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## Research article

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# Diversity of the extinct land snail genus *Chilonopsis* of St Helena (Mollusca: Gastropoda: Achatinidae)

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**Abstract.** The extinct land snail genus *Chilonopsis* (Achatinidae) endemic to St Helena is revised, based on existing and new material collected during palaeontological investigations in 2022–2023. We recognise nine species, including one from the new material that was previously undescribed: *Chilonopsis lanceoloideus* sp. nov. We review the nomenclature of all species and confirm the recent, but largely overlooked, validation of *C. aurisvulpina*, and the correct spelling of *C. melanioides*. We designate lectotypes for *C. aurisvulpina* and *C. subtruncatus* and synonymise *Bulimus relegatus* Benson with the former. Two species were recorded alive in 1878 and 1884–86 (*C. melanioides* and *C. turtoni*), but neither have been found alive since; the others have only ever been found as subfossil material.

**Keywords.** Extinction, fossil land snails, South Atlantic, taxonomy.

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## Introduction

St Helena is a remote island in the Atlantic Ocean, ~1300 km from the nearest land (Ascension Island) and ~1850 km from Africa and ~3300 km from South America. It is just 121.7 km<sup>2</sup> in area. Being formed from volcanic activity around 14 Mya, its non-marine snail fauna comprises colonising species and, being so isolated, few species are present, derived from even fewer colonisations. Thirty native

snail species (all endemic) have been recorded from eight endemic genera (Crowley & Pain 1977), alongside 23 introduced species (Key *et al.* 2021). Only three of these native species survive today, the others were lost due to the extensive and rapid habitat destruction on the island due to human activity. Although debated, the Portuguese were the first nation to discover St Helena, most likely on May 21, 1502, but it may have been earlier (Bruce 2022). At that time the island was uninhabited and covered with vegetation, ranging from open, stunted shrubland to tall canopy forests (Ashmole & Ashmole 2000). The Portuguese never permanently settled, using the island as a port of call *en route* to and from the East Indies, but did introduce goats, asses, pigs and game birds, which quickly multiplied and went feral, as well as agricultural trees and plants (Melliss 1875; Disney 2009). Competition between the Dutch, British and Portuguese East India Companies over the spice trade resulted in conflict, and the Dutch intended to claim the island before the British settled there in 1659 (Ashmole & Ashmole 2000). The Dutch briefly captured St Helena in 1673, but the British retook it a few months later, and it has remained under British rule ever since (Melliss 1875; Ashmole & Ashmole 2000). The population remained small for the next century; however, deforestation and introduced livestock profoundly affected the environment, resulting in an irreversible destruction of much of the flora (Cronk 1988, 1989). The first botanical survey, conducted by William John Burchell from 1802 to 1807 (Buchanan 2016), was a significant milestone in understanding the negative ecological changes on the island. Invasive plants and further introductions of non-native mammals such as rabbits resulted in St Helena having one of the highest levels of habitat loss in the world, with only around 3.5% of native plant areas remaining today (Cronk 1988; Lambdon & Cronk 2020). By 1694, timber was noted to be scarce (Cronk 1983) and by 1771 natural forest was restricted to the peaks of the island (Banks 1796). In 1805, the lower parts of the island were described as “black, ragged and mouldering, without any tree, shrub or trace of verdure” although the highest parts of the hills were well vegetated but with many invasives (Duncan 1805: 3). Faunal extinctions followed the habitat destruction; of the extinct snails, the largest and most abundant are those in the genus *Chilonopsis* Fischer von Waldheim, 1848, some of which were noted to be extinct as early as 1834 (Seale 1834).

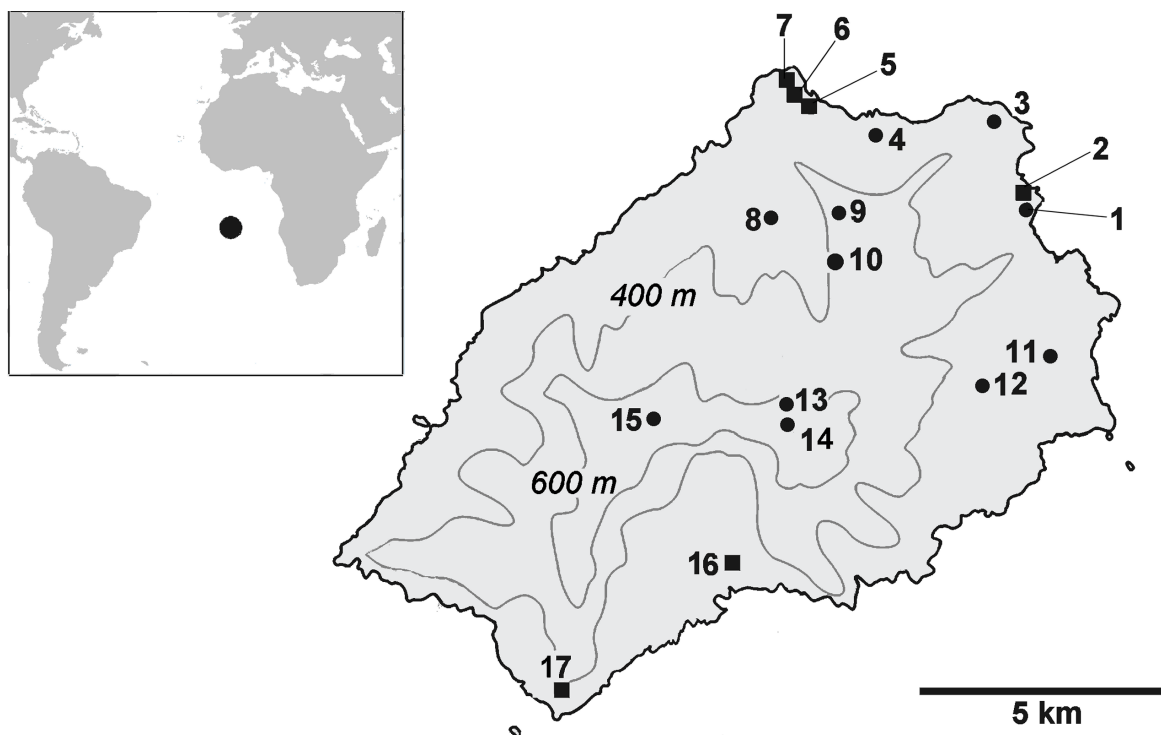
The first published record of snails from Saint Helena is the 1795 description of *Auris vulpina* by Chemnitz (now *Chilonopsis aurisvulpina* (Holten, 1802)) in a work that has been rejected as non-binomial (ICZN 1944). Other isolated specimens of this species were documented subsequently (e.g., Perry 1811). Early collections were made by visitors from ships calling at the island, most notably William Buckham Lorrain in 1824, William Henry Benson in 1832 and Joseph Dalton Hooker in 1840. More extensive material was accumulated by island residents: Robert Francis Seale in the 1820s, George Grey in 1840, Edward William Alexander in the 1840s.

Seale (1834: 6) was the first to draw attention to the subfossil nature of most shells: “the presence of those helices, which are to be met with in three or four parts of the Island, indicate that those parts (at least of Saint Helena) existed anterior to the recession of the waters, inasmuch as they are not strata of shells, but depositions which have been made upon several projecting flats on the sides of some of the hills, and, in one instance, upon an extensive plain. The variety of the helix here alluded to, is never found in a living state upon any part of the coast.” It was this observation that inspired Charles Darwin to make a particular search for shells when the *Beagle* called at St Helena in 1836: “Guided by information from Mr Seale I searched the sea-side of Flagstaff Hill to discover certain shells, supposed to be of marine origin, & found at considerable elevations. ... Beneath such an accumulation [of earth and stones] of about twenty feet thickness, the lower one or two yards or three feet resting on the volcanic tufa [error for tuff] contained scattered fragments of shells; one larger was slightly hardened apparently by calcareous matter & was full of shells.— Amongst them far the most abundant kind was a large appeared to me to be allied to *Bulimus*; there were delicate fragments which appeared to belong to young individuals.” (Darwin 1836: 934).

Benson collected some live snails in 1832 (Preece *et al.* 2022), and further attempts to find live snails were made by John Charles Melliss, a noted resident amateur naturalist who collected extensively in 1860–71 when he was the government surveyor of the island (Melliss 1875). After this time collections were made by increasingly professional scientists visiting the island: John Harcourt Blofeld, Thomas Vernon and Edith Wollaston and John Edward Gray in 1875–76, William Harry Turton in 1884–86, and Arthur and Mary Loveridge in 1961–72 (Sowerby 1844; Blofeld 1852; Forbes 1852; Melliss 1875; Wollaston 1878; Smith 1892; Crowley & Pain 1977; Woodward 1991). Snails were collected by the Musée royale de l’Afrique centrale (Tervuren, Belgium) in 1965 and 1967 but did not include *Chilonopsis*. In 2022 the “AtlantAves” palaeontological research programme collected material at several sites on Saint Helena as part of a study of the palaeoecology of the island, with particular reference to the avifauna. Mollusc specimens were collected and are preserved in NHMUK and MSH. This included new material of the extinct genus *Chilonopsis* (Achatinidae).

## Material and methods

All new material was collected on Saint Helena as part of palaeontological investigations in August–September 2022 by the “AtlantAves” team (Antoine Louchart, Julian Hume, Gavin Ellick, Anaïs Duhamel, Julien Joseph and Rebecca Cairns-Wicks). The localities are described below and located on Figure 1.



**Fig. 1.** Map of St Helena showing localities mentioned in the text, inset – location of St Helena in the Atlantic Ocean. 400 and 600 m contour lines shown. Locations of new material marked with squares. 1. Ridge leading to Bryan’s Rock. 2. Turks Cap. 3. The Barn. 4. Flagstaff Hill. 5. Sugar Loaf 3 and ridge. 6. Sugar Loaf 1 and quarry. 7. Sugar Loaf 2 and summit. 8. Side Path (‘side of the hill overlooking the Briars’). 9. Deadwood Plain. 10. Longwood. 11. Prosperous Bay Plain. 12. Dry Gut. 13. Between Mt Actaeon and Diana’s Peak. 14. Diana’s Peak. 15. High Peak. 16. Sandy Bay. 17. Castle Rock Plain.

Turks Cap (TC1. 15°55'48.29" S, 5°39'09.26" W). Dry, exposed weathering igneous rock with pockets of fine to coarse (clast size >50 mm) breccia deposits. Very rare terrestrial snails on surface in wind-protected pockets of sediment.

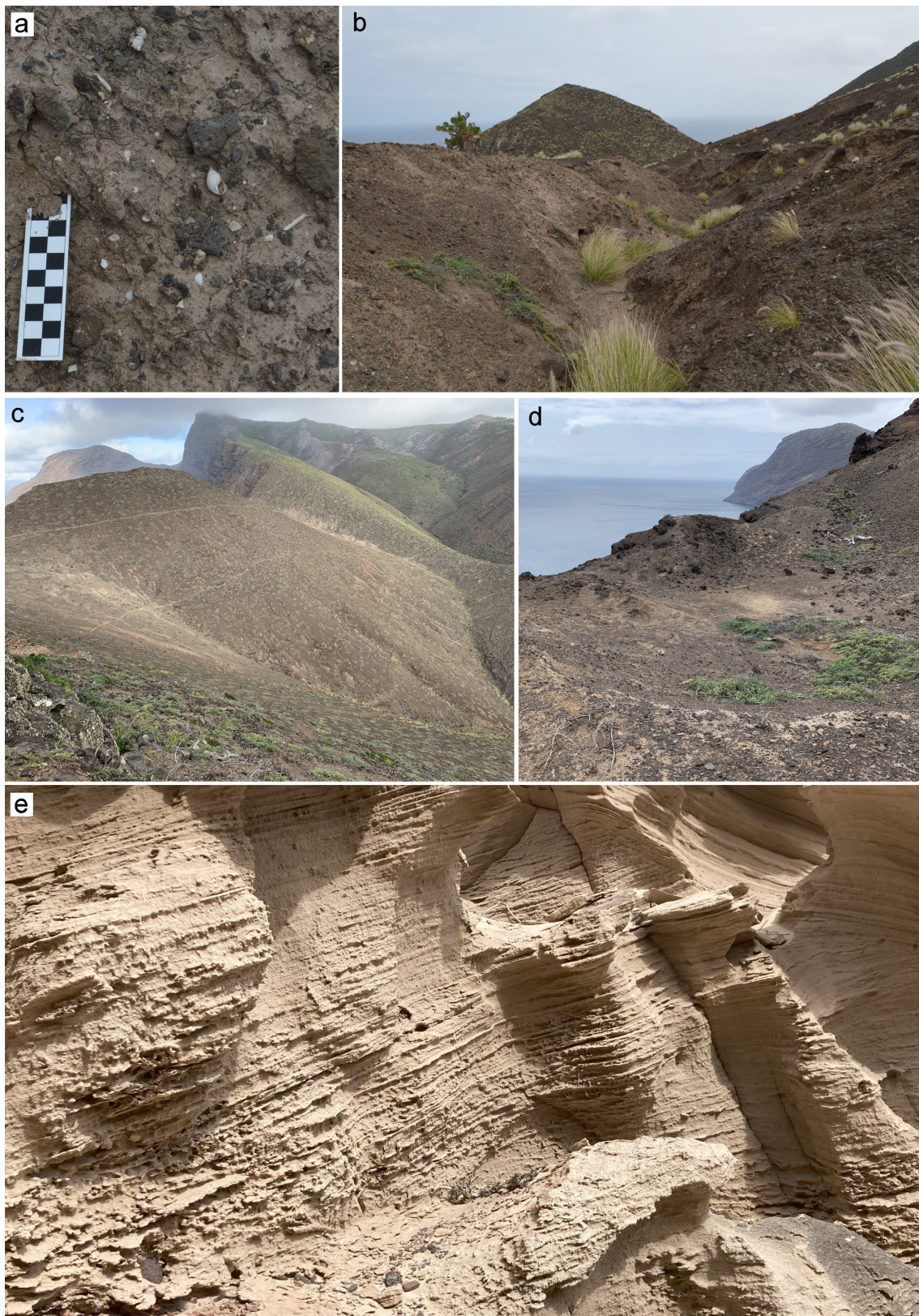
Dry Gut (DG1. 15°57'53.4" S, 5°39'22.9" W). Alluvial deposits forming terraces partly covered by (actual) colluvial sediments derived from nearby reliefs. Alluvial sediments consist of brownish fine silts and clays overlying unconformably weathered igneous rocks; they are interpreted as overbank deposits in an alluvial plain. The alluvial plain accreted from ephemeral flood events, with water overflowing nearby channels. Within this are gulleys 1–2.5 m in length and 80–120 mm deep. The base comprises a dry channel with silt intermixed with 0.5–25 mm breccia, denser on the upper surface. Snails found in the top 40 mm, some exposed on surface, others buried.

Sandy Bay (northern valley leading to Potato Gut) (PG1. 15°59'54.3" S, 5°42'42.7" W). Extensive aeolian calcareous sands situated over the side of the Sandy Bay valley leading to Potato Gut. Aeolian sands exhibit large-scale cross-bedding composed of well-sorted medium to coarse-grained skeletal carbonate grains of marine origin (calcareous containing coral, bivalve and gastropod clasts) with a small admixture of lithic grains (basalts) cemented by calcium carbonate; these deposits are interpreted as calcareous aeolianites. Aeolianites correspond to wind-borne topographically-controlled sand accumulations transported from the sea (i.e., aeolian sand dunes). Pristine rhizoliths are commonly found in the aeolianites, and usually form weathered rhizolith-rich beds ranging between 20 and 50 cm in thickness (Fig. 2e). Rhizoliths occur as vertical to tortuous pedogenetic cylindrical structures formed of well-cemented sediment, linked to the decay of plant roots on the surface of palaeo-sand dunes. Erosion creates sand slumps that extend to the valley walls. Eroded sandstone face has fine lamination (10–20 mm) dipping 45° E. Snails found on the surface.

Sugar Loaf 1 (15°54'36.9" S, 5°41'53.3" W; Fig. 2a–b). This is Site 1 of Olson (1975), situated 395 m above SL. Snails (*Chilonopsis* spp. and *Helsingia sanctaehelena*) are encountered in two distinct (and superposed) sedimentary formations: (i) calcareous aeolianites characterised by very well sorted (and rounded) coarse sands of marine origin (similar to that described at Sandy Bay), including rhizoliths, underlain by (ii) light brown alluvial deposits forming a low-angle terrace dissected by a modern ravine. Alluvial sediments consist of silts and (mostly) sands deposited from turbulent flows downslope, judging from the presence of current ripple cross laminations, planar laminations and trough cross-bedding. Boulders of calcareous aeolianite are found as reworked material within alluvial sediments. Scree deposits (<100–150 mm gravel and boulders), including finer sediments, occur as interbedded layers within the sandy alluvium and imply lateral inputs of colluvial deposits. Alluvial terraces are finally overlain by scree slope deposits made of a clitter of angular clasts and finer debris dipping 15° to the ravine. Numerous scattered terrestrial snails are found on the surface of alluvial deposits.

