

**Studies on the Streptaxidae
(Mollusca, Gastropoda Pulmonata) of Malaŵi 8.
A revision of '*Marconia*' *hamiltoni* (Smith), the largest local
streptaxid, with the description of a new genus¹**

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In memoriam Koos den Hartog

Bruggen, A.C. van & A.J. de Winter. Studies on the Streptaxidae (Mollusca, Gastropoda Pulmonata) of Malaŵi 8. A revision of '*Marconia*' *hamiltoni* (Smith), the largest local streptaxid, with the description of a new genus.

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'*Marconia*' *hamiltoni* s.l. is known from two discrete mountainous areas in Malaŵi, i.e. the (southern) Mt. Mulanje complex, and the (more northern) Zomba Plateau s.l. These uplands are separated by about 65 km of lower lying land with different types of vegetation and climate. Material from these two regions may be distinguished as separate species, the southern populations having comparatively small and broad shells with some apertural dentition ('*M.* *hamiltoni*', lectotype designated), while the northern populations have noticeably larger and more slender shells with a more reduced apertural dentition ('*M.* *malavensis*'). Discussion of the type localities for both taxa shows that these are either localized in an unlikely place ('*M.* *hamiltoni*') or unclear ('*M.* *malavensis*'). Radula and genital anatomy of '*M.* *hamiltoni*' are described and depicted for the first time. Both species are ovoviviparous, a rarely reported phenomenon in the Streptaxidae. The genitalia are markedly different from what is known in various streptaxid genera with which these species may be or have been classified. In spite of the confused streptaxid taxonomy, a new genus, *Austromarconia*, is introduced with *Ennea hamiltoni* as type species.

Introduction

With a maximum shell length of nearly 30 mm what is generally known as *Marconia hamiltoni malavensis* has arguably the largest shell among the many streptaxid snails of the rich malacofauna of Malaŵi. Only the far bulkier *Afristreptaxis elongatus* (Fulton, 1899) may reach almost the same size. The former is so far only known with certainty from the Zomba Plateau s.l., whilst the nominate subspecies is known to inhabit the Mt. Mulanje complex of Malaŵi, about 65 km further to the south-east. These two mountainous areas are distinctly separated by a stretch of relatively low-lying country with an altitude of about 700-800 m and a different type of vegetation and climate. Records from elsewhere in Malaŵi seem unreliable and unlikely; the

¹ For no. 7 in this series see: Bruggen, A.C. van, 2002. Studies on the Streptaxidae (Mollusca, Gastropoda Pulmonata) of Malaŵi 7. *Gulella hildae* spec. nov., a rarity from the Mt. Mulanje complex. – *Basteria* 65: 101-104.

country may now be considered to be fairly well surveyed for land molluscs. The size of the shell and the occurrence of the species in areas of easy access and popular with travellers has caused it to be picked up frequently, so that it is present in a number of collections world-wide. Apparent absence elsewhere suggests that '*M.* *hamiltoni* s.l. is endemic to south-east Malaŵi. The present paper attempts to revise these two taxa and their distribution. Also, their generic assignment is critically discussed.

Museum acronyms are the following: BM for The Natural History Museum [formerly British Museum (Natural History)], London; IRSNB for Institut Royal des Sciences Naturelles de Belgique, Brussels; MCZ for Museum of Comparative Zoology, Harvard University, Cambridge (Mass.), U.S.A.; MRAC for Musée Royal de l'Afrique Centrale, Tervuren, Belgium; RMNH for the collection of the Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden; SMF for Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main, Germany. Other abbreviations are alc. for specimens in alcohol, l/d for the ratio length/major diameter of shells as an indication of the shape of the shell, and HMM for leg. Ms Hazel M. Meredith. Geographical details have been extracted from the National Atlas of Malawi (1983).

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Description of the two species

Ennea hamiltoni var. *malavensis* Kobelt, 1904, was described from a single shell. An analysis of the quite considerable range of variation in shell characters of all examined material of '*M.* *hamiltoni* s.l. shows that indeed two taxa can be distinguished on account of shell size, shape and apertural dentition (see table 1, fig. 7). Most other characters used by Kobelt (1904) to define his var. *malavensis* as compared to the

Table 1. Measurements of shells of *Austromarconia hamiltoni* and *A. malavensis* (all from Malaŵi). Nos. 1-31 refer to specimens from the Mt. Mulanje complex (*A. hamiltoni*), nos. 32-52 refer to shells from the Zomba Plateau s.l. (*A. malavensis*). No. 23 (asterisk) is the lectotype of *A. hamiltoni* (see fig. 1) and no. 43 (two asterisks) the holotype of *A. malavensis*; note that both the type specimens are probably wrongly localized. No. 6 is figured in figs. 3 and 5, no. 22 in fig. 2, and no. 52 in figs. 4 and 6. The last column (d) refers to the angular process in the apertural dentition, i.e.: - = no trace of any form of denticle; + = mere trace of swelling or tubercle; ++ = swelling or incipient tubercle; +++ = noticeable denticle or tubercle. Note the differences in size and apertural dentition of the two species.

