (50): 112–120, 275–279.
- MANDAHL-BARTH G 1950 [for 1943] Systematische Untersuchungen über die Heliciden-Fauna von Madeira. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **469**: 1–93.
- NEUBERT E & GROH K 1998 Contributions to the nomenclature and phylogeny of *Boettgeria* O. Boettger, 1863, with description of *Loosjesiella* n. subgen. (Gastropoda: Pulmonata: Clausiliidae). *Basteria* **62** (3/4): 157–168.
- NOBRE A 1931 *Moluscos terrestres, fluviais e das águas salobras do arquipélago da Madeira*. 208 pp, Porto, Barcelos.
- PAIVA A DA COSTA [=Barão de Castelo de Paiva] 1866 Description de dix espèces nouvelles de mollusques terrestres de l'archipel de Madère. *Journal de Conchyliologie* **14**: 339–343.
- PAIVA A DA COSTA [=Barão de Castelo de Paiva] 1867 Monographia molluscorum terrestrium fluvialium, lacustrum, insularium Maderensium. *Memorias da Academia real das sciencias de Lisboa. Classe de sciencias mathematicas, physicas e naturaes* **4** (1): 1–168.
- SERVIÇO DO PARQUE NATURAL DA MADEIRA (SPNM) 2005 The Desertas Islands, *Secretaria Regional do Ambiente e dos Recursos Naturais*, Funchal, 1–94.
- SEDDON MB 2008 The landsnails of Madeira. An illustrated compendium of the landsnails and slugs of the Madeiran archipelago. *Studies in Biodiversity and Systematics of Terrestrial Organisms from the National Museum of Wales. Biotir Reports* **2**: 1–204.
- SEDDON MB, ABREU C, CAMERON R & TEIXEIRA D 2017 *Amphorella gracilis*. The IUCN Red List of Threatened Species **2017**: e.T171418A1325864.
- TEIXEIRA, D 2017 *Atlantica calathoides*. The IUCN Red List of Threatened Species **2017**: e.T107353425A107353451
- TEIXEIRA D, POKRYSZKO BM, CAMERON RAD, SILVA I & GROH K 2019 Taxonomic revision of the late-Pleistocene/Holocene land-mollusc fauna (Gastropoda: Eupulmonata) of the Desertas Islands, Madeiran Archipelago, with the description of 6 new species and 2 new subspecies. *Archiv für Molluskenkunde* **148** (2): 137–159.
- TEIXEIRA D, CAMERON R, GROH K & SEDDON MB 2018b *Geomitra grabhami* (errata version published in 2019). The IUCN Red List of Threatened Species **2018**: e.T156368A144802430.
- TEIXEIRA D, SILVA I, CAMERON R & GROH K 2018a *Geomitra coronula*. The IUCN Red List of Threatened Species **2018**: e.T121001523A121001604.
- WALDÉN HW 1983 Systematic and biogeographical studies of the terrestrial Gastropoda of Madeira. With an annotated check-list. *Annales Zoologica Fennici* **20**: 255–275.
- WOLLASTON TV 1878 *Testacea Atlantica, or the land and freshwater shells of the Azores, Madeiras, Salvages, Canaries, Cape Verdes, and Saint Helena*. xi+588 pp. London: Reeve.

pulchra Paiva, 1867 (in part), *Actinella* (*Plebecula*) *nitidiuscula saxipotens* – Mandahl-Barth, 1950.

A fossil species described by Wollaston (1878) from Bugio under the name *Helix vulgata* var. ϵ saxipotens. It is present as a fossil on both Deserta Grande and Bugio (Teixeira *et al.*, 2019), and its status is confirmed by co-existence in some deposits with *P. nitidiuscula*. It was first recorded as a fossil on Deserta Grande by Cameron & Cook (1999) and has been found in other sites since (Teixeira *et al.*, 2019). It is not known alive.

Plebecula anaglyptica (Reeve, 1852)

Helix anaglyptica Reeve, 1852, *Helix* [*Plebecula*] *vulgata* var. α major Paiva, 1867 (in part), *Helix* [*Plebecula*] *vulgata* var. β [sic! pro α] deserticola Wollaston, 1878, *Actinella* (*Plebecula*) *anaglyptica* – Mandahl-Barth, 1950.

An extant endemic species of the island of Chão only, from where it was named by Paiva (1867) *Helix vulgata* var. α major and by Wollaston (1878) var. β deserticola. Nevertheless, it was described by Reeve 36 years earlier. Cameron & Cook (1999) recorded it from Chão under *A. nitidiuscula*. It remains living there (IFCN, 2020).

