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REVISION OF THE GENUS *ACAVUS* FROM SRI LANKA (GASTROPODA: ACAVIDAE)

BERNHARD HAUSDORF¹ and KALIKA K. PERERA²

¹Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Martin-Luther-King-Platz 3,
D-20146 Hamburg, Germany; ²134-12, Highlevel Road, Maharagama, Sri Lanka.

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ABSTRACT

The genus *Acavus* from Sri Lanka includes three species, *Acavus haemastoma* (Linnaeus), *Acavus superbus* (L. Pfeiffer) and *Acavus phoenix* (L. Pfeiffer) with two subspecies, *Acavus phoenix phoenix* (L. Pfeiffer) and *Acavus phoenix castaneus* new subspecies. The conchological and anatomical differences between these species, as well as their intraspecific variation are described. Their distribution is shown on maps and all locality records are listed. The presence of extensive intraspecific polymorphism, the development of geographical subspecies and the presumable hybridization between some species show that the *Acavus* species are not isolated relict species, but that speciation is in progress and that the radiation of the *Acavus* species is probably much younger than the radiation of the acavid genera. The three *Acavus* species are not acutely endangered at present. In contrast to many other land snails, there is no risk of a rapid decline of the *Acavus* species due to deforestation, because these species also occur in synanthropic habitats.

INTRODUCTION

The Acavidae of Sri Lanka early attracted the attention of naturalists because they are colourful and attractive. The Acavidae are represented in Sri Lanka by two endemic genera, *Acavus* and *Oligospira*. Already Linnaeus (1758) described the first *Acavus* species, *A. haemastoma*. Colour and form varieties of this species were described later by Born (1778), Albers (1854, 1857), Westerlund (1887) and Pilsbry (1890a, 1890b), partly as separate species. The two other species recognized in the present paper, *A. superbus* (L. Pfeiffer, 1850) and *A. phoenix* (L. Pfeiffer, 1854), were described a century after Linnaeus by L. Pfeiffer (1850, 1854). Finally, additional colour varieties of *A. superbus* were described by L. Pfeiffer (1856) and Nevill (1881).

In his revision of *Acavus*, Pilsbry (1890a)

maintained *H. fastosus* Albers, 1854 and *H. prosperus* Albers, 1857 as separate species besides the three already mentioned, *A. haemastoma*, *A. superbus* and *A. phoenix*, because he has not seen specimens of these forms. Randles (1900) published an important comparative anatomical investigation of the anatomy of the *Acavus* species. He followed the classification of Pilsbry (1890a). Sykes (1900) and Gude (1914) also followed Pilsbry (1890a). However, Sykes (1900) already suspected that *A. prosperus* was only a variety of *A. haemastoma* and that *A. fastosus* was also closely allied to *A. haemastoma*. Barnacle (1962) classified *A. fastosus* and *A. prosperus* as varieties of *Acavus haemastoma* (Linnaeus). On the other hand, he ranked *Acavus roseolabiatus* (Nevill, 1881), formerly considered a variety of *Acavus superbus*, as distinct species. In the most recent survey of the landsnail fauna of Sri Lanka, Ratnapala (1984) accepted *A. roseolabiatus* as a separate species and also listed *A. fastosus* and *A. prosperus* as distinct species.

The exact distribution of the *Acavus* species in Sri Lanka was poorly known until Barnacle (1962) presented a distribution map. Unfortunately, Barnacle did not list exact localities. Therefore, it is not clear on what data his map is based. There are voucher specimens from only six localities in Barnacle's collection in the BMNH. Barnacle (1962) stated that each *Acavus* species inhabits a separate area and that the different species do not occur sympatrically. Since Barnacle (1962) has not shown or discussed the distribution of the various 'varieties', it remained unclear which 'varieties' represent geographical subspecies and which represent only infrasubspecific variations. Only recently more exact locality data of the various *Acavus* forms became available (Perera, 1992; Priyadarshana, 1995; Raheem & Butterworth, 1998).

Acavus is essentially restricted to the wet zone in the south-west of Sri Lanka, including

the foothills of the central massif, up to more than 600 m altitude. One *Acavus* species is also present at Ritigala, an isolated 600 m altitude patch of moist forest within the north-central dry zone. Sri Lanka's south-western wet zone (annual precipitation more than 2500 mm) was mostly covered by evergreen rain forest, but now the remaining patches of primary forest are being severely fragmented.

In this paper, we present a revision of the taxonomy of the *Acavus* species of Sri Lanka and discuss their distribution.

MATERIAL AND METHODS

Counting of the shell whorls follows Kerney & Cameron (1979: 13). Measurements from some populations are given to illustrate the size variation. If there are distinct size variations between populations, measurements of some of the extreme populations are given. The terms proximal and distal refer to the position in relation to the gonad. In the locality lists the localities are ordered according to their coordinates.

In most museum collections there are numerous *Acavus* samples from 'Ceylon'. Such inexact locality data are useless. Therefore, only samples with more exact locality data are listed. Most samples with exact locality data have been collected in the last decade and are concentrated in a few collections.

Abbreviations for collections: BMNH: The Natural History Museum, London; HEM: Collection J. Hemmen, Wiesbaden; LIN: Collection G. Lindner, Reinbek; PER: Collection K. K. Perera, Maharagama; SMF: Senckenberg-Museum, Frankfurt a. M.; ZMB: Zoologisches Museum der Humboldt-Universität, Berlin; ZMH: Zoologisches Institut und Zoologisches Museum der Universität Hamburg

Voucher specimens from the collection Perera have been deposited in the National Museum of Sri Lanka in Colombo.

Additional abbreviations: det. anat. = anatomically determined; D = shell diameter; H = shell height.

SYSTEMATIC ACCOUNT

Acavus Montfort, 1810

Acavus Montfort, 1810: 235. Type species (by original designation): *Helix haemastoma* Linnaeus, 1758.

Diagnosis: *Acavus* differs from the depressed-globular *Oligospira* in the conical-globular shell with more than 3½ whorls and the lack of a distal constricted penis section.

Remarks. The general anatomy of *Acavus* has been described in detail by Randles (1900). In agreement with the findings of Randles (1900), no constant differences in anatomical characters besides the penial structure between the *Acavus* species have been found. Therefore, only the penial structure is described in detail in the following.

The body colour of the *Acavus* species varies intraspecifically between light brownish or greyish to chocolate brown or black. No constant interspecific differences have been found.

Acavus haemastoma (Linnaeus, 1758) (Figs 1–13, 19)

Helix Haemastoma Linnaeus, 1758: 773. Locus typicus: not given.

Helix Melanotragus Born, 1778: 400. Locus typicus: not given.

Helix Haematragus Born, 1778: 400. Locus typicus: not given.

Helix fastosa Albers, 1854: 213. Locus typicus: 'peninsula Malaccana'.

Helix prospera Albers, 1857: 93, pl. 1 fig. 7–8. Locus typicus: 'Insula Ceylon'.

Helix (Acavus) haemastoma var. *aliostoma* Westerlund, 1887: 187. Locus typicus: 'Point de Galle'.

Helix (Macroon [Acavus]) haemastoma var. *conus* Pilsbry, 1890a: 79, pl. 16 fig. 7. Locus typicus: not given.

Helix haemastoma var. *concolor* Pilsbry, 1890b: 59. Locus typicus: not given.

Acavus haemastoma monochroa Pilsbry, 1931: 100. Nomen novum pro *Helix haemastoma* var. *concolor* Pilsbry, 1890 non A. E. Férussac, 1821.

