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## First Record of *Amphidromus* from Australia, with Anatomical Notes on Several Species (Mollusca:Pulmonata:Camaenidae)

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ABSTRACT. *Amphidromus cognatus* Fulton, 1907, described from a single specimen without locality data, is here recorded from several places north of Darwin in the Northern Territory. This is the first record from Australia of this South-east Asian to Timor genus of arboreal snails. Dissections of the genotype, *Amphidromus perversus* (Linné, 1758) from Bali and *A. poecilochrous jaeckeli* Laidlaw, 1954, from Flores, Indonesia, provide comparative data on genital and radular structures of *A. cognatus*. There are easily observable species differences in the terminal genitalia, although shell variation is great and confusing.

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*Amphidromus* Albers, 1850, is a genus of colourful tree-dwelling land snails that has long been popular with shell collectors. Species now referred to this genus are known in the region from the Garo and Khasi Hills of Assam throughout South-east Asia and Indonesia as far as the Celebes, Banda Islands, Timor, and Tanimber Islands. The northern limits seem to be the Southern Philippines (Mindanao and the Balabac-Palawan chain), Vietnam, Thailand, Burma and Assam. *Amphidromus* is replaced in New Guinea and parts of Wallacea by the papuinid complex of genera (Solem, 1959: 274, fig. 21). The occurrence of *Amphidromus* on Melville and Bathurst Islands and the Cobourg Peninsula, Northern Territory, Australia is thus a significant range extension.

Early well-illustrated studies by Fulton (1896) and Pilsbry (1900) are still the standard references for identification of *Amphidromus* species and colour forms from shell features. The synoptic catalogue of Laidlaw and Solem (1961) incorporates post-1900 literature and summarizes current knowledge. Description of two colour varieties from Komodo Islands, Indonesia (Djajasasmita, 1963); a review of variation in Thailand taxa (Solem, 1965); brief anatomical notes on *A. palaceus* (Mousson, 1848), *A. javanicus* (Sowerby, 1841), *A. heerianus* (Pfeiffer, 1871), and *A. porcellanus* (Mousson, 1848) by Bishop (1977), and on the terminal genitalia of *A. poecilochrous jaeckeli* Laidlaw, 1954 by Minato (1979), are the only subsequent papers other than catalogue listings in faunal checklists. The most significant contribution to knowledge of *Amphidromus* remains the masterly account of variation in East Timor species by Haniel (1921). Subsequent commentaries by Rensch (1931,

1935) on the systematics of the Timor populations only emphasize the complex nature of local variation and the inadequacies of using shell morphology alone to determine species limits.

The data on anatomical variation presented below, when interpreted with the aid of concepts on species recognition structures developed in studies of Australian camaenids (Solem, 1979, 1981a,b), confirm that variations in the terminal genital structures are most useful in recognizing species limits. Radular teeth of *Amphidromus* show several unique features that depart significantly from the normal pattern found in the family Camaenidae.

### ABBREVIATIONS

AM: Australian Museum, Sydney.  
 BM(NH): British Museum (Natural History), London.  
 FMNH: Field Museum of Natural History, Chicago.

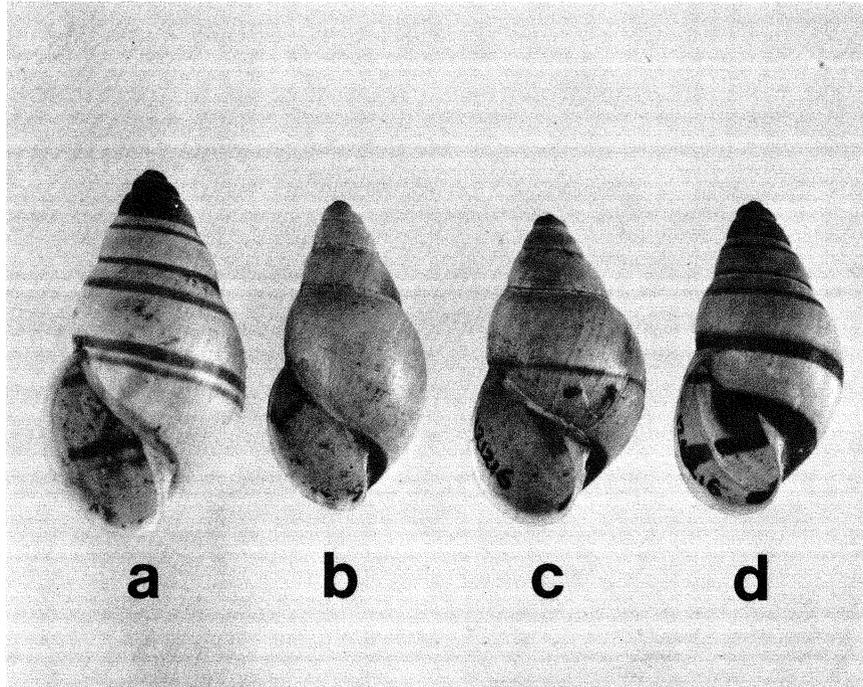
### Family CAMAENIDAE Pilsbry, 1893

#### Genus *Amphidromus* Albers, 1850

#### *Amphidromus cognatus* Fulton, 1907

Figs 1-7, 14, 23, 24

*Amphidromus cognatus* Fulton, 1907: 151, pl. IX, fig. 7.—  
 Laidlaw and Solem, 1961: 592, 610.



**Fig. 1.** Shells of *Amphidromus cognatus* Fulton. **a**, trees near beach, Bathurst I., near Darwin, Northern Territory, Australia, AM C.122528; **b-d**, on trees, Milikapiti Bay, Melville I., Northern Territory, Australia, AM C.121216. Height of largest shell is 29.7 mm.

**Holotype.** BM(NH) 1907.5.3.122.

**Type locality.** Port Essington, Cobourg Peninsula, Northern Territory, Australia (here restricted).

**Records.** Port Essington, Cobourg Peninsula (2 adults: BM [NH] 51.11.15.37, AM C.122527); alive on trees near beach, Bathurst I., near Darwin (1 adult, AM C.122528, collected by P. Carrol in 1976-1977); Milikapiti Bay, rain forest pocket between waterpumps, c. 500 m from beach, Melville I., near Darwin (22 adults, 20 juveniles, AM C.121216, collected by V. Kessner, 5 April 1980); Milikapiti Bay, rain forest behind pumps, Melville I. (15 live adults, 6 live juveniles, AM C.126706, FMNH 198760, collected by V. Kessner, 11 November 1980); 10 km from Milikapiti Bay on way to Kerslake, Melville I. (3 dead adults, AM C.126705, collected by Vince Kessner, 10 December 1980); along creek at bridge 3-4 km from Paru, Melville I., near Darwin (2 adults, 4 juveniles, AM C.121192, collected by P.H. Colman and V. Kessner, 21 March 1980).

**Description of shell.** Relatively small, sinistral, height 20.9–32.7 mm (mean 25.91 mm), diameter 12.15–17 mm (mean 14.35 mm). H/D ratio 1.56–2.12 (mean 1.80). Whorl count  $4\frac{7}{8}$  to 6 (mean  $5\frac{3}{8}$ ), sutures shallow, whorl contour rather flat. Lip very weakly to moderately expanded, sharply reflected, a very narrow umbilical chink remaining. Shell surface with only occasional weak radial growth lines. Colour pattern variable.