number	length \times maj.diam.	l/d	length last whorl	aperture height \times diam.	number of whorls	d
1	17.5 \times 9.0 mm	1.95	11.6 mm	6.6 \times 5.7 mm	5 1/2	-
2	17.7 \times 8.7 mm	2.03	12.0 mm	7.4 \times 5.7 mm	5+	+
3	18.2 \times 8.8 mm	2.07	12.0 mm	8.0 \times 5.9 mm	5 1/2	+++
4	18.3 \times 9.4 mm	1.95	12.2 mm	7.9 \times 5.7 mm	>5	+
5	18.7 \times 9.3 mm	2.01	12.5 mm	7.9 \times 6.0 mm	<5 1/2	+
6	18.7 \times 9.4 mm	1.99	12.0 mm	7.5 \times 6.2 mm	-	-
7	18.8 \times 9.6 mm	1.96	12.7 mm	8.1 \times 6.1 mm	5+	+
8	19.0 \times 9.0 mm	2.11	11.9 mm	8.0 \times 5.7 mm	6	++
9	19.0 \times 9.1 mm	2.09	12.5 mm	6.9 \times 5.6 mm	5 1/2	++
10	19.0 \times 9.3 mm	2.04	12.5 mm	7.7 \times 5.6 mm	5 1/4	+
11	19.1 \times 9.9 mm	1.92	12.7 mm	7.7 \times 6.2 mm	5 1/2	+
12	19.2 \times 9.3 mm	2.07	13.1 mm	7.6 \times 6.1 mm	5 1/2	++
13	19.2 \times 9.4 mm	2.04	12.5 mm	8.6 \times 6.2 mm	>5 1/2	+
14	19.2 \times 9.6 mm	2.00	12.7 mm	7.6 \times 6.1 mm	5 1/2	+
15	19.2 \times 10.0 mm	1.92	13.1 mm	8.5 \times 6.2 mm	<5 1/4	+
16	19.3 \times 8.9 mm	2.17	12.5 mm	7.1 \times 6.0 mm	5 1/2	+
17	19.3 \times 9.2 mm	2.09	12.9 mm	7.7 \times 6.2 mm	5 1/2	-
18	19.4 \times 9.0 mm	2.15	13.2 mm	8.0 \times 6.0 mm	5 1/2	+
19	19.5 \times 9.4 mm	2.07	12.5 mm	7.6 \times 6.2 mm	-	+++
20	19.6 \times 9.1 mm	2.15	12.7 mm	7.7 \times 6.0 mm	5 1/2	++
21	19.7 \times 9.3 mm	2.12	15.0 mm	8.1 \times 5.7 mm	5 1/2	+
22	19.8 \times 9.7 mm	2.04	12.6 mm	8.4 \times 6.2 mm	5 1/2	+++
23*	19.9 \times 9.3 mm	2.14	13.1 mm	8.2 \times 6.0 mm	5 1/4	++
24	20.0 \times 8.8 mm	2.27	12.5 mm	7.7 \times 5.9 mm	5 1/2	+++
25	20.0 \times 9.1 mm	2.19	12.6 mm	8.0 \times 6.2 mm	5 3/4	+
26	20.2 \times 8.6 mm	2.35	12.5 mm	7.6 \times 6.0 mm	5 1/2	+
27	20.8 \times 9.7 mm	2.14	13.4 mm	8.5 \times 6.2 mm	5 3/4	+
28	21.4 \times 9.6 mm	2.23	14.2 mm	8.2 \times 6.2 mm	5 3/4	+
29	21.4 \times 10.3 mm	2.08	14.2 mm	8.7 \times 6.2 mm	5 1/2	-
30	21.5 \times 10.7 mm	2.01	14.5 mm	9.5 \times 7.1 mm	5 1/2	+
31	23.5 \times 12.3 mm	1.91	15.0 mm	9.7 \times 7.4 mm	5 1/2	+
32	23.7 \times 10.9 mm	2.17	16.0 mm	9.4 \times 7.6 mm	5 3/4	-
33	24.0 \times 11.1 mm	2.16	15.0 mm	9.4 \times 8.0 mm	5 3/4	+++
34	25.2 \times 10.6 mm	2.38	15.9 mm	10.2 \times 7.2 mm	5 3/4	-
35	25.2 \times 11.2 mm	2.25	16.9 mm	10.1 \times 8.0 mm	5 3/4	-
36	25.2 \times 11.5 mm	2.19	15.6 mm	9.6 \times 7.7 mm	<6	-
37	25.2 \times 12.1 mm	2.09	16.0 mm	9.2 \times 8.0 mm	5 1/2	-
38	25.7 \times 12.7 mm	2.02	15.9 mm	9.4 \times 7.9 mm	5 3/4	-
39	25.8 \times 12.1 mm	2.13	16.5 mm	10.0 \times 8.1 mm	5 3/4	-
40	26.0 \times 11.3 mm	2.30	15.0 mm	9.1 \times 7.6 mm	<6	+
41	26.0 \times 11.6 mm	2.24	15.6 mm	10.1 \times 8.0 mm	<6	-

42	26.4 × 12.0 mm	2.20	17.0 mm	10.0 × 8.5 mm	<6	-
43**	26.5 × 11.5 mm	2.30	16.2 mm	10.5 × 8.0 mm	6	+
44	26.5 × 11.8 mm	2.24	17.4 mm	10.2 × 8.4 mm	<6	-
45	26.8 × 11.7 mm	2.29	16.9 mm	10.0 × 8.0 mm	<6	-
46	26.9 × 12.2 mm	2.20	16.2 mm	10.6 × 8.1 mm	<6	-
47	26.9 × 12.4 mm	2.17	16.9 mm	10.2 × 8.7 mm	<6	-
48	27.4 × 11.8 mm	2.32	17.5 mm	10.7 × 8.2 mm	5 3/4	-
49	27.7 × 11.7 mm	2.37	17.4 mm	10.5 × 8.2 mm	5 3/4	+
50	27.7 × 12.2 mm	2.27	16.2 mm	10.7 × 8.4 mm	<6	-
51	28.4 × 12.2 mm	2.33	16.9 mm	10.0 × 8.2 mm	6	-
52	29.0 × 12.2 mm	2.38	16.9 mm	11.2 × 8.5 mm	5 3/4	+

'typical' form, i.e. relative height of the aperture, greater number of whorls, deeper suture, and more convex final whorls, appear not to be diagnostic. Shells of '*M' malavensis*' are generally longer and wider than those of '*M' hamiltoni*', but are statistically significantly more slender (Mann-Whitney test: $Z = -4.5$, $p < 0.001$).

It is a moot point whether these taxa be called species or subspecies of the one species. In the absence of any arguments favouring the alternative hypothesis, the present authors have opted to consider the two taxa full species. The fact that these two taxa are geographically separated suggests this to be a classical, almost textbook, case of allopatric speciation.

Incidentally, a superficial search for kindred patterns of distribution in animals and plants, i.e. obviously allied taxa on the Mt. Mulanje complex on the one hand and on the Zomba Plateau *sensu lato* on the other hand, has so far not led to a satisfactory result.

The species may be differentiated as follows:

- a - Shell comparatively small and broad, 17.5-23.5 × 8.6-12.3 mm (mean 19.5 × 9.4 mm), 1/d 1.91-2.35 (median 2.07), angular process in the aperture generally present, Mt. Mulanje area (figs 1-3, 6) '*M' hamiltoni*
- b - Shell larger and relatively more slender, 23.7-29.0 × 10.6-12.7 mm (mean 26.3 × 11.8 mm), 1/d 2.02-2.38 (median 2.24), angular process in the aperture generally absent, Zomba Plateau *s.l.* (figs 4-5) '*M' malavensis*

'Marconia' hamiltoni (E.A. Smith, 1897) (figs 1-3, 6-21)

Ennea johnstoni Smith, 1893 (nec Smith, 1887): 633, pl. 59 fig. 1 (type locality Fort Johnston [= Mangochi], Upper Shire River [see below], BM 93.8.23.16-22, lectotype, 3 paralectotypes and 3 juv.).

Ennea hamiltoni Smith, 1897: 364 (nom. nov. for *Ennea johnstoni* Smith, 1893 nec 1887).

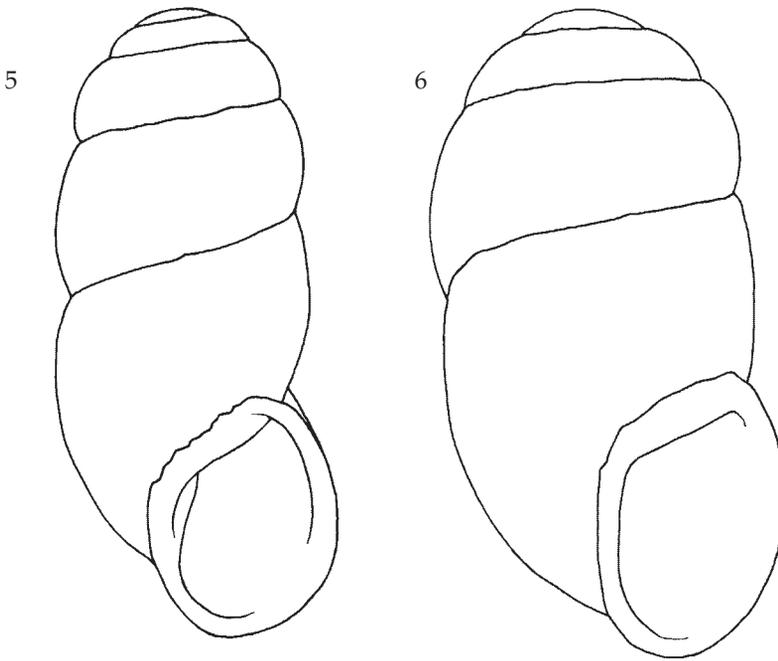
Edentulina hamiltoni; Kobelt, 1904: 295, pl. 36 figs. 21-22 (coloured); Kobelt, 1909: 56; Kobelt, 1910: 167.