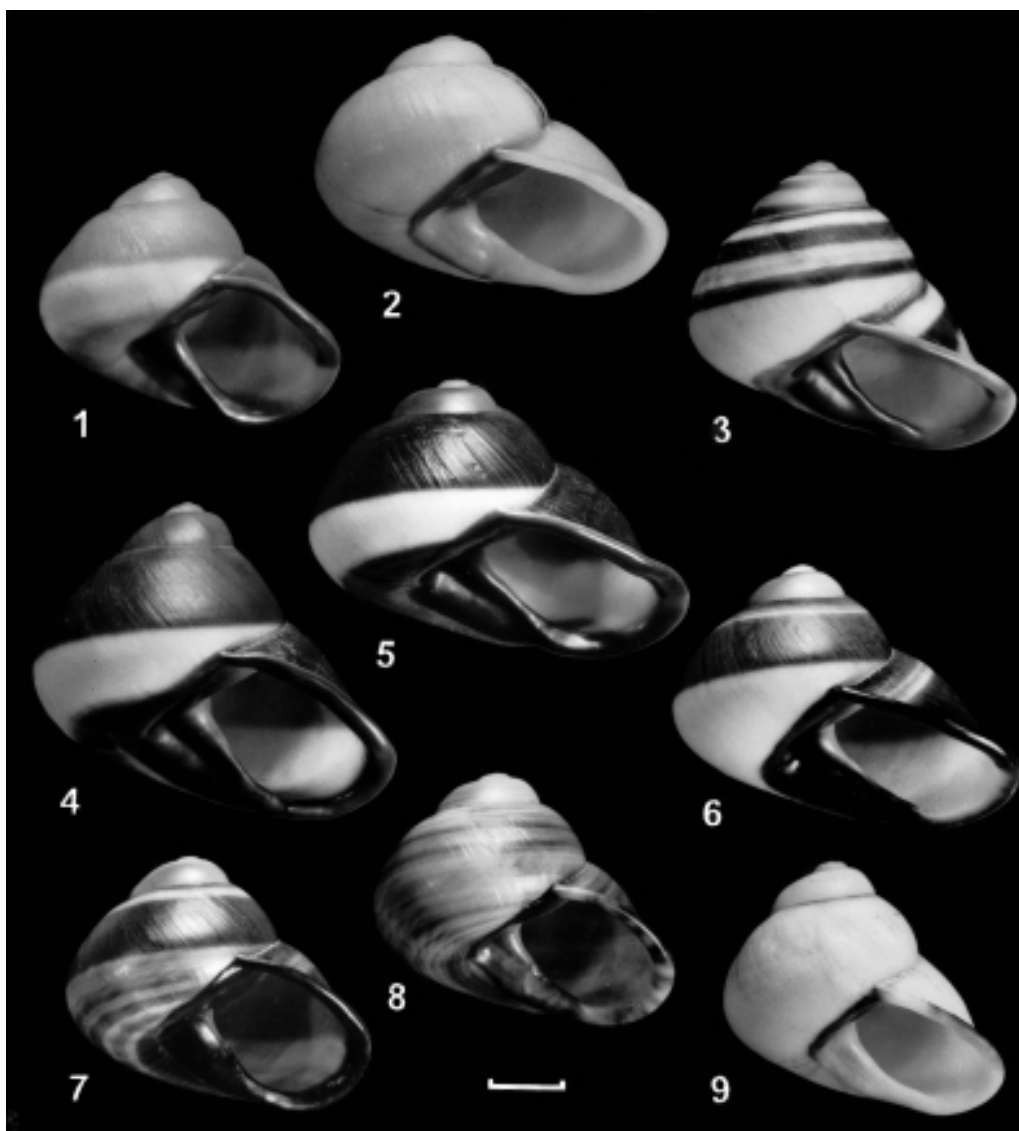
Shell (Figs 1–9): conical-globular; with 4–4½ convex whorls; protoconch with 2½–¾ whorls, pinkish, yellowish or brownish, with inconspicuous growth-ridges, more or less distinctly delimited from the teleoconch; teleoconch with inconspicuous growth-ridges; whitish, whitish with a variable brownish banding pattern or unicoloured brownish; body whorl rounded or very obtusely angular, slightly or distinctly descending towards the aperture; aperture oblique elliptical; the insertions of the aperture are connected by a heavy parietal callus; peristome thickened, expanded and reflexed; columellar margin of the peristome oblique, adnate to the base, not truncated, with a curved excavation at the place of the umbilicus, the peristome and the parietal callus are rose, purple, brown or whitish with a rose or brown touch.

Measurements. f. *haemastoma*: Kathaluwa (n = 50); D: 30.5–46.2 mm, $\bar{x} = 38.8 \pm 3.1$ mm; H: 31.1–47.6 mm, $\bar{x} = 38.2 \pm 3.1$ mm; D/H: 0.92–1.15, $\bar{x} = 1.02 \pm 0.05$.

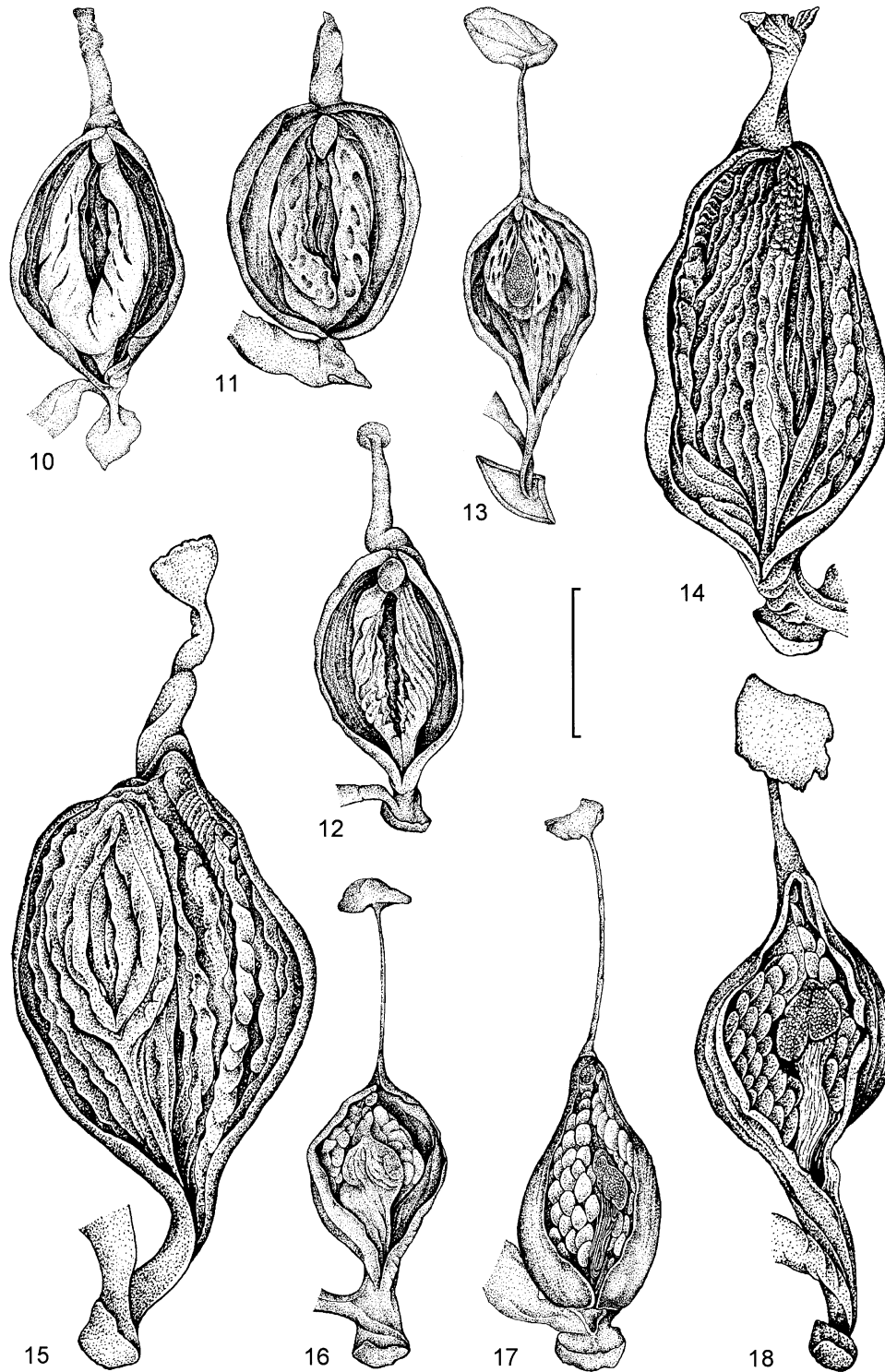
f. *melanotragus*: Baddegama (n = 25): D: 31.6–41.6 mm, $\bar{x} = 37.5 \pm 2.6$ mm; H: 32.3–40.1 mm, $\bar{x} = 37.2 \pm 1.9$ mm; D/H: 0.82–1.10, $\bar{x} = 1.01 \pm 0.06$. Elpitiya (n = 25): D: 40.8–52.7 mm, $\bar{x} = 46.7 \pm 3.1$ mm; H: 37.3–53.0 mm,

$\bar{x} = 47.0 \pm 3.4$ mm; D/H: 0.88–1.13, $\bar{x} = 1.00 \pm 0.06$.