Genus *Geomitra* Swainson, 1840

Geomitra coronula (R. T. Lowe, 1852)

Helix [*Coronaria*] *coronula* R. T. Lowe, 1852, *Helix* [*Octephila*] *coronula* – Paiva, 1867 (in part), *Helix* [*Coronaria*] *coronula* – Wollaston, 1878, *Geomitra* (*Geomitra*) *coronula* – Mandahl-Barth, 1950, *Craspedaria* (*Coronaria*) *coronula* – Bank *et al.*, 2002, *Geomitra coronula* – Seddon, 2008.

An extant and fossil endemic species of both southern Desertas islands. Whilst it was described as a fossil by R. T. Lowe in 1852 and thought by Wollaston (1878) to be restricted to Bugio alone, recent finding of living specimens on Deserta Grande (Pedregal, leg. D.T., I.S.), where it is rare (Teixeira *et al.*, 2018a), make it probable that Moniz (in Paiva, 1867) found it alive there and that Paiva did not mix it up with the following species. This is the first documented living record from Deserta Grande where it also was detected at several fossil sites, as also on Bugio, where it has not been found alive (Teixeira *et al.*, 2019).

Geomitra grabhami (Wollaston, 1878)

Helix [*Octephila*] *coronula* – Paiva, 1867 (in part), *Helix* [*Coronaria*] *Grabhami* Wollaston, 1878,

Geomitra (*Geomitra*) *grabhami* – Mandahl-Barth, 1950, *Craspedaria* (*Coronaria*) *grabhami* – Bank *et al.*, 2002, *Geomitra grabhami* – Seddon, 2008.

An extant endemic species of the north of Deserta Grande where Moniz first detected it in the 1860s (Paiva, 1867). It still lives on Deserta Grande (Fajã Grande, leg. D.T., I.S.), where it is rare (Teixeira *et al.*, 2018b) and is also now known as fossils from the north end of the island (leg. Gerber, Groh & Hemmen, 1985; Cameron & Cook, 1999; Teixeira *et al.*, 2019).

? *Geomitra* (*Geomitra*) *tiarella* (Webb & Berthelot, 1833)

Helix tiarella Webb & Berthelot, 1833, *Helix* [*Coronaria*] *tiarella* Wollaston, 1878, *Geomitra* (*Geomitra*) *tiarella* – Mandahl-Barth, 1950, *Craspedaria* (*Coronaria*) *tiarella* – Bank *et al.*, 2002, *Geomitra tiarella* – Seddon, 2008.

Wollaston (1878) regarded this species as endemic to Madeira itself, where closely related populations still live – in shrinking numbers – as rock-dwellers in the north of the island in coastal areas, but it is abundant as a fossil in the Quaternary beds of the Ponta São Lourenço. The indication by Bank *et al.* (2002) that it also occurs on Deserta Grande as a fossil seems unlikely. We have no good evidence for the existence of *G. tiarella* in the Desertas.

***Geomitra* (*Geomitra*) sp. indet. juv. (n. sp.?)

This fossil species, of which only juveniles are known (Fig. 3b), is endemic to Deserta Grande and probably closely related to a yet undescribed species that lives in the south of Madeira mainland (Fig. 3a) (Teixeira *et al.*, 2019; in prep.).

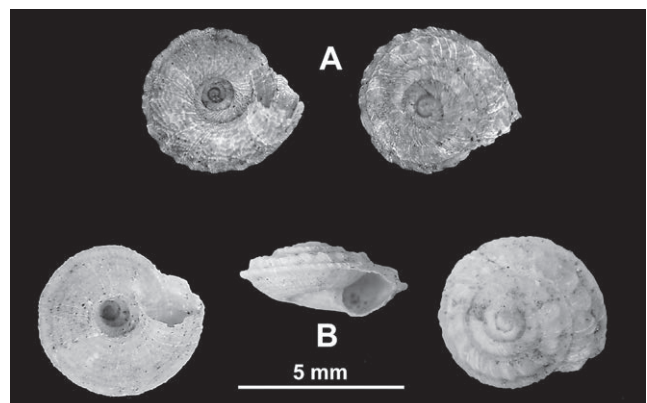


Figure 3 Undetermined *Geomitra* species. **A:** fresh from SW Madeira (leg. KG); **B:** fossil from Deserta Grande (site 3 of Teixeira *et al.*, 2019).