Marconia hamiltoni; Richardson, 1988: 227.

Marconia hamiltoni hamiltoni; Meredith, 1983: 248; Van Bruggen & Meredith, 1984: 161.

Figs 1-4. *Austromarconia* shells. 1, lectotype of *Ennea hamiltoni*, length 19.9 mm (no. 23 in table 1), "Fort Johnston" (= Mangochi, probably erroneous locality, see discussion in text) (BM 93.8.23.16-22, the mark on the shell was probably made by Major M.C. Connolly, although a lectotype was never properly selected by publication); 2, *A. hamiltoni*, shell with periostracum, length 19.8 mm (no. 22 in table 1), Mt. Mulanje, Lichenya Plateau (RMNH ex MCZ); 3, *A. hamiltoni*, length 18.7 mm (no. 6 in table 1, see also fig. 5), Mt. Mulanje, Sombani-Chinzama path (RMNH); 4, *A. malavensis*, length 29.0 mm (no. 52 in table 1, see also fig. 6), Zomba Plateau, Chingwe's Hole (RMNH). Photos A. 't Hooft.





Figs 5-6. Shell outlines of the two species of *Austromarconia* to show differences in shape when size differences are absent. 5, *A. malavensis*, length 29.0 mm (no. 52 in table 1, see also fig. 4), Zomba Plateau, Chingwe's Hole (RMNH); 6, *A. hamiltoni*, length 18.7 mm (no. 6 in table 1, see also fig. 3), Mt. Mulanje, Sombani-Chinzama path (RMNH). E. Koopmans del.

Material examined (numbers refer to table 1). **Malawi**. – Mulanje Dist., Lichenya Plateau, 6,000 ft. [= c. 2000 m], viii.1948, leg. A. Loveridge (Loveridge, 1953: 451-453, MCZ 184723; nos. 3, 11, 12, 16, 22, duplicates in RMNH, fig. 2); Lichenya Plateau, c. 1900 m, xi.1977, HMM (nos. 9, 21, RMNH); Lichenya Plateau, *Widdringtonia* forest, leaf litter, 2000 m, 4.xi.1981, leg. Dr R. Jocqué (alc., MRAC 801.061); Lichenya Plateau, grassland, 17.xi.1981, leg. Dr R. Jocqué (MRAC 801.081); Lichenya Plateau, under *Helichrysum*, 2000 m, xi.1981, leg. Dr R. Jocqué (alc., MRAC 801.134); Lichenya Plateau, c. 1900 m, 24.v.1985, leg. L.J. Happold (alc., RMNH); Lichenya Plateau, burnt grassland (one juv. in *Helichrysum nitens* plant), c. 1900 m, 6.ix.1986, HMM (nos. 1, 2, 4, 5, 7, 13, 14, 18, 26, RMNH); Mt. Mulanje complex, Little Lichenya R., near Mini-Mini Estate settling tank, leaf litter, c. 800 m, 22.ii.1987, HMM (no. 31, RMNH); Sapatwa Peak, red route, under tufts of grass, 2750 m, 12.xi.1981, leg. Dr R. Jocqué (alc., MRAC 801.078); Chambe Plateau, *Podocarpus* gully, c. 2000 m, 14.vi.1980, HMM (RMNH); Chambe N. face shelf, evergreen forest, 1450 m, v.1986, leg. M. Spurrier (RMNH); Thuchila Plateau, 1950 m, 1.iv.1977, HMM (no. 10, RMNH); Mulanje Forest Reserve near Nandalanda Peak, between Thuchila and Chinzama Huts, rocky valley with scanty vegetation, on wet rock in wet gully, 15°53.8'S 35°37.7'E, 2280 m, 15.i.2002, leg. K.-D.B. Dijkstra (alc., 1 immat., RMNH, fig. 10); Sombani-Chinzama path, c. 2000 m, 30.x.1976, and Thuchila, 1950 m, iv.1977, HMM (no. 6, figs 3 and 6, RMNH); Sombani Plateau, on newly cleared firebreaks, c. 2000 m, 28.v.1983, HMM (nos. 15, 24, 25, 27, 28, 29, RMNH); ibidem, 3.vii.1983, leg. Dr. J. Patterson (nos. 17, 19, 20, RMNH); Sombani Plateau, grassland, c. 2000 m, 8.i.1985, leg. Dr. J. Patterson (alc., RMNH); Mt. Mulanje, 1987 or 1988, leg. J. Chapman (no. 30, RMNH); Mt. Mulanje, "7,200 ft. [= c. 2400 m] in a marsh", 15.xi.1969, leg. J. Mtunda (no. 8, RMNH).

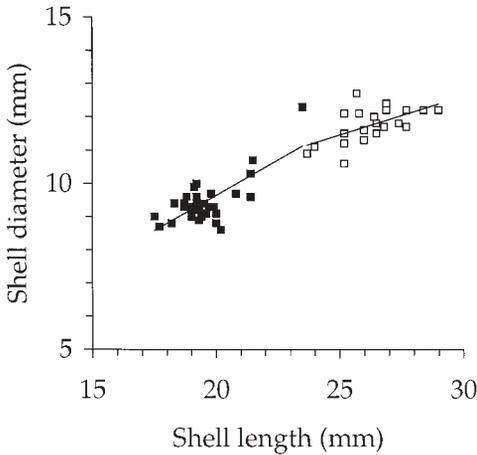


Fig. 7. Shell height (length) plotted against shell diameter for *Austromarconia hamiltoni* (■) and *A. malavensis* (□).

Possibly wrongly localized material: "Fort Johnston [= Mangochi], Upper Shire River", leg. A. Whyte [BM 93.8.23.16-22, **lectotype** (here designated, no. 23, fig. 1), 3 paralectotypes and 3 juv.]; "top of Mt. Zomba", 6000 ft. [= c. 2000 m], A. Sharpe (BM 95.5.14.1, the shell measures 19.6×9.7 mm and therefore seems to belong to '*M. hamiltoni*'); "Malosa (Nyassa)", ex S. Putzeys colln. (MRAC 16954; the shell measures 15.9×9.6 mm and therefore seems to belong to '*M. hamiltoni*'); "Lake Nyasa", ex Sowerby & Fulton, M. Connolly colln. (BM 1937.12.30.467, 19.2×9.6 mm); "Lac Nyassa", ex H.C. Fulton, ex P. Dupuis colln. (IRSNB, 19.4×9.5 mm).

