CAMAENID LAND SNAILS FROM WESTERN AND CENTRAL AUSTRALIA (MOLLUSCA: PULMONATA: CAMAENIDAE)

II

TAXA FROM THE KIMBERLEY, *AMPLIRHAGADA* IREDALE, 1933

ALAN SOLEM*

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INTRODUCTION

This is the second report on the semi-arid zone dominant land snails of Western and central Australia, which belong to the Camaenidae, *sensu lato*. It reviews 28 species-level taxa in *Amplirhagada* Iredale, 1933, a genus apparently restricted to and undergoing extensive speciation in the Kimberley Region. Part I of this series (Solem, 1979) covered the genera with trans-Australian distributions (*Hadra* Albers, 1860; *Xanthomelon* von Martens, 1860; *Damochlora* Iredale, 1938; and *Torresitrachia* Iredale, 1939), plus related *Chloritis*-like genera from eastern Australia.

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LIST OF TAXA

SYSTEMATIC REVIEW

GENUS *AMPLIRHAGADA* IREDALE, 1933

Amplirhagada Iredale, 1933, Records Australian Mus., **19:** 52—type species *Helix (Hadra) sykesi* Smith, 1894 by original designation; Iredale, 1938, Australian Zool., **9** (2): 113-114—list of species; Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 65-68—monograph of genus.

Thetagada Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 63—nude name for *Rhagada astuta* Iredale, 1939.

Tenuigada Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 68—type species *Tenuigada percita* Iredale, 1939 by original designation.

Diagnosis

Shell generally medium in size, spire moderately to strongly and evenly elevated, occasionally dome-shaped, umbilicus narrowly open to completely closed by reflected lip, rarely with a closing callus. Apical sculpture of radially elongated pustulations, varying from fine **(Plate 14e)** to very coarse **(Plate 13d)**, sometimes **(Plate 14d)** coalesced into weak radial ribs. Postapical sculpture above periphery ranging from very weak radial growth lines **(Plate 14c)** to very sharply defined radial ribs **(Plate 12c)** or grossly broadened radial ribs **(Plate 12b)**. Shell base with incised spiral lines **(Plate 14f)** that extend onto spire when radial ribbing greatly reduced. Body whorl not **(Fig. 43f)** to sharply **(Fig. 67c)** deflected behind lip, which is usually sharply reflexed and expanded in adults, but occasionally only slightly expanded. Shell periphery evenly rounded to occasionally carinated **(Fig. 43a)**. Basal lip without to with a high tuberculate protrusion **(Fig. 59f)**, parietal wall with a thin callus. Shell colour variable, white in *A. napierana*, horn coloured in *A. percita* (Iredale, 1939), horn coloured with reddish markings in remaining species. Typically with both a subsutural and a supraperipheral spiral colour band, a small to extensive columellar colour patch in species with a closed umbilicus, and an individually variable reddish suffusion on the spire, some features lacking in some species. Genitalia with size of ovotestis seasonally variable, size and shape of hermaphroditic duct also correlated with activity stage, talon (GT) receiving hermaphroditic duct laterally except in *A. questroana* **(Fig. 40a)** where the insertion is almost terminal. Spermatheca (S) normally with expanded base, narrowed shaft and ovate head that lies just above vas deferens-free oviduct origin. Interior of spermatheca base and vagina (V) normally **(Fig. 64a)** with narrow corrugated pilasters and a ridged, highly expandable pad surrounding opening of free oviduct (UVO), altered **(Fig. 64b)** under conditions of sympatry. Length of free oviduct (UV) and vagina (V) variable among species. Penis complex with a thin, expandable sheath extending from slightly above atrium (Y) to insertion of penis retractor muscle (PR) onto vas deferens (VD). No epiphallus or caeca on male system. Vas deferens (VD) entering penis sheath from halfway up to near apex, usually folded in an S-loop to tightly coiled below insertion of vas deferens, except immediately after mating and for the next few days. Vas deferens entering penis through a short **(Fig. 57a)** to very long **(Figs 66a-b)** tubular to conical verge (PV) with terminal and usually simple pore. Tip of verge modified in two Napier Range taxa **(Figs 51b-c)**. Walls of penis chamber with basal ridges (PP) of variable length, pustules (PPR) on upper wall except in *A. elevata*, a main stimulatory pilaster (PT) surmounted by narrow to wide corrugations whose anterior edges are lined with a few to many sharp points **(Figs 36-37)**. Main pilaster secondarily greatly reduced **(Figs 36d-f)** under congeneric sympatry.

Type species: *Helix (Hadra) sykesi* Smith, 1894 by original designation.

Previous studies and nomenclature

Smith (1894) described a few specimens collected in the Napier Range by W.W. Froggatt before 1884 and by J.J. Walker, an officer on the survey ship *Penguin* during its charting of Montague Sound and the Admiralty Gulf in 1890 and 1891: *Amplirhagada sykesi* (Smith, 1894), *A. imitata* (Smith, 1894), *A. montalivetensis* (Smith, 1894), *A. burnerensis* (Smith, 1894), and *A. combeana* Iredale, 1938 (new name for *Helix imitata* var. *cassiniensis* Smith, 1894 not *Helix millepunctata* var. *cassiniensis* Smith, 1894) date from this study. Iredale (1933, 1938) provided a cryptic description of the genus and a few years later he published a list of species and the needed substitute name. The only major study, Iredale (1939), resulted in the proposal of several species names and two generic names. *Tenuigada* is a subjective synonym of *Amplirhagada* and *Thetagada* is a nude name for *A. astuta* (Iredale, 1939). Of the species proposed by Iredale, *Amplirhagada herbertena* Iredale, 1939, *A. novelta* Iredale, 1939, and *Rhagada astuta* Iredale, 1939 were based on single worn shells. Only the latter is represented in collections by additional specimens. *A. burrowsena* Iredale, 1939 is here considered to be a synonym of *A. imitata* (Smith, 1894); *A. terma* Iredale, 1939 is based on small examples from the type lot of *A. burnerensis burnerensis* (Smith, 1894); and *Tenuigada ignara* Iredale, 1939 is placed as a synonym of *A. percita* (Iredale, 1939), since both names were based on shells from the same lot.

Except for the above descriptions, no data has been recorded in the literature on either shell variation or anatomical structures.