All specimens have the umbilical chink interior showing only the ground colour. A prominent spiral band of chocolate brown (except in the single Bathurst Island specimen, Fig. 1a) lies on the columella around the umbilicus. Additive colour elements present on some

to most specimens may include a peripheral spiral chocolate brown colour band (Fig. 1a, d), a distinctly subsutural chocolate brown colour band (Fig. 1a, d), and a purplish brown apical suffusion (Fig. 1a, c, d). The width of the upper spiral bands and columellar colour band vary (Fig. 1). The additive elements do not appear completely linked. While no specimen with a prominent spire suffusion lacks the peripheral colour band, the subsutural band may or may not be present with spire suffusion. No specimens have any of the spirals broken up into flammulations. Lip white or with a faint yellowish cast. Ground colour medium yellow in fresh examples, on body whorl occasionally showing tonal irregularities along growth lines, fading on spire and in worn examples.

**Distribution and habitat.** Modern records from Bathurst and Melville Islands near Darwin, Northern Territory, are in addition to the pre-1850 record from Port Essington, Cobourg Peninsula. Some of the specimens collected alive on Melville Island have been taken from the plant *Opilia amentacea* Roxburgh.

**Remarks.** The unlocalized holotype and two specimens of *Amphidromus cognatus* from Port Essington all have the complete suite of colour features, are three of the four specimens over 30 mm in shell height, and have the shell lip more strongly reflected and more broadly expanded. The restriction of the type locality to Port Essington is based on this identity of material. It is quite probable that all three were collected at the same time, but that the holotype subsequently became separated from its locality data and thus was

described as "locality unknown". Specimens with full colour elements from Melville Island differ from the Port Essington specimen only in their noticeably smaller size (Fig. 1b-d), thinner shell, and much less broadly reflected and expanded shell lip.

The Bathurst Island example (Fig. 1a) also has a full colour complement on the spire, except that the peripheral colour band is split into a wider upper and narrower lower portion. The columellar colour band is absent. Its lip is strongly expanded, and it is 29.7 mm high, with 5½ + whorls, thus almost equalling the size of the types.

Of the dead Melville Island examples taken in April, 1980, 18 adults and 13 juveniles could be scored as to colour pattern. Four adults and eight juveniles were so worn that either no colour pattern was left, or only partial traces existed. Of the juveniles, 5 have a weak subsutural and umbilical patch; 4 have apical colour suffusion, a strong peripheral, and an enlarged to double width umbilical colour band; and 4 have a heavy spire suffusion, heavy subsutural, heavy peripheral, and prominent umbilical colour band. Of the adults, 5 have a heavy spire suffusion, medium to strong peripheral, weak to strong subsutural, and prominent umbilical colour band (Fig. 1d); 1 has a weak peripheral colour band that fades out before the lip edge (Fig. 1c), and a prominent umbilical colour band; and 14 have only the umbilical colour band (Fig. 1b). Size variation in the 22 dead adults collected 5 April 1980 (AM C.121216) is:

	Mean	S.E.M.	Range
Shell height	25.90 mm	0.428	21.55–29.35 mm
Shell diameter	14.42 mm	0.206	12.3–16.75 mm
H/D ratio	1.80	0.013	1.68–1.90
Whorls	5¾	—	5 to 5¾
Aperture length	13.33 mm	0.200	11.6–15.0 mm

The two live adults (AM C.121192) collected 21 March 1980 are slightly smaller than average, but typical.

The live material from Milikapiti Bay taken 11 November 1980 included 15 live adults, several of which had only very thinly expanded lips. Loose eggs in the preservative indicated that at least one animal was in the process of egg laying. Dissection of four adults failed to discover any eggs in the female tract. Colour variation in the adult shells was quite similar to that in the dead April collections. Of the 15 adult specimens, 4 had only the umbilical patch and in one of these it was very weak; 4 had a weak spire suffusion and prominent umbilical patch; 1 had a weak spire suffusion, weak subsutural band, and prominent umbilical patch; 1 had a heavy spire suffusion, prominent peripheral band, and prominent umbilical patch; 3 had all colour components; and 1 had all colour components with the bands widened.

Size variation in the live collected adults was extensive:

	Mean	S.E.M.	Range
Shell height	25.17 mm	0.756	20.9–32.7 mm
Shell diameter	13.69 mm	0.260	12.15–15.7 mm
H/D ratio	1.83	0.036	1.56–2.12
Whorls	5¼ +	—	4¾ to 6
Aperture length	13.07 mm	0.322	10.9–15.5 mm

The total size range is clearly extended, but the mean differences are not significant. The three dead adults from on the way to Kerslake had all colour components and were within the range of variation for shell measurements.

Determining the nearest relatives of *Amphidromus cognatus* must await anatomical studies of Timor to Celebes species. Although Haniel (1921) provided much data on external aspects of the terminal genitalia, and illustrated variation ranges for several species, he did not discuss or illustrate the interior surfaces of the terminal genitalia, which is where the species recognition structures are located in the Camaenidae.

On conchological grounds, the most conspicuous species differences lie in the nature of the colour pattern. *Amphidromus cognatus* has the umbilical chink showing shell ground colour only and the umbilical band is sharply defined. All of the colour bands are chocolate brown, when present. Taxa such as *A. laevus* (Müller, 1774), *A. inconstans* Fulton, 1898, *A. contrarius* (Müller, 1774), and *A. columellaris* Möllendorff, 1892, have the colour extending into the umbilical chink (*A. columellaris*), bands of different colours on the shell (*A. laevus*), or strikingly flammulated colour patterns (*A. columellaris*, *A. inconstans*, *A. contrarius*). There are also clear differences in the way that the lip is expanded, in how the umbilical reflection terminates and in whorl contours. Unfortunately, these are difficult to communicate verbally, and would require extensive illustrations to document. Fortunately, the colour differences are adequate for identification.

### *Amphidromus perversus* (Linné, 1758)

#### var. *interruptus* (Müller, 1774)

Figs 8–9, 20–21

*Helix perversa* Linné, 1758: 772.—locality unknown.

*Amphidromus perversus*.—Laidlaw and Solem, 1961:533–534.