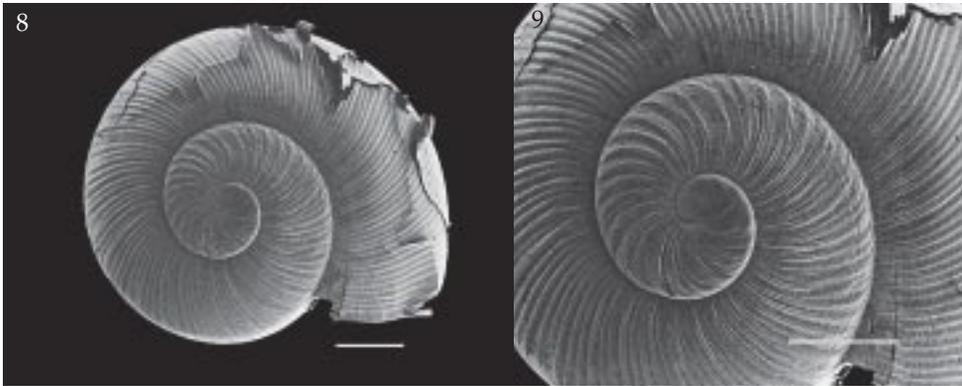
Diagnosis.— The smaller and least slender of the two species: shell 17.5-23.5 \times 8.6-12.3 mm, mean 19.5×9.4 mm, l/d 1.91-2.35, median 2.07 (fig. 7), length last whorl 11.6-15.0 mm, aperture height \times major diameter 6.6-9.7 \times 5.6-7.4 mm,

apertural dentition usually in the form of a more or less developed angular process.

Description of shell.— Shell (figs 1-3, 6) medium-sized, elongate cylindrical, narrowly rimate or with closed umbilicus, with dark greenish-brown (deciduous) periostracum (fig. 2), body whorl very slightly transparent when fresh, shell white and sub-transparent when dead. Spire produced, sides subparallel to parallel, apex flattened to depressed mamillate, costulate. Embryonic shell (ex utero, figs 8-9) up to 2.3 whorls (largest examined specimen), nearly 1.6 times as wide as high, periphery somewhat angulate, open but narrowly umbilicate (umbilicus c. 0.1 of shell width), sculptured with regular, oblique and somewhat curved, radial ribs from about $\frac{1}{4}$ whorl onwards; this sculpture is usually rather worn in adult shells. Transition between embryonic shell and later whorls not marked by an interruption of or change in sculpture. Total whorls of adult shell slightly more than five to as many as six, hardly convex. Postembryonal whorls sculptured with fairly coarse, straight and oblique, somewhat distant and little prominent, costulae, interstices narrower than costulae; sutures shallow though somewhat impressed, subcrenellate to crenellate. Aperture elongate ovate, labrum slightly incrassate and reflected, with two-fold to nearly completely absent dentition, viz. (1) an angular process which varies from almost complete absence to a proper tubercle and even rarely an inrunning lamella, but usually in the shape of a mere swelling, and (2) a columellar lamella which varies from complete absence (the usual condition) to a faint twist of the columella.

Animal. — A living adult with a shell of about 20 mm from the Thuchila Plateau exhibited a bright yellow dorsum, creamy yellow sides and red tentacles (field notes of Ms Meredith, 1.iv.1977). A subadult was bright orange (fig. 10).

Genitalia.— Four specimens were dissected (Lichenya Plateau, under *Helichrysum*, 2000 m, xi.1981, leg. Dr R. Jocqué, MRAC 801.134, figs 11-15). Atrium small, indistinct. Penis about 14 mm long, rather simple, elongate, slender and muscular. The vas deferens enters the penis subapically, cutting off a glandular(?) penial caecum of about 1.5



Figs 8-9. Embryonic shell of *Austrorconia hamiltoni* ex utero (Mt. Mulanje, Lichenya Plateau). SEM photos J. Goud. Scale bars 1 mm

mm long. Penial retractor wide but unbranched, originating from the columellar muscle complex and inserting on the penial apex where it covers both the caecum and the point of entrance of the vas deferens. Numerous hard and tiny spines cover much of the internal wall of the penis except for the caecum and the uppermost part of the penis surrounding the outlet of the vas deferens; a spine-free corridor runs from the point of entrance of the vas deferens towards the atrium, becoming less distinct on the lower half of the penis. The density of these spines is lowest near the atrium (less than 40 per 0.25 mm²) and highest in the upper quarter of the penis, where they constitute a dense carpet with up to 200-300 spines per 0.25 mm². The spines (fig. 15) are dark brown, rather uniform, long and slender with a curved apex. They vary in size to a limited extent but seem always <100µm, the ones measured being 80-93 µm long. Vas deferens free, i.e. not partly enveloped by a penis sheath; it is little convoluted and of about equal width along its course alongside the penis, to which it is attached by tissue fibres, but widens from the peniovaginal junction to its point of exit from the spermoviduct. Vagina somewhat dilated and swollen, c. 1.5-2.0 mm long, immediately above of which the duct of the bursa copulatrix starts. At this point some straps of muscle tissue are present that attach the female genitalia to the body wall. Duct of bursa copulatrix long and thin, with two convolutions and terminally an elongate-ovate bursa. Animal ovoviviparous; the greatly enlarged oviduct contains various (up to about five) embryos in different developmental stages, the largest possessing a shell of 2.3 whorls (for details of embryonic shell see sub 'Description of shell'). Hermaphrodite duct not strongly convoluted, but with two diverticula, the upper very long, slender, coiled, not covered by the albumen gland, the lower shorter, strait, slender and only visible after removal of some albumen gland tissue. The terminology of the organs associated with the carrefour region is rather confused. Following studies by Visser (1973) on *Gonaxis gwandaensis* (Preston, 1912), the long, exposed diverticulum is termed vesicula seminalis ('fertilization pouch' of Tompa, 1984), the hidden one receptaculum seminis ('spermathecal sac' of Tompa, op. cit.). Schileyko (2000) appears to use the term 'talon' for the former.

Radula.— Two radulae (figs 16-19) were studied by SEM. When stretched and



Fig. 10. *Austromarconia hamiltoni*, photograph of live immature from Mt. Mulanje, Mulanje Forest Reserve near Nandalanda Peak, shell length 16.0 mm, $5\frac{1}{4}$ whorls (RMNH, alc.). Photo K.-D. B. Dijkstra.