Amplirhagada was well described by Iredalean standards. Although the type species has not been dissected, its close similarity to the Mitchell Plateau taxa leaves little doubt but that it is correctly referred to this genus. *Thetagada* Iredale (1939: 63) was not adequately diagnosed and is considered to be a nude name, since '...this species may prove very distinct, and in order to keep this point in view a new subgeneric name, *Thetagada,* with this *[Rhagada astuta]* as type, is introduced' hardly qualifies as a valid description. *Tenuigada* Iredale (1939: 68) was adequately described, but in anatomy is only slightly different **(Figs 51b-c)** from *A. napierana,* a nearly typical *Amplirhagada* in all but colour and shell sculpture. *Tenuigada* is thus a subjective synonym of *Amplirhagada.*

Distribution and basic ecology

Amplirhagada was not collected in the Ningbing Ranges, but has been found near El Questro Station south of Wyndham. The genus **(Fig. 73)** has been then found in the Drysdale River Reserve and near Kalumburu Mission. It then ranges south to Koolan Island, Harding Range, and Napier Range, but is absent from the Oscar Range and the many ranges between there and Halls Creek. Discussion of distribution and species identification has been presented after the species accounts because of the mosaic pattern of structural variation and rather extensive sympatry.

Throughout most of its range, *Amplirhagada* is rock associated, primarily talus situations, but species also aestivate in crevices of large boulders or on the roof and walls of caves. Many of the species seal themselves to rocks or other shells, but others such as *A. mitchelliana, A. castra,* and *A. carinata* are 'free sealers', lying at the soil surface under logs or rocks and secreting a recessed calcified epiphragm across the aperture. In the Napier Range, *A. percita* (Iredale, 1939), and *A. burnerensis* (Smith, 1894) at times occur abundantly in caves and crevices.

The most varied ecology involves the Mitchell Plateau taxa. *A. castra* and both races of *A. varia* are restricted to vine thickets, *A. alta crystalla* is large boulder and tree associated near Crystal Creek, *A. confusa* is a large boulder and rock crevice or talus pile species in slightly more sheltered niches than *A. mitchelliana,* which often occurs in the same rock piles (but with a different aestivation pattern), but also is found under logs and small rocks on more open slopes than the usual habitat of *A. confusa*. The latter two species frequently are microsympatric. They occur up to the margins of the vine thickets, but only dead and bleached (washed in?) shells of them have been collected inside the vine thickets. Only a few specimens of *A. varia* have been collected outside of vine thickets, and *A. castra* has been found within only two vine thickets. They are thus micro-allopatric with the more widely distributed taxa.

In the Napier Range, the three endemic *Amplirhagada* were observed feeding by Carl Christensen and Laurie Price. Sixteen individuals were feeding on flowers, dead leaves and twigs, one juvenile was found apparently browsing on algae, and one individual scraping on a macroscopically barren rock. They thus appear to be feeding primarily on dead plant matter, quite in contrast with the *Westraltrachia* series, which are algal-fungal feeders. More detailed reports will be given elsewhere (Solem & Christensen, in preparation).

Patterns of shell variation

Amplirhagada is in a stage of extensive speciation. While most species found in one locality are easily recognizable by shell features, there are many similarities among allopatric populations, and in a number of situations reference to the soft parts is necessary for certain identification. There are few clearly linear trends or geographically limited variations. Instead, there are mostly mosaic patterns and few clear correlations between variations. For many features, the variation range is almost continuous, and, in the case of shell sculpture, almost impossible to characterize verbally.

Size and shape of shell—The total range in shell diameter for adult *Amplirhagada* is 11.5 to 25.55 mm. For individual species, of course, the size range is much less. Taxa for which 19 or more adult shells could be measured, have had the range of diameter calculated as a percentage of the minimum diameter **(Table 11)**. The remaining nine taxa show an artificially reduced range caused by the low number of observations. In **Table 11,** the low percentage ranges for *A. alta* and *A. elevata* probably are caused by their dome-shaped spires, since this growth pattern effectively reduces the extent of variation in shell diameter. The taxa have been grouped geographically. The greater variability of the Napier Range taxa probably reflects the greater annual variation in rainfall at this southern limit of distribution. The near identity in variability for the several Mitchell Plateau species is somewhat sur-

Table 11: Adult Size Variability in *Amplirhagada*

	Number of Adults	Diameter Range		Number of Adults	Diameter Range
Inland Taxa			Mitchell Plateau		
drysdaleana	19	35.0%	*mitchelliana*	561	46.8%
pusilla	59	39.8%	*confusa*	375	45.4%
carinata	60	25.7%	*castra*	150	39.1%
elevata	31	18.7%	*varia varia*	703	49.3%
wilsoni	76	35.5%	*v. depressa*	34	46.1%
Napier Range			Island Taxa		
percita	934	77.4%	*katerana*	30	30.2%
napierana	1,261	66.8%	*alta crystalla*	34	23.5%
burnerensis burnerensis	1,371	56.1%	*a. intermedia*	21	9.0%
			imitata	139	35.2%
b. umbilicata	628	54.7%	*combeana*	108	32.7%

prising. *A. mitchelliana* has an essentially continuous distribution in the open forests, and is more exposed to local vagaries in moisture supply. *A. confusa* tends to a clumped, and more sheltered, habitat in rock piles or cracks in large boulders, while *A. castra* and *A. varia* are restricted essentially to the densely vegetated vine thickets. While there are distinct size differences among populations from different vine thickets (see **Tables 29, 30**), the uniform total range of variation for these species may reflect common and recent ancestry, since the vine thickets may be a phenomenon of the last 15,000 years. The range of variation in the Mitchell Plateau taxa is only slightly greater than for either the Inland or Island taxa, if the effect of dome-shaped spire (*A. elevata* and *A. alta*) is discounted. The very depressed and acutely carinated *A. carinata* also has a lessened size range.

This very consistent size range in *Amplirhagada* contrasts rather markedly with the variation recorded for *Xanthomelon* and *Torresitrachia* (Solem, 1979: 57), where both greater and lesser diameter variations are found.

The total range of adult shell height is 7.3 to 22.7 mm, with 14 species showing 10% or more greater variability than in diameter, only two species (*A. drysdaleana* and *A. wilsoni*) with less, and three species (*A. napierana, A. mitchelliana, A. castra*) having essentially the same range of variation. The three most variable species, *A. percita* (Iredale, 1939) (98.6%), *A. burnerensis umbilicata* (93.8%) and *A. varia varia* (83.2%), greatly exceed in range the remaining Napier Range and Mitchell Plateau taxa (41.9% to 66.7%). Only *A. imitata* (Smith, 1894), which shows spire elevation differences from island to island **(Table 33)**, approaches (63.9%) this degree of variability. Most of the remaining taxa cluster in the 25-50% range.

The H/D ratio is affected by the degree of spire elevation, whorl count, doming effect or its absence, tightness of whorl coiling, and slightly by the degree of lip flaring. Thus the few species with a very high mean whorl count (6¾ or more), have a mean H/D ratio of 0.796-0.953 (*A. elevata, A. alta crystalla, A. a. intermedia*). The smaller *A. v. varia, A. confusa,* and *A. sykesi* (Smith, 1894) reach equivalent mean H/D ratios (0.804-0.847) with a lower whorl count (6⅛ to 6½). Otherwise there seem to be no clear trends in H/D ratio variation.