Sugar Loaf 2 (15°54'26.2" S, 5°41'57.9" W; Fig. 2c). This is Site 2 of Olson (1975). Directly below Sugar Loaf Mountain, Site 2 comprises a long gully with high runoff, the gully approximately 4 m across narrowing to a 1 m channel. As for Sugar Loaf 1 site, sediments consist mostly of light brown silts and sands overlying here a poorly exposed calcareous aeolianite. Snail subfossils on the surface separating the brownish silty sands from the upper stony layer of colluvial deposits. Samples are now divided into south-east (SE) and north-west (NW) sublocalities, which show significantly different faunal compositions (in birds, but also in land snails) and preservation (for example the NW part yields complete bird eggs and skulls, not found in the SE part).

Sugar Loaf 3 (15°55'36.2" S, 5°41'47.2" W; Fig. 2d). This is Site 3 of Olson (1975). A highly weathered fossil locality, strewn with large deposits of boulder scree, but also with silt to fine-grained sand deposits. Fine-grained silty sand deposits overlay a basal layer of calcareous aeolian sands, as in Sugar Loaf sites 1 and 2. Heavily weathered with subfossil terrestrial snails.



**Fig. 2.** **a.** *Chilonopsis* Fischer von Waldheim, 1848 subfossil shells in-situ at Sugar Loaf 1 (scale bar in cm). **b.** View of Sugar Loaf 1. **c.** Sugar Loaf 2. **d.** Sugar Loaf 3. **e.** Sandy Bay cross-bedding with rhizolith-rich intervals (photos: a–b = J. Hume; c–d = A. Louchart; e = P. Sorrel).

**Table 1.** Measurements (means±standard deviation in mm) and proportions of shells of *Chilonopsis* Fischer von Waldheim, 1848.

	height		diameter		height/diameter		mouth height/ width		n
	range	mean	range	mean	range	mean	range	mean	
<i>aurisvulpina</i>	33.1–48.8	42.20±4.26	20.1–31.5	25.57±3.50	1.52–2.00	1.67	1.40–2.10	1.79	34
<i>helena</i>	15.1–22.3	18.29±1.61	7.4–12.7	9.50±1.04	1.64–2.20	1.91	1.48–1.80	1.71	119
<i>blofeldi</i>	25.9–30.2	28.30±1.40	14.1–17.1	15.59±1.09	1.68–2.04	1.82	1.52–1.85	1.72	7
<i>lanceoloideus</i> sp. nov.	15.9–21.3	17.76±1.67	10.1–12.1	11.09±0.76	1.51–1.76	1.605	1.63–1.93	1.80	10
<i>exulatus</i>	17.2–21.5	19.83±1.41	7.5–9.2	8.63±0.52	2.24–2.39	2.30	1.63–2.25	2.13	8
<i>subtruncatus</i>	29.0–31.5	29.95±1.17	12.5–14.2	13.30±0.88	2.17–2.23	1.82	1.66–1.97	1.77	5
<i>subplicatus</i>	17.0–25.4	20.05±3.63	5.3–9.2	7.57±1.45	2.15–3.24	2.79	1.79–1.99	1.91	31
<i>melanioides</i>	23.8–24.8	24.23±0.51	7.4–8.0	7.77±0.32	3.01–3.22	3.12	1.44–1.95	1.72	4
<i>turtoni</i>	14.7–18.4	16.22±1.47	8.1–9.2	8.37±0.52	1.67–2.10	1.92	1.31–1.78	1.63	9

Measurements were taken with digital callipers to the nearest 0.1 mm. Height of the body whorl was defined as the distance from the base of the shell to the mid-point of the suture. Measurements are summarised in Table 1, and diagnostic characters in Table 2. Sculpture was examined under a light microscope ( $\times 40$  magnification) for all species, further detail was examined using scanning electron microscopy with the Verios 460 SEM at the Cambridge Advanced Imaging Centre; due to the irreplaceable nature of the material, this was only possible for species represented in the new collections. Suitably preserved specimens were available for four species although two specimens proved to be too worn to provide clear images.

Species were separated on the basis of conchological features of shell shape, sculpture and detail of the columellar and apertural region. In addition, morphometrics were compared using a principal components analysis of shell height and diameter, aperture height and width, height of the body whorl from base to the mid-point of the suture, distance from base to the widest part of the shell, maximum width of lip expansion, number of whorls of the protoconch and the teleoconch. The factor loadings are shown in Table 3 and the plot of the first two principal components in Figure 3. Almost all species were clearly separated on the first two principal components; those where there was overlap differ clearly in other features.

#### Institutional acronyms

ANSP	=	Academy of Natural Sciences of Drexel University, Philadelphia, USA
CM	=	Carnegie Museum of Natural History, Pittsburgh, USA
DMNH	=	Delaware Museum of Natural History, Delaware, USA
FMNH	=	Field Museum of Natural History, Chicago, USA
LIV	=	Liverpool Museum, Liverpool, UK
MCZ	=	Museum of Comparative Zoology, Harvard, USA
MM	=	Manchester Museum, Manchester, UK
MNHN	=	Museum national d'Histoire naturelle, Paris, France
MRAC	=	Musée royal de l'Afrique centrale, Tervuren, Belgium
MSH	=	Museum of St Helena, St Helena

**Table 2.** Diagnostic features of species of *Chilonopsis* Fischer von Waldheim, 1848. A = shape (1–ovate, 2–lanceoloid, 3–conical, 4–elongate); B = apex (0–rounded, 1–acute); C = maximum number of whorls; D = widest point of body whorl (1–middle, 2–below middle); E = body whorl (1–rounded, 2–shouldered, 3–carinate); F = sutures (0–straight, 1–wavy); G = maximum number of protoconch whorls; H = protoconch sculpture (0–reduced, 1–distinct); I = sutural bosses (0–absent, 1–present); J = teleoconch radials (0–reduced, 1–regular, 2–irregular); K = teleoconch scalloping (0–absent, 1–present); L = umbilicus (0–closed, 1–open); M = lip expanded (0–not, 1–narrowly, 2–widely); N = lip (0–curved, 1–sinuous); O = aperture at base (1–rounded, 2–angled, 3–flared); P = columella truncate (0–no, 1–yes); Q = columella (1–vertical, 2–oblique, 3–curved, 4–twisted); R = columellar surface (0–flat, 1–ridge, 2–concavity); S = parietal nodule (0–absent, 1–present).

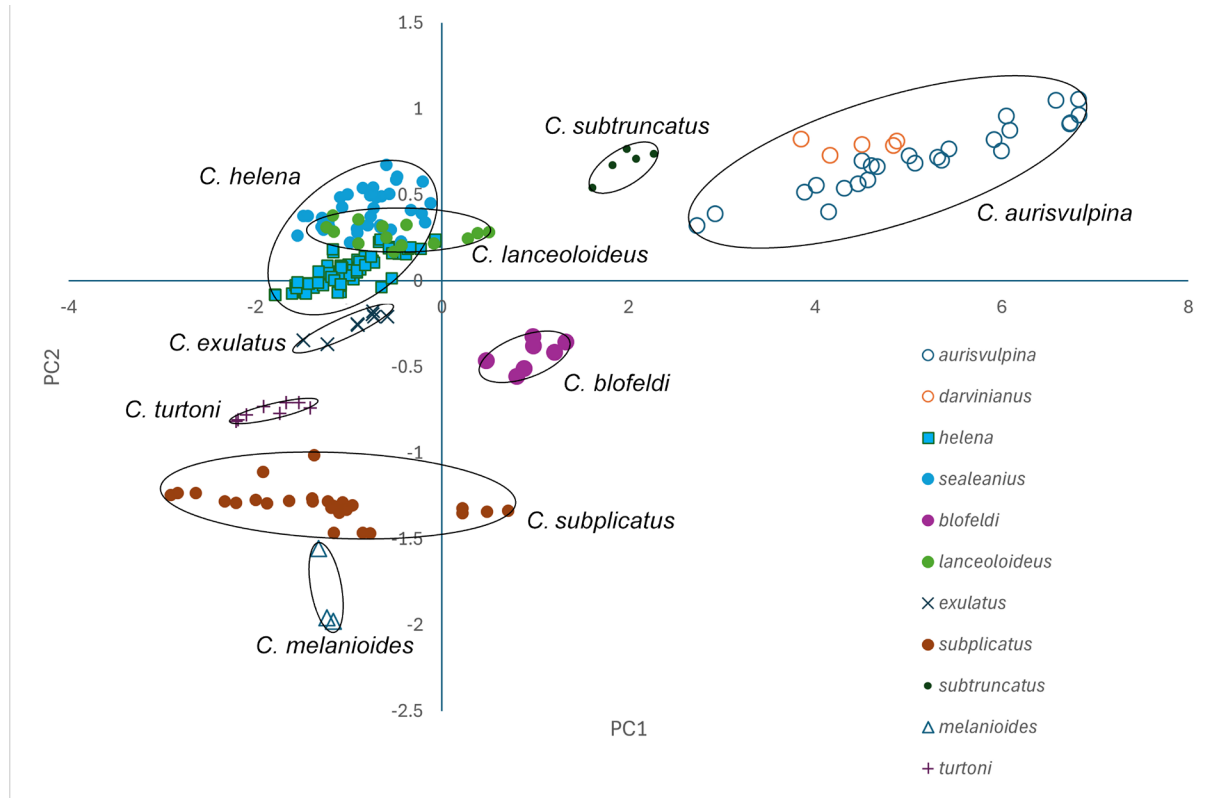
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
<i>aurisvulpina</i>	1	0	7	1	2	0	0.75	1	1	1	0	1	2	1	2	1	2	1	1
<i>helena</i>	1	0	7	2	2	0	2	1	0	1	1	0	1	0	2	0	1	0	0
<i>blofeldi</i>	1	1	6	1	1	0	2	?	0	1	?	0	1	0	2	0	1	0	0
<i>lanceoloideus</i> sp.nov.	2	0	5.25	2	1	0	1.75	1	0	2	1	0	1	0	1	0	2	0	0
<i>exulatus</i>	4	1	7	1	2	0	2	1	0	2	1	1	1	0	2	1	1	0	0
<i>subtruncatus</i>	4	0	7	1	1	0	2	0	0	0	0	1	1	0	3	1	1	0	0
<i>subplicatus</i>	4	0	7	1	2	0	1.5	1	1	1	0	0	1	0	2	1	4	2	1
<i>melanioides</i>	4	1	9	1	3	1	1	0	1	1	0	1	1	0	2	1	4	0	0
<i>turtoni</i>	3	1	7	1	1	0	2	1	0	1	0	0	0	0	1	1	1	0	0

**Table 3.** Principal components analysis results and factor loadings. The first two principal components account for 97.0% of the variance.

	PC1	PC2
Eigenvalue variance	93.9%	3.1%
Shell height	0.64259	-0.60532
Shell diameter	0.43408	0.07405
Aperture height	0.32617	-0.06742
Aperture width	0.17887	0.01387
Body whorl height	0.45811	0.61912
Widest point	0.21749	0.43773
Lip expansion	0.04906	0.01751
Teleoconch	0.00864	-0.21081
Protoconch	-0.02511	0.06086

- NHMD = Natural History Museum of Denmark, Copenhagen, Denmark  
 NHMUK = Natural History Museum, London, UK  
 NMBE = Naturhistorisches Museum der Burgergemeinde Bern, Bern, Switzerland  
 NMNZ = Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand  
 NMW = National Museum of Wales, Cardiff, UK  
 RBINS = Royal Belgian Institute of Natural Sciences, Brussels, Belgium  
 RMNH = Naturalis Biodiversity Center (formerly Nationaal Natuurhistorisch Museum, Leiden), Netherlands

- SANBI = South African National Biodiversity Institute, Cape Town, South Africa  
 UF = Florida Museum of Natural History, Gainesville, USA  
 UMMZ = University of Michigan Museum of Zoology, Michigan, USA  
 UMZC = University Museum of Zoology, Cambridge, UK  
 USNM = Smithsonian Institution, National Museum of Natural History, Washington D.C., USA  
 ZMA = Naturalis Biodiversity Center (formerly Zoological Museum Amsterdam), Netherlands



**Fig. 3.** Distribution of specimens across the first two principal components (Table 3). The main forms (species and recognisable varieties) are shown, with ellipses grouping the specimens of species recognised here.

## Results

### *Taxonomy*

Phylum Mollusca Linnaeus, 1758  
 Class Gastropoda Cuvier, 1797  
 Order Stylommatophora A. Schmidt, 1855

Family **Achatinidae** Swainson, 1840

### **Diagnosis**

Relatively large, usually dextral shells (to 200 mm in length), elongate to broadly conical. Whorls usually rounded, with moderately impressed sutures. Apex usually globose. Aperture ovate, basally expanded along columella margin, forming a channel. Columella often truncated, narrow to moderately wide and often thickened, usually with a twist or fold. Umbilicus very small or absent. Other shell features vary by genus.

*Chilonopsis* shows the basally expanded, channelled aperture typical of the family, and the columella fold is distinct in some species. It has been placed in three subfamilies: Stenogyrinae P. Fischer & Crosse, 1877 by Pilsbry (1905); Petriolinae Schileyko, 1998 by Schileyko (1998); and Coeliarinae Pilsbry, 1907 by Preece *et al.* (2022). These subfamilies are not clearly defined conchologically and are not fully monophyletic (Fontanilla *et al.* 2017). We therefore refrain from assigning *Chilonopsis* to any subfamily.

Genus ***Chilonopsis*** Fischer von Waldheim, 1848

*Chilonopsis* Fischer von Waldheim, 1848: 236.

*Nesobia* Ancey, 1887: 39.

*Cleostyla* Dall, 1896: 419.

*Helena* Germain, 1931: 169.

**Type species**

*Chilonopsis sulcata* Fischer von Waldheim, 1848: 236, by original designation (= *Chilonopsis aurisvulpina* (Holten, 1802)).

**Diagnosis**

Shells ovately conical to narrowly elongate; thin to moderately thick; whorls moderately convex, sometimes shouldered; protoconch with fine spiral striae of variable prominence; teleoconch sculpture of spiral and radial striae, intersecting to produce a scalloped or wavy effect; suture sometimes raised into bosses of variable prominence. Lip usually only slightly expanded, not thickened; umbilicus closed or nearly so; aperture subvertical, ovate; columella obliquely truncate to subtruncate, often with a ridge or nodule.

**Remarks**

The larger St Helena snails were recognised as a separate genus, *Chilonopsis* by Fischer von Waldheim in 1848. The genus was placed in the Achatinidae by Fischer (1883) (as the ‘Stenogyridae’) and further supported by Pilsbry (in Dall 1896) based on the form of the jaw and radula. Schileyko (1998) placed one species (*Chilonopsis helena* (Quoy & Gaimard, 1832), as *Nesobia helena*) in the Pachnodidae Steenberg, 1925 without explanation. He placed the other species (as *Chilonopsis* and *Cleostyla*) in the Petriolinae of the Subulinidae P. Fischer & Crosse, 1877 (Schileyko 1999). Subulinidae, along with Petriolinae, are now regarded as being within the Achatinidae (Bouchet *et al.* 2017). Similarly, Petit & Coan (2008) did not explain their listing of one species (*Chilonopsis aurisvulpina*) under Ferussaciidae Bourguignat, 1883. As all species share similar aspects of sculpture they are considered all to belong to the same family.

Dall (1896) and Pilsbry (1904) listed two subgenera: *Chilonopsis* (*Chilonopsis*) for species possessing sutural bosses (*C. aurisvulpina*, *C. melanioides*, *C. subplicatus*) and *Chilonopsis* (*Cleostyla*) for more elongate species lacking bosses. These were treated as separate genera by Schileyko (1999) but given that the development of the bosses is variable and *C. aurisvulpina* appears more similar to *C. helena* in all features other than the bosses than to the other ‘*Cleostyle*’ species, we consider them to be artificial groupings and retain all species in *Chilonopsis*.

***Chilonopsis aurisvulpina*** (Holten, 1802)

Figs 4a, 5–6, 7a–b

*Auris vulpina* Chemnitz, 1795: 287, pl. 210 figs 2086–2087 (non binomial).