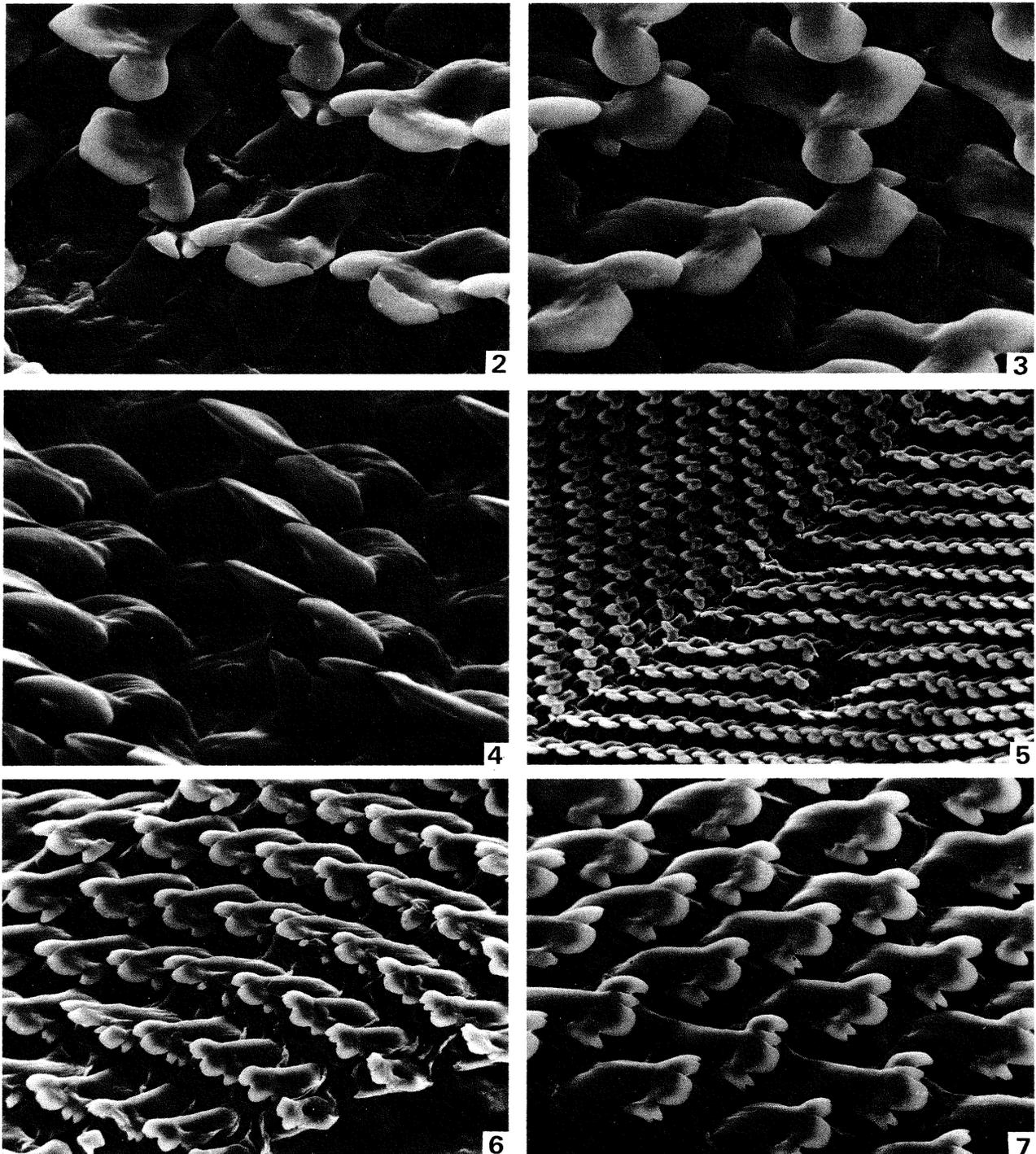
**Material.** Sanur, 50–200 metres from beach, Bali, Indonesia (8 adults, 3 juveniles, FMNH 198757, collected by Renate Wittig Skinner 5–17 May 1977).

**Remarks:** Both sinistral and dextral individuals, all referable to the colour form *interruptus* (Müller, 1774), were available.

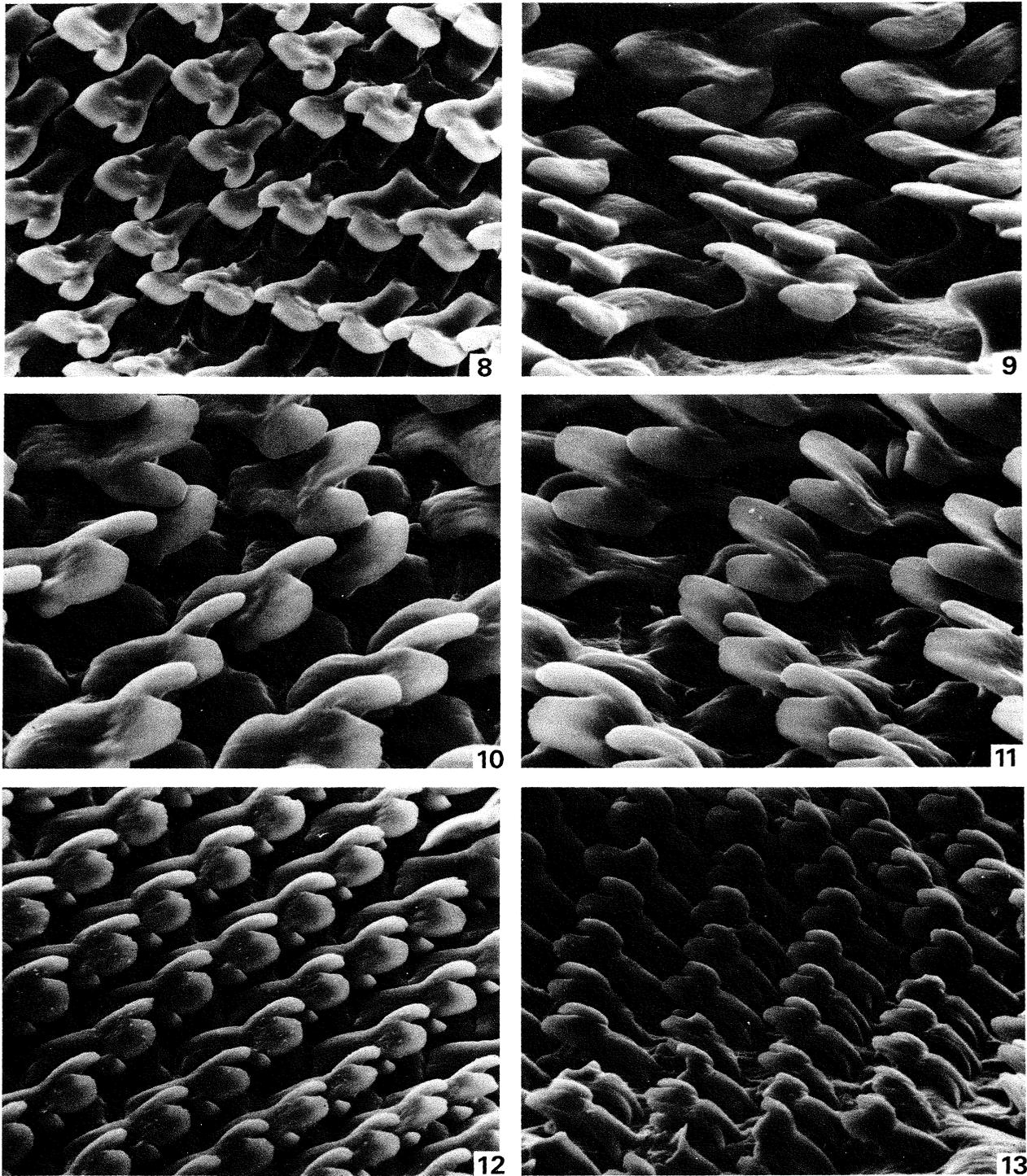
### *Amphidromus poecilochrous jaeckeli* Laidlaw, 1954

