

Streptaxidae (Mollusca: Gastropoda: Pulmonata) of the Seychelles Islands, Western Indian Ocean

J. Gerlach & A.C. van Bruggen

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The taxonomy of the species of the terrestrial carnivorous snail family Streptaxidae of the Seychelles archipelago is reviewed with the exception of the three species of the genus *Priodiscus* (vide Gerlach, 1995). All 18 species are restricted to the northern, granitic islands. This paper describes 15 species, including two new genera (*Silhouettia* and *Careoradula*), and four new subspecies (*Edentulina dussumieri reservae*, *E. d. silhouettae*, *E. d. praslina*, *Stereosteles nevillei paroidentata*). The nominal taxon *Streptaxis* (*Imperturbatia*) *constans* var. *silhouettae* is raised to species level to become the type species of the new genus *Silhouettia*. The type species of *Careoradula* is *Streptaxis* (*Imperturbatia*) *perelegans*. Anatomical descriptions and figures are provided for 13 species; the new genus *Careoradula* is distinct from all other streptaxids by the complete absence of a radula and associated structures. Distribution is featured on individual maps for each species. The paper concludes with a key to the shells of all species, those of *Priodiscus* included, and some preliminary considerations on the distribution of this group in the Seychelles archipelago.

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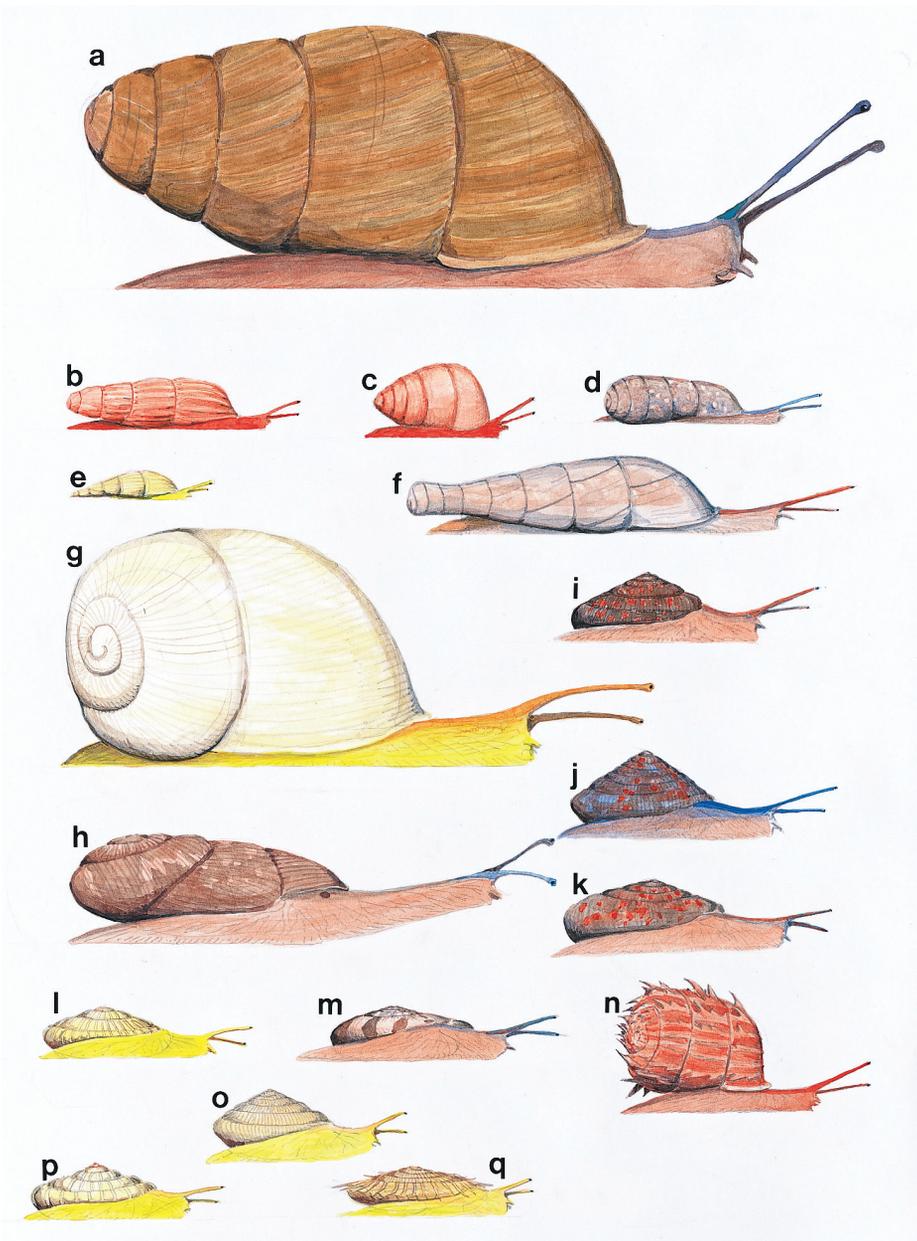


Plate 1. Living Seychelles Streptaxidae, all highly enlarged (all on the same scale, for shell measurements see text). (a) *Edentulina dussumieri*; (b) *Gulella bicolor*; (c) *Gulella silhouettensis*; (d) *Gulella gardineri*; (e) *Streptostele acicula*; (f) *Stereostele nevilli*; (g) *Gonaxis quadrilateralis* (alien species introduced from Kenya); (h) *Gonaxis souleyetianus*; (i) *Imperturbatia constans*; (j) *Imperturbatia violascens*; (k) *Silhouettia silhouettae*; (l) *Careoradula perelegans*; (m) *Augustula braueri*; (n) *Acanthennea erinacea*; (o) *Priodiscus costatus*; (p) *Priodiscus serratus*; (q) *Priodiscus spinosus*. J. Gerlach pinx.

Introduction

The terrestrial mollusc faunas of the islands of the western Indian Ocean are notable for their high degree of endemism and for the exceptionally large component of the fauna represented by the carnivorous pulmonate family Streptaxidae. The Seychelles fauna contains a large number of endemic species, many of which have been assigned to endemic genera. The specific and generic limits within the Streptaxidae are very poorly defined (many authors, e.g. Verdcourt, 1961) with existing classifications placing great reliance on external shell characters.

Small collections of Seychelles species date back to 1836 (Dufo, 1840) and 1866 (Adams, 1868; Nevill, 1868; for data on Martens vide Kabat & Boss, 1997). Much larger collections were made by A. Brauer in 1895 (Martens & Wiegmann, 1898) and the Percy Sladen Memorial Expedition in 1905 and 1908-1909 (Sykes, 1909). Brauer's collection included the first spirit material of Seychelles streptaxids which was described by Wiegmann (Martens & Wiegmann, 1898) in what remains one of the most extensive accounts of streptaxid anatomy. The next significant collection was made in 1972 by Benoit & Van Mol (1978). This contained very large numbers of specimens, both dry and in spirit, from a wide range of sites. The excellent nature of the preservation of this material and the associated locality data has provided us with the opportunity to examine individual, geographical and ontogenetic variation in a range of streptaxid species. Combined with the extensive shell collection of the Nature Protection Trust of Seychelles (collected in 1986-1997) this provides a clearer picture of the specific and generic limits within the Seychelles streptaxids, with implications for streptaxid faunas elsewhere and has resulted in a number of taxonomic changes. The present paper uses this material of 911 specimens to review all Seychelles streptaxids with the exception of the endemic genus *Priodiscus* Martens, 1898, which was reviewed in 1995 (Gerlach, 1995; see also pl. 1o-q). A representative series of duplicates is lodged in the National Museum of Natural History, Leiden.

Biogeographical background

The Seychelles islands comprise two main groups; the northern, granitic islands and the southern, coralline islands. The granitic islands are the remnants of the Seychelles microcontinent which was isolated following the break-up of Gondwanaland 65-100 million years ago. These islands are predominantly comprised of granite (mostly some 750 million years old), with some volcanic intrusions (Stephens, 1996) and reach up to 905 metres above sea level. In contrast, the southern islands are 8 m high at most and represent raised coral atolls or sand cays resting on the summit of submerged volcanoes (Matthews & Davies, 1966; Stoddart et al., 1971). Their geological history is much shorter, and most were submerged by higher sea levels some 35,000 years ago (Stoddart et al., 1971).

These differences between the granitic and coralline islands result in their supporting very distinctive faunas. The coralline islands have immigrant faunas that are composed of colonizing species originating from nearby land masses (mostly Madagascar and Africa). The granitic islands also have an immigrant component but many taxa must be relicts of forms which inhabited Gondwanaland prior to its fragmenta-

tion. As a result, the granitic island faunas have a strong Oriental (especially Indian) affinity, in contrast to the Ethiopian affinity of the coralline islands. Additionally, the height of the granitic islands gives them greater habitat diversity (fig. 1) and, most importantly, high rainfall. The rainfall allows the development of rain forest habitats which have high species diversity.

For the streptaxid mollusc faunas these differences are especially apparent - the granitic islands support 17 native species, mainly with Oriental affinities, compared to only a single living, African species, found on only three of the coralline islands (Aldabra, Assumption and Cosmoledo) (Van Bruggen, 1975, 1986). These two islands have supported a wider range of taxa in the past as indicated by subfossil material (*Gulella peakei* Van Bruggen, 1975, and *G. insulincola* Van Bruggen, 1975, in addition to the living *G. gwendolinae aldabrae* Van Bruggen, 1975) (Van Bruggen, 1975).

The limited streptaxid fauna of the coralline islands has been described in detail previously (Van Bruggen, 1975, 1986) and is not included in the present review which is restricted to the granitic islands of the Seychelles group.

Localities

Streptaxids have been collected on ten islands in the granitic Seychelles islands; Mahé, Anonyme, South-east, Cerf, St. Anne, Silhouette, Praslin, Curieuse, Félicité and La Digue (with a doubtful record from Frégate). The sites studied on each island (fig. 2) are described below with notes on the history of research at each site and their conservation value. Conservation value is noted according to the following scale:

- No native species present = 0
- 1 native species present, no endemics = 1
- 1 endemic species present = 2
- 2 endemic species present = 3
- 3-5 endemic species present = 4
- 5-10 endemic species present = 5
- An endemic species restricted to this site = 10

Mahé

1. Crève Coeur - Secondary forest dominated by *Cinnamomum verum* Presl and *Memecylon caeruleum* Hook. f., 386 metres above mean sea-level. West slope (300 m) visited by P.L.G. Benoit & J.-J. Van Mol on 11.vi.1972. Two species of streptaxid located (1 widespread endemic); conservation value = 2.

2. Beau Vallon - Mare Anglaise - Coastal suburb and secondary forest at sea-level. Visited by P.L.G. Benoit & J.-J. Van Mol (12.vi.1972) and J. Gerlach (1986-1997). Two species (1 native); conservation value = 1.

3. Victoria - Urban habitat at sea-level. Visited by G. Nevill (1866), P.L.G. Benoit & J.-J. Van Mol (13.vi.1972) and J. Gerlach (1985-1997). The only streptaxids recorded here are alien species; conservation value = 0.

4. Roche Caiman Bird Sanctuary (fig. 1a) - coastal *Casuarina equisetifolia* J.R. & G. Forst. forest resulting from plantation on land reclaimed in 1986. Visited by J. Gerlach (1986-1997). Two introduced species; low conservation value = 0.

5. Bel Air - Mid-altitude (150 m) suburban gardens. Visited by J. Gerlach (1985-1997). Three species (1 native); low conservation value = 1.



Fig. 1. Habitats of the granitic islands of the Seychelles archipelago. (a) Coastal plantation - Roche Caiman Bird Sanctuary, Mahé; (b) Palm forest - Vallée de Mai, Praslin; (c) *Pisonia sechellarum* forest, Silhouette; (d) Mt. Dauban, Silhouette; (e) Moss forest - Mt. Dauban, Silhouette. All photographs by J. Gerlach.

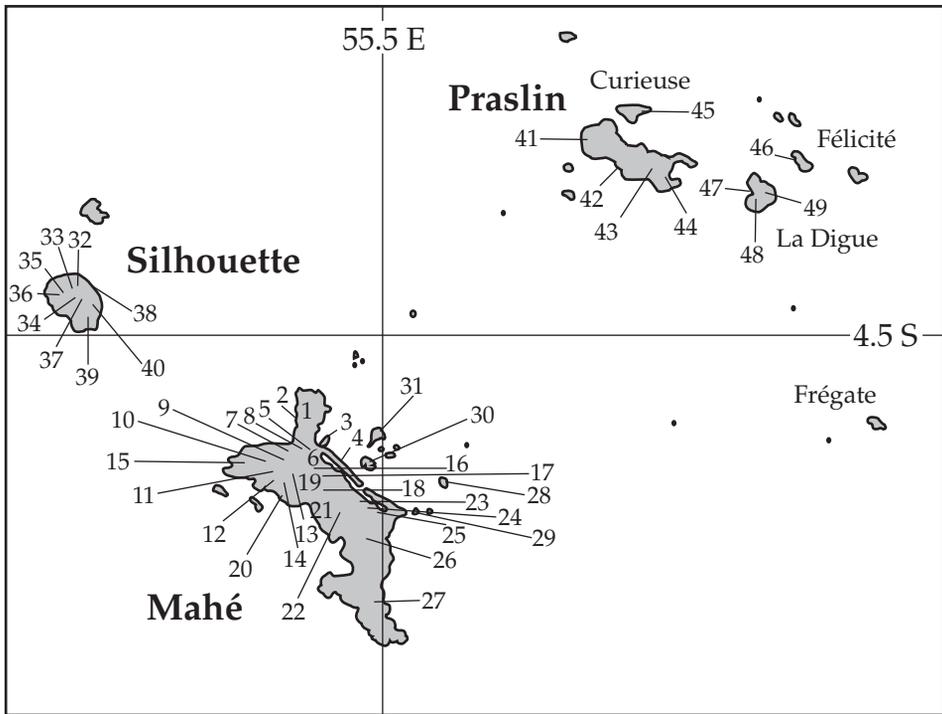


Fig. 2. Granitic islands of the Seychelles group, showing localities mentioned in the text.

6. Rochon Dam - Mid-altitude (230 m) suburban gardens and secondary forest. Visited by J. Gerlach (17.vii.1986). One introduced species; conservation value = 0.

7. Le Niol - Mid-altitude (250 m) suburban gardens. Visited by J. Gerlach (1988-1997). Two introduced species; conservation value = 0.

8. Trois Frères - High-altitude (270-450 m) secondary forest, dominated by *Cinnamomum verum* and other alien trees. Visited by Percy Sladen Memorial Expedition (xii.1908) and J. Gerlach (13.viii.1987, 31.viii.1988). Five species (all endemic); conservation value = 4.

9. Morne Seychellois - High-altitude to moss forest (500-850 m), heavily invaded, lower slopes dominated by alien vegetation. Visited by A. Brauer (1895), Percy Sladen Memorial Expedition (25.x.1905, 4.ii.1909), P.L.G. Benoit & J.-J. Van Mol (13-17.vii.1972) and J. Gerlach (26.vii.1991). Ten species (all endemic); conservation value = 5.

10. Congo Rouge - High-altitude (600-760 m) moss forest with predominantly endemic vegetation. Extensive invasion by alien plants (especially *Cinnamomum verum*). Visited by J. Gerlach (1987-1996). Five species (all endemic); conservation value = 4.

11. Morne Blanc - High-altitude (450-667 m) forest, mixed native and invasive alien plants. Some areas are almost pure native moss forest but much of the site is entirely alien. Visited by A. Brauer (1895), Percy Sladen Memorial Expedition (10.x.-25.xi.1908, 5.ii.1909), P.L.G. Benoit & J.-J. Van Mol (23.vi.1972, 8-9.viii.1972) and J. Gerlach (1986-1996). Eleven species (all endemic); conservation value = 5.

12. Morne Noir - Mid-high-altitude (400 m) forest, heavily invaded by *Cinnamomum verum*. Visited by P.L.G. Benoit & J.-J. Van Mol (1972). Two species (1 widespread endemic); conservation value = 2.

13. Mission - High-altitude (430-460 m) forest dominated by alien species (especially *Pterocarpus indicus* Willd.). Visited by J. Gerlach (1986-1992). One widespread endemic species; conservation value = 2.

14. Casse Dent - High-altitude (430-520 m) forest dominated by alien species (especially *Cola nitida* A. Chevalier and *Artocarpus heterophyllus* Lam.). Visited by J. Gerlach (1987-1994). Two species (endemic); conservation value = 3.

15. Mare aux Cochons - High-altitude (400-450 m) native forest with marshy areas in *Pandanus* and *Cyathea* tree-fern forest. Since the middle of the 20th century it has become secondary and degraded native forest. Visited by A. Brauer (1895), Percy Sladen Memorial Expedition (1905, 26.i.1909, 3.ii.1909), P.L.G. Benoit & J.-J. Van Mol (2-8.vii.1972) and J. Gerlach (17.vii.1989, 21.vii.1996). Four species (all endemic) conservation value = 4.

16. Copolia - Mid-high-altitude (350-497 m) endemic *Dillenia ferruginea* Gilg. forest. Extensive invasion by *Cinnamomum verum*. This site is identifiable as the 'Morne Impracticable' of Martens (1898) (Gerlach, 1990). Visited by A. Brauer (1895) and J. Gerlach (1988-1993). Six species (all endemic); conservation value = 5.

17. Fairview - Mid-altitude (350 m) suburban gardens. Visited by J. Gerlach (5.xii.1989). Only one introduced species has been recorded from this site; conservation value = 0.

18. La Misère - Mid-altitude (370 m) secondary forest dominated by *Cinnamomum verum*. Visited by P.L.G. Benoit & J.-J. Van Mol (16-17.vi.1972, 12.vii.1972) and J. Gerlach (10.viii.1986). One widespread endemic species; conservation value = 2.

19. Chateau Margot - Until the middle to the 20th century this site was on the edge of semi-native mid-altitude (350 m) forest; it is now suburban. Visited by Percy Sladen Memorial Expedition (xi.1905) and J. Gerlach (1989-1992). Four species (all endemic) were recorded in 1905-1909 but no native streptaxids remain at this site; conservation value = 0.

20. Beoliere - Low-altitude (150-180 m) secondary *Chrysobalanus icaco* L. scrub. Visited by J. Gerlach (12.iii.1988). Only one introduced species recorded; conservation value = 0.

21. Bernica - Mid-altitude (200 m) secondary forest, dominated by *Cinnamomum verum*. Visited by J. Gerlach (24.viii.1989). Only one widespread endemic species has been recorded; conservation value = 2.

22. Montagne Planeau (Mt. Harrison) - High-altitude (300-650 m) forest with areas of moss forest. Largely native with some invasion by *Cinnamomum verum*. Visited by A. Brauer (1895), Percy Sladen Memorial Expedition (xi.1905) and J. Gerlach (2.ix.1989). Four species (all endemic); conservation value = 5.

23. Cascade - Mid-altitude (240-500 m) forest. In the early part of the 20th century the upper parts of the valley were the Cascade Estate managed by H.P. Thomassett. Since the estate was abandoned in the 1930s it has changed to degraded secondary forest, dominated by alien plants. The lower slopes are now suburban. Visited by A. Brauer (1895), Percy Sladen Memorial Expedition (xi.1905, ix.1908, 21.xii.1908-25.i.1909, 15.ii.1909, 3.iii.1909) and J. Gerlach (3 and 17.viii.1986, 6.viii.1987). Nine

species (all endemic, including one restricted to this site) were recorded in 1905-1909; since then only 1 widespread endemic and 1 introduced species have been recorded and present conservation value = 2.

24. Mont Alphonse - Two endemic streptaxids were recorded from this site by the Percy Sladen Memorial Expedition (1905). From the localities listed by Sykes (1909) it appears to have been next to the Cascade valley. It is not marked on any map or described and the precise location is unknown.

25. Mont Sebert - Mid-altitude (500 m) 'glacis' - this is a granite dome covered by patches of endemic, partially xerophytic vegetation. Visited by Percy Sladen Memorial Expedition (xi.1905) and J. Gerlach (5.i.1989, 10.ix.1989, 12.vii.1992). Six species (all endemic); conservation value = 5.

26. La Réserve, Brulée - Mid-altitude (300-501 m) endemic palm forest. This site has a diverse native flora and is dominated by the endemic palms *Phoenicophorium borsigianum* (C. Koch) Stuntz., *Nephrosperma vanhouetteanum* (H. Wendl.) Balf. and *Verschaffeltia splendida* H. Wendl. Visited by J. Gerlach (1986-1996). Ten species (all endemic); conservation value = 5.

27. Montagne Capucins ('mountain at Pointe Capucin' - Martens, 1898) - Low-altitude (150 m) site, reported to have a forested summit in 1895 (Martens, 1898) but eroded slopes. Visited by A. Brauer (1895). Two species (both endemic); conservation value = 3.

28. Anonyme - This small (9.6 ha) islet was visited by the Percy Sladen Memorial Expedition (1905, 8-9.i.1909) who collected *Gulella gardineri*. It is covered by coastal vegetation (dominated by *Cocos nucifera* L. and *Calophyllum inophyllum* L.). It appears to be an unlikely site for *G. gardineri*, but has not been studied for invertebrates since 1909. Conservation value = unknown.

29. South-east - This small (3 ha) islet was one of the sites for the introduction of *Gonaxis quadrilateralis* in 1957. In 1971 it was joined to Mahé by coastal reclamation.

30. Cerf - This island was an introduction site for *Gonaxis quadrilateralis* in 1957. It is covered by coastal vegetation (*Cocos nucifera*, *Calophyllum inophyllum* and *Terminalia catappa* L.) with extensive invasion by *Tabebuia pallida* Miers, *Chrysobalanus icaco* and *Memecylon caeruleum*. Visited by Percy Sladen Memorial Expedition (27.x.1905) and J. Gerlach (1996-1997). No native streptaxids have been recorded; conservation value = 0.