*Voluta auris-vulpina* Holten, 1802: 45.

*Melania Nonpareil* Perry, 1811: pl. 29 fig. 4.

*Bulimus* (*Pachyotus*) *alopecotis* Beck, 1838: 56 (replacement name for *Voluta auris-vulpina*).

- Chilonopsis sulcata* Fischer von Waldheim, 1848: 236.  
*Bulimus relegatus* W.H. Benson, 1851: 31.  
*Bulimus darwinianus* Forbes, 1852: 4, pl. 5 fig. 1.  
*Bulimus auris-muris* (non Moricand) Shuttleworth, 1852a: 200 (preoccupied).  
*Bulimus auris-myoxi* Shuttleworth, 1852b: 289 (replacement name for *Bulimus auris-muris*).
- Voluta auris-vulpina* – Dillwyn 1817: 503. — Reeve 1849: pl. 30 fig. 180.  
*Helix auris-vulpina* – Férussac 1822: 57.  
*Pupa Auris vulpina* – Gray 1825: 413.  
*Bulimus auris-vulpina* – Griffith & Pidgeon 1834: 596, pl. 37 fig. 7. — Lamarck 1838: 257. — Deshayes 1839: 257. — Küster 1844: 39. — Pfeiffer 1848: 93; 1853: 371; 1854: xii; 1859: 440; 1868: 77. — Jeffreys 1872: 264. — Melliss 1875: 121. — Wollaston 1878: 547 (including var. *subspiralis*, *obliteratus*). — Smith 1892: 265.  
*Cochlogena auris-vulpina* – G.E. Sowerby I 1844: 155.  
*Bulimus relegatus* – Pfeiffer 1853: 417; 1868: 123. — Melliss 1875: 122.  
*Bulimus auris-vulpina* – Wollaston 1878: 547.  
*Bulimus Darwinianus* – Wollaston 1878: 549 (misspelling).  
*Buliminus (Pachyotus) auris vulpina* – Kobelt 1902: 656.  
*Chilonopsis nonpareil* – Pilsbry 1904: 174. — Crowley & Pain 1977: 553. — Schileyko 1999: 532.  
*Chilonopsis nonpareil* var. *darwinianus* – Pilsbry 1904: 176.  
*Chilonopsis (Chilonopsis) non pareil* – Germain 1931: 169.  
*Chilonopsis nonpareil darwinianus* – Crowley & Pain 1977: 555.  
*Chilonopsis* [sic] *nonpareil* – Woodward 1991: 4.  
*Chilonopsis aurisvulpina* – Petit 2003: 41. — Petit & Coan 2008: 244.

### Diagnosis

The largest *Chilonopsis* (height 33.1–48.4 mm), unique in having the body whorl angled near the shoulder and with very prominent sutural bosses. The lip is sinuous and there is usually a nodule on the parietal callus; the lip and callus are unusually thickened.

### Type material

#### Lectotype of *Auris vulpina* (here designated)

SAINT HELENA • shell; “China”; Spengler collection; NHMD-1725954 (Fig. 5a).

#### Remarks

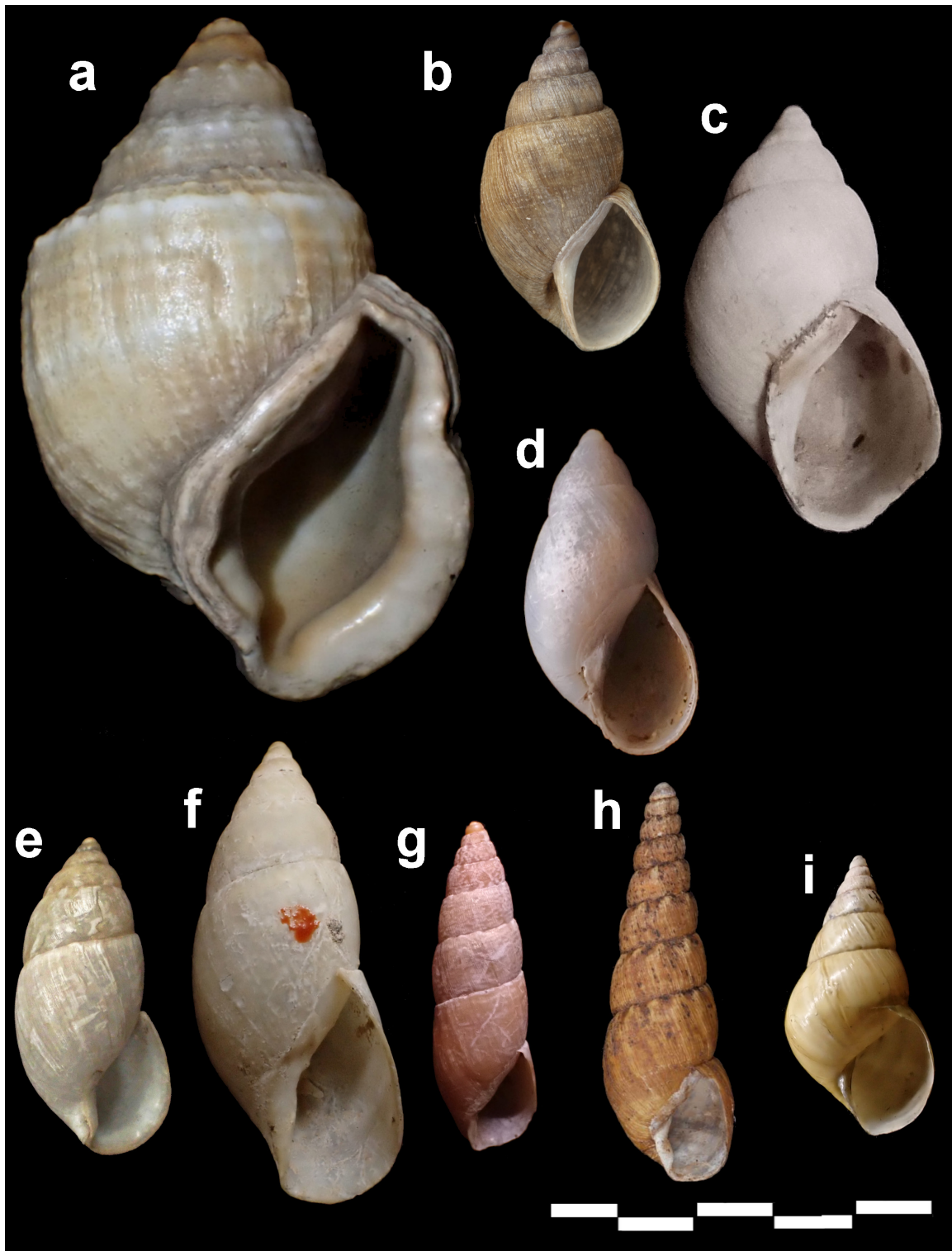
This is the shell figured (Fig. 5b) by Chemnitz (1795: 287, pl. 210 figs 2086–2087); the description was also based on two immature specimens, which have not been located. The immature specimens were bought from the Humfrefrdianum Museum auction in Hamburg in 1794; the auction catalogue gave their origin as Saint Helena (Holten 1802). The figured specimen was supposedly from China. We designate this specimen as the lectotype (Fig. 5a). In addition to the type material, Spengler had a second specimen labelled “St. Helena, 20 feet deep in the rock” (NHMD-1725961), this is worn, with the lip broken.

#### Type of *Melania Nonpareil*

Not located, Perry's (1811) figure (Fig. 5c) appears to be a copy of Chemnitz's figure of *Auris vulpina* but he states that it was ‘from a specimen in Mr. Lloyd's Museum.’ (probably William Horton Lloyd 1784–1849).

#### Type of *Chilonopsis sulcata*

Not located; ‘St. Jago Americae meridionalis’, figured by Fischer von Waldheim (1848) (Fig. 5d).



**Fig. 4.** Species of *Chilonopsis*. **a.** *C. aurisvulpina* (Holten, 1802) (NHMD-172594). **b.** *C. helena* (Quoy & Gaimard, 1832) (NHMUK 20240185). **c.** *C. blofeldi* (Forbes, 1852) (NHMUK). **d.** *C. lanceoloideus* sp. nov., holotype (NHMUK 20240171). **e.** *C. exulatus* (Reeve, 1849) (UMZC I.105095). **f.** *C. subtruncatus* (E.A. Smith, 1892) (NHMUK 92.2.24.224-8). **g.** *C. turtoni* (E.A. Smith, 1892) (NHMUK 1892.2.24.209-218). **h.** *C. subplicatus* (G.B. Sowerby I, 1844) (MSH). **i.** *C. melanioides* (Wollaston, 1878) (ANSP 97326). Scale bar = 25 mm.

**Holotype or syntype of *Bulimus relegatus***

SAINT HELENA • Lt. Lefroy; UMZC I.105005 (Fig. 5e).

**Remarks**

In the Robert McAndrew collection, ex W.H. Benson (Preece *et al.* 2022). It is unclear whether this is the holotype or a syntype: Preece *et al.* (2022) listed it as a syntype, but the original description gives no indication as to whether it was based on one or more specimens. This is the only specimen known to have been collected by Lefroy.

**Holotype of *Bulimus auris-myoxi***

SAINT HELENA • no locality; ex Marguiger 1845; NMBE-WL-19055 (Fig. 5f). Figured by Neubert & Gasteli (2003).

**Syntypes of *Bulimus darvinianus***

SAINT HELENA • 2 shells; collected by Edward Alexander; NHMUK-PI G 25274-5 (Fig. 5g–h). Figured by Forbes (1852: pl. 5 fig. 1); presented by E. Alexander to Museum of Practical Geology, later transferred to NHMUK.

**Other material examined**

20<sup>th</sup> century specimens include one worn specimen found in 1964 (Woodward 1991). Crowley & Pain (1977) noted that none could be found in Turton's localities by the MRAC Expedition (Flagstaff, Sugarloaf, Barn) and thought that the last remaining specimen was the one taken in 1972 by A. Loveridge at 300 m on the slopes of Bencoolen (Dry Gut), all others having been lost through erosion. However, the MRAC expedition concentrated only on recent and living animals, and the discovery of new material demonstrates that specimens can still be found.

**Typical form**

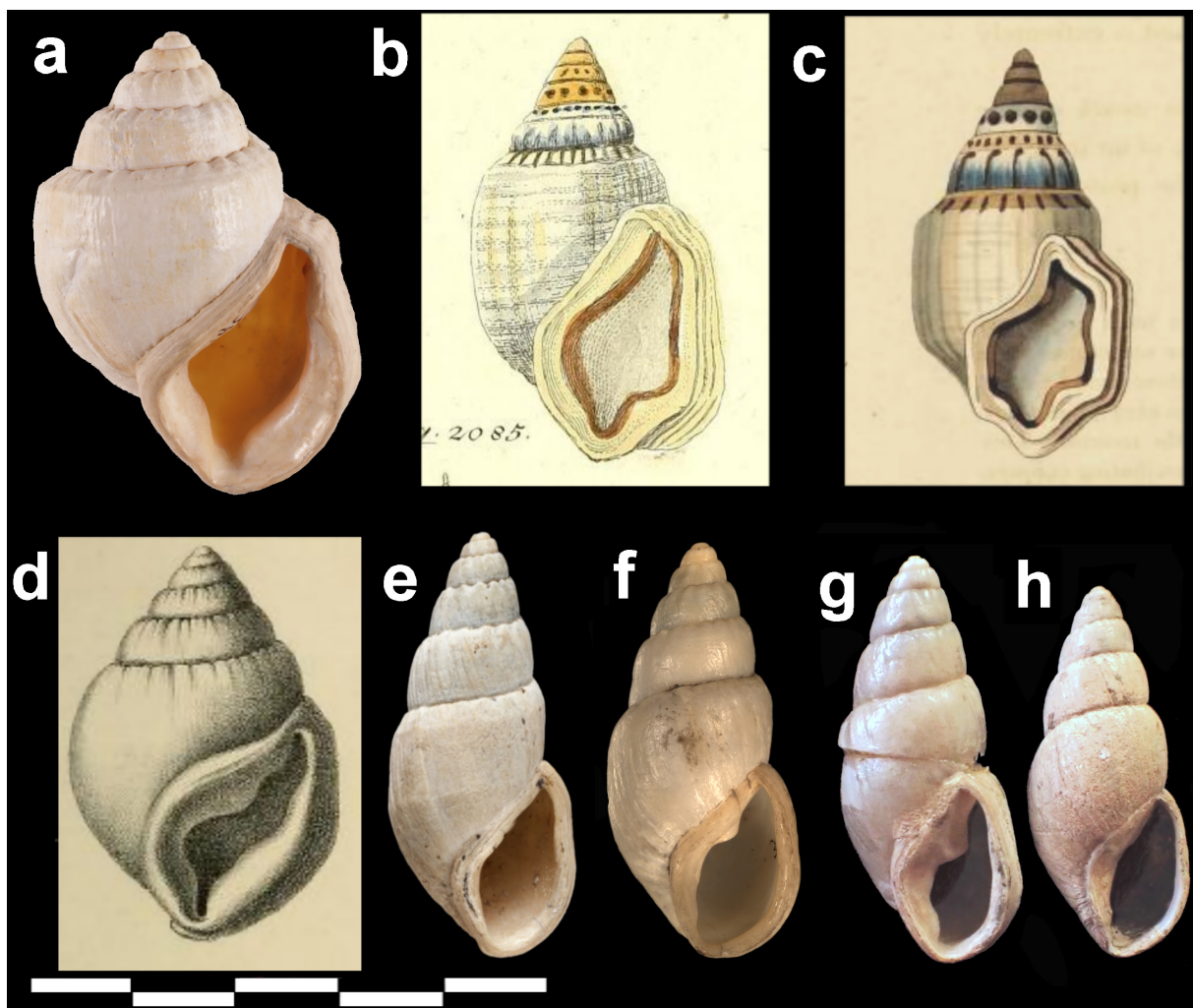
SAINT HELENA • 3 shells; coll. J.S. Phillips; ANSP MAL 330769 • 3 shells; ex T.B. Wilson; ANSP MAL 330770 • 1 broken shell; CM 62.6934 • 1 shell; Sugarloaf Ridge; ex Walton 10855; DMNH 142088 • 1 shell; FMNH 36152 • 1 shell; FMNH 48078 • 1 shell; on ridge leading to Bryan's rock; 27 May 1963; A. Loveridge leg.; FMNH 173184 • 1 shell; Sugarloaf Ridge, N coast facing E.; elev. ca 1000 ft; 30 Oct. 1963; A. and M. Loveridge leg.; FMNH 173185 • 2 shells; Sugarloaf Ridge, N coast facing E; A. and M. Loveridge leg.; FMNH 173186 • 1 shell; Sugarloaf Ridge from bases of *Suaeda fruticosa*; 30 Oct. 1963; A. Loveridge leg.; FMNH 173190 • 1 shell; LIV • 2 shells; off west coast; MCZ 141183 • 10 shells; Deadwood Plain; elev. 1500 ft; 1 Feb. 1949; MCZ 203239 • 1 shell; MCZ 381633 • 1 shell; Spence, Layard and Darbyshire collections; MM • 1 shell; A. Loveridge leg.; MRAC • 6 shells; Prosperous Bay Plain; 1995; P. and M. Ashmole leg.; MSH (1 used for SEM – Fig. 7a–b) • 1 spec.; Dry Gut; Aug.–Sep. 2022; “AtlantAves” leg., MSH • 1 shell; transferred from Museum of Practical Geology, presented by E. Alexander; NHMUK-PI G25278 • 1 shell; J. Brown collection 1860; NHMUK G25284-6 • 8 shells; W.H. Turton leg.; NHMUK 1892.2.24.1-7 • 5 shells; NHMUK 1892.2.24.10-5 • eggs; W.H. Turton leg.; NHMUK 1892.2.24.166-170 • 2 shells; Trechmann collection; NHMUK 2176 • 17 shells; NHMUK • 1 shell; Sugarloaf Ridge; Tomlin collection ex Blok collection; NMW • 1 shell; Putzeys collection; RBINS:IG.27761-INV.66549 • 1 shell; P. Dupuis collection ex Fulton; RBINS:IG8907-HIST.5 • 5 shells; J.C. Coops leg.; Sep. 1916; RMNH.MOL.269631-3 • 1 shell; Sowerby and Fulton collection (original provenance not documented); SANBI MB-A034375 • 4 shells; SANBI MB-A054185 • 4 shells; J.R. Tomlin leg.; UMMZ 141296 • 2 shells; USNM 104990 • 1 shell; USNM 126261 • 8 shells; USNM 703393 • 4 shells; USNM 709840 • 2 shells; USNM 713598.