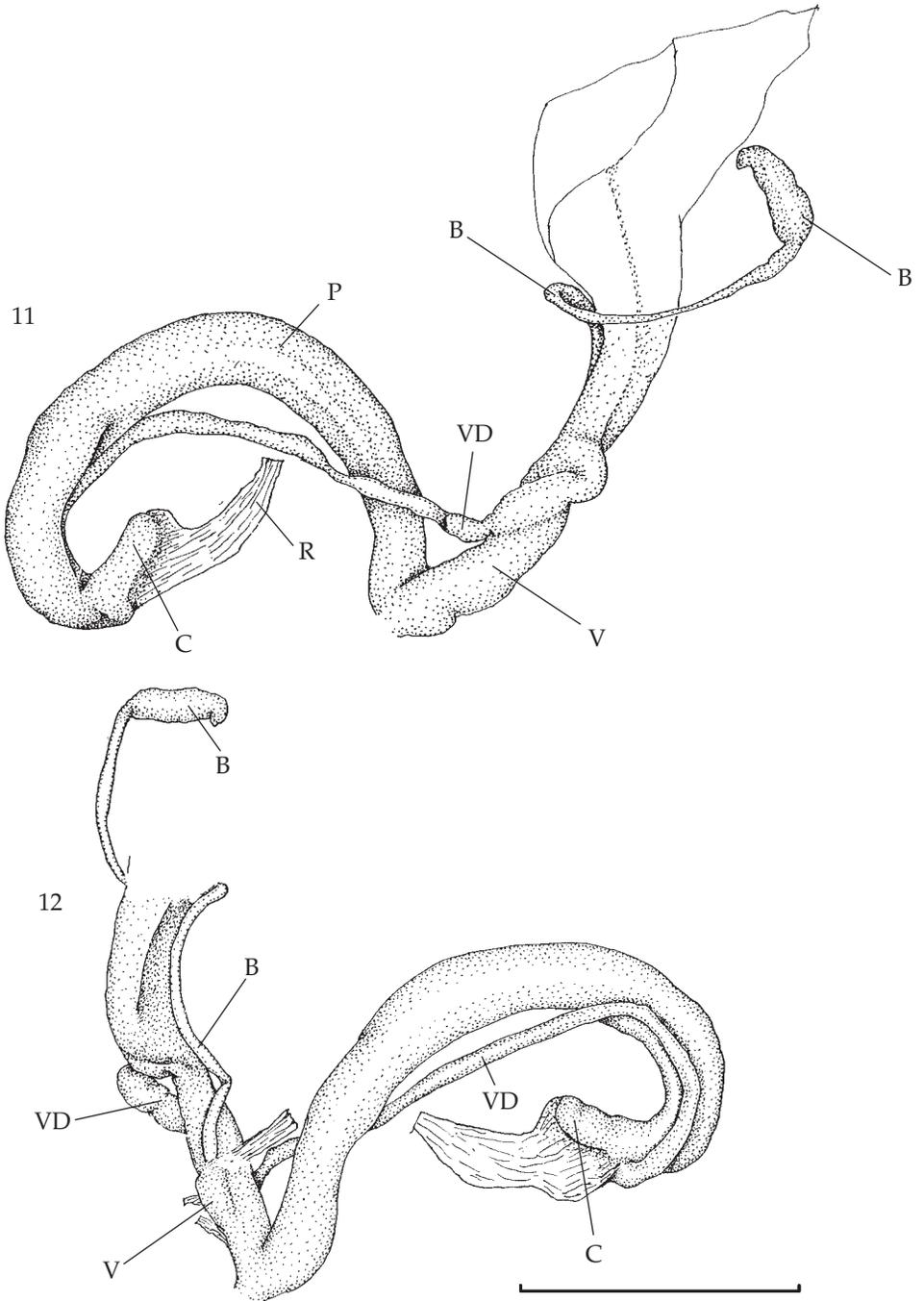
dried, these are 14-15 mm long and at most about 2.5 mm wide. Teeth are arranged in about 55 rows; central tooth absent. Formula of half a row: 0-8-11 and 0-7-12. Teeth rather simple and uniform, without side cusps. The teeth increase in size until the 7th or 8th tooth, after which the teeth gradually become smaller towards the outer edge. Apart from size little difference in shape was observed between the laterals and marginals.

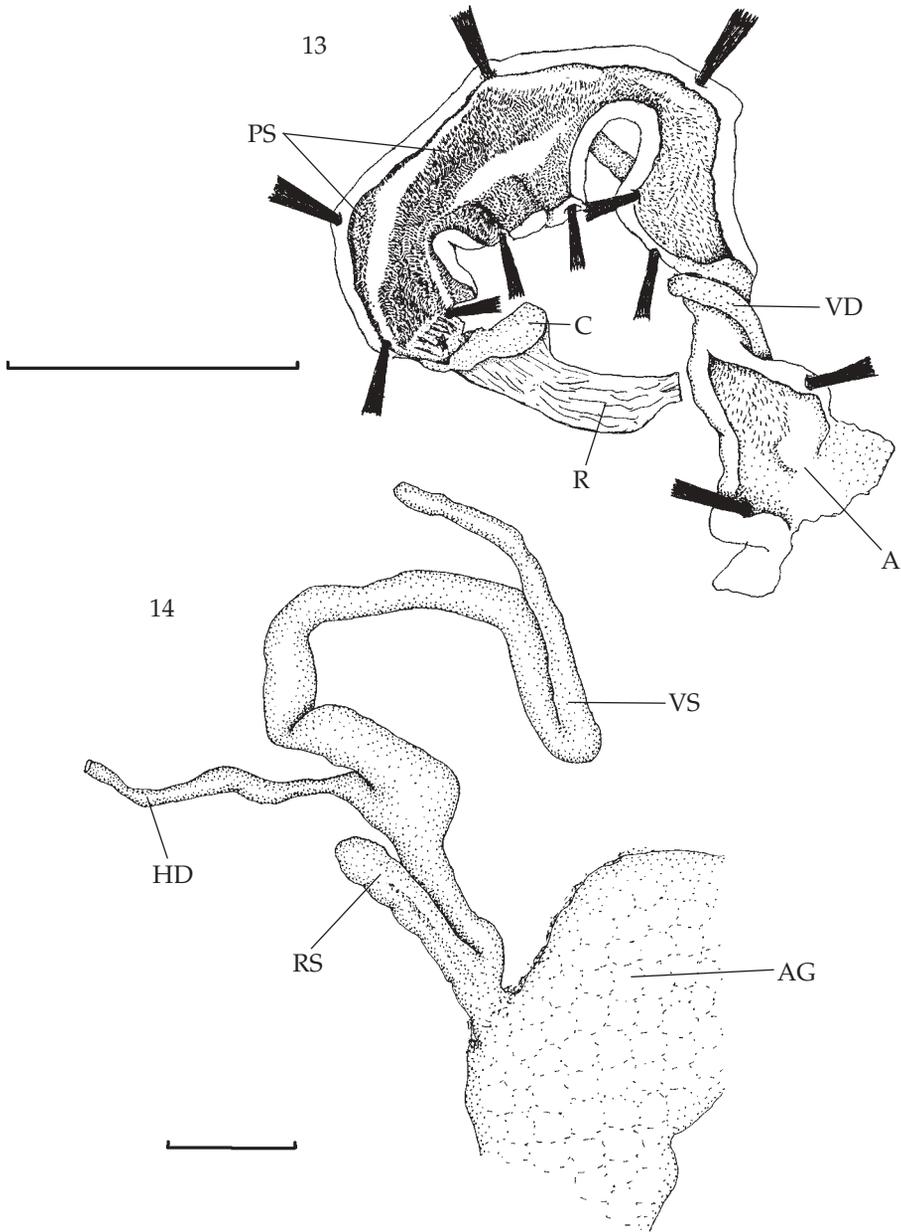
Distribution.— Mt. Mulanje area in south-eastern Malaŵi (roughly between $15^{\circ}51'$ and $16^{\circ}01'S$ and between $35^{\circ}31'$ and $35^{\circ}44'E$, i.e. an area of c. 18×23 km, fig. 20).

Type locality.— The type locality of *Ennea johnstoni* is “Fort Johnston [now Mangochi], Upper Shire River”. The species has never again been found there, although a number of collectors, inclusive of Ms. Meredith and the senior author, have worked in the area. Mangochi marks the exit of Lake Malaŵi in the form of the Shire R. and is situated in an area of around 500 m. The habitat in or near Mangochi seems unsuitable for *M. hamiltoni* and it is unlikely that the species actually lives at the type locality (fig. 20A). There may have been a mix-up of labels.