Genus *Discula* R. T. Lowe, 1852**Subgenus *Discula* s. str.*****Discula (Discula) cameroni* Pokryszko, Groh & Teixeira, 2019**

Endemic. First detected as fossils on Deserta Grande (Teixeira *et al.*, 2019) and subsequently living at the southern end of Deserta Grande (Planalto Sul and Rocha do Amarelo, leg. D.T., IFCN 2020), and at the northern end of Bugio (leg. & coll. I.S.) (Teixeira *et al.*, in prep.).

***Discula (Discula) tetrica* (R. T. Lowe, 1862)**

Helix tetrica R. T. Lowe, 1852, *Helix [Discula] tetrica* – Wollaston, 1878, *Discula (Discula) tetrica* – Mandahl-Barth, 1950.

Endemic. Live and fossil on Bugio only (Wollaston, 1878), but also found both fresh and fossil recently (leg. I.S.) (Teixeira *et al.*, in prep.).

***Discula (Discula) polymorpha* (R. T. Lowe, 1831)**

Helix [Helicella] polymorpha R. T. Lowe, 1831, *Helix [Discula] polymorpha* – Wollaston, 1878.

There are many described subspecies of this very variable species (Bank *et al.*, 2002), found on both Madeira and the Desertas. While it is clear that many do not represent clearly defined and geographically replacing taxa, those listed below have been recorded on the Desertas. Patterns of distribution suggest a degree of convergent evolution or phenotypic plasticity among them. Molecular analysis of forms from all three islands is needed to establish relationships.

***Discula (Discula) polymorpha minor* Mandahl-Barth, 1950**

Discula (Discula) polymorpha minor – Waldén, 1983, *Discula (Discula) polymorpha poromphala* – Bank *et al.*, 2002. Note remarks on *Actinella (Actinella) fecundaerrata* above.

A form of *D. polymorpha* described from Chão by Mandahl-Barth (1950) which closely resembles *D. polymorpha poromphala* (see below), to which it appears to be assigned by Wollaston (1878). H. W. Waldén (unpublished) regarded it as endemic to Chão, while the very similar form found in the northern part of Deserta Grande he assigned to *D. polymorpha poromphala*. Recent studies (D.T. unpublished) suggest that there is

a single form common to Chão and the north of Deserta Grande as far as Pedregal.

***Discula (Discula) polymorpha nebulata* (R. T. Lowe, 1855)**

Helix [Discula] senilis (non *Helix senilis* Morelet, 1851) var. α *nebulata* R. T. Lowe, 1855, *Helix [Discula] salebrosa* R. T. Lowe, 1862, *Helix [Discula] polymorpha* var. β . *salebrosa* – Wollaston, 1878, *Discula (Discula) polymorpha senilis* – Mandahl-Barth, 1950, *Discula (Discula) polymorpha salebrosa* – Waldén, 1983, *Discula (Discula) polymorpha nebulata* – Bank *et al.*, 2002.

Found both living and fossil on Deserta Grande (Teixeira *et al.*, 2019). Wollaston (1878), under var. β . *salebrosa*, records it live from Madeira and all three Desertas, and as fossil from both Madeira and Bugio. While Madeiran records need reassessment, our surveys have found it only on Deserta Grande. All specimens of *D. polymorpha* recently found both living and fossil from Bugio have been assigned to *D. p. poromphala* (below).

***Discula (Discula) polymorpha poromphala* (R. T. Lowe, 1852)**

Helix [Discula] poromphala R. T. Lowe, 1855, *Discula (Discula) polymorpha poromphala* – Mandahl-Barth, 1950, Waldén, 1983, *Discula (Discula) polymorpha pusilla* – Waldén, 1983 (non *Helix senilis* var. γ *pusilla* R. T. Lowe, 1855=*Actinella (Actinella) fecundaerrata* Groh & Cameron, 2019).

Endemic to the Desertas. While it has been recorded recently both as a fossil and alive on Bugio (Teixeira *et al.*, 2019), it is not known as a fossil from Deserta Grande. Wollaston (1878) records it alive from all three Deserta Islands. H.W. Waldén (unpublished), as stated above under *D. polymorpha minor*, assigned the form from the north of Deserta Grande to this subspecies, while D.T. (unpublished) regarded these as the same as those on Chão. It is clear that the systematics of these taxa is unresolved.