“*darwinianus* form”

SAINT HELENA • 2 shells; FMNH 126262a • 1 shell; Sugarloaf Ridge, N coast facing E; elev. ca 1000 ft; 1963; A. and M. Loveridge leg.; FMNH 173185 • 1 shell; Sugarloaf Ridge; 1963; A. Loveridge leg.; FMNH 173190 • 1 shell; Sugarloaf Ridge; W.H. Turton leg.; Darbyshire collection; MM • 1 shell; Woodward and McAndrew collections; UMZC • 1 shell; W.H. Turton leg.; USNM 126262 • 2 shells; USNM 707830 • 4 shells; USNM 710416.

**Description**

The largest *Chilonopsis* (33.1–48.4 mm high; Table 1). Shell moderately thin, often solid in subfossil specimens. Usually ovate, sometimes narrowly ovate to elongate. 6.5–7 convex whorls, body whorl high shouldered, angled at shoulder and margin. Protoconch of 0.75 whorls, ornamented with 5–6 spiral striae,



**Fig. 5.** *Chilonopsis aurisvulpina* (Holten, 1802) types. **a.** *Auris vulpina* Chemnitz, 1795, lectotype figured by Chemnitz (NHMD-1725954). **b.** *Auris vulpina* figure (Chemnitz 1795). **c.** *Melania Nonpareil* Perry, 1811 figure (Perry 1811). **d.** *Chilonopsis sulcata* Fischer von Waldheim, 1848 figure (Fischer von Waldheim 1848). **e.** *Bulimus relegatus* W.H. Benson, 1851 (UMZC I.105005). **f.** *Bulimus Auris-Myoxi* Shuttleworth, 1852, holotype (NMBE-WL-19055). **g–h.** *Bulimus darwinianus* Forbes, 1852, syntypes (NHMUK-PI G 25274-5). Scale bar = 50 mm. Photos: a = M. Vinther Sørensen, NHMD; c = NHMUK; e = UMZC; f = E. Neubert, NMBE.

which are only distinct in the freshest specimens (Fig. 7a). Teleoconch with low, coarse radial ridges raised into bosses at suture, overlain by fine radial ridges from second whorl. Faint spiral striae on first whorl, only distinct on the bosses, giving a granular appearance to the spire. On all other whorls these develop into strong, well separated spiral cords (Fig. 7b). Umbilicus compressed or closed. Lip expanded and thickened, curved inwards in middle part, compressing aperture. Columella slanting, obliquely subtruncated. Parietal callus thick, usually with a recessed parietal nodule of variable prominence.

Colour in the best-preserved specimens varying from whitish (probably faded) to red-brown, aperture orange-red, columella pink, parietal callus orange-red.

A variable species; four varieties have been recognised by Wollaston (1878) and listed by Pilsbry (1904):

Typical form – trochiform with whorls angled near the suture, coarse radial striae, umbilicus largely obscured, lip thickened, right margin bends inwards, aperture lacking nodules

“var. *subspiralis*” – as typical form but with more pronounced spiral striae and weaker radial ridges, closed umbilicus, a parietal nodule within the aperture

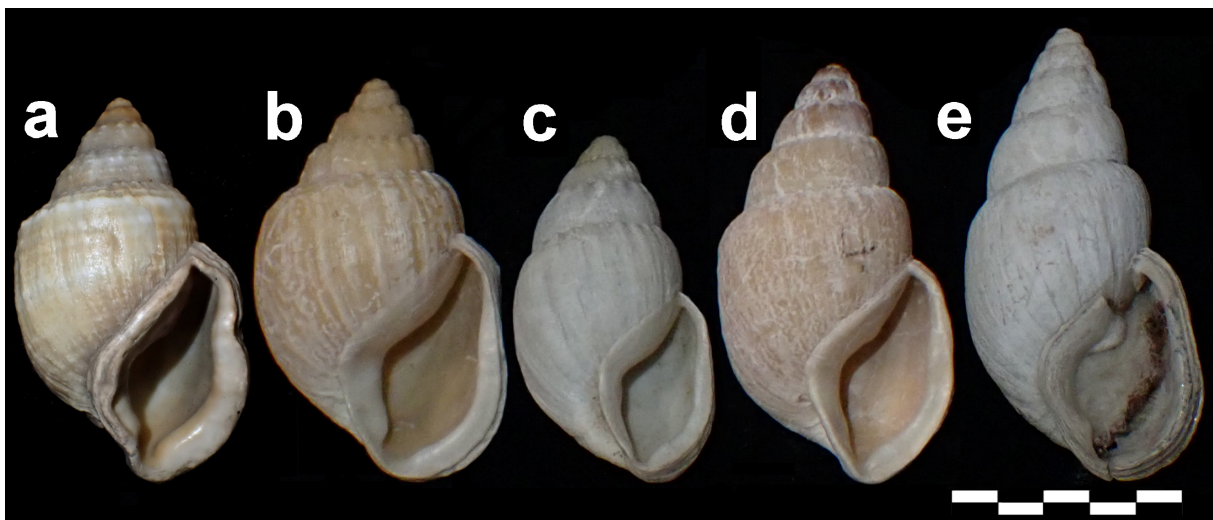
“var. *obliteratus*” – as typical form but whorls less angled, lip thinner and straighter on outer margin, umbilicus covered, a low parietal nodule deep within the aperture

“var. *darwinianus*” – narrow with an elongate spire, smoother, umbilicus closed, parietal tubercle usually well developed

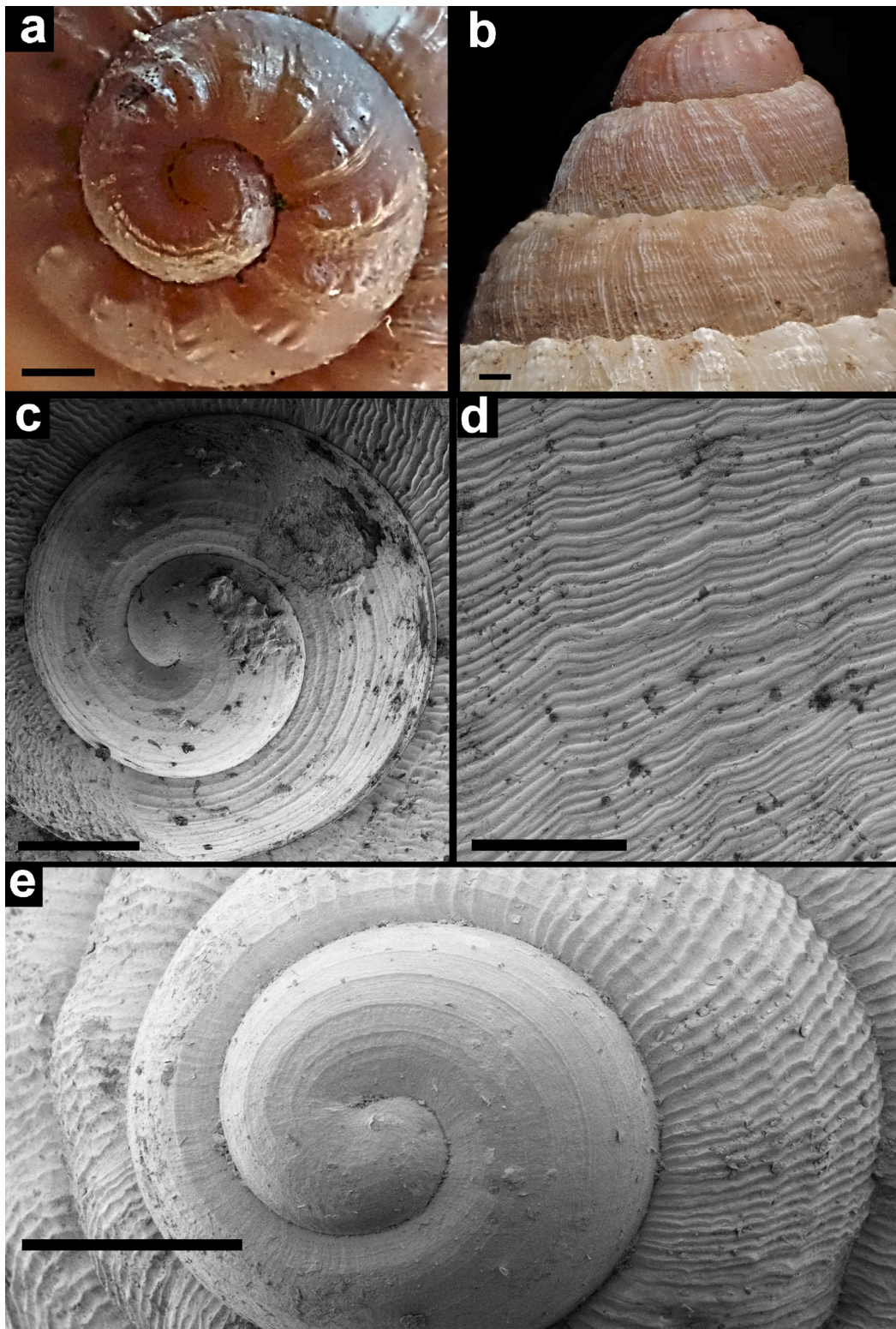
“Var. *darwinianus*” was kept as a subspecies by Crowley & Pain (1977) as it was ‘remarkably constant in form and size’ but varied in nodule development. All the varieties were sympatric on the Sugarloaf where they intergrade. As they were sympatric and lacked clear dividing lines none of the varieties can be maintained as a subspecies.

### Distribution

Eastern third of the island (Fig. 11): behind Longwood (Blofeld 1852); all along Sugarloaf Ridge (over 30 specimens from Turton, in Smith 1892; Wollaston 1878); Flagstaff (Wollaston 1878); towards The Barn



**Fig. 6.** *Chilonopsis aurisvulpina* (Holten, 1802) variation in a single sample (NHMUK un-numbered). Scale bar = 20 mm.



**Fig. 7.** Sculature of species of *Chilonopsis*. **a–b.** *Chilonopsis aurisvulpina* (Holten, 1802) (Prosperous Bay Plain, P. & M. Ashmole, 1995), protoconch (a) and spire (b). **c–d.** *Chilonopsis helena* (Quoy & Gaimard, 1832) (Turks Cap summit, “AtlantAves”, Aug. 2022) scanning electron micrographs of protoconch (c) and body whorl (d). **e.** *Chilonopsis lanceoloideus* sp. nov. (Castle Rock Plain, P. & M. Ashmole, 1995) scanning electron micrograph of protoconch and spire. Scale bars = 500  $\mu$ m.

(Wollaston 1878); Dry Gut (Woodward 1991; new); ridge leading to Bryan's Rock (FMNH 173184); Deadwood Plain (MCZ); Prosperous Bay Plain (MSH). Melliss (1875: 122) recorded it "embedded in the surface-soil in the ravines formed by rain, on the north-eastern quarter of the Island, at altitudes from 1200 to 1700 feet above the sea."

Both the typical variety and the rarer *darwinianus* form were found together on Sugarloaf, Flagstaff and Barn (Wollaston 1878).

Extinct; never recorded living.

### Remarks

According to Petit & Coan (2008), Holten's (1802) list validates Chemnitz's non-binomial names, making *Voluta auris-vulpina* Holten, 1802 available. Accordingly, the correct name for this species is *Chilonopsis aurisvulpina* (Holten, 1802).

*Bulimus relegatus* W.H. Benson, 1851 was synonymised with *C. helena* by Wollaston (1878) and this was followed by Crowley & Pain (1977) and Preece *et al.* (2022), however it falls within the range of variation of the "darwinianus" form of *C. aurisvulpina*. Thus, we consider it a junior synonym of *C. aurisvulpina*.

Melliss (1875: 121) described possible live records from the late 19<sup>th</sup> century: "Being exceedingly anxious to discover if this creature still lived, I explored the locality very carefully, about four years ago, and enlisted the sympathies of some of the peasantry in my cause. The wife of a labouring man, living in a small cottage in the valley at the back of Longwood, assured me that she often saw them alive, and that after heavy rains they came out of the earth and fed upon the Hottentot Fig plants. Thinking she meant the common garden snail (*Helix aspersa*), so abundant in the same neighbourhood, I examined her on this point; but so positive was she that she had seen the real, living *Bulimus auris-vulpina*, and that her children had used them as playthings, which statement the children confirmed, that I felt scarcely able to doubt their existence still in a living state. Possibly some few may lurk hidden somewhere; but, considering the changes which have taken place in the physical character of that part of the Island, and that the offer of a liberal reward to my sanguine acquaintance failed to produce a living specimen, I must confess that I am still sceptical upon this point."

Darwin (1844: 90) collected most of his specimens from the north-west side of Flagstaff Hill: "It is very remarkable that all the shells of this species found by me in one spot, form a distinct variety, as described by Mr. Sowerby, from those procured from another locality by Mr. Seale... have shown in my Journal, that the extinction of these land-shells possibly may not be an ancient event; as a great change took place in the state of the island about 120 years ago, when the old trees died, and were not replaced by young ones, these being destroyed by the goats and hogs, which had run wild in numbers, from the year 1502."

### *Chilonopsis helena* (Quoy & Gaimard, 1832)

Figs 4b, 8a–e, 7c–d

*Helix helena* Quoy & Gaimard, 1832: 111.

*Bulimus fossilis* G.E. Sowerby I, 1844: 156.

*Bulimus digitale* Reeve, 1849: pl. 47 fig. 308.

*Bulimus sealeianus* Forbes, 1852: 4, pl. 5 fig. 3.

*Bulimus helena* – Pfeiffer 1848: 198; 1859: 77; 1868: 121. — Melliss 1875: 122. — Wollaston 1878: 542. — Smith 1892: 266.

*Bulimus fossilis* – Forbes 1852: 4. — Jeffreys 1872: 264. — Melliss 1875: 122. — Wollaston 1878: 545.

*Bulimus (Naesiotus) helena* – Pfeiffer 1856: 698.  
*Bulimus sealeianus* – Melliss 1875: 122.  
*Bulimus Seleianus* [sic] – Wollaston 1878: 546.  
*Bulimus Helenae* [sic] – Ancey 1887: 39 (for n. gen. *Nesobia*).  
*Helenopachnodus helena* – Germain 1931: 169.  
*Chilonopsis helena* – Crowley & Pain 1977: 560.  
? *Nesobia helena* – Schileyko 1998: 182.

### Diagnosis

A distinctly shaped ovate *Chilonopsis* in having very high shouldered whorls and being the only ovate species with a distinctly produced apex; sculpture more prominently scalloped than in other species.

### Type material

#### Syntypes of *Helix helena*

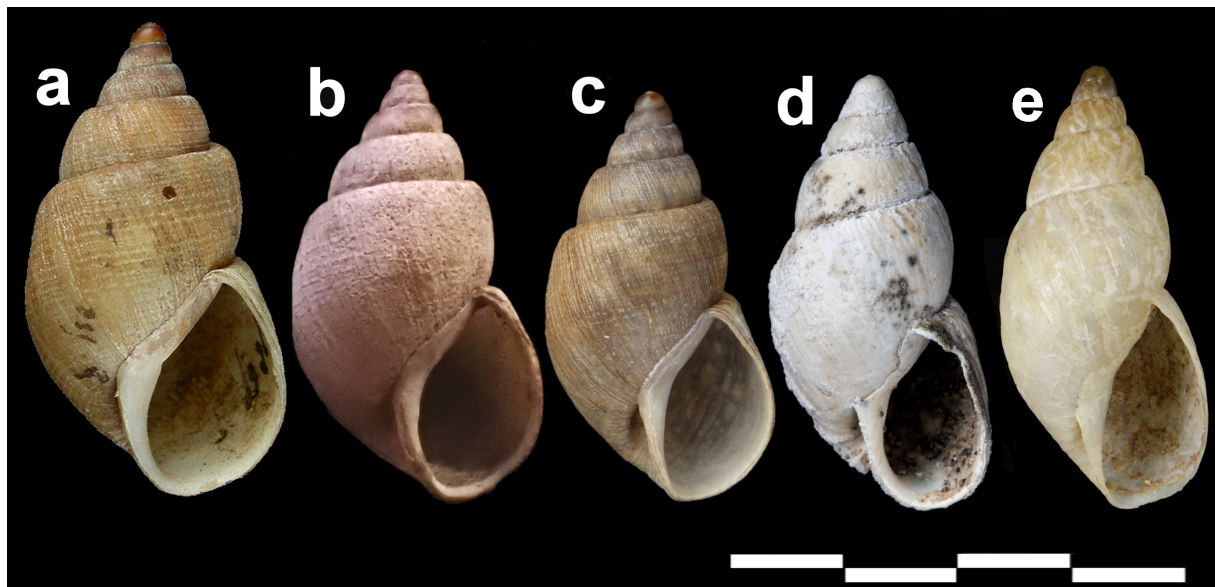
SAINT HELENA • 2 shells; St Helena; M. Seel [= Seale]; MNHN-IM-2000-4649 (Fig. 8a).