31. St. Anne - *Gonaxis quadrilateralis* was introduced to this island unofficially. Its vegetation is highly degraded and is almost completely alien. Visited by Percy Sladen Memorial Expedition (28.x.1905) and J. Gerlach (11.ix.1988). No native streptaxids have been recorded; conservation value = 0.

Silhouette

32. Mont Pot à Eau - High altitude (500-621 m) forest dominated by native hygrophyllic plants. Visited by Percy Sladen Memorial Expedition (xi.1905, viii.1909) and J. Gerlach (1990-1994). Two species (both endemic); conservation value = 3.

33. *Pisonia sechellarum* F. Friedmann forest (fig. 1c) - High-altitude (450-500m) endemic forest. Visited by J. Gerlach (1990-1996). Seven endemic species (including one restricted to this site and Mon Plaisir); conservation value = 5.

34. Mon Plaisir - High-altitude (550 m) forest dominated by *Northea hornei* Pierre and *Dillenia ferruginea*. In 1990-1994 the summit was dominated by the alien weed *Clidemia hirta* D. Don; it has now regenerated to its natural state (Gerlach, 1996). Visited by Percy Sladen Memorial Expedition (xi.1905, 25.vii-21.viii.1908) and J. Gerlach (1990-1997). Five endemic species (including one restricted to this site and the *Pisonia sechellarum* forest); conservation value = 5.

35. Mont Dauban (figs 1d-e) - High-altitude (650-740 m) moss forest dominated by endemic plants, especially *Glionnetia sericea* (Baker) D.D.Tirvengadam. Visited by Percy Sladen Memorial Expedition (xi.1905, ix.1908), P.L.G. Benoit & J.-J. Van Mol (5 and 7.vii.1972) and J. Gerlach (1990-1993). Five endemic species (including one endemic to the site); conservation value = 10.

36. Mare aux Cochons - High-altitude (500 m) marsh. Naturally covered by ferns and herbaceous plants. Since 1959 it has been partially drained and converted to coffee (*Coffea canephorum* Pierre ex Froehn.) plantation, now abandoned. Visited by Percy Sladen Memorial Expedition (xi.1905, 21.viii-29.ix.1908), P.L.G. Benoit & J.-J. Van Mol (2 and 8.vii.1972) and J. Gerlach (vii.1992, 14.xii.1993). Four endemic species (including the only recent site for the endemic *Edentulina moreleti*); conservation value = 4.

37. Jardin Marron - Mid-high-altitude (300-500 m) forest. Invaded by alien plants (*Psidium cattleianum* Sabine, *Artocarpus heterophyllus* and *Clidemia hirta*) but retaining a diverse native flora. Visited by J. Gerlach (1990-1997). Seven species (all endemic), conservation value = 5.

38. La Passe - Coastal suburb. Visited by J. Gerlach (1987-1998). Only 1 widespread native streptaxid has been recorded; conservation value = 0.

39. Mont Corgat - Mid-altitude (350 m) dry forest. Visited by Bristol University Expedition (Barnacle, 1972). Only 1 endemic streptaxid has been recorded; conservation status unknown.

40. Gratte Fesse - High-altitude (450-500 m) forest with large stands of *Pandanus hornei* Balf. f. and *Verschaffeltia splendida*. Visited by J. Gerlach (1991-1998). Nine endemic species; conservation value = 5.

Praslin

41. Anse Kerlan - Lowland marsh. Visited by J. Gerlach (20-22.vii.1996, 18-19.i.1997). The only evidence of streptaxids at this site are subfossil shells probably washed from nearby hills.

42. Grande Anse - Coastal suburb. Visited by J. Gerlach (1991-1997). Only 1 introduced species has been recorded; conservation value = 0.

43. Vallée de Mai (fig. 1b) - Coco-de-mer [*Lodoicea maldivica* (Gmel.) Pers.] palm forest, 170-190 m. This is a unique area of native forest. Visited by Percy Sladen Memorial Expedition (xi.1905, 29-30.xi.1908), P.L.G. Benoit & J.-J. Van Mol (22-23.vii and 20-23.viii.1972) and J. Gerlach (1986-1997). One species (endemic); conservation value = 2.

44. Fond Ferdinand - Coco-de-mer (*Lodoicea maldivica*) palm forest, 100-150 m. This forest was almost completely destroyed by fire in the 1990s. Visited by P.L.G. Benoit & J.-J. Van Mol (24.vii.1972). One species (endemic); since the fire it has been of reduced conservation value although regenerating rapidly.

45. Curieuse - Heavily fire damaged Coco-de-mer (*Lodoicea maldivica*) and coastal forest. Most of the island is now exposed earth and rock. Visited by Percy Sladen Memorial Expedition (xi.1905) and P.L.G. Benoit & J.-J. Van Mol (27.vii and 17.viii.1972). One widespread endemic species has been recorded; conservation value = 2.

46. Félicité - Naturally covered in coastal forest, dominated by *Calophyllum inophyllum*. Since the early 20th century most of the island has been converted to coconut (*Cocos nucifera*) plantation. Visited by Percy Sladen Memorial Expedition (xi.1905, 14-18.xii.1908). One endemic species recorded in 1908; current conservation value unknown.

La Digue

47. La Réunion - Lowland suburb with small patches of *Calophyllum inophyllum* woodland. Visited by Percy Sladen Memorial Expedition (xi.1905) and by J. Gerlach (8.i.1996, 24-26.vii.1996). The only streptaxid material is subfossil.

48. Belle Vue - Mid-altitude (100-200 m) secondary forest dominated by *Cinnamomum verum*. Visited by O. Griffiths (vii.1990) and J. Gerlach (23.iii.1992). One widespread endemic species recorded; conservation value = 2.

49. Mont La Digue - Mid-altitude (250-333 m) secondary forest dominated by *Cinnamomum verum*. Visited by P.L.G. Benoit & J.-J. Van Mol (28 and 31.vii.1972). Only one widespread endemic species has been located; conservation value = 2.

Frégate - Only one species has been recorded from this island. The record cannot be substantiated and is probably erroneous.

Abbreviations

Institutional abbreviations used in the text are as follows:

BMNH - British Museum (Natural History), London; MNHN - Muséum National d'Histoire Naturelle, Paris; MRAC - Musée Royal de l'Afrique Centrale, Tervuren; NPTS - Nature Protection Trust of Seychelles; RMNH - National Museum of Natural History (formerly Rijksmuseum van Natuurlijke Historie), Leiden; SMF - Senckenberg Museum, Frankfurt am Main; ZMB - Zoologisches Museum (Museum für Naturkunde der Humboldt-Universität), Berlin. The material in MRAC was all collected by Drs P.G.L. Benoit and J.-J. Van Mol in 1972. The NPTS material was collected by J. Gerlach between 1987-1997, unless stated otherwise

Measurement abbreviations: H - shell height; D - shell diameter; the ratio H/D indicates the shape of the shell. Most dimensions have been tabulated. The abbreviation alc. stands for (specimens kept in) alcohol.

Genus *Edentulina* Pfeiffer, 1856

The genus *Edentulina* is characterised by large bulimoid shells with slightly convex whorls. The sculpture is restricted to irregular growth ridges, coarse spiral striae may be present. The aperture is large and edentulous with a thickened, reflected labrum. The umbilicus is open but narrow. The penis is elongate and sheathed. The

short epiphallus is attached to the terminal part of the sheath. Penial ornamentation comprises complex arrangements of well developed chitinous spinules.

Distribution.— Tropical Africa, Madagascar, Comoros islands, Seychelles islands.

Traditionally the following two species have been classified with *Edentulina*. However, it is a moot point whether the Seychelles radiation may be compared to that on the African continent.

Edentulina dussumieri (Dufu, 1840)

Pupa Dussumieri Dufu non Férussac, 1840: 198.

Bulimus Dussumieri; Reeve, 1846: 457; Pfeiffer, 1841: 362.

Ennea Dussumieri; Morelet, 1860: 75, pl. 5 fig. 9; Germain, 1921: 122.

Gibbus (Gibbulina) Dussumieri; Nevill, 1868: 260.

Ennea (Edentulina) Dussumieri; Martens & Wiegmann, 1898: 7-8, pl. 1 figs 7-10.

Edentulina dussumieri; Moellendorff & Kobelt, 1904: 298, pl. 33 figs 6-8; Schouteden, 1936a: 139; Zilch, 1961: 80.

Ennea dussumieri; Sykes, 1909: 59; Barnacle, 1962: 54; Lionnet, 1984: 240; Gerlach, 1987: 10, 3 col. figs.

Material.— 190 adults: 72 NPTS (M1997.11, 12 & 13; Mahé, Silhouette and Praslin; alc. and dry; additional juvenile material), 91 MRAC (with duplicates in RMNH) (798.758, 804, 829-830, 835, 814, 885, 909, 947, 959; Mahé, Silhouette and Praslin; alc. and dry; additional juvenile material), 2 RMNH (Mahé, ex. H.C. Fulton), 15 MNHN (4 Mahé, leg. A. Peyrieras, iv.1972, colln. Mme. Blanc 1975, all alc.; 3 'Seychelles', colln. Denis; 6 syntypes 'des Séchelles 1839'; 2 "Seychelles", colln. Denis, handwriting on label is that of the dealers Sowerby or Sowerby and Fulton), 8 G. Lionnet colln. (Mahé; Silhouette; Praslin), 1 B. Colville colln. (Praslin, Vallée de Mai, 14.iv.1994), 1 O. Griffiths colln. (La Digue, VII.1990).

Material dissected.— Twenty adults and juveniles from Mahé, Silhouette and Praslin (NPTS M1997.11, 12 & 13; MRAC 798.804, 798.885).

Type material.— Six syntypes "des Séchelles 1839" (MNHN); 5 juvenile/subadult, 1 adult lectotype. Type locality: Mahé (according to original description). Lectotype measurements agree with the above data on specimens from north Mahé.

Shell (fig. 3a).— Shell of 7-8 whorls and 2 spirally ridged nuclear whorls, dull except around aperture, dark brown. Bulimoid, broad and slightly tapering towards the flat apex. The whorls are slightly rounded, without sutural ridges. Fine growth striae and irregular ribs are present, irregular spiral ridges are present on all whorls but are most distinct towards the apex. Aperture large, edentulous; lip incassate and reflected. Umbilicus narrow, deep and rimate. The thin brown periostracum is often deciduous towards the apex.

Dimensions.— See table 1.

Body (pl. 1a).— Foot orange to pink; tentacles dark grey with purple bases. Sole orange. Rare individuals have a yellow foot and sole.

Anatomy.

Salivary gland.— Short and broad, roughly triangular in shape; 5 mm long.

Radula (fig. 3f).— Four radula morphs are present in the four subspecies (described below). Radula 0.9 × 7.0-10.9 mm, 62-70 rows, rows curved. Central tooth long and narrow, symmetrical, 0.1 mm long. Laterals simple, decreasing in size. Last lateral greatly reduced (0.03 mm).

Reproductive anatomy (figs 3b-e).— Spermooviduct broadened terminally; 8-14

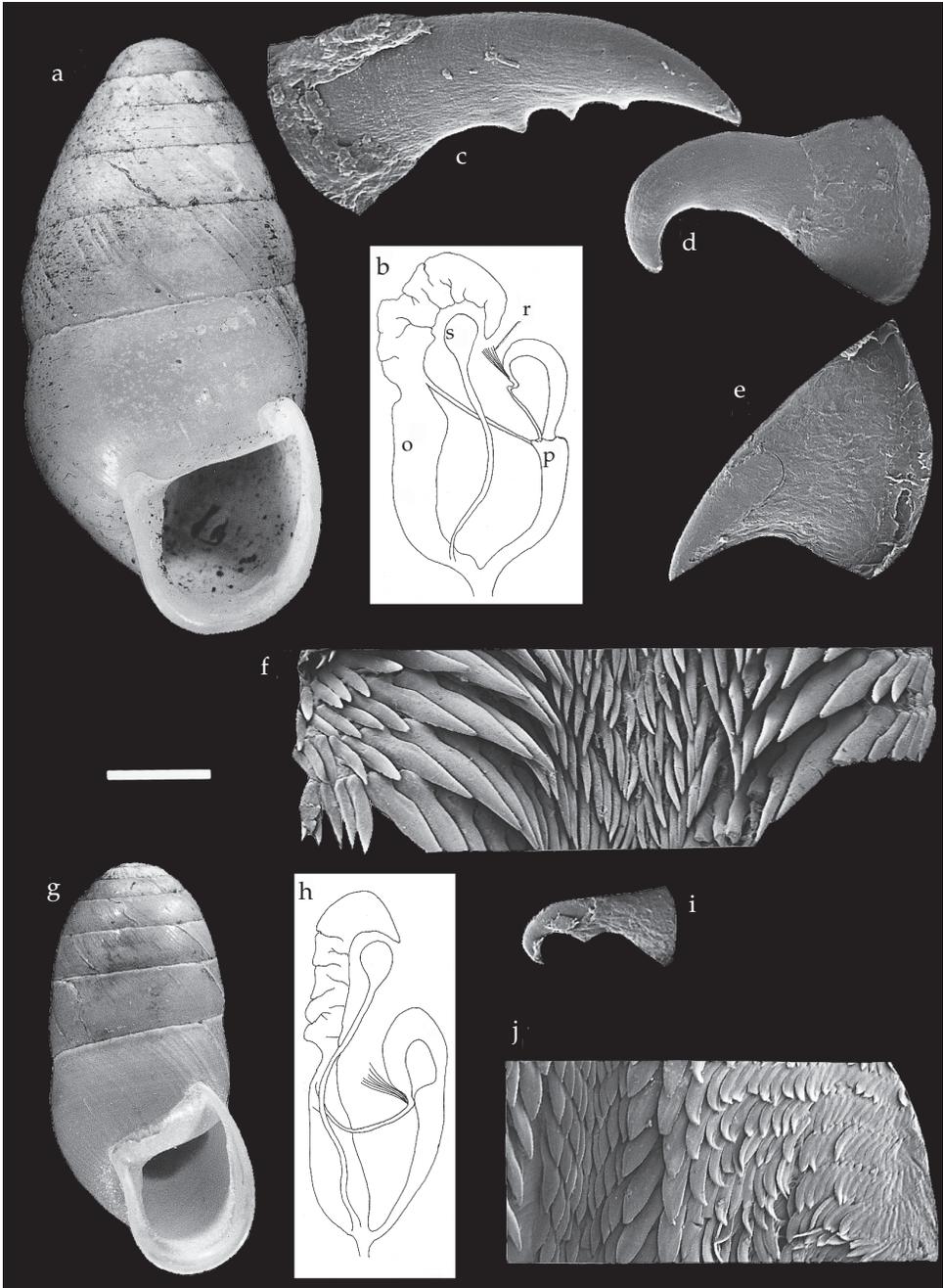


Fig. 3. *Edentulina* species. (a-f) *Edentulina dussumieri*, (a) shell (MRAC 798.758) (scale bar 3 mm), (b) reproductive anatomy (scale bar 0.05 mm), (c) spinule type A (scale bar 0.05 mm), (d) spinule type B (scale bar 0.1 mm), (e) spinule type C (scale bar 0.1 mm), (f) radula (scale bar 0.1mm); (g-j) *Edentulina moreleti*, (g) shell (MRAC 798.865) (scale bar 1.3 mm), (h) reproductive anatomy (scale bar 3 mm), (i) spinule (scale bar 0.05 mm), (j) radula (scale bar 0.1 mm).

Table 1. *Edentulina dussumieri* dimensions (mm).

	Height		Diameter		H/D		Whorls		N
	range	mean (sd)	range	mean (sd)	range	mean (sd)	range	mean	
Lectotype	17.9	-	8.8	-	2.03	-	7.75	-	1
Mahé	13.4-19.6	16.4 (1.70)	7.8-10.2	8.6 (0.50)	1.52-2.28	2.04 (2.02)	7-8	8.0	101
North Mahé	13.4-18.2	15.6 (1.21)	7.8-9.2	8.5 (0.42)	1.59-2.24	2.24 (0.13)	7-8	8.0	36
South Mahé	14.2-18.8	16.3 (1.21)	7.4-10.2	9.0 (0.58)	1.45-20.6	1.80 (2.52)	7.5-8	8.0	37
Praslin	15.5-18.7	17.4 (0.69)	7.4-8.9	8.0 (0.45)	1.78-2.35	2.17 (0.32)	7-8	7.4	8
La Digue	16.9	-	8.5	-	1.99	-	8	-	1
Silhouette	16.7-20.0	18.3 (1.42)	8.4-10.0	9.2 (0.62)	1.91-2.22	2.07 (1.45)	7-8.5	8.0	70
Total	15.4-20.0	17.1 (1.54)	7.4-9.8	8.8 (0.54)	1.92-2.35	2.04 (1.72)	7-8.5	8.0	180

mm long. Spermatheca ovoid, 3 mm long; spermatheca duct narrow, 20 mm long; base broad, 2 mm long. Penis elongate (11-15 mm). Penis sheath present on lower half. Short epiphallus (3 mm long) attached to terminal part of sheath. Penis constricted basally and at attachment of sheath. Penial retractor muscle terminal. Penis regularly ornamented with chitinous, black spinules which are visible externally. Three spinule forms are recognisable: elongate (0.15 mm), multi-cuspid (type A); hooked, bicuspid (type B); and small (0.05 mm), simple (type C). The arrangement of spinules is constant within well defined populations and defines subspecific taxa.

Notes on juvenile anatomy.— A range of juvenile and subadult specimens was dissected. No differences were found between these and mature adults in radula structure/formula or in the salivary gland. The reproductive organs were only detectable in subadult specimens with shells over 14.5 mm long.

Cerebral ganglia.— Cerebral ganglia fused; cerebro-pedal connectives long (equal to width of fused ganglia); pleural ganglia close to pedal ganglia; pedal-visceral connectives long; visceral ganglia fused and median. This is the typical streptaxid pattern (Tillier, 1990) which is found in all other Seychelles taxa (Gerlach, personal observations).

Distribution (fig. 4).— Mahé (Mare aux Cochons, Trois Frères, Morne Blanc, Morne Seychellois, Montagne Planeau, La Réserve & Brulée), Silhouette (Jardin Maron, Mon Plaisir, Mont Pot à Eau, Mont Dauban, *Pisonia sechellarum* forest, Mare aux Cochons, Gratte Fesse), Praslin (Vallée de Mai, subfossils at Anse Kerlan), La Digue (subfossil only).

Geographical variation.— The adult shells differ significantly in size and shape between the three islands; there are also significant differences between populations on Mahé. The data are summarized in table 1. The sample from Praslin is too small for significance testing. From these comparisons it is apparent that the Silhouette form is larger and broader than the others, the north Mahé population has the smallest shells. Shells of the Praslin population appear to be intermediate in size and proportions and have slightly less convex whorls than in any other population. These conchological differences are also reflected in the soft-body anatomy (specifically in radula formula and penial spinule arrangement) and allow four subspecies to be rec-

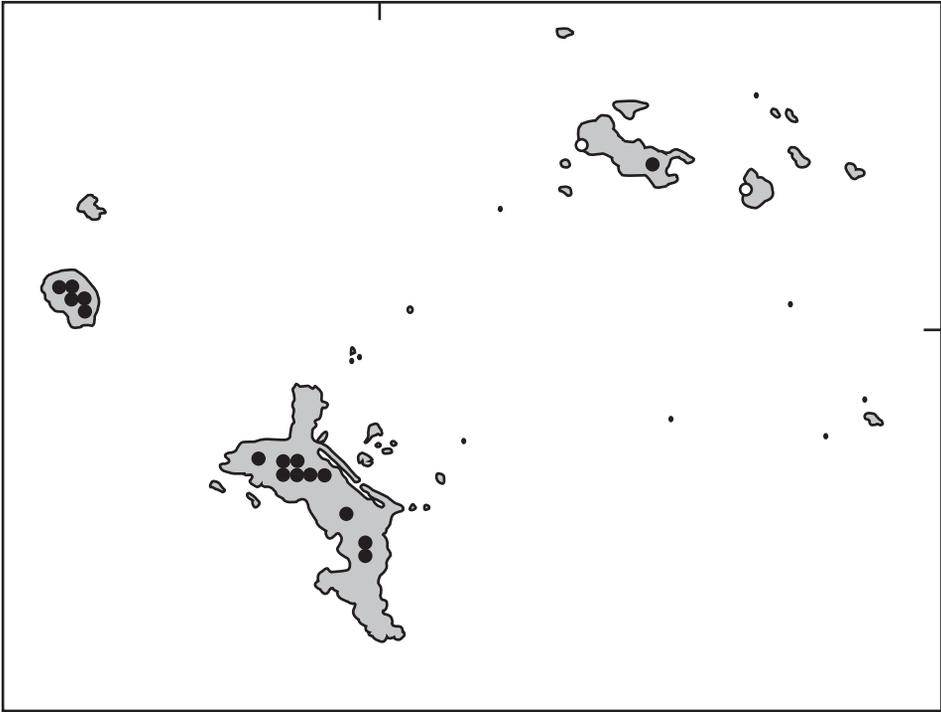


Fig. 4. Distribution of *Edentulina dussumieri*.

ognized. There is only a single subfossil shell from La Digue; this is insufficient to identify to subspecies level.

Edentulina dussumieri dussumieri (Dufo, 1840)

Material studied.— 36 adults from 72 NPTS (NPTS M1997.11 Mahé; alc. and dry; additional juvenile material), 91 MRAC (with duplicates in RMNH) (MRAC 798.814, 829, 830, 857, 909, 935, 947 Mahé; alc. and dry; additional juvenile material), 2 RMNH (Mahé, ex. H.C. Fulton), 13 MNHN (4 Mahé, leg. A. Peyrieras, iv.1972, colln. Mme. Blanc 1975, all alc.; 3 'Seychelles', colln. Denis; 6 syntypes 'des Séchelles 1839'), 4 G. Lionnet colln.; 10 adult and juvenile alc. specimens were dissected from NPTS and MRAC collections (NPTS M1997.11; MRAC 798.804, 798.885).