Figs 10–13, 15, 22

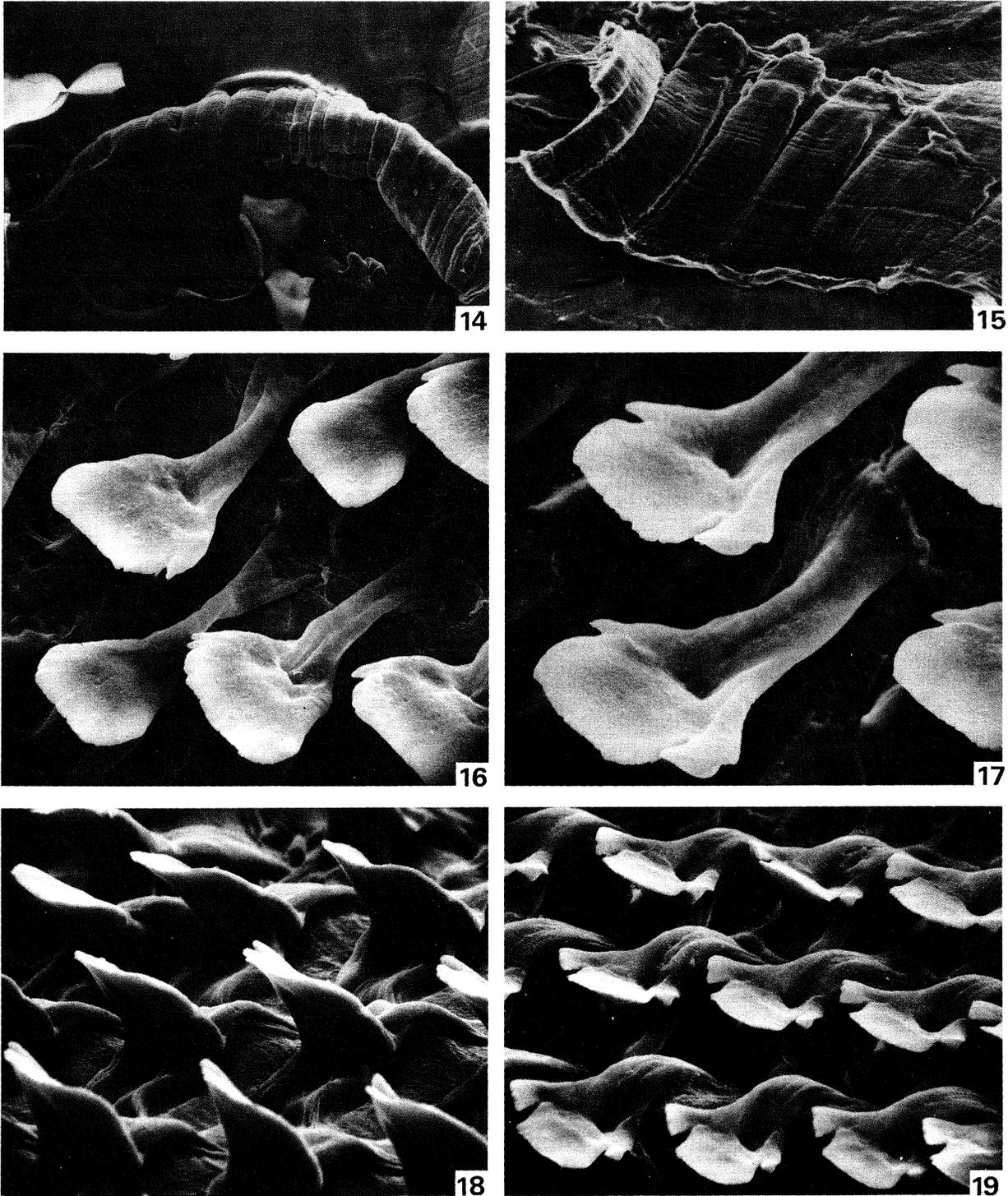
*Amphidromus contrarius floresii*.—Haltenorth and Jaeckel, 1940: 174–175, figs 3, 4—Kampong Mosen, West Flores, Indonesia (not Bartsch, 1917).



**Figs 2-7.** Radular teeth of *Amphidromus cognatus* Fulton. Melville I., Northern Territory, Australia. AM C.121192. 2, 4, 5, 6, are Dissection A. 3, 7, are Dissection B. 2, Rachidian and early laterals, 810 X. 3, Rachidian and early laterals, 907 X. 4, Low angle view of rachidian and early laterals, 1,150 X. 5, Part row view from high posterior angle, 160 X. 6, Outer marginal teeth, 405 X. 7, Mid-marginal teeth, 480 X.



**Figs 8–13.** Radular teeth of *Amphidromus perversus* (Linné), and *A. poecilochrous jaeckeli* Laidlaw. **8–9**, *A. perversus* (Linné). Sanur, Bali, Indonesia, FMNH 198757. **8**, Rachidian and several laterals showing variation in shape of anterior basal plate, 410 X. **9**, Laterals from left side of radula showing deflection of anterior basal plate margin, 800 X. **10–13**, *A. p. jaeckeli* Laidlaw. Konga, Flores, Indonesia, FMNH 198758. **10** and **12** from Dissection A, **11** and **13** from Dissection B. **10**, Rachidian and early laterals showing presence of ectocone and anterior basal plate margin deflection, 860 X. **11**, Rachidian and early laterals showing absence of ectocones on these early laterals, 780 X. **12**, Lateromarginal transition area showing change in basal plate length, 465 X. **13**, Outermost marginals from right side of radula, 415 X.



**Figs 14-19.** Jaws of *Amphidromus* and radula of *Papuina phaeostoma medinensis* Rensch. **14,** Jaw of *Amphidromus cognatus* Fulton, 50 X. **15,** Detail of jaw of *A. p. jaeckeli* Laidlaw. Note worn tips on upper margin. 152 X. **16-19,** *Papuina phaeostoma medinensis* Rensch. 80 miles southeast of Kavieng Village, New Ireland, Bismarck Archipelago (3°02' 30"S, 151° 40'E), FMNH 168394. **16,** Rachidian and first laterals in near-vertical view showing anterior basal plate margins, 930 X. **17,** Mid-lateral teeth showing serrated mesocone margin and enlargement of endocone (lower) and ectocone (upper), 1,075 X. **18,** Lateral teeth viewed from a posterior about 45° angle showing deflection of anterior basal plate, 850 X. **19,** High angle view of mid-lateral teeth showing basal plate anterior deflection, 660 X.

*Amphidromus contrarius jaeckeli* Laidlaw, in Butot, 1954: 106–107, figs 2, 3—Komodo Island, Indonesia.

*Amphidromus poecilochrous jaeckeli*.—Laidlaw and Solem, 1961: 569–570, 631, fig. 16A; Minato, 1979: 15–17.

**Material.** Hill near Konga, Flores, Indonesia (3 live adults, FMNH 198758, collected by Renate Wittig Skinner June 1975).

**Remarks.** The three specimens available, except for having the ground colour extend partly onto the reflected lip, agree with the type illustrations and are thus referred to this subspecies.

### Radular Structure

Previous observations on the radula of *Amphidromus* have focused on the angled nature of the rows, and the pattern of cusp shape. Haniel (1921: 49–57, figs 14–21) indicated that there was considerable minor variation in the cusping of the rachidian tooth, but seriously misinterpreted the anterior basal plate margin because of the tooth row overlap inherent in vertical viewing with optical equipment. Bishop (1977: fig. 2) showed only outlines of anterior cusp margins.

Within the context of the Camaenidae, the radula of *Amphidromus* is highly modified, correlating with the arboreal habitat and microfloral food. The only clear indication that this tooth form is derived from the basic camaenid pattern can be seen in teeth approximately midway on the radula between the rachidian and outermost marginals. In *A. p. jaeckeli* (Fig. 12), the persistence of a simple inter-row basal support mechanism at the point of lateral marginal transition can be seen. At the upper right of this illustration, one tooth is angled, showing the altered anterior margin of the tooth, while the next tooth in the same row has the same margin resting on the posterior basal plate of the next tooth in line. In the lower left of this illustration, the basal plates have become noticeably shortened, the posterior basal margin is receding, and the pattern evident in outer marginals of a bifurcated, non-interacting anterior margin (Fig. 13) is set.