Penis (Figs 10–12): The opening of the vas deferens is situated in a longitudinal furrow bordered by two tumid lips. The furrow is enclosed by a high, u-shaped, more-or-less corrugated and ridged thickening. Sometimes there are some additional lateral pleats to this



Figures 1–9. 1–5. *Acavus haemastoma* (Linnaeus, 1758) (f. *haemastoma*). 1. Ahangama (ZMH 2705). 2. Ahangama (ZMH 2706). 3. Ahangama (ZMH 2707). 4. Imaduwa (ZMH 2708). 5. Galle (ZMH 2704). 6–9. *Acavus haemastoma* (Linnaeus, 1758) (f. *melanotragus*). 6. Beruwala (ZMH 2709). 7. Akurala (ZMH 2711). 8. Akurala (ZMH 2712). 9. Akurala (ZMH 2710). Scale bar (for all figures) = 10 mm.



Figures 10–18. Inner structures of the penis: **10.** *Acavus haemastoma* (Linnaeus, 1758) (f. *haemastoma*), Imaduwa (ZMH 2708). **11.** *Acavus haemastoma* (Linnaeus, 1758) (f. *melanotragus*), Yakkamulla near Imaduwa (ZMH 2713). **12.** *Acavus haemastoma* (Linnaeus, 1758) (f. *melanotragus*), Akurala (ZMH 2712). **13.** *Acavus haemastoma* (Linnaeus, 1758) (possible hybrid with *A. superbus*), Haycock (BMNH). **14.** *Acavus phoenix phoenix* (L. Pfeiffer, 1854), Imaduwa (ZMH 2722). **15.** *Acavus phoenix castaneus* new subspecies, Kitulgala (holotype ZMH 2725). **16.** *Acavus superbus* (L. Pfeiffer, 1850) (f. *superbus*), Kahawatta (ZMH 2714). **17.** *Acavus superbus* (L. Pfeiffer, 1850) (f. *grevillei*), Kuruwita (ZMH 2718). **18.** *Acavus superbus* (L. Pfeiffer, 1850) (f. *roseolabiatum*), Yatiyantota (ZMH 2720). Scale bar (for all figures) ± 10 mm.

thickening. There is a rather large, almost smooth terminal papilla. The proximal top of the penis which contains the terminal papilla is bent in relation to the rest of the penis.

Remarks. No anatomical differences have been found between the red-lipped form (f. *haemastoma*: Figs 1–5, 10) and the brown-lipped form (f. *melanotragus*: Figs 6–9, 11–12) of *A. haemastoma*. Although the banding pattern is very variable in *A. haemastoma*, the colour patterns of the red-lipped and of the brown-lipped specimens in sympatric populations (e.g., from Elpitiya) are very similar. The size variation of the red-lipped and of the brown-lipped specimens in sympatric populations is also similar. For example, the specimens of both the red-lipped and the brown-lipped form from Elpitiya are extraordinarily large. These data indicate that the two forms probably interbreed and cannot be considered separate species.

Barnacle (1962) supposed that the two forms might be separate species, because he did not find them in association. However, at several localities in the interior of the wet zone red-lipped and brown-lipped specimens occur sympatrically (Fig. 19). The red-lipped form dominates in the south coast region of Sri Lanka between Galle and Matara, whereas the brown-lipped form dominates in the west coast region between Beruwala and Gintota. Because the ranges of the two forms are not distinctly separated, these forms can hardly be considered to be geographic subspecies. Nevertheless, it would be interesting to examine, why the colour of the peristome is fixed in the populations along the coast, whereas the populations in the interior are polymorphic.

The holotype of *H. prospera* Albers (ZMB) is a depressed, almost uniform brown specimen of the red-lipped form of *A. haemastoma* which is within the normal variation of the species.

There are intermediate forms between *H. fastosa* Albers (holotype ZMB) which is characterized by several fine brown bands (Fig. 8) and the normal brown-lipped form of *A. haemastoma* with broad brown zones (Fig. 7). Because

H. fastosa occurs only in some populations of the normal brown-lipped form and because no anatomical differences between these forms have been found, *H. fastosa* too is placed in the synonymy of *A. haemastoma*. Perera (1992) erroneously recorded a red-lipped form as *H. fastosa*.

H. haemastoma var. *aliostoma* Westerlund with a brownish-red lip and the unicolour chestnut *H. haemastoma* var. *concolor* Pilsbry are colour variations within the normal variability of *A. haemastoma*. The same is true for *H. haemastoma* var. *conus* Pilsbry which is based on more elevated specimens.

Some populations of *A. haemastoma* are very polymorphic and include all described banding patterns from forms with numerous fine or a few broader bands, forms with partly fused bands or broad brown zones to unicoloured whitish or brown specimens.

D. Raheem found two specimens at the Haycock which are intermediate between *A. haemastoma* and *A. superbus* concerning the penial structures (Fig. 13). The opening of the vas deferens is situated on a protruding thickening in the middle of the penis as in *A. superbus*. However, there are no rows of large tubercles proximal of this central thickening as in *A. superbus*, but, as in *A. haemastoma*, the thickening is enclosed by a u-shaped pilaster formed by ridges fused to a reticulate network. The size of the smooth terminal papilla is also intermediate between *A. haemastoma* and *A. superbus*. The shells resembled those of typical *A. haemastoma* (D. Raheem, pers. comm.). *A. haemastoma* and *A. superbus* are distinct throughout most of their range. The Haycock, situated at the border of the distribution areas of *A. haemastoma* and *A. superbus*, is the only locality from which intermediate specimens are known. These facts indicate that the specimens from the Haycock might be hybrids between *A. haemastoma* and *A. superbus*.

Distribution (Fig. 19): *A. haemastoma* occurs in an approximately 25 km broad zone in the lowland along the south-western coast of Sri Lanka