Body whorl contour ranges from evenly rounded to sharply angulated, with juveniles of most taxa showing sharply angulated peripheries. Thus smaller examples of species such as *A. varia* and *A. burnerensis* may show a faint angulation to the periphery, although most examples will have an evenly rounded body whorl. Species such as *A. wilsoni* **(Fig. 56)** and *A. kalumburuana* are truly variable in contour, but most have a rounded periphery. *A. pusilla, A. drysdaleana, A. katerana, A. herbertena* Iredale, 1939, and the very strongly angulated taxa *A. astuta* (Iredale, 1939) and *A. carinata* depart furthest in the direction of carination.

Mean whorl count varies considerably, correlating reasonably well with shell height and shell diameter **(Table 12)**. Increased peripheral angulation (*A. carinata* and *A. astuta*), unusual spire depression (*A. varia depressa*), and unusual single specimens (*A. novelta, A. herbertena*) are the reasons for the few departures from a normal incremental pattern. The total range in adult whorl count is greatest in the Napier Range taxa (1⅜ to 2¼), which also show the greatest range in height and diameter, followed by the Mitchell Plateau taxa, *A. imitata* and *A. katerana* (1⅛ to 1⅝). Most of the other taxa, where more than a dozen adults were studied, show a range of ⅝ to ⅞ whorls.

Umbilical features—Nine species of *Amplirhagada* have a narrowly open umbilicus that is wide enough to measure and then calculate a D/U ratio. The total range of umbilical width in these taxa is 0.3-3.1 mm. Partial closure of their umbilici is effected by reflexion of the lip. The extent of such closure varies widely **(Figs 38b, d, f)**, but at least a slight measurable opening remains. In juveniles of all species, the umbilicus is completely open. Three of the umbilicated taxa are from offshore islands, *A. herbertena* Iredale, 1939, *A. astuta* (Iredale, 1939) and *A. montalivetensis* (Smith, 1894). The others are from inland areas, *A. questroana, A. drysdaleana, A. pusilla, A. carinata,* plus *A. percita* (Iredale, 1939) and *A. burnerensis umbilicata* from the Napier Range. *A. katerana* and *A. kalumburuana* **(Fig. 43d)** have a slight to no opening, and most other species retain a weak lateral crack **(Fig. 70f)** or have a hair-line crevice visible **(Fig. 70c)**. In the latter situation, or even when this crevice is completely absent, the animal has not completely closed the crevice by extending a shell layer fully onto the outer shell surface from the lip. This is thus an incompletely closed umbilicus, even when the opening is essentially shut. The only exception to

Table 12: Whorl count and size correlation in *Amplirhagada*

Mean Whorl Counts:	5 ⅜-5 ⅝			5¾-6¼	
Taxon	$\bar{x}$ Height in mm	$\bar{x}$ Diameter in mm	Taxon	$\bar{x}$ Height in mm	$\bar{x}$ Diameter in mm
drysdaleana	10.51	16.73	*questroana*	13.21	20.02
pusilla	9.93	16.73	*kalumburuana*	12.84	18.19
carinata	11.54	19.98[1]	*napierana*	13.41	18.71
astuta	11.68	19.45[1]	*b. burnerensis*	13.12	18.65
percita	10.90	17.15	*castra*	13.65	18.09
burnerensis umbilicata	10.25	16.75	*varia varia*	13.98	17.32
			v. depressa	11.07	16.27
			montalivetensis	14.27	20.39
			imitata	14.74	18.97
			novelta	16.80	21.50
Mean Whorl Counts:	6 ⅜-6½			6¾-7¼	
katerana	15.27	21.56	*elevata*	16.54	20.77
wilsoni	15.09	21.57	*a. crystalla*	20.64	22.67
alta alta	15.43	20.06	*a. intermedia*	19.31	22.05
confusa	16.44	20.10	*alta* subsp.	20.40	22.00
sykesi	17.44	20.56	*mitchelliana*	16.09	21.98
herbertena	15.80	21.20			

[1]Diameter increased by depressed spire and peripheral carination.

this is *A. novelta* Iredale, 1939 **(Fig. 72c)**, in which the umbilical area has been covered by a complete callus. Whether this is the result of repaired injuries to the shell, or indicates that the single very worn specimen actually belongs to another genus is unknown. Without collection of additional materials, its status will be uncertain.

Aperture and lip features—In general the differences shown in this area of the shell are rather subtle. Descension of the body whorl behind the lip ranges from not at all in some carinated species **(Fig. 43f)**, very slight and gradually in others **(Figs 43a, c)** and then through almost insensible gradations to the abruptly deflected pattern seen in *A. varia depressa* **(Fig. 67c)**. In some sympatric species pairs the differences are quite noticeable. *A. confusa* **(Fig. 55a)** has much sharper body whorl descension than does *A. mitchelliana* **(Fig. 55c)**, while *A. elevata* **(Fig. 55f)**, the higher spired of the other species pair, has much less descension than does *A. wilsoni* **(Fig. 55e)**. The differences partly correlate with the degree of peripheral carination.

For simple physical factors, it is more difficult to attach below an angulation than on a rounded surface. The tendency of angulated or carinated taxa to have little or no body whorl descension probably relates to simple growth limitations.

Expansion of the lip varies both within and among species. Such taxa as *A. burnerensis burnerensis* **(Figs 48c-d)** have a very narrowly expanded lip, in great contrast to the situation seen in more typical species such as *A. carinata* **(Fig. 43a)**. The least lip expansion is shown by *A. burnerensis umbilicata* **(Fig. 49h)**. Because the lip varies in width from upper palatal margin to basal region, sometimes there is weak thickening of the lip internally, and the basal lip protrusion is highly variable, I did not quantify the lip differences. The intraspecific variation was large enough that I suspect any species differences would be masked in most instances.

The presence of a basal lip protrusion reaches its highest degree of development in *A. alta* subsp. from Wollaston Island **(Fig. 59f)**, where it is a very high tubercle. The other races of *A. alta* **(Figs 59a-e)** have a moderately prominent to quite prominent protrusion. *A. sykesi* (Smith, 1894) **(Fig. 70b)**, *A. katerana* **(Figs 43e-f)**, and *A. combeana* Iredale, 1938 **(Fig. 71h)** have a weak or no basal lip protrusion, the Napier Range and Prince Regent River Reserve taxa, *A. drysdaleana, A. questroana,* and *A. astuta* (Iredale, 1939) lack the protrusion, while in the Mitchell Plateau, Admiralty Gulf, Montague Sound and Buccaneer Archipelago taxa it is moderately to strongly developed. Its expression comes in the final phase of adult shell growth, so that in materials collected at the end of the wet season, it can be much smaller in newly adult examples. There is moderate intraspecific variation, so that although *A. confusa* generally has a stronger basal lip protrusion than does the sympatric *A. mitchelliana* **(Figs 55a-b)**, the difference is not constant. The function of this structure is unknown.