Basic row shape in all three species examined agrees with that of *A. cognatus* (Fig. 5)—V-shaped, with the arms of the V directed anteriorly. The rachidian tooth is greatly reduced in size and highly variable in cusp shape (Figs 2, 3, 8, 10, 11). Such variation in cusping on teeth of reduced size, and hence probably reduced function, is well-documented in other land snail taxa, for example, in the athoracophorid slug, *Aneitea* (Solem, 1959: 47). In *A. perversus* (Fig. 8), the rachidian is broadly monocuspid and less reduced in size than in the specimens of *A. p. jaeckeli* (Figs 10, 11). One of these has larger ectocones than the other, and I presume that examination of additional material would increase the range of variation. A much greater contrast was observed in the two specimens of *A. cognatus* (Figs 2, 3). In one specimen (Fig. 3) the mesocone is broad and with truncated posterior cusp margin; in the other (Fig. 2) the mesocone is greatly reduced in size to a Y-shaped nubbin. Both examples have relatively prominent ectocones on the rachidian. When observed from a

lower viewing angle, the cusps are seen to be elevated at almost a 90° angle, but their tips lie distinctly below the plane of the surrounding laterals and thus probably do not function in feeding.

Structure of the lateral teeth is consistent in all three species. Two cusps, a mesocone and an endocone, with the latter distinctly narrower, are elevated in the same cutting plane (Figs 4, 5, 8, 9, 10). This contrasts greatly with the pattern observed in arboreal enids (Solem, 1973: figs 9, 11, 12) and partulids (*ibid.*, figs 13–16, 18, 20) where the two-cusp pattern involves striking differences in both the plane of highest elevation for each cusp and the identity of the second cusp. In these taxa, the mesocone makes initial contact with the food surface followed a microsecond later by an equally elevated ectocone, giving two scrapes from the same tooth. In both of these families there is great overlap between basal plates (*ibid.*, figs 7, 12, 13, 15, 16, 18, 20, 21). In the Partulidae, the inter-row support involves sliding along a significant surface length, while in the Enidae (*ibid.*, fig. 7) there is a more traditional raised point of interlock. *Amphidromus* shows a gross difference (Figs 2, 4, 6, 8, 9, 11). There is, for the lateral teeth, no inter-row support system. Instead, the anterior margin of each lateral tooth is sharply deflected downward (Fig. 4) with its anterior tip lying between the posterior margins of two teeth in the next row. Presumably this curved anterior margin is correlated with surface curvature on the underlying support cartilage during functional rotation of the radular ribbon into the mouth during a feeding stroke. This support system and the elaboration of an endocone into a *simultaneous* cutting edge are two features that I am not aware of being present in any other family of arboreal land snails. Previous illustrations have shown the posterior basal plate margin as abruptly truncated in *Amphidromus*, as the sharply narrowed anterior deflection would be hidden in vertical view by the cusps of the next anterior row.

A modification of this pattern is seen in *Papuina phaeostoma medinensis* from Kavieng, New Ireland, Bismarck Archipelago (Figs 16–19). The central and early laterals are almost monocuspid (Fig. 16), with only a slight endocone trace. After the first few laterals, there is significant ectoconal enlargement and endoconal development (Fig. 17). Most of the functioning laterals (Fig. 18) show the same anterior margin deflection reported above for *Amphidromus*, although the earliest laterals (Solem, 1974: 136) have a simpler structure (Fig. 16). Early marginals (Fig. 19) show enlargement of the side cusps and accentuation of the anterior deflection. This suggests, as has been hypothesized previously on other grounds, that *Amphidromus* and the papuinid complex of genera are parallel experiments in arboreal living, but probably are not monophyletic.

The process of transition to marginal teeth in *Amphidromus* (Fig. 12) can be pin-pointed to a small region of basal plate shortening. In all three species, gradual development of an ectocone has been proceeding for a number of teeth, accompanied by size

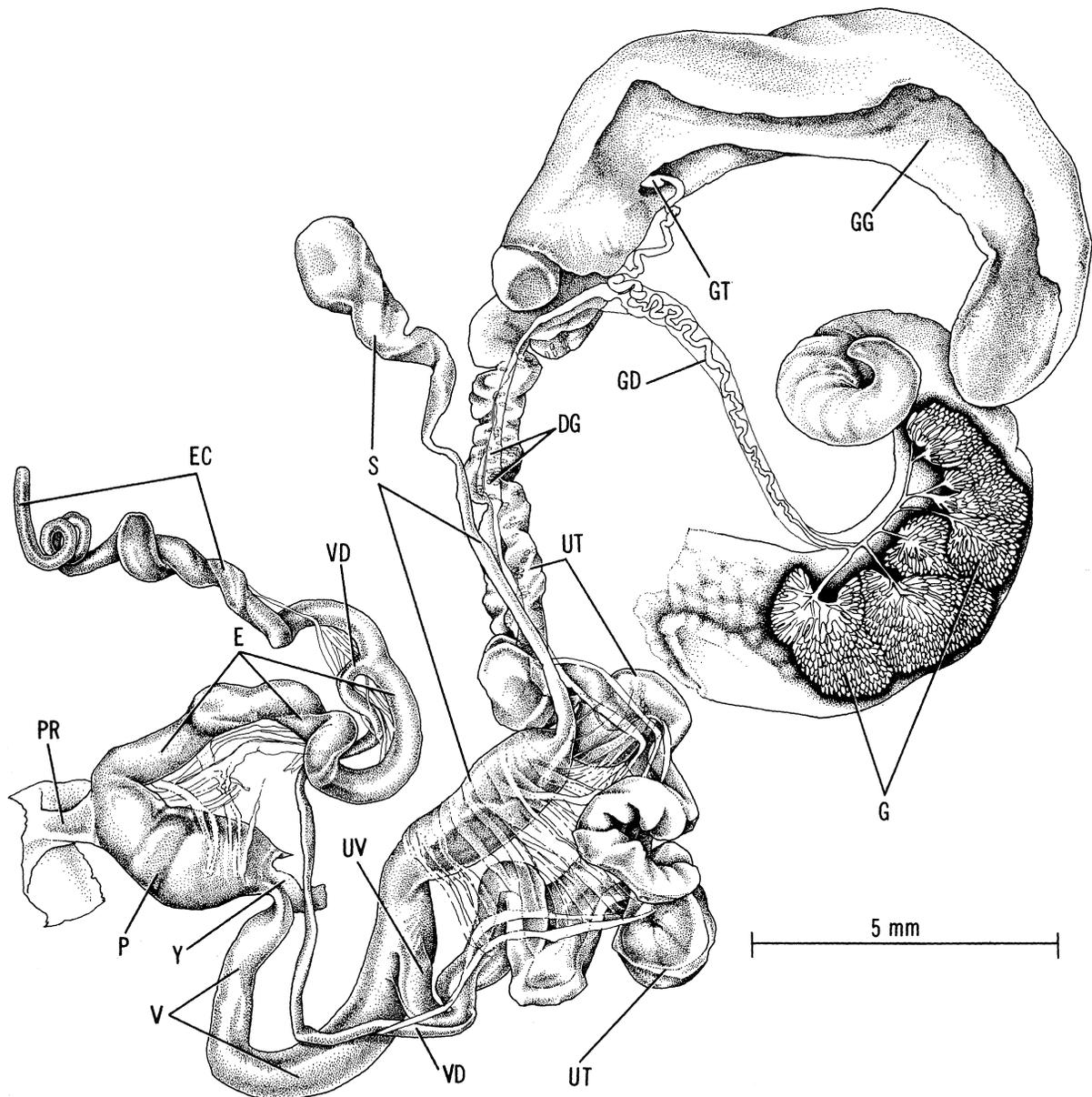


Fig. 20. Genitalia of *Amphidromus perversus* (Linné). On trees, Sanur, Bali, Indonesia, FMNH 198757. Collected by R.W. Skinner between 5-17 May 1977. Scale line equals 20 mm.

reduction of both the mesocone and the endocone. The tri-cuspid situation begins to be noticeable about 15 laterals outward and is a gradual shift. Outer marginals (Figs 6, 7, 13) are highly variable, may show splitting of all or no cusps, and have considerable individual variation in shape of the basal plate. The apparent differences illustrated for the three species are at least partly bridged by variation in other radulae studied, and should not be cited as indicative of species differences.