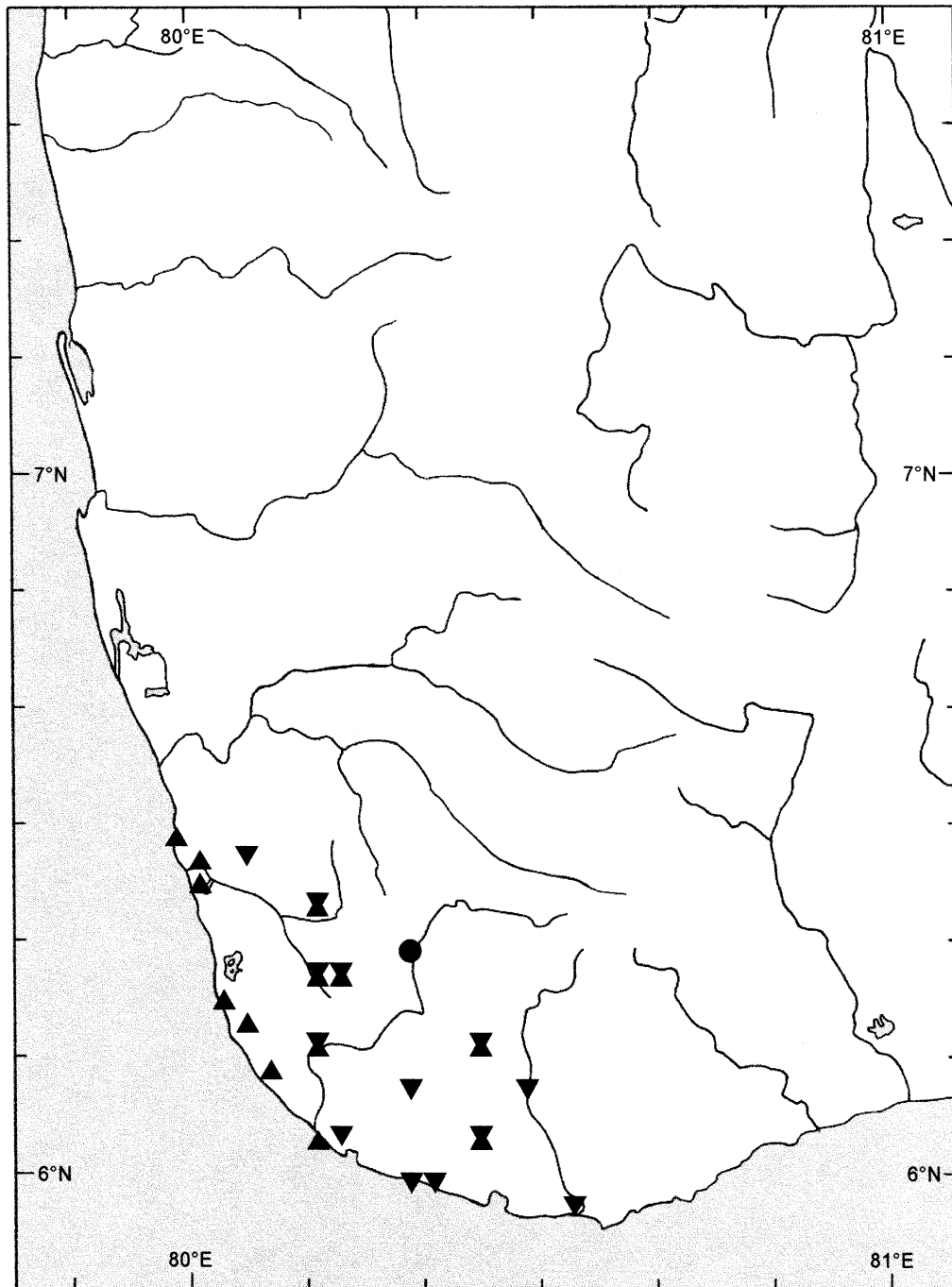


Figure 19. Distribution of *Acavus haemastoma* (Linnaeus, 1758) in Sri Lanka (2°-squares): *f. haemastoma* ▼, *f. melanotragus* ▲, presumable hybrid with *Acavus superbis* (L. Pfeiffer, 1850) ●.

between Beruwala and Matara up to about 100 m altitude.

Material: f. *haemastoma*: Matara, 5°57'N 80°32'E (BMNH); Ahangama, 5°58'N 80°21'E (det. anat.; PER, leg. 1990; ZMH 2705, leg. 1996; ZMH 2706, leg. 1996; ZMH 2707, leg. 1996; ZMH 2750, leg. 1989); Habaraduwa, 5°59'N 80°18'E (PER, leg. 1990); Kathaluwa, 5°59'N 80°20'E (PER, leg. 1990, 1991; ZMH 2752, leg. 1991); Yakkamulla near Imaduwa, 6°02'N 80°24'E (det. anat.; PER, leg. 1996; ZMH 2708, leg. 1996); Galle, 6°03'N 80°13'E (det. anat.; BMNH; HEM; LIN; PER, leg. 1992; SMF 91417, leg. 1899; ZMH 2704, leg. 1996); Kombala-Kottawa, 6°06'N 80°18'E (Raheem & Butterworth, 1998); Beraliya (Akuressa), 6°06'N 80°29'E (Raheem & Butterworth, 1998); Baddegama, 6°10'N 80°11'E (BMNH); Dediyaigala, 6°10'N 80°25'E (Raheem & Butterworth, 1998); Beraliya (Kudagala), 6°16'N 80°13'E (Raheem & Butterworth, 1998); Elpitiya, 6°17'N 80°10'E (PER, leg. 1988; ZMH 2753, leg. 1988); Yagirala, 6°22'N 80°10'E (Priyadarshana, 1995); Munamalwatta, 6°27'N 80°05'E (BMNH).

f. *melanotragus*: Yakkamulla near Imaduwa, 6°02'N 80°24'E (det. anat.; ZMH 2713, leg. 1996); Gintota, 6°03'N 80°11'E (PER, leg. 1987); Hikkaduwa, 6°08'N 80°06'E (HEM; PER, leg. 1992); Baddegama, 6°10'N 80°11'E (BMNH; PER, leg. 1990; ZMH 2751, leg. 1990); Dediyaigala, 6°10'N 80°25'E (Raheem & Butterworth, 1998); Akurala, 6°12'N 80°04'E (det. anat.; PER, leg. 1992; ZMH 2710, leg. 1996; ZMH 2711, leg. 1996; ZMH 2712, leg. 1996; ZMH 2755, leg. 1996); Ambalangoda, 6°14'N 80°03'E (PER, leg. 1987); Beraliya (Kudagala), 6°16'N 80°13'E (Raheem & Butterworth, 1998); Elpitiya, 6°17'N 80°10'E (PER, leg. 1988; ZMH 2754, leg. 1988); Yagirala, 6°22'N 80°10'E (Priyadarshana, 1995); Bentota, 6°25'N 80°00'E (HEM, leg. 1972); Alutgama, 6°26'N 80°00'E (PER, leg. 1996); Beruwala, 6°29'N 79°59'E (det. anat.; PER, leg. 1992, 1996; ZMH 2709, leg. 1996).

Presumed hybrids with *A. superbus*: Haycock, 6°19'N 80°18'E (BMNH, leg. 1995).

***Acavus phoenix* (L. Pfeiffer, 1854)**
(Figs 14–15, 20–26)

Shell (Figs 20–25): conical-globular; with 4–4½ convex whorls; protoconch with 2½–3 whorls, pinkish, yellowish or brownish, with inconspicuous growth-ridges, more or less distinctly delimited from the teleoconch; teleoconch with inconspicuous growth-ridges; whitish, pinkish, pinkish with brownish bands above the periphery or at the suture, whitish with a variable brown banding pattern, or unicoloured brownish; body whorl rounded or obtusely angular, slightly or distinctly descending towards the aperture; aperture oblique elliptical; the insertions of the aperture are connected by a heavy

parietal callus; peristome thickened, expanded and reflexed; columellar margin of the peristome oblique, adnate to the base, truncated or not truncated, with a curved excavation at the place of the umbilicus; the peristome and the parietal callus are white or brown.

Penis (Figs 14–15): The opening of the vas deferens is situated on a longitudinal fold in a longitudinal furrow bordered by two tumid lips. At each side of the furrow there is a longitudinal elevation and there is a third longitudinal elevation opposite to the furrow. These elevations as well as the space between them are sculptured by several long rows of large tubercles. There is no distinct terminal papilla. The penis is very large and is spindle-shaped or almost cylindrical.

Remarks: The large, globose, partly pinkish *A. phoenix phoenix* can easily be distinguished from *A. haemastoma* (Linnaeus) and *A. superbus* (L. Pfeiffer). However, the shells of some specimens of *A. phoenix castaneus* new subspecies can be distinguished from unicoloured brown forms of *A. haemastoma* (Linnaeus) only by their larger size. Some specimens of *A. phoenix castaneus* new subspecies with an angular body whorl cannot be distinguished from brown-lipped *Acavus superbus* (L. Pfeiffer) by shell characters.

Anatomically, the inner structure of the very large penis of *A. phoenix* differs from that of *A. haemastoma* and of *A. superbus* by lacking a distinct terminal papilla, the three longitudinal elevations and the sculpture covering almost the complete wall of the penis with rows of large tubercles.

