

**Descriptions of New Species of the Diverse and Endemic
Land Snail *Amplirhagada* Iredale, 1933
from Rainforest Patches across the Kimberley, Western Australia
(Pulmonata: Camaenidae)**

FRANK KÖHLER

Department of Environment and Conservation of Western Australia,
Science Division, Wildlife Place, Woodvale WA 6026, Australia and

Australian Museum, 6 College Street, Sydney NSW 2010, Australia
frank.koehler@austmus.gov.au

ABSTRACT. Fifteen species of the camaenid land snail *Amplirhagada*, which are endemic to the Kimberley region in Western Australia, are newly described in the present work based on material collected in 1987 during the Kimberley Rainforest Survey of the then Dept. Conservation and Land Management, Western Australia. These species were listed previously as new discoveries under preliminary species identifications but have never been validly described. All of them were collected in rainforest and vine thicket patches across the Kimberley, where they generally occur as narrow-range endemics. The species are most typically characterized by a peculiar penial anatomy while other morphological structures, such as the shell or radula, provide characters less or not suitable for unambiguous species identification. Three manuscript taxa listed as potentially new are here preliminarily subsumed under an already described taxon, *A. carinata* Solem, 1981. By contrast to all other species treated herein, *A. carinata* has a fairly large distribution around the Walcott Inlet in the Southwest Kimberley. This taxon also reveals a comparatively large amount of morphological variation not only with respect to the shell but also to its genital anatomy. This unusual morphological variation is discussed as being potentially indicative of on-going lineage differentiation and the presence of a species complex, which cannot be satisfactorily resolved at the present stage.

KÖHLER, FRANK. 2011. Descriptions of new species of the diverse and endemic land snail *Amplirhagada* Iredale, 1933 from rainforest patches across the Kimberley, Western Australia (Pulmonata: Camaenidae). *Records of the Australian Museum* 63(2): 167–202.

The Kimberley region in northwesternmost Western Australia has been found to harbour a hyper-diverse radiation of camaenid land snails, which matches in species richness some of the most diverse land snail faunas worldwide (Köhler, 2010a). Despite the valiant work of Alan Solem (1931–1990) over many years, a large proportion of this land snail fauna has remained undescribed. In contrast to many other groups of helicoid land snails worldwide, the

Camaenidae in northwesternmost Australia (i.e., in the Kimberley and immediately adjacent regions of the Northern Territory) have micro-ranges and are usually restricted to small islands of rainforests and vine thickets, where they occur as local endemics.

Recently, molecular comparisons have revealed high levels of mitochondrial divergence between *Amplirhagada* species from several offshore islands along the Kimberley

coast. The amount of genetic differentiation of the island species had not been expected, for the islands have repeatedly been connected with the mainland during the past 500,000 years (Johnson, O'Brien & Fitzpatrick, 2010; Köhler, 2010b). Based on this observation, it has been concluded that the origin of species predates the formation of the islands and that the phylogeographic relationships among *Amplirhagada* species may reflect earlier events, likely connected to the fragmentation of rainforest habitats since about the late Miocene or early Pliocene (Köhler, 2010a).

In terms of species numbers, *Amplirhagada* Iredale, 1933 arguably is the most diverse camaenid genus in the Kimberley. Representatives of this group are found along the Kimberley coast within a distributional range from the Buccaneer Archipelago in the south to Kalumburu in the north as well as in inland areas of the Napier, Oscar, Harding, and King Leopold Ranges, the Drysdale River Reserve, Mt Elizabeth Station and the region south of Wyndham (Solem, 1981, 1988). Thirty species were described previously by nineteenth and twentieth century authors, such as Smith (1894), Iredale (1938, 1939) and Solem (1981, 1988), while an additional twenty-six species were recently described by Köhler (2010b) bringing the total number of currently recognized species to 56. However, this number does include only a few of the allegedly 23 new species briefly listed under preliminary taxon identifications in the inventory

of the Kimberley rainforests (Solem, 1991), which have remained undescribed. These species were collected in rainforest and vine thicket patches across the Kimberley, where they were mostly found as micro-endemics (Fig. 1). The relevant material has since been kept in the Field Museum of Natural History, Chicago, where it has remained essentially untouched after Alan Solem passed away in 1990 (Cameron, Pokryszko & Wells, 2005).

To revise the status of these manuscript taxa and formally describe those that are considered to represent valid species is the foremost goal of the present publication as a contribution towards a more complete knowledge of the Camaenidae of the Western Australian Kimberley.

Material and methods

This study is primarily based on ethanol preserved specimens and supplementary dry shell material collected during the Kimberley Rainforest Survey (RFS) of the then Department of Environment and Land Management, Western Australia (now Department of Environment and Conservation, DEC) in 1987–1988. This material has been kept in the Field Museum of Natural History, Chicago (FMNH). The specimen series have now been split and shared with the Western Australian Museum, Perth (WAM) and the Australian Museum, Sydney (AM).

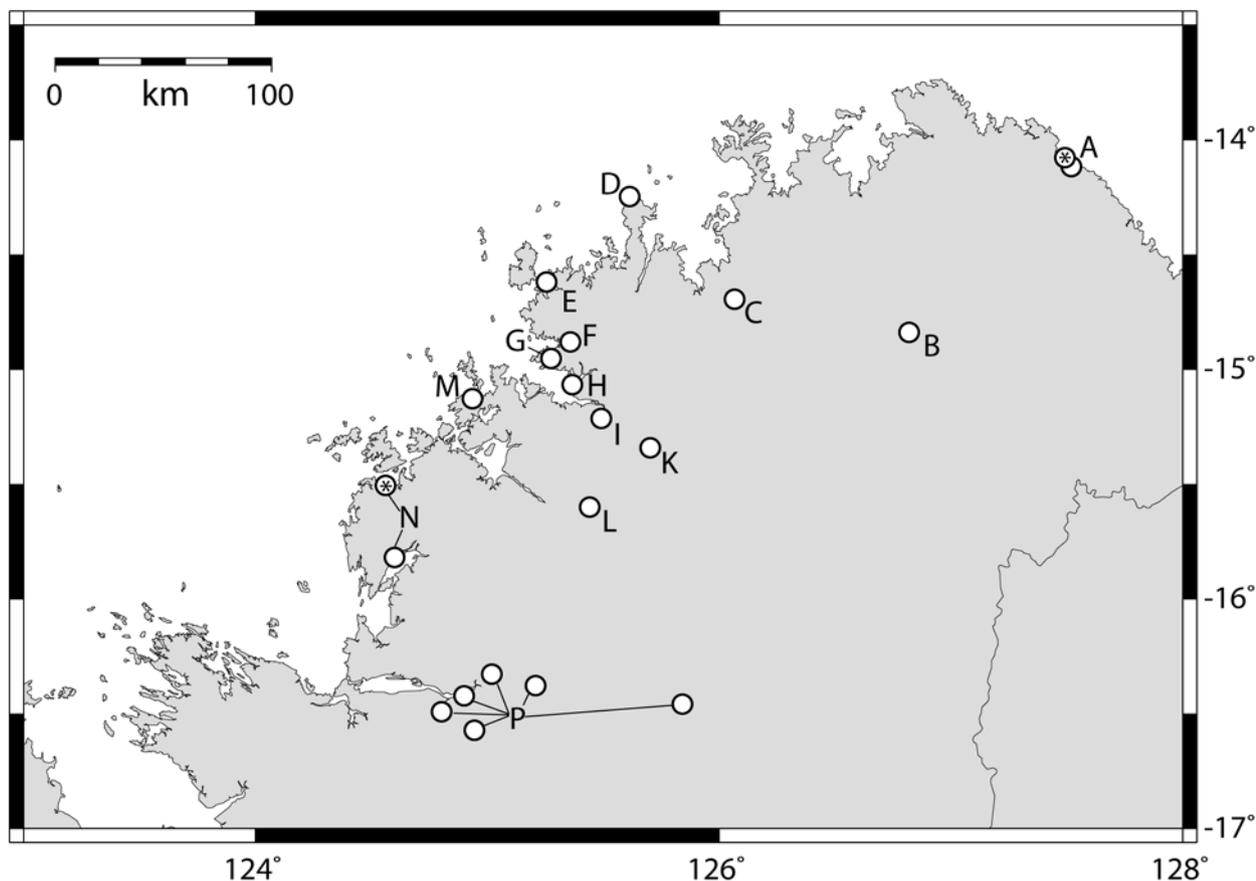


Figure 1. Distribution of *Amplirhagada* species described in the present work. (A) *A. atlantis* n.sp. (B) *A. carsoniana* n.sp. (C) *A. alicunda* n.sp. (D) *A. davidsoniana* n.sp. (E) *A. vialae* n.sp. and *A. discoidea* n.sp. (F) *A. forrestiana* n.sp. (G) *A. inusitata* n.sp. and *A. epiphallia* n.sp. (H) *A. lindsayae* n.sp. (I) *A. angusticauda* n.sp. (K) *A. moraniana* n.sp. (L) *A. gardneriana* n.sp. (M) *A. bendraytoni* n.sp. (N) *A. coffea* n.sp. (P) *A. carinata* Solem, 1981. When species occur at more than one locality, the type locality of newly described taxa is marked with an asterisk.

Morphological descriptions focus on characters of the shell, genital organs, and the radula. Morphometric shell parameters of adult shells (with calloused outer lip), such as height of shell (H), diameter of shell (D) and height of last whorl (LW) were measured with Vernier callipers precise to 0.1 mm. The numbers of whorls (N), including the protoconch, were counted as described in Barker (1999: Fig. 6). The parameter “angle of aperture” describes the angle formed between aperture and the horizontal in degrees when the shell is in an upright position. Anatomy of mantle and genital organs was studied using a binocular microscope with drawing mirror. The final inking of anatomical drawings was done by Martin Püschel (Sydney). Radulae and jaws were extracted manually, cleaned by soaking in 10% KOH solution for about six hours followed by rinsing in water and ethanol. They were mounted on carbon specimen tabs for electron scanning microscopy. Radular tooth formula gives the numbers of teeth as follows: C (central row of teeth) + number of lateral rows of teeth + number of transitional rows of teeth + number of marginal rows of teeth. Whenever the number of available specimens allowed, the anatomy was studied in two (in small series) to five specimens per sample in order to confirm that morphological features are consistently found among conspecific specimens.

Terminology for anatomical features is not always consistent and Alan Solem employed some terms that are otherwise not widely used. In order to gain clarity, terms used here are defined as follows. Anterior part of oviduct refers to the proximal portion of the oviduct from the atrium to the point where uterus and prostate fuse forming the spermooviduct. The anterior oviduct consists of vagina (most anterior portion between atrium and opening to bursa copulatrix) and free oviduct (between opening to bursa copulatrix and distal end of anterior part of oviduct). Spermooviduct consists of uterus and prostate fused to each other. Bursa copulatrix is the term used for the spermatolytic gland, which has erroneously been referred to as “spermatheca” by Alan Solem. The inner penial wall may support different structures, such as pustules (small, conical elevations) and pilasters (projecting longitudinal column). The main stimulatory pilaster is significantly larger than any other potentially present pilasters and frequently also differs in shape and structure.

Systematic descriptions

Gastropoda

Heterobranchia

Stylommatophora

Camaenidae Pilsbry, 1895

Amplirhagada Iredale, 1933

Amplirhagada Iredale, 1933: 52; Solem, 1981: 147–320; Solem, 1988: 28–32; Solem, 1991: 187–202; Solem & McKenzie, 1991: 247–263; McKenzie *et al.*, 1995: 251; Johnson, O’Brien & Fitzpatrick, 2010: 141–153; Köhler, 2010b: 217–284. Type species *Helix (Hadra) sykesi* Smith, 1894 by original designation.
Tenuigada Iredale, 1939: 68. Type species *Tenuigada percita* Iredale, 1939 by original designation.

Diagnosis

Rock or free sealer with medium sized (H = 8–23 mm, D = 15–30 mm, H/D = 0.5–1.1) shell, from thin and translucent to moderately thick, broadly conical to dome-shaped with moderately to strongly elevated spire. Umbilicus narrowly winding, entirely open to completely concealed by columellar reflection, frequently variable within species. Protoconch with weak to strongly developed radially elongated pustulations, transition to teleoconch inconspicuous. Teleoconch sculpture variable, ranging from presence of very weak axial growth lines only to presence of well-developed, regular radial lirae, which may be prominent on entire whorl surface or only on upper parts of whorls. Last whorl moderate to wide in cross-section, periphery well rounded to slightly angulated (often transitions are found within single populations). Shell colour variable, background often yellowish brown to horn, frequently banded, with brown sub-sutural and peripheral bands, or more rarely uniform with lighter base.

Mantle cavity extending between half and more than entire last whorl of shell; mantle roof with variably spotted or marbled, black pigmentation; kidney extending about half to two thirds of mantle cavity.

Genitalia typically camaenid with prostate and uterus being fused forming spermooviduct; development of gonads depending on seasonal activity and maturity. Penis with well-developed sheath, extending entire length, usually thin proximally, thick distally. Typically without well-developed epiphallus, rarely vas deferens reflecting as simple, elongated epiphallus. Penial retractor muscle attached at apex of penial complex, variable in length. Vas deferens entering penial sheath from halfway up to almost apically; entering penial chamber through variably developed verge. Inner penial wall supporting characteristic pustulation and basal pilasters (often species-specific); a main stimulatory pilaster may or may not be present, varying in development, shape and sculpture (often species-specific). Bursa copulatrix relatively simple, short, reaching or slightly extending base of spermooviduct; head usually well differentiated (inflated); inner wall of vagina and bursa copulatrix with longitudinal pilasters that vary in development and finer structure.

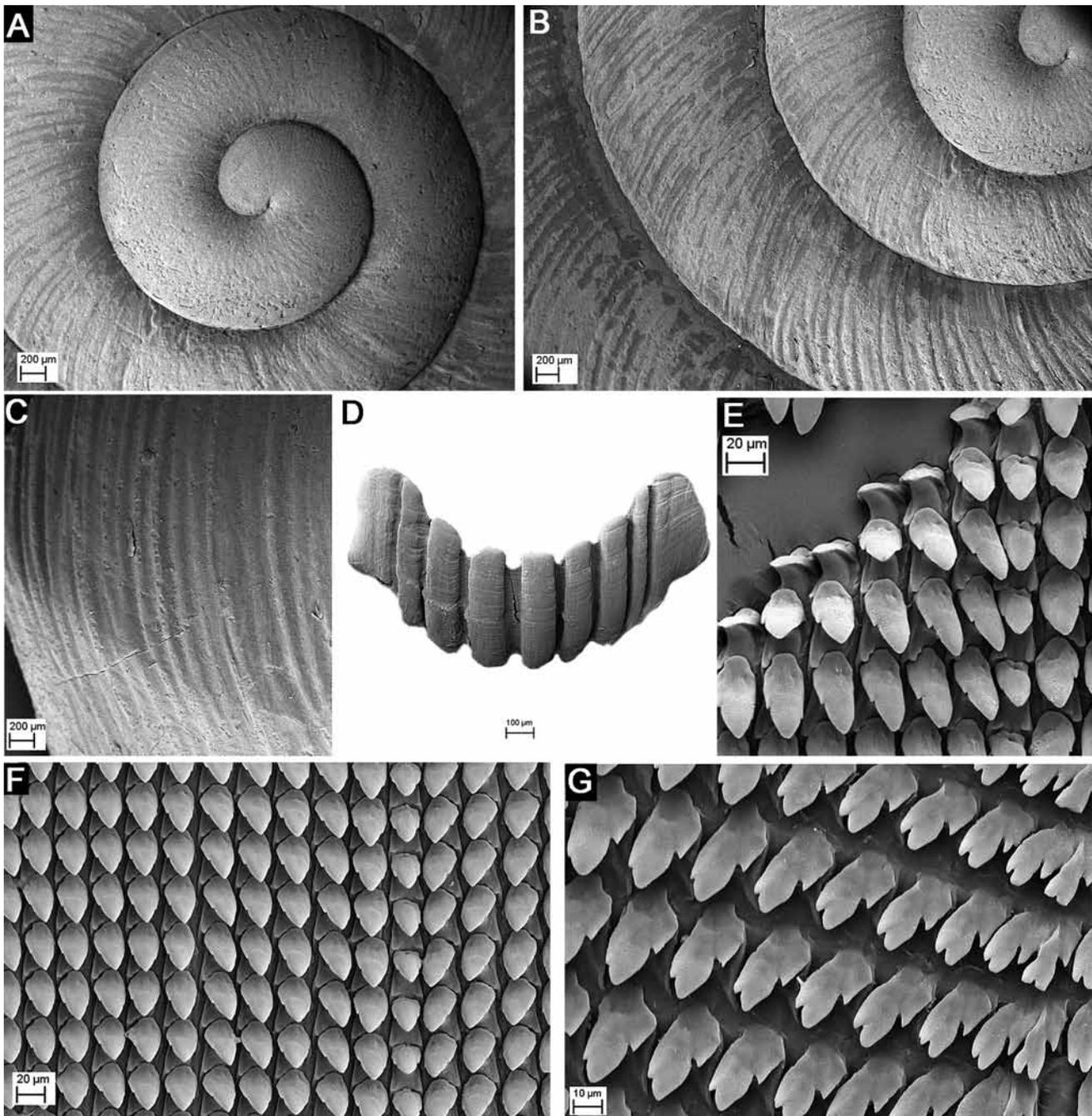


Figure 2. *Amplirhagada atlantis* n.sp. SEM of shell (AM C.472919), radula and jaw (AM C.472918). (A) Protoconch viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Close-up showing sculpture on last whorl. (D) Jaw. (E) Close-up showing morphology of central and inner lateral teeth. (F) Central and lateral teeth viewed from above. (G) Inner and central marginal teeth viewed from above. Scale bars: A–C, 200 µm; D, 100 µm; E–F, 20 µm; G, 10 µm.

Albumen gland elongated. Talon embedded in albumen gland within proximal portion of albumen gland. Hermaphroditic duct tightly undulating. Radula rectangular in shape, usually between 3.5 and 5.5 mm long with 120–170 rows of teeth. Tooth formula variable, C + 12–20 + 3–4 + 15–22. Central teeth with pointed triangular mesocones, shorter than base of tooth; ectocones vestigial. Lateral teeth with bluntly pointed triangular mesocones, length equal to base of tooth; vestigial to small ectocones; endocones vestigial. Marginal teeth multicuspid, mesocones and endocones similar in length, ectocones smaller than endocones, occasionally subdivided. Species aestivating as rock or free sealers.

Amplirhagada atlantis n.sp.

Type locality. Western Australia, NW Kimberley, Joseph Bonaparte Gulf, 8.6 km SSE of Cape Bernier; 14°04'40"S 127°29'25"E (RFS-04-1; coll. V. Kessner, 04 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34704 (preserved specimen) (Pl. 1.1; Table 1). Paratypes AM C.472918 (4 preserved specimens), WAM S34705 (8 preserved specimens), FMNH 220006 (12 preserved specimens), AM C.472919 (3 dried shells), WAM S34706 (10 dried shells), FMNH 220005 (13 dried shells).

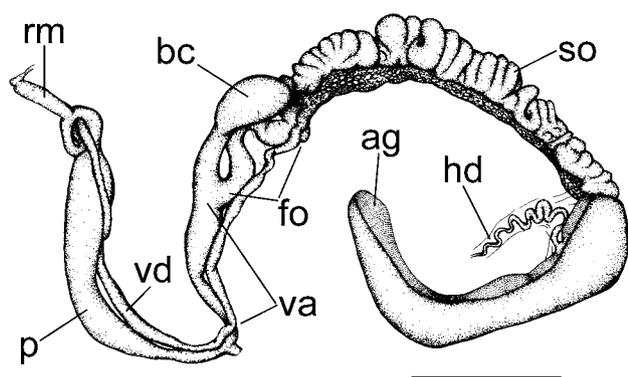


Figure 3. Genitalia of *Amplirhagada atlantis* n.sp. (AMC.472918). Abbreviations: *ag*, albumen gland; *bc*, bursa copulatrix; *fo*, free oviduct; *hd*, hermaphroditic duct; *p*, penis; *rm*, penial retractor muscle; *so*, sperm oviduct; *va*, vagina; *vd*, vas deferens. Scale bar = 5 mm.

Additional material (not dissected). WAM S34751 (5 preserved specimens), FMNH 220327 (10 preserved specimens), WAM S34752 (8 dried shells), FMNH 220328 (7 dried shells), all from 5.6 km W of Evelyn Island, mainland, behind beach and mangroves; 14°06'55"S 127°31'10"E (RFS 10-2; coll. V. Kessner, 10 Jun 1987).

Etymology. Specific name referring to the name of the seaplane "Atlantis 1925" of the two German aviators Hans Bertram and Adolph Klausmann, who in 1932 undertook a goodwill flight from Cologne, Germany, to Australia. On 14 May 1932 the aviators took off from Timor bound for Darwin but were stranded due to bad weather near Bertram Cove, where they survived for 40 days before being rescued. Being a noun the species epithet keeps its male suffix.

Description

Shell (Pl. 1.1, Fig. 2A–C). Broadly conical with moderately elevated spire. Rather thin but solid, translucent. Periphery well rounded to slightly angulate; upper and basal sectors rounded. Umbilicus 80–90% concealed by columellar reflection. Background colour horn to almost crème; no spiral bands visible; outer and inner lip colour whitish. Protoconch 2.6 mm in diameter, comprising about 1.5 whorls, with weak radially elongated pustulations. Teleoconch with faint, regular axial growth lines, evenly distributed across whorls of shell and across whorl diameter. Angle of aperture 45–60 degrees; outer lip thin, well rounded, well expanded, not or slightly reflected; basal node absent or weak. Parietal wall of inner lip inconspicuous. Average shell size $11.8 \pm 0.8 \times 16.2 \pm 0.9$ mm (Table 1).

Radular and jaw morphology (Fig. 2 D–G). Tooth formula C + 14 + 4 + ?; average number of rows of teeth 130 ($n = 2$). Jaw with nine plates.

Genital morphology (Figs 3–4). Penis straight, more or less of same length as anterior part of oviduct. Penial sheath delicate. Length of penial retractor muscle equivalent to about $\frac{1}{4}$ of length of penial complex. Penial verge extending about $\frac{1}{4}$ of length of penial chamber, slender with rounded tip. Almost entire inner penial wall covered by strongly developed pustules, which are arranged to form several corrugated longitudinal pilasters. Main stimulatory pilaster

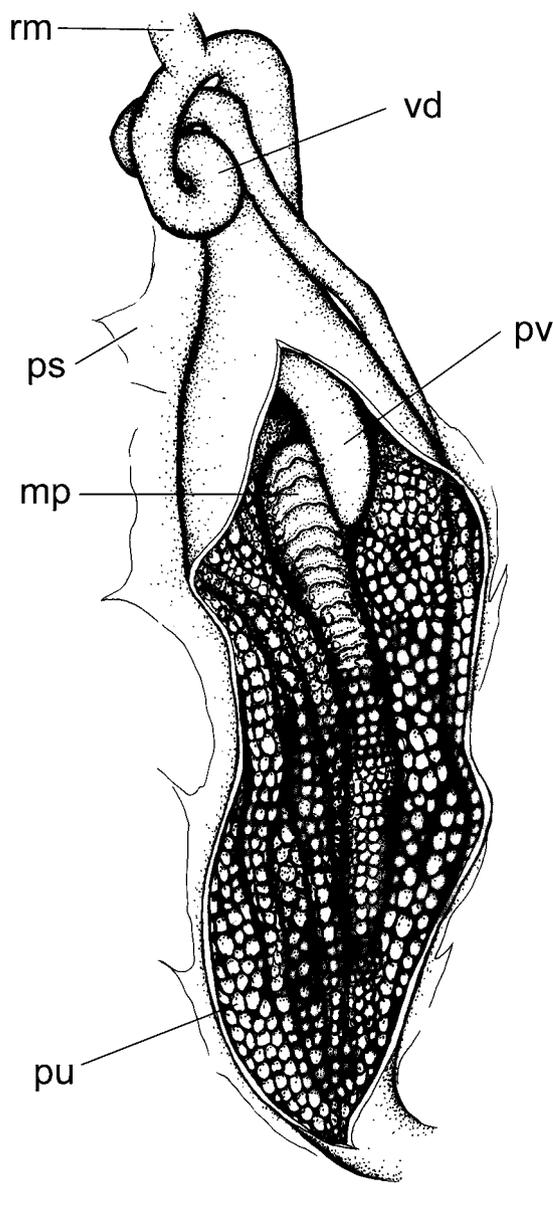


Figure 4. Penial anatomy of *Amplirhagada atlantis* n.sp. (AMC.472918). Abbreviations: *mp*, main pilaster; *ps*, penial sheath; *pu*, penis wall pustulation; *pv*, penial verge; *rm*, penial retractor muscle; *vd*, vas deferens. Scale bar = 3 mm.

well developed, elongate, comprising proximal third of inner penial wall; sculptured by smooth lateral ridges being formed by fused and flattened pustules. Vas deferens entering penial sheath near apex of penial complex. Vagina long, tubular, posteriorly slightly inflated; inner vaginal wall and inner wall of spermathecal duct support continuous, well-developed, smooth longitudinal pilasters. Bursa copulatrix short, reaching base of spermoviduct; head elongately inflated, connected with spermoviduct by connective tissue, wall of head delicate, smooth. Free oviduct rather straight comprising less than half of length of anterior part of oviduct. Spermoviduct longer than anterior part of oviduct.