#### Syntypes of *Bulimus fossilis*

SAINT HELENA • 2 shells; NHMUK PI G 25270 to NHMUK PI G25272 (Fig. 8b). Originally in the Museum of Practical Geology (Sowerby 1844).

#### Syntypes of *Bulimus digitale*

SAINT HELENA • 2 shells; “H. Helena... = *B. digitale* Reeve f 208”; NHMUK 20240185 (Fig. 8c). Exact matches for Reeve’s (1849) figure and description of specimens of unknown origin in the Cuming collection.



**Fig. 8.** *Chilonopsis helena* (Quoy & Gaimard, 1832). **a.** *Helix helena* Quoy & Gaimard 1832, syntype MNHN-IM-2000-4649. **b.** *Bulimus fossilis* G.E. Sowerby I, 1844 (NHMUK PI G 25270-2). **c.** *Bulimus digitale* Reeve, 1849, syntype (NHMUK 20240185). **d–e.** *Bulimus sealeianus* Forbes, 1852, syntype (NHMUK 1857.10.16.33). **e.** Elongate specimen (NMW.1955.158.27974). Scale bar = 25 mm. Photos: a = D. Brabant, MNHN; c–d = NHMUK; e = H. Wood, NMW.

**Syntypes of *Bulimus sealeianus***

SAINT HELENA • 2 shells; Sugar Loaf; E. Alexander leg.; NHMUK 1857.10.16.33 (Fig. 8d) • 2 shells; Sugar Loaf; E. Alexander leg.; NHMUK P G25276-7. The latter transferred from the Museum of Practical Geology.

**Other material examined**

**Typical form**

SAINT HELENA • 1 shell; FMNH 48075 • 2 shells; FMNH 48250 • 3 shells; S foot of Sugarloaf Pt, gully; 9 Jun. 1961; M. and A. Loveridge; FMNH 173187 • 24 shells; The Barn; A. Loveridge leg.; MCZ 203249 • 1 shell; Summit of the Barn; Spence and Layard collection; MM • 1 shell; Sugar Loaf 1, 0–30 m; “AtlantAves”; Aug.–Sep. 2022; MSH • 1 shell; Trechmann collection; NHMUK 2176 • 1 shell; The Barn; E. Alexander leg.; NHMUK 1857.10.16.25 • 4 shells; Melliss leg.; Fulton collection; NHMUK 1873.11.19.44 • 4 shells; Melliss leg.; NHMUK 1873.11.19.112 • 1 shell; Side Path; W.H. Turton leg.; NHMUK 1892.2.24.229 • 4 shells; The Barn; W.H. Turton leg.; NHMUK 1892.2.24.235-8 • 3 shells; Turks Cap Summit surface finds; Aug.–Sep. 2022; “AtlantAves” leg.; NHMUK 20240173 (1 used in SEM – Fig. 7c–d) • 5 shells; Sugar Loaf 1; Aug.–Sep. 2022; “AtlantAves” leg.; NHMUK 20240175 • 3 shells; Sugar Loaf 2 SE, 0–30 cm: Aug.–Sep. 2022; “AtlantAves” leg.; NHMUK 20240176 • 1 shell; McAndrew collection ex Fulton; NHMUK • 2 shells; valley east of Bank’s; C. Lewis leg.; NHMUK • 1 shell; Tomlin collection; NMW • 1 shell; G eret 1919; P. Dupuis collection; RBINS:IG:8907-HIST.3 • 1 shell; RMNH. MOL.251844 • 1 shell; Sugarloaf Ridge; UF 564271 • 11 shells; USNM 126265 • 1 shell; USNM 197823 • 1 shell; USNM 703395 • 1 shell; ZMA.MOLL.379088.

**“sealeianus form”**

SAINT HELENA • 3 shells; Sugar Loaf Hill; 600 ft; 12 Feb. 1949; Mrs A. Loveridge leg.; MCZ 203243 • 2 shells; Sugarloaf; W.H. Turton leg.; NHMUK 1892.2.24.18.2-5 • 5 shells; Sugarloaf; W.H. Turton leg.; NHMUK 1892.2.24.134-9 • 3 shells; Sugar Loaf 1, 0–30 cm; Aug.–Sep. 2022; “AtlantAves” leg.; NHMUK 20240177 • 55 shells; same data as for preceding; NHMUK 20240178 • 20 shells; Sugar Loaf 2 SE, 0–30 cm; Aug.–Sep. 2022; “AtlantAves” leg.; NHMUK 20240179 • 5 shells; Sugar Loaf 2 SE; Aug.–Sep. 2022; “AtlantAves” leg.; NHMUK 20240180 • 5 shells; Sugar Loaf 3; Aug.–Sep. 2022; “AtlantAves” leg.; NHMUK 20240181 • 1 shell; Trechmann collection; NHMUK • 1 shell; J.J. McAndrew collection ex Fulton; NHMUK • 1 shell; NMW.1955.158.27974 • 3 shells; USNM 126266.

**Description**

Relatively small (height 15.1–22.3 mm; Table 1). Ovately conical, very rarely elongate. Thick, slightly shiny in fresh specimens. Apex rounded, projecting distinctly. 5–7 convex whorls, usually high-shouldered, body whorl rounded. Sutures very deeply impressed and whorls strongly shouldered near suture. Protoconch of 1.5–2 whorls ornamented with 8–10 fine spiral striae (Fig. 7c). Teleoconch with 8–10 strong spiral ridges and fine, raised radial ridges. Radials bent where they cross the spirals, giving a scalloped effect (Fig. 7d). Aperture ovate, distinctly angled at base. Lip narrowly expanded; margins united by a thick callus. Callus runs onto the scalloped sculpture, giving an irregularly serrated appearance. Columella straight. Umbilicus open, surrounded by a slight ridge.

Protoconch reddish, rest of shell yellowish or pinkish to light brown with irregular zig-zag patterns of white streaks in well preserved specimens. The freshest specimens have a dark brown periostracum (NHMUK 92.2.24.18.25, 73.11.10.44). Aperture white.

**Distribution**

Restricted to the north and east of the island (Fig. 11); The Barn over 600 m above sea level to the summit (Melliss 1875; Wollaston 1878; Smith 1892); Side Path (Melliss 1875 as *B. fossilis*); Sugarloaf

Ridge, Quarry and summit (Wollaston 1878 as *B. fossilis*; Smith 1892; Forbes 1898 as *B. fossilis*; Lewis, 2008); Turks Cap (new); Dry Gut (DG07 – Cairns-Wicks & Lambdon 2013).

The *sealeianus* form has only been found on the Sugar Loaf area.

Extinct: “although the shells are now dead, they appear of more recent date than the former species [most *Chilonopsis*]” (Melliss 1875: 122). Only dead shells were found by Wollaston, but not all were buried: “occurs rather abundantly on the extreme summit of the Barn, and in that immediate neighbourhood, lying loosely on the surface soil, beneath the shrubs of *Salsola*, &c., – where it has much the appearance of having lived at a comparatively recent period. At all events many of the examples have their colour and outer cuticle completely preserved, – though it is equally true that the majority of them are decomposed, decorticated, and colourless.” (Wollaston 1878: 544). Smith thought it probably extinct in 1892 although he thought some may have been surviving at the time (Smith 1892). Two specimens collected by Turton in the 1880s (NHMUK 57.10.16.25) are in perfect condition with, intact periostracal layers and appear to have been fresh when collected.

### Remarks

*Bulimus fossilis* was considered a ‘somewhat unimportant modification’ of *C. helena* by Wollaston (1878) and synonymised with this species by Smith (1892), along with *B. sealeianus*. Crowley & Pain (1977) also included as synonyms *B. digitatus* Reeve, 1849 and *B. relegatus* W.H. Benson, 1851, which are regarded here as synonyms of *C. aurisvulpina*. *Bulimus sealeianus* is a recognisable form, partially separated in the principal component analysis (Fig. 3) but intergrades with typical *C. helena*, it differs in being straight-sided, not shouldered; narrower; an aperture forming 55–60% of shell height, rather than less than 55%; and a more evenly rounded base to the aperture. Crowley & Pain (1977) suspected NMW.1955.158.27974 to be a distinct species but the range of specimens examined here shows it to fall within the range of variation of the present species.

### *Chilonopsis blofeldi* (Forbes, 1852)

Figs 4c, 9a–c

*Bulimus Blofeldi* Forbes, 1852: 4, pl. 5 fig. 2.

*Bulimulus blofeldi* – Melliss 1875: 122. — Wollaston 1878: 546. — Smith 1892: 265.

*Helenopachnodus Blofeldi* – Germain 1931: 169.

*Chilonopsis blofeldi* – Crowley & Pain 1977: 561.

### Type material

Not located, collected by J.H. Blofeld, “in a reddish clay or loam on the side of a hill overlooking the “Briars” in the cutting of the road from James Town to Longwood, about 1200 feet above the sea-level” (Blofeld 1852).

### Other material examined

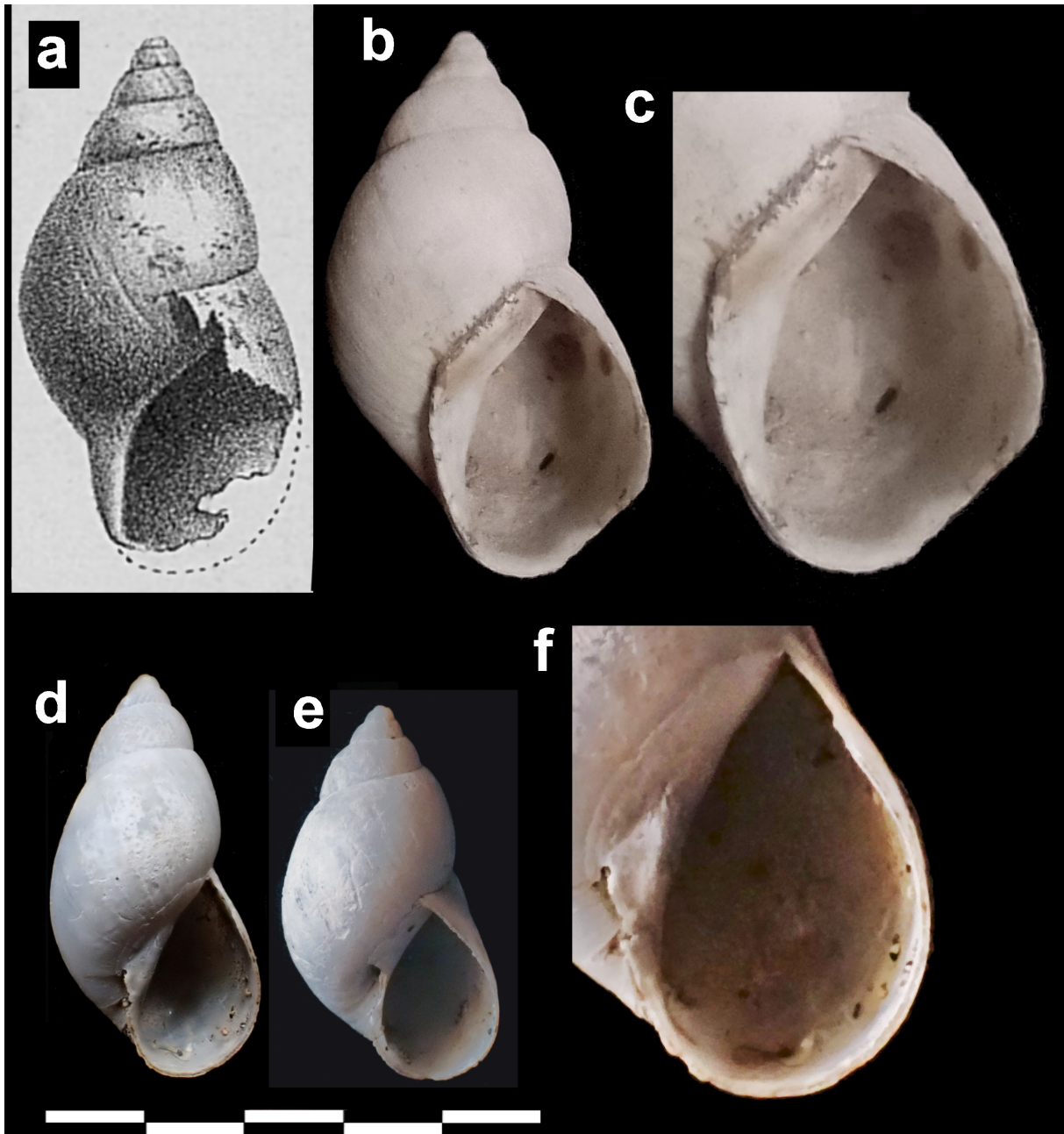
SAINT HELENA • 1 shell; Captain Geoge Grey leg.; NHMUK 1841.4.19.734 • 1 shell; 1840; Dr J. Hooker leg.; NHMUK 1868.12.26.1 • 1 shell; J.C. Melliss leg.; NHMUK 1873.11.19.43 • 1 shell; W.H. Turton leg.; NHMUK 1892.2.24.219-223 • 1 shell; Tomlin collection; NMW.1955.158.27974 • 2 shells; sidepath road, above the Briars; 1200 ft; W.H. Turton leg.; Pain collection; NMW.1981.118 • 7 shells; W.H. Turton leg.; USNM 126263.

### Diagnosis

A uniquely evenly ovate *Chilonopsis* with a broadly expanded body whorl; columella simple but distinctly curved on the left margin.

**Description**

A large species (height 25.9–30.2 mm; Table 1). Ovate conical. Thin. Apex acute. 5–6 convex whorls, body whorl ovate, widest at mid-point from apex to base of aperture. Sutures deep, slightly impressed. Protoconch of 1.5–2 whorls, with at least one indistinct spiral stria (all specimens are worn so probably more striae were present). Teleoconch with fine transverse striae, one faint spiral stria visible on the first whorl (probably more were present). Aperture ovate, angled below. Lip very narrowly expanded at base. Margins joined by a palatal callus of variable thickness. Columella vertical; left margin curved, not obscuring umbilicus (Fig. 9c). Umbilicus open, narrow.



**Fig. 9.** a–c. *Chilonopsis blofeldi* (Forbes, 1852). d–f. *C. lanceoloideus* sp. nov. a. *Bulimus Blofeldi* Forbes, 1852 figure (Forbes 1852). b. Specimen NHMUK un-numbered (ex Melliss). c. Aperture. d, f. Holotype (NHMUK 20240171). e. Paratype NHMUK 20240172. f. Aperture. Scale bar = 25 mm.

All specimens are bleached and worn, lacking any trace of original colour and details of sculpture are eroded.

### Distribution

Known only from Side Path (Fig. 11). Very common according to Turton (in Smith 1892). Probably extinct by 1852 as Blofeld recorded only buried shells. All specimens seen are bleached subfossils.

*Chilonopsis lanceoloideus* sp. nov.

[urn:lsid:zoobank.org:act:15C89CAB-ED18-4EFC-9B26-805DFB4FF0BB](https://zoobank.org/urn:lsid:zoobank.org:act:15C89CAB-ED18-4EFC-9B26-805DFB4FF0BB)

Figs 4d, 7e–f, 9d–f

### Diagnosis

A moderately elongate *Chilonopsis* with an evenly lanceoloid shape. Adults with fewer whorls than other *Chilonopsis* (4.5–5.25 mm compared to 5.0–9.0 mm). Teleoconch sculpture with distinctively wavy radial striae, not as prominent as the scalloped radials of *C. helena*. The only non-elongate *Chilonopsis* with a columellar ridge.

### Etymology

Named due to its lanceoloid shape, which is unique in the St Helena terrestrial mollusc fauna.

### Type material

#### Holotype

SAINT HELENA • adult shell; Sandy Bay PG1 valley toward Potato Gut, surface finds; 15°59'54.3" S, 5°42'42.7" W; Aug.–Sep. 2022; “AtlantAves” leg.; NHMUK 20240171.

#### Paratypes

SAINT HELENA • 1 subadult, 4 juvenile shells; same data as for holotype; NHMUK 20240172.

### Other material examined

SAINT HELENA • 6 shells (3 adults, 2 subadult, 1 broken); Castle Rock Plain (GB 882 SH); 1995; P. and M. Ashmole leg.; MSH (1 used in SEM – Fig. 7e).