Type material.— Six syntypes "des Séchelles 1839" (MNHN); 5 juvenile/subadult, 1 adult lectotype. Type locality: Mahé (according to original description). Lectotype measurements agree with the above data for this subspecies.

Shell.— 7-8 whorls. Bulimoid, broad and relatively short (height/diameter = 1.80-0.13). This taxon is significantly broader than any other subspecies (t test of height/diameter $T > 2.471$, $P < 0.02$).

Dimensions - See table 1.

Body.— As for species description.

Anatomy.

Radula.— Formula 18 + 1 + 18.

Reproductive anatomy.— In the proximal half of the penis spinules are of type C, at the mid-point they are of type B, and type A occurs terminally. The number of cusps increases towards the end except for the spinules in the terminal fifth which are without cusps and S-shaped.

Distribution.— Mahé (Mare aux Cochons, Trois Frères, Morne Blanc, Morne Seychellois, La Misère).

Edentulina dussumieri reservae subspec. nov.

Material studied.— 37 adults: 36 NPTS (NPTS M1997.12 Mahé; alc. and dry; additional juvenile material), 1 UMZ (I.22,540 Mahé; dry); 15 adult and juvenile specimens were dissected from NPTS collections (NPTS M1997.12).

Type material.— Holotype NPTS M1997.12a. Paratypes M1997.12b&c, UMZ I.22,540. All La Réserve, Mahé, 17.vii.1989, coll. J. Gerlach. Type locality: Mahé, La Réserve.

Shell.— 7.5-8 whorls. Bulimoid, broad and relatively short (height/diameter = 2.24-0.52), although not statistically significantly different from the Silhouette population. Significantly longer and narrower than the Silhouette population ($t = 7.909$ and $t = 6.712$ respectively, $P < 0.001$ in both cases).

Dimensions.— See table 1.

Body.— As for species description.

Anatomy.

Radula.— Formula 17 + 1 + 17.

Reproductive anatomy.— Penial spinule arrangement is as in the nominate subspecies except that type B spinules are replaced by type C.

Distribution.— Mahé (La Réserve, Brulée, Montage Plateau).

Edentulina dussumieri silhouettae subspec. nov.

Material studied.— 70 adults, 95 juveniles: 72 NPTS (NPTS M1997.13 Silhouette; alc. and dry), 91 MRAC (with duplicates in RMNH) (MRAC 798.758, 804, 835, 836, 959 Silhouette; alc. and dry), 2 G. Lionnet colln.; 4 adult and juvenile alc. specimens were dissected (NPTS M1997.13, MRAC 798.804).

Type material.— Holotype MRAC 798.804, Mare aux Cochons (500 m, 'forêt endémique'), Silhouette, 2 and 8.vii.1972, coll. P.L.G. Benoit & J.-J. Van Mol. Paratypes NPTS M1997.13a, Jardin Marron, Silhouette, 14.vii.1990, coll. J. Gerlach. Type locality: Silhouette, Mare aux Cochons.

Shell.— 7.5-8 whorls. Bulimoid, broad. Resembling *E. d. reservae* except significantly shorter and broader.

Dimensions.— See table 1.

Body.— As for species description.

Anatomy.

Radula.— Formula 25 + 1 + 25.

Reproductive anatomy.— Penial spinule arrangement is as in the nominate subspecies except that type B spinules are absent and type A spinules continue to the apex of penis.

Distribution.— Silhouette (Jardin Marron, Mon Plaisir, Mont Pot à Eau, Mont Dauban, *Pisonia sechellarum* forest, Gratte Fesse).

Edentulina dussumieri praslina subspec. nov.

Material studied.— Seven adults: 1 NPTS (NPTS M1997.14 Praslin; dry), 3 MRAC (MRAC 798.885; alc.), 1 G. Lionnet colln. 1 B. Colville colln.; 1 adult alc. specimen dissected (MRAC 798.885).

Type material.— Holotype MRAC 798.885, Vallée de Mai, Praslin, 22-23.vii.1972 coll. P.L.G. Benoit & J.-J. Van Mol. Paratype NPTS M1997.14, Vallée de Mai, Praslin, 17.vii.1987, coll. J. Gerlach. Type locality: Praslin, Vallée de Mai.

Shell.— 7-8 whorls. Bulimoid, broad and slightly tapering towards the flat apex. Insufficient specimens for significance testing.

Dimensions.— See table 1.

Body.— As for species description.

Anatomy.

Radula.— Formula 27 + 1 + 27.

Reproductive anatomy.— Spinule arrangement as in the nominate taxon except that type A spinules are only bicuspid and are S-shaped.

Distribution.— Praslin (Vallée de Mai, Anse Kerlan - subfossil fragment only).

Edentulina moreleti (Adams, 1868)

Gibbus (*Gibbulina*) *Moreleti* Adams, 1868: 291.

Pupa Moreleti; Pfeiffer, 1841: 350, pl. 28 fig. 10; Nevill, 1868: 64.

Ennea (*Edentulina*) *Moreleti*; Martens in Möbius, 1880: 205; Martens, 1898: 8.

Ennea moreleti; Barnacle, 1962: 54; Lionnet, 1984: 240; Gerlach, 1987: 9, 3 text figs.

Edentulina moreleti; Moellendorff & Kobelt, 1904: 298, pl. 33 figs 9-10.

Material studied.— 30 specimens from Silhouette (17 BMNH) unnumbered; 12 MRAC 798.865, 872, 953 & 958; alc. and dry; 1 P. Topley colln.), 4 Mahé (3 MNHN: leg. A. Peyrias, iv.1972, colln. Mme. Blanc, 1975; 1 G. Lionnet colln.).

Material dissected.— Two specimens from Silhouette (MRAC 798.872 & 953).

Type material.— The holotype (Silhouette, colln. G. Nevill 1867) cannot be located in the collections of the BMNH. Type locality: Silhouette.

Shell (fig. 3g).— Shell bulimoid; 6.75-7.75 whorls with 2 nuclear whorls. Whorls flattened and rounded towards the flat apex. Radial ridges present on protoconch. Surface dull, brown. Irregular growth ridges present, some forming slight ribs. Aperture edentulous; lip incrassate, reflected and slightly thickened. Umbilicus rimate. Periostracum thin.

Dimensions.— See table 2; t tests of the measurement data from Mahé and Silhouette indicate that Mahé shells are significantly larger than those from Silhouette (height $t = 5.70$, diameter $t = 2.43$, H/D $t = 2.66$; $P < 0.05$ for all cases). However, the Mahé sample is limited to four shells and, although statistical significance is attained by these differences, the data are considered insufficient from which to draw reliable conclusions.

Body.— Uniform off-white in spirit specimens, red in life (Martens, 1898).

Anatomy.

Salivary gland.— Broad, bilobed; 5 × 2 mm.

Radula (fig. 3j).— Formula 29 + 1 + 29. Central tooth short, simple, lateral simple. Radula sac 10 mm long.

Table 2. *Edentulina moreleti* dimensions (mm).

	Height		Diameter		H/D		Whorls		N
	range	mean (sd)	range	mean (sd)	range	mean (sd)	range	mean	
Mahé	12.9-14.0	13.0 (0.17)	5.6-6.5	5.8 (0.17)	2.15-2.30	2.24 (0.05)	7.5-7.75	7.7	4
Silhouette	11.0-12.2	11.6 (0.30)	5.3-5.7	5.3 (0.15)	2.04-2.23	1.68 (0.59)	6.75-7.5	7.1	30
Total	11.0-14.0	12.0 (0.27)	5.3-6.5	5.4 (0.15)	2.04-2.30	1.79 (0.45)	6.75-7.75	8.8	34

Reproductive anatomy (figs 3h-i).— Spermoviduct enlarged near base into broad, muscular brood chamber 10 mm long. Spermatheca ovoid, 2 mm long; spermatheca duct narrow, 20 mm long. Penis elongate (16-18 mm), covered by sheath. Constriction between penis and epiphallus. Long epiphallus (15 mm); curved, terminal part attaching in terminal part of penis. Penial retractor muscle terminal. Penis not ornamented, epiphallus regularly ornamented with only weakly chitinized orange spinules. Spinules 0.2 mm long, hooked and bicuspid. Spermatophore long and simple (7.0 × 0.5 mm).

Distribution (fig. 5).— Mahé (Copolia, Mare aux Cochons, Morne Blanc, Morne Seychellois), Silhouette (Mare aux Cochons).

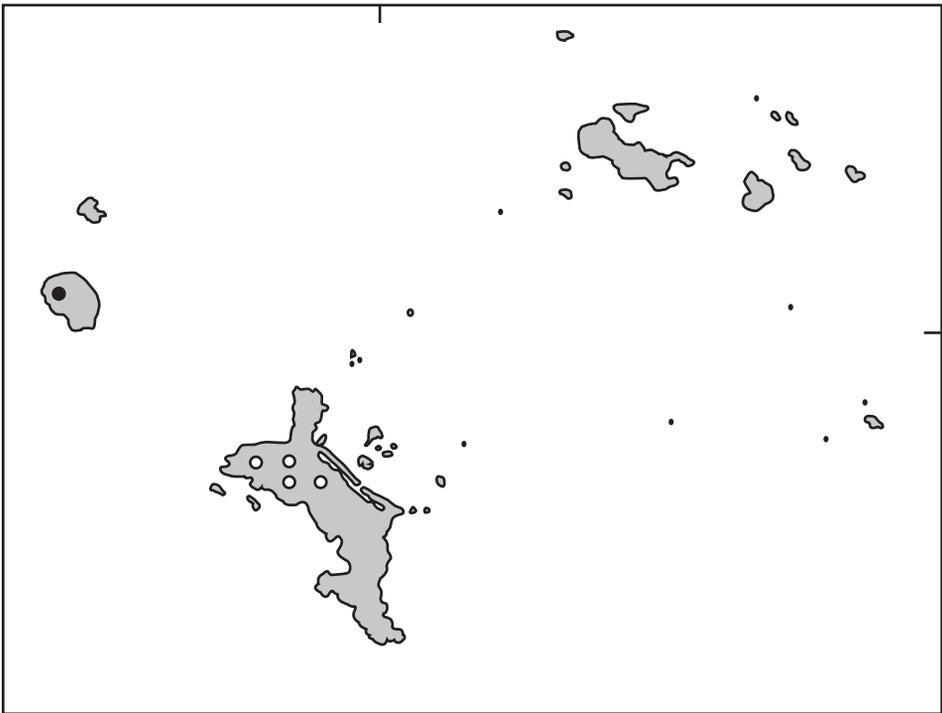


Fig. 5. Distribution of *Edentulina moreleti*.

Genus *Gulella* Pfeiffer, 1856

A poorly defined genus, speciose and almost certainly polyphyletic. Species referred to this genus are generally pupiform to elongate. Most species have a complex arrangement of apertural denticles and lamellae. Anatomically they may perhaps be characterized by having a short, club-shaped penis. Penial spinule arrangement is variable but all published dissections of *Gulella* note the presence of a large terminal spinule. Four Seychelles species have been referred to this genus, only one with reasonable certainty.

Distribution.— Africa south of the Sahara, Comoro Islands, Madagascar, Seychelles Islands, Mascarene Islands.

Gulella bicolor (Hutton, 1834)

Pupa bicolor Hutton, 1834: 86, 93.

Ennea (*Huttonella*) *bicolor*; Pfeiffer, 1856: 120.

Huttonella bicolor; Stoliczka, 1871: 169; Nevill, 1878: 6.

Ennea bicolor; Nevill, 1869: 64; Barnacle, 1962: 54; Lionnet, 1984: 240; Gerlach, 1987: 10, 2 col. figs.

Gulella bicolor; Naggs, 1989: 165-168.

Material studied.— Nine adults, 1 juvenile: Mahé (NPTS M1997.15), Praslin (NPTS M1997.16), "Seychellen" (SMF 169623/5, 169222/1; colln. C. Bosch, from dealer H. Rolle).

Type material.— Syntypes BMNH 1856.9.15.75, coll. Capt. T. Hutton, India 'Mirzapore and Agra'.

Shell (fig. 6a).— Shell elongate conical, slightly tapering with a blunt and flattened apex. Seven whorls with 1.5 nuclear whorls. Glossy, transparent; regular costulae on all whorls (8 mm⁻¹), strongly marked only at the sutures. Lip incrassate and reflected, four teeth in the aperture: a strong, almost vertical angular lamella, a prominent midlabral denticle, a small denticle to the left of the base and a prominent shelf-like columellar lamella.

Dimensions.— See table 3.

Table 3. *Gulella bicolor* dimensions (mm) of Seychelles specimens.

	Shell			whorls	Aperture		N
	height	diameter	H/D		height	width	
Range	4.3-6.8	1.5-2.3	2.57-3.37	6-8	1.1-1.7	0.9-1.5	10
Mean (sd)	5.94 (0.70)	1.91 (0.23)	3.12 (0.24)	7.3 (0.54)	1.51 (0.20)	1.32 (0.22)	

Body (pl. 1b).— Body, visceral mass, foot and tentacles vermilion.

Anatomy.

Radula.— Formula 9 + 1 + 9 (from Stoliczka, 1871).

Reproductive anatomy (fig. 7b) (from Stoliczka, 1871).— Spermoviduct and spermatheca elongate but simple in shape. Penis elongate; slightly inflated terminally. Presence of penis sheath or ornamentation not recorded. Epiphallus not distinct from penis. Penial retractor muscle terminal.

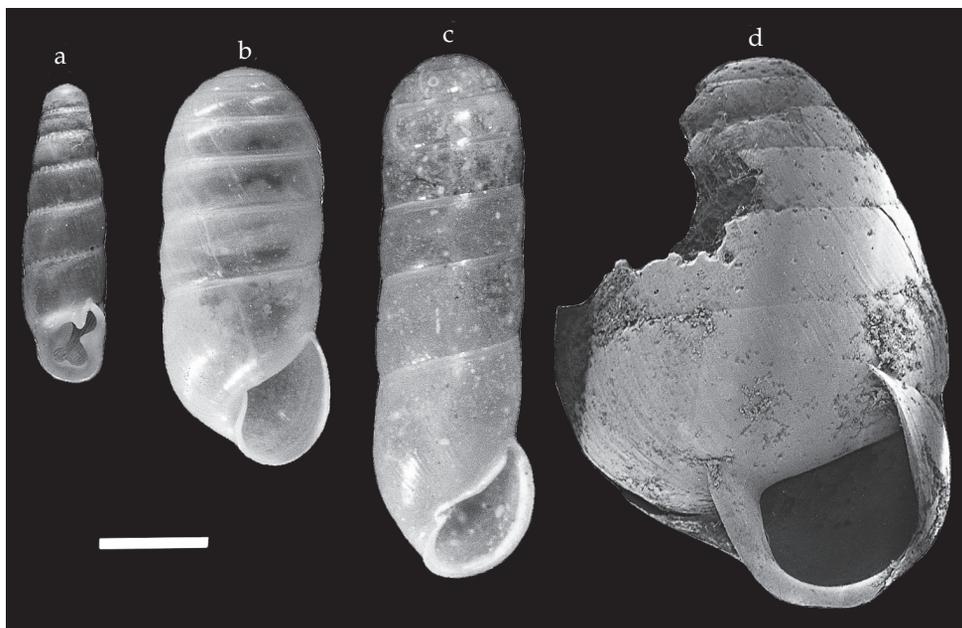


Fig. 6. Shells of *Gulella* species. (a) *Gulella bicolor* (SMF 169623/5) (scale bar 2 mm); (b) *Gulella gardineri* (BMNH 1910.6.20.12-14) (scale bar 1.6 mm); (c) *Gulella thomassetti* (BMNH 1910.6.28.11) (scale bar 0.85 mm); (d) *Gulella silhouettensis* (NPTS M1997.18) (scale bar 1 mm).

Distribution (fig. 8).— Mahé (Bel Air), Praslin (Grande Anse). A widely distributed species of unknown origin (probably Afro-Oriental), introduced to Seychelles in the mid 1800s (first recorded 1867 - Nevill, 1869). Also recorded from the Mascarenes.

'Gulella' silhouettensis Verdcourt, 1994

Gulella silhouettensis; Verdcourt, 1994: 141-143, figs 1-2.

Material studied.— Two adults, 2 juveniles (SMF 310151-2; NPTS M1997.17-18).

Type material.— Holotype SMF 310151; paratypes SMF 310152 (radula SMF 310153), NPTS M1997.18 (ex colln. J. Gerlach). All Mt. Dauban, Silhouette, 21.vii.1990, J. Gerlach leg.

Shell (fig. 6d).— Shell ovoid-conical with 7 convex whorls; rounded protoconch of 2.5 whorls. Sculpture restricted to some raised growth lines and very faint transverse striate near the suture, a few faint, widely spaced ribs near the aperture. Suture shallow, most pronounced on fifth whorl. Aperture edentulous, oblique, expanded and reflexed only on the lower margin, very thin at junction with whorl; columella thickened, angled at 45° to the axis; parietal callus very thin. Underside very convex, keeled at margin in juveniles; umbilicus closed (narrowly open in juveniles). Opaque creamy white, translucent in juvenile shells.

Dimensions.— See table 4.

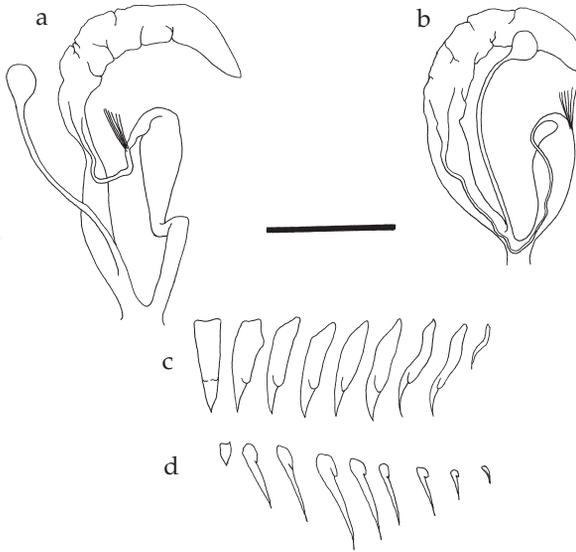


Fig. 7. Anatomy of *Gulella* species. (a) *Gulella gardineri*, reproductive anatomy (scale bar 3 mm); (b) *Gulella bicolor*, reproductive anatomy (scale bar 3 mm); (c) *Gulella silhouettensis*, radula (teeth C, 1, 2, 4, 5, 10, 15, 20, 25, 29); (d) *Gulella gardineri*, radula (teeth C, 1, 2, 5, 10, 15, 18, 20, 23, 25).

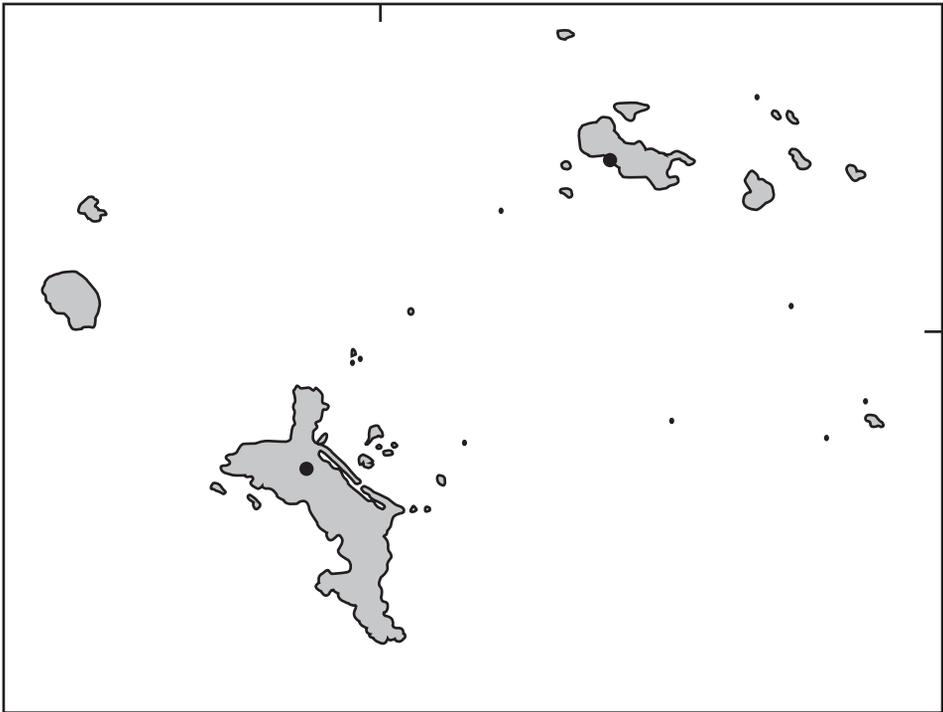


Fig. 8. Distribution of *Gulella bicolor* in the Seychelles group.

Table 4. '*Gulella silhouettensis* dimensions (mm).

	height	Shell			Aperture	
		diameter	H/D	whorls	height	width
Holotype (SMF 310151)	5.5	4.0	1.38	7	2.4	2.25
Paratype (NPTS M1997.18)	5.6	4.0	1.40	6.25	2.2	1.5

Body (pl. 1c).— Red with vermilion spots on the mantle, tentacles pink; foot pale grey, 5.5 mm long.

Anatomy.

Salivary gland.— Unknown.

Radula (fig. 7c).— Formula 29 + 1 + 29. Central tooth well developed. Radula sac 2 mm long; 44 V-shaped rows of teeth (Verdcourt, 1994).

Reproductive anatomy.— Unknown.

Distribution (fig. 9).— Silhouette; restricted to 7 ha of moss forest above 700 m on Mont Dauban.

Notes.— In the absence of data on the genital anatomy this species can only be provisionally placed in *Gulella*.