Aestivation strategy. Free or rock sealer, in talus throughout vine thicket patches.

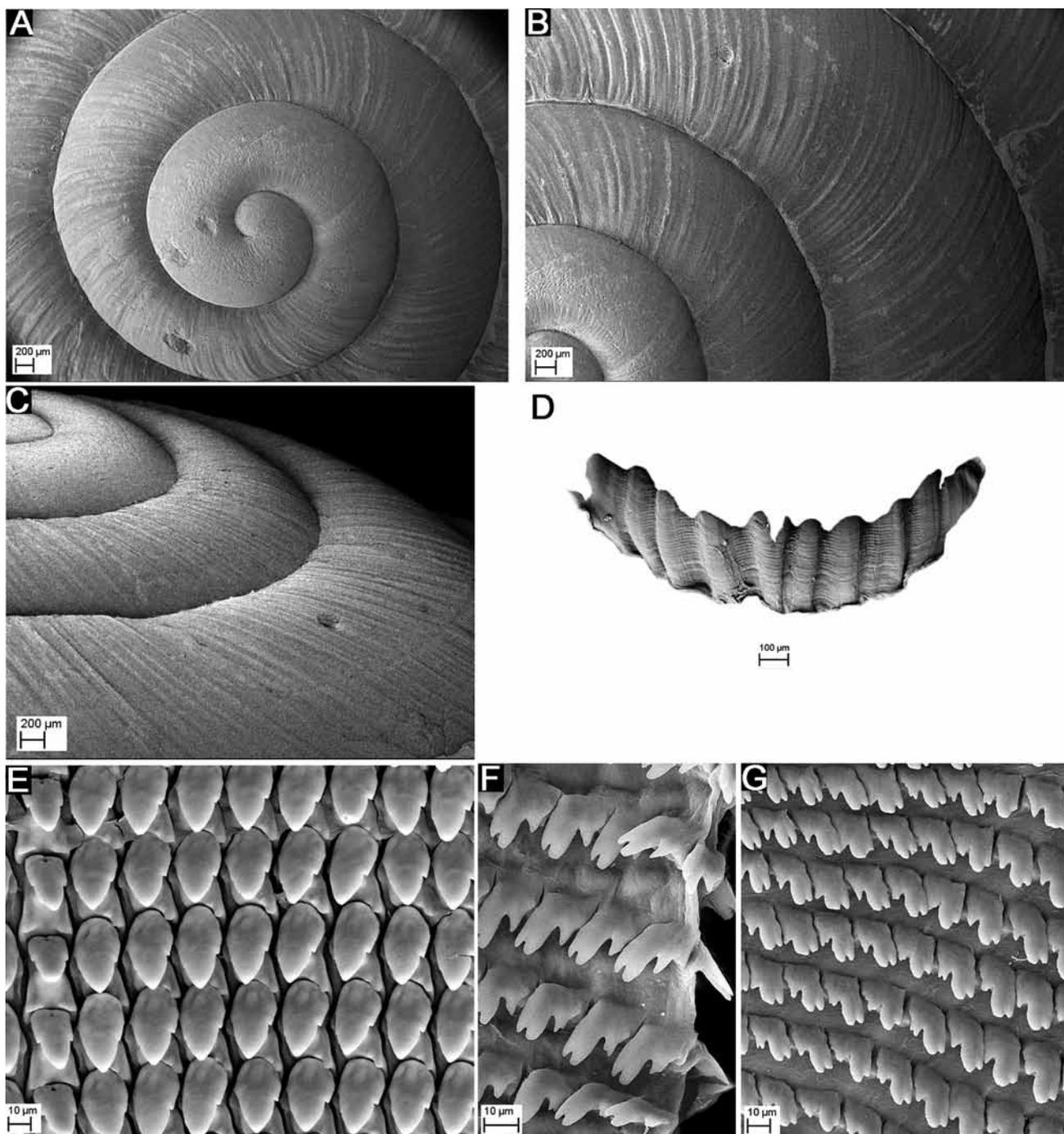


Figure 5. *Amplirhagada carsoniana* n.sp. SEM of shell (AM C.472920), radula and jaw (WAM S34708). (A) Protoconch viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) First teleoconch whorls viewed obliquely from above. (D) Jaw. (E) Central and lateral teeth viewed from above. (F) Close-up of marginal teeth. (G) Inner and central marginal teeth viewed from above. Scale bars: A–C, 200 µm; D, 100 µm; E–G, 10 µm.

Remarks. Anatomical description based on dissections of two type specimens. The non-type sample contains predominantly immature individuals not suitable for anatomical dissections. Listed by Solem (1991) as “*Amplirhagada* NSP17”.

***Amplirhagada carsoniana* n.sp.**

Type locality. Western Australia, NW Kimberley, Carson Escarpment, 2.5 km N of Face Point, base of escarpment;

14°50'20"S 126°49'10"E (RFS 10-4, coll. V. Kessner, 10 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34707 (preserved specimen) (Pl. 1.2; Table 1). Paratypes WAM S34708 (preserved specimen), FMNH 220344 (preserved specimen), AM C.472920 (5 dried shells), WAM S34709 (12 dried shells), FMNH 220343 (17 dried shells).

Etymology. In reference to the Carson Escarpment, where this species was found.

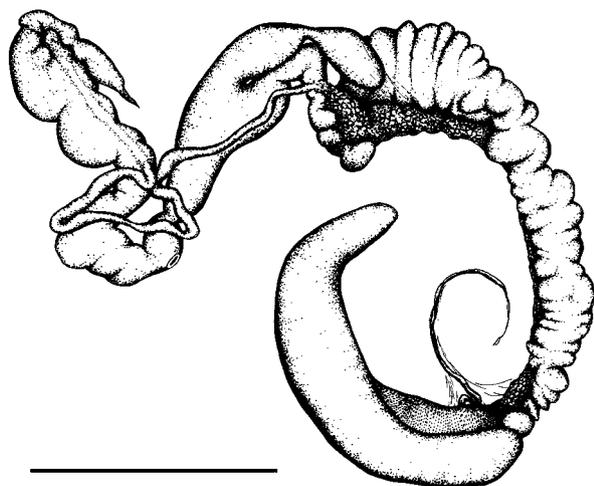


Figure 6. Genitalia of *Amplirhagada carsoniana* n.sp. (WAM S34708). For labelling of structures see Fig. 3. Scale bar = 5 mm.

Description

Shell (Pl. 1.2; Fig. 5 A–C). Broadly conical with low spire, almost discoid. Thin to delicate, translucent. Periphery rounded to slightly angulate; upper and basal sectors of whorls well rounded. Umbilicus 10–30% concealed by columellar reflection. Background colour brownish horn; peripheral band absent or well marked, thin, brown, visible on most whorls; sub-sutural diffuse, thin, visible on most whorls; outer and inner lip colour whitish. Protoconch 2.6 mm in diameter, comprising about one whorl, with weak radially elongated pustulations. Teleoconch with faint, regular axial growth lines, evenly distributed across shell surface. Angle of aperture about 45 degrees; outer lip thin, well rounded, expanded, weakly reflected; basal node absent. Parietal wall of inner lip absent or very inconspicuous. Average shell size $9.8 \pm 0.6 \times 16.3 \pm 0.8$ mm (Table 1).

Radular and jaw morphology (Fig. 5 D–G). Tooth formula C + 12–14 + 4 + 18–20; average number of rows of teeth 130 (n = 2). Jaw with ten plates.

Genital morphology (Figs 6–7). Penis coiled within thick penial sheath; penial complex about as long as anterior part of oviduct. Length of penial retractor muscle equivalent to about half of length of penial complex. Penial verge extending about 1/5 of length of penial chamber, slender with pointed tip. Inner penial wall entirely covered by dense pustulation; pustules forming indistinct, corrugated pilasters. Main stimulatory pilaster indistinct, formed by prolonged pustules, comprising proximal half of inner penial chamber. Vas deferens entering penial sheath within proximal third of penial complex. Vagina moderately long, distally inflated. Bursa copulatrix short, reaching base of spermoviduct. Free oviduct coiled, shorter than vagina. Spermoviduct longer than anterior part of oviduct.

Aestivation strategy. Free sealer.

Remarks. Description based on dissection of one specimen. Listed by Solem (1991) as “*Amplirhagada* NSP18” to be distinct from *A. drysdaleana* Solem, 1981. Both taxa are indeed very similar but *A. carsoniana* differs by coiled, shorter penis with shorter main pilaster, no extended basal pilasters of inner penial wall and shorter vagina. Vas deferens

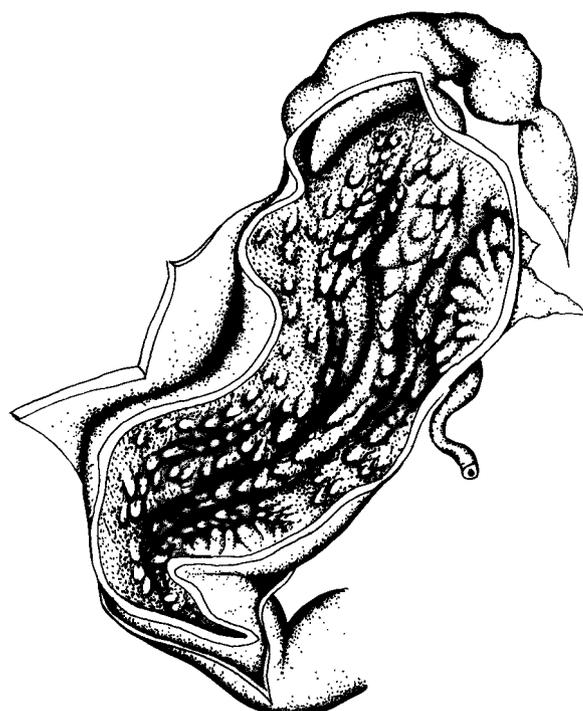


Figure 7. Penial anatomy of *Amplirhagada carsoniana* n.sp. (WAM S34708). For labelling of structures see Fig. 4. Scale bar = 3 mm.

entering sheath half way up in *A. carsoniana* but within upper sector of penial sheath in *A. drysdaleana*. Being similar overall and occurring in close proximity to each other, both species are likely sister taxa.

Amplirhagada alicunda n.sp.

Type locality. Western Australia, NW Kimberley, 27 km SE Walsh Point, ca. 16 km SSW of Mt. Connor, 13 km from coast; $14^{\circ}41'45''\text{S } 126^{\circ}04'04''\text{E}$ (RFS 11-4, coll. V. Kessner, 11 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34710 (preserved specimen) (Pl. 1.3; Table 1). Paratypes WAM S34711 (2 preserved specimens), FMNH 220384 (2 preserved specimens), AM C.472921 (10 dried shells), WAM S34712 (16 dried shells), FMNH 220385 (25 dried shells).

Etymology. Species epithet derived from “alicunde” (Latin = from somewhere, from any place), in reference to the remote type locality, far away from any named place.

Description

Shell (Pl. 1.3; Fig. 8 A–D). Broadly conical to semi-globose with elevated spire. Solid, not translucent. Periphery slightly compressed to slightly angulate; upper sector of whorl flattened, basal sectors rounded. Umbilicus 70–100% concealed by columellar reflection. Background colour crème to horn; peripheral band conspicuous, usually well developed, rather thin, clearly visible on most whorls;

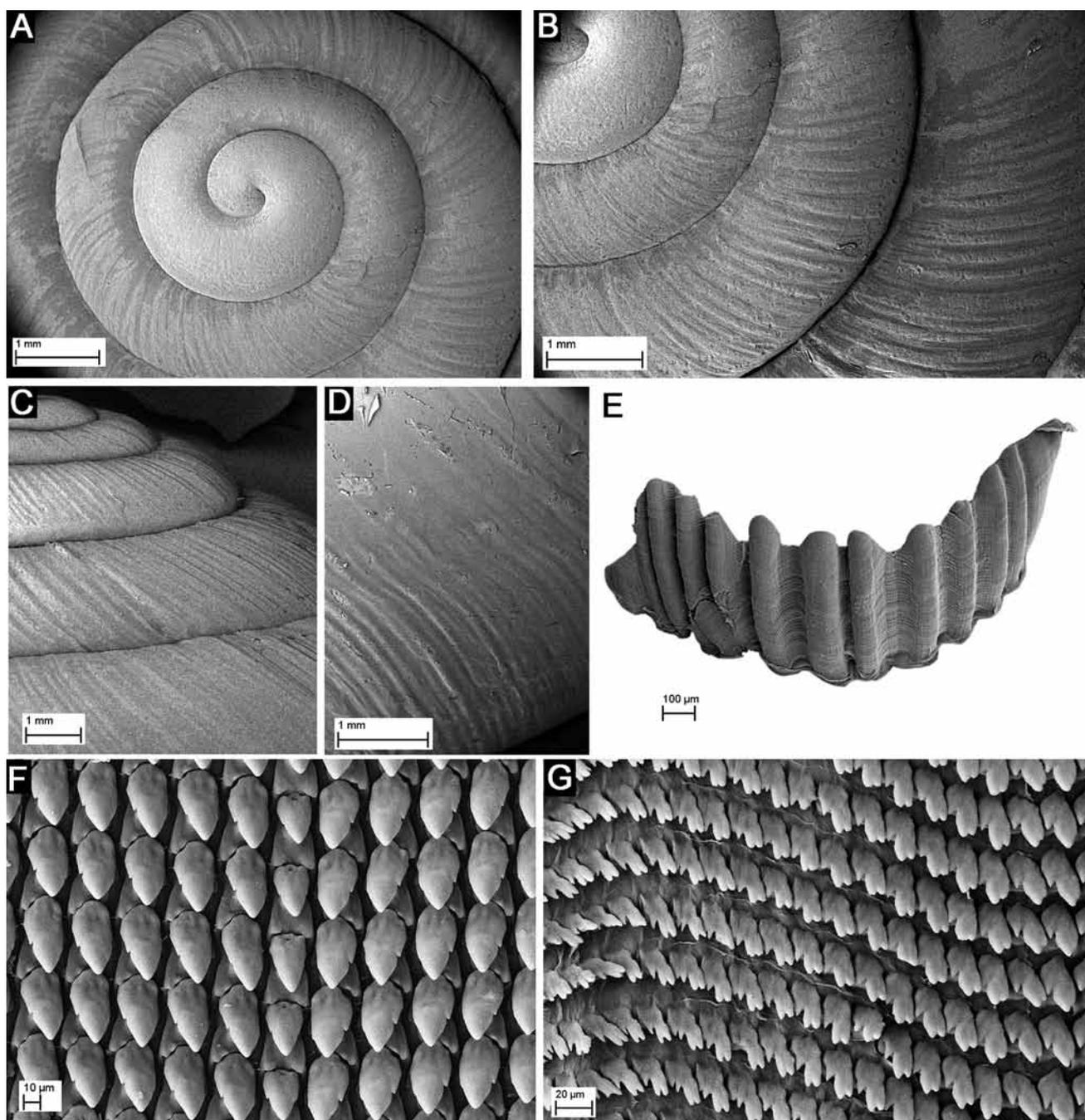


Figure 8. *Amplirhagada alicunda* n.sp. SEM of shell (AM C.472921), radula and jaw (WAM S34711). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) First teleoconch whorls viewed obliquely from above. (D) Close-up showing sculpture on last whorl. (E) Jaw. (F) Central and inner lateral teeth viewed from above. (G) Marginal teeth viewed from above. Scale bars: A–D, 1 mm; E, 100 µm; F, 10 µm, G, 20 µm.

sub-sutural band broad, diffuse to well developed, brown, clearly visible on most whorls; outer and inner lip colour white, conspicuously contrasting shell colour. Protoconch 2.4 mm in diameter, comprising about one whorl, with very weak radially elongated pustulations. Teleoconch with faint, regular axial growth lines, evenly distributed across shell. Angle of aperture about 60 degrees; outer lip moderately thick, well rounded, slightly expanded, not reflected; basal node absent or weak. Parietal wall of inner lip very inconspicuous. Average shell size $16.0 \pm 1.4 \times 20.2 \pm 0.7$ mm (Table 1).

Radular and jaw morphology (Fig. 8 E–G). Tooth formula C + 16–18 + 4 + 18–20 (n = 1). Jaw with 12 plates.

Genital morphology (Figs 9–10). Penis straight, more or less of same length as anterior part of oviduct; distal part of penis proper narrow, proximal part inflated. Penial sheath delicate. Length of penial retractor muscle equivalent to about $\frac{1}{4}$ of length of penial complex. Penial verge extending about $\frac{1}{10}$ of length of penial chamber, slender with pointed tip. Proximal part of inner penial wall entirely covered by extremely fine pustulation. Main stimulatory pilaster strongly enlarged, comprising proximal half of inner penial chamber,

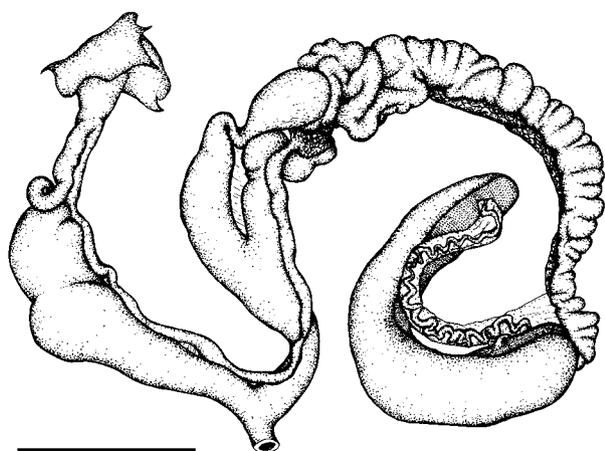


Figure 9. Genitalia of *Amplirhagada alicunda* n.sp. (WAM S34711). For labelling of structures see Fig. 3. Scale bar = 5 mm.

cone-shaped, sculptured by regularly spaced, lateral ridges that support dense rows of little hooks. Vas deferens entering penial sheath within proximal third of penial complex. Vagina moderately long, tubular; inner vaginal wall and inner wall of bursa copulatrix with continuous, well-developed, smooth longitudinal pilasters. Bursa copulatrix short, reaching base of spermoviduct. Free oviduct rather straight comprising less than half of length of anterior part of oviduct. Spermoviduct longer than anterior part of oviduct.

Aestivation strategy and ecology. Free sealer, inhabits locally restricted vine thicket.

Remarks. Anatomical description based on dissection of one specimen. Listed by Solem (1991) as “*Amplirhagada* NSP19”. Shell similar to other relatively large, broadly conical species with spiral bands, such as *A. combeana* Iredale, 1938 and *A. michelliana* Solem, 1981 but anatomy of inner penial wall clearly different.

Amplirhagada moraniana n.sp.

Type locality. Western Australia, NW Kimberley, 25.6 km SSW of Mitchell River Homestead, N bank of Moran River, 15°20'30"S 125°42'05"E (RFS-18-2: coll. V. Kessner, 18 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34713 (preserved specimen) (Pl. 1.4; Table 1). Paratypes WAM S34714 (2 preserved specimens), FMNH 220725 (3 preserved specimens), FMNH 220724 (20 dried shells), WAM S34715 (15 dried shells), AM C.472922 (6 dried shells).

Etymology. Named after the Moran River.

Description

Shell (Pl. 1.4; Fig. 11 A–E). Broadly conical with low to moderately elevated spire; thin, translucent. Periphery well rounded to slightly angulate; upper and basal sectors of whorls rounded. Umbilicus 70–90% concealed by columellar reflection. Background and ventral colour pale brownish horn; peripheral and sub-sutural bands usually absent or diffuse, visible on last whorl only; outer and inner lip whitish. Protoconch ~2.5 mm in diameter, comprising about 1.5

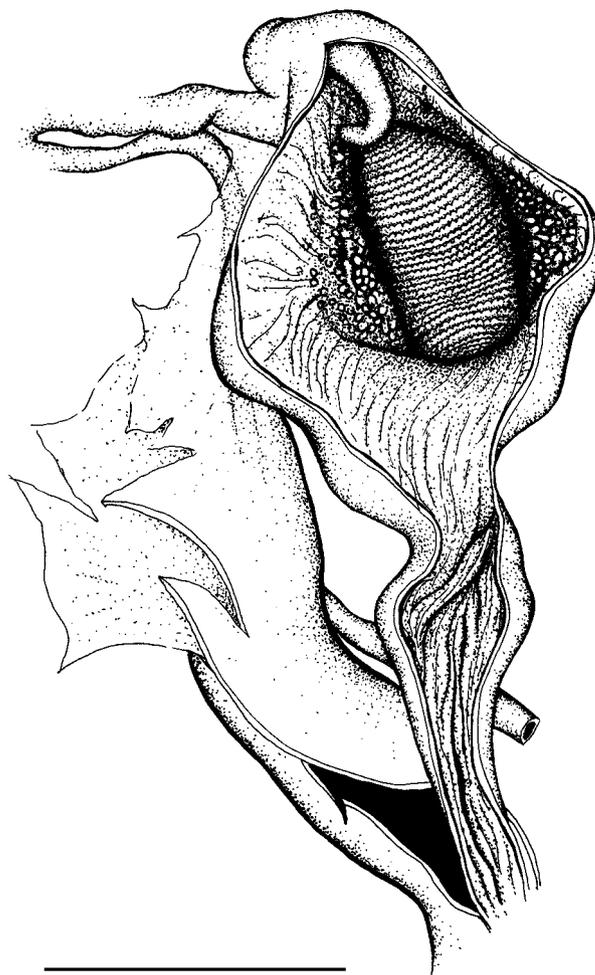
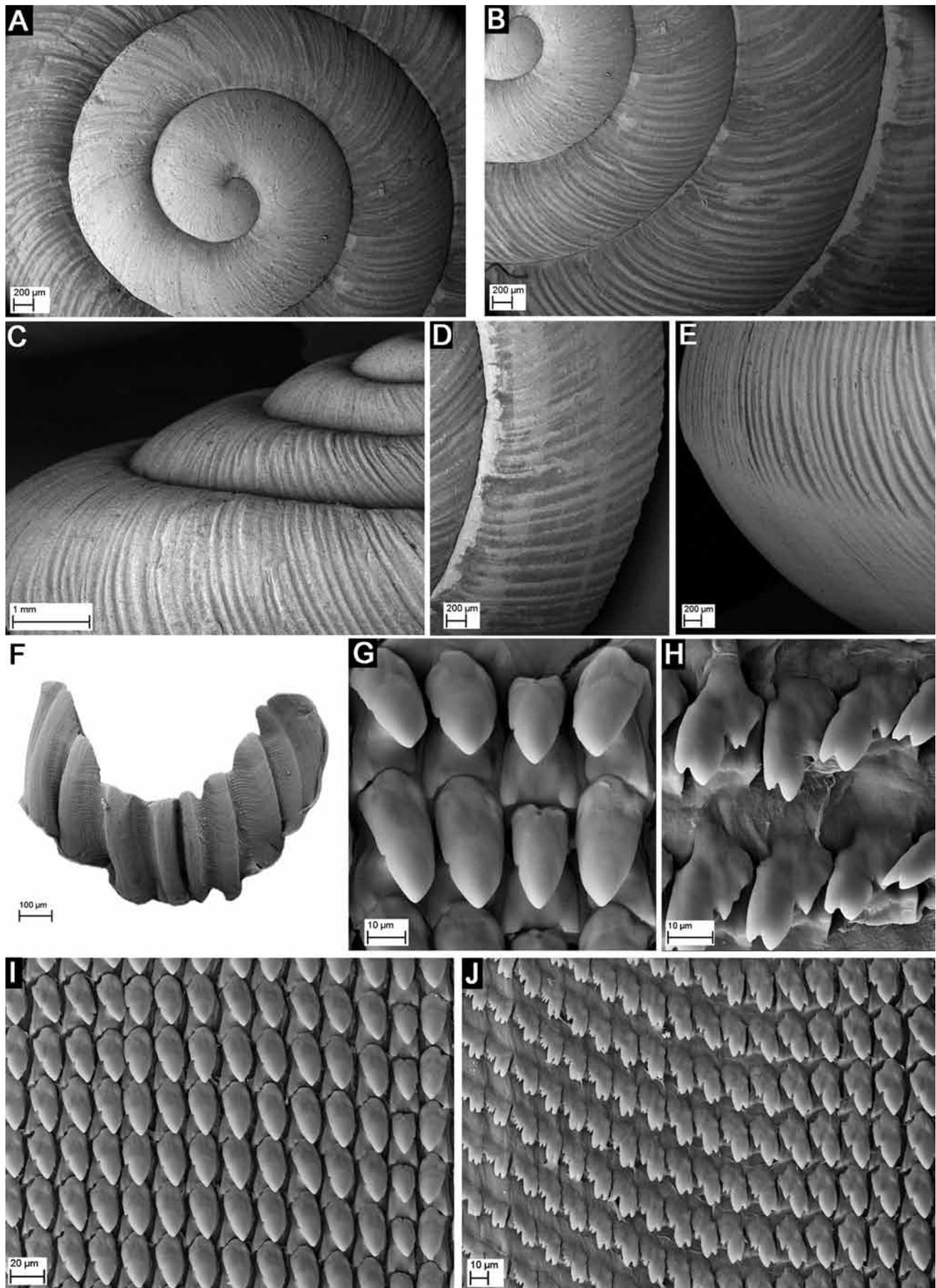


Figure 10. Penial anatomy of *Amplirhagada alicunda* n.sp. (WAM S34711). For labelling of structures see Fig. 4. Scale bar = 3 mm.

whorls, with radially elongated pustulations. Teleoconch with regular axial lirae, evenly distributed across shell surface. Angle of aperture about 45 degrees; outer lip thin, well rounded, slightly expanded, slightly reflected; basal node absent or weak. Parietal wall of inner lip inconspicuous. Average shell size $10.9 \pm 1.5 \times 15.9 \pm 1.5$ mm (Table 1).