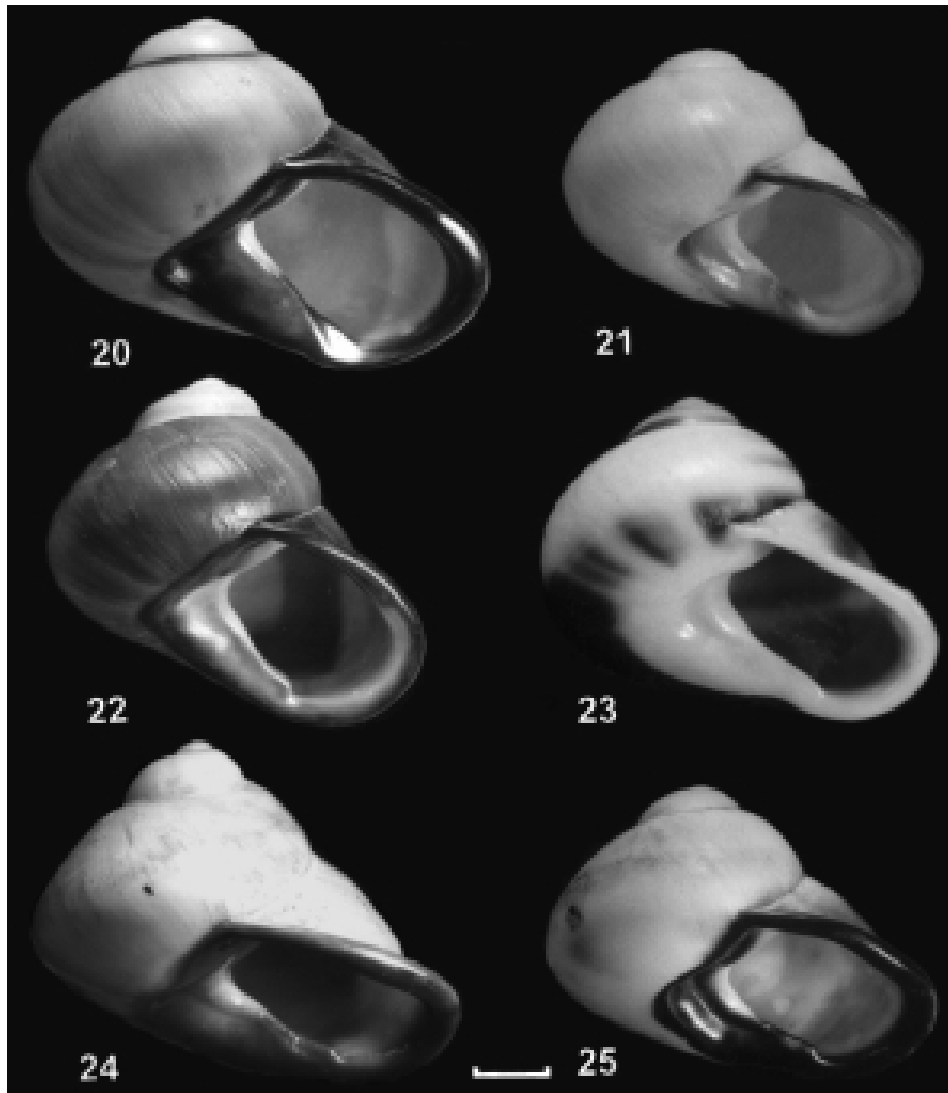
***Acavus phoenix phoenix* (L. Pfeiffer, 1854)**
(Figs 14, 20–21, 26)

Helix Phoenix L. Pfeiffer, 1854: 53. Locus typicus: 'Ceylon'.

Helix seposita Strobel, 1854: 71. Locus typicus: not given.

Diagnosis: The nominotypical subspecies is characterized by the large, globose shell with an at least partly pinkish body-whorl (except in albino specimens).

Measurements: Horana (n = 25): D: 43.1–58.6 mm, \bar{x} = 52.5 ± 4.7 mm; H: 34.4–59.7 mm, \bar{x} = 50.3 ± 5.9 mm; D/H: 0.94–1.62, \bar{x} = 1.06 ± 0.16.



Figures 20–25. 20–21. *Acavus phoenix phoenix* (L. Pfeiffer, 1854). 20. Maharagama (ZMH 2721). 21. Sri Lanka (ZMH 2739). 22–25. *Acavus phoenix castaneus* new subspecies. 22. Kitulgala (holotype ZMH 2725). 23. Kitulgala (paratype ZMH 2726). 24. Kandy (paratype ZMH 2728). 25. Ritigala Mountain (paratype ZMH 2727). Scale bar (for all figures) = 10 mm.

Remarks: Ziegler has labeled specimens of *A. phoenix* with the name *H. seposita*. Strobel (1854) stated that this name has priority over *H. phoenix* L. Pfeiffer. However, *H. seposita* actually is a junior synonym of *H. phoenix*, because it was published after the description of *A. phoenix*.

Distribution (Fig. 26): *A. p. phoenix* is widespread in the south-central part of the wet zone

and in the coastal region between Kalutara and Colombo upwards to about 500 m altitude.

Material: Weligama, 5°58'N 80°25'E (SMF 28398, leg. 1912); Imaduwa, 6°02'N 80°24'E (det. anat.; PER, leg. 1990; ZMH 2722, leg. 1996); Dediagala, 6°10'N 80°25'E (Rahem & Butterworth, 1998); Kanneliya, 6°15'N 80°21'E (PER, leg. 1997); Haycock, 6°19'N 80°18'E (Raheem & Butterworth, 1998); Deniyaya, 6°20'N 80°33'E (PER, leg. 1990); Kudawa near Wed-