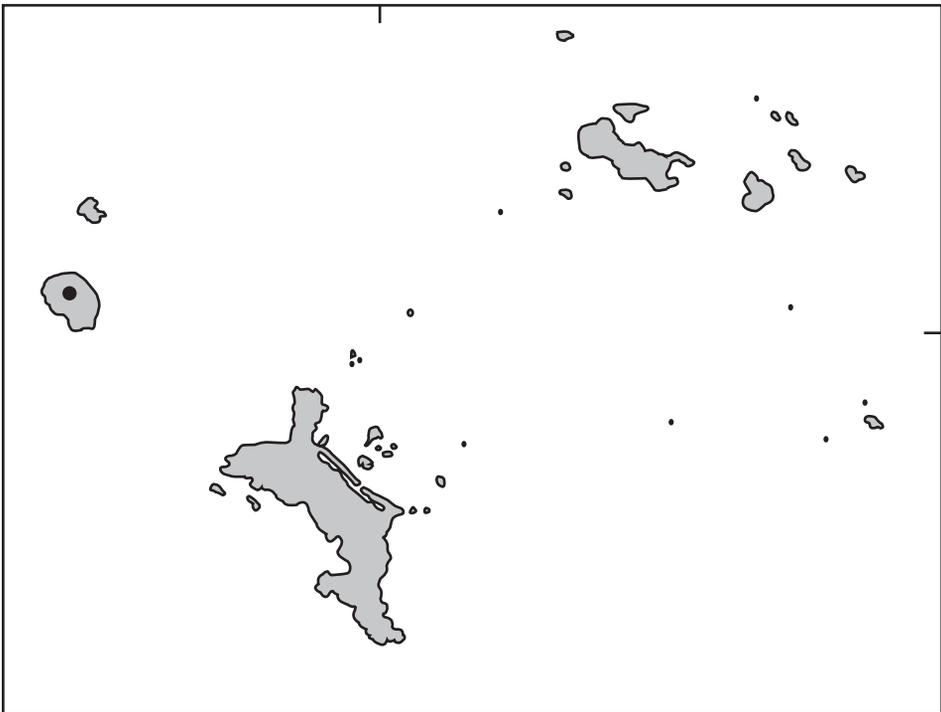


Fig. 9. Distribution of *Gulella silhouettensis*.

'Gulella' thomassetti (Sykes, 1909)

Ennea thomassetti Sykes, 1909: 57, 59-60, fig 2; Barnacle, 1962: 54; Lionnet, 1984: 240; Gerlach, 1987: 13, 2 col. figs.

Gulella thomassetti; Connolly, 1925: 259; Germain, 1934: 122.

Material studied.— Only a single specimen is known (BMNH 1910.6.28.11).

Type material.— Holotype BMNH 1910.6.28.11. Type locality: Mahé, Cascade.

Shell (fig. 6c).— Shell elongate, cylindrical with 7.5 whorls and 1.5 nuclear whorls. Glossy, colourless and translucent. Surface smooth with only irregular growth lines. Lip slightly reflected, columella twisted, umbilicus closed. A long, slanting parietal lamella borders the apex of the labrum, but does not contact the columella and is, therefore, completely free. This may be an autapomorphic character.

Dimensions.— See table 5.

Table 5. *'Gulella' thomassetti* dimensions (mm).

	Shell height	diameter	H/D	whorls	Aperture height	Last whorl width
Holotype	4.4	1.3	3.46	7.5	1.0	0.9

Body.— Unknown.

Anatomy.— Unknown.

Distribution (fig. 10).— Mahé, "Mountain Forest, Cascade." (Sykes 1909: 60).

Notes.— It should be noted that the original figure (Sykes, 1909: 60 fig. 2) is incorrect in measurements, shape and enlargement.

In the absence of data on the genital anatomy this species can only be provisionally placed in *Gulella*.

'Gulella' gardineri (Sykes, 1909)

Ennea gardineri Sykes, 1909: 57, 59, fig. 1 (includes var. a); Barnacle, 1962: 54 (includes var. A); Lionnet, 1984: 240; Gerlach, 1987: 13, 2 col. figs.

Gulella gardineri; Connolly, 1925: 259-260; Germain, 1934: 119, 122.

Material studied.— 40 adults, 14 juveniles; Mahé, Anonyme, Silhouette (BMNH 1937.12.30.259-260, 1825, unnumbered; MRAC 798.862; NPTS M1997.19-20, 1998.7); alc. and dry.

Material dissected.— Two adults, Silhouette (NPTS M1997.20a, 1998.7).

Type material.— Holotype BMNH 1910.6.28.12-14, coll. J.S. Gardiner, 1905; Mahé, Cascade forest.

Shell (fig. 6b).— Shell of 5-8 whorls with 2 nuclear whorls, glossy, translucent and colourless. Pupiform, whorls slightly rounded, no sutural ridge, apex rounded. Irregular growth lines present, no other sculpture. Mouth edentulous; lip slightly reflected and incrassate. Columella characteristically twisted; this twist is already present in

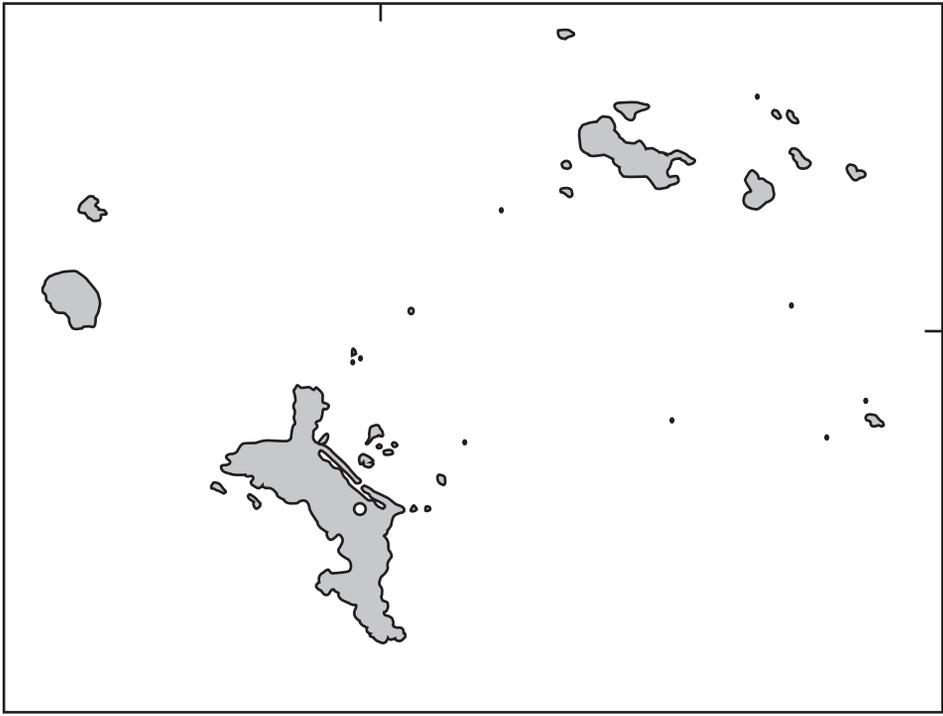


Fig. 10. Distribution of *Gulella thomassetti*.

early stages of the shell, such as a 2.7 mm long juvenile (3 whorls) from Mt. Sebert, Mahé (BMNH 1825). Umbilicus closed.

Dimensions.— See table 6. There is no significant geographical variation in measurements (t-test $P > 0.05$ for all comparisons).

Table 6. '*Gulella*' *gardineri* dimensions (mm).

	Height		Diameter		H/D		Whorls		N
	range	mean (sd)	range	mean (sd)	range	mean (sd)	range	mean	
Holotype	6.5	-	2.7	-	2.41	-	7.5	-	-
Mahé	4.6-6.8	5.3 (0.51)	2.0-3.0	2.4 (0.31)	2.02-2.50	2.28 (0.12)	6-8	6.7 (0.75)	24
Anonyme	4.2-4.4	4.3 (0.1)	2.0	2.0 (0)	2.10-2.20	2.15 (0.05)	5.5	5.5 (0)	2
Silhouette	4.0-6.3	5.4 (0.54)	1.8-2.7	2.4 (0.26)	2.00-2.52	2.20 (0.18)	6-8	6.8 (0.66)	12
Total	4.2-6.8	5.3 (0.52)	1.8-3.0	2.4 (0.28)	2.00-2.52	2.25 (0.20)	5.5-8	6.7 (0.74)	36

Body (pl. 1d).— Uniform off-white in spirit specimens, tentacles and dorsum of head red in life.

Anatomy.

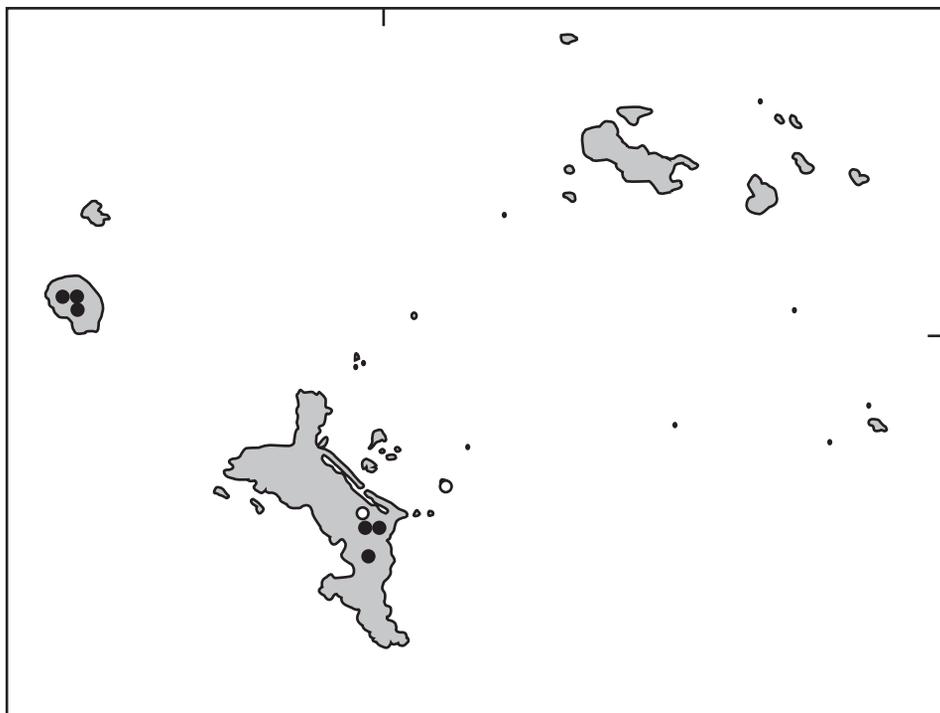


Fig. 11. Distribution of *Gulella gardineri*.

Salivary gland.— Unknown..

Radula (fig. 7d).— Formula $25 + 1 + 25$. Central tooth reduced, symmetrical. Laterals increase in size to the 10th tooth, then reduce. The 3 outer marginals are reduced. All laterals and marginals needle-shaped.

Reproductive anatomy (fig. 7a).— Base of spermoviduct elongate (6 mm), slightly inflated. Spermatheca not located. Penis elongate at base, becoming broad distally (6 mm). Penis sheath absent. Long, narrow epiphallus (3 mm long). Penial retractor muscle terminal. The distal, inflated part of the penis is ornamented with small spinules, these may be weakly or fully chitinized, measuring 0.03 mm long. These are regularly arranged and are uniformly simple in shape. The lower part of the penis bears only weakly developed papillae.

Distribution (fig. 11).— Mahé (Cascade, Mt. Sebert, Mt. Alphonse, Chateau Margot, La Réserve), Anonyme, Silhouette (Jardin Marron, Mon Plaisir, *Pisonia sechellarum* forest, Morne Dauban, Gratte Fesse).

Notes.— Attention should be drawn to the incorrect measurements given by Sykes (1909: 59), viz. 6.0×2.6 mm, which gives an H/D of 2.31; his figure gives an H/D of 2.16, the enlargement is also incorrect.

Sykes (1909) also records a "Var. a. Smaller and narrower in proportion" from Cascade Forest, Mahé. There are two shells of this variety from Anonyme in the Connolly collection (BMNH 1937.12.30.259-260) labelled "forma minor". Connolly (1925: 260) recorded almost exactly the same type of shells from Silhouette (4.3×2.0 mm,

H/D 2.15); there is also a shell of this form from Silhouette in the NPTS. Obviously dwarf forms occur throughout the range of the species. There are no noticeable gaps in the series of measurements and there is no clear size or proportionate distinction between large adults of "var. a" and small typical shells. Comparisons of the percentage of "var. a" (defined as adults below 4.5 mm high) suggests that there are differences between populations (56% from Mahé, 10% from Silhouette), however, the samples available are too small to be reliable (N = 27 and 10 respectively).

Although the pupiform shape of the shell resembles that of many *Gulella* species this is not a typical member of that genus. The edentulous aperture is uncommon in *Gulella* and the reproductive anatomy is notably distinct; the penis is unusually elongate and the large terminal spinule probably typical of the genus is absent. These differences indicate that '*G' gardineri*' is distinct at either generic or subgeneric level. However, until the anatomy of the type of *Gulella* [*G. menkeana* (Pfeiffer, 1853)] is determined this species has to be retained in the genus provisionally.

Genus *Streptosteles* Dohrn, 1866

This is a genus of many similar, poorly defined nominal species. All have elongate, slender shells with convex whorls ornamented with radial ridges. The surface is usually glossy and colourless. The aperture has a reflected, thickened lip and a few or no denticles. The reproductive anatomy is poorly known (Adam, 1965: 16).

Distribution.— Tropical Africa.

Streptosteles acicula (Morelet, 1877)

Ennea acicula Morelet, 1877: 339, pl. 13 fig. 3.

Streptosteles (Raffraya) maheensis Connolly, 1925: 258.

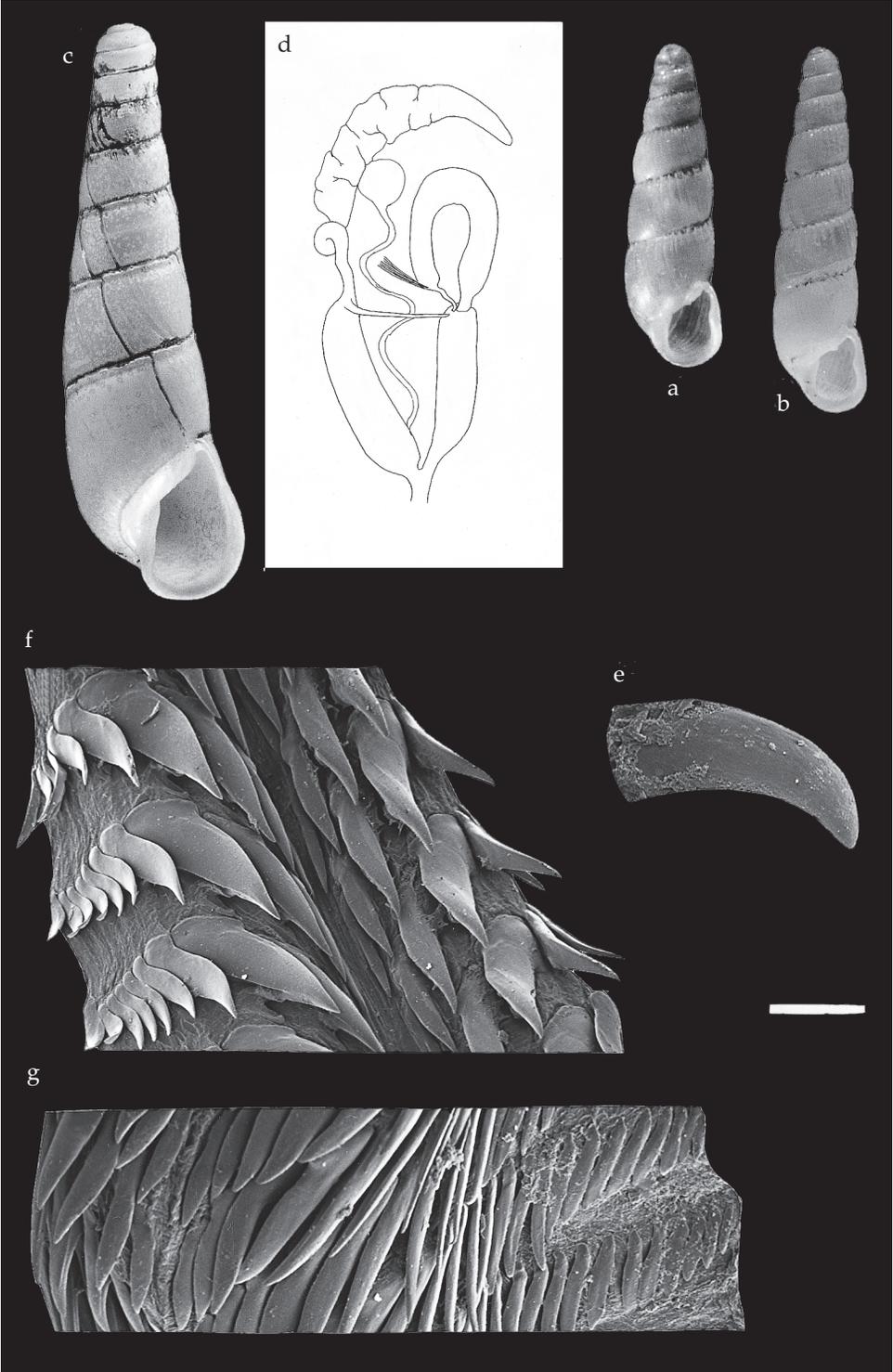
Streptosteles acicula; Barnacle, 1962: 54; Lionnet, 1984: 240; Gerlach, 1987: 11, 2 col. figs.

Material studied.— Seychelles - 29 adults; Mahé (BMNH Connolly, 1925, BMNH 2110; NPTS M1997.21), Silhouette (NPTS M1997.22). Aldabra (O. Griffiths colln.). Amirantes - Poivre (O. Griffiths colln.). Madagascar - 2 adults; Nossi Bé (SMF 136566/2). Mayotte - 4 adults (SMF 169236/1, 136567/2; RMNH ex. H.B. Preston). Mauritius - 9 adults (NPTS M1997.23; Madge (1939); RMNH Venmans colln., ex Madge colln.).

Type material.— Holotype of *S. acicula*: BMNH 93.2.4.21-2. Holotype of *S. maheensis*: Natal Museum (Pietermaritzburg, South Africa); paratype in BMNH (1937.12.30.208).

Shell (figs 12a-b).— Shell elongate, long and slender, gently tapering to a blunt apex. 7-8 whorls with 1.5 nuclear whorls. Glossy, although often obscured with dirt, colourless and translucent. Whorls slightly rounded with widely spaced regular radial costulae (9 mm⁻¹) and irregular faint growth lines. The radial costulae are most prominent at the sutures. Lip incrassate and reflected, thickened to form a small labral denticle. There are two parietal processes near the apex of the aperture, a superficial outer and a smaller inner one just below the former, in addition to an insignificant shelf-like columellar lamella. In a paratype of *S. maheensis* (BMNH 1937.12.30.208) the parietal processes are fused to form a lamella running into the aperture.

Dimensions.— See table 7. Measurements of the different island populations were



compared using t tests. These show that the Seychelles shells are significantly larger and proportionately broader than Mascarene and Comoros shells (height $t = 3.80$, diameter $t = 3.23$, H/D $t = 2.14$, $P < 0.05$ for all). These differences indicate that the granitic islands Seychelles population can be recognized as a distinct subspecies for which the name *Streptostele acicula maheensis* (Connolly, 1925) is available. Specimens from the southern coralline islands appear to be closer to the Comoros shells. Unfortunately material is insufficient to determine whether these represent a distinct sub-specific form.

Table 7. *Streptostele acicula* dimensions (mm).

		height	diameter	H/D	whorls	N
Holotype		4.6	1.4	3.25	7.25	1
<i>S. maheensis</i> holotype		5.9	1.5	3.93	8	1
Mahé	range	4.7-6.5	1.3-2.0	2.27-4.46	6.8	20
	mean (sd)	5.3 (0.73)	1.7 (0.24)	3.11 (0.49)	7.5 (0.60)	
Silhouette	range	4.8-5.1	1.8-1.9	2.67-2.68	7-8	2
	mean (sd)	5.0 (0.15)	1.9 (0.05)	2.68 (0.01)	7.5 (0.50)	
GRANITIC SEYCHELLES total	range	4.7-6.5	1.4-2.0	2.27-4.46	6-8	22
	mean (sd)	5.3 (0.57)	1.7 (0.22)	3.16 (0.43)	7.4 (0.59)	8
Aldabra	range	3.9-4.5	1-1.1	3.55-4.19	7	
	mean (sd)	4.1 (0.21)	1.1 (0.05)	3.77 (0.22)	7(0)	
Poivre	range	4.8-5	1.2	4-4.17	7	3
	mean (sd)	4.9 (0.12)	1.2 (0)	4.11 (0.10)	7 (0)	
SOUTHERN SEYCHELLES total	range	3.9-5	1-1.2	3.55-4.23	7	11
	mean (sd)	4.3 (0.44)	1.1 (0.06)	3.77 (0.25)	7 (0)	
MADAGASCAR	range	5.3	1.5	3.53	7.5	2
	mean (sd)	5.3 (0)	1.5 (0)	3.53 (0)	7.5 (0)	
COMOROS	range	4.5-5.7	1.3-1.4	3.25-4.11	7.25-8	5
	mean (sd)	4.9 (0.42)	1.4 (0.05)	3.61 (0.24)	7.4 (0.30)	
MASCARENES	range	4.1-5.0	1.1-2.1	2.52-3.85	7-8	13
	mean (sd)	4.6 (0.42)	1.4 (0.27)	3.4 (0.42)	7.25 (0.38)	

Body (pl. 1e).— Uniform pale yellow.

Anatomy.— Unknown.

Distribution (fig. 13).— Mahé (Victoria, Bel Air, Beau Vallon, Mare Anglaise), Silhouette (La Passe). Also known from Aldabra, Poivre (Amirantes), Mauritius, Réunion, Rodriguez, Anjouan, Mayotte, Nossi Bé (Madagascar).