Etymology.— Originally the species was called *Ennea johnstoni* by E.A. Smith in 1893. However, this name was preoccupied by *E. johnstoni* E.A. Smith, 1887, so that in 1897 Smith himself had to propose the nomen novum *Ennea hamiltoni*. Both names refer to the outstanding Victorian pioneer Sir Harry Hamilton Johnston (1858-1927), first administrator (styled ‘Consul’) of Nyasaland (1891-1897), whose collector Alexander Whyte (1831-1912) obtained the type series of the species.

Ecology.— ‘*M. hamiltoni*’ is a mountain forest/grassland ecotone dweller. It has





Figs 11-14. Genital anatomy of *Austromarconia hamiltoni* from Mt. Mulanje, Lichenya Plateau. 11-12, different views of distal genitalia; 13, penis, cut open to give an impression of the internal organisation and distribution of the spines (these are actually more numerous, not every individual spine is shown); 14, carrefour region. Abbreviations: A, atrium; AG, (remains of) albumen gland; B, bursa copulatrix; C, penial caecum; HD, hermaphrodite duct; P, penis; PS, penial spines; R, penial retractor muscle; RS, receptaculum seminis; V, vagina; VD, vas deferens; VS, vesicula seminalis. Scale bar 1 mm.



Fig. 15. Penial spines from upper portion of penis, see fig. 13. Scale bar 100 μ m. Photo E.J. van Nieukerken.

family Urocyclidae] from the Thuchila evergreen forest and young *Achatina*" (field notes of Ms. Meredith, 1.iv.1977).

'Marconia' malavensis (Kobelt, 1904) (figs 4-5, 7, 20)

Ennea (*Uniplicaria*) *hamiltoni*; Smith, 1899: 580 (this should refer to '*M' malavensis* as the localities mentioned, Mt. Zomba and Malosa, both at 6000 ft., are within the range of that species).

Edentulina hamiltoni var. *malavensis* Kobelt, 1904: 296 [not pl. 35 fig. 8 (coloured) - this figure depicts *Ennea johnstoni* Smith, 1887, now *Edentulina johnstoni*, a West African species from Cameroon, etc.] (type loc. Nyassaland [= Malawi], Malava [see below], holotype SMF 8417, vide Zilch, 1961: 88, pl. 6 fig. 28).

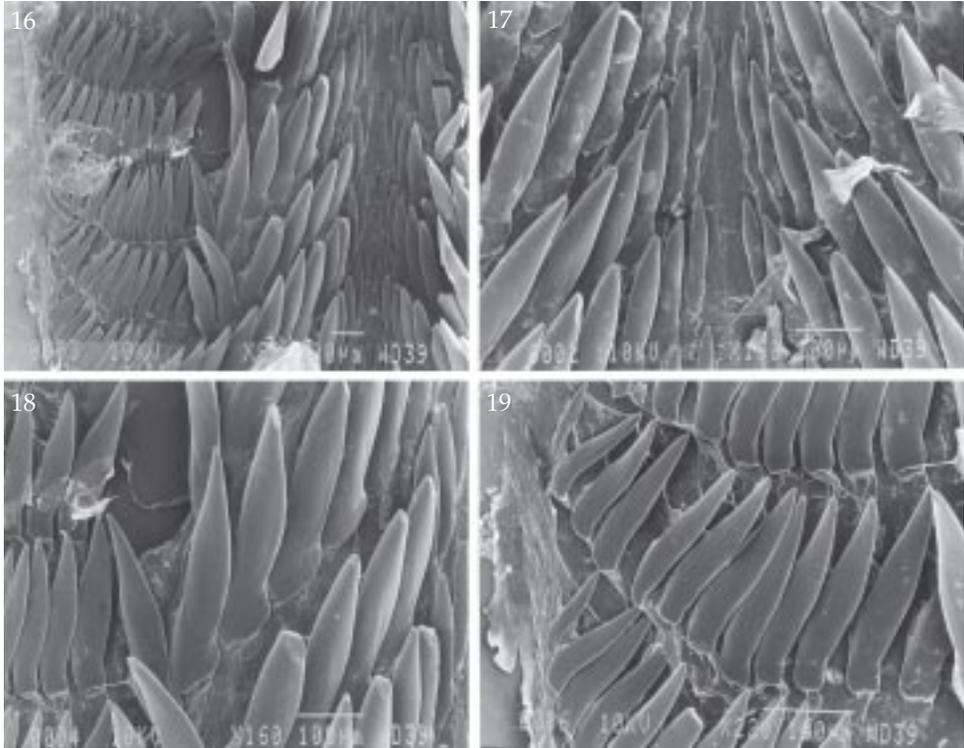
Marconia hamiltoni malavensis; Zilch, 1961: 88, pl. 6 fig. 28; Meredith, 1983: 248; Van Bruggen & Meredith, 1984: 161.

Material examined (numbers refer to table 1). **Malawi**, Zomba Dist., Zomba Plateau, grassland on slope below radio masts, 1860 m, 17.viii.1986, HMM (nos. 35, 41, RMNH); forest below radio mast, leaf litter, 1860 m, 26.vii.1988, HMM (RMNH); slopes of Malumbe, burnt grassland, c. 2000 m, 17.x.1985, HMM (nos. 33, 34, 36, 44, 51, RMNH); Chingwe's Hole, firebreak at edge of trial pine plantation, c. 1900 m, iv.1976, HMM (nos. 45, 46, 47, 52, figs 4 and 5, RMNH); Chingwe's Hole, grassland, c. 1900 m, 17.i.1983, leg. Dr. B. Owen (no. 39, RMNH); firebreak at edge of trial pine plantation, c. 1900 m, 1.vi.1977, HMM (nos. 38, 49, 50, RMNH); burnt grassland near trial pine plantation, c. 1900 m, 28.viii.1983, HMM (nos. 37, 42, 48, RMNH); Malava [see below], ex H.C. Fulton, O. von Moellendorff colln. (no. 43, SMF 8417, **holotype**; Zilch, 1961: 88, pl. 6 fig. 28 - this is also the shell depicted in colour in Kobelt, 1904: 296, pl. 36 figs 21-22); "Malosa & Zomba Plateau", 1800-1900 m, 10.x.1976, HMM (nos. 32, 40, RMNH); "Malosa", 6000 ft. [= c. 2000 m] (BM 97.12.31.54-7, 5 shells: 24.1-27.6 \times 11.5-13.0 mm, l/d 1.86-2.26, all 5 1/2 whorls, denticle absent to very poorly developed - in pencil on original label 'Types': impossible because type material consists solely of holotype!); "co-type Nyassa", ex S. Putzeys colln. (MRAC 16957, this cannot be a cotype = syntype, see above; it measures 27.0 \times 14.0 mm and therefore belongs to the species *malavensis*); "Nyika Malasa, Nyassaland 6,000 ft. [= c. 2000

been found to occur in grassland bordering mountain forests and is usually exposed in the form of empty shells in numbers on the ground after grass fires (fig. 21). A shell from the Sombani Plateau (Mt. Mulanje complex), collected on 28 May 1983, is closed by an epiphragm. In this part of Africa the month of May represents the dry winter season.