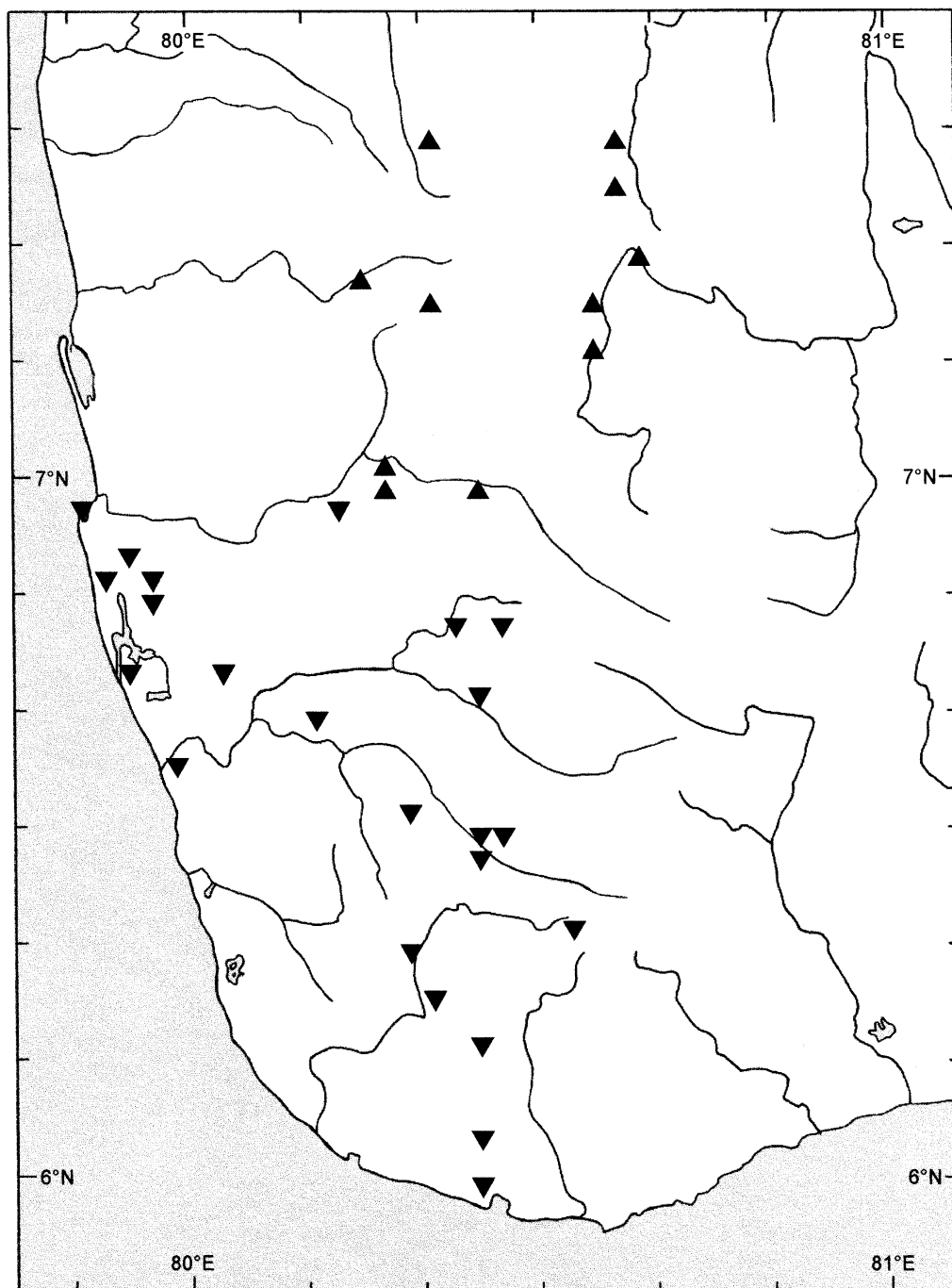


Figure 26. Distribution of *Acavus phoenix* (L. Pfeiffer, 1854) in Sri Lanka (2°-squares): *Acavus p. phoenix* (L. Pfeiffer) ▼, *Acavus phoenix castaneus* new subspecies ▲. The occurrence of *Acavus phoenix castaneus* at Ritigala Mountain is outside of the area shown in the map.

dagala, 6°26'N 80°24'E (PER, leg. 1990); Weddagala, 6°28'N 80°25'E (PER, leg. 1990); Kudumiriya, 6°28'N 80°27'E (Raheem & Butterworth, 1998); Morapitiya-Runakanda, 6°30'N 80°19'E (Raheem & Butterworth, 1998); Kalutara, 6°34'N 79°58'E (PER, leg. 1987); Bulathsinhala, 6°38'N 80°10'E (PER, leg. 1989); Ratnapura, 6°41'N 80°24'E (HEM); Panadura, 6°43'N 79°54'E (PER, leg. 1987); Horana, 6°43'N 80°03'E (det. anat.; HEM, leg. 1988; PER, leg. 1989; ZMH 2723, leg. 1996; ZMH 2756, leg. 1989); Kuruwita, 6°46'N 80°22'E (PER, leg. 1989); Gilimale, 6°46'N 80°26'E (Raheem & Butterworth, 1998); Piliyandala, 6°48'N 79°56'E (Priyadarshana, 1995); Mount Lavinia, 6°50'N 79°52'E (LIN); Dehiwala, 6°51'N 79°52'E (Priyadarshana, 1995); Maharagama, 6°51'N 79°57'E (det. anat.; ZMH 2721, leg. 1996); Kotte, 6°53'N 79°54'E (PER, leg. 1988); Colombo, 6°56'N 79°51'E (BMNH; SMF 28384; SMF 91431, leg. 1904); Avissawella, 6°57'N 80°13'E (HEM; PER, leg. 1989).

***Acavus phoenix castaneus* new subspecies**
(Figs 15, 22–26)

Diagnosis: *A. phoenix castaneus* is characterized by the colour of the body-whorl which is unicoloured brown or whitish with a brown banding pattern. Moreover, many populations of *A. phoenix castaneus* are on average smaller and often more depressed (partly with an angulated periphery) than those of the nominotypical subspecies.

Measurements: Kitulgala (n = 50): D: 46.2–57.0 mm, \bar{x} = 50.2 ± 3.0 mm; H: 41.0–50.0 mm, \bar{x} = 46.3 ± 2.2 mm; D/H: 0.85–1.22, \bar{x} = 1.09 ± 0.07.

Remarks: No constant anatomical differences between *A. phoenix castaneus* and *A. phoenix phoenix* have been found. It is likely that the two forms are conspecific, because the species specific inner penial structures of both are corresponding. However, D. Raheem (pers. comm.) found conspicuous differences between one spermatophore of *A. phoenix phoenix* from Gilimale and one of *A. phoenix castaneus* from Ritigala. This is surprising, because the spermatophores are formed in the lumen of the penis and, thus, differences in the spermatophore structure should also be found in the inner penial structures. Examination of more spermatophores of the two forms are necessary to resolve the issue.

A. phoenix castaneus in which the body-whorl is unicoloured brown or whitish with a brown banding pattern can be considered as geographic subspecies, because its range is separate

from that of the nominotypical form in which the body-whorl is at least partly pinkish.

A. phoenix castaneus has erroneously been identified with *A. haemastoma* f. *melanotragus* by Jousseaume (1894) and with *A. superbus* f. *grevillei* by Longstaff (1912). Randles (1900) has already recognized that the form belongs to *A. phoenix*. Perera (1992) has recorded the form partly under *A. phoenix* and partly under *A. superbus* f. *grevillei*.

Etymology: After the brownish (lat. *castaneus* = of the colour of chestnuts) shell.

Distribution (Fig. 26): *A. phoenix castaneus* is widespread in the northern, interior part of the wet zone from about 30 m to more than 600 m altitude. An apparently isolated population has been found on Ritigala Mountain in the dry zone.

Type material: Holotype: Kitulgala, 6°59'N 80°25'E (det. anat.; ZMH 2725, leg. 04.02. 1997, Measurements: D = 50.5 mm. H = 48.0 mm). Paratypes: Kitulgala, 6°59'N 80°25'E (BMNH; PER, leg. 1990; ZMH 2724, leg. 1997; ZMH 2726, leg. 1997; ZMH 2758, leg. 1990); Kandy, 7°18'N 80°38'E (det. anat.; BMNH; PER, leg. 1990; SMF 28382, leg. 1912; SMF 28395; SMF 181360; ZMH 2728, leg. 1996; ZMH 2730; ZMH 2763, leg. 1997); Ritigala Mountain, above 600 m altitude, 8°07'N 80°40'E (det. anat.; PER, leg. 1997; ZMH 2727, leg. 1997).

Other material: Dehiwita, 6°58'N 80°16'E (PER, leg. 1990); Yatiyantota, 7°01'N 80°17'E (PER, leg. 1990); Gampola, 7°10'N 80°34'E (field observation); Kegalla, 7°15'N 80°21'E (Priyadarshana, 1995); Peradeniya, 7°15'N 80°35'E (ZMH 2729, leg. 1904); Alawwa, 7°17'N 80°14'E (LIN); Alawatugoda, 7°25'N 80°36'E (D. Raheem, pers. comm.); Matale, 7°28'N 80°37'E (SMF 91437, leg. 1904); Kurunegala, 7°29'N 80°21'E (field observation).

***Acavus superbus* (L. Pfeiffer, 1850)**
(Figs 16–18, 27–33)

Helix superba L. Pfeiffer, 1850: 71. Locus typicus: 'in sylvis montanis insulae Ceylon'.

Helix grevillei L. Pfeiffer, 1856: 387, pl. 36 fig. 8. Locus typicus: 'Ceylon'.

Helix (Acavus) superba var. *roseolabiata* Nevill, 1881: 134. Locus typicus: 'Ceylon'.