***Discula (Discula) polymorpha docaensis* Teixeira & Groh, 2019**

Endemic to Deserta Grande, where it has been found both living (leg. R. A. D. Cameron and L. M. Cook) and fossil (Teixeira *et al.*, 2019) only in the vicinity of Doca. This subspecies is both highly distinctive and geographically localised.

***Discula (Discula) lyelliana* (R. T. Lowe, 1852)**

Helix [*Tectula*] *lyelliana* R. T. Lowe, 1852, *Helix* [*Tectula*] *Bulwerii* var β Albers, 1854, *Helix* [*Tectula*] *lyelliana* var. β *gigas* Wollaston, 1878, *Discula (Discula) lyelliana* – Mandahl-Barth, 1950, *Discula (Discula) lyelliana gigas* – Mandahl-Barth, 1950.

Endemic. Both alive (Risco, leg. D.T. & I.S.) and fossil (Teixeira *et al.*, in prep.) on Deserta Grande. Fossil on Bugio, west side of south plateau at 210m (leg. & coll. I.S. 20.8.2008). This is the first record for Bugio.

Subgenus *Mandahlia* Forcart, 1965****Discula (Mandahlia) tectiformis ludovici* (Albers, 1854)**

Helix [*Crenea*] *Ludovici* Albers, 1854, *Discula (Tectula) tectiformis ludovici* – Mandahl-Barth, 1950, *Discula (Mandahlia) tectiformis ludovici* – Waldén, 1983.

Known as a fossil from a single site on Deserta Grande, above Doca (South) at 60m (leg. & coll. I.S. 9.8.2008). This extinct subspecies was previously known only from Porto Santo (Bank *et al.*, 2002), where there is a living subspecies *D. tectiformis tectiformis* (G. B. Sowerby I, 1824). First record for the Desertas.

Genus *Steenbergia* Mandahl-Barth, 1950

The genus *Steenbergia* was separated on anatomical characters by Mandahl-Barth (1950) from a closely related monospecific genus usually known as *Heterostoma* Hartmann, 1843, a name that is unfortunately preoccupied by an older homonym proposed by De Filippi (1837) for a platyhelminth. Genital anatomy, however, does not correlate well with shell morphology, and is complicated by the occurrence, sometimes syntopically, of hemiphallics (Craze & Lace, 2000). While there may be a close relationship between *Steenbergia/Heterostoma* and *Spirorbula* (Brozzo *et al.*, 2018), it seems that all taxa previously referred to as *Heterostoma* should be referred to as *Steenbergia*.

Steenbergia desertae* (Mandahl-Barth, 1950)**Steenbergia duplex desertae* Mandahl-Barth, 1950**

Known alive from all three Desertas, and as fossils from Deserta Grande and Bugio (Teixeira *et*

al., in prep.). The status of described species of *Steenbergia* requires clarification; there may be a complex of forms attributable to *S. paupercula* (R. T. Lowe, 1831). Bank *et al.* (2002) treat it as a species of *Heterostoma*, Seddon (2008) figures it as a form of *Steenbergia paupercula*.

Genus *Spirorbula* R. T. Lowe, 1852****Spirorbula squalida* (R. T. Lowe, 1852)**

Helix [*Irus*] *squalida* R. T. Lowe, 1852, *Spirorbula squalida* – Mandahl-Barth, 1950.

Known only as fossil from Deserta Grande. (Teixeira *et al.*, in prep.), but also living on Madeira (Seddon, 2008).

? *Spirorbula* sp. indet. (n.sp.?)**

A single, damaged and fossil specimen from the north of Deserta Grande appears not to match *S. squalida* (Teixeira *et al.*, 2019).

Genus *Leptaxis* R. T. Lowe, 1852**Subgenus *Leptaxis* s. str.*****Leptaxis (Leptaxis) simia* (A. Férussac, 1832)**

As with *Discula polymorpha* (see above), this species has a number of designated subspecies. The fossil material is frequently fragmented, making allocation among these doubtful. Three such subspecies are recorded for the Desertas.

***Leptaxis (Leptaxis) simia advenoides* (Paiva, 1867)**

Helix [*Leptaxis*] *erubescens* var. γ *advenoides* Paiva, 1867, *Leptaxis (Leptaxis) erubescens advenoides* – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Leptaxis) simia advenoides* – Bank *et al.*, 2002.