Radular and jaw morphology (Fig. 1 F–J). Tooth formula C + 12–13 + 3–4 + 16–18, with 120 rows of teeth ($n = 1$). Jaw with nine plates.

Genital morphology (Figs 12–13). Penis straight, tubular, longer than anterior part of oviduct. Penial sheath very delicate. Length of penial retractor muscle very short, equivalent to about 1/10 of length of penial complex. Penial verge very long, extending about 3/4 of length of penial chamber, slender with pointed tip. Inner penial wall almost entirely covered by reloped, rhomboid pustules that are arranged in honey-comb pattern. No main stimulatory pilaster differentiated; three to four longitudinal pilasters formed by fused, more elevated pustules are present, extending most of inner penial chamber, giving rise to corrugated longitudinal pilasters comprising distal end of inner penial wall. Vas deferens very thick, not undulating, entering penial sheath within proximal third of penial complex. Vagina long, tubular; inner vaginal wall and inner wall of bursa copulatrix with continuous, well-developed, smooth longitudinal pilasters. Bursa copulatrix slightly



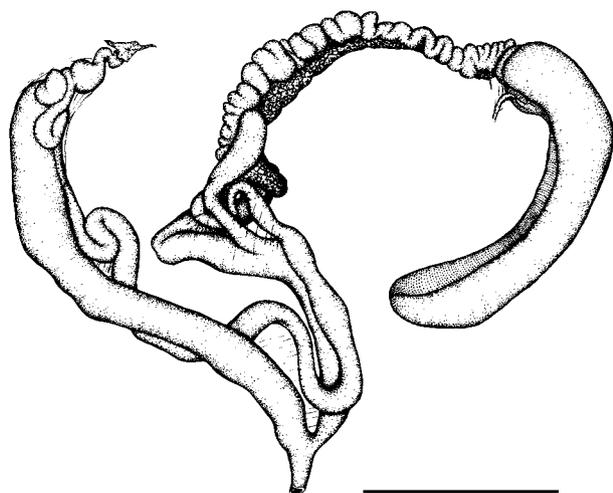


Figure 12. Genitalia of *Amplirhagada moraniana* n.sp. (WAM S34714). For labelling of structures see Fig. 3. Scale bar = 5 mm.

extending base of spermoviduct. Free oviduct comprising less than half of length of anterior part of oviduct. Spermoviduct about as long as anterior part of oviduct.

Aestivation strategy: Free sealer.

Remarks. Anatomical description based on dissection of one specimen. Listed by Solem (1991) as “*Amplirhagada* NSP20”. One of the smallest species with respect to shell height and diameter; a similar shell with respect to size and shape is only found in *A. angustocauda* described further below. Elongated shape of penis and markedly elongated penial verge (almost as long as penial chamber), corrugated penial wall sculpture, and very thick vas deferens is combination of features typical only for this species.

Amplirhagada davidsoniana n.sp.

Type locality. Western Australia, NW Kimberley, Admiralty Gulf, 2.6 km E Davidson Point, near Voltaire Passage; 14°14'55"S 125°36'50"E (RFS 09-2; coll. V. Kessner, 9 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34716 (preserved specimen) (Pl. 1.5; Table 1). Paratypes AM C.472923 (14 preserved specimens), WAM S34717 (30 preserved specimens), FMNH 220282 (44 preserved specimens), paratypes AM C.472924 (15 shells), WAM S34718 (36 dried shells), FMNH 220283 (54 shells).

Etymology. In reference to Davidson Point.

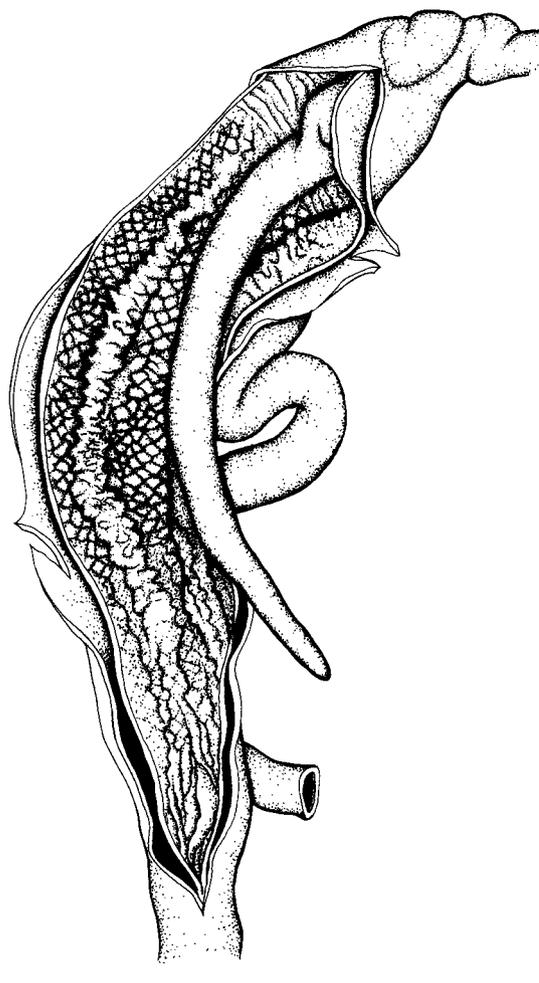


Figure 13. Penial anatomy of *Amplirhagada moraniana* n.sp. (WAM S34714). For labelling of structures see Fig. 4. Scale bar = 3 mm.

Description

Shell (Pl. 1.5; Fig. 14 A–C). Broadly conical with moderately elevated spire. Thin to solid, translucent. Periphery evenly rounded to slightly angulate; upper and basal sectors of whorls well rounded. Umbilicus 50–80 percent concealed by columellar reflection. Background colour horn to yellowish brown; peripheral band absent to well developed, usually diffuse, rather thin, brown, visible on last whorls only; sub-sutural band absent or diffuse and very thin, brown, visible on last whorls only; ventral and outer lip colour horn; inner lip translucent, pale white. Protoconch c. 2.4 mm in diameter, comprising about one whorl, with well-developed, radially elongated pustulations. Teleoconch with fine, regular axial growth lines, rounded in cross-section; spaces equal to thickness of lines; sculpture evenly distributed across whorls of shell and across whorl diameter, height of lirae reduced

Figure 11 (facing page). *Amplirhagada moraniana* n.sp. SEM of shell (AM C.472922), radula and jaw (WAM S34714). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) First teleoconch whorls viewed obliquely from above. (D) Close-up showing sculpture on last whorl, viewed from above. (E) Close-up showing sculpture on last whorl, lateral view. (F) Jaw. (G) Close-up showing detail of central and inner marginal teeth. (H) Close-up showing detail of central marginal teeth. (I) Central and inner lateral teeth viewed from above. (J) Marginal teeth viewed from above. Scale bars: A–B, D–E, 200 µm; C, 1 mm; F, 100 µm; G–H, J, 10 µm; I, 20 µm.

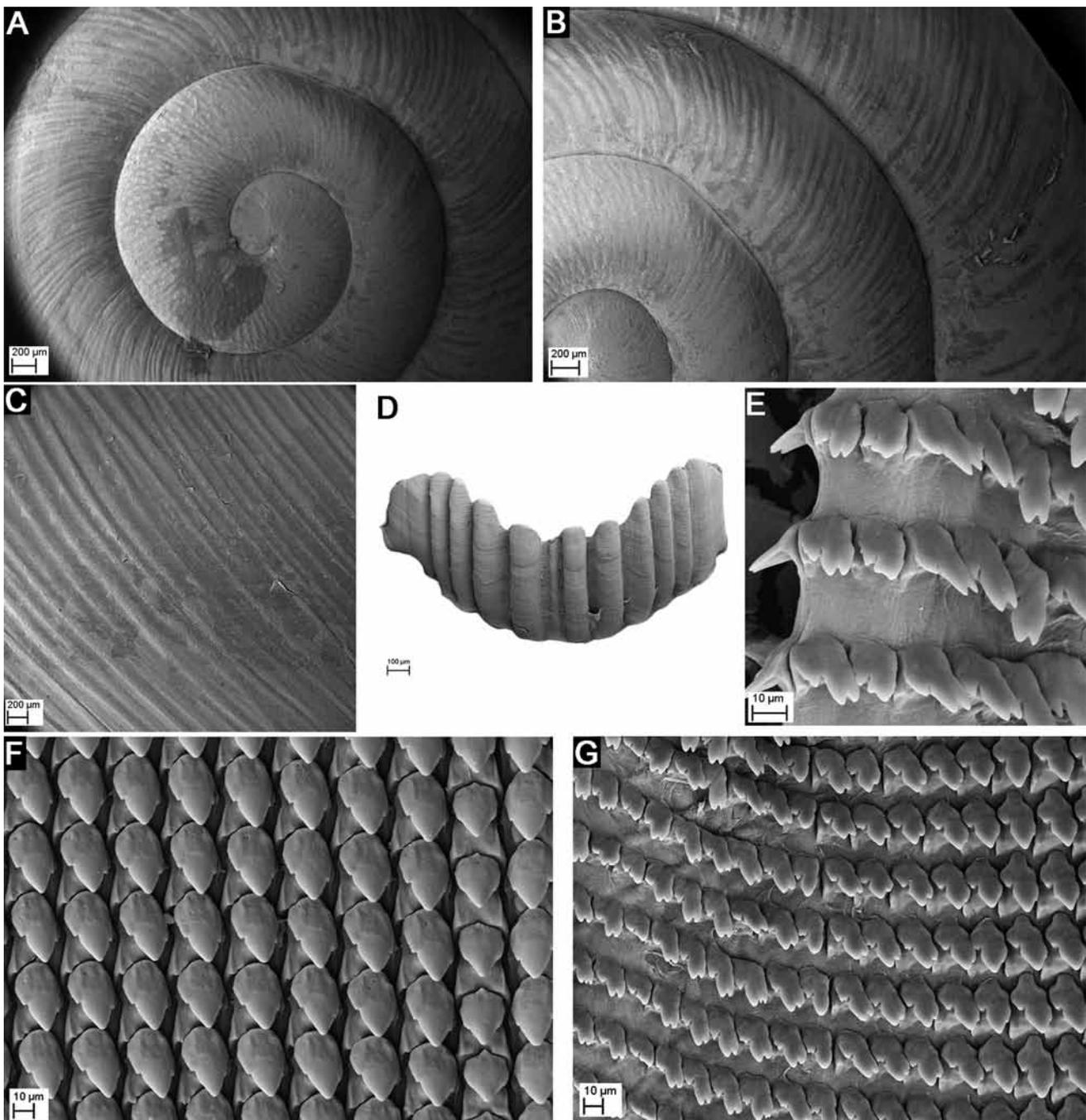


Figure 14. *Amplirhagada davidsoniana* n.sp. SEM of shell (AM C.472924), radula and jaw (AM C.472923). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Close-up showing sculpture on last whorl, viewed from above. (D) Jaw. (E) Close-up showing detail of central marginal teeth. (F) Central and inner lateral teeth viewed from above. (G) Marginal teeth viewed from above. Scale bars: A–C, 200 µm; D, 100 µm; E–G, 10 µm.

underneath suture. Angle of aperture less than 45 degrees; outer lip sharp to moderately thick, rounded, expanded, slightly reflected; basal node absent or very weak. Parietal wall of inner lip inconspicuous. Average shell size $13.1 \pm 0.8 \times 18.3 \pm 0.9$ mm (Table 1).

Radular and jaw morphology (Fig. 14 D–G). Tooth formula C + 12–14 + 4 + 24–28, with 150–160 rows of teeth ($n = 2$). Jaw with 11 plates.

Genital morphology (Figs 15–16). Penis straight, tubular, slightly longer than anterior part of oviduct. Penial sheath very delicate. Length of penial retractor muscle equivalent

to length of penial complex. Penial verge elongately conical, with pointed tip, extending about 1/5 of length of penial chamber. Inner penial wall entirely covered by well-developed pustules arranged in longitudinal rows or pilasters. Main stimulatory pilaster relatively short, cone-shaped comprising proximal third of inner penial wall; with lateral corrugations. Vas deferens very thick, not undulating, entering penial sheath within proximal third of penial complex. Vagina long, tubular; inner vaginal wall with rows of laterally expanded pustules that are densely arranged in longitudinal rows. Rows of pustules giving rise

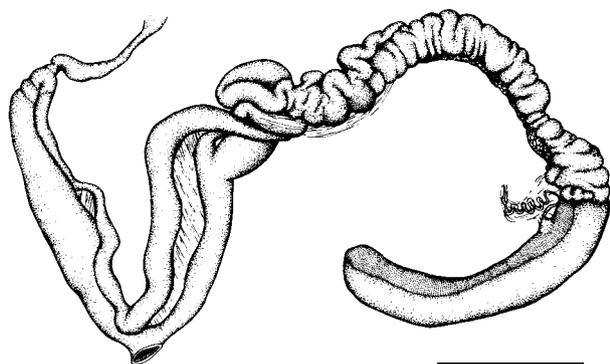


Figure 15. Genitalia of *Amplirhagada davidsoniana* n.sp. (AM C.472923). For labelling of structures see Fig. 3. Scale bar = 5 mm.

to corrugated pilasters at proximal end of vagina. Inner wall of bursa copulatrix with smooth longitudinal pilasters. Bursa copulatrix slightly extending base of spermoviduct. Free oviduct short, comprising less than half of length of anterior part of oviduct. Spermoviduct about longer than anterior part of oviduct.

Aestivation strategy: Rock sealer.

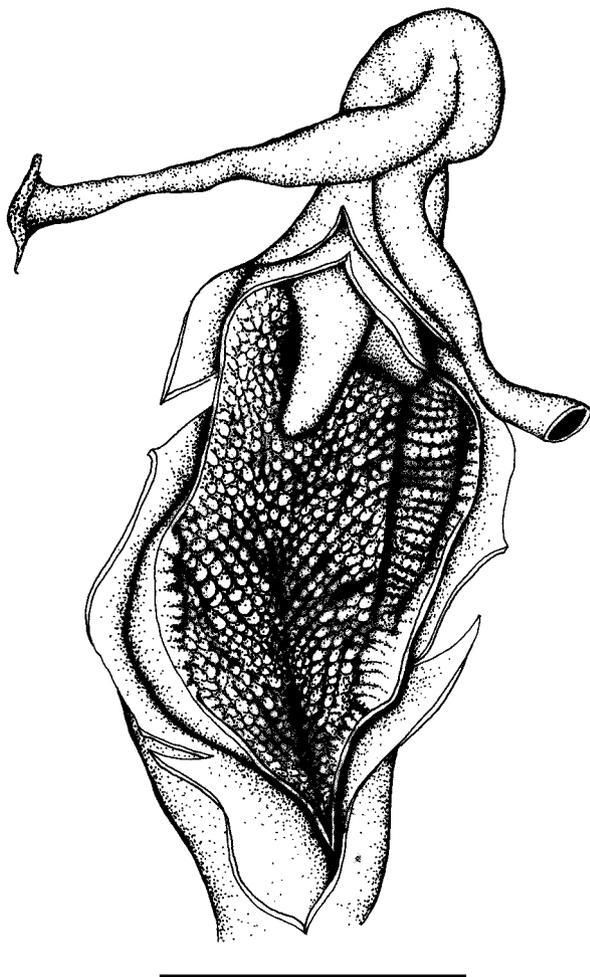


Figure 16. Penial anatomy of *Amplirhagada davidsoniana* n.sp. (AM C.472923). For labelling of structures see Fig. 4. Scale bar = 3 mm.

Remarks. Anatomical description based on dissections of three specimens. Listed by Solem (1991) as “*Amplirhagada* NSP21”. Shell similar to *A. imitata* (Smith, 1894), *A. solemiana* Köhler, 2010 and *A. indistincta* Köhler, 2010, but differing by shell size, distinct corrugation of inner penial wall and much longer vagina.

Amplirhagada vialae n.sp.

Type locality. Western Australia, NW Kimberley, Bonaparte Archipelago, Montague Sound, Scott Strait, 8.3 km E of Savage Hill; 14°37'15"S 125°15'15"E (RFS-05-2; coll. V. Kessner, 05 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34719 (preserved specimen) (Pl. 1.6; Table 1). Paratypes AM C.472925 (2 preserved specimens), WAM S34720 (5 preserved specimens), FMNH 220066 (9 preserved specimens), AM C.472926 (4 shells), WAM S34721 (10 dried shells), FMNH 220065 (12 shells).

Etymology. Named in honour of Marlene Vial in recognition for her help with SEM and other work.

Description

Shell (Pl. 1.6; Fig. 17 A–D). Semi-globose with highly elevated spire. Solid, not translucent. Periphery well rounded to slightly compressed, occasionally slightly angulate; upper sector of whorl flattened to slightly shouldered underneath suture, basal sectors rounded. Umbilicus completely concealed by columellar reflection. Background colour pale yellowish brown to horn; peripheral band conspicuous, well developed, moderately broad, clearly visible on last whorls; sub-sutural band broad, diffuse to well developed, brown, clearly visible on last whorls; both bands may blend into each other covering shell with a dark brown tone; outer and inner lip colour white, conspicuously contrasting shell colour. Protoconch 3.4 mm in diameter, comprising about 1.5 whorls, with weak radially elongated pustulations. Teleoconch with faint, regular axial growth lines, evenly distributed across shell. Angle of aperture about 30 degrees; outer lip moderately thick, well rounded, slightly expanded, not reflected; basal node absent or weak. Parietal wall of inner lip inconspicuous. Average shell size $17.1 \pm 1.8 \times 19.8 \pm 1.0$ mm (Table 1).

Radular and jaw morphology (Fig. 17 E–G). Tooth formula C + 14–16 + 4 + 20–22, with 160 rows of teeth ($n = 1$). Jaw with 10 plates.

Genital morphology (Figs 18–19). Penis curved, medially inflated, about as long as anterior part of oviduct. Penial sheath very delicate. Length of penial retractor muscle equivalent to about 1/3 of length of penial complex. Penial verge elongately conical, with pointed tip, short, extending about 1/10 of length of penial chamber. Inner penial wall entirely covered by well-developed, elongate pustules densely arranged in longitudinal rows. Main stimulatory pilaster huge, cone-shaped comprising 3/4 of length of inner penial wall; with regular lateral corrugations that support dense and regular rows of hooks. Vas deferens thick, not undulating, entering penial sheath close to penial apex. Vagina long, inflated; inner vaginal wall and wall of

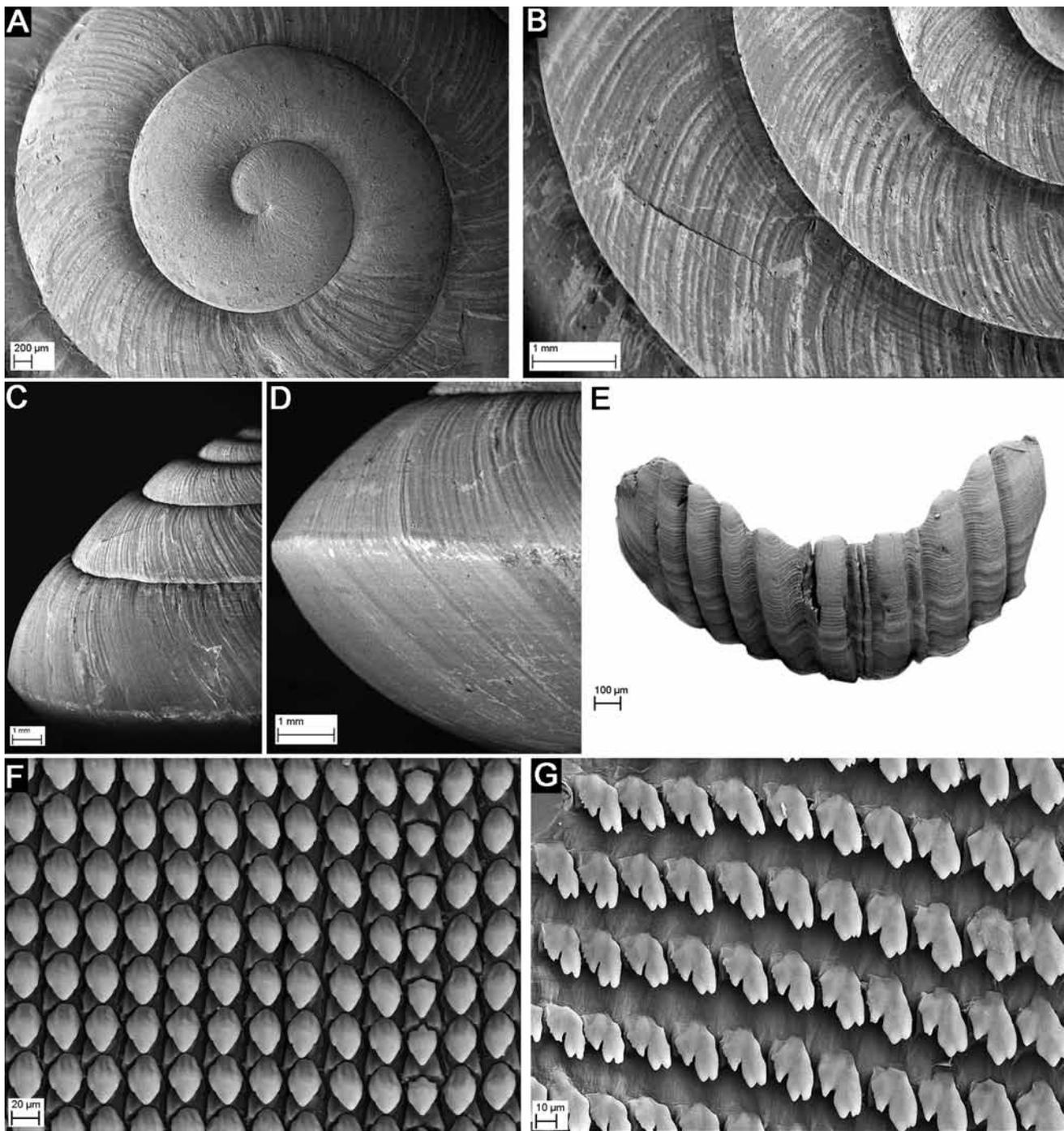


Figure 17. *Amplirhagada vialae* n.sp. SEM of shell (AM C.472926), radula and jaw (AM C.472925). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Lateral view of shell. (D) Lateral view of last whorl. (E) Jaw. (F) Central and inner lateral teeth viewed from above. (G) Marginal teeth viewed from above. Scale bars: A, 200 μm ; B–D, 1 mm; E, 100 μm ; F, 20 μm ; G, 10 μm .

bursa copulatrix with smooth longitudinal pilasters. Bursa copulatrix reaching base of spermooviduct. Free oviduct rather long, tubular, comprising about half of length of anterior part of oviduct. Spermooviduct not much longer than anterior part of oviduct.

Aestivation strategy: Free sealer.

Remarks. Anatomical description based on dissections of two specimens. Listed by Solem (1991) as “*Amplirhagada* NSP22”. The “bee-hive” shaped shell is similar to that of *A. decora* Köhler, 2010 (Bigge Island) and *A. boongarensis* Köhler, 2010 (Boongaree Island), but these species differ in shell colour. All three species are characterized by a huge,

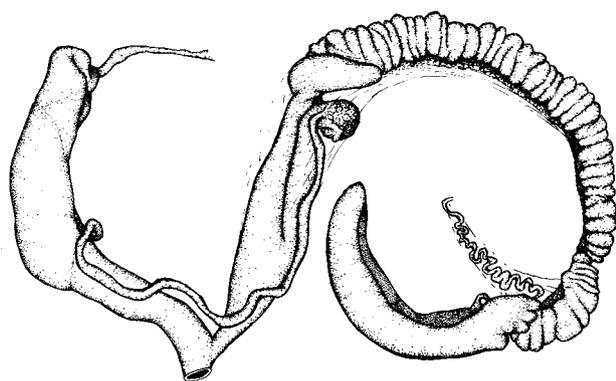


Figure 18. Genitalia of *Amplirhagada vialae* n.sp. (AM C.472925). For labelling of structures see Fig. 3. Scale bar = 10 mm.