Notes.— So far the species has been identified on the Comoros, Nossi Bé (Madagascar), Seychelles, Amirantes, Aldabra, and Mascarenes. The long history in the western Indian Ocean resembles a natural distribution pattern. A host of very similar

Fig. 12. Shells of *Streptostele* and *Stereostele* with anatomical details of the latter. (a-b) *Streptostele acicula* (scale bar 1.3 mm), (a) *S. a. acicula* (BMNH 1893.2.4.21-2), (b) *S. acicula maheensis* (BMNH 1937.12.30.208); (c-g) *Stereostele nevilli*, (c) shell (MRAC 798.849) (scale bar 3 mm), (d) reproductive anatomy (scale bar 2 mm), (e) spinule (scale bar 0.025 mm), (f) *S. nevilli parvidentata* radula (scale bar 0.03 mm), (g) *S. n. nevilli* radula (scale bar 0.01 mm).

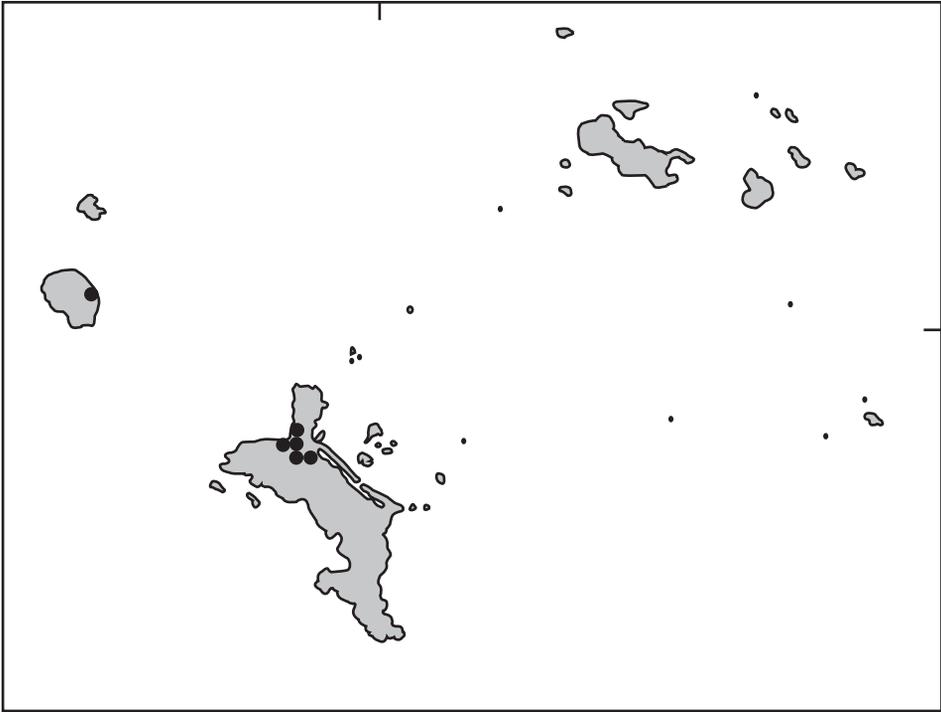


Fig. 13. Distribution of *Streptostele acicula* in the Seychelles group.

species of the subgenus *Raffraya* has been described from continental Africa. Some of these have very wide distributions, such as *S. (R.) herma* Connolly, 1912, which occurs from the Kruger National Park, Transvaal (now Mpumalanga and Northern Province), to Shimoni in Kenya (Van Bruggen, 1967; Verdcourt, 1978), a distance of roughly 2500 km in a straight line. This is comparable to the size of the natural range of *S. (R.) acicula*. Some of these poorly discriminated African species (e.g. see key in Verdcourt, 1978: 24) may be synonyms of the species under discussion. A revision of the African species should take into account those occurring on the islands of the western Indian Ocean.

Genus *Stereostele* Pilsbry, 1919

Stereostele was proposed by Pilsbry (1919) (as a subgenus of *Streptostele* Dohrn, 1866) without a description. The genus is monotypic, being restricted to *Ennea (Elma) nevilli* Adams, 1868, from the Seychelles islands.

The first proper description is that of Thiele (1931: 732): “Schale glatt, Spindel deutlich gedreht, aber nicht abgestutzt, Mundrand etwas erweitert.” Zilch (1960: 568) raised *Stereostele* to full generic status and provided a fairly long diagnosis: “Gehäuse ziemlich festschalig, glänzend, schlank, getürmt kegelförmig; 9 schwach gewölbte Umgänge, nur mit undeutlichen Anwachsstreifen, fast glatt; Endwindung unten gerundet, ungenabelt; Mündung senkrecht, eiförmig; Mundrand schmal umgeschla-

gen, dünn; Spindel etwas gewunden in dass Innere ziehend, unten mit einer gerundeten Ecke in den Basalrand übergehend, nicht abgestutzt." A free translation of this is as follows: "Shell comparatively solid, shining, slender, conically turreted; 9 weakly convex whorls, with only vague growth striae, almost smooth; body whorl rounded at the base, no umbilicus; aperture perpendicular, ovate; labrum narrowly reflected, thin; columella slightly twisted towards the inside, at its base smoothly merging into the labrum, not truncate."

We may add to this diagnosis that *Stereosteles* also differs from allied genera in its comparatively large size (17.0-20.1 mm; *Varicosteles* Pilsbry, 1919, 11.6-18.0 mm; *Streptosteles* 2.8-26.0 mm, but usually only up to c. 15 mm); the shell is also much more solid than in *Streptosteles*. Further details are given in the species description.

Distribution.— Seychelles, endemic.

Stereosteles nevillei (Adams, 1868)

Ennea (Elma) nevillei Adams, 1868: 291, pl. 28 fig. 12; Nevill, 1869: 63.

Streptosteles (Elma) nevillei; Martens in Möbius, 1880: 205; Martens, 1898: 14-15, pl. 2 figs 9-12.

Streptosteles (Elma) nevillei var. *dubia* Wiegmann, 1898: 52, pl. 3 fig. 6, pl. 4 fig. 7.

Streptosteles (Stereosteles) nevillei; Pilsbry, 1919: 183; Thiele, 1931: 732.

Stereosteles nevillei; Moellendorff & Kobelt, 1904: 338, pl. 41 figs 3-4; Zilch, 1960: 568.

Streptosteles nevillei; Sykes, 1909: 62; Barnacle, 1962: 54; Lionnet, 1984: 240; Gerlach, 1987: 15, 2 col. figs.

Material studied.— 18 adults and 10 juveniles Mahé (MRAC 798.870, 849, 911; alc. and dry; BMNH unnumbered - E.R. Sykes colln. 1905/8; NPTS M1997.24), 20 adults, 5 juveniles Silhouette (MRAC 798.833, 957; BMNH 2268.06.1.1, 1978.1.28.70; NPTS M1997.25; alc. and dry), 2 adults La Digue (MRAC 798.821; alc. and dry; O. Griffiths colln. A1502, 1 damaged shell).

Material dissected.— Mahé (MRAC 798.870); La Digue (MRAC 798.821); Silhouette (NPTS M1997.25a).

Type material.— Syntypes (BMNH 1978.1.28.70) "Selected from the collection of the late Henry Adams", "Purchased of Mr. Geale". Type locality: Silhouette (Nevill 1869). The largest shell has been selected as lectotype.

Shell (fig. 12c).— Shell elongate, long and slender, gently tapering to a blunt and slightly bulbous apex; 8-9 whorls with 2 nuclear whorls, all flattened and smooth with only faint growth lines and some well defined old peristomes; a slight sutural ridge is present. The long axis of the shell is not always completely straight; some specimens are slightly curved to the right. Aperture edentulous; labrum slightly incrassate and reflected; umbilicus closed. Columella distinctly twisted. The thin periostracum is pale to olive brown.

Dimensions.— See table 8.

Body (pl. 1f).— Body and tentacles dark purple-grey, sole reddish brown. Dorsal part of tail pink, flattened with a very narrow medial longitudinal groove. Mantle purple, with irregular vermilion patches. Mantle border reddish brown. The pneumostome is fringed by one anterior and one posterior mantle lobe.

Anatomy.

Salivary gland.— Elongate oval, 5 × 3 mm.

Radula (figs 12f-g).— Radula formula varies on different islands; there is no central tooth. Populations on Mahé and La Digue have a radula formula of 16 + 0 + 16,

Table 8. *Stereostele nevilli* dimensions (mm).

	Height		Diameter		H/D		Whorls		N
	range	mean (sd)	range	mean (sd)	range	mean (sd)	range	mean	
Lectotype	20.1	-	6.0	-	3.35	-	9	-	1
Paralectotype	19.3	-	6.0	-	3.22	-	8	-	1
Mahé	14.0-20.0	17.1 (2.33)	4.7-6.4	5.5 (0.41)	2.71-3.63	3.08 (0.33)	8-9.5	8.1 (0.70)	17
La Digue	18.7	-	5.7	-	3.28	-	8.25	-	1
Silhouette	14.4-20.1	17.6 (1.37)	4.5-6.2	5.5 (0.29)	2.94-3.43	3.25 (0.13)	7-9	8.3 (0.60)	20
Total	14.0-20.1	17.4 (1.83)	4.5-6.4	5.5 (0.35)	2.71-3.63	3.20 (0.22)	7-9	8.2 (0.65)	38

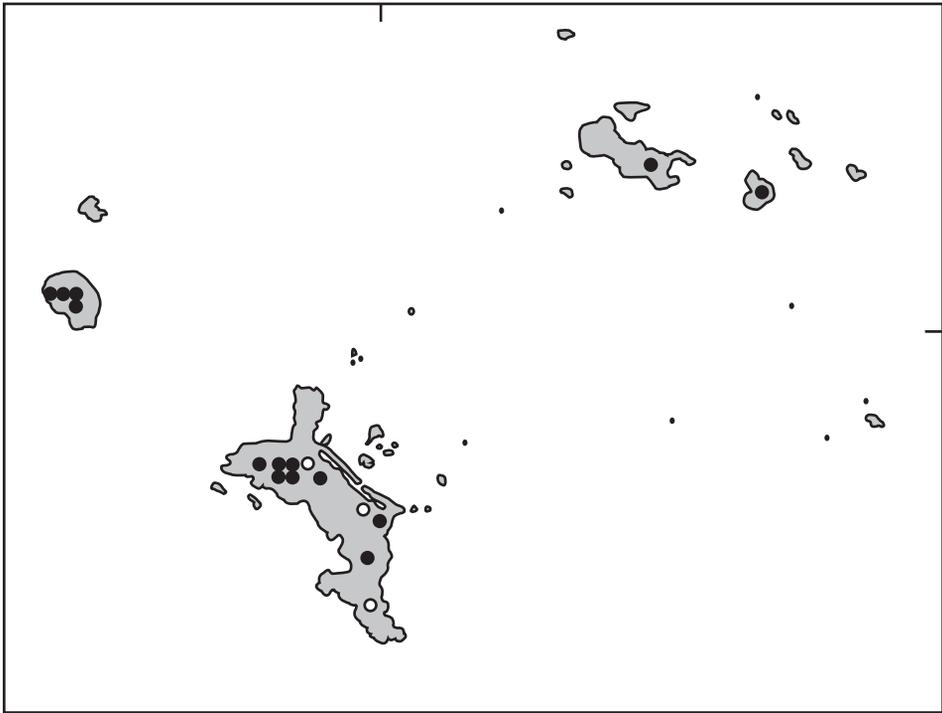
Silhouette populations have the formula 21 + 0 + 21. The reduced central tooth reported for 'Var. *dubia*' (Wiegmann in Martens & Wiegmann, 1868) has not been traced in any of the specimens examined. Wiegmann further cites the radula formula as 23 + 0 + 23 for this variety and 16 + 0 + 16 for the typical variety, both from Mahé. Examination of both forms from Mahé and Silhouette shows that radula formulae are constant within islands and not related to shell morph. Consequently it is probable that the 'Var. *dubia*' specimen was incorrectly labelled and was in fact collected on Silhouette. The shape of the first 6 laterals differs on different islands; conical on Silhouette and flattened on Mahé and La Digue. The next 4 are needle-shaped and the remaining 6-12 reduced.

Reproductive anatomy (figs 12d-e).— Spermoviduct broadened basally; 8-11 mm long. Spermatheca spherical, 3 mm long; spermatheca duct narrow, 20 mm long. Penis elongate (3-4 mm), distal half strongly curved and attached by vas deferens to the penis sheath which is present on the lower half. Epiphallus absent. Penis constricted at attachment of sheath. Penial retractor muscle terminal. Terminal half of penis regularly ornamented with chitinous, black spinules which are visible through the penis wall. A small number of spinules are present near the base. Spinules 0.01 mm long. Vas deferens short.

'Var. *dubia*' is described as having a short penis, long vas deferens and hooked spinules with 3-5 cusps. The differences in penis size and shape are ascribable to the immaturity of the specimen described. The curvature of the spinules in 'Var. *dubia*' is also found in Silhouette specimens, although they are monocuspid. This is further evidence that 'Var. *dubia*' refers to animals from Silhouette, and not from Mahé as reported by Wiegmann (1898).

Distribution (fig. 14).— Mahé (Mare aux Cochons, Morne Blanc, Congo Rouge, Morne Seychellois, Chateau Margot, Copolia, Cascade, Mt. Sebert, La Réserve, Pointe Capucin), Silhouette (Jardin Marron, Mon Plaisir, *Pisonia sechellarum* forest, Mare aux Cochons, Gratte Fesse), Praslin (Vallée de Mai), La Digue (Belle Vue). The record of a fossil shell from Aldabra (Taylor et al., 1979) refers to a wrongly identified subulinid (see note below).

Note.— *S. nevilli* has often been confused with subulinids, particularly *Subulina octona* (Bruguère, 1789) (e.g. Taylor et al., 1979; Edlinger, 1988). This species, howev-

Fig. 14. Distribution of *Stereostele neville*.

er, has a slightly but distinctly truncate columella and the labrum is not thickened. In addition, adult *Stereostele neville* are broader ($H/D < 3.25$) than similarly sized subulinids which have at least one more whorl, a less coarse and dome shaped apex, and more convex whorls. Shells compare as follows:

<i>Stereostele neville</i>	20.1 × 6.2 mm, H/D 3.24, 9 whorls
	19.3 × 6.0 mm, H/D 3.22, c. 8 whorls
<i>Subulina octona</i>	21.9 × 4.8 mm, H/D 4.56, 10 whorls
2, Java, Batavia (= Jakarta), RMNH	19.2 × 4.4 mm, H/D 4.36, 9.25 whorls

Stereostele neville neville (Adams, 1868)

Type material.— The lectotype for the species is the lectotype specimen for this subspecies (BMNH 1978.1.28.70).

Shell and body.— As for species description above.

Dimensions.— See table 8, not significantly different from the other populations.

Radula.— Formula 21 + 0 + 21. First 6 laterals conical.

Reproductive anatomy.— As for the species description above.

Distribution.— Silhouette.

Stereostele nevilli parvidentata subsp. nov.

Type material.— Holotype MRAC 'loc. 18' (Morne Blanc, 23.VI.1972, coll. P.L.G. Benoit & J.-J. Van Mol), 2 paratypes MRAC 798.870 (Morne Blanc, 23.vi.1972, coll. P.L.G. Benoit & J.-J. Van Mol), NPTS M1997.24a (Morne Blanc, 22.vii.1988, coll. J. Gerlach). Type locality: Morne Blanc, Mahé.

Shell and body.— As for species description above.

Dimensions.— See table 8, not significantly different from the Silhouette population.

Radula.— Formula 16 + 0 + 16. First 6 laterals flattened.

Reproductive anatomy.— As for species description above.

Distribution.— Mahé (Mare aux Cochons, Morne Blanc, Congo Rouge, Morne Seychellois, Chateau Margot, Copolia, Cascade, Mt. Sebert, La Réserve, Pointe Capucin), La Digue (Belle Vue). The Praslin population probably also belongs to this subspecies but no spirit material is available from which to determine the radula formula.

Genus *Gonaxis* Taylor, 1877

The shell of *Gonaxis* is distinctly distorted with the discoidal juvenile whorls displaced to one side by the broader last two whorls of the adult shell. Sculpture is typically restricted to a coarse costulation. The aperture is usually edentulous; the labrum is usually slightly reflected. This genus comprises several distinct forms and is probably polyphyletic. A full revision is required before the true generic limits can be defined.

Distribution.— Tropical Africa, Seychelles (one species widely distributed by man in the Indo-Pacific).

Subgenus *Macrogonaxis* Bequaert & Clench, 1936*Gonaxis (Macrogonaxis) quadrilateralis* (Preston, 1910)

Ennea quadrilateralis Preston, 1910: 527, pl. 7 fig. 2; Schouteden, 1936b: 499; Adam, 1971: 57.

Gonaxis quadrilateralis; Verdcourt, 1960: 259; Mead, 1961: 134, fig. 3; Verdcourt, 1961: 9, 15, 17, 20, fig. 10; Lionnet, 1971: 90, 122; Ranaivosoa, 1971a: 342, 344; Ranaivosoa, 1971b: 360, 365; Chang, 1975: 10, 12, 20, fig. 2; Mead, 1979: 13, 15, 24, 46, 57, 60, 64, 98.

Gonaxis (Macrogonaxis) quadrilateralis; Bequaert & Clench, 1936: 265, 269; Adam, 1965: 6-8, fig. 1 (radula, identification questionable because of immaturity of specimen); Verdcourt, 1983: 229.

Gonaxis quadrilateris (sic); Barnacle, 1962: 53; Lionnet, 1984: 240; Gerlach, 1987: 10, 3 col. figs

Eustreptaxis quadrilateralis; Zilch, 1961: 81.

Streptaxis (Gonaxis) Craveni E.A. Smith var. *minor* Germain, 1918: 252.

Material studied.— 18 adults, 8 juveniles Mahé (dry and spirit material MRAC (duplicates in RMNH) MRAC 798.745, 754-5, 775, 915, 923; NPTS M1997.26; alc. and dry); 6 adults St. Anne (NPTS M1997.27); 5 adults, 2 juveniles Kenya.

Material dissected.— Two adults, 2 subadult, 1 juvenile Mahé (NPTS M1997.26).

Type material.— Holotype MRAC 16940 (Kenya, 'Shimbi Hills', ex H.B. Preston; R. Kemp leg.); paratypes BMNH 1911.10.12.160-161 and 1937.12.30.84-85, RMNH (same data as holotype). Only 1 specimen mentioned in original description. There is also a specimen labelled 'syntype' at SMF (SMF 5078).

Shell (fig. 15e).— Shell thin, inflated and somewhat distorted; juvenile shell helioid, adult whorls becoming displaced to the right. 5-6 whorls with 2 nuclear whorls; first 2 smooth, the remainder with very strong, regular growth lines (3 mm^{-1}). Surface glossy, opaque and translucent or white. Umbilicus open, narrow (10% of underside), broader in juveniles (20% of underside). Lip slightly incrassate, reflected, not thickened, receding apically in profile; aperture edentulous. There is no periostracum.

Dimensions.— See table 9.

Table 9. *Gonaxis quadrilateralis* dimensions (mm).

	Height		Diameter		H/D		Whorls		N
	range	mean (sd)	range	mean (sd)	range	mean (sd)	range	mean	
Holotype	26.3	-	17.9	-	1.47	-	6.25	-	1
Mahé	23.2-26.1	24.5 (0.82)	15.5-17.0	16.3 (0.58)	1.41-1.65	1.50 (0.07)	5.75-6.5	6.10	18
St. Anne	23.3-25.4	24.5 (0.68)	15.2-20.3	17.8 (0.41)	1.25-1.53	1.38 (0.02)	5.75-6	6.04	6
Africa	24.0-26.3	25.0 (1.13)	15.5-17.9	16.5 (0.92)	1.41-1.65	1.52 (0.08)			6
Zanzibar	16.0	-	12.0	-	1.33	-			1
Total	23.2-26.3	23.9 (0.89)	15.5-17.9	16.0 (0.66)	1.4-1.65	1.47 (0.06)			31

Body (pl. 1g).— Uniform bright orange-yellow.

Anatomy.

Salivary gland.— Bilobed, elongate.

Radula (fig. 15g).— Formula $17 + 1 + 17$. Central tooth asymmetrical. Laterals 1-6 simple, 7-10 broad, 11-16 short and fine, 17 rudimentary.

Reproductive anatomy (fig. 15f).— Spermatheca broadened basally into a chamber 10-15 mm long. Spermatheca oval; duct long and thin; attached to broadened base of oviduct near genital atrium. Penis broad and simple, slightly expanded terminally; retractor muscle terminal; no epiphallus. Terminal half of penis irregularly ornamented with short orange spinules. Spinules simple, 0.25 mm long, weakly chitinized. Unchitinized spinules present in sexually mature 11 mm diameter juvenile.

Distribution (fig. 16).— Mahé, all lowland sites to 300 m above sea level, Cerf, St. Anne. The species was introduced from Kenya in 1958 to control the two pest species *Achatina fulica* Bowdich, 1822, and *A. immaculata* Lamarck, 1822 [= *A. panthera* (Férussac, 1832)] (Lionnet, 1971). It was released on Mahé, South-East, Praslin, La Digue and Cerf islands and is still present on Mahé (including South-East Island which is now joined to Mahé) and Cerf. It has also been located on St. Anne. It has been reported to have exercised "effective" control of *Achatina* on Cerf; however, observations by the senior author in January 1996 demonstrate that this is incorrect: *Achatina* species remain abundant on Cerf. The species has been widely introduced in the failed biological control of *A. fulica* (vide Mead, 1979). In contrast to its wide (artificial) distribution outside Africa, the natural range of *G. quadrilateralis* appears to be very restricted (recorded from the Shimba Hills and Kwale in Kenya and from Zanzibar).