Shell colour—**Table 13** summarizes the variation in shell colour patterns on a 'presence or absence' basis. In this table, a '+' means present, a '–' means absent, and '( )' means a rare to infrequent condition. Where a colour pattern is reduced in prominence, this has been mentioned under the particular species, but this is a somewhat subjective feature. There are four basic additions to the ground colour scheme: two spiral bands, a columellar colour patch of variable extent, and an added colour suffusion on the spire that may extend down to the body whorl. The supraperipheral colour band is reddish to dark orange, narrow to wide, but almost always clearly visible just above the suture of the succeeding whorl. Just below the suture, a narrow band of white separates the suture from the subsutural colour band, also red or orange-red in tone, and equally variable in width. On many figures of shells viewed from the side, these bands have been indicated by dotted lines. The supraperipheral colour band is absent only in the Napier Range taxa and in some specimens of *A. drysdaleana*. The subsutural colour band also is absent in the Napier Range taxa. *A. kalumburuana,* sometimes in *A. castra, A. carinata* and *A. drysdaleana,* and normally absent in *A. katerana*. At times the periphery of some light coloured shells may show a translucent whitish colour zone, but generally this is seen in faded, worn examples and may be only a remnant of a colour zone.

Table 13: Patterns of Color Variation in *Amplirhagada*

Taxon	Supraperipheral Band	Subsutural Band	Columellar Patch	Spire Suffusion
drysdaleana	+ to −	+ to −	−	−
questroana	+	+	−	+
pusilla	+	+	−	−
katerana	+	(+) to −	(+) to −	+
kalumburuana	+	−	−	+
carinata	+	+ to −	−	(+) to −
astuta	+	+	−	−
percita	−	−	−	−
napierana	−	−	−	−
burnerensis burnerensis	−	−	+	−
b. umbilicata	−	−	+	−
elevata	+	+	+	+
wilsoni	+	+	+ to (−)	(+) to −
alta alta	+	+	+	+
a. crystalla	+	+	+	+
a. intermedia	+	+	+	+
mitchelliana	+	+	+	+
confusa	+	+	+	+
castra	+	+ to −	(+) to −	+
varia varia	+	+	+	+
v. depressa	+	+	+	(+) to −
sykesi	+	+	+	(+) to −
montalivetensis	+	+	+	−
imitata	+	+	+	+ to (−)
combeana	+	+	+ to −	−

The reddish columellar colour patch is highly variable, when present, and also variable in its presence or absence. The umbilicated taxa, except *A. montalivetensis* (Smith, 1894) lack the patch, as do *A. kalumburuana,* and *A. napierana.* It is rarely absent in *A. wilsoni,* rarely present in *A. castra* and *A. katerana,* and variable in *A. combeana* Iredale, 1938. All other species have it strongly developed. It may be restricted to the rim of the umbilicus, or extend partly onto the basal lip and parietal wall. In *A. burnerensis* it is very strongly developed, extending not only onto the basal lip, but along and behind the lip, then up to the suture and for a variable distance along the suture on the body whorl. This latter phenomenon could be interpreted as a remnant of the subsutural colour band, but its ontogeny is uncertain.

Absence of the colour patch in the umbilicated taxa may be a primitive condition, but its loss in taxa with a closed umblicus probably is secondary.

The addition of colour to the spire can occur in at least two ways: by extension of the supraperipheral band upwards to the suture, or by adding colour that diminishes from the suture toward the periphery by extending the subsutural colour band. In cases of very dark spires, it is impossible to say which alternative has been followed. Both are lumped under the heading of spire suffusion. This is rarely present in *A. carinata, A. wilsoni, A. varia depressa,* and *A. sykesi* (Smith, 1894), absent in the Napier Range taxa, *A. drysdaleana, A. pusilla, A. astuta* (Iredale, 1939), and *A. combeana* Iredale, 1938, rarely absent in *A. imitata* (Smith, 1894), and strongly developed in the other taxa. At times the spire suffusion, particularly in some examples of *A. castra,* will be much darker than and overwhelm the spiral bands, approaching a reddish-purple in tone.

At the other extreme, a few individuals of *A. mitchelliana* were collected in which all colour had been lost from the shells. The animals retained normal pigmentation, so that true albinism is not involved.

Shell sculpture—There are three basic sculptural elements that show mainly qualitative differences among the species of *Amplirhagada:* an apical sculpture of radially elongated pustulations; postapical radial ribs or growth lines that are present only above the periphery; and incised spiral lines that always can be seen on the shell base and that may be detectable on the spire when the radial elements are greatly reduced. SEM photographs from an essentially vertical angle **(Plates 12-14)** give an indication of the sculptural variety, and will help in many cases to discriminate between species. The differences in the radial elements are quite subtle, differential surface wear among specimens frequently confuses the situation, and moderate intraspecific variation does exist. Thus shell sculpture is not a feature that can be used in key construction.

The apical sculpture, in all species for which unworn material could be examined, consisted of radially elongated pustulations. They range in prominence from the very fine and crowded pustulations found in *A. percita* (Iredale, 1939) **(Plate 14e)** to the very coarse pustules seen in *A. castra* **(Plate 13d)**, *A. carinata* **(Plate 13e)**, and *A. varia* **(Plate 13c)**. In some individuals, such as the figured example of *A. napierana* **(Plate 14d)**, the pustulations partly coalesce into weak radial ridges. There may be a correlation between the fineness of the apical pustulations and the degree of reduction in the radial ribbing, but only worn material of those species with strong radial ribbing was available for SEM analysis and their apical sculpture could not be studied. This pattern of apical sculpture is quite distinctive from that seen in *Torresitrachia* and *Damochlora* (Solem, 1979: Plates 2-4, 8).