### Description

Relatively small (height 15.9–21.3 mm; Table 1). Ovately conical to lanceoloid. Thin. Apex obtuse. 4.5–5.25 moderately convex whorls; no trace of shouldering. Body whorl ovate, widest below mid-point from apex to base of aperture. Sutures shallowly impressed, very slight bossing apparent (Fig. 7e). Protoconch of 1.25–1.75 whorls ornamented with 7–12 fine spiral striae (Fig. 7e). Teleoconch ornamented with 6 indistinct spiral striae, largely obscured by fine wavy radial striae and coarse radial growth lines. The overlapping of the radial and spiral striae creates a fine scalloped pattern (Fig. 7e). Aperture ovate, rounded at base (angled in subadult). Lip very narrowly and evenly expanded, not thickened, reflected onto umbilicus. Margins joined by a thin, shiny parietal callus. Columella oblique, thickened at insertion and forming a low ridge with a concavity on its surface (Fig. 9f); slightly pressed over umbilicus. Umbilicus open, narrow.

All shells bleached but white zig-zag markings are visible on the spire, fading but still detectable onto the body whorl.

### Distribution

Known only from the south of St Helena (Fig. 11): Sandy Bay and Castle Rock Plain.

### Remarks

Closely resembles *C. blofeldi*; both species lacking apertural thickenings and being superficially similar in shape, but the present species is smaller and wider (maximum length 21.3 mm compared to 25.9 mm for the smallest *C. blofeldi* and height/diameter 1.51–1.76 compared to 1.68–2.04), and is more evenly lanceoloid in shape. The presence of a slightly expanded lip and parietal callus demonstrates that *C. lanceoloideus* sp. nov. are not merely immature *C. blofeldi*. The present taxon differs from *C. blofeldi* in size; having a rounded apex; having less convex whorls, the widest part of the shell below the mid-point from apex to base of aperture; shallower sutures and a rounded base to the aperture; a slightly expanded lip; angled columella with a low vertical ridge and slight depression.

### *Chilonopsis exulatus* (Reeve, 1849)

Figs 4e, 10a

*Achatina exulata* Benson MS in Reeve, 1849: pl. 78 fig. 77 (in text for pl. 21).

*Achatina exulata* – Melliss 1875: 123.

*Bulimus exulatus* – Wollaston 1878: 542. — Smith 1892: 266.

*Bulimus (Cleostyla) exulatus* – Dall 1896: 419.

*Chilonopsis (Cleostyla) exulatus* – Pilsbry 1904: 181. — Germain 1931: 170.

*Chilonopsis exulatus* – Crowley & Pain 1977: 559.

*Cleostyla exulata* – Schileyko 1999: 531.

### Diagnosis

Smallest of the two ovately elongate *Chilonopsis* (17.2–21.5 mm compared to 29.0–31.5 mm); differs from *C. subtruncatus* in having a less flared aperture and, well developed sculpture. The wrinkled radial striae on the teleoconch are unique and give an irregular scalloping effect.

### Type material

#### Possible holotype of *Chilonopsis exulatus*

SAINT HELENA • UMZC I.105095 (Fig. 10a).

### Remarks

Reeve (1849) states it was collected by Lieut. Lefroy. Reeve's description of a specimen in the Benson collection does not enable any particular specimen to be identified. The figure (Reeve 1849: pl. 78 fig. 572) appears to show a more striped shell than the UMZC specimen, but this may have faded. It is impossible to be certain that this is the holotype, although it is the only specimen known to be associated with Benson.

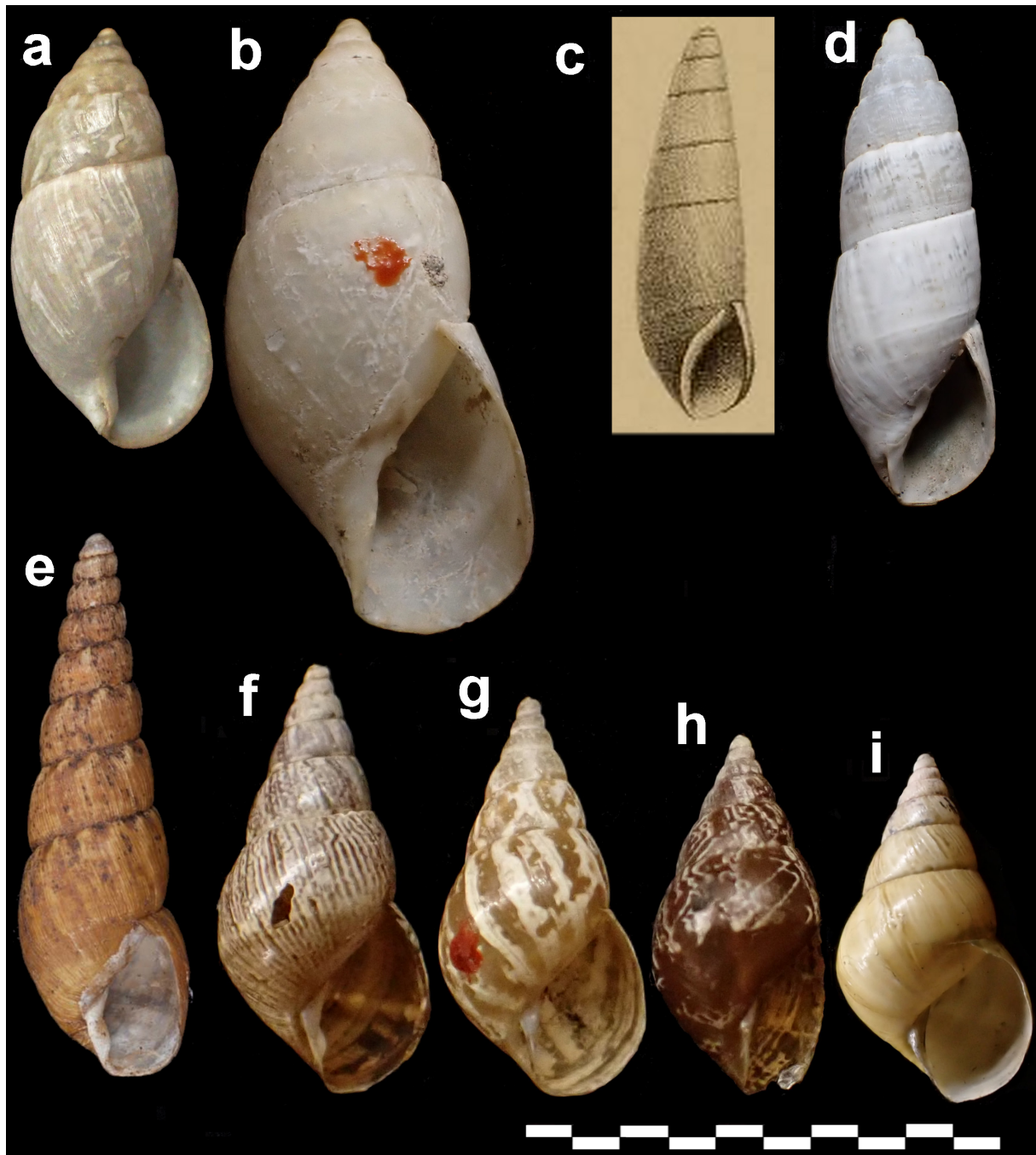
### Other material examined

SAINT HELENA • 1 shell; ANSP 69979 • 1 shell; Sugarloaf Ridge, N coast facing E; A. Loveridge leg.; FMNH 173183 • 4 shells; W.H. Turton leg.; NHMUK 1893.2.24.171-5 • 1 shell; Trechmann collection; NHMUK 2176 • 1 shell; W.H. Turton leg.; Tomlin collection; NMW • 5 shells; W.H. Turton leg.; USNM 126267.

### Description

A small species (height 17.2–21.5 mm; Table 1). Shell elongately ovate, thin. Apex rounded, projecting. 6.5–7 convex whorls, first 4 slowly widening, the rest very rapidly widening and less convex. Whorls very narrowly shouldered, sutures impressed. Protoconch of 1.5–2 whorls, ornamented with 6–8 very fine spiral striae, usually indistinct at apex. Teleoconch with irregular growth-lines and wrinkled radial ridges, crossed by spiral striae. Aperture ovate. Lip thin, very narrowly expanded, flaring at base. Columella short, with a prominent internal fold, truncate at base. Umbilicus closed.

Fresh shells glossy, off-white to pale grey with white markings. Apical 3 whorls yellowish. Surface very glossy.



**Fig. 10.** Elongate species of *Chilonopsis*. **a.** *C. exulatus* (Reeve, 1849), possible holotype (UMZC I.105095). **b.** *C. subtruncatus* (E.A. Smith, 1892), lectotype (NMHUK 92.2.24.224-8). **c–d.** *C. subplicatus* (G.B. Sowerby I, 1844). **c.** *Cochlicopa terebellum* G.B. Sowerby I, 1844 figure (Forbes 1892). **d.** Typical *C. subplicatus* specimen (NHMUK 20240182). **e.** *Chilonopsis melanioides* (Wollaston, 1878), syntype (ANSP 97326). **f–i.** *Chilonopsis turtoni* (E.A. Smith, 1892), syntypes. **f–h.** NHMUK 1892.2.24.209-218. **i.** NHMUK 1860.1.23.49. Scale bar = 20 mm.

**Distribution**

Restricted to the north of the island (Fig. 11); recorded from Sugarloaf Ridge (Smith 1892) and Side Path (Melliss 1875). Melliss had them only from surface-soil (1875) but some of Turton's 1884–86 specimens appear to be fresh, being shiny and pigmented.

*Chilonopsis subtruncatus* (E.A. Smith, 1892)

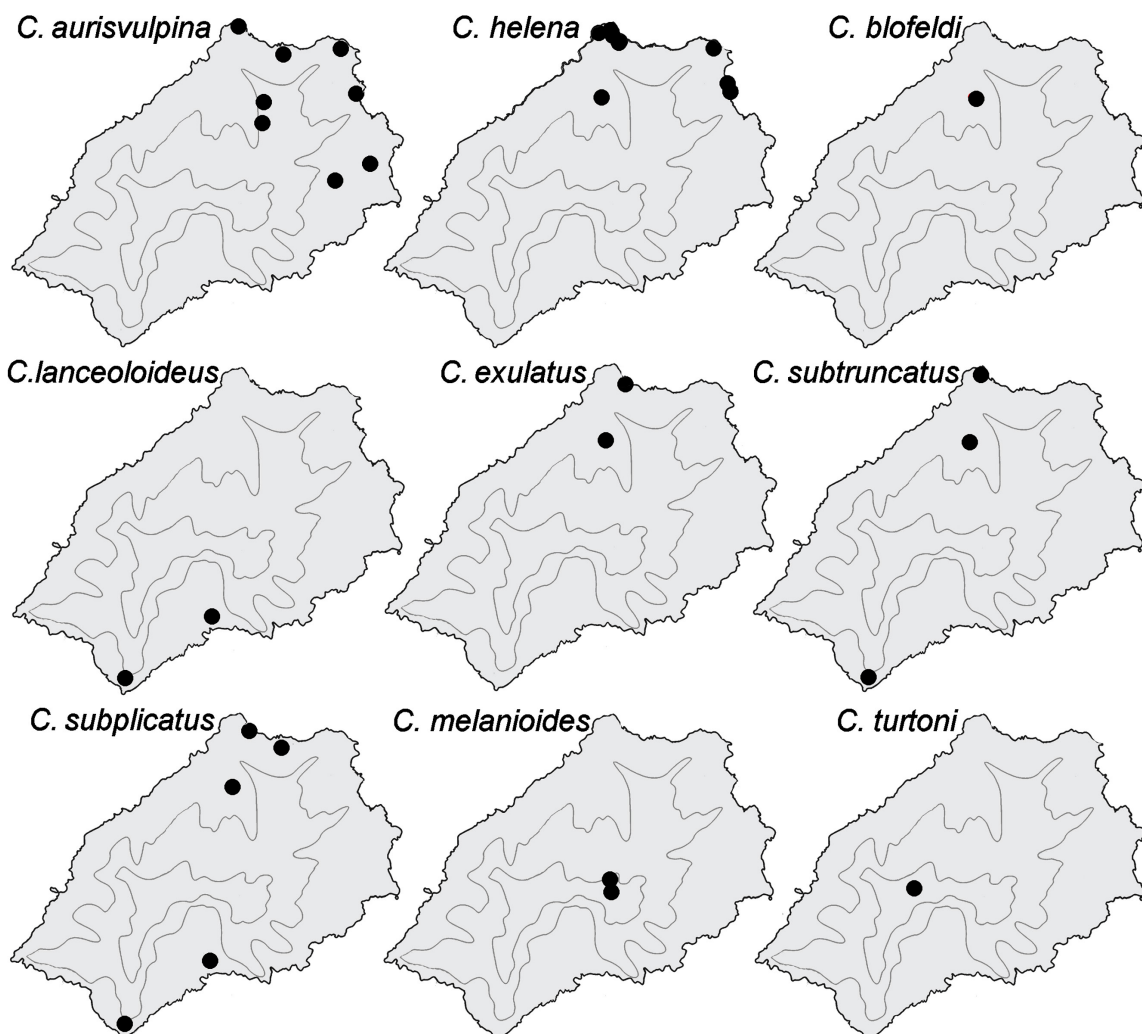
Figs 4f, 10b

*Bulimulus subtruncatus* E.A. Smith, 1892: 266.

*Bulimus (Cleostyla) subtruncatus* – Dall 1896: 419.

*Chilonopsis (Cleostyla) subtruncatus* – Pilsbry 1904: 180. — Germain 1931: 170.

*Chilonopsis subtruncatus* — Crowley & Pain 1977: 556.



**Fig. 11.** Distributions of species of *Chilonopsis* Fischer von Waldheim, 1848.

### Diagnosis

The larger of two elongately ovate species of *Chilonopsis* (29.0–31.5 mm compared to 17.2–21.5 mm). Sculpture reduced; aperture distinctly flared at base.

### Type material

#### Lectotype (here designated)

SAINT HELENA • shell; Side Path; W.H. Turton leg.; NHMUK 1892.2.24.224-8 (Fig. 10b). One of the syntypes marked as a holotype, corresponding to the specimen measured by Smith (1892) although no holotype was designated. We designate this specimen as the lectotype.

#### Paralectotypes (here designated)

SAINT HELENA • 4 shells; same data as for lectotype; NHMUK 1892.2.24.224-8.

### Other material examined

SAINT HELENA • 1 shell; ANSP 69868 • 2 shells; Sugarloaf Point; ex Jackson 10856; DMNH 148893 • 1 shell; G ret 1919; P. Dupuis collection; RBINS:IG:8907-HIST.6 • 1 shell (broken subadult); Castle Rock Plain (GB 882 SH); 1995; P. and M. Ashmole leg.; MSH • 1 shell; Tomlin collection; NMW.1955.158 • 1 shell; Side Path; W.H. Turton leg.; Pain collection; NMW.1981.118.04854 • 2 shells; USNM 126264.

### Description

A large species (height 29.0–31.5 mm; Table 1). Elongately ovate. Apex conical, slightly projecting. 7 slightly convex whorls, suture deep. Protoconch of 2 whorls with fine spiral striae, usually very faint. Teleoconch with fine growth-lines and very shallow radial striae, crossed by sparse, shallow spiral striae. Aperture ovate to slightly auricular. Lip thin, very slightly expanded, distinctly flaring slightly toward base, margins united by a thin callus. Columella oblique with a vertical ridge. Last whorl obliquely sloping, but slightly ascending to the lip. Lip thin, slightly spreading or expanded in front. Umbilicus closed.

All specimens bleached white, mostly heavily worn. Oblique white streaks very faintly visible around the middle of each whorl and just above the sutures.

### Distribution

All but one specimen from the north of the island (Fig. 11): Side Path (Smith 1892) and Sugarloaf Point (DMNH). One shell from Castle Rock Plain in the south (MSH). Shells were common in 1884–86 but already extinct (Smith 1892).

### Remarks

Very similar to *C. exulatus* but larger, more fusiform, columella less truncate, similar oblique intersecting opaque-white markings.

#### *Chilonopsis subplicatus* (G.B. Sowerby I, 1844)

Figs 4g, 7g–h, 10c–d

*Cochlicopa subplicata* G.B. Sowerby I, 1844: 156.

*Cochlicopa terebellum* G.B. Sowerby I, 1844: 156.

*Bulimus subplicatus* – Forbes 1852: 199. — Melliss 1875: 122.