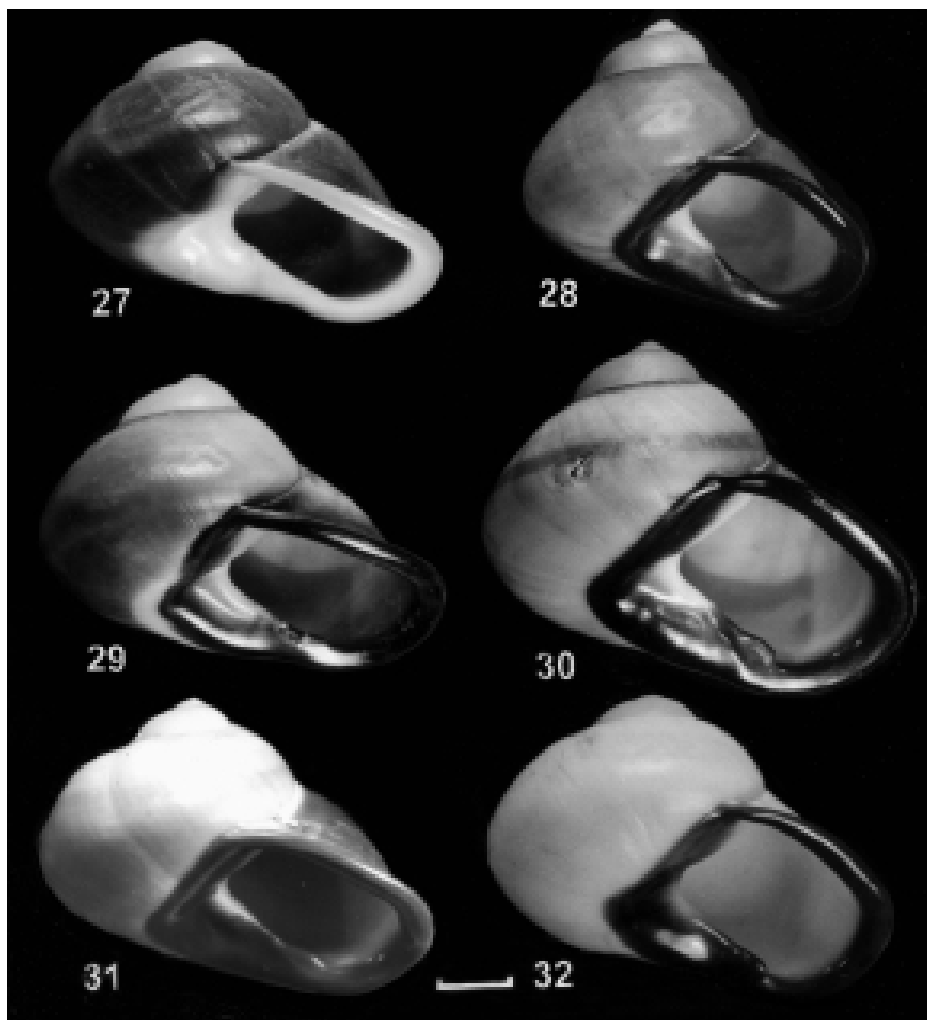
Shell (Figs 27–32): conical-globular; with 3½–4¼ convex whorls, body whorl flattened or even slightly concave; protoconch with 2½–2¾ whorls, pinkish or brownish, with inconspicuous growth-ridges, more or less distinctly delimited from the teleoconch; teleoconch with inconspic-

uous growth-ridges and sometimes coarsely malleated; the impressions sometimes form obliquely descending grooves; pinkish, reddish-brownish or brownish, sometimes with a darker brownish band above the periphery; body whorl obtusely angular, slightly or distinctly descending towards the aperture; aperture oblique elliptical; the insertions of the aperture are connected by a heavy parietal callus; peristome thickened, expanded and reflexed; columellar margin of the peristome oblique, adnate to the base, more or less truncated, with a curved excavation at the place of the umbilicus, the peristome and

the parietal callus are white with an orange or brownish margin, dark brownish or rose.

Measurements: f. *superbus*: Rakwana (n = 25): D: 33.6–52.5 mm, $\bar{x} = 47.2 \pm 3.7$ mm; H: 33.9–47.8 mm, $\bar{x} = 42.7 \pm 2.9$ mm; D/H: 0.88–1.35, $\bar{x} = 1.11 \pm 0.08$.

f. *grevillei*: Ratnapura (n = 25): D: 41.0–51.4 mm, $\bar{x} = 46.0 \pm 2.4$ mm; H: 40.5–48.5 mm, $\bar{x} = 44.1 \pm 1.8$ mm; D/H: 0.93–1.24, $\bar{x} = 1.04 \pm 0.07$. Kanneliya (n = 10): D: 34.6–45.6 mm, $\bar{x} = 39.7 \pm 3.6$ mm; H: 38.2–43.7 mm, $\bar{x} = 40.8 \pm 1.7$ mm; D/H: 0.89–1.10, $\bar{x} = 0.98 \pm 0.07$.



Figures 27–32. 27. *Acavus superbis* (L. Pfeiffer, 1850) (f. *superbus*). Kahawatta (ZMH 2714). 28–30. *Acavus superbis* (L. Pfeiffer, 1850) (f. *grevillei*). 28. Kanneliya (ZMH 2716). 29. Pelmadulla (ZMH 2717). 30. Kuruwita (ZMH 2715). 31–32. *Acavus superbis* (L. Pfeiffer, 1850) (f. *roseolabiatus*). 31. Kitulgala (ZMH 2719). 32. Yatiyantota (ZMH 2720). Scale bar (for all figures) = 10 mm.

f. *roseolabiatus*: Kitulgala (n = 25): D: 48.0–58.6 mm, \bar{x} = 53.6 \pm 2.2 mm; H: 42.9–52.4 mm, \bar{x} = 48.4 \pm 2.5 mm; D/H: 1.00–1.19, \bar{x} = 1.11 \pm 0.06.

Penis (Figs 16–18): The opening of the vas deferens is situated on a protruding thickening in the middle of the penis. There are several long rows of large tubercles left and right proximal to the thickening. The terminal papilla is small (and sometimes sculptured with some smaller tubercles) or even apparently missing (or at least not distinguishable from other tubercles, e.g. in the three examined specimens of f. *roseolabiatus*). The penis is pear-shaped because of the distal thickening.

Remarks: *A. superbus* is characterized by the obtusely angular body whorl and the inner structure of the pear-shaped penis.

The relation of the typical form of *A. superbus* (Figs 16, 27) with a white peristome with an orange or brownish margin, the brown-lipped form (f. *grevillei*; Figs 17, 28–30) and the rose-lipped form (f. *roseolabiatus*; Figs 18, 31–32) resembles that of the red-lipped form and the brown-lipped form of *A. haemastoma*. They are colour forms with broadly overlapping ranges and several sympatric occurrences (Fig. 33). We therefore do not consider these forms to be geographic subspecies.

Barnacle (1962) considered *roseolabiatus* to be specifically distinct from *A. superbus*. However, *roseolabiatus* differs from the other forms of *A. superbus* only in the colour of the peristome and the parietal callus. The lack of malleations is not a constant difference, the malleations also being absent in many specimens of the other forms of *A. superbus*. There are also no constant anatomical differences. Contrary to the opinion of Barnacle (1962), the range of *roseolabiatus* overlaps with that of the other forms.

Distribution (Fig. 33): *A. superbus* is widely distributed in southern and western foothills of the central massif from about 30 m to more than 600 m altitude. The f. *superbus* occurs mainly in the eastern part of the Ratnapura district, whereas the f. *roseolabiatus* predominates in the northern part of the range, especially in the Kelani valley where no other forms of *A. superbus* live.

Material: f. *superbus*: Kudawa near Weddagala, 6°26'N 80°24'E (PER, leg. 1989); Rakwana, 6°28'N 80°36'E (HEM; PER, leg. 1989, 1993; ZMH 2757, leg.