Jaw structure in *Amphidromus* (Figs 14, 15) compared with the average camaenid structure, shows reduction phenomena. The jaw is much thinner and less rigid, narrower, significantly elongated, and with greatly reduced vertical ribs. Haniel (1921: 40-45, figs 11, 12) illustrated the extreme variability in numbers of vertical

ribs within single populations. The jaw cannot be used for differentiating among species of *Amphidromus*.

#### Major Variations in the Genitalia

The few notes in early literature on the basic genital anatomy of *Amphidromus* are summarized by Laidlaw and Solem (1961: 516). For most of these, it is not possible to determine today which species was being studied. Haniel (1921: 57-68, figs 22-27) demonstrated considerable local variation in the length of the epiphallallic caecum and in the external appearance of many genital features. He did not study the functioning surfaces of the genitalia. Haniel's outline drawings and poorly reproduced photographs make further analysis

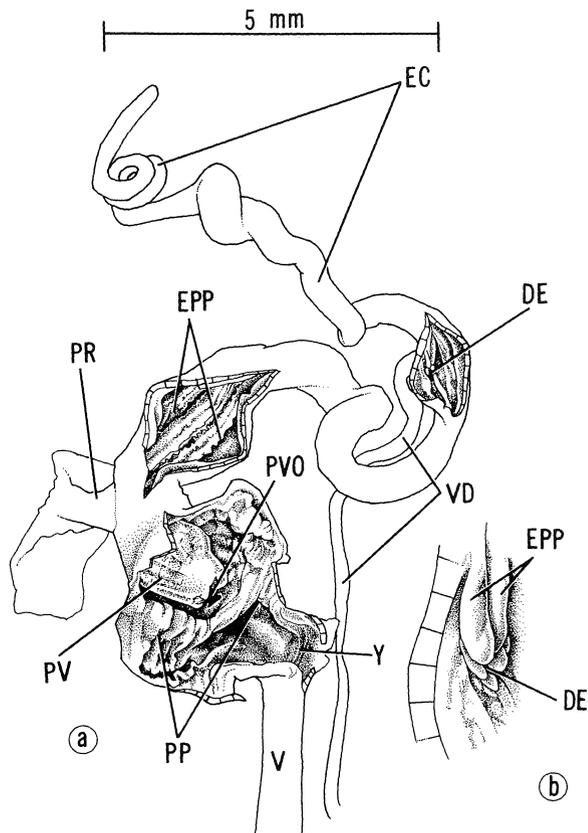


Fig. 21. Functioning surfaces of male terminal genitalia in *Amphidromus perversus* (Linné). On trees, Sanur, Bali, Indonesia, FMNH 198757. Scale line equals 10 mm. a, interior of penis chamber and epiphallus; b, detail of vas deferens opening into epiphallus.

of his data extremely difficult. Bishop (1977) found vergic differences among four Indonesian species and confirmed differences in lengths of the epiphallic caecum, but presented no quantitative data and his simplified drawings are very difficult to interpret. Minato (1979) outlined the terminal genitalia of *A. poecilochrous jaeckeli*, but gave no internal details.

The three species reported on here are from widely separated localities, were collected in different seasons, are of different relative maturities, and were preserved in different ways, and initially a maximum of two individuals could be dissected for each. It is thus possible to present only preliminary notes and suggest lines of investigation. Even these limited data do, however, confirm the camaenid position of *Amphidromus* and show that the patterns of variation in the terminal male system exactly parallel patterns observed in West Indian species of *Pleurodonte* which are sympatric. This suggests that species recognition structural shifts also exist in *Amphidromus* and that study of the terminal genitalia functioning surfaces will permit ready determination of species limits. This will permit unravelling and organizing the bewildering shell colour variations that exist both allopatrically and sympatrically. A recent note on *A. perversus* by Skinner (1981) contained data suggesting that colour variations in the shells of *Amphidromus* may have the same type

of physiologically linked, ecological correlations that occur in the much more completely studied European *Cepaea*.

The genitalia of *A. perversus* (Figs 20, 21) show only a few unusual features for a camaenid. The mass of the ovotestis is tightly clumped, the hermaphroditic duct enters very near to the head of the talon (GT), there is a very tightly kinked lower portion of the prostate-uterus that is bound by fibres to the spermathecal shaft, and the epiphallic caecum (EC) is very long. Laidlaw and Solem (1961: 520) point out that, in general, the epiphallic caecum is elongated in members of *Amphidromus, s.s.*, when compared with members of the subgenus *Syndromus*. This difference is confirmed by the conditions of *A. poecilochrous jaeckeli* (Fig. 23a), *A. cognatus* (Fig. 22a), and *A. porcellanus* (Bishop, 1977: 204, fig. 5f).

The penis of *A. perversus* is quite short, slightly bulbous, and has the walls (Fig. 21a) with vague spiral ridges. The verge (PV) is short, conic, with a very wide terminal pore (PVO). The epiphallus (E) has weak, slightly crenulated ridges basally that become smooth near the entrance of the vas deferens (VD), which is flanked (Fig. 21b) by a series of low, finger-like pilasters.

The dissected individuals of *Amphidromus poecilochrous jaeckeli* are 'new adults' with the characteristic minute albumen gland (GG, Fig. 22a), and extremely slender prostate-uterus area. The ovotestis is broken up into a series of distinct lobules, there is near-apical entrance of the hermaphroditic duct (GD) into the talon (GT), the spermatheca is quite slender for its entire length, and the epiphallic caecum (EC) is quite short.

*Amphidromus poecilochrous jaeckeli* (Fig. 22b) has corrugated longitudinal pilasters lining the penis interior, the verge (PV) is grossly enlarged to a flattened tip with the pore (PVO) shifted to one side and located almost half-way toward the verge apex. Epiphallic sculpture is less clearly developed and the pattern of ridges around the entrance of the vas deferens is simplified compared with that found in *A. perversus*.

In *A. cognatus* (Figs 23a-d, 24a, b), there is clear lateral entrance of the hermaphroditic duct onto the talon (Figs 23c, 24a), the ovotestis is also clearly divided into lobules (Figs 23b, 24b), and the epiphallic caecum is quite short (EC). *A. cognatus* is unusual in having the vagina (Fig. 23a) folded over with connective tissue binding the folded area, whereas in *A. perversus* it is the lower prostate-uterus (Fig. 20) that is folded and bound to the spermathecal shaft. The immature genitalia of *A. poecilochrous jaeckeli* do not permit study of this region. The walls of the penis chamber in *A. cognatus* (Fig. 23d) are smooth, with vague longitudinal pilasters below. The verge is conical, with strongly wrinkled surface, slightly subterminal pore (Fig. 23e, PVO), and with epiphallic pilasters lining the inner verge surface (Fig. 23e, EPP).