The radial ribbing shows a nearly continuous series of changes from the sharply defined ribs in *A. pusilla* **(Plate 12c)** to the nearly smooth surface of *A. burnerensis umbilicata* **(Plate 14c)**. The change is not a linear sequence, since the enlarged, rounded ribs of *A. imitata* (Smith, 1894) **(Plate 12a)** and *A. combeana* Iredale, 1938

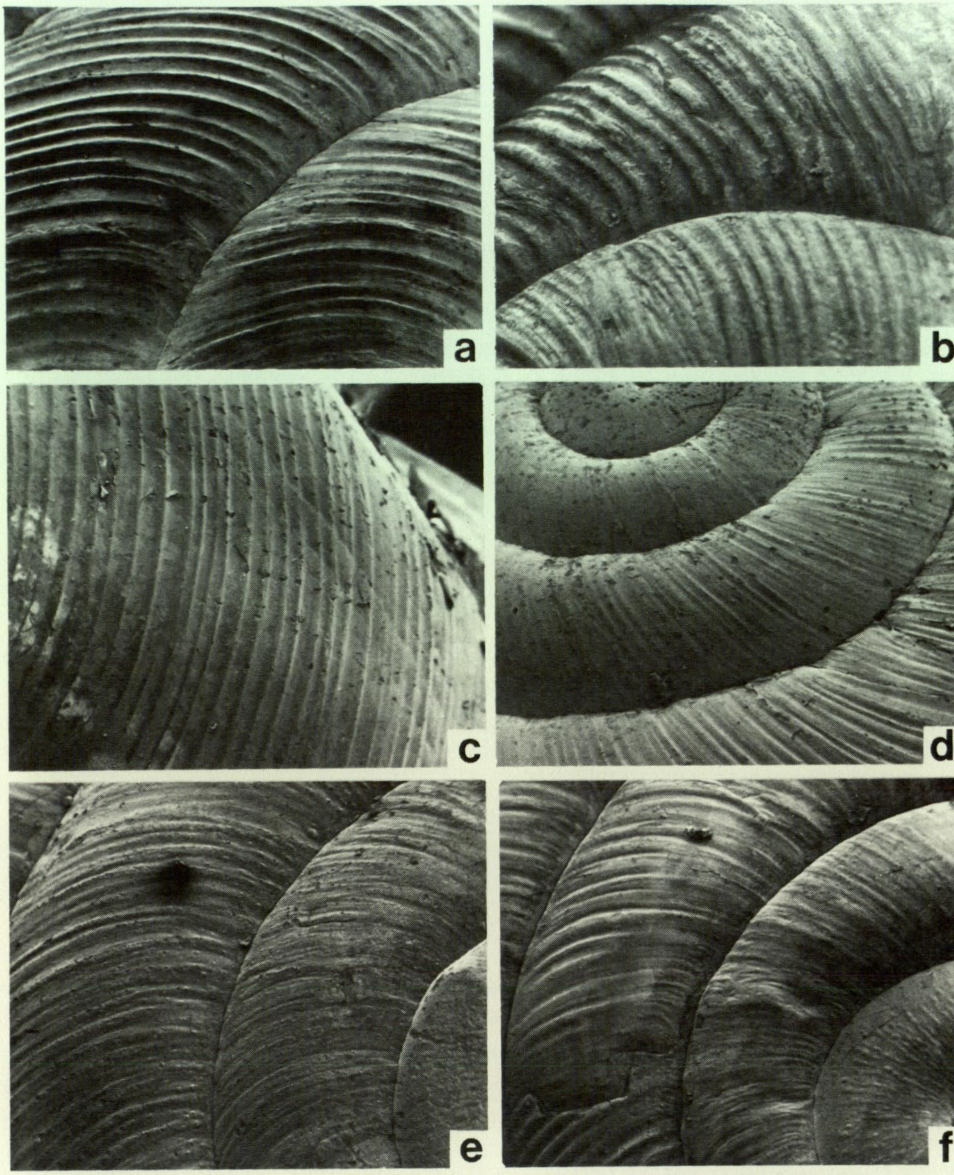


Plate 12: Shell sculpture in *Amplirhagada,* a) *A. imitata* (Smith, 1894), FMNH 41588, Baudin Id., Admiralty Gulf, 3rd and 4th whorls at 21X; b) *A. combeana* Iredale, 1938, FMNH 200825, Cassini Id., Admiralty Gulf, 3rd and 4th whorls at 21X; c) *A. pusilla,* WAM 628.77, Pitta Creek, Prince Regent River Reserve, body whorl behind lip at 21X; d) *A. drysdaleana,* WAM 627.77, Sta. B1-7, Drysdale River National Park, apex and spire at 16.5X; e) *A. questroana,* WAM 607.77, Sta. WA-222, El Questro Station, apex and spire at 21X; f) *A. kalumburuana,* WAM 617.77, Sta. WA-220, Kalumburu Mission, apex and spire at 21X.