*Bulimus terebellum* – Forbes 1852: 199. — Melliss 1875: 122.

- Achatina subplicata* – Melliss 1875: 123.  
*Subulina subplicata* – Wollaston 1878: 552.  
*Subulina terebellum* – Wollaston 1878: 552.  
*Bulimus* (*Peroneus* ?) *subplicatus* – Smith 1892: 266.  
*Pachyotus subplicatus* – Dall 1896: 419.  
*Chilonopsis subplicatus* – Pilsbry 1904: 178. — Crowley & Pain 1977: 558.  
*Chilonopsis subplicatus* var. *terebellum* – Pilsbry 1904: 179.  
*Chilonopsis* (*Chilonopsis*) *subplicatus* – Germain 1931: 170.

### Diagnosis

The only fusiform *Chilonopsis*; spiral striae on the base coarser than in other species; columellar ridge distinctively concave.

### Type material

#### Type of *Cochlicopa subplicata*

Not located, collected by Charles Darwin, Flagstaff hill (Darwin 1836).

#### Type of *Cochlicopa terebellum*

Not located, collected by Charles Darwin, Flagstaff hill (Darwin 1836); said to be in the collection of Charles Lyell (Forbes 1852), figured by Forbes (1852) (Fig. 10c). The Darwin specimens have not been located in the Lyell collections of the Oxford University Museum or the NHMUK (J. Ablett, E. Howlett, C. Sendino pers. com.).

### Other material examined

SAINT HELENA • 2 shells; ANSP MAL 69938 • 1 shell; MCZ 381472 • 18 shells; Castle Rock Plain (GB 882 SH); 1995; P. and M. Ashmole leg.; MSH (1 used in SEM) • 1 shell; Flagstaff Hill; E.W. Alexander leg.; NHMUK 1857.10.16.34 • 5 shells; W.H. Turton leg.; NHMUK 1892.2.24.176-181 • 1 shell; A.J. Piele collection; NHMUK 2242 • 3 shells; Sandy Bay PG1 valley toward Potato Gut, surface finds; Aug.–Sep. 2022; “AtlantAves” leg.; NHMUK 20240182 • 3 shells; burrow 100 m NE of Olsen site A, Sandy Bay; Aug.–Sep. 2022; “AtlantAves” leg.; NHMUK 20240183 • 1 shell; above Potato Bay; 1981; D.G. Llewellyn leg.; 1981; NHMUK • 1 shell; W.H. Turton leg.; Tomlin collection; NMW • 3 shells; Tomlin collection; UMMZ 141297 • 6 shells; USNM 126270.

### Description

A relatively small species (height 17.0–25.4 mm; Table 1). Elongately fusiform. Apex flat. 5.5–7 very slightly convex whorls. Protoconch of 1.5 whorls ornamented with 5 very fine spiral striae. Teleoconch with fine spiral striae on first three whorls, interrupted by radial ridges; coarse spiral ridges on lower half of each whorl, visible just above suture and on body whorl. Strong radial ridges on all whorls, sinuous at the sutures and where they cross the spiral striae. Semi-regular radial ridges forming raised bosses at suture on 3<sup>rd</sup>–6<sup>th</sup> whorls; body whorl of large adults smooth. Body whorl slightly angled at margin. Aperture distinctly slanting, ovate, becoming broadened and with a flaring lip in fully mature individuals (“*C. terebellum*”). The outer lip is simple, margins joined by a thin parietal callus. Columella dilated, twisted in middle, forming a concavity. Umbilicus very narrow. Grey-brown to reddish with white mottling and diagonal streaks markings, sutural bosses white. Apex usually reddish.

### Distribution

Widespread (Fig. 11). Published material is restricted to the north of the island; Flagstaff Hill (Darwin 1836), Sugarloaf Ridge (Smith 1892); Side Path (between Jamestown and Longwood, side of the hill overlooking the Briars – Wollaston 1878). New material collected from the south of the island: Sandy

Bay (new). *Chilonopsis terebellum* only recorded from Flagstaff Hill (Darwin 1836) and Sugarloaf Ridge (NHMUK 1892.2.24.176–181). Considered extinct in 1892 (Smith 1892), although some of Turton's specimens from 1884–86 were fresh.

### Remarks

*Bulimus terebellum* was synonymised with *C. subplicatus* by Smith (1892), a lead followed by Germain (1931), whereas Pilsbry (1904: 179) retained var. *terebellum* Sowerby as a larger, smoother form with a more expanded aperture; these differences can mostly be attributed to different stage of maturity and some samples (e.g., MSH and NHMUK 1892.2.24.176–181) include both forms from the same locality.

### *Chilonopsis melanioides* (Wollaston, 1878)

Figs 4h, 10e

*Subulina melanioides* Wollaston, 1878: 550.

*Bulimulus melanioides* – Smith 1892: 267.

*Pachyotus melanioides* – Dall 1896: 416.

*Chilonopsis melanioides* – Pilsbry 1904: 177. — Crowley & Pain 1977: 557.

*Chilonopsis (Chilonopsis) melanioides* – Germain 1931: 170.

### Diagnosis

The most elongate *Chilonopsis* (mean height/diameter 3.12 compared to 1.31–2.79) with the most whorls (7.5–9.0 compared to 4.5–7.0); sutures distinctively wavy. Low irregular sutural bosses present and teleoconch sculpture irregular and coarse.

### Type material

#### Syntypes of *Subulina melanioides*

SAINT HELENA • 1 shell; Lowe-Wollaston collection; ANSP 97326 (Fig. 10e) • 3 shells; NHMUK 1896.42.197 • 1 shell; RMNH.MOL.269649.

Wollaston described the species based on all the specimens collected by Mrs Wollaston, himself and Mr P. Whitehead mid-way between Actaeon and Diana's Peak.

### Other material examined

SAINT HELENA • 2 radula slides (presumably extracted from ANSP 97326); ANSP 69937 • 2 shells; DMNH 184024 • 1 shell; FMNH 76902 • 1 shell; Diana's Peak; 2000 feet; W.H. Turton leg.; NHMUK 1892.2.24.204-8 • Diana's Peak; presented by G.T. Angas; NHMUK 1878.5.23.1 • 1 shell; J. Ponsonby, Suter collection; NMNZ M.209881 • 1 shell; Diana's Peak; elev. over 2000 feet; W.H. Turton leg.; Tomlin collection; NMW • 1 shell; P. Dupuis collection ex Fulton; RBINS:IG:8907-HIST.4 • 3 shells; Ponsonby collection; UMMZ 141295 • 3 shells; W.H. Turton leg.; USNM 197822, 126269.

### Description

A long species (height 23.8–24.8 mm; Table 1). Elongately conical. Shell moderately thick. Apex acute. 7.5–9 slightly convex whorls. Body whorl with a distinct, low carina just below the margin. Sutures deep, wavy. Protoconch of 1 whorl with faint traces of spiral striae. Teleoconch with fine spiral striae crossed by coarse radial ridges, forming a coarse scalloping pattern. Spirals clearest at middle and lower half of each whorl. Irregular very widely spaced low bosses present at the sutures. Aperture narrowly ovate, slightly oblique. Lip narrow, simple, margins joined by a very thin palatal callus. Columella vertical, with a prominent oblique fold, truncated at base. Umbilicus almost completely covered.

Most specimens are fresh with the periostracum intact: apical 1.5 whorls yellowish, rest dark red-brown to black, with irregular ochre streaks on the sutural bosses extending to near the margin of each whorl.

### Distribution

Known only from Diana's Peak (Fig. 11) over 600 m above sea level (Turton in Smith 1892) and between Mt Actaeon and Diana's Peak (Wollaston 1878).

### Remarks

A single live animal and fresh shells were recorded in 1878 (Wollaston 1878). Reports of it being extant after this date (Smith 1892; Germain 1931) are both in reference to the original description rather than evidence of continued survival.

Wollaston (1878: 551) described the habitat in which they found the specimens: "... though a single living example which was secured by Mr. P. Whitehead in an immediately adjoining locality sufficed abundantly to indicate the *modus vivendi* of the species, – it having been taken at the roots of one of the damp masses of intermingled moss and grass which pad the base of the perpendicular rocks formed by the excavation of what is known as the 'Cabbage-Tree Road'. There can be little doubt, consequently, that the *S. melanooides* will be ascertained to occur in humid places generally along the northern slopes of the ridge below Diana's Peak."

### *Chilonopsis turtoni* (E.A. Smith, 1892)

Figs 4i, 10f–i

*Bulimulus turtoni* E.A. Smith, 1892: 255.

*Chilonopsis turtoni* – Pilsbry 1904: 181. — Crowley & Pain 1977: 560.

*Chilonopsis (Cleostyla) Turtoni* – Pilsbry 1904: 181. — Germain 1931: 170.

### Diagnosis

The only conical *Chilonopsis*; shell thinner than in other species; sutures very shallowly impressed; sculpture very weakly developed.

### Type material

#### Syntypes of *Bulimulus turtoni*

SAINT HELENA • 1 juv. shell; ex Museum of Economic Geology; NHMUK 1860.1.23.50 • 1 adult shell; ex Museum of Economic Geology; NHMUK 1860.1.23.49 • 10 adult, 2 juv. shells; near High Peak; Capt. Turton R.E. leg.; NHMUK 1892.2.24.209-218 (Fig. 10f–h).

The main syntype series were collected by Turton but Smith's description also includes the specimens then in the Museum of Economic Geology (NHMUK 1860.1.23.49–50), collected by E. Alexander and donated by Forbes, this collection later became part of NHMUK.

Forbes (1852: 3) referred to these specimens as "an existing undescribed species found by Mr. Alexander feeding on the cabbage-trees only on the highest points of the island."

### Other material examined

SAINT HELENA • 2 shells; ANSP MAL 69936 • 4 shells; W.H. Turton leg.; Melvill-Tomlin collection; NMW.1955.158.27975 • 1 shell; W.H. Turton leg.; Pain collection; NMW.1981.118.04853 • 1 shell; G eret 1919; P. Dupuy collection; RBINS:IG:8907-HIST.7 • 3 shells; Ponsonby collection; UMMZ 141298 • 5 shells; W.H. Turton leg.; USNM 126268.

### Description

A relatively small species (height 14.7–18.4 mm; Table 1). Shell conical, thin, glossy. Apex rounded, produced. 7 slightly convex whorls, body whorl evenly rounded. Sutures very shallowly impressed. Protoconch of 2 whorls with faint spiral striae. Teleoconch with oblique growth-lines and low ridges, crossed by low, indistinct spiral ridges. Aperture ovate, acuminate above. Lip not expanded; margins united by a thin, shiny callus. Columella truncate, upper margin narrowly reflexed, with a small fold or nodule on the middle. Umbilicus open, narrow.

All specimens are fresh with periostracum intact: dark to mid-brown, with irregular oblique white streaks and spots, often interrupted. Streaks may be fine or broad, some deflected into a zig-zag pattern. One specimen ochre with indistinct darker streaking and a dark brown columella (Fig. 10i).

### Distribution

High Peak (Turton in Smith 1892) (Fig. 11). Last recorded alive in 1884–86 when Turton reported it as living in native vegetation (Smith 1892), and his specimens are mostly recent.

### Discussion

The nine species of *Chilonopsis* recognised here appear to represent a notable radiation of moderately large snail species on a small island. However, in the absence of any anatomical material it is impossible to be certain that they are all congeneric and descended from a single colonisation. There may have been some degree of ecological specialisation as indicated by the great variation in form between the ovoid and lanceolate species. However, this is speculation as all species are extinct. Shells have been found in sympatry most commonly for *C. aurisvulpina*, *C. helena* and *C. subplicatus*. *Chilonopsis helena* has also been found with *C. blofeldi*, *C. exulatus* and *C. subtruncatus*. *Chilonopsis lanceoloideus* sp. nov. has been found with *C. subplicatus*. The only completely exclusive species were the high forest *C. melanioides* and *C. turtoni*. However, ranges were probably more extensive and showed a greater degree of overlap than available data indicate; in the present study *C. subplicatus* was found in the south of the island, where it had previously only been recorded from the north.

Charles Darwin noted their extinction as early as 1836: Amongst “I believe it is a Land shell; but whatever it may be, there is no question, but what in this is an extinct species.” (Darwin 1836: 934). The fact that the extinction of species of *Chilonopsis* was recent was noted as early as 1838 (Lamarck 1838) in reference to *C. aurisvulpina*. Darwin (1845) seems to be the first to have attributed this to habitat loss: “On the higher parts of the island, considerable numbers of a shell, long thought a marine species, occur embedded in the soil. It proves to be a Cochlogena, or land-shell of a very peculiar form; with it I found six other kinds; and in another spot an eighth species. It is remarkable that none of them are now found living. Their extinction has probably been caused by the entire destruction of the woods, and the consequent loss of food and shelter, which occurred during the early part of the last century... There can be little doubt that this great change in the vegetation affected not only the land-shells, causing eight species to become extinct, but likewise a multitude of insects” (Darwin 1845: 934).

With the early and extensive habitat destruction on St Helena, the majority of endemic snail species were lost by the mid 19<sup>th</sup> century. For *Chilonopsis* we can infer the possible dates of extinction for different species varying from the early 1800s (there being only subfossil material of *C. aurisvulpina*, *C. blofeldi* and *C. lanceoloideus* sp. nov.) to around 1880 (good material collected by Turton 1884–86 of *C. helena*, and live *C. melanioides* in 1878) and shortly after 1886 (live or fresh material collected by Turton 1884–86: *C. exulatus*, *C. subtruncatus*, *C. subplicatus* and *C. turtoni*). The only species known to have been collected alive (*C. melanioides* and *C. turtoni*) are known to have been collected in the high areas where forest fragments have survived best (High Peak to Diana’s Peak).

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## References

- Ancey C.F. 1887. Description of new genera or sub-genera of Helicidae. (Continued). *The Conchologists' Exchange* 2 (2): 22–23.  
Available from <https://www.biodiversitylibrary.org/item/90481#page/116/mode/1up> [accessed 16 Mar. 2024].
- Ashmole P. & Ashmole M. 2000. *St Helena and Ascension Island: A Natural History*. Anthony Nelson, Trowbridge, Wiltshire.
- Banks J. 1796. *Journal of the Right Hon. Sir Joseph Banks Bart., K.B., P.E.S. during Captain Cook's first voyage in H.M.S. Endeavour in 1768–71 to Tierra del Fuego, Othaite, New Zealand, Australia, the Dutch East Indies, etc.* Macmillan & Co., London. <https://doi.org/10.5962/bhl.title.56795>
- Beck H. 1838. *Index molluscorum praesentis aevi musei principis augustissimi Christiani Frederici*. Beck, Copenhagen. <https://doi.org/10.5962/bhl.title.46251>
- Benson W.H. 1851. Descriptions of new land shells from St. Helena, Ceylon, and China. *Annals and Magazine of Natural History* (2) 7 (40): 262–266.  
Available from <https://www.biodiversitylibrary.org/page/13787854> [accessed 22 Jul. 2025].
- Blofeld J.H. 1852. Notes on St. Helena. *Quarterly Journal of the Geological Society* 8: 195–196.  
<https://doi.org/10.1144/GSL.JGS.1852.008.01-02.24>
- Bouchet P., Rocroi J.P., Hausdorf B., Kaim A., Kano Y., Nützel A., Parkhaev P., Schrödl M. & Strong E.E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* 61 (1–2): 1–526. <https://doi.org/10.4002/040.061.0201>
- Bruce I. 2022. The discovery of St Helena. *Wirebird* 51: 26–43.
- Buchanan S. 2016. *Burchell's Travels: The Life, Art and Journeys of William John Burchell, 1781–1863*. Penguin Books (South Africa), Cape Town.
- Cairns-Wicks R. & Lambdon P. 2013. *Habitat Survey Report: Dry Gut and the Southern Ridge of Prosperous Bay Plain. Final report*. Unpublished. Available from <https://www.sainthelena.gov.sh/wp-content/uploads/2017/08/Habitat-and-Invertebrate-Survey-Dry-Gut-and-the-Southern-Ridge-March-2013.pdf> [accessed 16 Mar. 2024].