Specimens collected 11 November 1980 had the ovotestis enlarged (Fig. 24b) and the prostate-uterus (Fig. 24a) distinctly more swollen than in adult

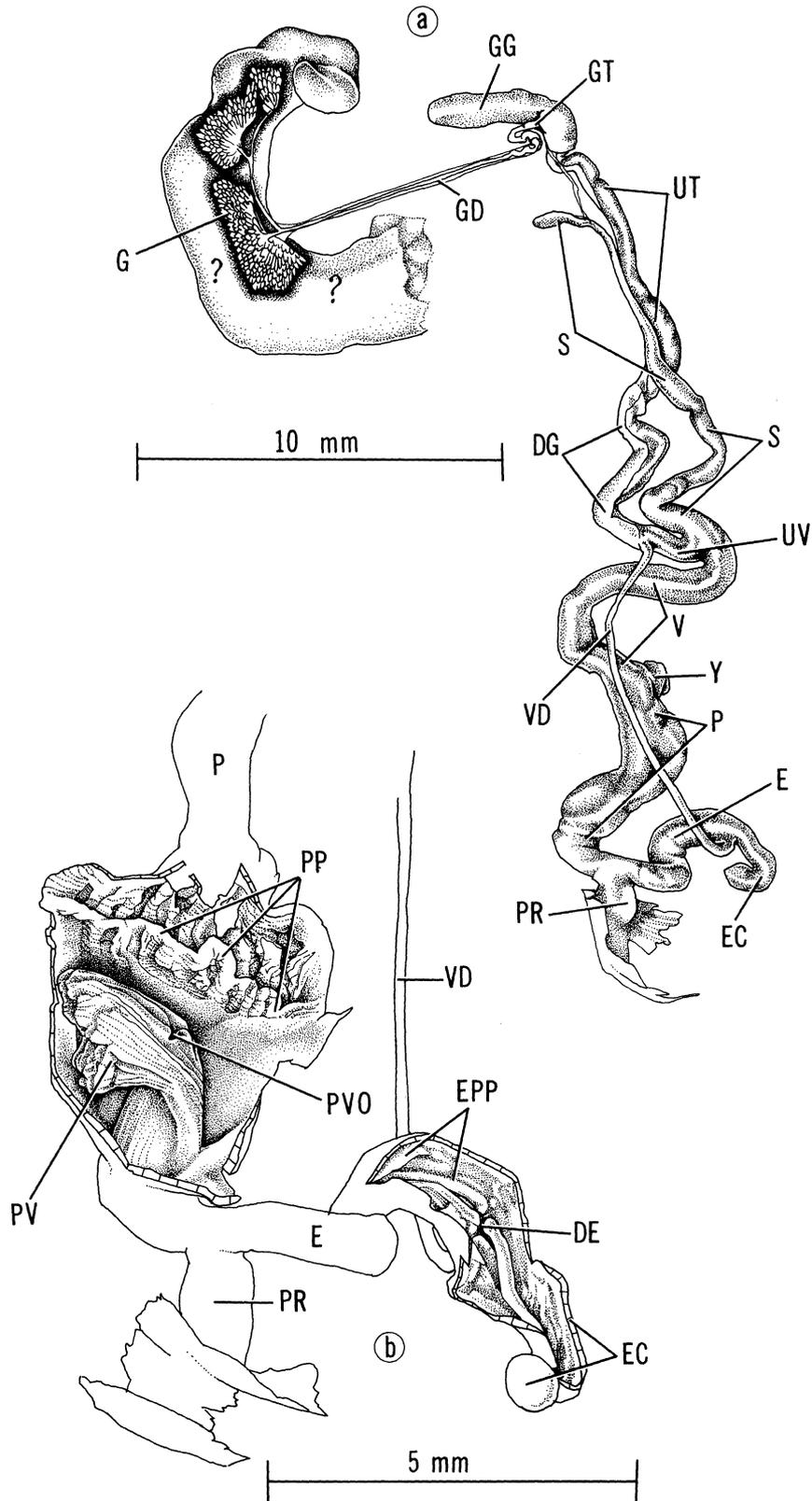
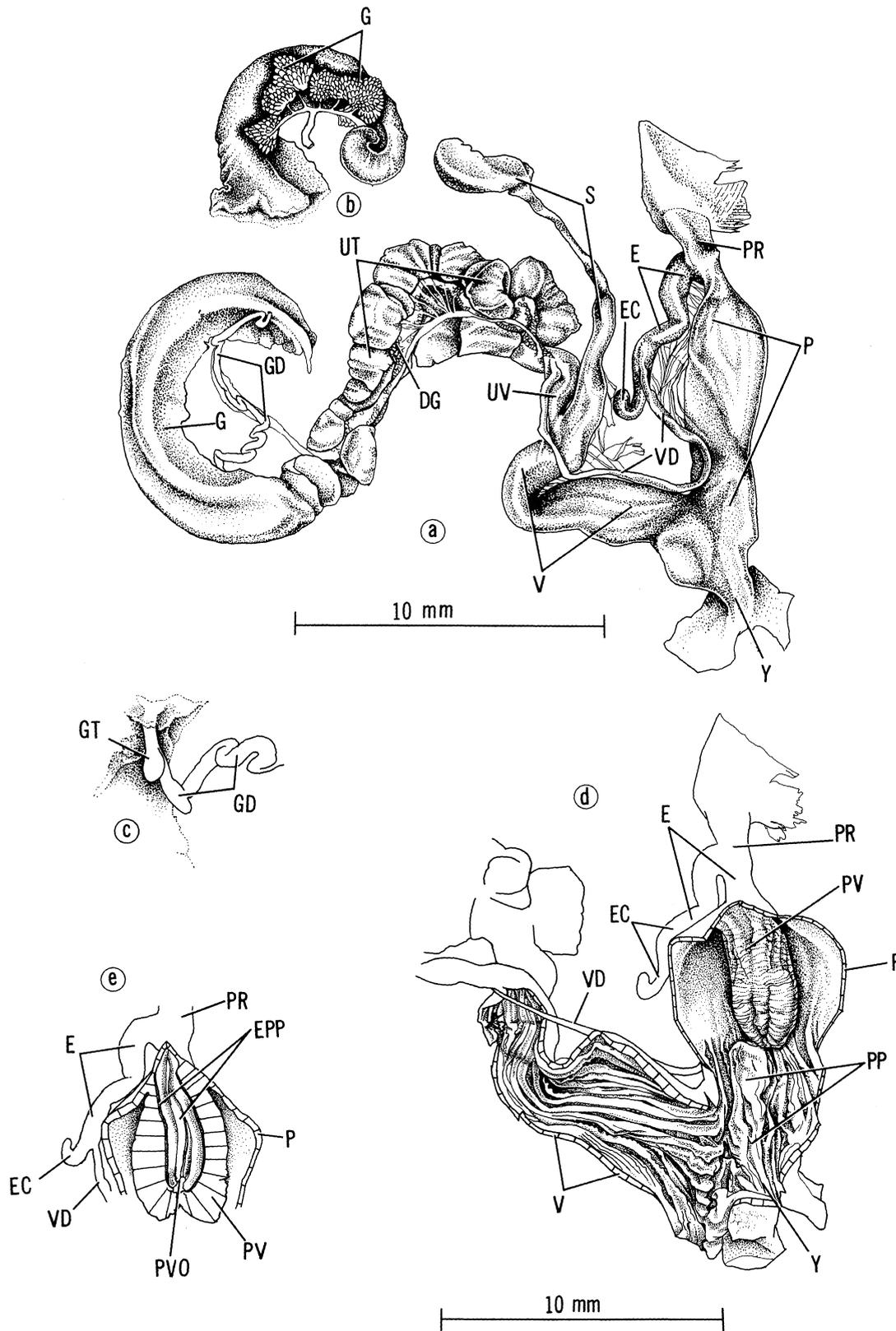


Fig. 22. Genitalia of *Amphidromus poecilochrous jaeckeli* Laidlaw. Jungle near Konga, Flores, Indonesia, FMNH 198758. Collected by R.W. Skinner in June 1975. Scale lines as marked. a, whole genitalia, male adult phase; b, interior of penis chamber and epiphallus.