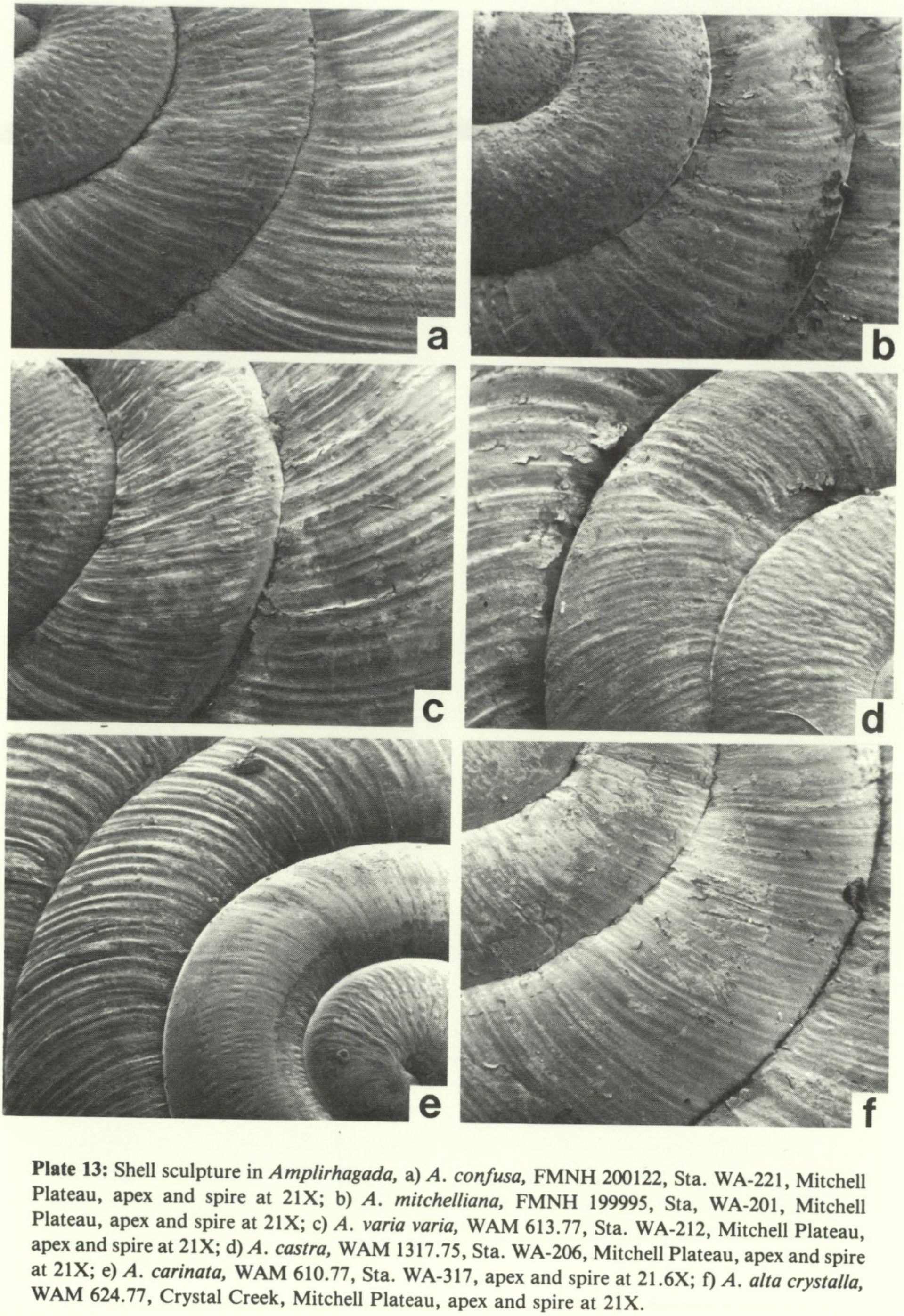


Plate 13: Shell sculpture in *Amplirhagada,* a) *A. confusa,* FMNH 200122, Sta. WA-221, Mitchell Plateau, apex and spire at 21X; b) *A. mitchelliana,* FMNH 199995, Sta, WA-201, Mitchell Plateau, apex and spire at 21X; c) *A. varia varia,* WAM 613.77, Sta. WA-212, Mitchell Plateau, apex and spire at 21X; d) *A. castra,* WAM 1317.75, Sta. WA-206, Mitchell Plateau, apex and spire at 21X; e) *A. carinata,* WAM 610.77, Sta. WA-317, apex and spire at 21.6X; f) *A. alta crystalla,* WAM 624.77, Crystal Creek, Mitchell Plateau, apex and spire at 21X.

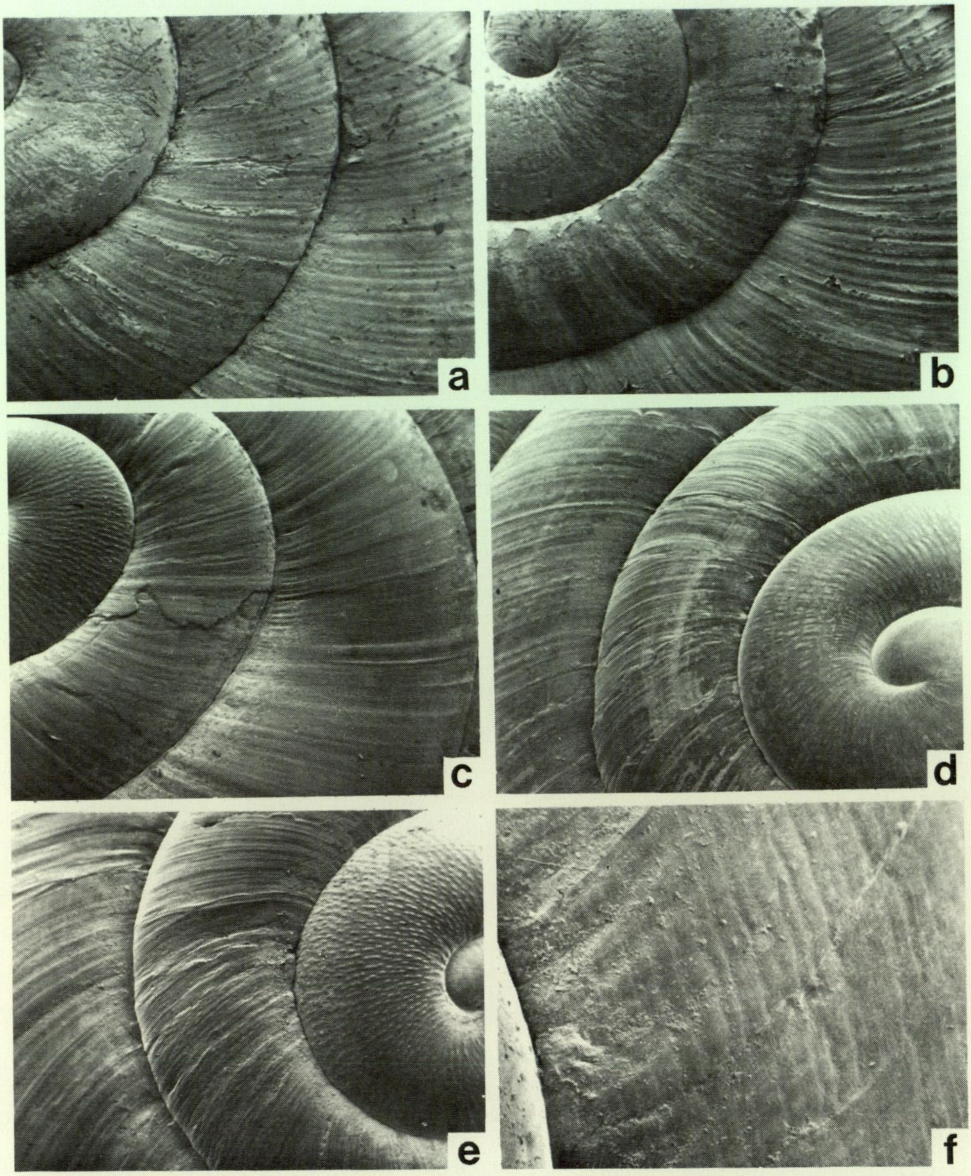


Plate 14: Shell sculpture in *Amplirhagada,* a) *A. elevata,* WAM 623.77, Sta. W6 (1), Prince Regent River Reserve, apex and spire at 21X; b) *A. wilsoni,* WAM 622.77, Sta. E5 (7), Prince Regent River Reserve, apex and spire at 21X; c) *A. burnerensis umbilicata,* FMNH 199446, Sta. WA-198, Napier Range, apex and spire at 21.8X; d) *A. napierana,* FMNH 199862, Sta. WA-192, Napier Range, apex and spire at 21X; e-f) *A. percita* (Iredale, 1939), FMNH 199401, Sta. WA-199, Napier Range, e is apex and spire at 20.5X, f is body whorl showing incised spiral lines at 45X.