Originally described as a fossil from the Ponta de São Lourenço (Paiva, 1867: 14), it is also recorded extant on Chão (Wollaston, 1878). While also recorded from the north of Deserta Grande by Mandahl-Barth (1950), recent finds of *L. simia* from the northern two-thirds of Deserta Grande refer to *L. simia simia* (leg. D.T.). Bank *et al.* (2002) state that it is only fossil on Madeira and living on Ilhéu Chão, whilst Seddon (2008) restricts the subspecies to Ilhéu Chão alone.

***Leptaxis (Leptaxis) simia hyaena* (R. T. Lowe, 1852)**

Helix [*Leptaxis*] *hyaena* R. T. Lowe, 1852, *Helix* [*Leptaxis*] *erubescens* var. β Paiva, 1867, *Helix* [*Leptaxis*] *erubescens* var. δ *hyaena* – Wollaston, 1878, *Leptaxis (Leptaxis) erubescens hyaena* – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Leptaxis) simia hyaena* – Bank *et al.*, 2002.

Known both alive and fossil from Bugio (Teixeira *et al.*, in prep.) and alive from the southern part of Deserta Grande, where early records (Paiva, 1867; Wollaston, 1878) have recently been confirmed (leg. D.T., I.S., IFCN 2020).

***Leptaxis (Leptaxis) simia simia* (A. Férussac, 1832)**

Helix (Helicogena) simia A. Férussac, 1832, *Helix [Helicogena] erubescens* R. T. Lowe, 1831 (non *Helix erubescens* Solander, 1786), *Helix [Leptaxis] erubescens* var. β [normalis] Wollaston, 1878, *Leptaxis (Leptaxis) erubescens erubescens* – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Leptaxis) simia simia* – Bank *et al.*, 2002.

Native to Madeira and Deserta Grande where it is known both alive and fossil (Teixeira *et al.*, in prep.). Fossils from Deserta Grande are placed here with caution. Introduced to São Miguel and Terceira in the Azorean islands (Bank *et al.*, 2002).

*****Leptaxis (Leptaxis) furva grandissima*
T. Cockerell, 1922**

Leptaxis furva var. *grandissima* T. Cockerell, 1922

Found at one site at the north end of Deserta Grande, represented by one empty shell of uncertain age (Teixeira *et al.*, 2019). This taxon was also recorded as fossil from Madeira (Cockerell, 1922), and originates most probably from the Ponta de São Lourenço. This is the only evidence for the occurrence of *L. furva* (R. T. Lowe, 1831) s. lat. on the Desertas; it is extant on Madeira.

*****Leptaxis (Leptaxis) isambertoii* Teixeira & Cameron, 2019**

Endemic to Deserta Grande, known only as fossils (leg. & coll. I.S.) (Teixeira *et al.*, 2019). Clearly closely related to *L. furva*.

Subgenus *Cryptaxis* R. T. Lowe, 1855***Leptaxis (Cryptaxis) groviana* (A. Férussac, 1832)**

Helix (Helicogena) groviana A. Férussac, 1832, *Helix [Helicogena] undata* R. T. Lowe, 1831 (non *Helix undata* Gmelin, 1791).

As with *Discula polymorpha*, the status of forms within this species requires clarification. Only one subspecies, *L. groviana groviana* (see below) is recognised on Madeira itself, while a variety of forms are recognised on the Desertas Islands. With the exception of *Leptaxis groviana antiqua* (see below), there is clinal variation along the island chain and the division into subspecies is somewhat arbitrary. With the exception of the following two subspecies, the others are listed as they occur from north to south.

***Leptaxis (Cryptaxis) groviana groviana* (A. Férussac, 1832)**

Leptaxis (Cryptaxis) undata undata – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Cryptaxis) groviana groviana* – Bank *et al.*, 2002.

Endemic to Madeira, where it is widespread, but with a single population from the Castanheira valley, Deserta Grande. This is a suspected introduction from Madeira, with evidence of hybridisation with *L. groviana vulcania* or *L. groviana vulcania* var. β *desertae*, see discussion in Teixeira *et al.* (2019), and below.

*****Leptaxis (Cryptaxis) groviana antiqua*
Cameron & Teixeira, 2019**

Endemic to Deserta Grande, known only as fossils (Teixeira *et al.*, 2019). This subspecies is clearly distinct from all living forms on conchological grounds.

***Leptaxis (Cryptaxis) groviana vulcania* (R. T. Lowe, 1852)**

Helix [Leptaxis] vulcania R. T. Lowe, 1852, *Helix [Cryptaxis] vulcania* – Wollaston, 1878, *Helix [Cryptaxis] vulcania* var. β *desertae* – Wollaston, 1878, *Leptaxis (Cryptaxis) undata vulcania* – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Cryptaxis) groviana vulcania* – Bank *et al.*, 2002.