Notes.— The Mahé and St. Anne material agree well with the type, particularly as regards the costulate sculpture, which is very marked in the type. Germain (1918) described a small and squat Zanzibar specimen (16.0 × 12.0 mm, H/D 1.33) as *Strep-*

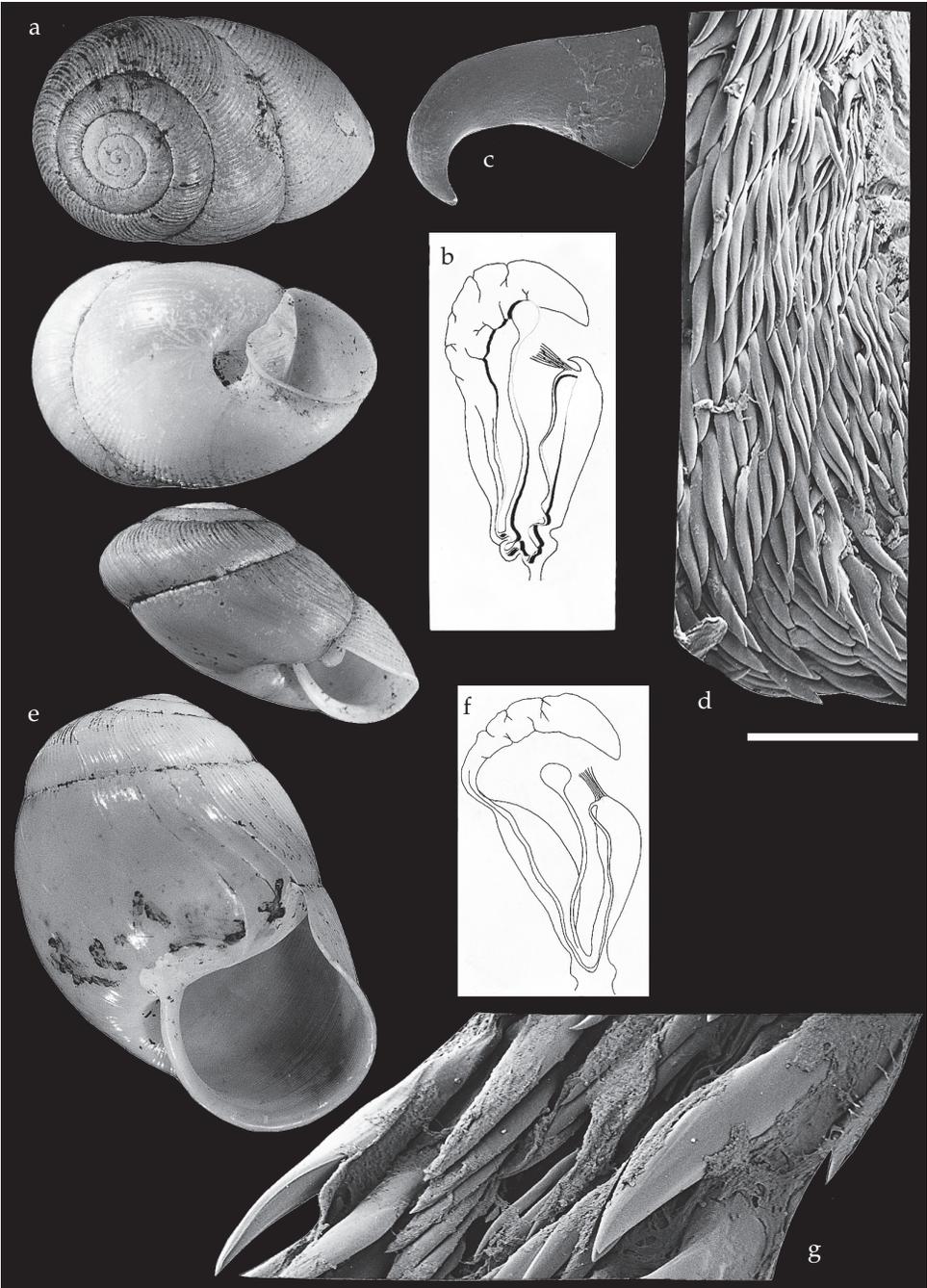


Fig. 15. a-d. *Gonaxis* species. (a-d) *Gonaxis souleyetianus*, (a) shell (MRAC 798.811) (scale bar 6 mm), (b) reproductive anatomy (scale bar 10 mm), (c) spinule (scale bar 0.04 mm), (d) radula (scale bar 1.75 mm); (e-g) *Gonaxis quadrilateralis*, (e) shell (MRAC 798.755) (scale bar 6 mm), (f) reproductive anatomy (scale bar 10 mm), (g) radula (scale bar 0.3 mm).

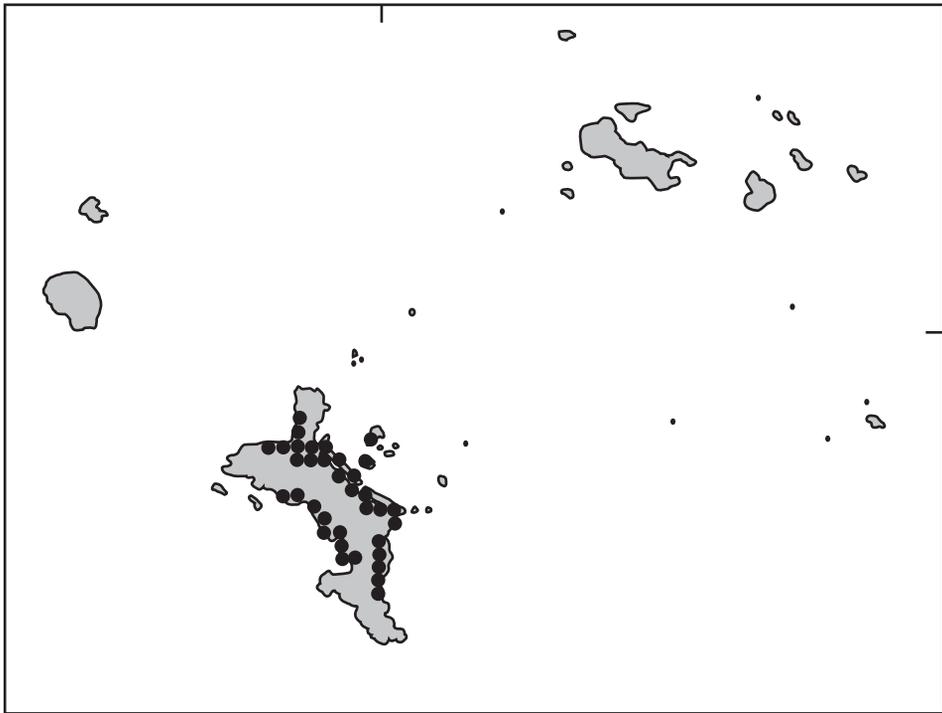


Fig. 16. Distribution of *Gonaxis quadrilateralis* in the Seychelles group.

taxis (*Gonaxis*) *craveni* var. *minor*. In case the Zanzibar populations are separated on a subspecific level, this name would be available. The species is superficially similar to the east African *G. kibweziensis* (E.A. Smith, 1894), which is distinguishable by its much smaller maximum length. Further spirit material from East Africa is required before the taxonomic distinctions between *G. quadrilateralis*, *G. kibweziensis* and the Zanzibar population can be resolved.

Sexual maturity is apparent in 'juvenile' shells. Microscopic, immature genitalia were detected in one specimen 9.0 mm in diameter (3.25 whorls). Almost fully developed genitalia were present in a 'juvenile' of 11.3 mm (4 whorls), these were approximately half the size of adult genitalia and penis spinules were present only as papillae; however, this specimen was gravid with 3 spherical shelled eggs measuring 2.5 mm diameter. Sexual maturity prior to the attainment of the adult shell has not been reported for any other streptaxid.

A species s.n. '*Gonaxis*' s.s.

'*Gonaxis*' *souleyetianus* (Petit, 1841)

Helix Dussumieri (part) Dufo 1840: 199; Pfeiffer, 1841: 11.

Helix Souleyetiana Petit, 1841: 99.

Streptaxis Souleyetianus; Pfeiffer, 1841: 8; Philippi, 1847: 130, pl. 8 fig. 6; Pfeiffer, 1846: pl. 102 figs 21-23; Nevill, 1868: 260; Nevill, 1869: 69.

Gonaxis souleyetianus; Kobelt, 1905: 17, pl. 43 figs 16-19.

Streptaxis souleyetianus; Sykes, 1909: 60; Barnacle, 1962: 54. Lionnet, 1984: 240; Gerlach, 1987: 9, 3 col. figs; Edlinger, 1988: 390.

Material studied.— 11 juveniles, 134 adults; Mahé (MRAC 798.750, 756-757, 763, 768, 777, 779, 811, 828, 847, 851, 858, 866, 895, 901, 906, 908, 916, 919, 921, 927, 948, 949; alc. and dry, duplicates in RMNH); NPTS M1997.28), Silhouette (MRAC 798.759, 776, 834, 840, 863, 871, 952, 960, 961; alc. and dry; NPTS M1997.29); Praslin (MRAC 798.842, 888, 932; alc. and dry; NPTS M1997.30), Curieuse (MRAC 798.860, alc.); La Digue (MRAC 798.822-3, 882; alc. and dry; NPTS M1997.31; O. Griffiths colln A1502).

Material dissected.— Six adults from Mahé, Silhouette and La Digue (NPTS M1997.28-9, 31; MRAC 798.822, 906). A spirit specimen from Praslin (MRAC 798.842) was contracted and not suitable for dissection.

Type material.— Petit gives no details of the collector of the type specimens and provides only a vague locality: "habite, dit-on, une des les Seychelles" (Petit, 1841). His measurements are 13 × 9 × 6 mm. The specimen should be in the Paris museum but according to Dr. S. Tillier (in litt., 4.vii.1980) it could not be found. Among the Paris material there is a sample labelled Seychelles from 'M. Dussumier et Dufo'. One of these specimens measures 13.8 × 8.7 × 7.0 mm. Dussumier and Dufo collected in the Seychelles in 1840 and may have been the collectors of Petit's specimen. If neotype designation were to become necessary, this Paris specimen might be considered to qualify.

Shell (fig. 15a).— Shell typically very distorted to the right, noticeably flattened and compressed; 5-6 whorls and two nuclear whorls; dull on the upper-surface, shiny below. First two whorls smooth, the remainder sculptured with strong, regular ribs (8

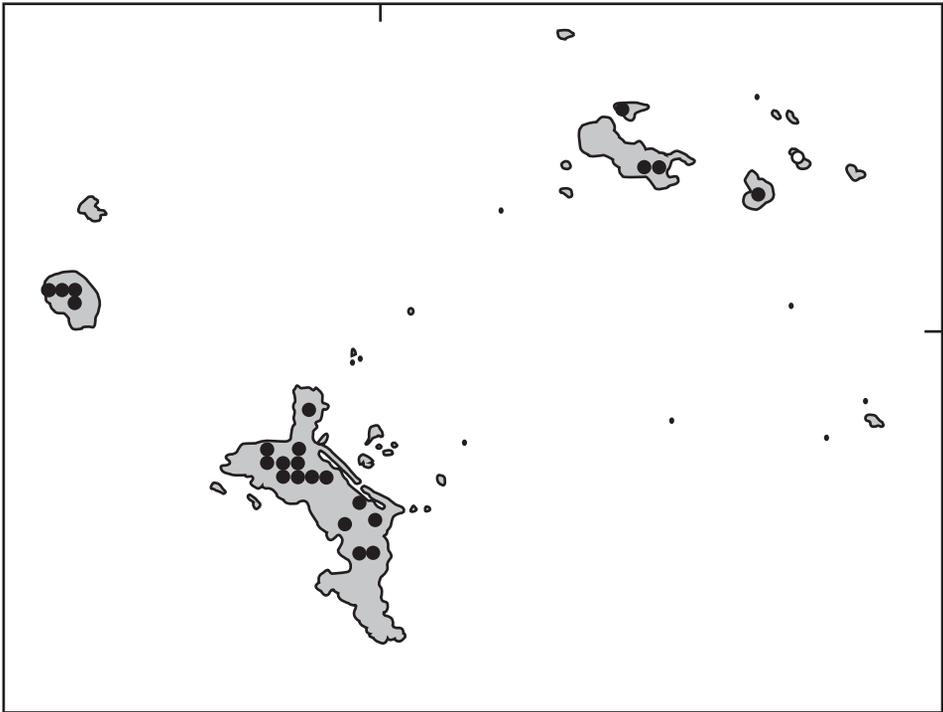


Fig. 17. Distribution of *Gonaxis souleyetianus*.

mm⁻¹). Underside with few irregular ribs (4 mm⁻¹), appearing almost smooth. Aperture with incrassate and reflected lip; there is a short parietal lamella in adult specimens. Umbilicus broad, occupying about 11% of the underside of the shell; very shallow. The thin yellow-brown periostracum is deciduous.

The shell changes shape considerably during growth. The first 4 whorls are discoidal, with a wide umbilicus (30% of the underside) which extends almost to the apex. The 5th represents a short intermediate stage when the labrum starts curving downward and the umbilicus is rapidly closed by the lower margin of the labrum. Subsequent whorls are in the adult form. The intermediate and subadult stages are apparently of short duration as very few specimens have been obtained compared to the abundant helicoid juveniles.

Dimensions.— See table 10. '*G*'. *souleyetianus* is subject to considerable variation in size and minor variations in development of the apertural process and sculpture. The considerable size variation does not appear to be of taxonomic significance as morphometric data show continuous variation between the size extremes and no anatomical variations are apparent. Size differences are not significant between island populations (for t-tests $t > 0.45$, $P > 0.1$ for all comparisons). In table 10 maximum measurements (length × major diameter) are given, which is the only practical way of measuring these distorted shells

Table 10. *Gonaxis souleyetianus* dimensions (mm).

	Height		Diameter		H/D		Whorls range	N	
	range	mean (sd)	range	mean (sd)	range	mean (sd)		range	mean
Mahé	9.3-12.9	10.9 (1.17)	6.2-8.5	7.2 (0.95)	1.39-1.59	1.49 (0.04)	5-6	5.9	81
Praslin	11.4-14.4	12.9 (1.15)	7.8-9.1	8.4 (0.85)	1.44-1.58	1.51 (0.06)	5-5.75	5.5	4
Silhouette	10.0-12.1	11.0 (1.10)	6.2-8.2	7.2 (0.94)	1.45-1.61	1.53 (0.10)	5-5.25	5.3	40
La Digue	12.4-14.9	12.8 (1.20)	8.1-10.3	8.7 (0.80)	1.45-1.53	1.52 (0.05)	5-5.75	5.4	9
Total	9.3-14.9	17.7 (1.15)	6.2-10.3	7.3 (0.93)	1.39-1.61	1.50 (0.06)	5-6	5.7	134

Body (pl. 1h).— Dark purple; sole orange-brown; mantle beige, mottled with vermilion spots, some individuals also have purple patches on the mantle.

Anatomy.

Salivary gland.— Elongate, simple.

Radula (fig. 15d).— Formula 28 + 0 + 28. No central tooth. First 16 laterals elongate cones (0.2 mm), last 12 reduced, needle-like. 87-90 rows. Radula sac 12 mm long.

Reproductive anatomy (figs 15b-c).— Spermoviduct 10-21 mm, elongate with a very narrow base. Spermatheca elongate, to 7 mm, duct narrow, attaching 4-9 mm from base of spermoviduct. Penis elongate, 5-15 mm with terminal blind process. Epiphallus subterminal, short (1-2 mm), not differentiated from vas deferens. Penial retractor muscle attaching terminally to epiphallus. Penis ornamented with regular, closely arranged spinules. Terminal half with short hooked spinules, 0.05-0.1 mm long, basal half with more diffuse arrangement of curved spinules. Spinules replaced by un-chitinized papillae in 33% of adults (both large and small morphs). Penis sheath absent.

Distribution (fig. 17).— Mahé (Bel Ombre, Creve Coeur, Trois Frères, Morne

Blanc, Morne Noir, Morne Seychellois, Mission, Copolia, La Misère, Fairview, Chateau Margot, Congo Rouge, Montagne Planeau, Cascade, Mt. Sebert, La Réserve and Brulée), Silhouette (Jardin Marron, Mon Plaisir, Mont Dauban, *Pisonia sechellarum* forest, Mare aux Cochons, Gratte Fesse), Praslin (Vallée de Mai, Fond Ferdinand), Curieuse, La Digue (Mt. La Digue, Belle Vue). Also reported from Félicité (Nevill, 1868; Sykes, 1909) and Frégate (Germain, 1934). Probably extinct on Félicité; no recent data. No specimens or other records from Frégate; searches in 1972 (Benoit & Van Mol) and 1987 (Gerlach) failed to find the species. This is probably an erroneous record.

Note.— This species almost certainly deserves to be classified with a genus of its own because of its position on the outlying Seychelles group. Obviously it is the product of a long evolution in isolation. However, the authors refrain from naming and defining such a genus because of the absence of comparative anatomical details as regards the many *Gonaxis* s.l. species on the African continent (see e.g. Verdcourt, 1961; Adam, 1965).

Genus *Imperturbatia* Martens, 1898

The shell of *Imperturbatia* is depressed helicoid with an angulate periphery and many regularly increasing whorls. The initial c. 1.2 whorls are smooth, the remainder are covered with coarse prominent ribs, usually less prominent to almost absent below the periphery, but returning in strength around the umbilicus. The aperture is edentulous; the labrum is usually slightly incrassate and reflected. The penis is simple and ornamentation is lacking or restricted to simple hooks. For differences with shells of other *Imperturbatia*-like genera see generic diagnoses below.

Imperturbatia constans (Martens, 1898)

Streptaxis (*Imperturbatia*) *constans* Martens, 1898: 11-12; Sykes, 1909: 60.

Imperturbatio constans; Kobelt, 1905: 23, pl. 44 figs 1-2.

Imperturbatia constans; Thiele, 1931: 728; Zilch, 1960: 536; Barnacle, 1962: 54; Barnacle, 1971: 386; Lionnet, 1984: 240; Gerlach, 1987: 10, 3 col. figs.

Material studied.— 34 juveniles, 42 adults (MRAC 798.890; NPTS M1997.32; alc. and dry; BMNH 1825, 1937.12.30.281-2, unnumbered; ZMB 57280-1).

Material dissected.— 1 adult (NPTS M1997.32).

Type material.— Holotype ZMB 57280; 3 paratypes ZMB 57281; coll. A. Brauer, 1895. Type locality: Mahé, no locality specified.

Shell (fig. 18b).— Shell discoidal to subconical; 7-8 straight sided whorls with 2.5 nuclear whorls. First 2.5 whorls smooth, remainder ornamented with fine, regular radial ribs (7-9 mm⁻¹); ribs extend onto undersurface. High shouldered keel present. Surface dull, white or colourless. Umbilicus open, broad (16-23% of the undersurface). Aperture narrow (height/diameter 0.56-0.84); lip reflected, slightly thickened; edentulous. Periostracum absent.

Dimensions.— See table 11.

Table 11. *Imperturbatia constans* dimensions (mm).

	Height		Diameter		H/D		Whorls		N
	range	mean (sd)	range	mean (sd)	range	mean (sd)	range	mean	
Lectotype	2.6	-	4.6	-	0.57	-	7	-	1
Mahé	2.1-3.6	2.9 (1.02)	3.7-6.0	5.1 (0.55)	0.55-0.69	0.62(0.05)	5-8	7.6 (0.57)	42

Body (pl. 1i).— Reddish brown with black speckling.

Anatomy.

Salivary gland.— Elongate, simple, 3 mm long.

Radula (fig. 24a).— Formula 33 + 1 + 33. Central tooth large, lateral gradually decreasing in size.

Reproductive anatomy (fig. 19a).— Sperмовидuct simple, 10 mm long. Spermatheca short, spermatheca and duct not distinguished, 3 mm long, attached near base of sperмовидuct. Penis simple, elongate; penial retractor muscle terminal; epiphallus 4 mm long, not differentiated. No penial ornamentation apparent.

Distribution (fig. 20).— Mahé (Trois Frères, Morne Blanc, Morne Seychellois, Cascade, La Réserve & Brulée).

Note.— Martens noted the similarity between this species and the description of *Helix Le Vieuxi* Nevill, 1871. The possibility that this may be a senior synonym of *I. constans* was noted by Barnacle (1971). The type material of this species cannot be traced and the description is too imprecise to distinguish between the different *Imperturbatia* species. With the addition of uncertainty over the possible transposition of the measurements in the original description of *Helix Le Vieuxi* this name is considered to be a nomen dubium.

Imperturbatia violascens (Martens, 1898)

Streptaxis (Imperturbatia) violascens Martens, 1898: 12, pl. 2 fig. 7.

Imperturbatio violascens; Kobelt, 1905: 24, pl. 44 figs 5-6.

Imperturbatia violascens; Thiele, 1931: 728; Barnacle, 1962: 54; Lionnet, 1984: 240; Gerlach, 1987: 9, 3 col. figs.

Material studied.— 13 adults; Mahé (MRAC 798.757, 869, 908; alc. and dry; BMNH unnumbered (ex E. von Martens, *Helix enneagyra* Mts.); NPTS M1997.33; ZMB 57294). An unpublished dissection drawing (labelled *Imperturbatia constans*) provided by Dr. A.A. Schileyko was also examined.

Material dissected.— One adult (MRAC 798.757); a dry specimen rehydrated, only penis and albumen gland extracted. Additional anatomical data provided by Dr. A.A. Schileyko.

Type material.— Holotype ZMB 57294; coll. A. Brauer, 1895. Type locality: Mahé, Mt. Harrison (Montagne Planeau).

Shell (fig. 18a).— Shell subconical; 7-8.25 whorls with 2 nuclear whorls. First two whorls smooth, remainder ornamented with fine S-shaped radial ribs (6 mm⁻¹); ribs extending onto undersurface. Surface dull, colourless. High shouldered, rounded keel present; whorls distinctly convex. Umbilicus open, relatively narrow (18-24% of undersurface), deep (extending to apical whorls). Aperture slightly broadened (height/



Fig. 18. Shells of *Imperturbatia* and *Silhouettia* species (scale bar 2 mm). (a) *Imperturbatia violascens* (MRAC 798.759); (b) *Imperturbatia constans* (BMNH 1937.12.30.281-2); (c) *Silhouettia silhouettae* (MRAC 798.954).