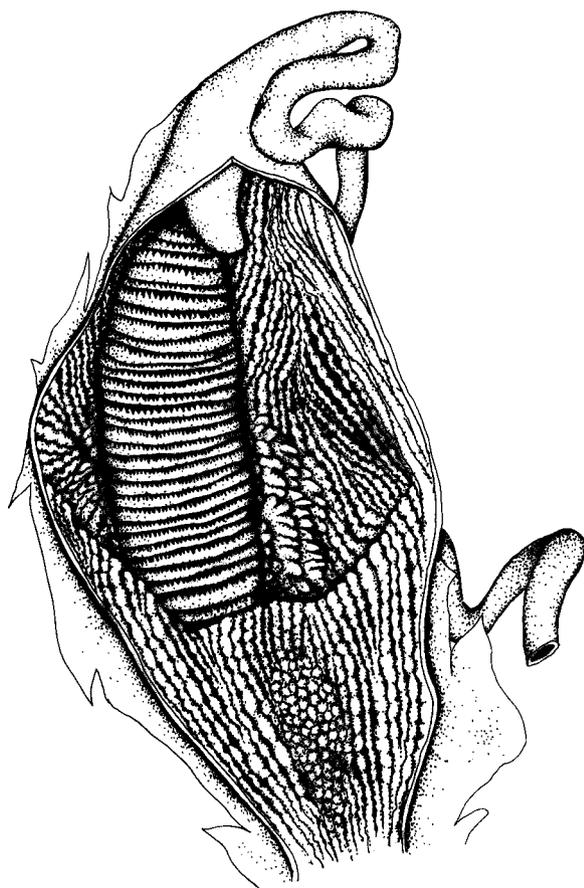


Figure 19. Penial anatomy of *Amplirhagada vialae* n.sp. (AM C.472925). For labelling of structures see Fig. 4. Scale bar = 3 mm.

cone-shaped main pilaster and by their inner penial wall being densely covered with large pustules. *Amplirhagada boongareensis* differs by possessing two additional pilasters and *A. decora* Köhler, 2010 has a shorter bursa copulatrix. The present species occurs in sympatry with *A. discoidea* n.sp. being described in the following.

Amplirhagada discoidea n.sp.

Type locality. Western Australia, NW Kimberley mainland, Scott Strait, 8.3 km E of Savage Hill on Bigge Island; 14°37'15"S 125°15'15"E (RFS 05-2; coll. V. Kessner, 5 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34722 (preserved specimen) (Pl. 1.7; Table 1). Paratypes AM C.472927 (3 preserved specimens), WAM S34723 (5 preserved specimens), FMNH 220064 (8 preserved specimens), AM C.472928 (6 dried shells), WAM S34724 (12 dried shells), FMNH 220063 (20 dried shells).

Etymology. In reference to discoidal shape of shell.

Description

Shell (Pl. 1.7; Fig. 21A–D). Broadly conical with low spire, discoid. Rather thin but solid, slightly translucent. Periphery angulate; upper and basal sectors slightly flattened. Umbilicus 10–20% concealed by columellar reflection. Background colour light yellowish brown; peripheral band conspicuous, well developed, moderately broad, clearly visible on last whorl only; sub-sutural band broad, well developed, brown, visible on last whorl only; both bands may blend into each other covering shell with a dark brown tone; outer and inner lip colour white, conspicuously contrasting shell colour. Protoconch 3.1 mm in diameter, comprising about one whorl, with inconspicuous radially elongated pustulations. Teleoconch almost smooth, with very faint, regular axial growth lines. Angle of aperture about 45 degrees; outer lip thin, well rounded, slightly expanded, not or slightly reflected; basal node. Parietal wall of inner lip thin. Average shell size $12.4 \pm 0.7 \times 20.9 \pm 0.9$ mm (Table 1).

Radular and jaw morphology (Fig. 21 E–G). Tooth formula C + 13–15 + 4 + 16–22, with 120 rows of teeth ($n = 2$). Jaw with c. 10 plates.

Genital morphology (Figs 20, 22). Penis rather straight, tubular, about as long as anterior part of oviduct. Penial sheath very delicate, distally thicker. Length of penial retractor muscle equivalent to about 1/3 of length of penial complex. Penial verge elongately conical, with blunt tip, short, extending about 1/4 of length of penial chamber. Inner penial wall entirely covered by densely arranged, very small pustules. Several more or less developed longitudinal

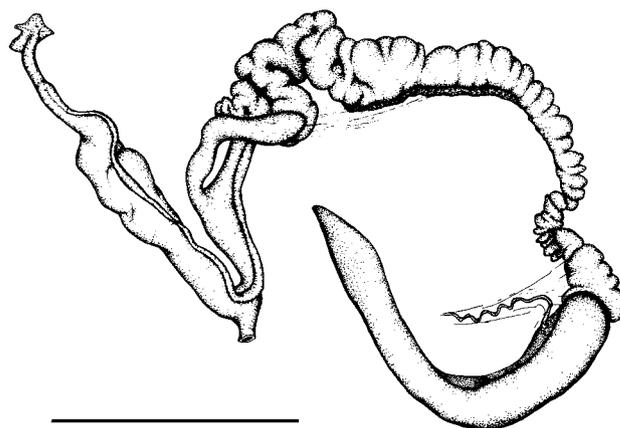


Figure 20. Genitalia of *Amplirhagada discoidea* n.sp. (AM C.472927). For labelling of structures see Fig. 3. Scale bar = 10 mm.

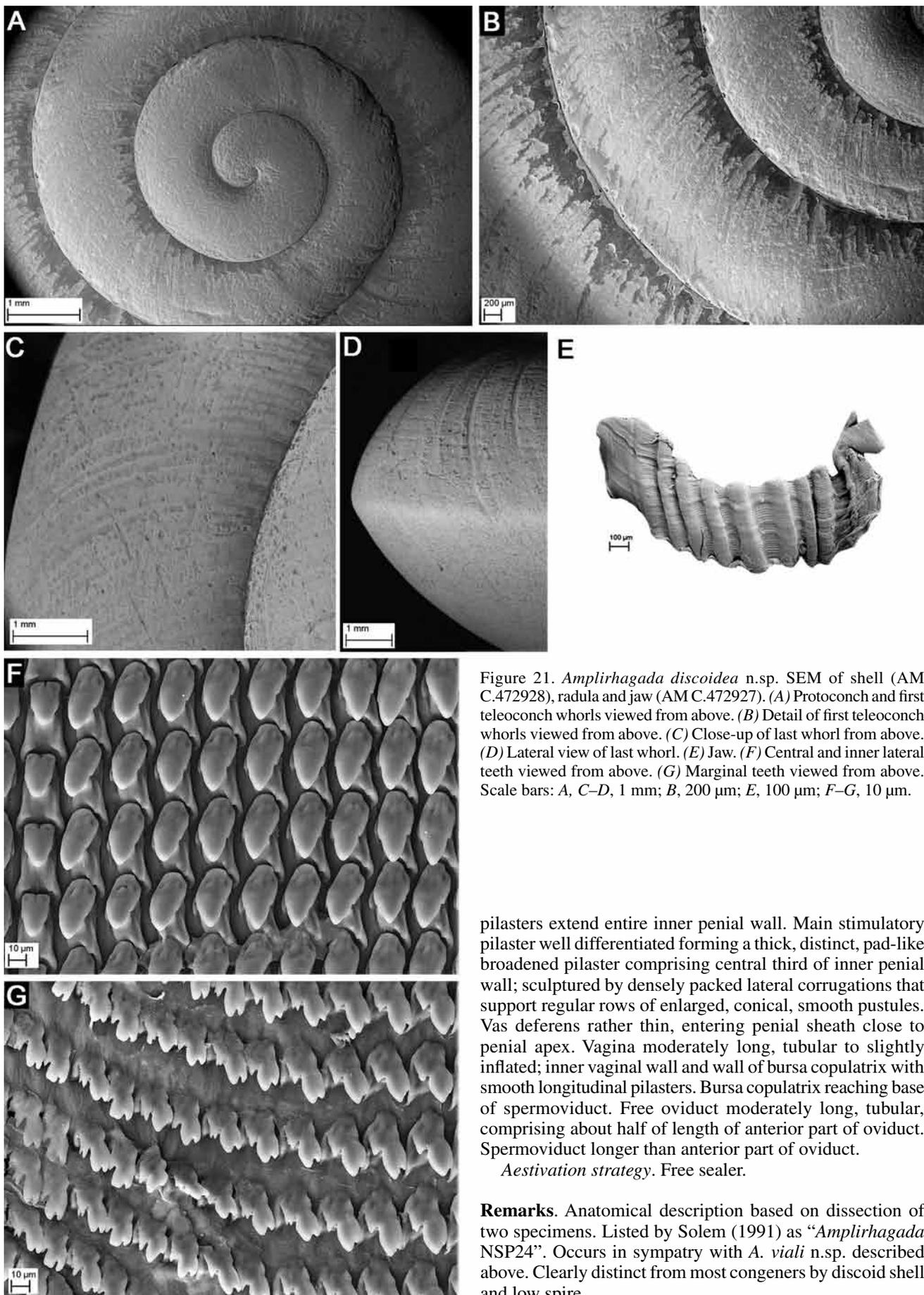


Figure 21. *Amplirhagada discoidea* n.sp. SEM of shell (AM C.472928), radula and jaw (AM C.472927). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Close-up of last whorl from above. (D) Lateral view of last whorl. (E) Jaw. (F) Central and inner lateral teeth viewed from above. (G) Marginal teeth viewed from above. Scale bars: A, C–D, 1 mm; B, 200 µm; E, 100 µm; F–G, 10 µm.

pilasters extend entire inner penial wall. Main stimulatory pilaster well differentiated forming a thick, distinct, pad-like broadened pilaster comprising central third of inner penial wall; sculptured by densely packed lateral corrugations that support regular rows of enlarged, conical, smooth pustules. Vas deferens rather thin, entering penial sheath close to penial apex. Vagina moderately long, tubular to slightly inflated; inner vaginal wall and wall of bursa copulatrix with smooth longitudinal pilasters. Bursa copulatrix reaching base of spermoviduct. Free oviduct moderately long, tubular, comprising about half of length of anterior part of oviduct. Spermoviduct longer than anterior part of oviduct.

Aestivation strategy. Free sealer.

Remarks. Anatomical description based on dissection of two specimens. Listed by Solem (1991) as “*Amplirhagada* NSP24”. Occurs in sympatry with *A. viali* n.sp. described above. Clearly distinct from most congeners by discoid shell and low spire.

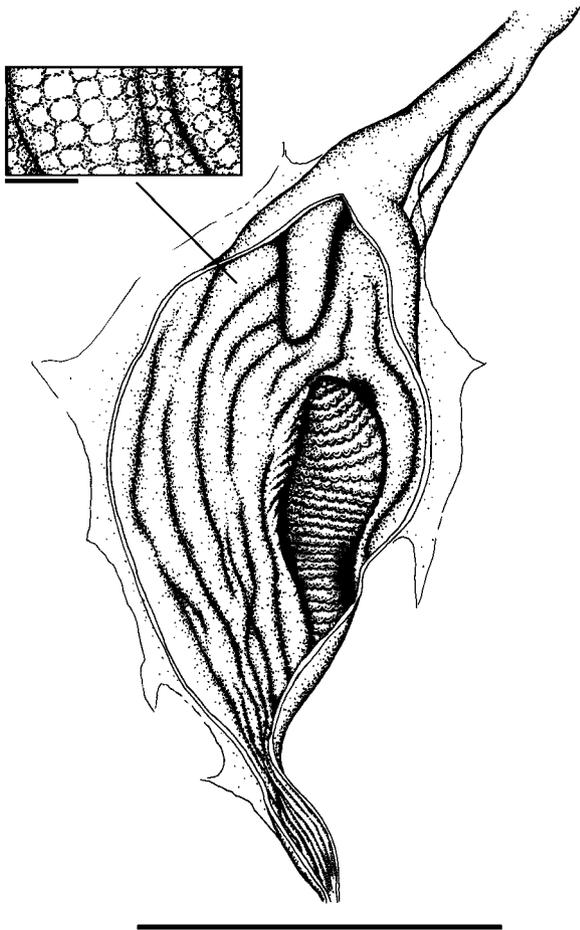


Figure 22. Penial anatomy of *Amplirhagada discoidea* n.sp. (AM C.472927). For labelling of structures see Fig. 4. Scale bar = 5 mm. Scale bar (inset) = 0.25 mm.

Amplirhagada forrestiana n.sp.

Type locality. Western Australia, NW Kimberley, York Sound, Prince Frederick Harbour, 9.7 km NW of Mt. Anderdon, 4 km from coast; 14°52'50"S 125°21'30"E (RFS-05-3; coll. V. Kessner, 05 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34725 (preserved specimen) (Pl. 1.8; Table 1). Paratypes AM C.472930 (2 preserved specimens), WAM S34726 (5 preserved specimens), FMNH 220084 (8 preserved specimens), AM C.472931 (5 dried shells), WAM S34727 (9 dried shells), FMNH 220083 (12 dried shells).

Etymology. Named after Matthew Forrest, first Kimberley explorer, who in 1879 was instructed to map out the country between the De Grey River in Western Australia and the Victoria River in the Northern Territory.

Description

Shell (Pl. 1.8; Fig. 25 A–C). Broadly conical with low spire, almost discoid. Thin, translucent. Periphery sharply angulate; upper and lower sectors of whorls rounded. Umbilicus narrowly winding, 30–80% concealed by columellar reflection. Background colour pale brownish horn; peripheral band absent or diffuse, if present moderately broad, diffuse, brown, visible on last whorls only; sub-sutural band absent or diffuse, brown, visible on last whorls only; outer and inner lip colour whitish. Protoconch 4.7 mm in diameter, comprising about 1.5 whorls, with indistinct radially

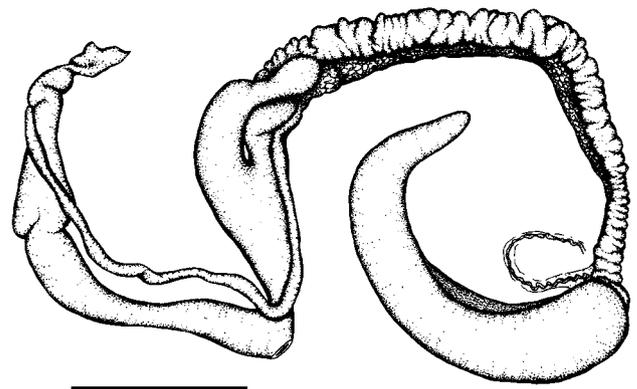


Figure 23. Genitalia of *Amplirhagada forrestiana* n.sp. (AM C.472930). For labelling of structures see Fig. 3. Scale bar = 5 mm.

elongated pustulations. Teleoconch with well-developed, regular lirae, evenly distributed across shell surface. Angle of aperture 45–60 degrees; outer lip thin, well rounded, slightly expanded, slightly reflected; basal node absent or weak. Parietal wall of inner lip inconspicuous. Average shell size $11.6 \pm 0.8 \times 19.4 \pm 1.0$ mm (Table 1).

Radular and jaw morphology (Fig. 25 D–G). Tooth formula C + 11 + 4 + 16; 150 rows of teeth ($n = 1$). Jaw with nine plates.

Genital morphology (Figs 23, 24). Penis rather straight, tubular, longer than anterior part of oviduct. Penial sheath delicate, proximally thicker. Penial retractor muscle stubby. Penial verge comparatively long, elongately conical, extending about $\frac{1}{3}$

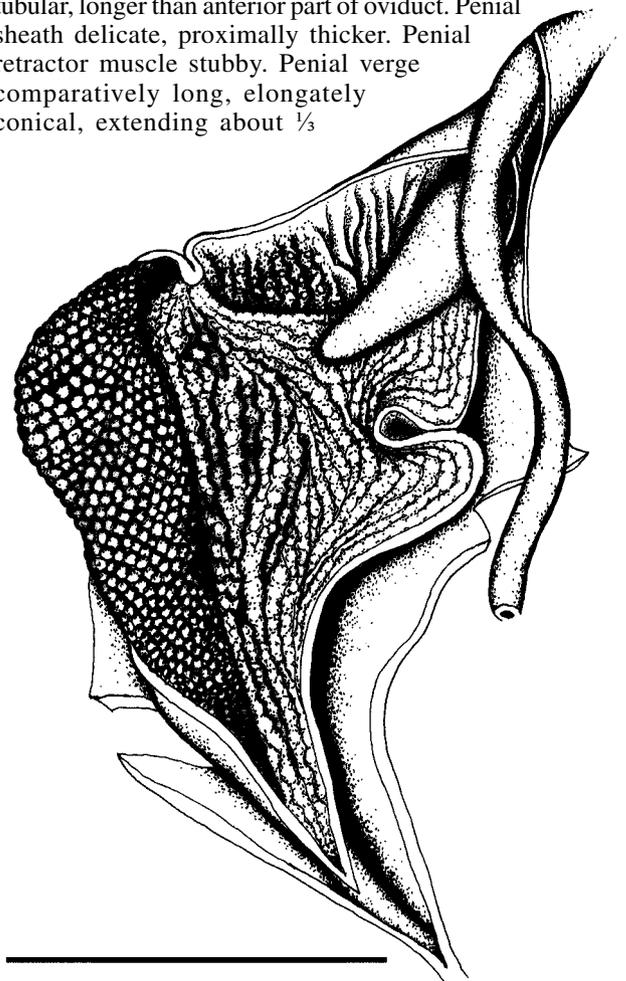


Figure 24. Penial anatomy of *Amplirhagada forrestiana* n.sp. (AM C.472930). For labelling of structures see Fig. 4. Scale bar = 3 mm.

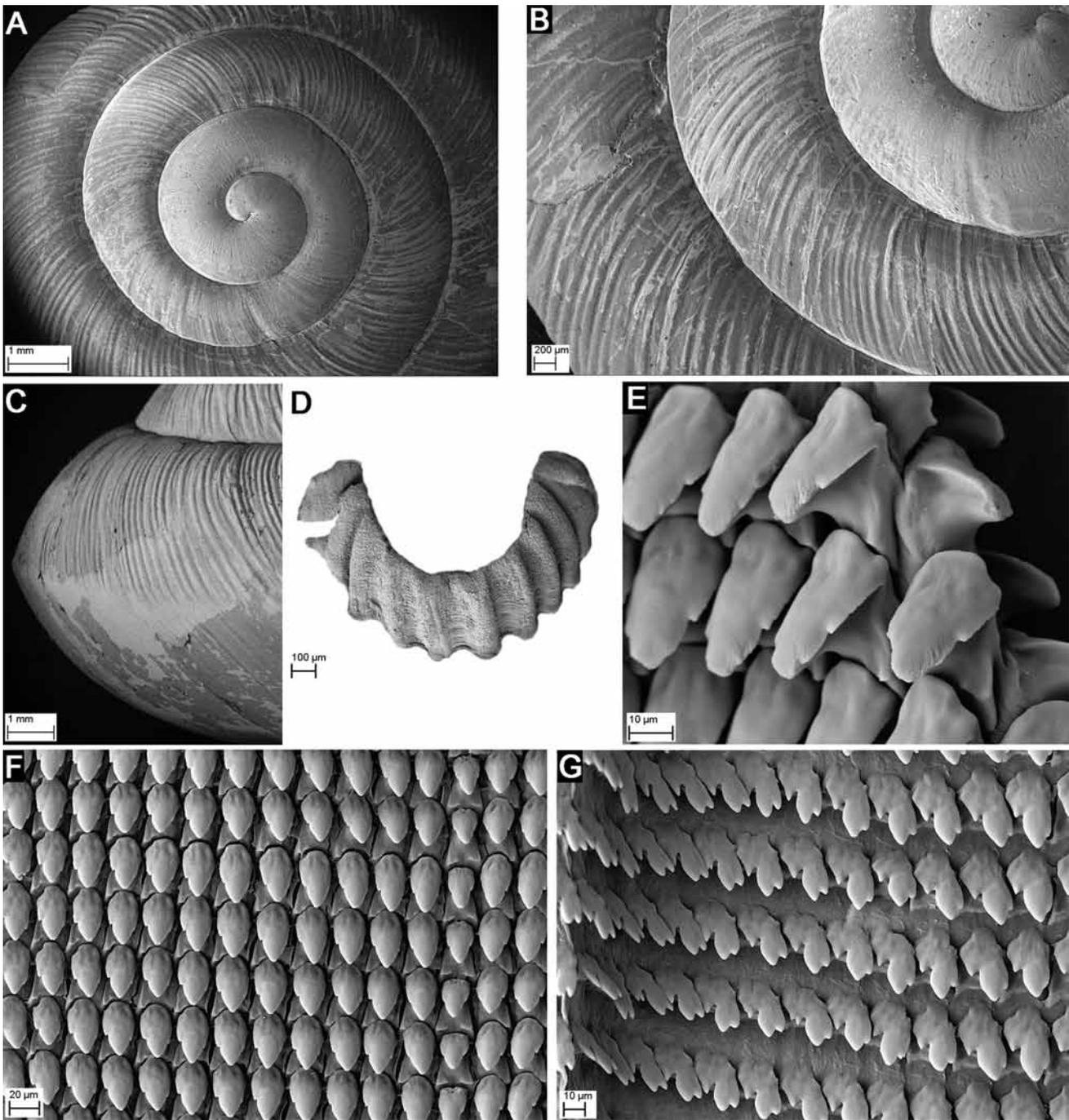


Figure 25. *Amplirhagada forrestiana* n.sp. SEM of shell (AM C.472931), radula and jaw (AM C.472930). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Lateral view of last whorl. (D) Jaw. (E) Close-up of inner lateral teeth. (F) Central and lateral teeth viewed from above. (G) Marginal teeth viewed from above. Scale bars: A, C, 1 mm; B, 200 µm; D, 100 µm; E, G, 10 µm; F, 20 µm.

of length of penial chamber. Inner penial wall entirely covered by densely in honey-comb pattern arranged, small and regular pustules. No main stimulatory pilaster. Vas deferens rather thin, entering penial sheath close to penial apex, long and winding. Vagina moderately long, distally inflated; inner vaginal wall and wall of bursa copulatrix with smooth longitudinal pilasters. Bursa copulatrix very wide, slightly extending base of spermoviduct. Free oviduct very long, tubular, coiling, comprising $\frac{3}{4}$ of length of anterior part of oviduct. Spermoviduct about as long as anterior part of oviduct.

Aestivation strategy. Free sealer.

Remarks. Listed by Solem (1991) as “*Amplirhagada* NSP25”. A single specimen from Naturalist Island, assigned to the same manuscript name in the collection of the Field Museum (FMNH 220692) was not studied. Amongst medium-sized species, shell differs from other congeners by markedly wider diameter, resulting in a discoidal shape (shell proportions and size only similar in *A. discoidea*). *Amplirhagada discoidea* differs by having a more angulated shell periphery and a conspicuously different penial anatomy, with a large main pilaster (absent in *A. forrestiana*), rather smooth inner penial wall (markedly pustulose in *A. forrestiana*) and rather narrow bursa copulatrix (wide on *A. forrestiana*).

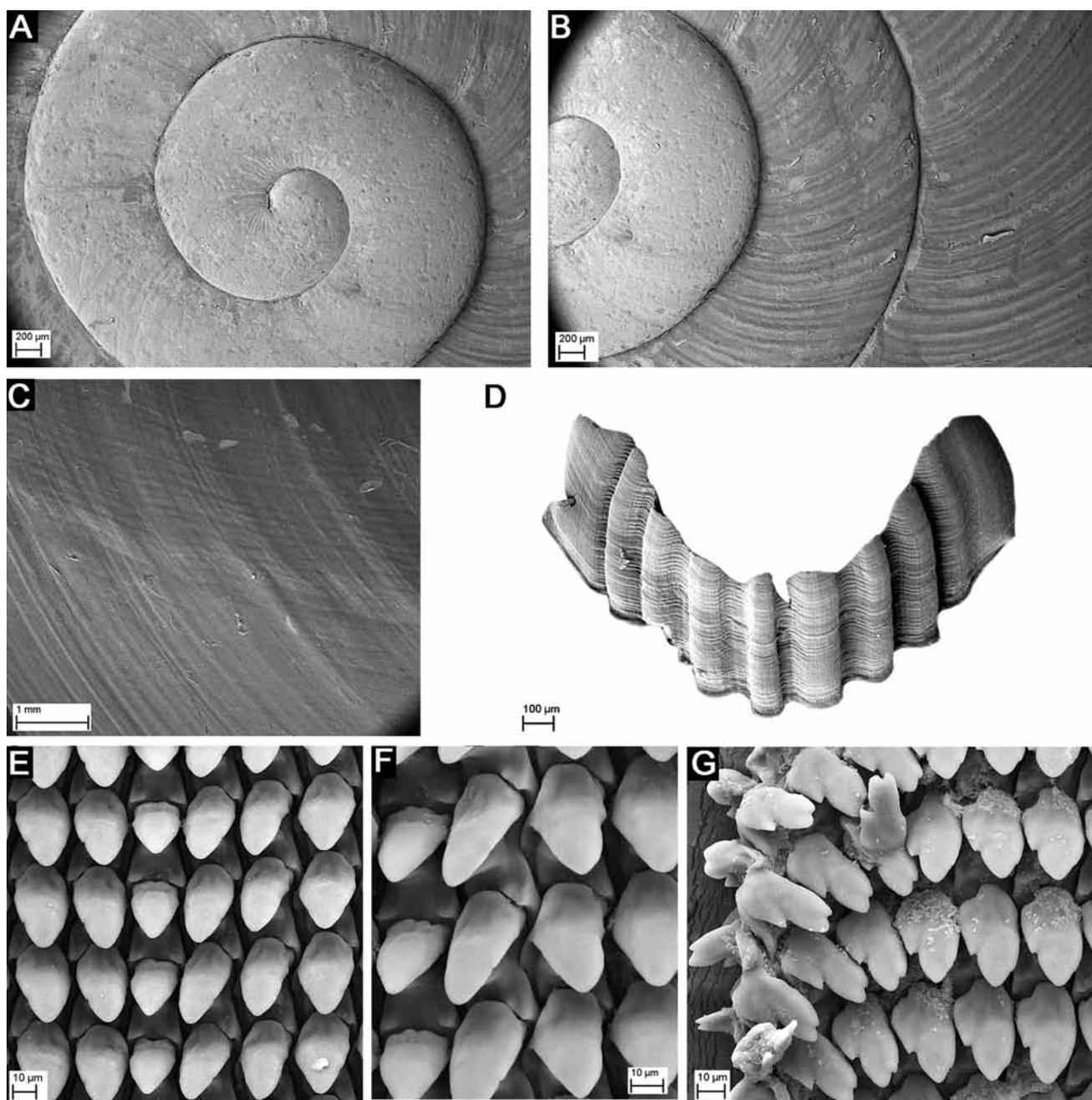


Figure 26. *Amplirhagada inusitata* n.sp. SEM of shell (AM C.472929), radula and jaw (WAM S34728). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Close-up of sculpture on last whorl, lateral view. (D) Jaw. (E) Central and inner lateral teeth. (F) Close-up of central and lateral teeth viewed from above. (G) Transition from outer lateral to inner marginal teeth viewed from above. Scale bars: A–B, 200 µm; C, 1 mm; E–G, 10 µm.