A Desertan endemic, found living and abundant, but not certainly as a fossil on Chão and

the northern two-thirds of Deserta Grande. Fossil records listed in Cameron & Cook (1999) were based on fragments; they cannot be distinguished from *L. groviana antiqua*. Wollaston (1878) described what appears to be clinal variation, with those from Deserta Grande labelled as var. β desertae being slightly larger. There is indeed a cline within Deserta Grande, with more southerly populations being larger (Teixeira *et al.*, 2019). The status of var. β desertae from Deserta Grande remains to be determined.

***Leptaxis (Cryptaxis) groviana leonina* (R. T. Lowe, 1852)**

Helix [*Leptaxis*] *leonina* R. T. Lowe, 1852, *Helix* [*Cryptaxis*] *leonina* – Wollaston, 1878, *Helix* [*Cryptaxis*] *leonina* var. α *intermedia* Wollaston, 1878, *Leptaxis (Cryptaxis) undata leonina* – Mandahl-Barth, 1950, Seddon, 2008, *Leptaxis (Cryptaxis) groviana leonina* – Bank *et al.*, 2002.

Desertan endemic recorded both alive and fossil from Bugio (Teixeira *et al.*, 2019 and coll. I.S.) and alive only from the southern end of Deserta Grande (Wollaston, 1878; and coll. D.T.). Wollaston (1878) suggested clinal variation on Deserta Grande with *L. g. vulcania* and named those that appeared to be intermediate as var. α *intermedia*.

Family Helicidae Rafinesque, 1815

Subfamily Helicinae Rafinesque, 1815

Tribe Otalini G. Pfeffer, 1930

Genus *Idiomela* T. Cockerell, 1921

***Idiomela subplicata* (G. B. Sowerby I, 1824)**

Helix subplicata G. B. Sowerby I, 1824, *Helix (Idiomela) subplicata* – Mandahl-Barth, 1950, *Idiomela subplicata* – Hemmen & Groh, 1984.

Previously thought to be a Porto Santan endemic, living at present only on the Ilhéu de Baixo, but widespread as a fossil on Porto Santo and Ferro and Baixo islets. Recently found alive on Bugio, in the southeast slope at Planalto Sul (leg. I.S., 2019). Not present in the fossil records (Teixeira *et al.*, in prep.), it may represent an adventitious introduction. First record for the Desertas.

DISCUSSION

At the time the last annotated checklist of Desertan snails was produced (Cameron & Cook, 1999), the only certainly known fossil material came from the mid 19th century records from Bugio (Wollaston, 1878), and from a limited sample from the northern extremity of Deserta Grande (Cameron & Cook, 1999). Excluding dubious records and allowing for changes in taxonomic status, 27 living species-level taxa were known from the Desertas, plus a further three known only as fossils. Some of the living species had not been seen since the 19th century. That list made no attempt to distinguish subspecies.

The list presented here reflects the discovery of many fossiliferous deposits on Deserta Grande and more intensive sampling of the deposits on Bugio (Teixeira *et al.*, 2019). It also reflects a significant increase in the sampling of living species. Further, the eradication or reduction of introduced mammalian grazers and predators such as rabbits and mice has resulted in some habitat recovery (Bell, 2001; SPNM, 2005; IFCN, 2020). While the status of many subspecies is unclear, we have listed those from the Desertas that appear to be endemic. Some appear not to conform to the typical requirements of distinct, non-overlapping ranges, while others might prove to be regarded as species when modern molecular approaches are used.

In the list presented here, we regard the records of six species, *Oxychilus cellarius*, *Cochlicella acuta*, *Caseolus innominatus*, *Disculella spirulina*, *Geomitra tiarella* and *Actinella arcta* as unsubstantiated, although the last of these may be represented by a closely related taxon. A further putative species, *Amphorella melampoides*, not recorded as such, is also excluded. Without these, and allowing for a few cases of ambiguity, there are 55 species-level taxa recorded from the Desertas. Of these, four are widespread species; a further 28 are known alive or fossil elsewhere in the archipelago, and 23 appear to be endemic to the Desertas. These counts of species underestimate the degree of specifically Desertan endemism, as *Leptaxis groviana*, *Leptaxis simia* and *Discula polymorpha* are represented on the Desertas by more than one endemic subspecies, while the subspecies of *Caseolus abjectus* and *Helicomela punctulata* are also endemic to the Desertas.