Hypsometrical distribution is from 1450 to 2750 m. One specimen (no. 31 in the table, Mini Mini Estate) is from 800 m and Ms. Meredith comments (in litt., 1.xi.2002) "at a much lower altitude than the others. I wonder if it got washed down!"

The adult described above under 'Animal' fed on a specimen of "conical snail [*Trochozonites sharpei* Smith, 1899,



Figs 16-19. Radula of *Austromarconia hamiltoni* from Mt. Mulanje, Lichenya Plateau. 16, overview of a few rows of teeth on left side (note absence of central tooth and simple shape of laterals and marginals); 17, close view of centre of radula (note absence of side cusps on teeth); 18, further enlargement of part of fig. 16 (note shape and base of lateral teeth); 19, view of left margin of three rows (note shape and size of marginal teeth). All scale bars 100 μ m. SEM photos J. Goud.

m]”, “BRIT. MUS. exchange”, ex H.C. Fulton (MRAC 97404, the shell measures 25.8 \times 12.8 mm; the locality is obviously Malosa); “Malara 6,000 ft. [= c. 2000 m]”, ex H.C. Fulton, P. Dupuis colln. (IRSNB, 25.0 \times 12.0 mm); ibidem, ex H.C. Fulton (RMNH, 25.8 \times 11.8 mm); “Nyassa”, ex Sowerby & Fulton, Dautzenberg colln. (IRSNB, 25.4 \times 12.8 mm).

Diagnosis.— The larger and more slender of the two species: shell 23.7-29.0 \times 10.6-12.7 mm, mean 26.3 \times 11.8 mm, l/d 2.02-2.38, median 2.24 (fig. 7), length last whorl 15.0-17.5 mm, aperture height \times major diameter 9.1-11.1 \times 7.2-8.5 mm, apertural dentition usually absent.

Description of shell.— See above under ‘*M’ hamiltoni*’; the diagnosis emphasizes the differences with this species, i.e. size, shape and apertural dentition. The few examined embryonic shells are very similar to those of ‘*M’ hamiltoni*’ at a comparable number of whorls, perhaps a trifle larger, the largest comprising 2 1/2 whorls.

Animal.— Unknown.

Genitalia.— Unknown. Ovoviviparous.

Radula.— Unknown.



Fig. 21. Regenerating burnt grassland on Mt. Mulanje, Lichenya Plateau, with flowering *Helichrysum nitens* (Compositae), 6.ix.1986. When the fire goes through quickly, the grass tufts and particularly the clumps of *H. nitens* survive and must afford considerable shelter to *Austromarconia hamiltoni* snails. Photo J. Chapman, courtesy Ms. H.M. Meredith.

Distribution.— Zomba Plateau s.l. in south-eastern Malaŵi (roughly between 15°13' and 15°23'S and between 35°15' and 35°22'E, i.e. an area of c. 18 × 12 km, fig. 21). Malosa mountain forms a northern extension of the Zomba Plateau.

Type locality.— “Malava” (for discussion see below sub Etymology).

Etymology.— Fulton’s locality Malava could not be traced; it is not featured in three gazetteers consulted (Ansell & Dowsett, 1988; Atlas of Malawi, 1983; Benson & Benson, 1977) and is merely listed with a question mark in a fourth one (Meredith, 1983). In the official U.S. Malaŵi gazetteer (Malawi, 1970) there are three names resembling Malava, viz., Malasa (a stream at 16°05'S 35°29'E), Malavi (13°43'S 33°42'E), and Malaza (14°06'S 34°01'E).

◀ Fig. 20. Maps showing (A) types of vegetation in southern Malaŵi (note area “a” on Mt. Mulanje, which about equals the distribution of *Austromarconia hamiltoni*, and another area of this category, i.e. “Montane grassland/evergreen forest”, north of Zomba, which about equals the distribution of *A. malavensis*; Fort Johnston = Mangochi, the type locality of *A. hamiltoni*, is situated at the very top of this map between Lake Malombe and the swampy area to the north of this lake – it is clear that the species cannot exist here); (B) shadow relief map of southern Malaŵi with the gap between the ranges of *A. hamiltoni* (Mt. Mulanje area near the border with Mozambique to the south of Lake Chilwa is situated further north) and *A. malavensis* (part of Shire Highlands NE of Zomba); (C) the position of Malaŵi in Africa. Maps A and C are based on Van Bruggen & Meredith (1984: 157, fig. 1), map B represents part of the shadow relief map in Debenham (1958).

In the present authors' opinion, Malava could be a spelling variant of (Mt.) Malosa for two reasons, i.e. (1) large shells of the species have been found there, and (2) there is also the spelling 'Malara' on labels accompanying other large shells procured from the London shell dealer H.C. Fulton (IRSNB, MRAC, RMNH). The word Malava could also simply be due to faulty transcription of labels.

Ecology.— '*M. malawensis* is also a mountain forest/ecotone dweller. Hypsometrical distribution is from 1800 to 2000 m; this is within the range of what is known for '*M. hamiltoni*.

The sample collected on 1.vi.1977 (Zomba Plateau, firebreak at edge of trial pine plantation) encompassed one empty adult shell with four young shells inside showing that the species is ovoviviparous.

Ovoviviparity

It appears that both species are ovoviviparous, a manner of reproduction rarely encountered in the family Streptaxidae (see below). Ovoviviparity as a reproductive strategy (Tompa, 1984: 122) is usually considered to be an adaptation to adverse environmental conditions, i.e. it shortens the initial life phases so as to overcome e.g. a short summer season or a dry period. The species occur at fairly great altitudes in the mountains in comparatively open habitat. In the winter season climatic conditions may be severe at times, particularly as regards temperatures at night, but also in the daytime. For example, Chapman & White (1970: 14) write: "The mean annual temperature . . . of the high plateaux [is] less than 18.3°C (65°F). Ground frosts are frequent in June and July on the high plateaux, . . ." Conceivably ovoviviparity has survival value here. Correlation of this phenomenon with a large aperture hardly obstructed by lamellae and/or teeth, so that easy exit of the juvenile snails is guaranteed, should be noted.

Ovoviviparity has been relatively rarely explicitly reported in species of Streptaxidae, but does occur at least occasionally. Recently Emberton (2002: 71) found this to be the dominant mode of reproduction among Madagascan *Gulella*-like species, and he even used ovoviviparity as a character to distinguish these streptaxids from similarly-shelled subulinids. However, ovoviviparity also occurs in various African subulinid genera, e.g. *Pseudoglessula* Boettger, 1892 (Ortiz de Zárate & Ortiz de Zárate, 1959; De Winter, unpublished data). Herbert (2002) reported another case of ovoviviparity in his recently described South African *Gulella salpinx*. In the subfamily Streptaxinae ovoviviparity has been reported in a few species only, like *Gonaxis maugerae* (Gray, 1837) (Degner, 1934).

Conservation

The two species in this complex are still locally frequent. The habitat of these probably endemic Malawi taxa is not yet under threat because of its seemingly inhospitable character and limited suitability for agriculture, so that at present the continued existence of the species seems assured. Mounting human population pressure causes an increasing threat from fire as cultivation creeps further up the sides of the mountain. However, fire has spread up over the mountains for many years past and the snails have survived (Meredith, in litt., 1.xi.2002).