**Fig. 23.** Genitalia of *Amphidromus cognatus* Fulton. Along creek at bridge 3-4 km from Paru, Melville I., Northern Territory, Australia. AM C.121192. Collected by P.H. Colman and V. Kessner on 21 March 1980. Scale lines as marked. **a**, whole genitalia of fully mature individual; **b**, ovotestis; **c**, detail of hermaphroditic duct-talon junction; **d**, interior of terminal genitalia.

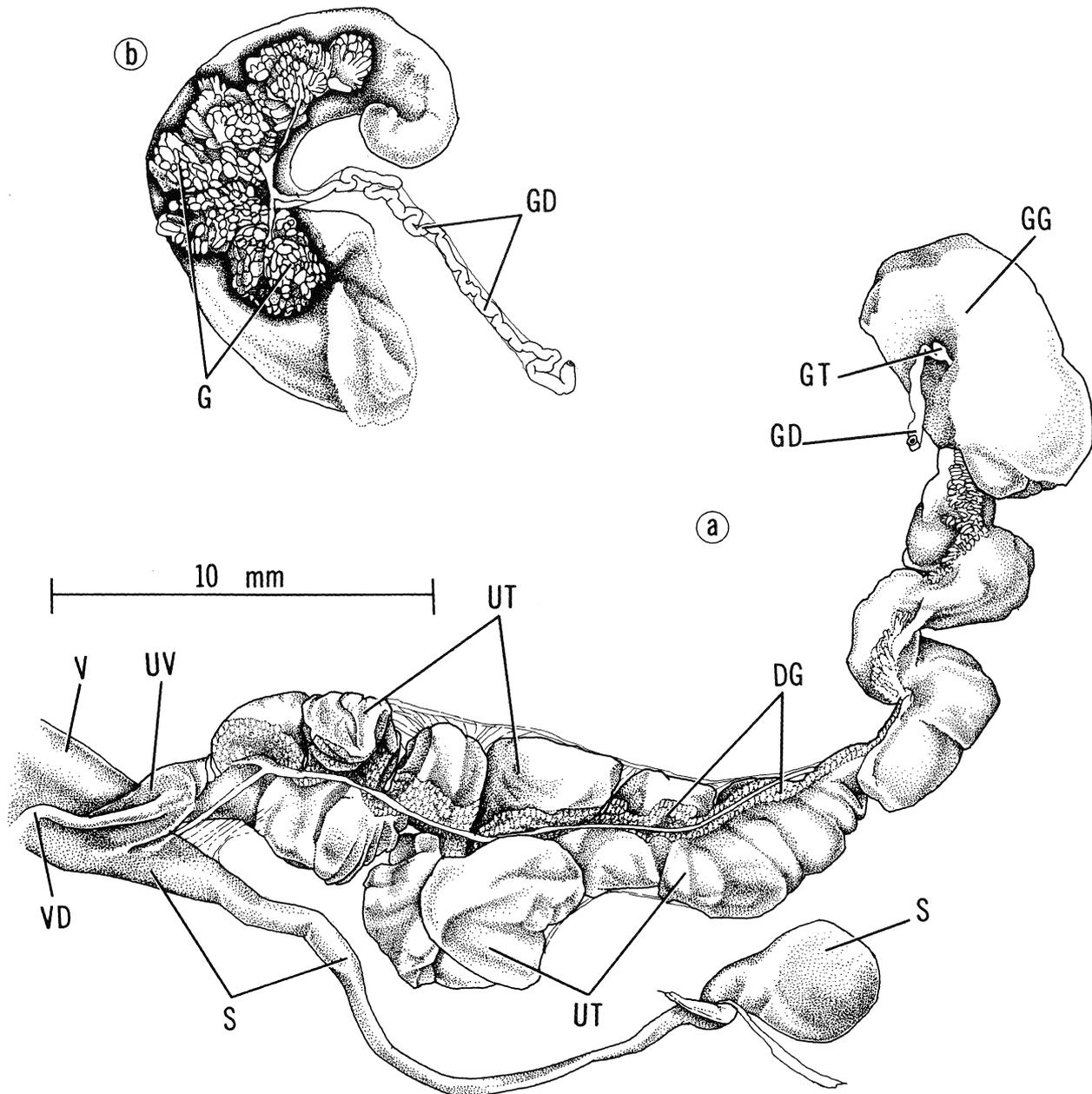


Fig. 24. Genital details of *Amphidromus cognatus* Fulton. Rain forest behind pumps, Milikapiti Bay, Melville I., near Darwin, Northern Territory, Australia, FMNH 198760. Collected by V. Kessner 11 November 1980. a, pallial and apical genitalia showing enlarged uterus, hermaphroditic duct; b, hermaphroditic gland.

specimens collected 21 March 1980. The former were from near the start of the wet season, the latter from near the late wet season. When the November specimens were received at the Australian Museum, about a dozen eggs were loose in the bottle. Dissecting four (of 15) adults was possible. One dissected individual had numerous calcium granules in the uterine walls, but none had eggs in the tract. It seems probable that during the drowning process, all encapsulated eggs would have been expelled, but we do not know how many eggs had been laid prior to collection.

Obvious differences among the species in regard to prostate-uterus length and development probably are mainly seasonal, since the specimens of *A. cognatus* were collected in March 1980, near the end of the wet season, but during a time of normal activity; those of *A. perversus* were taken in early to mid-May 1977, a time that approximates the normal start of dry season conditions; and those of *A. poecilochrous jaeckeli* were obtained in June 1975, during the dry season. The latter specimens were conchologically barely adult. The pattern of camaenids becoming male adult at the end

of one wet season, with the albumen gland and prostate-uterus areas remaining undeveloped until the middle or latter part of the following wet season, is typical for Australian genera, such as *Xanthomelon* and *Torresitrachia* (Solem, 1979), and *Amplirhagada* (Solem, 1981). Size and shape variations in these features thus have no systematic importance.

Changes in the point at which the hermaphroditic duct (GD) enters the talon (GT), length of the epiphallic caecum (EC), pattern of pilasters around the entrance of the vas deferens (VD) into the epiphallus (E), and details of vaginal (V) length, almost certainly will be useful in distinguishing species. The patterns of structural variation with the penis itself—smooth walls; spiral or longitudinal ridges that may be smooth or corrugated; verge shape variation from simple conical to elongate-oval to expanded tip; verge pore terminal, sublateral, or high lateral in position—are exactly the types of changes found in sympatric species of *Pleurodonte* on the island of Dominica, Lesser Antilles (Solem, in preparation). These changes are equivalent to the patterns for species recognition found in Australian camaenids (Solem, 1979, 1981 a, b, in press), and thus suggest that the general pattern for the Camaenidae is to use structures of the terminal genitalia for species recognition purposes. Such alterations can be on the functioning surfaces of the male and/or female terminalia (Solem, 1981 a, b). Bishop (1977) found shape differences in the verges of Javanese *Amphidromus*, but did not discuss or illustrate pore position and gave only rudimentary data on wall sculpture of the male system. Nevertheless, this confirms widespread variation patterns in the male system.

### Gross Anatomy

Externally, the body of *Amphidromus* is without unusual features. The head warts that are characteristic of *Rhagada* and some of the Japanese camaenid taxa are absent. Body colour is monochrome.

Pallial structures are typically camaenid, with a narrow and quite elongated kidney that abuts solidly against the most anterior intestinal loop at the apex of the pallial cavity. Despite the altered whorl count and profile in comparison with typical camaenids, no detectable pallial reorganization was discovered. Further comments and illustrations will be presented elsewhere.

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