Amplirhagada inusitata n.sp.

Type locality. Western Australia, NW Kimberley, N side of Prince Frederick Harbour, near mouth, 16 km W of Mt. Anderdon, 0.3 km from coast; 14°57'10"S 125°16'30"E (RFS 14-1; coll. V. Kessner, 14 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34728 (preserved specimen, dissected). Paratypes WAM S34729 (preserved specimen, juvenile), FMNH 220537 (preserved specimen), AM C.472929 (2 dried shells), WAM S34730 (3 dried shells) (Pl. 1.9), FMNH 220540 (6 dried shells).

Etymology. Species epithet derived from “*inusitata*” (Latin, unusual, uncommon, extraordinary; of female gender) in reference to its remarkably distinct penial morphology.

Description

Shell (Pl. 1.9; Fig. 26 A–C). Broadly conical with low spire. Thin, translucent. Periphery sharply angulate; upper sector of whorls flattened. Umbilicus 30–50% concealed by columellar reflection. Background colour pale yellowish brown; peripheral band diffuse to well developed, moderately broad, brown, visible on visible on last whorl only; sub-

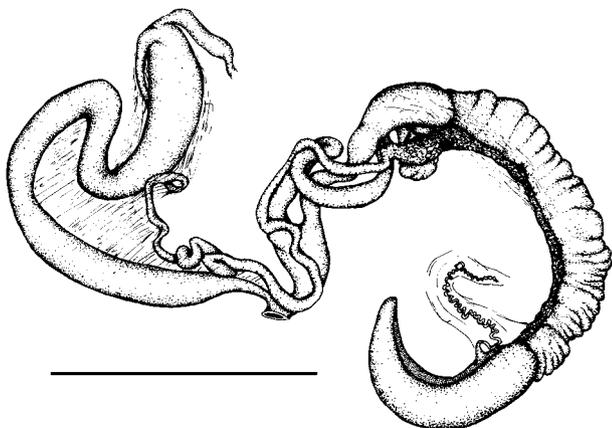


Figure 27. Genitalia of *Amplirhagada inusitata* n.sp. (WAM S34728). For labelling of structures see Fig. 3. Scale bar = 10 mm.

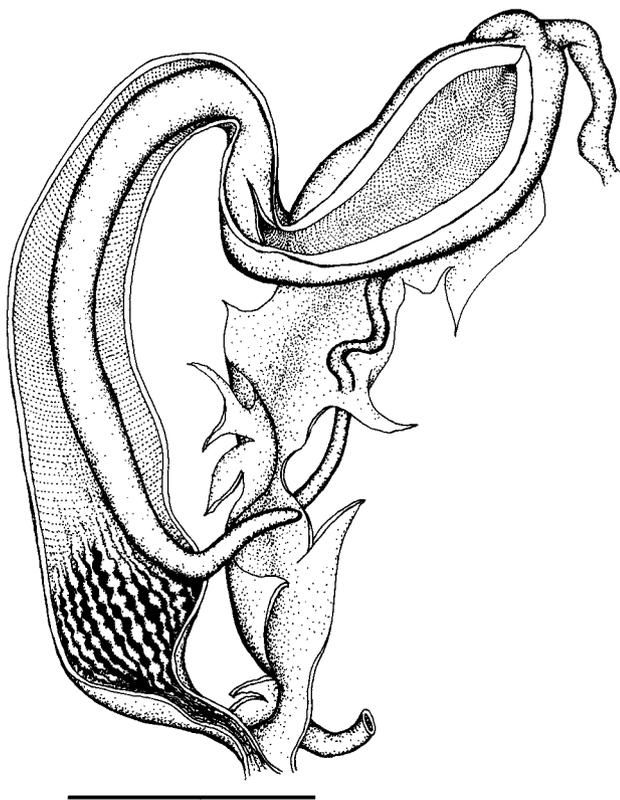


Figure 28. Penial anatomy of *Amplirhagada inusitata* n.sp. (WAM S34728). For labelling of structures see Fig. 4. Scale bar = 5 mm.

sutural band diffuse to well developed, brown, visible on last whorl only; outer and inner colour like shell. Protoconch 2.6 mm in diameter, comprising about one whorl, with very indistinct radially elongated pustulations. Teleoconch with faint axial growth lines, evenly distributed across shell surface. Angle of aperture 45–60 degrees; outer lip thin, well rounded, slightly expanded; basal node absent or weak. Parietal wall of inner lip inconspicuous. Average shell size $16.8 \pm 1.7 \times 21.4 \pm 0.7$ mm (Table 1).

Radular and jaw morphology (Fig. 26 D–G). Tooth formula C + 14–19 + 4 + ?; 125 rows of teeth ($n = 1$). Jaw with 10 plates.

Genital morphology (Figs 27–28). Penis long, curved to bending, tubular, clearly longer than anterior part of oviduct. Penial sheath very delicate. Penial retractor muscle very short. Penial verge extremely elongated, extending almost entire length of penis, with pointed tip, proximally the lumen of the penial verge forms an extended duct that is connected to vas deferens, possibly functioning as epiphallus. Penial chamber extending only distal half of entire length of penial complex, inner penial wall almost entirely smooth, in proximal third corrugated longitudinal pilasters are present consisting of fused pustules. No main stimulatory pilaster differentiated. Vas deferens rather thin, undulating, entering penial sheath close to penial apex. Vagina moderately long, tubular to slightly inflated; inner vaginal wall and wall of bursa copulatrix with smooth longitudinal pilasters. Bursa copulatrix reaching base of spermoviduct. Free oviduct long, bending, tubular, comprising more than half of length of anterior part of oviduct. Spermoviduct as long as anterior part of oviduct.

Aestivation strategy. Free sealer.

Remarks. Anatomical description based on dissection of the holotype. Listed by Solem (1991) as “*Amplirhagada* NSP26”. Shell similar to other relatively large and broadly conical species with spiral bands, such as *A. combeana* Iredale, 1938 and *A. mitchelliana* Solem, 1981, differing from all other congeners by extremely long and tubular penial verge, narrowly elongated penis, smooth penial wall with only short corrugated pilasters at its base. Found in sympatry with *A. pusilla* Solem, 1981 and *A. epiphallica* n.sp. described below.

Amplirhagada coffea n.sp.

Type locality. Western Australia, NW Kimberley, George Water, 16 km SW of Mt. Grey, near Barlee Impediment; $15^{\circ}49'10''\text{S } 124^{\circ}36'00''\text{E}$ (RFS-23-3; coll. V. Kessner, 23 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34731 (preserved specimen) (Pl. 1.10; Table 1). Paratypes AM C.472932 (3 preserved specimens, WAM S34732 (8 preserved specimens), FMNH 220945 (13 preserved specimens), AM C.472933 (6 dried shells), WAM S34733 (10 dried shells), FMNH 220948 (16 dried shells).

Etymology. Species epithet refers to the dark coffee-brown colour of the shell.

Description

Shell (Pl. 1.10; Fig. 29 A–C). Semi-globose, with rather high spire; solid. Periphery compressed to angulate; upper sector slightly shouldered, basal sector rounded. Umbilicus completely concealed by columellar reflection. Background colour crème to brown; sub-sutural and mid-whorl bands usually blend into each other covering entire shell surface in chestnut brown; ventral and outer lip colour light brownish horn; inner lip whitish. Shell surface glossy. Protoconch 3.3 mm in diameter, comprising about 1.2 whorls, with indistinct radially elongated pustulations. Teleoconch with well-developed, regular axial growth lines, evenly distributed

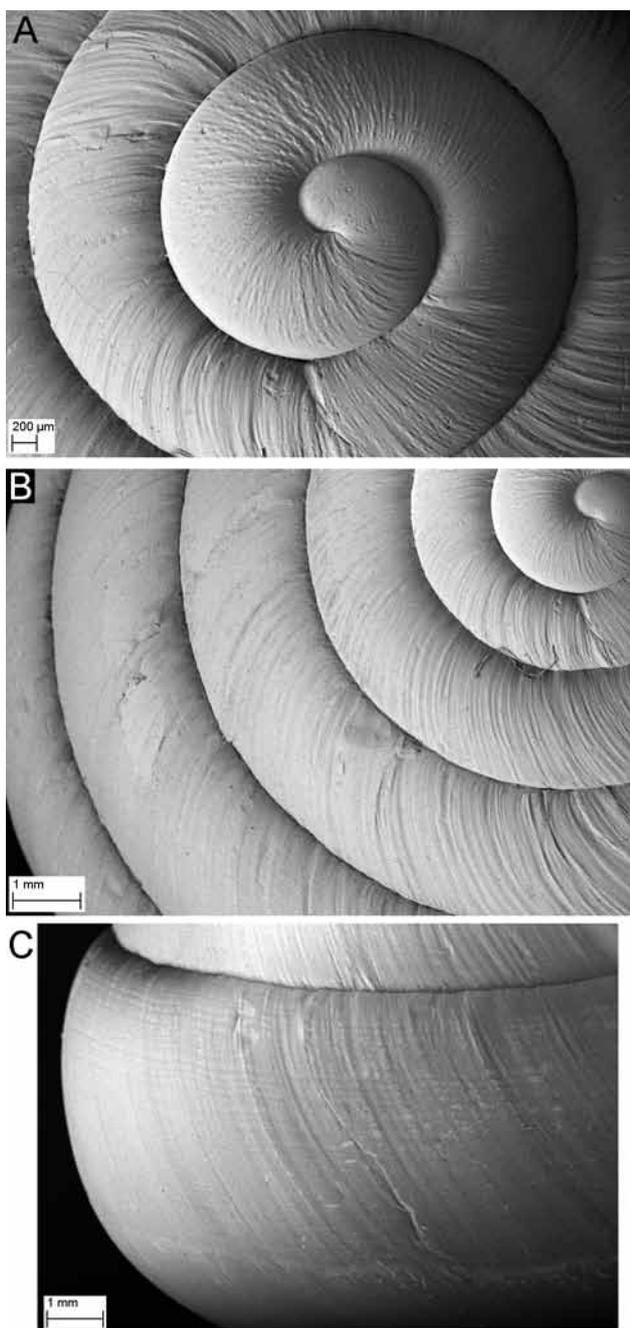


Figure 29. *Amplirhagada coffea* n.sp. SEM of shell (AM C.472933). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Close-up of sculpture on last whorl, lateral view. Scale bars: A, 200 µm; B–C, 1 mm.

across shell surface. Angle of aperture 30–45 degrees; outer lip rounded to slightly angulate, slightly expanded, well reflected, basal node of lip present, palatal node absent. Average shell size $17.9 \pm 1.6 \times 21.4 \pm 1.1$ mm (Table 1).

Genital morphology (Fig. 30). Penis straight, more or less of same length as anterior part of oviduct. Penial sheath proximally thick, distally delicate. Length of penial retractor muscle equivalent to about a third of length of penial complex. Penial verge slender, moderately long, extending about 1/6 of length of penial chamber. Distal part of inner penial wall entirely covered by regular pustulation; pustules relatively large, conical. Proximal part of inner penial wall

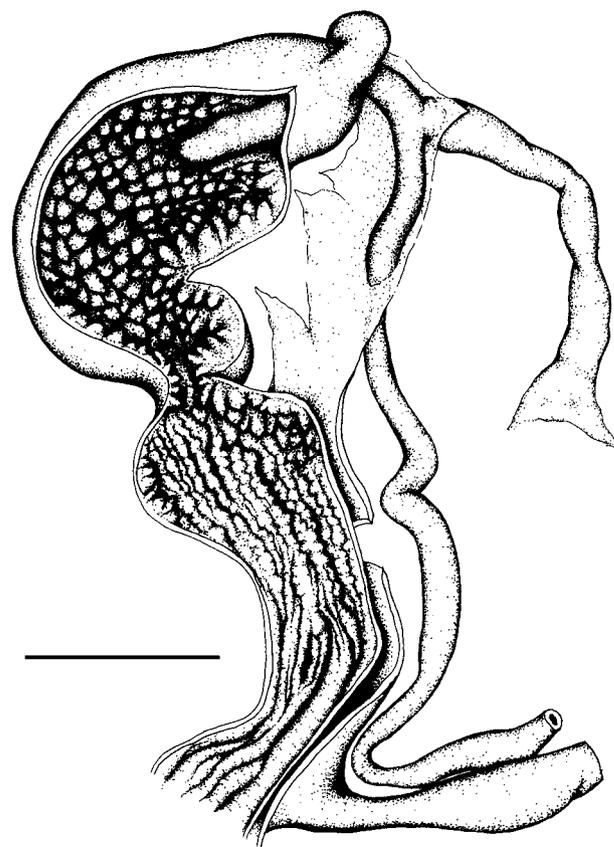


Figure 30. Penial anatomy of *Amplirhagada coffea* n.sp. (AM C.472932). For labelling of structures see Fig. 4. Scale bar = 3 mm.

covered by many irregular, corrugated pilasters formed from fused rows of pustules. No main stimulatory pilaster present. Vas deferens entering penial sheath within distal quarter of penial complex. Rest of genital system unknown.

Aestivation strategy. Rock sealer.

Remarks. Description based on dissection of one specimen. Listed by Solem (1991) as “*Amplirhagada* NSP27” together with dry shells found on Boongaree Island, which were tentatively considered conspecific as based on similar shell. The species from Boongaree was previously described as *A. boongareensis* Köhler, 2010. *Amplirhagada coffea* differs from the former by usually having a concealed umbilicus, different shell and inner lip colour, glossy surface, strongly reflected outer lip. Species with similar “bee-hive” shaped shells, such as *A. boongareensis*, *A. decora* Köhler, 2010 and *A. vialae* differ by having large cone-shaped main pilasters and distinct pustulation of inner penial wall. Material from a second sampling site at the mainland coast (RFS-26–3, Brecknock Harbour, opposite Camden Island) is tentatively being considered conspecific for its similar shell and penial anatomy.

Amplirhagada gardneriana n.sp.

Type locality. Western Australia, NW Kimberley, 15 km E of King Cascade, Princess May Ranges; $15^{\circ}36'00''\text{S } 125^{\circ}26'30''\text{E}$ (RFS 27-3; coll. V. Kessner, 27 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34734 (preserved specimen) (Pl. 1.11; Table 1). Paratypes AM C.472934 (8 preserved specimens), WAM S34735 (13 preserved specimens), FMNH 221084 (22 preserved specimens), AM

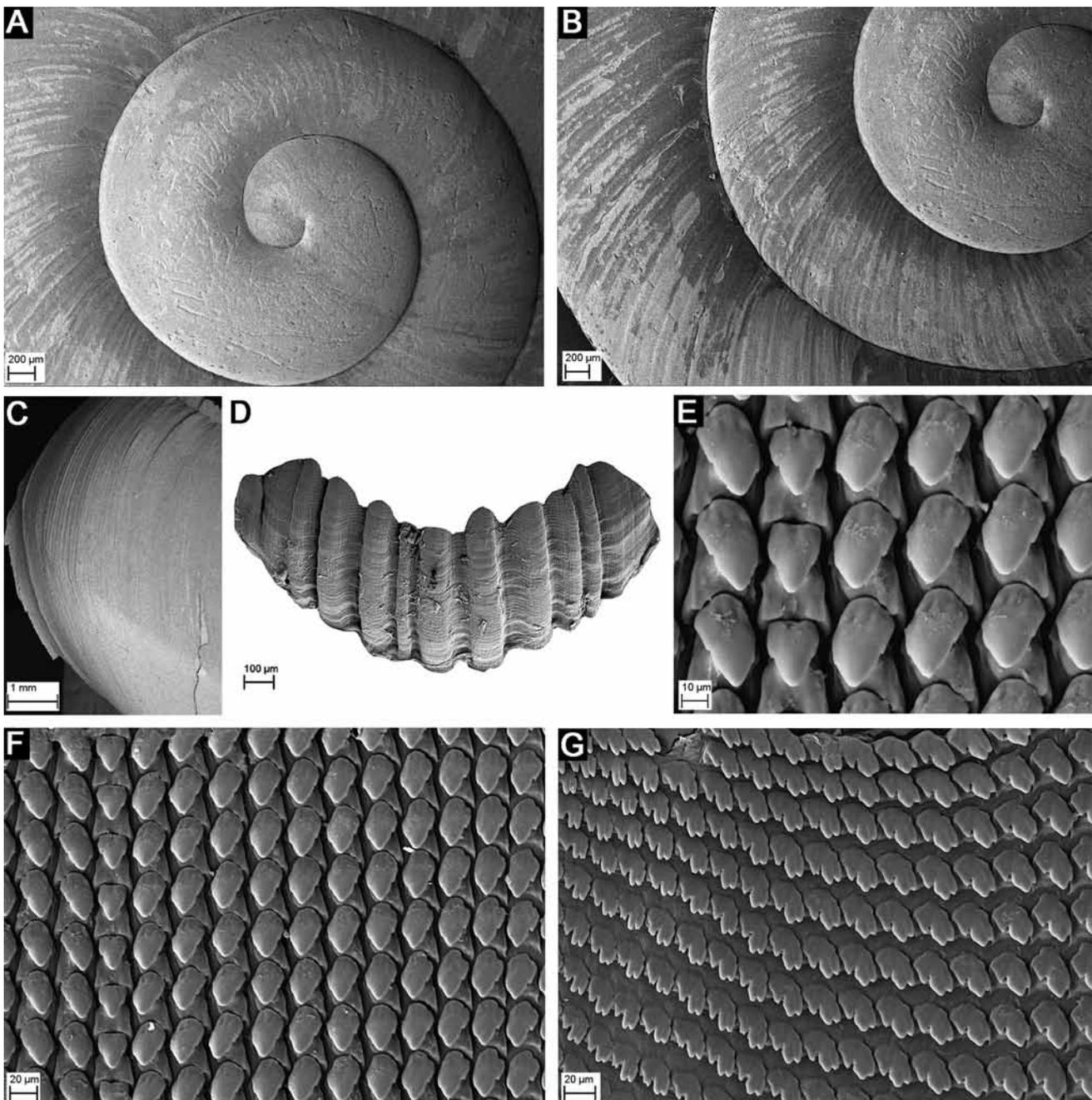


Figure 31. *Amplirhagada gardneriana* n.sp. SEM of shell (AM C.472935), radula and jaw (AM C.472934). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Close-up of sculpture on last whorl, lateral view. (D) Jaw. (E) Central and inner lateral teeth from above. (F) Marginal teeth viewed from above. Scale bars: A–B, 200 μ m; C, 1 mm; D, 100 μ m; E, 10 μ m; F–G, 20 μ m.

C.472935 (14 dried shells), WAM S34736 (25 dried shells), FMNH 221083 (34 dried shells).

Etymology. In reference to the Gardner Plateau, where this species occurs.

Description

Shell (Pl. 1.11; Fig. 31 A–C). Semi-globose with elevated spire. Solid, not translucent. Periphery well rounded to angulate; upper and basal sectors of whorls well rounded. Umbilicus narrowly winding, 50–80% concealed by columellar reflection. Background colour horn to pale brownish ochre; peripheral band rarely present, if present

rather distinct, thin, brown, visible on last whorl only; sub-sutural band absent or diffuse, brown, thin; outer and inner lighter than shell. Protoconch 2.6 mm in diameter, comprising about one whorl, with very indistinct radially elongated pustulations. Teleoconch with faint, regular axial growth lines; evenly distributed across shell surface. Angle of aperture 45–60 degrees; outer lip thin, well rounded, expanded, not reflected; basal node absent or weak. Parietal wall of inner lip thin. Average shell size $14.2 \pm 1.2 \times 18.0 \pm 0.7$ mm (Table 1).

Radular and jaw morphology (Fig. 31 D–G). Tooth formula C + 11 + 4 + 16; 125 rows of teeth (n = 1). Jaw with 10 plates.

Genital morphology (Figs 32–33). Penis straight, tubular,

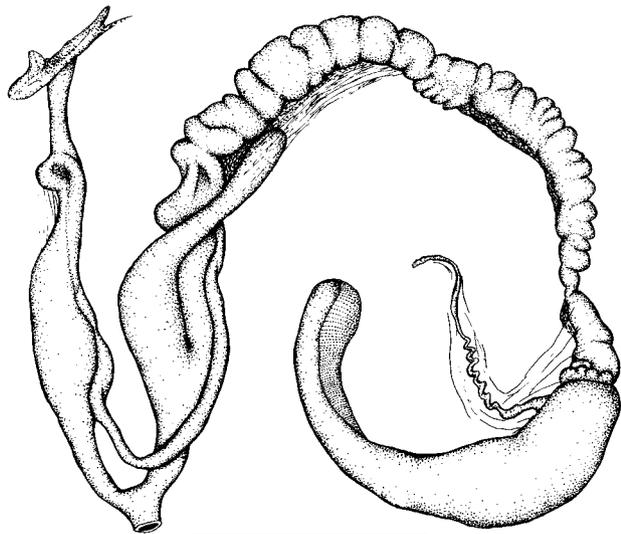


Figure 32. Genitalia of *Amplirhagada gardneriana* n.sp. (AM C.472934). For labelling of structures see Fig. 3. Scale bar = 5 mm.

thin, as long as anterior part of oviduct. Penial sheath distally thick, proximally delicate. Penial retractor about half as long as penis. Penial verge conical, with pointed tip, extending about $\frac{1}{4}$ of length of penial chamber. Inner penial wall entirely covered by very fine, dense pustulation. Main stimulatory pilaster weakly developed, extending distal half of inner penial wall, corrugated. Vas deferens rather thin, entering penial sheath in distal third of penial complex. Vagina moderately long, tubular to slightly inflated; inner vaginal wall and wall of bursa copulatrix with smooth longitudinal pilasters. Bursa copulatrix slightly extending base of spermoviduct. Free oviduct comprising about half of length of anterior part of oviduct. Spermoviduct longer than anterior part of oviduct.

Aestivation strategy. Free sealer.

Remarks. Anatomical description based on dissections of three specimens. Listed by Solem (1991) as “*Amplirhagada* NSP28”. According to Solem (1991) the species differs from *A. pusilla* Solem, 1981 by its narrower umbilicus and more elevated spire and from *A. drysdaleana* Solem, 1981 by a shorter vagina. It also differs by a distinct pustulation of inner penial wall.

Amplirhagada lindsayae n.sp.

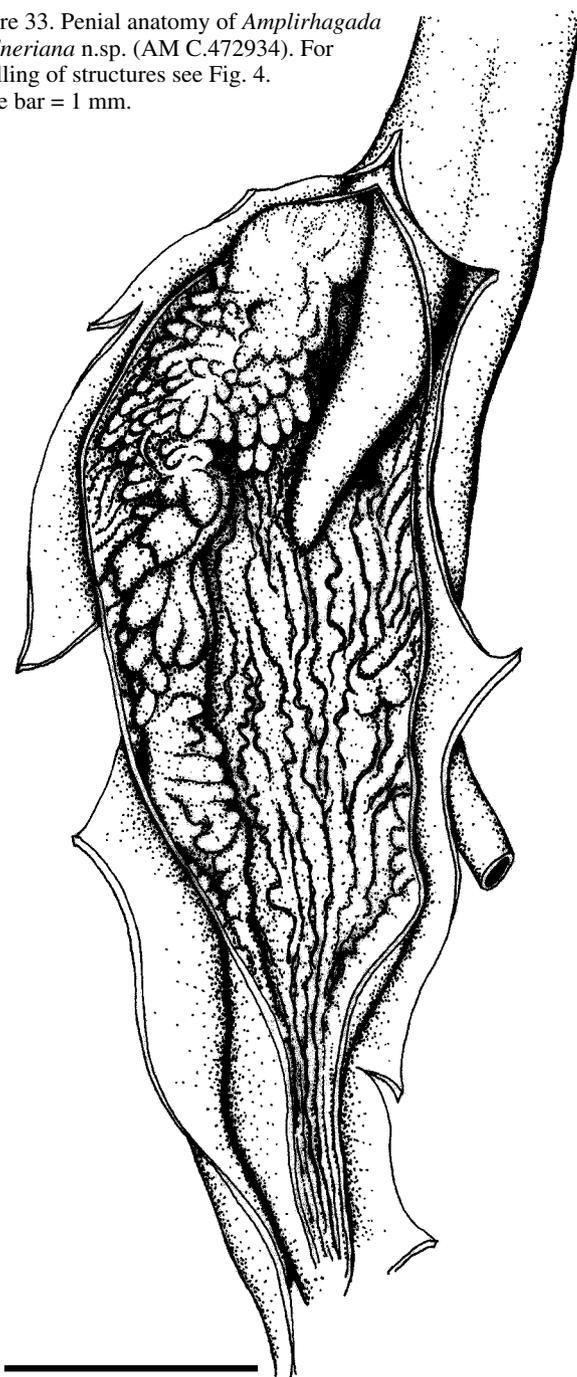
Type locality. Western Australia, NW Kimberley, Prince Frederick Harbour, 40.5 km NE of Mt. Trafalgar, S of Hunter River mouth; 15°03'55"S 125°21'55"E (RFS-14-2; coll. V. Kessner, 14 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34737 (preserved specimen) (Pl. 1.12; Table 1). Paratypes AM C.472936 (4 preserved specimens), WAM S34738 (12 preserved specimens), FMNH 220561 (18 preserved specimens), AM C.472937 (3 dried shells), WAM S34739 (8 dried shells), FMNH 220560 (12 dried shells).