(Plate 12b) can be derived by intensification and broadening of the basic type, while such taxa as *A. astuta* (Iredale, 1939), *A. drysdaleana* **(Plate 12d)**, *A. questroana* **(Plate 12e)**, *A. kalumburuana* **(Plate 12f)**, and *A. carinata* **(Plate 13e)** show a lower, less regular sculpture that can be interpreted as a result of size reduction and broadening of the basic rib pattern. A greater degree of irregularity, but generally greater prominence, is seen in *A. castra* **(Plate 13d)** and *A. varia* **(Plate 13c)**. Two species pairs, that in size are almost identical to each other, show an interesting pattern of heavier sculpture in one than in their sympater. *A. elevata* **(Plate 14a)** has much less prominent sculpture, but is much higher spired, than *A. wilsoni* **(Plate 14b)** from the same part of the Prince Regent River Reserve. On the Mitchell Plateau, the high spired *A. confusa* **(Plate 13a)** has noticeably heavier sculpture than the sympatric *A. mitchelliana* **(Plate 13b)**. There is an equivalent degree of sculptural difference between the species pairs, but the sculpture change does not correlate with shell shape or with any pattern of change in species recognition features of the genitalia.

The several Napier Range taxa, *A. burnerensis umbilicata* **(Plate 14c)**, *A. napierana* **(Plate 14d)** and *A. percita* (Iredale, 1939) **(Plate 14e)** plus the Admiralty Gulf *A. sykesi* (Smith, 1894), have the most reduced radial sculpture in the genus, with the radial element represented essentially by irregular growth wrinkles.

The spiral incised lines can be viewed optically at 15-50x magnification, but proved surprisingly hard to photograph **(Plate 14f)**. Most fresh examples show these lines on the shell base and up to the periphery. In the taxa with prominent radial sculpture above the periphery, they rarely can be detected. As the radial sculpture is reduced, the incised lines become more conspicuous above the periphery. In *A. sykesi* (Smith, 1894) and the Napier Range taxa, the spiral incised lines are predominant on the spire.

A general pattern of either intensification or reduction from the well defined rib seen in *A. pusilla* probably is an accurate depiction of the directions of character change in radial sculpture. The incised spiral lines become visible on the spire when the radials are reduced, and thus are interpreted as an additive element that normally is masked by the radial ribs.

Pattern of anatomical variation

Comments here are restricted to those features that show variation within the genus or are diagnostic of *Amplirhagada* in relation to other Western Australian camaenids. External body features, pallial organ features, and observations on the muscle system will be discussed in a general review.

Radula and jaw—Depending on the availability of preserved material, from one to five buccal masses of each species were treated with KOH, the dissected out radula and jaw cleaned with a sonic cleaner, and then mounted and prepared for SEM observation using the technique outlined by Solem (1972). Each mounted specimen was examined with a Cambridge S4-10 Stereoscan at Field Museum of

Natural History. Photographs were taken of at least one example for each species. The gross structure of the jaw, shape, number and spacing of its vertical ribs differed within populations so extensively that any differences between species were masked. The jaw structure seems to be standard in the Western Australian camaenids and thus no illustrations or discussions are presented here.

The radular observations were equally unproductive in finding species differences within *Amplirhagada.*

Genitalia—Necessary preliminaries to discussion of structural variation in the genital organs are surveys of microsympatry and seasonal variation in genitalia.

Of the 28 species level taxa in *Amplirhagada,* it was possible to at least partially dissect and illustrate 19. For nine of these, only single collections or collections made within a few days of each other were available; for five taxa I had collections made in two or three different months; and for five taxa, mainly from the Napier Range, I had collections made in four to seven different months. The dates of collection for dissected materials of *Amplirhagada* are summarized in **Table 14**. The most complete monthly coverage was for *A. burnerensis burnerensis.* Thus, the hypothesized basic reproductive sequence in the genus is based initially on the data from this species as summarized in **Fig. 53** and that species discussion. Data from the other species are fully consistent with the outlined events, differing only in the timing associated with the north-south gradient in normal start of the wet season.

Microsympatry involves immediate problems of species recognition by the snails. Mating in the Western Australian camaenids apparently is very quick, with the snails touching heads, immediately aligning the right sides of their heads together, with extrusion and insertion of the penis followed by mutual exchange of sperm masses. The whole process occurs in less than ten minutes. This has been seen in four genera so far. Mating in *Amplirhagada napierana* was observed by Christensen and Price at Sta. WA-325 on 4 and 12 January 1977. The 'snails appeared to run into each other, then touch heads a couple of times, and press the right sides of their heads together. Copulations lasted less than five minutes from initial contact to spontaneous separation' (field notes by Christensen, 4 January 1977). Dissection of the four individuals from two mating pairs (FMNH 200245), which were directly preserved in alcohol after spontaneous separation in the field, showed that mating was reciprocal. Fresh sperm masses were situated at the base of the spermathecal stalk in each individual. The shape of the sperm mass was the same as in *A. burnerensis burnerensis* **(Fig. 52e)**. All four individuals were fully adult in genitalia.

This quickness of mating effectively rules out species recognition by courtship rituals. The structural variation found in the penis chamber, particularly the main pilaster **(Figs 36-37)**, and lower female tract **(Fig. 64)** provides species recognition features for the snails. As would be expected, such differences are greater in cases of sympatric than allopatric species. Thus an understanding of the extent and nature of sympatry in *Amplirhagada* must be part of this review of genital variation.

Table 14: Dates of collection for Dissected *Amplirhagada*

Taxon	Jan	Feb	Mar	Ap	May	June	July	Aug	Sep	Oct	Nov	Dec
alta alta								1976				
a. crystalla			1977								1976	
b. burnerensis	1977	1977	1977		1977		1966			1976		1976
b. umbilicata	1977	1977										1976
carinata	1977	1977										1976
castra			1977			1975		1975		1976		
confusa			1977							1976		
drysdaleana								1975				
elevata								1974				
kalumburuana										1976		
katerana						1972						
mitchelliana	1973		1977					1976		1976		
napierana	1977	1977	1977		1977					1976		1976
percita	1977	1977	1977		1977					1976		1976
pusilla								1974				
questroana											1976	
v. depressa										1976	1976	
v. varia			1977							1976		
wilsoni								1974				