36 species have been recorded alive. 14 of these have not been recorded as fossils. Of these, four are widespread species probably introduced to the archipelago, two are confined, or nearly so, to Chão, and one, *Caseolus pittae*, has not been found since its initial discovery in the 19th century.

Among the 41 species recorded as fossils, 19 have not been found alive on the Desertas. Of these, eight are known alive elsewhere in the Madeiran Archipelago; eight are apparently extinct Desertan endemics and three are known only as fossils in any part of the Archipelago. Thus, it would appear that 48% of the known fossil fauna has become extinct on the Desertas, and 31% have disappeared completely. This contrasts with a total of 21 species known as fossils in 1999, of which only four (19%) had never been found alive. Even allowing for some revision as modern taxonomic techniques are applied, the scale of local extinction is far greater than previously thought. Further analysis of these fossil faunas is in preparation (Teixeira *et al.*, in prep.). Molecular and anatomical studies in progress will determine relationships and status of living taxa more precisely.

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REFERENCES

- ALBERS JC 1854 Malacographia Maderensis sive enumeratio molluscorum quae in insulis Madaerae et Portus Sancti aut vive extant aut fossilis reperiuntur. 94 pp, 17 pls. Berolini
- BANK RA 2009 Systematic list of the Recent terrestrial gastropods of the Madeiran archipelago. *Conchylia* 40(3/4): 61–64.
- BANK RA, GROH K & RIPKEN TH EJ 2002 Catalogue and bibliography of the non-marine Mollusca of Macaronesia. Pp. 89–235, 13 pp. explanations to 13 pls in: Falkner, M., Groh, K., & Speight, M.C.D (Eds) *Collectanea Malacologica, Festschrift für Gerhard Falkner*. Hackenheim & München: ConchBooks & Verlag der Friedrich-Held-Gesellschaft.
- BELL BD 2001. Removal of rabbits from Deserta Grande Island, Madeira Archipelago. *Arquipelago. Life and Marine Sciences. Supplement 2 (Part B)*: 117–119. Ponta Delgada. ISSN 0873–4704.
- BOURGUIGNAT JR 1856 Aménités Malacologiques. § L. Du genre *Caecilianella*. *Revue et Magasin de Zoologie* (2)8(9): 430, pl. 12, figs 21–22.
- BROZZO A, HARL J, DE MATTIA W, TEIXEIRA D, WALTHER F, GROH K, PALL-GERGELY B, GLAUBRECHT M, HAUSDORF B & NEIBER MT 2020 Molecular phylogeny and trait evolution of Madeiran land snails: radiation of the Geomitriini (Stylommatophora: Helicoidea: Geomitridae) *Cladistics* 36: 594–616.
- BRUGGEN AC VAN 1991 *Pupa tabularis* Melvill & Ponsonby, 1893, a new synonym of *Lauria cylindracea* (Da Costa, 1787) (Gastropoda Pulmonata: Pupillidae). *Basteria* 55: 21–24.
- CAMERON RAD & COOK LM 1999 Land snail faunas of the Deserta Islands, Madeiran Archipelago, past and present. *Journal of Conchology* 36: 1–15.
- CAMERON RAD, COOK LM, GOODFRIEND GA & SEDDON MB 2006 Fossil land snail faunas of Porto Santo, Madeiran Archipelago: change and stasis in Pleistocene to recent times. *Malacologia* 49: 25–60.
- COCKERELL TDA 1922 The helicoid genus *Leptaxis* Lowe. *Nautilus* 35: 101–103.
- CRAZE PG & LACE LA 2000 Spatial ecology, habitat and speciation in the Porto Santan land snail genus *Heterostoma* (Helicidae). *Biological Journal of the Linnean Society* 71: 665–676.
- DE FILIPPI F 1837 Descrizione di nuovi entozoi trovati in alcuni molluschi d'acqua dolce. *Biblioteca italiana: o sia Giornale di letteratura, scienze ed arti* 87: 333–340.