Additional, non-type material. WAM S34753 (6 dried shells), FMNH 219312 (7 dried shells), all from S side of Hunter River mouth, Prince Frederick Harbour; 15°02'58"S 125°23'53"E (KC-079; coll. V. Kessner, A. Longbottom, 22 Jul 1988).

Etymology. Named in honour of Sue Lindsay (Australian Museum) in recognition of her help with SEM work.

Figure 33. Penial anatomy of *Amplirhagada gardneriana* n.sp. (AM C.472934). For labelling of structures see Fig. 4. Scale bar = 1 mm.



Description

Shell (Pl. 1.12; Fig. 34 A–C). Semi-globose with elevated spire. Solid, not translucent. Periphery angulate to keeled; upper and basal sectors of whorls well rounded. Umbilicus almost entirely concealed by columellar reflection, forming a chink. Background colour pale greenish-ochre; peripheral band mostly visible, usually diffuse, blending into brownish tone that may cover upper part of whorls, thin to moderately broad, brown, visible on last whorls only; sub-sutural band absent or very inconspicuous and diffuse, brown, visible on last whorl only; ventral colour pale horn, outer lip like shell, inner lip pale white. Protoconch 2.8 mm in diameter, comprising about one whorl, with very indistinct radially elongated pustulations. Teleoconch with faint, regular axial

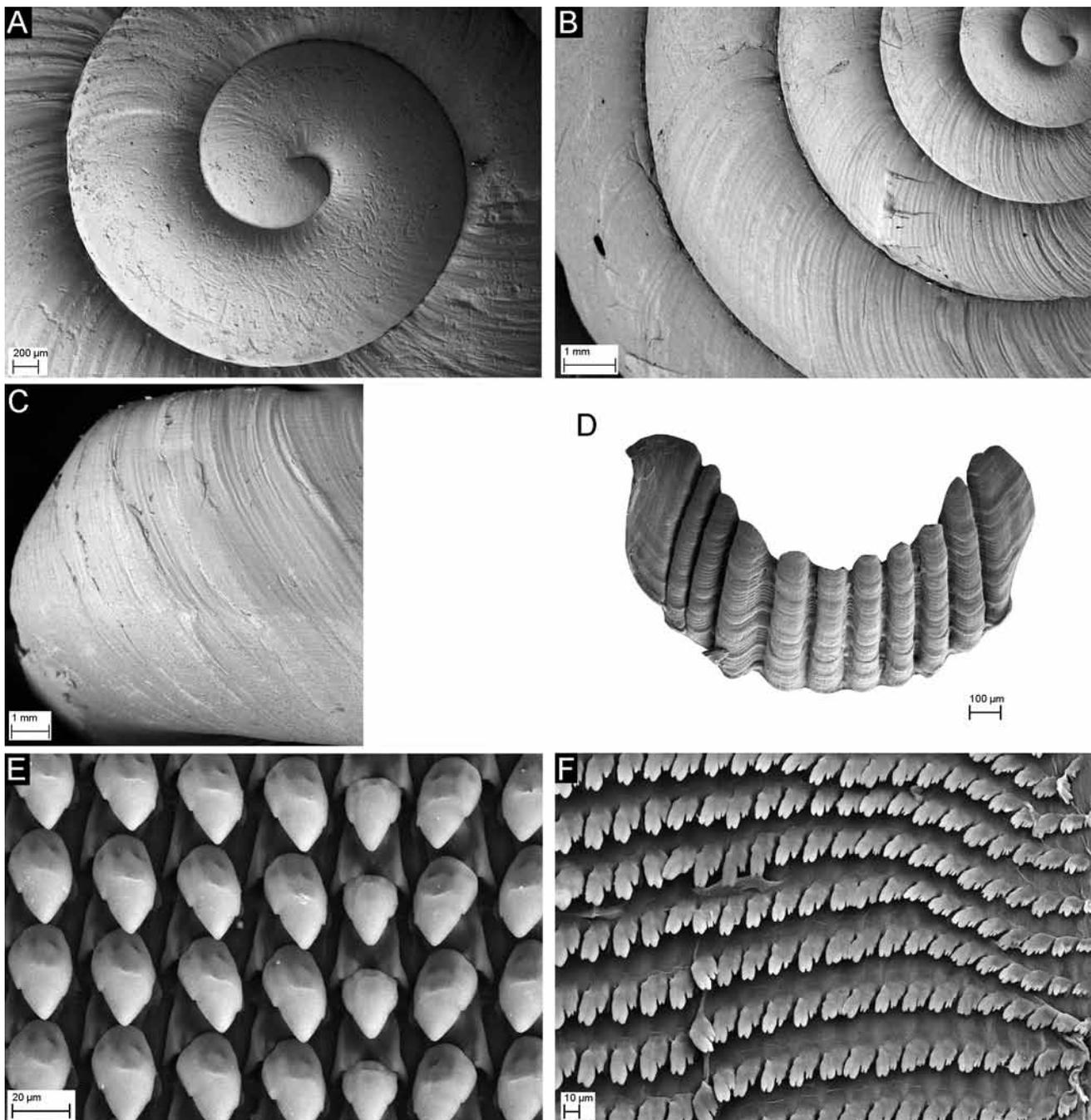


Figure 34. *Amplirhagada lindsayae* n.sp. SEM of shell (AM C.472937), radula and jaw (AM C.472936). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Close-up of sculpture on last whorl, lateral view. (D) Jaw. (E) Central and inner lateral teeth, detail from above. (F) Marginal teeth viewed from above. Scale bars: A, 200 µm; B–C, 1 mm; D, 100 µm; E, 20 µm; F, 10 µm.

growth lines; evenly distributed across shell surface. Angle of aperture about 45 degrees; outer lip sharp to moderately thick, well rounded, slightly expanded, not or slightly reflected; basal node absent or very weak. Parietal wall of inner lip thin. Average shell size $18.3 \pm 1.3 \times 22.4 \pm 0.8$ mm (Table 1).

Radular and jaw morphology (Fig. 34 D–F). Tooth formula C + 12–14 + 4 + 24–26, with 130 rows of teeth 130 ($n = 1$). Jaw with 11 plates.

Genital morphology (Figs 35–36). Penis straight, tubular, as long as anterior part of oviduct. Penial sheath distally thick, proximally thin. Penial retractor about as long as penis. Penial verge rather small, elongate with pointed tip. Inner

penial wall entirely covered by relatively large pustules that are arranged in longitudinal rows. Main stimulatory pilaster formed by row of enlarged (broadened, more elongate), triangular pustules, each supporting a single hook. A weak gutter forms along inner penial wall. Vas deferens moderately thick, entering penial sheath close to penial apex, forming an extended loop. Vagina long, tubular, moderately inflated; inner vaginal wall and wall of bursa copulatrix with smooth longitudinal pilasters. Bursa copulatrix comparatively long, clearly extending base of spermooviduct. Free oviduct comprising about half of length of anterior part of oviduct. Spermooviduct longer than anterior part of oviduct.

Aestivation strategy. Free sealer.

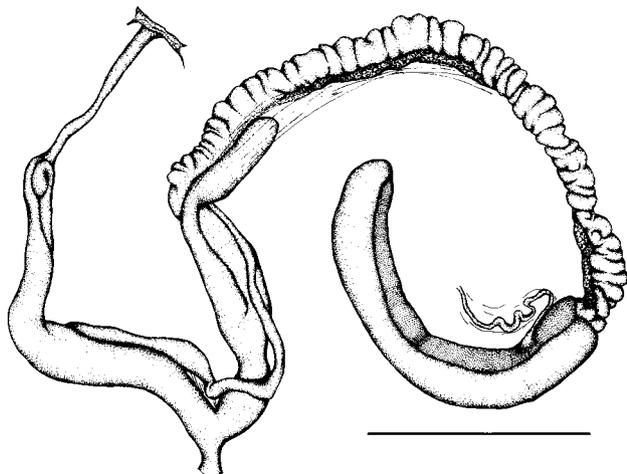


Figure 35. Genitalia of *Amplirhagada lindsayae* n.sp. (AM C.472936). For labelling of structures see Fig. 3. Scale bar = 10 mm.

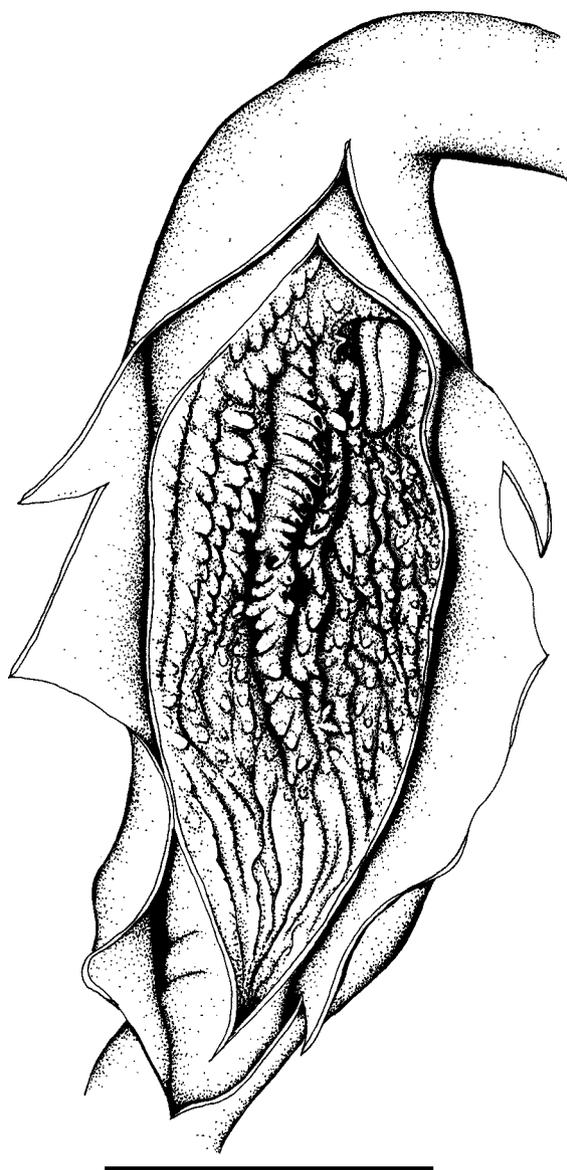


Figure 36. Penial anatomy of *Amplirhagada lindsayae* n.sp. (AM C.472936). For labelling of structures see Fig. 4. Scale bar = 3 mm.

Remarks. Anatomical description based on dissections of three specimens. Listed by Solem (1991) as “*Amplirhagada* NSP29”. The “bee-hive” shaped shell is similar to that of other species, such as *A. boongareensis* Köhler, 2010, *A. decora* Köhler, 2010 and *A. vialae*, all of which differ from present species by possessing a huge cone-shaped main pilaster.

Amplirhagada bendraytoni n.sp.

Type locality. Western Australia, NW Kimberley, York Sound, 4 km SE of Cape Brewster, S of Coronation Island, between beach and base of escarpment; 15°07'40"S 124°56'15"E (RFS 12-3; coll. V. Kessner, 12 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34740 (preserved specimen) (Pl. 1.13; Table 1). Paratypes WAM S34741 (2 preserved specimens), FMNH 220448 (3 preserved specimens), WAM S34742 (3 dried shells), FMNH 2200447 (5 dried shells).

Etymology. Named in honour of my friend and neighbour Ben Drayton from Sydney.

Description

Shell (Pl. 1.13; Fig. 37 A–B). Broadly conical to semi-globose with moderately elevated spire. Solid, not translucent. Periphery angulate; upper and basal sectors rounded. Umbilicus 50–80% concealed by columellar reflection. Background colour horn with a yellowish brown tone; spiral bands absent; outer and inner lip colour lighter than shell. Protoconch not differentiable on SEM micrograph. Teleoconch with very faint axial growth lines; evenly distributed across shell surface. Angle of aperture c. 45 degrees; outer lip moderately thick, well rounded, slightly expanded, not reflected; basal node absent. Parietal wall of inner lip absent. Average shell size $15.2 \pm 1.5 \times 21.3 \pm 1.3$ mm (Table 1).

Radular and jaw morphology (Fig. 37 C–G). Radular Tooth formula C + 13–18 + 4 + 18–22, with 130–140 rows of teeth ($n = 2$). Jaw with nine plates.

Genital morphology (Figs 38–39). Penis straight, tubular, thin, as long as anterior part of oviduct. Penial sheath thick. Penial retractor half as long as penis. Penial verge tiny, with pointed tip. Inner penial wall entirely smooth, with several rather indistinct longitudinal pilasters. Main stimulatory pilaster short, at proximal half of inner penial wall, corrugated by lateral lamellae, each lamella supporting usually three little hooks that are arranged into longitudinal rows that run along the central portion of the pilaster. Vas deferens thin, entering penial sheath close to penial apex, forming an extended loop. Vagina very short, proximally inflated; inner vaginal wall and wall of bursa copulatrix with smooth longitudinal pilasters. Bursa copulatrix slightly extending base of spermoviduct. Free oviduct comprising more than half of length of anterior part of oviduct. Spermoviduct longer than anterior part of oviduct.

Aestivation strategy. Free sealer.

Remarks. Anatomical description based on dissections of two specimens. Listed by Solem (1991) as “*Amplirhagada* NSP31”. The combination of an almost entirely smooth inner penial wall with a sort main pilaster, a tiny verge and a thick penial sheath are peculiar to only this species.

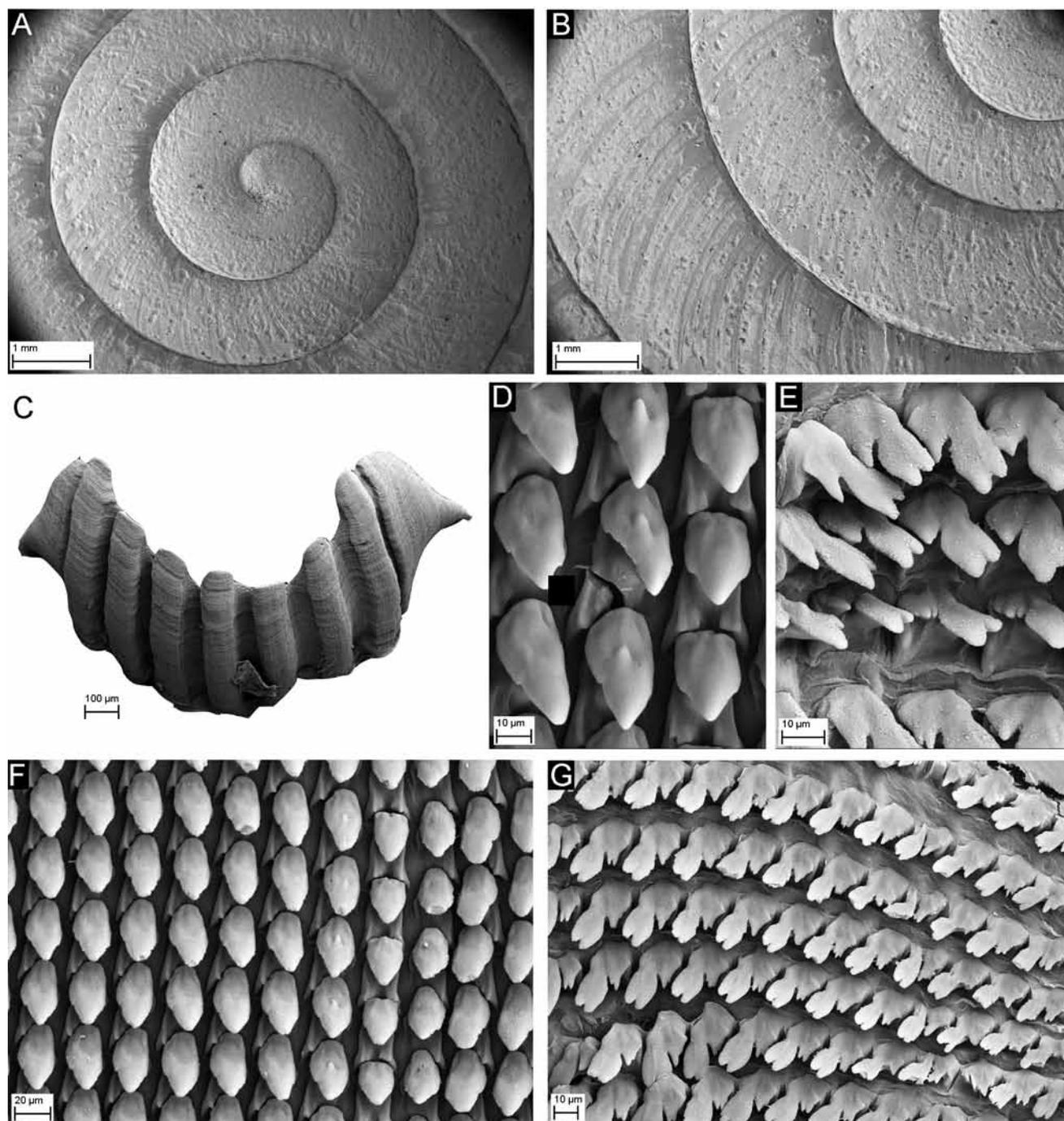


Figure 37. *Amplirhagada bendraytoni* n.sp. SEM of shell, radula and jaw (WAM S34741). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Jaw. (D) Close-up of central and inner lateral teeth. (E) Close-up of Marginal teeth. (F) Central and inner lateral teeth viewed from above. (G) Marginal teeth viewed from above. Scale bars: A–B, 1 mm; C, 100 μ m; D–E, G, 10 μ m; F, 20 μ m.

***Amplirhagada angustocauda* n.sp.**

Type locality. Western Australia, NW Kimberley, SE of Prince Frederick Harbour, 10.5 km E of Mt. Brookes, 6.5 km from coast; west bank tributary Roe River; 15°12'45"S 125°29'30"E (RFS 16-1; coll. V. Kessner, 16 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34743 (preserved specimen, dissected). Paratypes FMNH 220650 (preserved specimen) (Pl. 1.14), WAM S34744 (2 dried shells), FMNH 220654 (dried shell).

Etymology. The species epithet is derived from “angustus” (Latin = narrow) and “cauda” (Latin = penis), in reference to the narrow and elongate epiphallus being a characteristic of this species.

Description

Shell (Pl. 1.14; Fig. 40 A–C). Broadly conical with moderately elevated spire. Thin, translucent. Periphery sharply angulate; upper and basal sectors rounded. Umbilicus 30% concealed by columellar reflection. Background colour yellowish brown; spiral bands absent; outer and inner lip

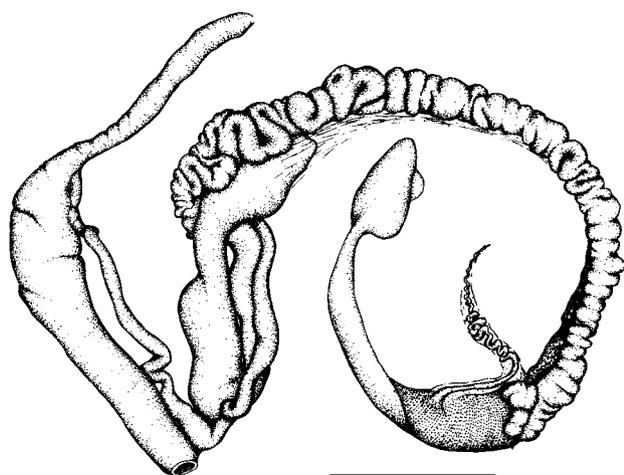


Figure 38. Genitalia of *Amplirhagada bendraytoni* n.sp. (WAM S34741). For labelling of structures see Fig. 3. Scale bar = 5 mm.

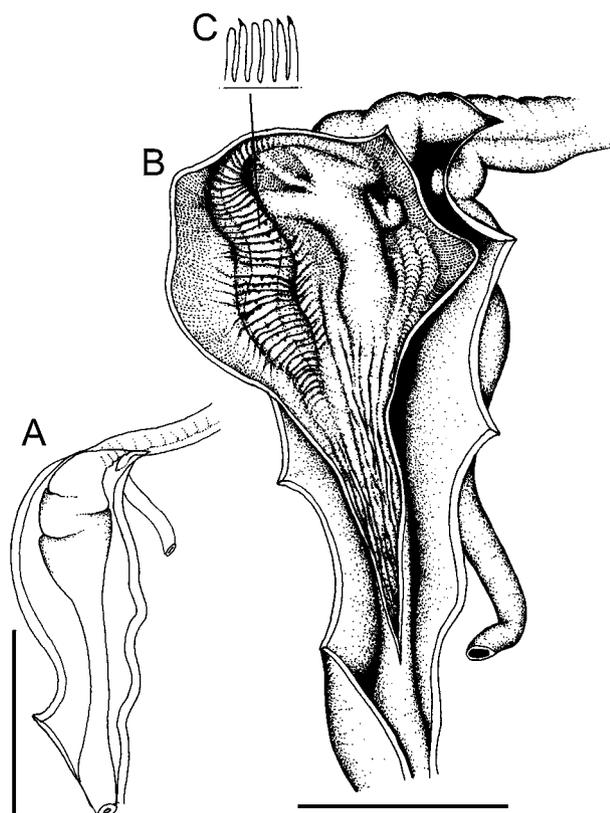


Figure 39. Penial anatomy of *Amplirhagada bendraytoni* n.sp. (WAM S34741). For labelling of structures see Fig. 4. (A) Schematic view of the penis with the penial sheath being removed. Scale bar = 5 mm. (B) Interior anatomy of the penial wall. Scale bar = 5 mm. (C) Schematic cross-section of the main pilaster (not to scale).

colour whitish. Protoconch 3.4 mm in diameter, comprising about 1.5 whorls, essentially smooth. Teleoconch with well-developed, irregular axial growth lines; evenly distributed across shell surface. Angle of aperture c. 60°; outer lip sharp, well rounded, slightly expanded; basal node absent. Parietal wall of inner lip absent. Average shell size $11.7 \pm 1.2 \times 15.7 \pm 0.7$ mm (Table 1).

Radular and jaw morphology (Fig. 40 D–F). Tooth formula C + 10–13 + 4 + 16, with 120 rows of teeth 130 (n = 1). Jaw with 11 plates.

Genital morphology (Figs 41–42). Penis straight, with a short, tubular, very thin penis proper; lumen of penial chamber short extending only about 1/3 to 1/4 of length of penial complex. Inner penial wall with few smooth longitudinal pilasters; no main stimulatory pilaster differentiated. Penial sheath distally thick, proximally thin. Penial retractor muscle stubby, no longer than 1/5 of penial complex. Vas deferens moderately thick, entering penial sheath at about half of length of penial complex, forming an extended loop, reflecting as an elongate, thin, tubular epiphallus, which gives rise to the short penis. Inner wall of epiphallus smooth, ciliated. Penial verge tiny, slender, with pointed tip. Vagina moderately long, proximally slightly inflated; inner vaginal wall and wall of bursa copulatrix with smooth longitudinal pilasters. Bursa copulatrix slightly extending base of spermoviduct. Free oviduct comprising about half of length of anterior part of oviduct. Spermoviduct longer than anterior part of oviduct.

Aestivation strategy. Unknown.

Remarks. Description is based on dissection of the holotype. The species was listed by Solem (1991) as “*Amplirhagada* NSP33”. Shell smaller than in most other congeners. Various features of the penial anatomy are very characteristic: vas deferens reflecting as a narrow, elongated epiphallus, the penial chamber is very short supporting longitudinal pilasters but no pustules. Species differs by its markedly different penial anatomy from *A. wilsoni* Solem, 1981, which also occurs at the banks of the Roe River not too far from the type locality of this species. For comparison with *A. moraniana* having also a similar shell see remarks under this species.

Amplirhagada epiphallica n.sp.

Type locality. Western Australia, NW Kimberley, N side of Prince Frederick Harbour, near mouth, 16 km W of Mt. Anderdon, 0.3 km from coast; 14°57'10"S 125°16'30"E (RFS 14-1; coll. V. Kessner, 14 Jun 1987) (Fig. 1).

Type material. Holotype WAM S34745 (preserved specimen) (Pl. 1.15; Table 1). Paratypes WAM S34746 (3 preserved specimens), FMNH 200539 (4 preserved specimens), WAM S34747 (2 dried shells), FMNH 220541 (2 dried shells).