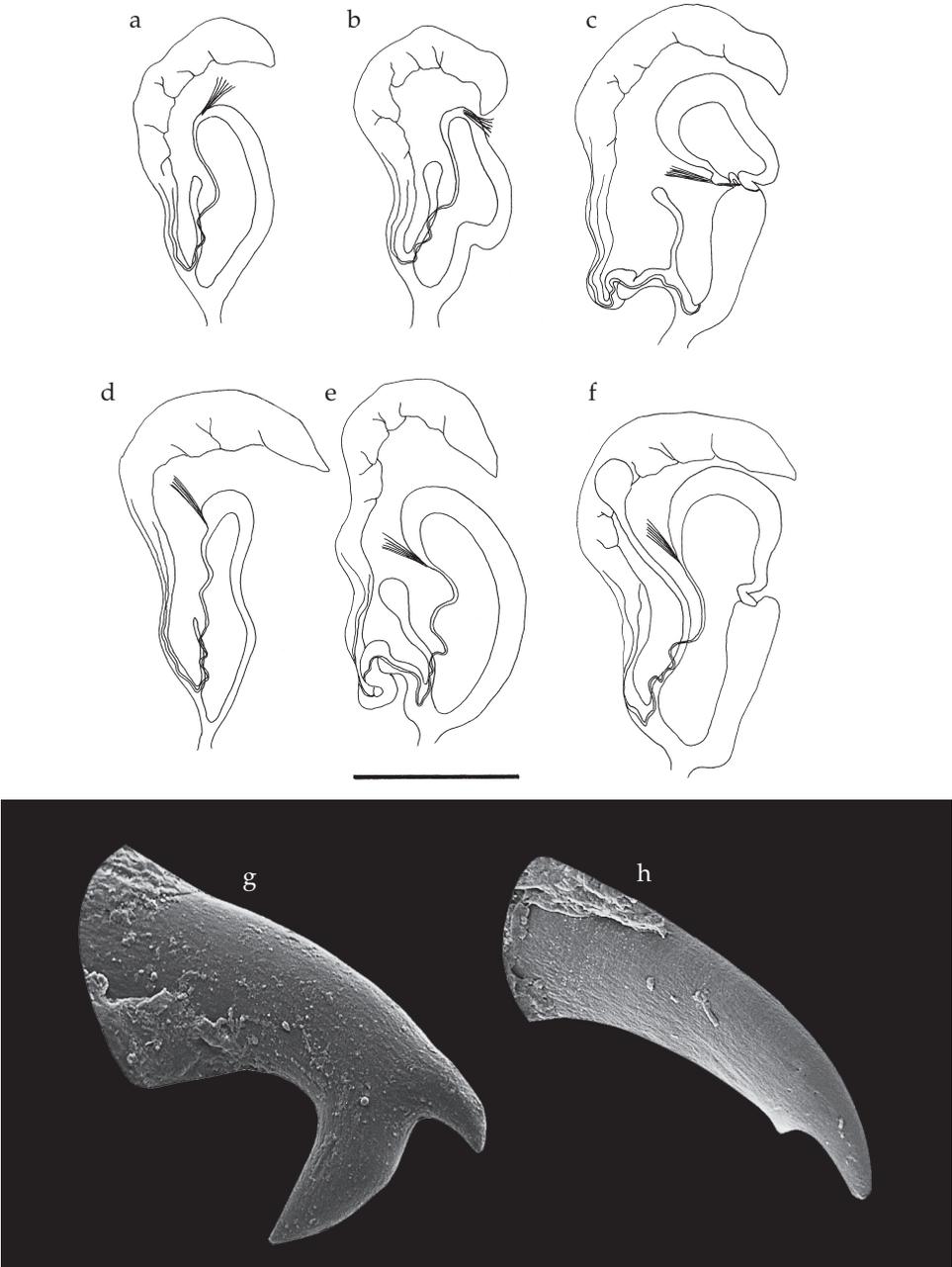


Fig. 19. Anatomy of *Imperturbatia*, *Silhouettia*, *Careoradula*, *Augustula* and *Acanthennea* species. (a) *Imperturbatia constans* (scale bar 2 mm); (b, g) *Imperturbatia violascens*, (b) reproductive anatomy (scale bar 3 mm), (g) spinule (scale bar 0.02 mm); (c) *Silhouettia silhouettae* (scale bar 2 mm); (d) *Careoradula perelegans* (scale bar 2.25 mm); (e) *Augustula braueri* (scale bar 2 mm); (f, h) *Acanthennea erinacea*, (f) reproductive anatomy (scale bar 5 mm), (h) spinule (scale bar 0.04 mm).

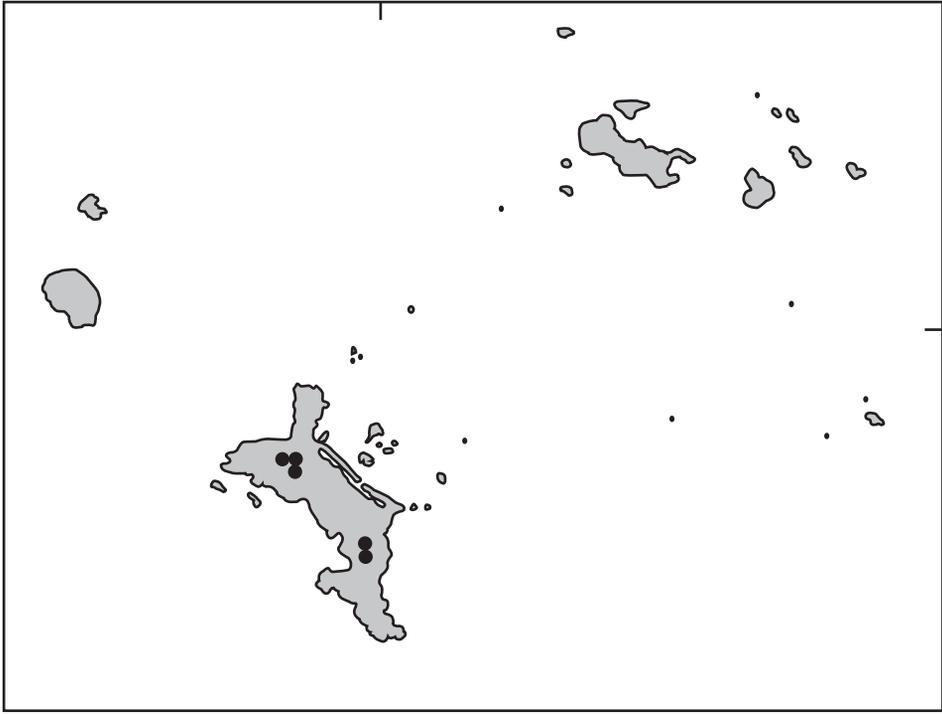


Fig. 20. Distribution of *Imperturbatia constans*.

diameter = 0.76-1.07); lip reflected and thickened; edentulous. Periostracum absent.
Dimensions.— See table 12.

Table 12. *Imperturbatia violascens* dimensions (mm).

	Height		Diameter		H/D		Whorls		N
	range	mean (sd)	range	mean (sd)	range	mean (sd)	range	mean	
Holotype	2.3	-	4.0	-	0.58	-	9	-	1
Mahé	3.1-4.0	3.5 (0.29)	4.6-5.5	5.1 (0.24)	0.55-0.82	0.67 (0.08)	7.5-8.25	7.9 (0.27)	12

Body (pl. 1j).— Body and mantle beige; mantle heavily streaked violet with few vermilion spots above the mantle border. Mantle border anteriorly developed into 3 lobes.

Anatomy.

Salivary gland.— Unknown.

Radula.— Unknown.

Reproductive anatomy (figs 19b, 19g).— Spermatheca spherical, spermatheca duct long. Penis elongate (4 mm long), narrow (0.4 mm wide), simple, without appendages. Penial sheath restricted to base. Spinules present throughout penis, all simple, measuring 0.02 mm long. Albumen gland very large (4 mm long).

Distribution (fig. 21).— Mahé (Morne Blanc, Montagne Planeau, La Réserve and Brulée, Beau Vallon, ca 600 m - A.A. Schilekyo personal communication).

Genus *Silhouettia* gen. nov.

The shell of this monotypic genus resembles that of *Imperturbatia* in being depressed helicoid with an angulate periphery and many regularly increasing whorls. The initial c. 1.2 whorls are smooth, the remainder are covered with coarse prominent ribs. The aperture is edentulous; the labrum is usually slightly incrassate and reflected. The sculpture is finer, more prominent on the underside and the surface glossier than in *Imperturbatia*. Anatomically penis structure (sheathed penis) and ornamentation (complex spinules) are distinct from *Imperturbatia*.

Type species.— *Silhouettia silhouettae* spec. nov.

Etymology.— *Silhouettia*, latinization of the type locality, Silhouette island.

Silhouettia silhouettae (Martens, 1898)

Streptaxis (*Imperturbatia*) *constans* var. *Silhouettae* Martens, 1898: 12.

Streptaxis (*Imperturbatia*) *constans* (part); Sykes, 1909: 60.

Imperturbatia levieuxi; Barnacle, 1971: 386; Lionnet, 1984: 240; Gerlach, 1987: 10.

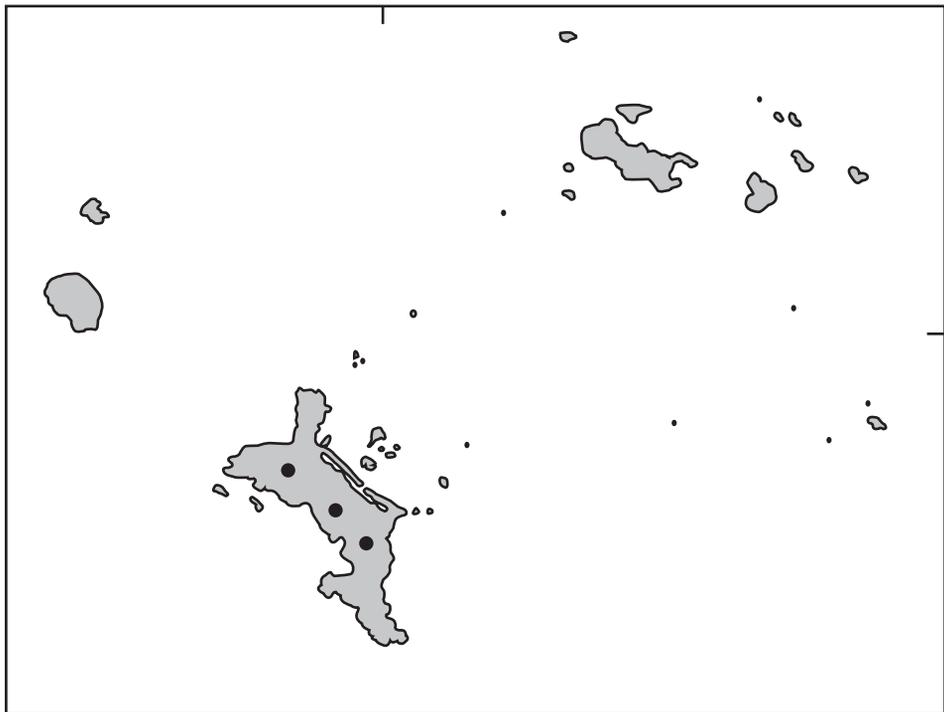


Fig. 21. Distribution of *Imperturbatia violascens*.

Material studied.— Five juveniles, 8 adults; Silhouette (MRAC 798.954, 961; NPTS M1997.34; alc. and dry; BMNH 1825; ZMB 57283).

Material dissected.— One adult (NPTS M1997.34a).

Type material.— Holotype MRAC 798.954 (coll. P.L.G. Benoit & J.-J. Van Mol, Mare aux Cochons, 500 m, forêt endémique, 2 and 8.vii.1972). Paratypes NPTS M1997.34a and b (coll. J. Gerlach, VIII.1990, *Pisonia sechellarum* forest). Type locality: Mare aux Cochons, Silhouette.

Shell (fig. 18c).— Shell subconical with a low spire; 8.5 whorls with 2.25 nuclear whorls. First 2.5 whorls smooth, the remainder ornamented with fine, regular radial ribs (15 mm^{-1}), ribs extending onto undersurface and into umbilicus. Ribs on the body whorl are widely spaced and very regular. Surface glossy, white. High shouldered keel present; whorls distinctly convex. Umbilicus open, relatively narrow (15–20%, mean = 19%, of the underside) and deep (extending to apical whorls). Aperture broad, square and angled at keel, middle of underside and umbilical margin; lip distinctly reflected and slightly thickened; edentulous. Periostracum absent.

Dimensions.— See table 13.

Table 13. *Silhouettia silhouettiae* dimensions (mm).

	Height		Diameter		H/D		Whorls		N
	range	mean (sd)	range	mean (sd)	range	mean (sd)	range	mean	
Holotype	3.8		6.2		0.61		8.5		1
Silhouette	3.8-5.5	4.5 (0.11)	6.2-6.6	6.3 (0.08)	0.64-0.83	0.72 (0.12)	8-8.5	8.4	8

Body (pl. 1k).— Foot fawn, tentacles dark vermilion-violet. Mantle beige with vermilion spots. Violet spots along mantle border and on mantle along ureter.

Anatomy.

Salivary gland.— Elongate, simple, 3 mm long.

Radula (figs 24b, 24e).— Formula 15 + 0 + 15. No central tooth, laterals simple, larger towards centre.

Reproductive anatomy (fig. 19c).— The genital atrium is long, the spermooviduct elongate (10 mm) but simple in shape, attached near base of spermooviduct. Spermatheca short, not distinguished from duct. Penis simple, elongate (6 mm); penial retractor muscle terminal. Penis sheath present on lower half. Epiphallus elongate (4 mm long), slightly inflated terminally, attaching to terminal part of sheath. Penis regularly ornamented with chitinous, black spinules which are visible through the penis wall and are simple in shape.

Distribution (fig. 22).— Silhouette (Jardin Marron, Mon Plaisir, Mont Pot à Eau, Mont Dauban, *Pisonia sechellarum* forest, Mont Corgat, Gratte Fesse).

Note.— This species was first noted by Martens who described it as a variety of *Imperturbatia constans*. His varietal name is formalized here as a species name. He noted the number of whorls, size and the different sculpture as distinguishing the taxon.

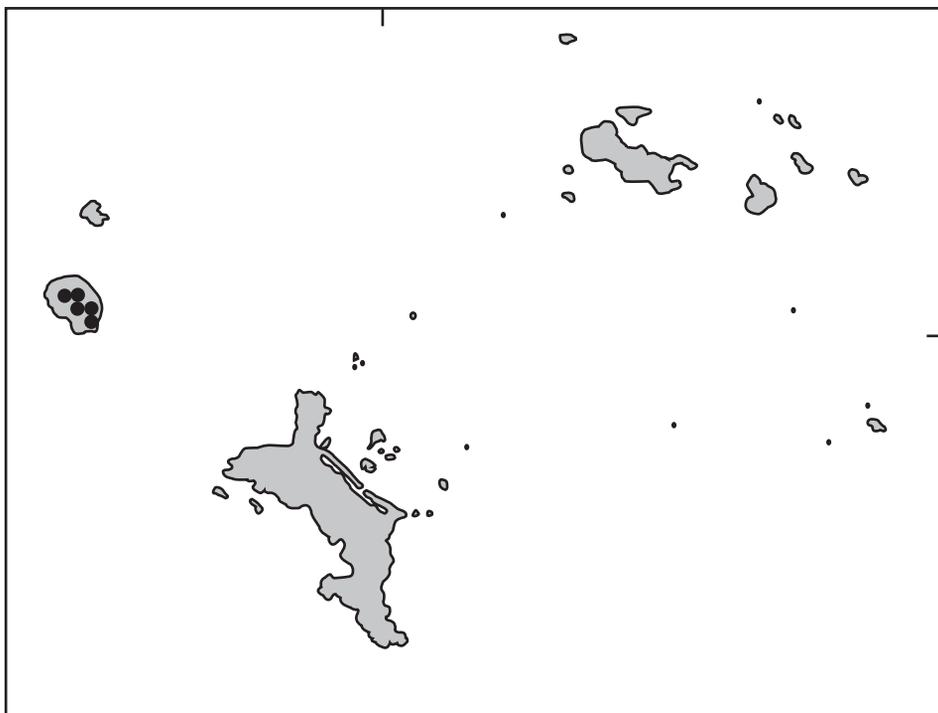


Fig. 22. Distribution of *Silhouettia silhouettae*.

Genus *Careoradula* gen. nov.

The monotypic genus *Careoradula* resembles *Imperturbatia* in its shell and basic anatomy. As with *Imperturbatia* the shell is depressed helicoid with an angulate periphery and many regularly increasing whorls. The aperture is edentulous; the labrum is usually slightly incrassate and reflected. It differs from *Imperturbatia* in having a more pronounced sculpture of very prominent, regular ribs, extending onto the underside to the umbilicus. Its reproductive anatomy is similar to that of *Imperturbatia* but it is distinct from all other streptaxids in the absence of a radula and associated structures (Gerlach & Van Bruggen, 1998).

Type species.— *Streptaxis (Imperturbatia) perelegans* Martens, 1898.

Etymology.— Composite of *careo*, lacking (Latin) and *radula*, gastropod feeding structure.

Careoradula perelegans (Martens, 1898)

Streptaxis (Imperturbatia) perelegans Martens, 1898: 12-13, pl. 2 fig. 6; Sykes, 1909: 60.

Imperturbatio perelegans; Kobelt, 1905: 24, pl. 44 figs 3-4.

Imperturbatia perelegans; Thiele, 1931: 728; Barnacle, 1962: 54; Lionnet, 1984: 240; Gerlach, 1987: 10, 3 col. figs.; Gerlach & Van Bruggen, 1998: 249.

Material studied.— Mahé 11 adults, 1 juvenile (MRAC 798.853; alc. and dry; NPTS M1997.35, BMNH 1825 (ex Sykes colln., 1905), 1937.12.30.283-5 (labelled Seychelles), ZMB 57279). Silhouette 5 adults (NPTS M1997.36, 1998.6).

Material dissected.— One adult from Mahé (MRAC 798.853).

Type material.— Martens described this species from three specimens collected by A. Brauer in 1895. Measurements were given for the largest specimen; this is designated lectotype (ZMB 57279).

Shell (fig. 23a).— Shell discoidal; 6-8 whorls with 2-2.5 nuclear whorls. High shouldered keel present. Spire slightly raised; whorls not strongly convex. Surface glossy, colourless and translucent. First 2-2.5 whorls smooth, the remainder ornamented with faint, irregular growth lines and raised regular ribs. The ribs are regularly arranged (2 mm^{-1}) and extend onto the underside where they are distinctly S-shaped. Umbilicus open, wide (occupying 53-65% of major diameter, mean 57.4%) and deep (extending to the apical whorls). Aperture edge thickened by one of the ribs, forming a narrow lip; edentulous. Periostracum absent.

Dimensions.— See table 14.

Table 14. *Careoradula perelegans* dimensions (mm).

	Height		Diameter		H/D		Whorls		N
	range	mean (sd)	range	mean (sd)	range	mean (sd)	range	mean	
Lectotype	2.3	-	5.1	-	0.45	-	7	-	1
Mahé	2.5-3.1	2.7 (0.29)	5.2-6.1	5.7 (0.31)	0.45-0.52	0.48 (0.05)	7-7.25	8.0 (0.68)	11
Silhouette	1.9-2.6	2.3 (0.10)	4.4-5.0	4.7 (0.08)	0.43-0.54	0.50 (0.00)	6-7	6.6 (0.23)	6

Body (pl. 11).— Uniform pale yellow (off-white in spirit material).

Anatomy.

Salivary gland.— Elongate (3 mm), simple.

Radula.— All radula and odontophore structures absent. The rostrum is well developed and strong.

Reproductive anatomy (fig. 19d).— Spermoviduct elongate, thin and simple in shape. Spermatheca not located. Penis elongate, thin ($3.5 \times 0.3 \text{ mm}$), slightly inflated terminally. No penis sheath located, no distinct epiphallus, penial retractor muscle terminal. No penial ornamentation.

Distribution (fig. 25).— Mahé (Morne Blanc, Morne Seychellois, Congo Rouge, Cascade, Mt. Sebert, La Réserve and Brulée), Silhouette (*Pisonia sechellarum* forest, Gratte Fesse).

Genus *Augustula* Thiele, 1931

The shell of the monotypic genus *Augustula* is depressed helicoid with regularly increasing whorls. The initial 1.5 whorls are smooth. Above the periphery the other whorls are covered with regular, fairly close and prominent costulae. In the interstices very weak growth lines may be detected and also a spiral component. Below the weakly angulate periphery the sculpture becomes obsolete so that the base of the shell seems to be almost smooth. The edentulous aperture has a sharp and thin



Fig. 23. Shells of *Careoradula*, *Augustula* and *Acanthennea* (scale bar 2 mm). (a) *Careoradula perelegans* (BMNH 1937.12.30.283-5); (b) *Augustula braueri* (BMNH 1937.12.30.286-9); (c) *Acanthennea erinacea* (BMNH 1825).