- GITTENBERGER, E, BUDHA, PB & BANK, RA (2020): Amazing *Paralaoma servilis* (Gastropoda, Pulmonata, Punctidae) in Nepal. *Basteria* **84** (1–3): 76–82.
- GOODFRIEND GA, CAMERON RAD, COOK LM, COURTY MA, FEDEROFF N, KAUFMAN A, LIVETT E & TALLIS J 1996 Quaternary eolianite sequence of Madeira: stratigraphy, chronology and palaeoenvironmental interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **120**: 195–234.
- GROH K & HEMMEN J 1986 Zur Kenntnis der Vitrinidenes Madeira Archipels (Pulmonata: Vitrinidae). *Archiv für Molluskenkunde* **116**: 1–39.
- GROH K, RÄHLE W, KITTEL K, HEMMEN J & BANK RM 2009 Corrections and additions to Mary B. Seddon's "The landsnails of Madeira. An illustrated compendium of the landsnails and slugs of the Madeiran archipelago" (2008). *Conchylia* **40**(3/4): 2–25.
- HUTTERER R & GROH K 1993 [for 1991] A review of Macaronesian *Truncatellina* (Gastropoda: Vertiginidae) with descriptions of four new species. *Bocagiana* **151**: 1–19.
- IFCN 2020 Final report of the LIFE Recover Natura project (LIFE12/NAT/PT/000195), Secretaria Regional do Ambiente, Recursos Naturais e Alterações Climáticas, Funchal.
- LOWE RT 1852 Brief diagnostic notices of new Madeiran land shells. *Annals and Magazine of Natural History* (2) **9** (50): 112–120, 275–279.
- MANDAHL-BARTH G 1950 [for 1943] Systematische Untersuchungen über die Heliciden-Fauna von Madeira. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **469**: 1–93.
- NEUBERT E & GROH K 1998 Contributions to the nomenclature and phylogeny of *Boettgeria* O. Boettger, 1863, with description of *Loosjesiella* n. subgen. (Gastropoda: Pulmonata: Clausiliidae). *Basteria* **62** (3/4): 157–168.
- NOBRE A 1931 *Moluscos terrestres, fluviais e das águas salobras do arquipélago da Madeira*. 208 pp, Porto, Barcelos.
- PAIVA A DA COSTA [=Barão de Castelo de Paiva] 1866 Description de dix espèces nouvelles de mollusques terrestres de l'archipel de Madère. *Journal de Conchyliologie* **14**: 339–343.
- PAIVA A DA COSTA [=Barão de Castelo de Paiva] 1867 Monographia molluscorum terrestrium fluvialium, lacustrum, insularium Maderensium. *Memorias da Academia real das sciencias de Lisboa. Classe de sciencias mathematicas, physicas e naturaes* **4** (1): 1–168.
- SERVIÇO DO PARQUE NATURAL DA MADEIRA (SPNM) 2005 The Desertas Islands, *Secretaria Regional do Ambiente e dos Recursos Naturais*, Funchal, 1–94.
- SEDDON MB 2008 The landsnails of Madeira. An illustrated compendium of the landsnails and slugs of the Madeiran archipelago. *Studies in Biodiversity and Systematics of Terrestrial Organisms from the National Museum of Wales. Biotir Reports* **2**: 1–204.
- SEDDON MB, ABREU C, CAMERON R & TEIXEIRA D 2017 *Amphorella gracilis*. The IUCN Red List of Threatened Species **2017**: e.T171418A1325864.
- TEIXEIRA, D 2017 *Atlantica calathoides*. The IUCN Red List of Threatened Species **2017**: e.T107353425A107353451
- TEIXEIRA D, POKRYSZKO BM, CAMERON RAD, SILVA I & GROH K 2019 Taxonomic revision of the late-Pleistocene/Holocene land-mollusc fauna (Gastropoda: Eupulmonata) of the Desertas Islands, Madeiran Archipelago, with the description of 6 new species and 2 new subspecies. *Archiv für Molluskenkunde* **148** (2): 137–159.
- TEIXEIRA D, CAMERON R, GROH K & SEDDON MB 2018b *Geomitra grabhami* (errata version published in 2019). The IUCN Red List of Threatened Species **2018**: e.T156368A144802430.
- TEIXEIRA D, SILVA I, CAMERON R & GROH K 2018a *Geomitra coronula*. The IUCN Red List of Threatened Species **2018**: e.T121001523A121001604.
- WALDÉN HW 1983 Systematic and biogeographical studies of the terrestrial Gastropoda of Madeira. With an annotated check-list. *Annales Zoologica Fennici* **20**: 255–275.
- WOLLASTON TV 1878 *Testacea Atlantica, or the land and freshwater shells of the Azores, Madeiras, Salvages, Canaries, Cape Verdes, and Saint Helena*. xi+588 pp. London: Reeve.