Generic classification with the description of a new genus

Generic assignment in the Streptaxidae is still mostly based on shell morphology; the anatomical data available do not yet materially contribute to this arrangement (but see Schileyko, 2000: 771-835). The taxa under consideration have been classified since Zilch (1961) with the genus *Marconia* Bourguignat, 1889 (type species *Ennea lata* E.A. Smith, 1880). According to Zilch's widely used manual (Zilch, 1960: 564) the '*M. hamiltoni*' complex belongs to the genus *Marconia*, subgenus *Stenomarconia* Germain, 1934 [type species *M. (S.) jeanneli* Germain, 1934, from Mt. Kenya; see also Anonymus, 1952: 161, pl. 7 fig. 1] by virtue of its cylindrical shell shape. In a later paper by Zilch (1961: 88) the species complex is simply shown under *Marconia*. However, at about the same time Verdcourt (1961: 18) gave *Stenomarconia* generic status, partly based on genitalia and radula data. Attention is drawn to his remark on the shell colour: "..... of a peculiar light to dark olive colour very unusual in this family". As regards relationships he states "This genus is, I believe, more related to *Streptostele* Dohrn and its allies than it is to *Gonaxis* Taylor or *Edentulina* Pfr."

In various older publications (see synonymy above) the '*M. hamiltoni*' complex is assigned to *Edentulina* L. Pfeiffer, 1856 (type species *Bulimus ovoidea* Bruguière, 1792). Although *Edentulina* is probably a heterogeneous assembly of species, the taxa attributed to this genus differ conchologically by e.g. an elongate ovate shell with a large, somewhat inflated, body whorl that may be slightly askew. A dark periostracum is hardly known among *Edentulina*. In some characters of the genital anatomy described in the literature (Degner, 1934; Ortiz de Zárate & Ortiz de Zárate, 1956; Verdcourt, 1961; Gerlach & Van Bruggen, 1999; Schileyko, 2000; unfortunately Emberton, 1999, has no anatomical data included), the species nowadays classified with *Edentulina* (see also Bequaert & Clench, 1936a; Richardson, 1988) differ markedly from the '*M. hamiltoni*' complex, e.g. in having a penis sheath partly enveloping the penis.

The regular cylindrical shape and size of *M. hamiltoni* is also found among the extensive streptaxid radiation of the Mascarene Is. (Mauritius, Réunion) for which the generic names *Gonospira* Swainson, 1840, and *Orthogibbus* Germain, 1919, are employed. Obviously in this case the resemblance is superficial and no doubt due to convergent evolution, which is confirmed by Steenberg's (1936) and Schileyko's (2000) anatomical data. The malacofauna of the Mascarenes, remnants of ancient Gondwanaland, displays a streptaxid radiation almost completely divorced from that on the African mainland, although the name *Gonospira* has been tentatively used for one East African species [*G. expatriata* (Preston, 1910), Verdcourt, 1983: 229].

We agree with Tattersfield (1999) that the generic assignment of African Streptaxinae species (in the sense of Zilch, 1960, and subsequent authors, and not according to Schileyko, 2000) is to a large degree arbitrary at the present state of knowledge. Too little is known of the anatomy of too few species to clarify the existing confusion. Since Tattersfield's (1999) paper, Schileyko (2000) significantly altered the traditional higher taxonomy of the Streptaxidae. For instance, he introduced a new subfamily Marconiinae, comprising the genera *Stenomarconia*, *Marconia* and *Macrogonaxis* Thiele, 1932 (of the last the anatomy being unknown!) and redefined other subfamilies by including genera largely on the basis of what seem rather trivial characters taken partly from specimens of which the generic assignment and species identification may be questionable.

In view of the large size and undistorted spire of the two species dealt with here, our taxa might be classified with the African genera *Afristreptaxis* Thiele, 1932, *Marconia*, and *Stenomarconia*. The nomenclatorially disputed genus *Eustreptaxis* L. Pfeiffer, 1878 [or 1879 (see Bequaert & Clench, 1936b), but not 1877, and not a nomen nudum as claimed by Schileyko, 2000], is left out of consideration here. *Gonaxis* Taylor, 1877 s.l. is traditionally (but by no means generally) used for species with more strongly distorted spires.

Thiele (1911) described the genital anatomy of the type species of *Afristreptaxis* (*Streptaxis vosseleri* Thiele, 1911) which appears to differ among others by having a distinct penis sheath. Schileyko only provided anatomical details of *A. elongatus*, a species which is otherwise anatomically different and unlikely to fit in *Afristreptaxis*, but of which the hermaphrodite duct seems to be very strongly convoluted (Van Bruggen, 1964, copied in Schileyko, 2000: 834). In any case the shells attributed to *Afristreptaxis* are more globose.

The two species have previously been classified (as subspecies of a single species) with the genus *Marconia*. Authors disagree about the identity of the type species of this genus, but seem to agree that *Marconia* species have a short, undistorted or very little distorted, shell quite unlike the elongate, cylindrical shell of the species dealt with here. In fact, the shells of the two taxa discussed here much more resemble those of *Stenomarconia jeanneli* in shape and colour. However, the description of the genitalia of this species by Verdcourt (1961) seems to preclude assignment to *Stenomarconia*: the penis of *Stenomarconia* is quite short and has a long caecum (Verdcourt, 1961). According to Schileyko's (2000) interpretation of the genus, *Marconia* differs by the possession of a short penis with a strongly developed lateral, rather than apical, penial caecum, the presence of a short penial sheath, the lack of a penial retractor muscle, less numerous and differently shaped penial hooks, and in having an inconspicuous talon in Schileyko's sense. However, Schileyko's (2000) description seems to be based on dissection of a specimen of *M. elgonensis* (Preston, 1913), of which the generic placement in *Marconia* is not undisputed.

In the absence of any likely or satisfactory genus to lodge the species, described above as '*M.* *hamiltoni*' and '*M.* *malavensis*', it seems appropriate to propose a new generic entity to provide a steady anchor in the chaotic higher classification of the Streptaxinae sensu Zilch (1960).

The new genus is the following:

Austromarconia gen. nov.

Diagnosis.— Shell fairly large (height 17.5–29 mm), cylindrical with regularly produced spire with flattened apex with most of the embryonic whorls regularly costulate, costulation continued on later whorls, covered with deciduous dark greenish-brown periostracum; aperture with or without a little prominent angular process. Reproduction characterized by ovoviviparity. Penis elongate with a terminal short caecum, internal wall densely covered with tiny, uniformly elongate, hard spines of <100 µm length. Vas deferens free, i.e. not covered by a penis sheath. Hermaphrodite duct not strongly convoluted, with a very long and exposed vesicula seminalis.

Type species.— *Ennea johnstoni* E.A. Smith, 1893 [now *Austromarconia hamiltoni* (Smith, 1897)].

Other species.— *Austromarconia malavensis* (Kobelt, 1904).

Distribution.— Southern Malaŵi uplands.

Etymology.— *Austromarconia* (gender: feminine), Latin, from *auster* = the south, and *Marconia*, to denote geographical origin and erstwhile generic assignment.

Differences between *Austromarconia* and kindred streptaxids are discussed above.

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² This is not an altogether commonly available book. However, there is an also somewhat obscure facsimile reprint published in 1969 by the Negro Universities Press (a division of Greenwood Publishing Corp.), New York, in which, unfortunately, all colour illustrations are reproduced in black-and-white.

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