Etymology. The species epithet refers to the presence of an epiphallus, which is a very distinctive feature among species of *Amplirhagada*.

Description

Shell (Pl. 1.15; Fig. 43 A–C). Broadly conical with low spire, almost discoid. Thin to delicate, translucent. Periphery rounded to angulate; upper and basal sectors of whorls well rounded. Umbilicus 10–50% concealed by columellar reflection. Background colour pale yellowish brown; peripheral band well marked, moderately thick, brown, visible on most whorls; sub-sutural well marked to diffuse, moderately thick, visible on most whorls; outer and inner lip colour whitish. Protoconch 2.5 mm in diameter, comprising about 1.2 whorls, essentially smooth. Teleoconch with regular axial growth lines; evenly distributed across shell surface. Angle of aperture about 45 degrees; outer lip thin, well rounded, expanded, not reflected; basal node absent or weakly developed. Parietal wall of inner lip inconspicuous. Average shell size $13.7 \pm 0.8 \times 20.1 \pm 0.7$ mm (Table 1).

Radular and jaw morphology (Fig. 43 D–F). Tooth formula C + 13–14 + 4 + 18–20, with 150 rows of teeth 130 (n = 1). Jaw with 11 plates.

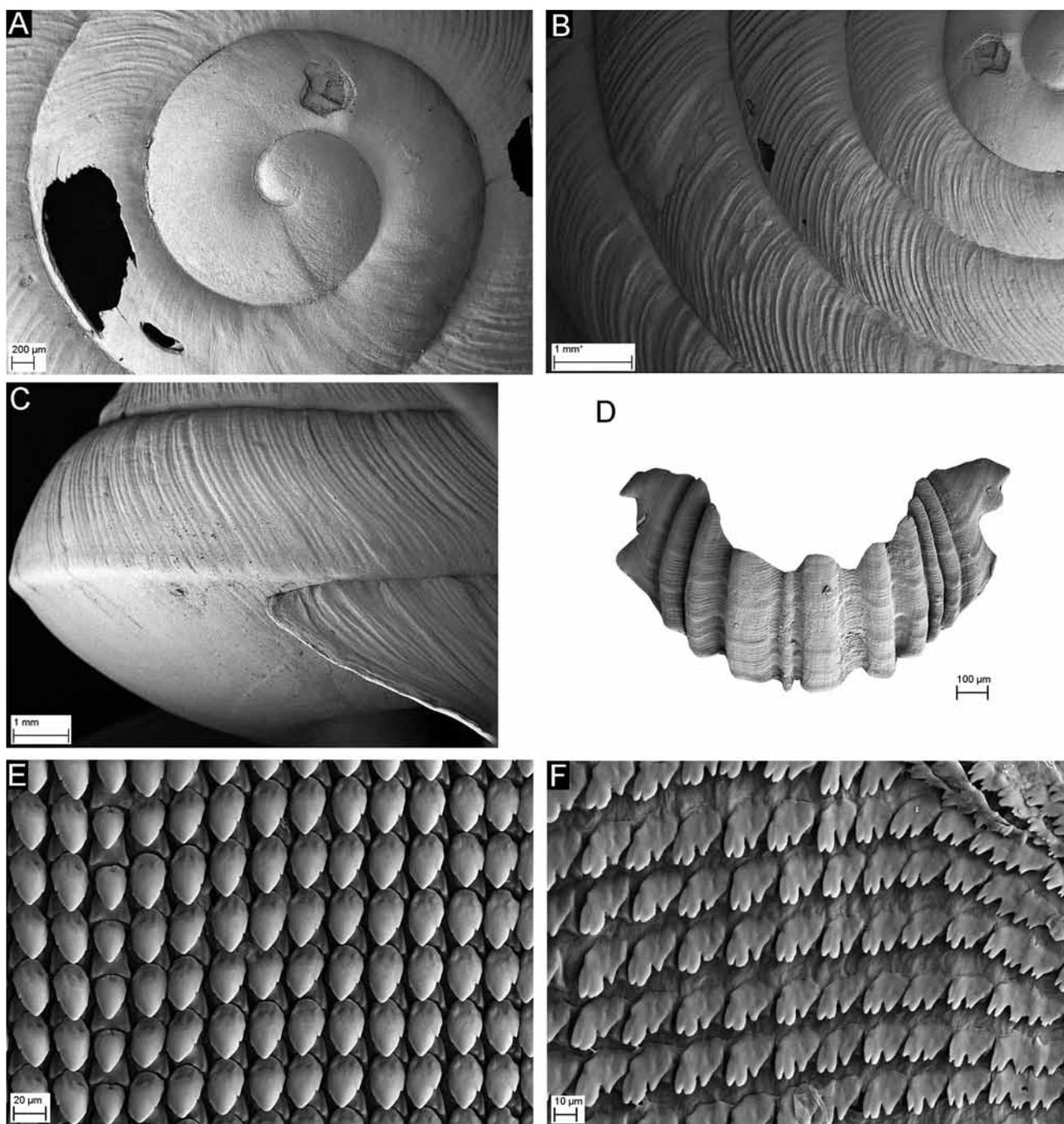


Figure 40. *Amplirhagada angustocauda* n.sp. SEM of shell, radula and jaw (WAM S34743). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Close-up of sculpture on last whorl, lateral view. (D) Jaw. (E) Central and inner lateral teeth viewed from above. (F) Marginal teeth viewed from above. Scale bars: A, 200 µm; B–C, 1 mm; D, 100 µm; E, 20 µm; F, 10 µm.

Genital morphology (Figs 44–45). Penis complex elongated, tubular, coiled; actual penis extending proximal two thirds of penial complex. Inner penial wall completely lined with regular, fine pustulation arranged in corrugated pilasters; no main stimulatory pilaster differentiated. Penial sheath thick. Penial retractor muscle stubby, no longer than 1/10 of penial complex. Vas deferens moderately thick, entering penial sheath at apical end of penial complex, forming an extended loop, reflecting as an elongate, thin, tubular epiphallus, which gives rise to the short penis. Inner wall of epiphallus smooth, ciliated. Penial verge

tiny, slender, forming a loop with pointed tip. Vas deferens elongated, winding before entering the uterus. Vagina long, tubular; inner vaginal wall and wall of bursa copulatrix with smooth longitudinal pilasters. Bursa copulatrix slightly extending base of spermoviduct, with bulbous head. Free oviduct elongated, coiled before entering the uterus, comprising more than half of length of anterior part of oviduct. Spermoviduct no longer than anterior part of oviduct. Albumen gland as long as spermoviduct.

Aestivation strategy. Free sealer.

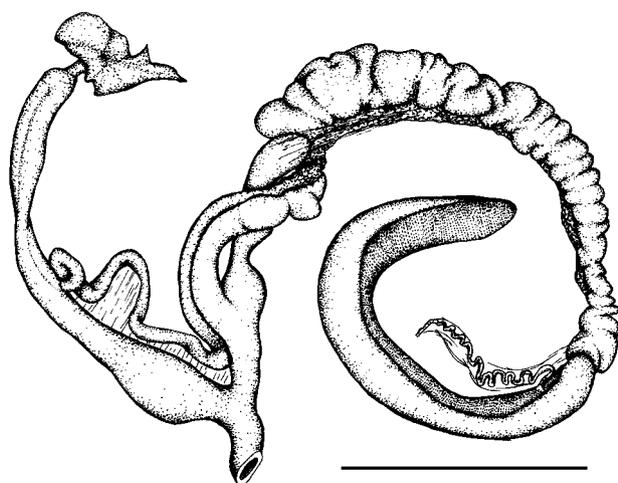


Figure 41. Genitalia of *Amplirhagada angustocauda* n.sp. (WAM S34743). For labelling of structures see Fig. 3. Scale bar = 5 mm.

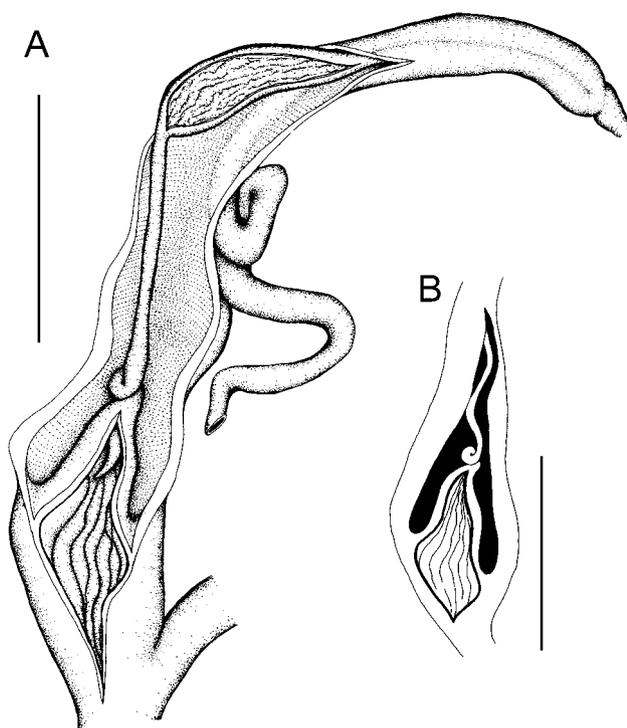


Figure 42. Penial anatomy of *Amplirhagada angustocauda* n.sp. (WAM S34743). For labelling of structures see Fig. 4. (A) Interior anatomy of the penial wall. (B) Schematic view of the penis with the penial sheath being removed. Scale bars = 3 mm.

Remarks. Anatomical description based on dissection of the holotype. Listed by Solem (1991) as “*Amplirhagada* NSP35” and found in sympatry with *A. inusitata* n.sp. and *A. pusilla* Solem, 1981. The flat shell is similar to that of *A. discoidea*. However, the genital anatomy of this species is very unusual for *Amplirhagada* showing a combination of exclusive features, such as a very long and winding vas deferens, a long tubular vagina, very long tubular penis and vas deferens reflecting as an epiphallus within the strongly developed penial sheath, and a short, thin and coiled penial verge.

Amplirhagada carinata Solem, 1981

Amplirhagada carinata Solem, 1981: 205–208, pl. 13e, figs. 37g, 43a–b, 45a–b

Type locality. Western Australia, SW Kimberley, 5 km N of Mt Hart Station, immediately W of Mt Matthew, Upper Barker Drainage, King Leopold Ranges.

Material examined (Fig. 1). WAM S34759 (8 preserved specimens), FMNH 220843 (7 preserved specimens), WAM S34760 (13 dried shells), FMNH 220842 (13 dried shells), all from 3.6 km SSE of Mt. Talbot, 3.2 km from coast, near Walcott Inlet; 16°29'25"S 124°48'05"E; RFS-21-3; coll. V. Kessner, 21 Jun 1987 (“NSP36”). WAM S34761 (8 preserved specimens), FMNH 221066 (8 preserved specimens), AM C.472938 (6 dried shells), WAM S34762 (13 dried shells), FMNH 221065 (19 dried shells), all from 34 km S of Mt. Kitchener, 9 km from coast, S of Calder River; 16°19'40"S 125°01'10"E; RFS-27-1, coll. V. Kessner, 27 Jun 1987 (“NSP36”). WAM S34763 (5 preserved specimens), FMNH 221096 (5 preserved specimens), AM C.472939 (5 dried shells), WAM S34764 (15 dried shells), FMNH 221095 (20 dried shells), all from NW hump of The Dromedaries, E of Isdell River; 16°34'20"S 124°56'40"E; RFS-28-1, coll. V. Kessner, 28 Jun 1987 (“NSP38”). WAM S34765 (4 preserved specimens), FMNH 220782 (4 preserved specimens), WAM S34766 (9 dried shells), FMNH 220781 (10 dried shells), all from Walcott Inlet, 6 km E of Mt. Talbot, 2 km from coast; 16°27'30"S 125°50'30"E; RFS 19-2, coll. V. Kessner, 19 Jun 1987 (“NSP42”). FMNH 220755 (2 preserved specimens), WAM S34767 (11 dried shells), FMNH 220755 (11 dried shells), all from Walcott inlet, 14.5 km E of Mt. Talbot; 16°25'20"S 124°54'00"E; RFS 18-4, leg. V. Kessner, 18 Jun 1987 (“NSP42”). AM C.472940 (6 preserved specimens), WAM S34768 (10 preserved specimens), FMNH 220987 (15 preserved specimens), WAM S34769 (17 dried shells), FMNH 220986 (16 dried shells), all from 25.3 km WSW of Mt. Blithe, on Charney River; 16°22'35"S 125°12'35"E; RFS 25-2, coll. V. Kessner, 25 Jun 1987 (“NSP42”).

Diagnosis

Shell (Pl. 1.16; Fig. 46 A–C) broadly conical to discoid with low spire, slightly to sharply angulated periphery, well rounded upper and basal sectors of whorls. Umbilicus 10–80% concealed by columellar reflection. Background colour pale yellowish brown; peripheral band usually diffuse, thin, brown, visible on most whorls; sub-sutural band diffuse, brown, thin; outer and inner lip colour like shell. Protoconch c. 1.5 mm in diameter, with about 1.5 whorls, with very indistinct radially elongated pustulations. Teleoconch with faint, regular axial growth lines; evenly distributed across shell surface. Angle of aperture 45–60 degrees; outer lip thin to moderately thick, well rounded, slightly to well expanded, not reflected; basal node absent or weak. Parietal wall of inner lip inconspicuous. Average shell size $10.7 \pm 16.9 \times 1.4 \pm 1.1$ mm (Table 1).

Radular tooth formula C + 12–14 + 4 + 16–20, with on average 130 of rows of teeth ($n = 4$), jaw with 10 plates (Fig. 46 D–E).

Penis heavily coiled within penial sheath, thick, longer than anterior part of oviduct, with thick penial sheath. Penial verge moderate in size, comprising c. 1/10 of length of penial chamber, conical, with rounded tip. Inner penial wall penial wall with dense, fine pustulation, main stimulatory pilaster weakly to well developed, extending about half of length of penial chamber, consisting of enlarged and partly fused pustules forming hooked corrugations or an elongated, conical pilaster; a gutter forming along inner penial wall. Vas deferens moderately thick, winding, entering

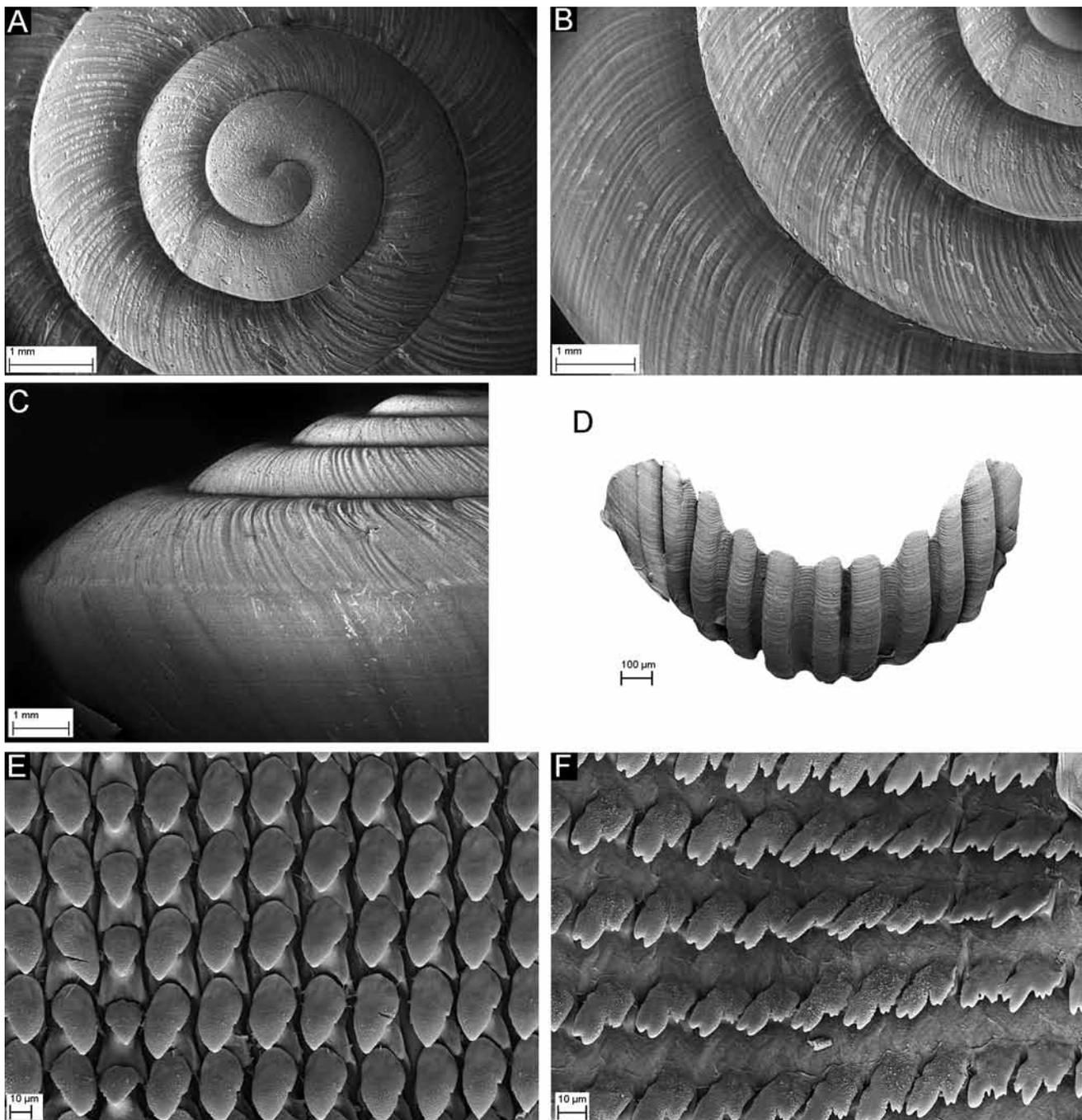


Figure 43. *Amplirhagada epiphallica* n.sp. SEM of shell, radula and jaw (WAM S34746). (A) Protoconch and first teleconch whorls viewed from above. (B) Detail of first teleconch whorls viewed from above. (C) Close-up of sculpture on last whorl, lateral view. (D) Jaw. (E) Central and inner lateral teeth viewed from above. (F) Marginal teeth viewed from above. Scale bars: A–C, 1 mm; D, 100 µm; E–F, 10 µm.

penial sheath close to penial apex. Vagina moderately long, distally inflated, inner wall with rows of densely arranged triangular pustules. Bursa copulatrix clearly extending base of spermooviduct (Figs 47–48). Aestivation strategy unknown.

Remarks. Description based on dissections of four specimens. Material of three distinct manuscript species differentiated by Solem (1991), *Amplirhagada* NSP36, NSP38, and NSP 42, are subsumed under *A. carinata* Solem, 1981. Solem (1991) indicated serious problems with the correct delimitation of *A. carinata* and was puzzled by its unusually large distributional range. However, there are other congeners, such as *A. burnereensis* (Smith, 1894),

A. pusilla Solem, 1981 and *A. osmondi* Solem, 1988, that occupy similarly large ranges in the interior of the SW and E Kimberley.

The various populations currently included within *A. carinata* indeed reveal considerable levels of anatomical differentiation. While inner penial wall always supports dense and conspicuous pustulation, a main stimulatory pilaster may or may not be developed. However, anatomical variation in shell and penial anatomy is large also within populations and I am not able to unequivocally delimit taxa by using these features. As outlined by Cameron (1992) for similar patterns of shell differentiation found in a number of camaenid species in the Oscar and Napier Ranges of the

Discussion

Significance of morphological characters for the delimitation of taxa

The genital anatomy, with special emphasis on penial anatomy, has been recognized as the most significant source of systematic information on all systematic levels within the Camaenidae (e.g., Solem, 1981). This observation was recently confirmed also for *Amplirhagada* by Köhler (2010b), who showed that the vast majority of species was characterized by distinct features, notably of inner penial wall and development of the main stimulatory pilaster. Species-taxa delineated by use of such features were consistently differentiated by large genetic distances in the mitochondrial marker *cytochrome c oxidase subunit 1* (COI).

Naturally, the development and relative size of some genital structures depends on the maturity of the animal and on its actual reproductive state. Among fully mature specimens (with adult shell features and fully developed albumen gland), a simple pattern of seasonal variation is found with the genitalia being inactive and reduced in size during the early to middle dry season between May and August (Solem & Christensen, 1984). As figures and descriptions of genital features herein are exclusively based on the examination of adult specimens collected during the dry season (June 1987), all reproductive organs should be in a comparable stage of seasonal development.

Species described herein (and earlier; Köhler, 2010b) reveal an amazing variety especially with respect to their penial anatomy. Most species are readily recognisable by a peculiarly developed inner penial wall (*A. alicunda*, *A. discoidea*, *A. bendraytoni*), the presence of an unusually long penial verge (*A. moraniana*, *A. inusitata*), a massively enlarged main pilaster (*A. alicunda*, *A. vialae*), absence of a main pilaster (*A. coffea*), peculiar shape of the main pilaster (*A. gardneriana*), an extremely elongated penis (*A. inusitata*), or even the presence of an epiphallus (*A. angustocauda*, *A. epiphallica*), and often a combination of several such characteristics.

The presence of an epiphallus in *A. angustocauda* and *A. epiphallica* is particularly remarkable because the lack of an epiphallus was thought to be a characteristic shared by all species of this genus. The species *A. epiphallica* is characterized by additional features, such as a very long and coiled penis plus a long and winding vas deferens and free oviduct, which sets it apart from all other congeners. These features indicate that this is a species that likely occupies a distinct position in the phylogenetic tree of *Amplirhagada*. Still, it is retained within *Amplirhagada* for the time being because of its typical shell, the presence of a penial sheath and a penial verge being similar to the typical shape. The elongated, tubular penis, the presence of an epiphallus and the long and winding vas deferens and free oviduct can be seen as derivations from the typical anatomy. It is considered more likely that these structures are plesiomorphic and were lost or reduced in all other congeners than assuming that they have developed in *A. epiphallica* independently from similar character states in other camaenid genera. This assumption implies that *A. epiphallica* may be the most primitive species within *Amplirhagada*. This remains to be tested by a phylogenetic analysis.

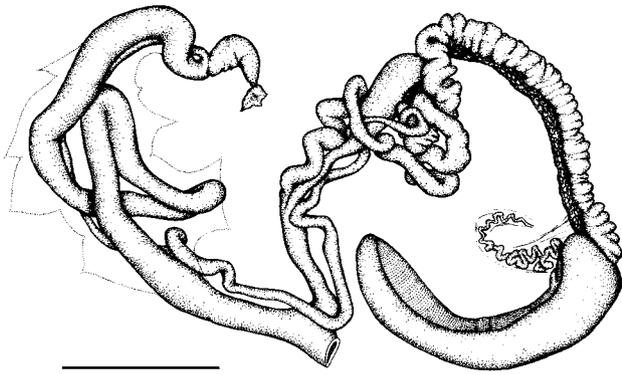


Figure 44. Genitalia of *Amplirhagada epiphallica* n.sp. (WAM S34746). For labelling of structures see Fig. 3. Scale bar = 5 mm.



Figure 45. Penial anatomy of *Amplirhagada epiphallica* n.sp. (WAM S34746). For labelling of structures see Fig. 4. (A) Interior anatomy of the penial wall. (B) Schematic view of the penis with the penial sheath being removed. Scale bars = 5 mm.

interior SW Kimberley, this might indicate the presence of unresolved species complexes that are currently undergoing the process of lineage differentiation (i.e., speciation). A careful analysis of the spatial patterns of anatomical and genetic differentiation is needed to resolve these problems and suggest a proper taxonomic solution for these species complexes.