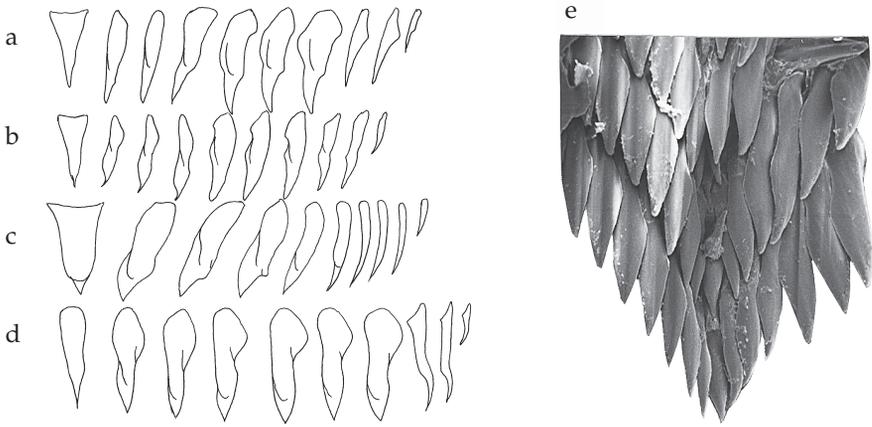


Fig. 24. Radulae of *Imperturbatia*, *Silhouettia*, *Augustula* and *Acanthennea* (scale bar 0.05 mm). (a) *Imperturbatia constans*; (b, e) *Silhouettia silhouettae*; (c) *Augustula braueri*; (d) *Acanthennea erinacea*.

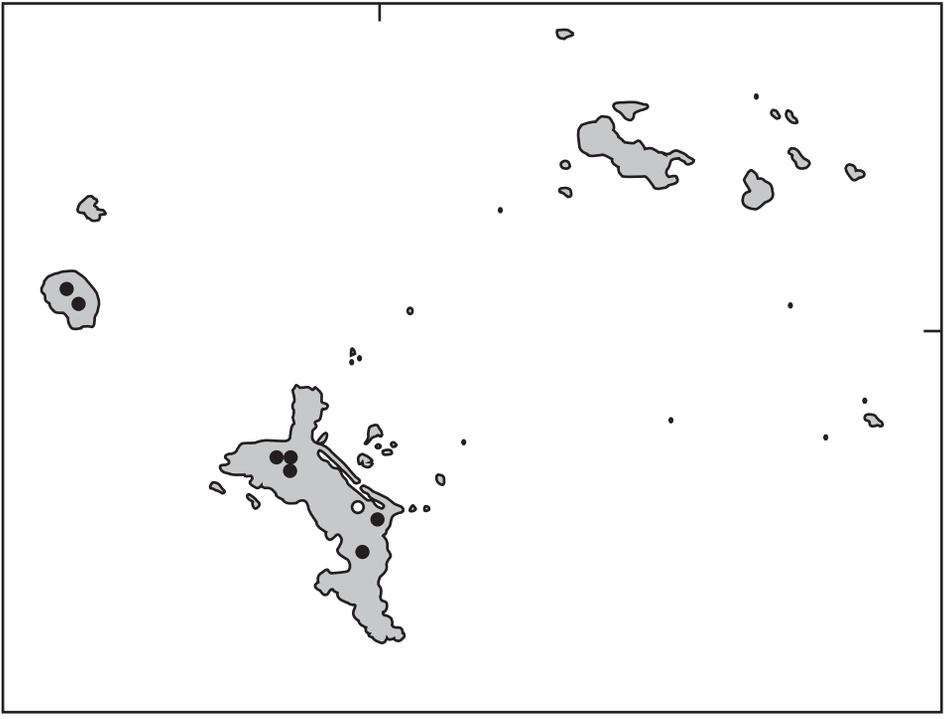


Fig. 25. Distribution of *Careoradula perelegans*.

labrum; the umbilicus is fairly narrow and deep. The shells of *Imperturbatia*, *Silhouettia* and *Careoradula* are smaller with more whorls, have a more noticeably angulate shell with a relatively wider umbilicus and costulae sculpture on the base at least

around the umbilicus, and a slightly incrassate and reflected labrum. Its genital anatomy is distinct from these genera in the club-shaped, papillate penis.

Augustula braueri (Martens, 1898)

Streptaxis (Imperturbatia) Braueri Martens, 1898: 13-14, pl. 2 fig. 9; Sykes, 1909: 60.

Imperturbatio braueri; Kobelt, 1905: 25, pl. 44 figs 7-8.

Augustula braueri; Thiele, 1931: 727, fig. 772; Zilch, 1960: 556.

Imperturbatia braueri; Germain, 1934: 122; Barnacle, 1962: 54; Lionnet, 1984: 240; Gerlach, 1987: 9, 3 col. figs.

Material studied.— 16 juveniles, 30 adults; Mahé (BMNH 1937.12.30.286-9, 1825; NPTS M1997.37; alc. and dry; ZMB 57292-7), Silhouette (NPTS M1997.38; ZMB 57298).

Material dissected.— One adult from Mahé (NPTS M1997.37).

Type material.— Ten syntypes (6 ZMB 57292-8; 4 BMNH 1937.12.30.286-9) coll. A. Brauer, 1895. Type locality: Mahé and Silhouette, no precise locality.

Shell (fig. 23b).— Shell discoidal; 4-5 whorls with 1.5 nuclear whorls. First 1.5 whorls smooth, the remainder ornamented with fine, regular radial ribs (8 mm⁻¹). The ribs do not extend to the undersurface which is only marked by irregular growth lines. Surface glossy, colourless or white. Umbilicus open and narrow, occupying less than 10% of the underside. Aperture broad; lip not thickened or reflected; edentulous. No periostracum.

Dimensions.— See table 15.

Table 15. *Augustula braueri* dimensions (mm).

	Height		Diameter		H/D		Whorls		N
	range	mean (sd)	range	mean (sd)	range	mean (sd)	range	mean	
Mahé	1.8-3.7	2.5 (0.45)	3.6-5.9	5.1 (0.60)	0.35-0.77	0.50 (0.09)	4-5	4.5 (0.43)	17
Silhouette	2.8-3.0	2.9 (0.1)	4.8-5.0	3.9 (0.1)	0.58-0.6	0.59 (0.01)	5	5	2

Body (pl. 1m).— Body and mantle vermilion.

Anatomy.

Salivary gland.— Elongate, simple.

Radula (fig. 19e).— Formula 29 + 1 + 29; central tooth and first 4 laterals broad, remainder slender and curved.

Reproductive anatomy (fig. 19e).— Penis long, club-shaped, retractor muscle terminal. Penis ornamented with weakly chitinized conical papillae (0.4 mm long). Spermatheca oval; duct short and wide. Muscular ridges are present inside the spermatheca and spermoviduct.

Distribution (fig. 26).— Mahé (Trois Frères, Morne Blanc, Morne Seychellois, Congo Rouge, Cascade, Mt. Sebert, La Réserve & Brulée), Silhouette (Jardin Marron, Gratte Fesse).

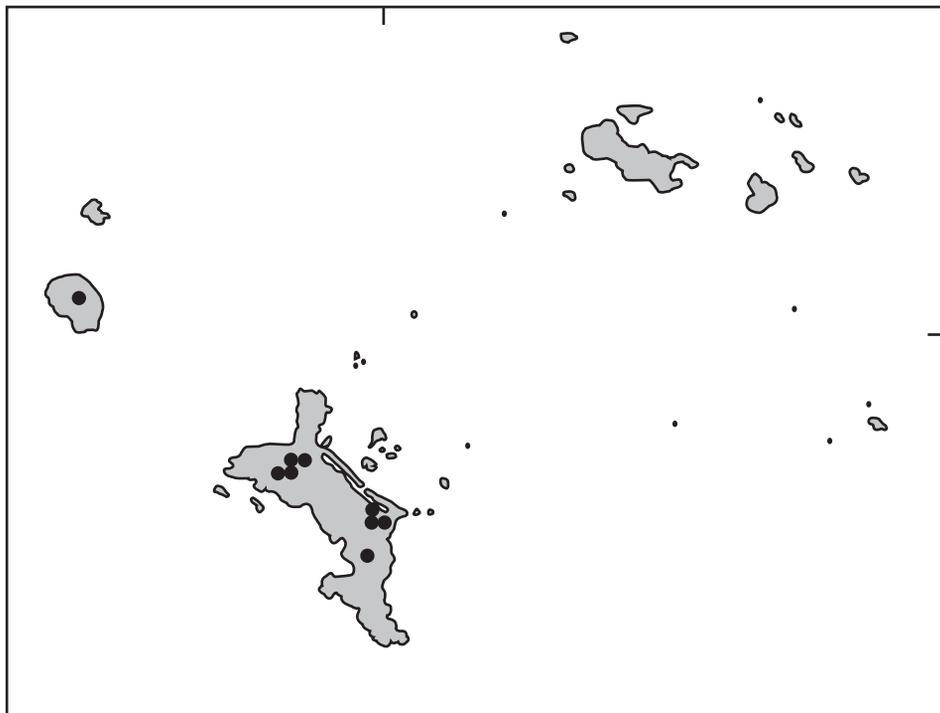


Fig. 26. Distribution of *Augustula braueri*.

Genus *Acanthennea* Martens, 1898

The shells of the monotypic genus *Acanthennea* are characterised by their flattened and almost sunken apex and short pupoid form; the whorls are covered with widely spaced lamella-like ribs with two prominent spines. The aperture is edentulous and the labrum is sharply receding in profile. The penis is long, sheathed and with bicuspid spinules.

Acanthennea erinacea (Martens, 1898)

Ennea (*Acanthennea*) *erinaceus* Martens, 1898: 8-10, pl. 1 figs 15-17; Moellendorff & Kobelt, 1904: 275, pl. 33 figs 16-18.

Acanthennea erinaceus; Thiele, 1931: 731; Zilch, 1960: 566, fig. 1982; Barnacle, 1962: 54; Lionnet, 1984: 240; Gerlach, 1987: 9, 3 col. figs.

Material studied.— 32 juveniles, 118 adults; 19 adults Mahé (BMNH 1825, 1937.12.30.275-6; SMF 8453/1; NPTS M1997.39; ZMB 56915-8), 99 adults Silhouette (NPTS M1997.40; alc. and dry).

Material dissected.— Three specimens Silhouette (NPTS M1997.40a).

Type material.— Holotype ZMB 56915, paratypes (juvenile) ZMB 56918, coll. A. Brauer, 1895. Type locality: Mahé, Morne Impracticable (Copolia).

Shell (fig. 23c).— Shell pupoid, squat with convex sides; 8-9 whorls with 2-2.25

flat nuclear whorls. First 2 whorls smooth, the remainder ornamented with widely spaced, flange-like ribs. Apical part of each rib with a large, laterally compressed spine; base with a similar, but smaller spine. The second spine may be absent [var. *uniseriata* (Martens, 1898: 10)] on at least some whorls. Surface glossy, colourless, translucent. Aperture large, more or less ovoid, height and width approximately equal, edentulous; lip reflected, receding apically with a sharp curve in profile. This is present in both subadults and adults. Umbilicus closed.

Juvenile shells are depressed and initially have an open umbilicus. The aperture may have from one to three basal processes, sometimes fused into a single incrassate horizontal lamella. In juveniles the width of the aperture exceeds its length. There are no noticeable differences between subadults and adults.

Dimensions.— See table 16. Comparison of the measurements of shells from Mahé and Silhouette reveals significant differences in proportions. Mahé shells are significantly shorter and broader than those from Silhouette [*t* (height) = 4.620, *P* < 0.001, *t* (diameter) = 2.329, *P* < 0.02, *t* (H/D) = 6.125, *P* < 0.001]. The number of whorls is not significantly different (*t* = 0.647, *P* > 0.1).

Table 16. *Acanthemea erinacea* dimensions (mm).

	Height		Diameter		H/D		Whorls		N
	range	mean (sd)	range	mean (sd)	range	mean (sd)	range	mean	
Lectotype	6.1	-	4.2	-	1.43	-	8.5	-	1
Mahé	4.4-6.2	5.2 (0.53)	3.7-4.5	4.0 (0.30)	1.19-1.43	1.30 (0.07)	7-8	7.9 (0.50)	13
Silhouette	4.2-6.3	6.0 (0.91)	3.8-4.6	4.2 (0.21)	1.24-1.45	1.44 (0.12)	7-9	8.0 (0.68)	99

Body (pl. 1n).— Body uniformly purple.

Anatomy.

Salivary gland.— Elongate, simple.

Radula (fig. 24d).— Formula 43 + 1 + 43.

Reproductive anatomy (figs 19f, 19h).— Spermatheca elongate and simple in shape. Penis elongate (9 mm) and extremely narrow (0.1 mm at base), becoming wider in distal half (0.3 mm). Penis sheath present on lower half. Long undifferentiated epiphallus (3 mm long) attaching to terminal part of sheath. Penis constricted at attachment of sheath. Penial retractor muscle terminal. Penis regularly ornamented with chitinous, black spinules which are visible through the penis wall. The spinules are long, gently curved and bicuspid; they measure 0.03 mm and are regularly arranged in 6 oblique columns on the distal half but only two columns are present in the basal half.

Distribution (fig. 27).— Mahé (Trois Frères, Morne Blanc, Morne Seychellois, Copolia, Montagne Planeau, Mt. Alphonse, Cascade, La Réserve & Brulée), Silhouette (Jardin Marron, *Pisonia sechellarum* forest, Gratte Fesse).

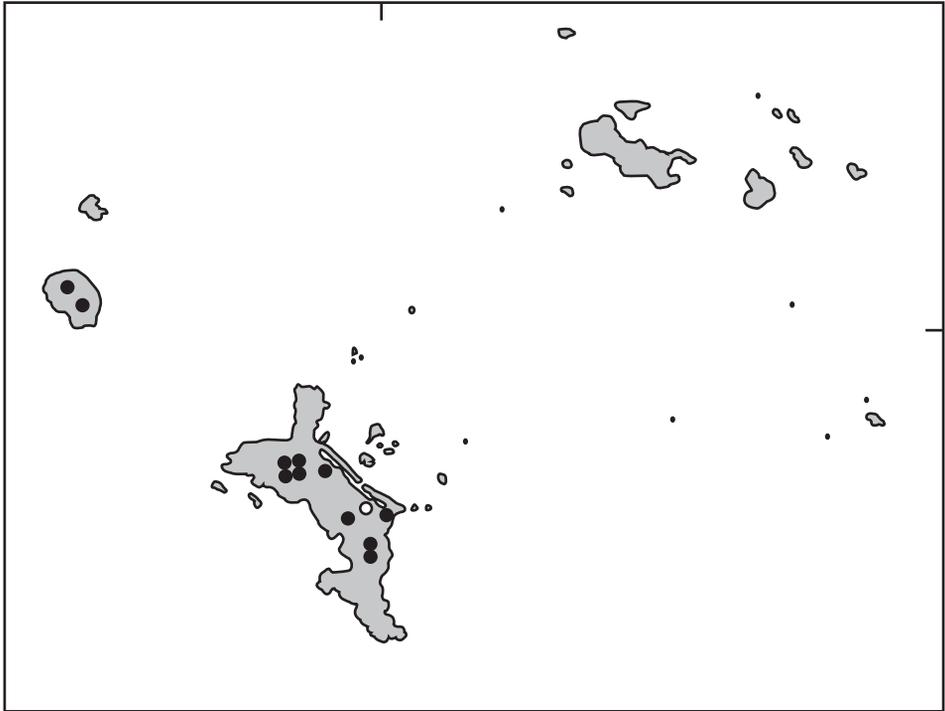


Fig. 27. Distribution of *Acanthennea erinacea*.

Key to the shells of the Seychelles Streptaxidae

The following key is for the identification of adult shells; the juveniles of some species may differ considerably in shape as compared to adult shells, accordingly identification from the key can only be provisional and should be supported by the descriptions above. The key includes all Streptaxidae recorded on the granitic islands of Seychelles (including the genus *Priodiscus*).

- 1. Shell markedly distorted 2
- Shell normal, not distorted 3
- 2. Shell large (>20 mm), bulbous and inflated, finely ribbed, aperture without denticles *Gonaxis quadrilateralis*
- Shell smaller (<16 mm), compressed, markedly costulate, aperture with mid-parietal lamella *Gonaxis souleyetianus*
- 3. Shell depressed helicoid or discoidal, width greater than height 4
- Shell with high spire (cylindrical, elongate pupoid or pupoid), height considerably greater than width 11
- 4. Shell with 4-5 whorls, umbilicus narrow (1/10-1/8 of major diameter), costulation not continued below the periphery, shell 2.0-2.6 × 4.9-6.0 mm ... *Augustula braueri*
- Shell with more than 5 whorls, umbilicus wider (1/7-1/2 of major diameter), cos-

- tulation continued on base of shell, sometimes almost smooth, but always with traces of costulation around the umbilicus 5
5. Shell discoidal with a prominent keel 6
- Shell depressed helicoid 8
6. Costulation coarse, prominent on both sides of shell *Priodiscus costatus*
- Costulation fine, regular, prominent at keel but reduced on underside 7
7. Keel finely serrated *Priodiscus serratus*
- Ribs projecting beyond keel, giving a spiny appearance *Priodiscus spinatus*
8. Costulation on base well marked 9
- Costulation on base absent or very weak, usually limited to traces around the umbilicus *Silhouettia silhouettae*
9. Costulation very coarse (c. 20 ribs on last half whorl), umbilicus large and tapering, showing all whorls from the inside, width >30% of major diameter, height of shell less than half major diameter, i.e. H/D <0.5, shell 2.0-4.2 × 4.2-5.9 mm *Careoradula perelegans*
- Costulation less coarse (at least 35 ribs on last half whorl), umbilicus much narrower and more cylindrical, less than 25% of major diameter, height of shell more than half major diameter, i.e. H/D >0.5 10
10. Costulation fine (c. 45 ribs on last half whorl), width of umbilicus 20-25% of major diameter, shell normally 2.6-3.1 × 4.5-5.3 mm, 7.25-7.5 whorls (larger forms known) *Imperturbatia constans*
- Costulation coarser (c. 35 ribs on last half whorl), width of umbilicus <20% of major diameter, shell normally 2.9-3.8 × 5.0-5.6 mm, 8-8.5 whorls (smaller forms known) *Imperturbatia violascens*
11. Shell comparatively large, i.e. H >12 mm 12
- Shell comparatively small, i.e. H <10 mm 14
12. Shell more or less ovoid or cylindrical, H/D <2.5 13
- Shell more or less ovoid or cylindrical, H/D >3.0 *Stereostele nevilli*
13. Shell cylindrical, sides sub-parallel (apical angle around 5°), no spiral sculpture on shell, H 11-14 mm *Edentulina moreleti*
- Shell somewhat tapering, sides converging (apical angle around 4°), body whorls somewhat bulbous, marked spiral sculpture, H 14-20 mm .. *Edentulina dussumieri*
14. Shell turritiform and slender, tapering, H/D >3.0, H 4-6 mm, aperture with two dental processes *Streptostele acicula*
- Shell (elongate) pupoid, rarely somewhat tapering (H/D <1.5 or >3.0), aperture edentulous, with one denticle or more than two denticles 15
15. Shell smooth or with weak growth striae, aperture either edentulous or with denticle, H/D >2.0 16
- Shell noticeably costulate, the ribs covered with one or more spines, aperture edentulous, H/D <1.5 *Acanthennea erinacea*
16. Shell conical, edentulous *Gulella silhouettae*
- Shell cylindrical or tapering 17
17. Shell somewhat tapering, aperture with four processes, columella not twisted *Gulella bicolor*
- Shell more or less cylindrical, aperture edentulous or with parietal lamella, columella twisted 18

- 18. Shell slender, up to 4.5 mm long, H/D >3.0, aperture with oblique parietal lamella *Gulella thomassetti*
- Shell somewhat squat, up to 6.5 mm long (dwarf forms only up to 4.5 mm long), H/D <2.0, aperture edentulous *Gulella gardineri*

Preliminary conclusions

The above data combined with those of the senior author’s earlier paper (Gerlach, 1995) give a complete overview of the Streptaxidae of the Seychelles islands. It is a moot point whether the streptaxid assemblage of this isolated group of islands reflects a single radiation. Endemism is marked, but there are very clear connections to the African mainland, certainly on the generic level. The great variety in shell and genital morphology almost precludes development from a common ancestor. The Streptaxidae very probably are a Gondwana family, i.e. a family that arose and initially developed on the complex of southern continents (viz., South America, Africa, India, Australia, Antarctica) known as Gondwanaland (cf. Van Bruggen, 1980, 1994). The granitic islands of the Seychelles archipelago are remnants of this late Triassic supercontinent and it is likely that early streptaxids were already present when Gondwanaland completed its disintegration in the late Cretaceous c. 65 million years ago, eventually resulting in the complete isolation of the islands. Therefore local isolation and concurrent evolution of the fauna is markedly ancient.

All indigenous species bar one (*Streptostele acicula*) are endemic to the archipelago. Seven of the eleven genera are also restricted to the Seychelles: *Stereostele*, *Imperturbatia*, *Silhouettia*, *Careoradula*, *Augustula*, *Priodiscus*, and *Acanthennea*. These genera seem to have Oriental affinities. The other species are provisionally classified with four (tropical) continental African genera, albeit with a large measure of doubt and reluctance: *Edentulina*, *Gulella*, *Gonaxis*. and *Streptostele*. A complicating factor here is that due to a dearth of anatomical data the continental genera have never been properly defined - while most of the numerous species in the Streptaxidae are well-marked, there are as yet no clear-cut differences between the genera.

As regards distribution, the western islands of Silhouette and Mahé appear to harbour the largest number of species, each with eleven species. Mahé is by far the largest island (15,252 ha; all data on surface area and elevation according to Skerrett & Skerrett, 1990) with the most diverse assemblage of habitats with altitudes of up to 905 m, but equally rich Silhouette is considerably smaller (1,995 ha, altitudes of up to 867 m). The eastern island Praslin (2,756 ha with altitudes of up to 367 m) with its satellite La Digue (1,010 ha, altitudes of up to 333 m) is noticeably larger than Silhouette but only harbours four species, which, however, are all represented on both of the two western islands. Therefore there is a striking difference between the western and eastern islands, which, incidentally, once again highlights the prominent conservation value of Silhouette and Mahé.

A proper and more complete biogeographical analysis has to await the detailed treatment of all indigenous land molluscs of the Seychelles archipelago.

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