1989); Nahiti Mukalana, 6°29'N 80°35'E (Raheem & Butterworth, 1998); Kalawana, 6°32'N 80°24'E (PER, leg. 1989); Madampe, 6°32'N 80°35'E (BMNH; PER, leg. 1990); Kahawatta, 6°34'N 80°34'E (det. anat.; PER, leg. 1990; ZMH 2714, leg. 1996); Ketetenna, 6°35'N 80°34'E (D. Raheem, pers. comm.); Ope-nayake, 6°36'N 80°37'E (PER, leg. 1993); Pelmadulla, 6°37'N 80°32'E (PER, leg. 1993); Arslena, 6°57'N 80°29'E (Randles, 1900).

f. *grevillei*: Oliyagankele, 6°05'N 80°32'E (Raheem & Butterworth, 1998); Viharekele, 6°07'N 80°37'E (Raheem & Butterworth, 1998); Kanneliya, 6°15'N 80°21'E (det. anat.; PER, leg. 1994; ZMH 2716, leg. 1996; ZMH 2760, leg. 1994); Kudawa near Weddagala, 6°26'N 80°24'E (PER, leg. 1990); Kudumiriya, 6°28'N 80°27'E (Raheem & Butterworth, 1998); Morapitiya-Runakanda, 6°30'N 80°19'E (Raheem & Butterworth, 1998); Madampe, 6°32'N 80°35'E (BMNH); Pelmadulla, 6°37'N 80°32'E (det. anat.; ZMH 2717, leg. 1996); Ratnapura, 6°41'N 80°24'E (HEM, leg. 1989; PER, leg. 1998); Kuruwita, 6°46'N 80°22'E (det. anat.; PER, leg. 1989; ZMH 2715, leg. 1996; ZMH 2718, leg. 1996); Gilimale, 6°46'N 80°26'E (Raheem & Butterworth, 1998); Eratne, 6°49'N 80°23'E (Raheem & Butterworth, 1998).

f. *roseolabiatus*: Ketetenna, 6°35'N 80°34'E (D. Raheem, pers. comm.); 8 km W of Balangoda, 6°37'N 80°38'E (D. Raheem, pers. comm.); Bopathella, 6°48'N 80°22'E (Priyadarshana, 1995); Eratne, 6°49'N 80°23'E (Raheem & Butterworth, 1998); Batatota, 6°50'N 80°22'E (Raheem & Butterworth, pers. comm.); Polgaswatte, 6°57'N 80°26'E (Raheem & Butterworth, 1998); Dehiowita, 6°58'N 80°16'E (PER, leg. 1990); Kitulgala, 6°59'N 80°25'E (det. anat.; BMNH; PER, leg. 1990, 1991; ZMH 2719, leg. 1997; ZMH 2759, leg. 1990); Kelani valley, forest reserve Nr. 191, 7°00'N 80°24'E (Raheem & Butterworth, 1998); Yatiyantota, 7°01'N 80°17'E (det. anat.; BMNH; PER, leg. 1990; ZMH 2720, leg. 1996; ZMH 2761, leg. 1990); Ullswater, 7°02'N 80°23'E (BMNH); Sembawatte, 7°02'N 80°26'E (Raheem & Butterworth, 1998); Yakdessa, 7°02'N 80°26'E (ZMH 2764).

GENERAL REMARKS

The *Acavus* species live on tree trunks, usually up to 5 m (but sometimes up to 25 m) above the ground. They often occur in groups of 5–30 or more. They have been found on palm trees, especially arecanut (*Areca catechu*) and kitul (*Caryota urens*) palms, banana (*Musa* sp.), and some branched trees such as jack and breadfruit (*Artocarpus* spp.). They also occur in anthropogenic habitats.

The three *Acavus* species are not acutely endangered at present, because they are widespread in Sri Lanka. There is no risk of a rapid decline due to deforestation, because, in contrast to many other endemic land snails, e.g. *Oligospira*, the *Acavus* species are not restricted

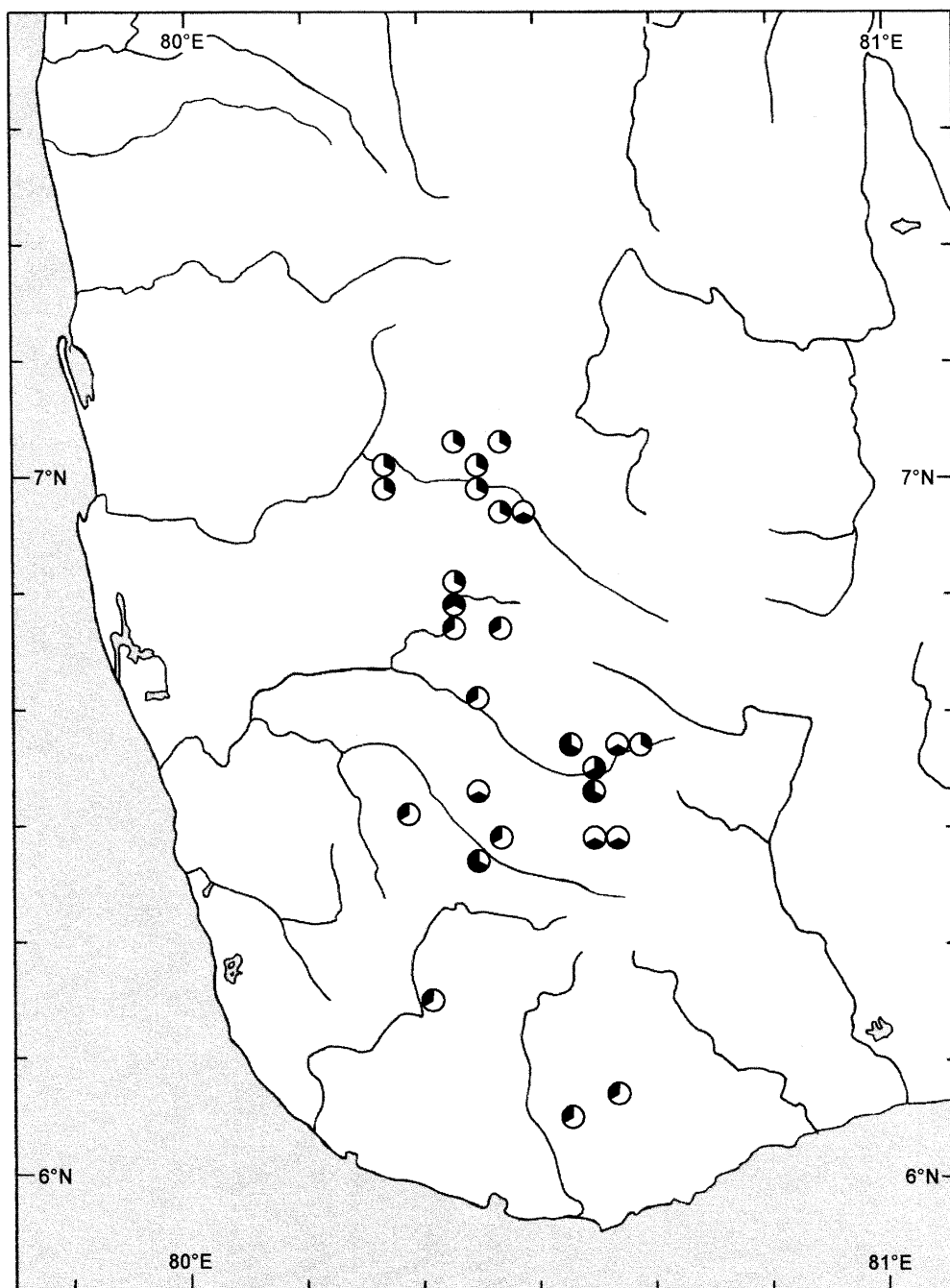





Figure 33. Distribution of *Acavus superbus* (L. Pfeiffer, 1850) in Sri Lanka (2°-squares): f. *superbus* H , f. *grevillei* H₁ , f. *roseolabiatus* H₂ .

to undisturbed forests, but also occur in synanthropic habitats.

The Acavidae have a disjunct distribution pattern on Madagascar, the Seychelles and on Sri Lanka and are therefore considered to be a Gondwanaland relict group (Emberton, 1990). The distribution pattern indicates that the Acavidae probably originated before the separation of India from Madagascar in the Late Cretaceous (Smith, Smith & Funnell, 1994). However, if the Sri Lankan acavid lineage is more than 60 million years old, one would expect to find many more species (as, e.g., on Madagascar) which are better isolated. Despite their supposed ancient age, the *Acavus* species are anything but isolated relict species. The presence of extensive intraspecific colour polymorphism, the development of geographical subspecies and the presumable hybridization between some species show that speciation is in progress. Perhaps this situation can be explained by the hypothesis that the Sri Lankan Acavidae (presumably there were not only one or two lineages in more than 60 million years) passed through a bottleneck in the Tertiary and that the recent radiation of *Acavus* (and *Oligospira*) is much younger than the origin of the family. The bottleneck in the Tertiary might have been caused by the abrupt climatic changes during the northward drift of India.

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