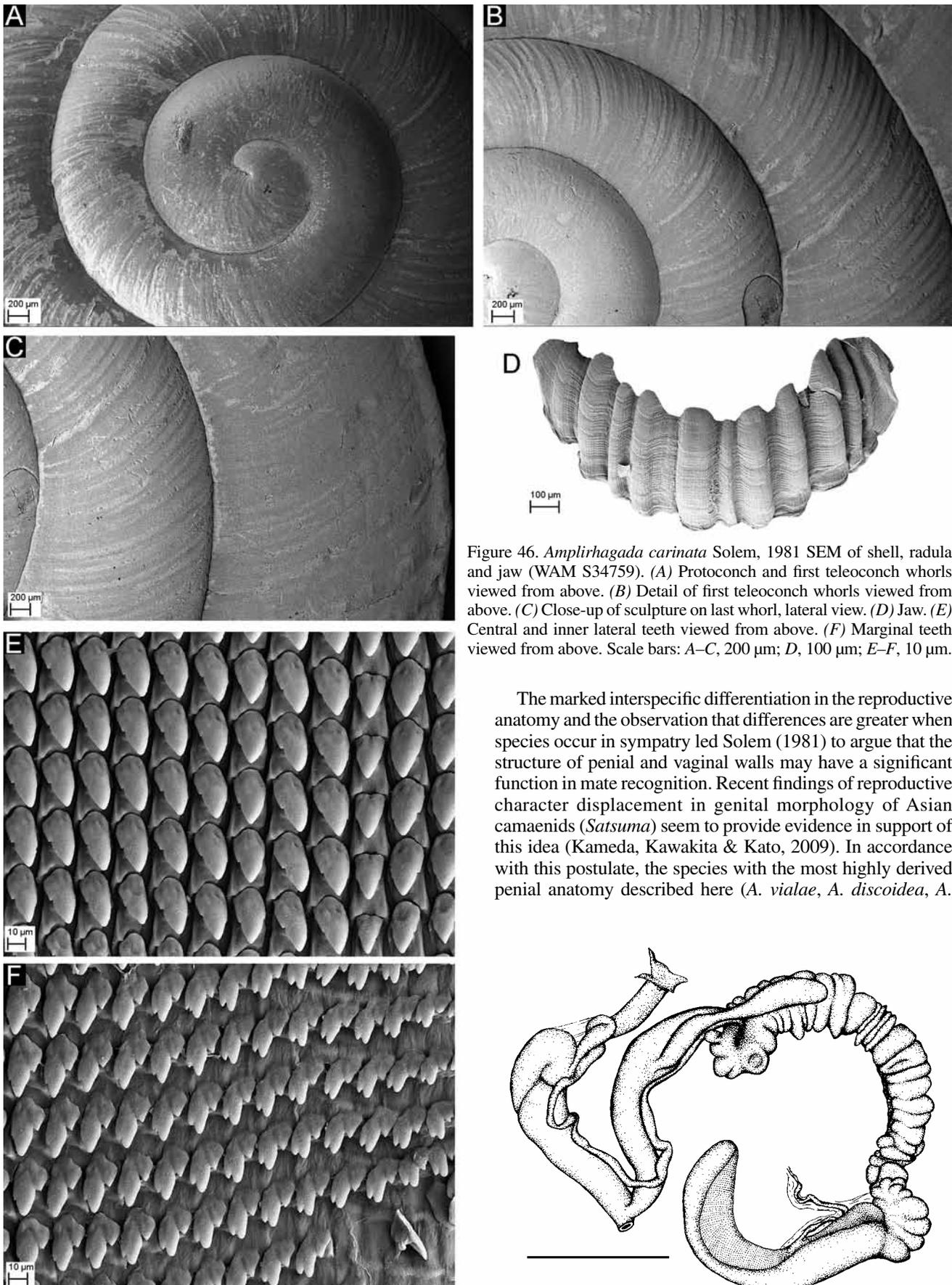


Figure 46. *Amplirhagada carinata* Solem, 1981 SEM of shell, radula and jaw (WAM S34759). (A) Protoconch and first teleoconch whorls viewed from above. (B) Detail of first teleoconch whorls viewed from above. (C) Close-up of sculpture on last whorl, lateral view. (D) Jaw. (E) Central and inner lateral teeth viewed from above. (F) Marginal teeth viewed from above. Scale bars: A–C, 200 µm; D, 100 µm; E–F, 10 µm.

The marked interspecific differentiation in the reproductive anatomy and the observation that differences are greater when species occur in sympatry led Solem (1981) to argue that the structure of penial and vaginal walls may have a significant function in mate recognition. Recent findings of reproductive character displacement in genital morphology of Asian camaenids (*Satsuma*) seem to provide evidence in support of this idea (Kameda, Kawakita & Kato, 2009). In accordance with this postulate, the species with the most highly derived penial anatomy described here (*A. vialae*, *A. discoidea*, *A.*

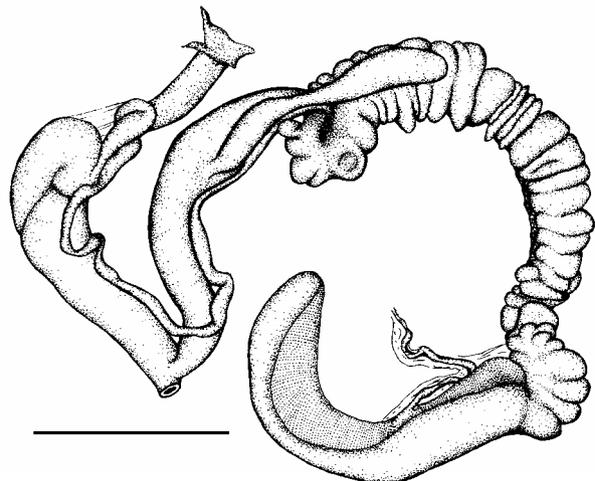


Figure 47. Genitalia of *Amplirhagada carinata* Solem, 1981 (WAM S34759). For labelling of structures see Fig. 3. Scale bar = 5 mm.

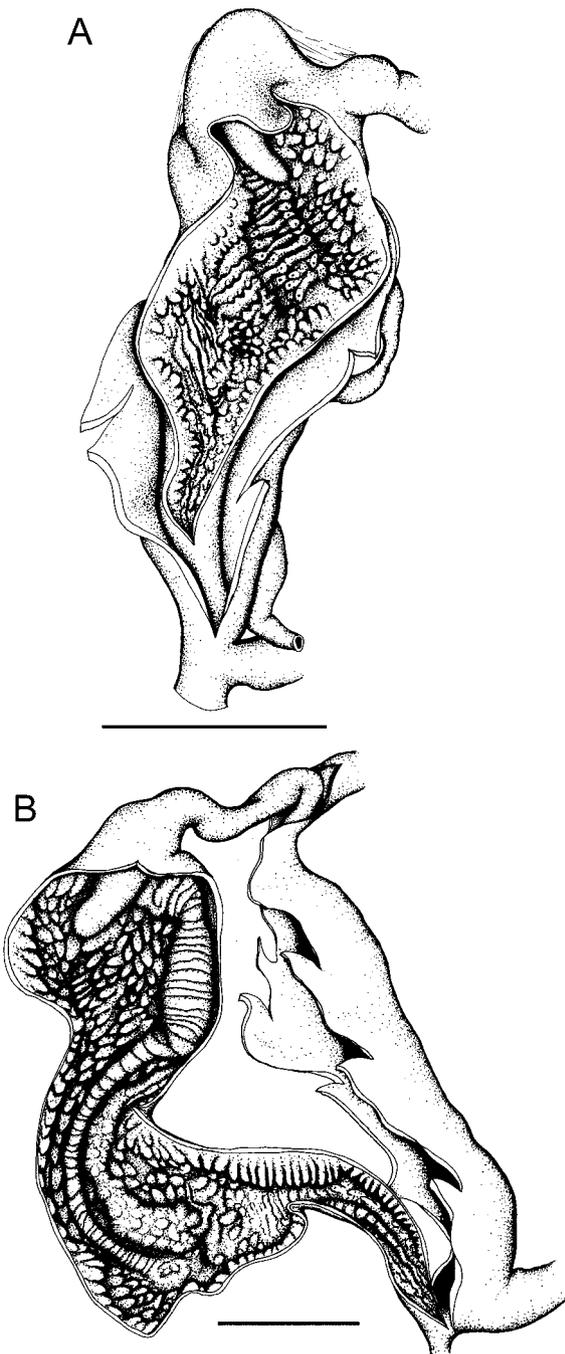


Figure 48. Penial anatomy of *Amplirhagada carinata* Solem, 1981. (A) Interior anatomy of the penial wall (WAM S34759). (B) Interior anatomy of the penial wall (WAM S34763). For labelling of structures see Fig. 4. Scale bars = 3 mm.

inusitata, *A. epiphallica*, *A. angustocauda*) consistently occur in sympatry with at least a second congener. However, the picture is not as simple as there are also species that possess unusual features but are not known to co-occur with a second species, such as *A. moraniana* and *A. alicunda*. In addition, another species not treated herein (*Amplirhagada* NSP37, as preliminarily identified by Alan Solem) and *A. carinata* have overlapping ranges and a similar penial anatomy. However, these two species were never found in sympatry. *Amplirhagada* “NSP37” was ignored in this paper because of its currently unresolved relationships with another undescribed species from islands in the Collier Bay, and will be dealt with in future publications.

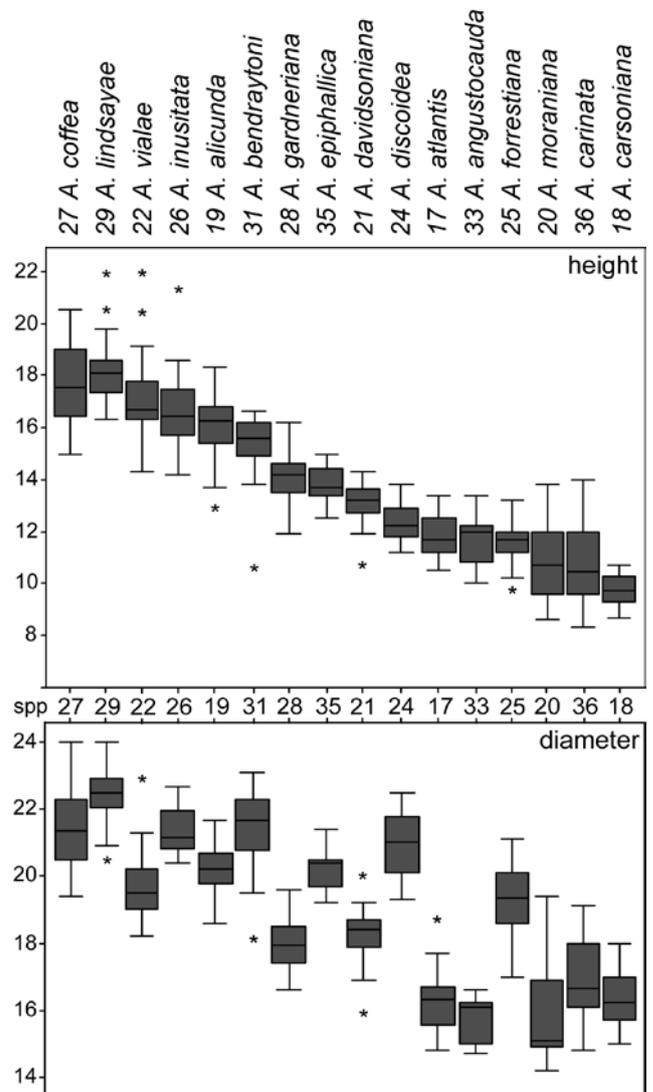


Figure 49. Shell size ranges of *Amplirhagada* species described herein. Box plot diagrams showing the median (line in box), the 25% (box) and 75% percentile (lines outside box) and extremes (asterisks) of shell height (above) and shell width (below) of species sorted by their height. Species numbers refer to the manuscript names of the described species as used by Solem (1991): 27, *A. coffea*. 29, *A. lindsayae*. 22, *A. vialae*. 26, *A. inusitata*. 19, *A. alicunda*. 31, *A. bendraytoni*. 28, *A. gardneriana*. 35, *A. epiphallica*. 21, *A. davidsoniana*. 24, *A. discoidea*. 17, *A. atlantis*. 33, *A. angustocauda*. 25, *A. forrestiana*. 20, *A. moraniana*. 36, *A. carinata*. 18, *A. carsoniana*.

Contrasting with the systematic significance of the reproductive anatomy, Solem (1981) found that shell features often are of limited value for the recognition of species. In the first place, species recognition by shell features is complicated though by the usually large amount of variation in shell shape and colouration. In general, species that occur under allopatric conditions may exhibit quite similar shells while conversely species found in sympatry usually have distinct shell shapes or sizes, which was discussed as being indicative of ecological niche partitioning (Solem, 1981; Cameron, 1992). Although shell characters are of limited utility for inferring relationships, they are still useful for the recognition of most species. Among species of *Amplirhagada*

there are two conspicuously different shell types. Many species have moderately flat and broadly conical shells (the “standard shape”) but some others have dome-shaped (or beehive-shaped) shells. Köhler (2010b) has shown that a least some of these species form a separate clade (*A. uwinensis* Köhler, 2010; *A. sphaeroidea* Köhler, 2010; *A. regia* Köhler, 2010; *A. camdenensis* Köhler, 2010) nested among other congeners. Species described here also differ in their shells with respect to shape, colour, and size (Table 1). With regard to adult shell height (H), they occupy ranges between about 10 and 22 mm (Fig. 49) with almost no overlap between the smaller (e.g., *A. moraniana*, *A. wilsoni*, *A. atlantis*) and the larger species (e.g., *A. coffea*, *A. lindsayae*). Even species of similar height may partly differ significantly in diameter (D), and thus also in their H/D ratio. This holds true, for example, for the species pairs *A. coffea*–*A. lindsayae*, *A. vialae*–*A. inusitata* or *A. discoidea*—all other species of similar height.

Besides shells and genitalia, radulae and jaws were considered rather useless for the differentiation of taxa at species level by Solem (1981), which is confirmed by the results of the present study. The radula was found to be highly conserved and therefore uninformative at the species and genus level.

Corresponding observations with regard to the significance of morphological characters in general were made in other Australian (Clark, 2009; Willan *et al.*, 2009; Köhler, 2010b, c, 2011), Asian (Chiba, 1999; Kameda, Kawakita & Kato, 2007; Chiba & Davison, 2008) and New Guinean Camaenidae (Jordaens *et al.*, 2009), respectively.

Patterns of distribution and lineage differentiation

The majority of *Amplirhagada* species are found exclusively in rainforest or vine thicket patches at more sheltered localities, which seems to indicate a strong correlation with this kind of habitat. Similar observations were made in most other camaenids in the Kimberley (Solem, 1991). As a result, species ranges are often very small; i.e., an average of 20 km in diameter (Solem & McKenzie, 1991). In accordance with this general statement, all but three species described herein were found only at one (or two very close) localities. Only *A. coffea* and *A. carinata* Solem, 1981 were found at localities that imply a larger distributional range. Other *Amplirhagada* species with larger distributions are *A. pusilla* Solem, 1981, *A. burnnerensis* (Smith, 1894), *A. osmondi* Solem, 1988, *A. napierana* Solem, 1981 and *A. percita* (Iredale, 1939) (Cameron, 1992; Solem, 1981). All these species are found in the semi-arid interior of southern and southeastern Kimberley, where they predominantly occur on limestone outcrops in more open woodland. These more inhospitable habitats differ considerably from the rainforest-type habitats of species that live in the rainfall-rich coastal regions of the NW Kimberley. Rainforest habitats may accommodate up to four sympatric *Amplirhagada* species plus a range of additional camaenids from other genera. In sympatry these species seem to occupy distinct ecological niches—a conclusion essentially based on differences in shell shapes and sizes (Solem, 1991).

Table 1. Shell measurements of the type series. Given are maximum–minimum (mean±standard deviation) of N measured adult shells. Abbreviations used: HT = holotype.

species	n	height (H)	diameter (D)	height of first whorl	number of whorls	H/D ratio
<i>A. atlantis</i>	19	10.5–13.4 (11.8±0.8)	14.8–18.7 (16.2±0.9)	6.6–8.4 (7.2±0.4)	4.0–5.0 (4.6±0.3)	0.65–0.81 (0.73±0.04)
	HT	12.8	18.7	8.4	5.0	0.68
<i>A. carsoniana</i>	20	8.7–10.7 (9.8±0.6)	15.0–18.0 (16.3±0.8)	5.3–6.9 (6.3±0.4)	4.5–5.0 (4.8±0.2)	0.53–0.69 (0.60±0.04)
	HT	8.8	16.1	6.5	5.0	0.55
<i>A. alicunda</i>	22	12.9–18.3 (16.0±1.4)	18.6–21.7 (20.2±0.7)	7.9–10.1 (9.0±0.5)	4.7–5.7 (5.2±0.2)	0.66–0.88 (0.79±0.05)
	HT	14.8	19.7	9.2	5.0	0.75
<i>A. moraniana</i>	21	8.6–13.8 (10.9±1.5)	14.2–19.4 (15.9±1.5)	5.8–8.3 (6.3±0.7)	3.5–5.5 (4.8±0.4)	0.59–0.77 (0.68±0.04)
	HT	9.5	15.1	6.7	5.0	0.63
<i>A. davidsoniana</i>	21	10.7–14.3 (13.1±0.8)	15.9–20.0 (18.3±0.9)	6.5–8.6 (7.6±0.5)	5.0–5.9 (5.4±0.3)	0.64–0.77 (0.72±0.03)
	HT	14.0	20.0	8.6	5.9	0.70
<i>A. vialae</i>	21	17.9–21.9 (17.1±1.8)	18.2–22.9 (19.8±1.0)	7.9–11.1 (9.1±0.7)	5.2–6.7 (5.8±0.4)	0.76–0.98 (0.86±0.06)
	HT	16.7	20.2	9.1	5.4	0.83
<i>A. discoidea</i>	21	11.2–13.8 (12.4±0.7)	19.3–22.5 (20.9±0.9)	6.9–8.2 (7.6±0.4)	5.1–5.9 (5.5±0.2)	0.55–0.64 (0.59±0.03)
	HT	13.3	22.5	8.2	5.2	0.59
<i>A. forrestiana</i>	22	9.8–13.2 (11.6±0.8)	17.0–21.1 (19.4±1.0)	6.3–8.2 (7.2±0.5)	5.0–6.1 (5.3±0.3)	0.55–0.64 (0.60±0.02)
	HT	12.0	20.3	7.1	6.1	0.59
<i>A. inusitata</i>	13	14.2–21.3 (16.8±1.7)	20.4–22.7 (21.4±0.7)	8.3–9.7 (8.9±0.4)	5.4–6.3 (5.7±0.3)	0.69–0.95 (0.79±0.07)
<i>A. coffea</i>	28	15.0–20.5 (17.9±1.6)	19.4–24.0 (21.4±1.1)	8.1–10.5 (9.3±0.6)	5.1–6.3 (5.8±0.3)	0.68–0.92 (0.84±0.05)
	HT	20.0	22.4	10.0	6.0	0.89
<i>A. gardneriana</i>	22	11.9–16.2 (14.2±1.2)	16.6–19.6 (18.0±0.7)	6.8–8.4 (7.6±0.4)	4.8–5.6 (5.4±0.2)	0.68–0.88 (0.79±0.05)
	HT	15.8	19.5	8.4	5.5	0.81
<i>A. lindsayae</i>	23	16.3–21.9 (18.3±1.3)	20.5–24.0 (22.4±0.8)	8.4–10.0 (9.2±0.4)	5.1–5.7 (5.4±0.2)	0.72–0.96 (0.81±0.05)
	HT	18.0	22.0	9.1	5.3	0.82
<i>A. bendraytoni</i>	13	10.6–16.6 (15.2±1.5)	18.1–23.1 (21.3±1.3)	8.2–12.0 (9.2±0.9)	5.0–6.0 (5.7±0.3)	0.59–0.78 (0.71±0.05)
	HT	15.4	21.7	9.0	6.0	0.71
<i>A. angustocauda</i>	5	10.0–13.4 (11.7±1.2)	14.7–16.6 (15.7±0.7)	6.2–7.1 (6.6±0.3)	5.0–5.6 (5.3±0.2)	0.67–0.81 (0.74±0.04)
<i>A. epiphallica</i>	9	12.5–15.0 (13.7±0.8)	19.2–21.4 (20.1±0.7)	7.6–8.1 (7.9±0.2)	5.6–6.0 (5.8±0.1)	0.63–0.75 (0.68±0.04)
	HT	13.7	21.4	7.6	6.0	0.64
<i>A. carinata</i>	63	8.3–14.0 (10.7±1.4)	14.8–19.1 (16.9±1.1)	5.6–8.6 (6.7±0.6)	4.5–6.1 (5.2±0.4)	0.51–0.76 (0.63±0.08)

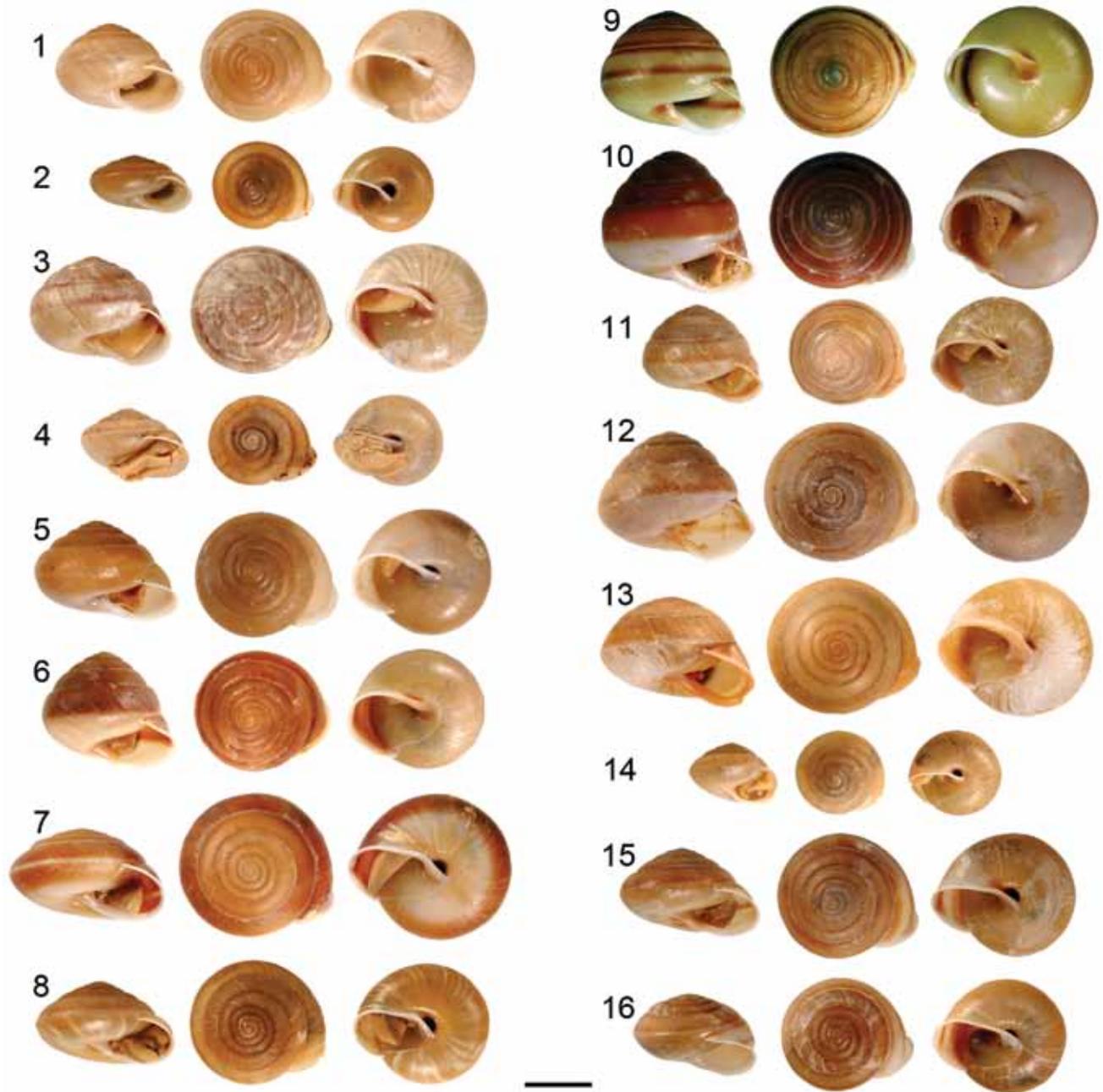


Plate 1. Shells of *Amplirhagada* species (from left to right viewed from side, above, and below). 1. Holotype of *A. atlantis* n.sp. WAM S34704. 2. Holotype of *A. carsoniana* n.sp. WAM S34707. 3. Holotype of *A. alicunda* n.sp. WAM S34710. 4. Holotype of *A. moraniana* n.sp. WAM S34713. 5. Holotype of *A. davidsoniana* n.sp. WAM S34716. 6. Holotype of *A. vialae* n.sp. WAM S34719. 7. Holotype of *A. discoidea* n.sp. WAM S34722. 8. Holotype of *A. forrestiana* WAM S34725. 9. Paratype of *A. inusitata* n.sp. AM C.472929. 10. Holotype of *A. coffea* n.sp. WAM S34731. 11. Holotype of *A. gardneriana* n.sp. WAM S34734. 12. Holotype of *A. lindsayae* n.sp. WAM S34737. 13. Holotype of *A. bendraytoni* n.sp. WAM S34740. 14. Paratype of *A. angustocauda* n.sp. FMNH 220650. 15. Holotype of *A. epiphallica* n.sp. WAM S34745. 16. Shell of *A. carinata* Solem, 1981 WAM S34759. Scale bar = 10 mm. Notice that soft bodies protrude from some shells.

By contrast, the open woodland/rock habitats in the drier interior support only one *Amplirhagada* species each. In these regions, *Amplirhagada* species with similar ecological adaptations replace each other on local scales, which was attributed to the lack of available ecological niches (Cameron, 1992). On the other hand, it has been shown that areas of exposed, layered rock can act as litho-refugia for the persistence of rainforest lineages in areas where rainforest is currently, or was historically, marginal

or absent (Couper & Hoskin, 2008). Rocks provide similar microclimatic conditions to rainforest, in being cool, moist, largely sheltered from fire and are stable and relatively buffered from short- and long-term climatic changes.

The species that are able to live in rocky landscapes outside of closed-canopy rainforests have generally larger distributions simply because the rocky ranges are spatially not as restricted as rainforest patches. These wider distributions in rather inhospitable landscapes provide

opportunities for differentiation along spatial gradients in concert with medium to long-termed climatic fluctuations, which may in the end lead to allopatric speciation (Cameron, 1992). Such processes are apparently responsible for the huge variation within *A. carinata* and other camaenid species from the drier interior of the Kimberley. Being apparently a more widespread phenomenon, they deserve the attention of future, more detailed studies.

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