- Chemnitz J.H. 1795. *Neues systematisches Conchylien-Cabinet* Vol. 11. Gabriel Nicolaus Raspe, Nürnberg. <https://doi.org/10.5962/bhl.title.120155>
- Cronk Q.C.B. 1983. The decline of the redwood *Trochetiopsis erythroxyton* on St Helena. *Biological Conservation* 26 (2): 163–174. [https://doi.org/10.1016/0006-3207\(83\)90064-2](https://doi.org/10.1016/0006-3207(83)90064-2)
- Cronk Q.C.B. 1988. W.J. Burchell and the botany of St Helena. *Archives of Natural History* 15: 45–60. <https://doi.org/10.3366/anh.1988.15.1.45>
- Cronk Q.C.B. 1989. The past and present vegetation of St Helena. *Journal of Biogeography* 16: 47–64. <https://doi.org/10.2307/2845310>
- Crowley T.E. & Pain T. 1977. La faune terrestre de l'île Sainte-Hélène IV. Mollusca not Charopidae. *Annales Musée royal de l'Afrique centrale* (8) 220: 534–575.
- Dall W.H. 1896. Insular landshell faunas, especially as illustrated by the data obtained by Dr. G. Baur in the Galapagos Islands. *Proceedings of the Academy of Natural Sciences of Philadelphia* 48: 395–460. Available from <https://biostor.org/reference/119623> [accessed 16 Mar. 2024].
- Darwin C.R. 1836. Geological diary: St. Helena. CUL-DAR38.920-935. Transcribed by Guido Chiesura and Kees Rookmaaker, edited by John van Wyhe. Darwin Online. Available from <https://darwin-online.org.uk/content/frameset?pageseq=1&itemID=CUL-DAR38.920-935&viewtype=text> [accessed 2 Feb. 2024].
- Darwin C.R. 1844. *Geological Observations on the Volcanic Islands Visited During the Voyage of H.M.S. Beagle, together with some Brief Notices of the Geology of Australia and the Cape of Good Hope. Being the Second Part of the Geology of the Voyage of the Beagle, under the Command of Capt. Fitzroy, R.N. during the Years 1832 to 1836.* Smith Elder & Co., London. <https://doi.org/10.1144/GSL.JGS.1845.001.01.101>
- Darwin C.R. 1845. *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S. Beagle Round the World, under the Command of Capt. Fitz Roy, R.N.* John Murray, London. <https://doi.org/10.5962/t.175052>
- Deshayes G.P. In: Deshayes G.P. & Milne-Edwards H. 1839. *Histoire naturelle des Animaux sans Vertèbres, Présentant les Caractères généraux et particuliers de ces Animaux, leur Distribution, leurs Classes, leurs Familles, leurs Genres, et la Citation des principales Espèces qui s'y rapportent: Précédée d'une Introduction offrant la Détermination des Caractères essentiels de l'Animal, sa Distinction du végétal et des autres Corps naturels: enfin, l'Exposition des Principes fondamentaux de la Zoologie; par J.B.P.A. de Lamarck, Revue et Augmentée de Notes Présentant les Faits nouveaux dont la Science s'est Enrichie jusqu'à ce jour.* 3<sup>rd</sup> ed. Vol 2. Meline, Cans, Brussels. <https://doi.org/10.5962/bhl.title.46287>
- Dillwyn L.W. 1817. *A Descriptive Catalogue of Recent Shells, Arranged According to the Linnaean Method; with Particular Attention to the Synonymy.* Vol. 1. John and Arthur Arch, London. <https://doi.org/10.5962/bhl.title.10437>
- Disney A.R. 2009. *The Portuguese in India and other Studies, 1500–1700.* Ashgate, Farnham, Surrey.
- Duncan F. 1805. *A Description of the Island of St. Helena; Containing Observations on its Singular Structure and Formation; and an Account of its Climate, Natural History and Inhabitants.* R. Phillips, London (attributed to Duncan by Gosse P. 1990. St Helena 1502–1938. Nelson, Oswestry, Shropshire).
- Férussac A.E.J.P.J.F. d'Audebard de. 1822. In: Bory de Saint-Vincent J. (ed.) *Dictionnaire classique d'Histoire naturelle*, vol. 2. Rey & Gravier, and Baudouin frères, Paris. <https://doi.org/10.5962/bhl.title.33901>
- Fischer P. 1883. *Manuel de Conchyliologie et de Paléontologie conchyliologique: ou, Histoire naturelle des Mollusques vivants et fossiles.* F. Savy, Paris. <https://doi.org/10.5962/bhl.title.13213>

- Fischer von Waldheim G. 1848. *Chilonopsis* novum genus testarum e familia helicum icone et descriptione illustratum. *Bulletin de la Société impériale des Naturalistes de Moscou* 21 (1): 233–236. Available from <https://www.biodiversitylibrary.org/page/34377789> [accessed 16 Mar. 2024].
- Fontanilla I.K., Naggs F. & Wade C.M. 2017. Molecular phylogeny of the Achatinoidea (Mollusca: Gastropoda). *Molecular Phylogenetics and Evolution* 114: 382–385. <https://doi.org/10.1016/j.ympev.2017.06.014>
- Forbes E. 1852. On the extinct land-shells of St. Helena. *Quarterly Journal of the Geological Society* 8: 197–199. Available from <https://www.biodiversitylibrary.org/item/109911#page/309/mode/1up> [accessed 16 Mar. 2024].
- Forbes H.O. 1898. Museums. In: *Forty-Fifth Annual Report of the Committee of the Free Public Museums of the City of Liverpool*. J.R. Williams & Co., Liverpool. Available from <https://www.biodiversitylibrary.org/page/12801997> [accessed 16 Mar. 2024].
- Germain L. 1931 (for 1929). L'origine et l'évolution de la faune malacologique de l'île de Sainte-Hélène. *Comptes rendus du Congrès des Sociétés savantes, Section des Sciences* (1929): 161–180
- Gray J.E. 1825. A list and description of some species of shells not taken notice of by Lamarck. *Annals of Philosophy* New Series 9 (6): 407–415. Available from <https://www.biodiversitylibrary.org/page/15880862> [accessed 16 Mar. 2024].
- Griffith E. & Pidgeon E. 1834. The Mollusca and Radiata. Vol. 12. In: E. Griffith, *The Animal Kingdom Arranged in Conformity with its Organization, by the Baron Cuvier*, [...]. Whittaker & Co., London. <https://doi.org/10.5962/bhl.title.113427>
- Holten H.S. 1802. *Enumeratio systematic Conchyliorum beat. J.H. Chemnitzii*. K.H. Seidelini, Copenhagen. Available from <https://www.biodiversitylibrary.org/bibliography/96191> [accessed 16 Mar. 2024].
- ICZN (International Commission on Zoological Nomenclature). 1944. Opinion 184. On the status of names first published in volumes 1 to 11 of Martini and Chemnitz, *Neues Systematisches Conchylien-Cabinet*, Nürnberg, 1769–1795. *Opinions and Declarations rendered by the ICZN* 3: 25–36. <https://doi.org/10.5962/p.149318>
- Jeffreys J.G. 1872. The Mollusca of St. Helena. *Annals and Magazine of Natural History, including Zoology, Botany, and Geology* 9: 262–264. <https://doi.org/10.1080/00222937208696579>
- Key R., Fowler L. & Pryce D. 2021. *Terrestrial & Freshwater Invertebrates of St. Helena*. Pisces Publications for St. Helena Nature Conservation Group.
- Kobelt W. 1902. Die Familie Buliminidae. *Systematisches Conchylien-Cabinet von Martini und Chemnitz* 1 (13) (2): 397–1051. <https://doi.org/10.5962/bhl.title.119523>
- Küster H.K. 1844. In: Küster H.K. & Pfeiffer L. (1840–1865) Die Bulimiden und Achatinen. In: *Abbildungen nach der Natur. Die Gattungen Bulimus, Partula, Achatinella, Achatina und Azeca*. In: *Abbildungen nach der Natur mit Beschreibungen. Systematisches Conchylien-Cabinet von Martini und Chemnitz* 1 (13) (1): 33–48. <https://doi.org/10.5962/bhl.title.119525>
- Lamarck J.-B.P.A.M. de 1838. *Histoire naturelle des Animaux sans Vertèbres présentant les Caractères généraux et particuliers de ces Animaux, leur Distribution, leurs Classes, leurs Familles, leurs Genres, et la Citation des principales Espèces qui s'y Rapportent; Précédée d'une Introduction*. Vol. 8: *Histoire des mollusques*. J.B. Baillière, London. <https://doi.org/10.5962/bhl.title.46287>
- Lambdon P. & Cronk Q. 2020. Extinction dynamics under extreme conservation threat: The flora of St Helena. *Frontiers in Ecology and Evolution* 8 (41): 1–10. <https://doi.org/10.3389/fevo.2020.00041>

- Lewis C.A. 2008. The Late Glacial and Holocene avifauna of the island of St Helena, South Atlantic Ocean. *Transactions of the Royal Society of South Africa* 63 (2): 128–144. <https://doi.org/10.1080/00359190809519217>
- Melliss J.C. 1875. *St. Helena: A Physical, Historical, and Topographical Description of the Island, Including its Geology, Fauna, Flora and Meteorology*. L. Reeve & Co., London. <https://doi.org/10.5962/bhl.title.120102>
- Neubert E. & Gosteli M. 2003. The molluscan species described by Robert James Shuttleworth. I. Gastropoda: Pulmonata. *Contributions to Natural History Special Papers from the Natural History Museum Bern* 1: 1–123.
- Olson S.L. 1975. Paleornithology of St. Helena Island, South Atlantic Ocean. *Smithsonian Contributions to Paleobiology* 23: 1–49. <https://doi.org/10.5479/si.00810266.23.1>
- Perry G. 1811. *Conchology, or the Natural History of Shells: Containing a New Arrangement of the Genera and Species, Illustrated by Coloured Engravings Executed from the Natural Specimens, and Including the Latest Discoveries*. W. Miller, London. <https://doi.org/10.5962/bhl.title.156640>
- Petit R.E. 2003. George Perry's molluscan taxa and notes on the editions of his *Conchology* of 1811. *Zootaxa* 377: 1–72. <https://doi.org/10.11646/zootaxa.377.1.1>
- Petit R.E. & Coan E.V. 2008. The molluscan taxa made available in the Griffith & Pidgeon (1833–1834) edition of Cuvier, with notes on the editions of Cuvier and on Wood's *Index testaceologicus*. *Malacologia* 50 (12): 219–264. <https://doi.org/10.4002/0076-2997-50.1.219>
- Pfeiffer L. 1848. *Monographia heliceorum viventium: sistens descriptiones systematicas et criticas omnium huius familiae generarum et specierum hodie cognitarum*. Vol. 2. Brockhaus, Leipzig. <https://doi.org/10.5962/bhl.title.14455>
- Pfeiffer L. 1853. *Monographia heliceorum viventium: sistens descriptiones systematicas et criticas omnium huius familiae generarum et specierum hodie cognitarum*. Vol. 3. Brockhaus, Leipzig. <https://doi.org/10.5962/bhl.title.10791>
- Pfeiffer L. 1854. In: Küster H.K. & Pfeiffer L. 1840–1865. Die Gattungen *Bulimus*, *Partula*, *Achatinella*, *Achatina* und *Azeca*. *Abbildungen nach der Natur mit Beschreibungen. Systematisches Conchylien-Cabinet von Martini und Chemnitz* 1 (13) (1): iii–xix. <https://doi.org/10.5962/bhl.title.119525>
- Pfeiffer L. 1856. Versuch einer Anordnung der Heliceen nach natürlichen Gruppen. *Malakozoologische Blätter* 2: 112–185. Available from <https://www.biodiversitylibrary.org/page/15864853> [accessed 16 Mar. 2024].
- Pfeiffer L. 1859. *Monographia heliceorum viventium: sistens descriptiones systematicas et criticas omnium huius familiae generarum et specierum hodie cognitarum*. Vol. 4. Brockhaus, Leipzig. Available from <https://www.biodiversitylibrary.org/page/11648889> [accessed 16 Mar. 2024].
- Pfeiffer L. 1868. *Monographia heliceorum viventium: sistens descriptiones systematicas et criticas omnium huius familiae generarum et specierum hodie cognitarum*. Vol. 6. Brockhaus, Leipzig. Available from <https://biodiversitylibrary.org/page/12932804> [accessed 16 Mar. 2024].
- Pilsbry H.A. 1904. *Manual of Conchology, Structural and Systematic, with Illustrations of the Species. Second Series: Pulmonata. Vol. 17: African Achatinidae*: 113–208. Conchological Department, Academy of Natural Sciences, Philadelphia. Available from <https://biodiversitylibrary.org/page/23563258> [accessed 16 Mar. 2024].
- Pilsbry H.A. 1905–1906. *Manual of Conchology; Structural and Systematic, with Illustrations of the Species. Second Series: Pulmonata. Vol. 18. Achatinidae: Stenogyrinæ and Cæloxinæ*: 1–357. Conchological Department, Academy of Natural Sciences, Philadelphia. Available from <https://biodiversitylibrary.org/page/23563258> [accessed 16 Mar. 2024].

- Preece R.C., White T.S., Raheem D.C., Ketchum H., Ablett J., Taylor H., Webb K. & Naggs F. 2022. William Benson and the golden age of malacology in British India: Biography, illustrated catalogue and evaluation of his molluscan types. *Tropical Natural History* 6 (Suppl.): 1–434. Available from <https://li01.tci-thaijo.org/index.php/tnh/issue/view/17479> [accessed 16 Mar. 2024].
- Quoy J.R.C. & Gaimard J.P. 1832. *Voyage de la Corvette l'Astrolabe: Exécuté par Ordre du Roi, pendant les Années 1826–1827–1828–1829, sous le Commandement de M.J. Dumont d'Urville*. Zoologie. Vol 2. 1–321; Atlas (Mollusques): pls 1–93. Tatsu, Paris. <https://doi.org/10.5962/bhl.title.2132>
- Reeve L.A. 1849. *Conchologia iconica, or, Illustrations of the Shells of Molluscous Animals*. Vol. 5. Reeve, London. Available from <https://biodiversitylibrary.org/page/8937038> [accessed 16 Mar. 2024].
- Schileyko A.A. 1998. Treatise on Recent terrestrial pulmonate molluscs. Part 2: Gastrocoptidae, Hypselostomatidae, Vertiginidae, Truncatellinidae, Pachnodidae, Enidae, Sagdidae. *Ruthenica* Supplement 2: 129–261.
- Schileyko A.A. 1999. Treatise on Recent terrestrial pulmonate molluscs. Part 4. Draparnaudiidae, Caryodidae, Macrocyclidae, Acavidae, Clavatoridae, Dorcasiidae, Sculptariidae, Corillidae, Plectopylidae, Megalobulimidae, Strophocheilidae, Cerionidae, Achatinidae, Subulinidae, Glessulidae, Micractaeonidae, Ferussaciidae. *Ruthenica* Supplement 2: 437–564.
- Seale R.F. 1834. *The Geognosy of the Island of St Helena, Illustrated in a Series of Views, Plans and Sections; Accompanied with Explanatory Remarks and Observations*. Ackermann & Co., London.
- Shuttleworth R.J. 1852a. Diagnosen neuer Mollusken. *Mitteilungen der Naturforschenden Gesellschaft in Bern* 1852 (248–249): 193–208. Available from <https://www.biodiversitylibrary.org/item/42749#page/201/mode/1up> [accessed 16 Mar. 2024].
- Shuttleworth R.J. 1852b. Diagnosen neuer Mollusken. *Mitteilungen der Naturforschenden Gesellschaft in Bern* 1852 (260–261): 289–304. Available from <https://www.biodiversitylibrary.org/item/42749#page/301/mode/1up> [accessed 16 Mar. 2024].
- Smith E.A. 1892. On the land-shells of St. Helena. *Proceedings of the Zoological Society of London* 1892: 258–270. Available from <https://biodiversitylibrary.org/page/31848767> [accessed 16 Mar. 2024].
- Sowerby G.B.I. 1844. Description of fossil shells – Extinct land-shells from St. Helena. Appendix to Part I. In: Darwin C.R., *Geological Observations on the Volcanic Islands, Visited during the Voyage of H.M.S. Beagle, together with some Brief Notices on the Geology of Australia and the Cape of Good Hope. Being the Second Part of the Geology of the Voyage of the Beagle, under the Command of Capt. Fitzroy, R.N. during the years 1832–1836*. Smith, Elder & Co., London. Available from <https://darwin-online.org.uk/content/frameset?itemID=F272&viewtype=text&pageseq=1> [accessed 2 Feb. 2024].
- Wollaston T.V. 1878. *Testacea Atlantica or the Land and Freshwater Shells of the Azores, Madeiras, Salvages, Canaries, Cape Verdes, and Saint Helena*. L. Reeve & co., London. <https://doi.org/10.5962/bhl.title.22119>
- Woodward F.R. 1991. Dr. William B. Lorrain and St. Helena's endemic land shells. *Hawaiian Shell News* 39 (11): 1, 4.

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