Fifteen of the 28 *Amplirhagada* are without congeneric sympaters; 13 are known to occur either microsympatrically or have very narrow zones of contact between taxa. All of these taxa have been dissected. The type of sympatry varies from area to area. In the Napier Range, *A. percita* (Iredale, 1939) and *A. napierana* have interdigitating but separate distributions with transition zones of 100 metres or less showing some indication of hybridization, while across Yammera Gap, *A. b. burnerensis* (Smith, 1894) and *A. b. umbilicata* have similar interdigitating occurences along the narrow range. In the Prince Regent River Reserve, *A. elevata* and *A. wilsoni* were taken at Sta. W6 (2) and W6 (5), *A. elevata* and *A. pusilla* at Sta. W6 (1). No data is available on their comparative ecology. In the vicinity of the Mitchell Plateau, a more complex pattern occurs. *A. mitchelliana* is the most widely distributed species, occurring sporadically in open woodlands and aestivating under medium sized boulders or large logs. In more sheltered and more densely vegetated ravines with large boulders by creek sides or in shallow rock talus on the floor of ravines, it occurs microsympatrically with *A. confusa. A. mitchelliana* lies free in the soil with an epiphragm across the aperture, while *A. confusa* seals to a rock or another shell. *A. confusa* at times occurs in immense numbers in this more restricted habitat. Neither species has been found living within the unusual vine thickets. *A. varia varia, A. v. depressa,* and *A. castra* almost always are confined to the isolated patches of vine thickets. Each population shows a slightly different average shell morphology. Live examples of the vine thicket and non-vine thicket taxa have been taken within five feet of each other, but not actually microsympatrically. *A. alta crystalla* occurs within the known range of *A. mitchelliana,* but the two taxa have not been found together yet. While shelter site selection, aestivating mechanism, and habitat preference differ among the species, normal microsympatric occurrence and chance mixing during the flash-floods of the wet season are inevitable on the Mitchell Plateau. Thus the several species of *Amplirhagada* found there have need for the clear differences in species recognition features found in the terminal genitalia.

The basic life history pattern, based on dissections and measurements of juveniles, dissection of barely mature adult snails from late wet season samples, and study of the seasonal samples taken for the Napier Range. *Amplirhagada,* is for crawling young to appear about a month after observed matings. They reach approximately half-size by the end of their first wet season. In the second wet season the shell reaches adult size and develops a reflected and thickened lip, the male organs reach full size, but the ovotestis, albumen gland and prostrate-uterus remain underdeveloped. Thus, at the start of their third wet season, the animal is presumed to be male active only. Individuals from October samples were common with enlarged ovotestis and prostate but with the albumen gland and uterus the same size as in February and March specimens whose shells were barely adult. I have no data as to whether these specimens become female active late in the third wet season, or if they are only male active that year with the albumen gland growing to functioning size during the third wet season. I consider that the latter option is more probable, and that there is a four year maturation process in at least the Napier Range and Mitchell Plateau *Amplirhagada.* Their length of life after reaching full sexual maturity is unknown. The pattern is different in some taxa from the Eastern States as reported by McLauchlan (1951). In *Meridolum,* and by implication other taxa, matings involve an older female phase animal and a younger (less than two years) male phase animal. Adult female state is reached in two years and maximum age of at least five years is obtained by some individuals.

Fully mature specimens, defined as examples with adult shell features and full sized albumen glands, show a clear and simple pattern of seasonality in the genitalia. In the early and middle parts of the dry season, the genitalia are inactive and occupy a considerably reduced portion of the body volume. The ovotestis **(Fig. 53)** is minute in size with tiny lobes, whereas the digestive gland is packed with granules and tissue. The hermaphroditic duct is extremely slender and varies from almost totally uncoiled **(Fig 53,** 3-VII) to a waved pattern (**Fig. 53,** 14-V). Both prostate and uterus are slender and noticeably narrower than at other seasons. The spermathecal head will have relatively loose masses of tissue occupying the space, and the vas deferens usually will be tightly coiled up against the head of the penis **(Fig. 53).** If the specimens are accidentally activated for a few hours before drowning and preservation, the uncoiled pattern of the vas deferens can be found, probably as a result of a mating attempt. The albumen gland does not reduce in length or apparent volume.

Shortly before the normal start of the wet season, a series of changes occur. The ovotestis swells dramatically, occupying a large portion of the upper whorls, the vas deferens thickens slightly and becomes much more tightly kinked, and the prostate enlarges greatly. The situation in snails that had not been activated yet by rain is shown by *A. mitchelliana* **(Fig. 62a)** and *A. castra* **(Fig. 63a)**. The situation in activated snails that have just mated is shown in *A. kalumburuana* **(Fig. 44a)**, and *A. burnerensis burnerensis* (Smith, 1894) **(Figs 52a, 53** on 5 December). Here the hermaphroditic duct is noticeably thicker than in the non-activated examples and there is a marked swelling to the upper portion of the vagina and lower part of the spermatheca, indicating the presence of a sperm mass. The timing of this change varies with the area and correlates with the normal start of the wet season. Thus, the Napier Range material from October is still in dry season condition, since the rains do not normally come until late in November or early December, whereas the Mitchell Plateau and Kalumburu examples are activated by mid-October, which correlates with the normal start of rains in those areas.

Once the wet season has started and mating taken place, the female system becomes activated. There is increased swelling of the hermaphroditic duct, the uterus expands dramatically **(Fig. 53)**, the prostate begins to decrease in volume, the ovotestis varies in size for a period of time and then starts to shrink, and the spermathecal head becomes tightly packed with exogenous sperm and other transferred material. Evidence for multiple mating comes from the two sources: the fluctuating degree of coiling in the vas deferens through the wet season, and the finding of several discrete sperm packets in varying stages of dissolution in the spermatheca of wet season samples. The vas deferens becomes straightened out during mating and stays that way for at least a few days (see *A. questroana,* **Fig. 40a,** *A. kalumburuana,* **Fig. 44a,** *A.b. burnerensis,* **Fig. 52a, c; Fig. 53)**. Deep retraction of the animal can partly hasten recoiling and also will increase the kinking of the hermaphroditic duct, for example in *A. alta alta* **(Fig. 60a)**.

Evidence that the activation of the female system is triggered by mating comes from study of *A. burnerensis burnerensis* (see Discussion under that species). Specimens collected in early October were kept inactive in a sealed package until late February. Prostate, ovotestis and hermaphroditic duct had greatly enlarged, but the uterus is still dry season size **(Fig. 53,** activated 25 February). Since by mid-February the field-collected snails **(Fig. 53,** 19 February) have a greatly shrunken ovotestis, hermaphroditic duct, and prostate, with the uterus still at least partially enlarged, and several hard masses in the spermatheca, the contrast of the enormous ovotestis, large prostate, and thick hermaphroditic duct in the delayed activation specimens is striking **(Fig. 53)**. These 'supermales' had the least material stored in the spermatheca of any examined specimens. The lack of any sign of activation in the female system suggests that the exchange of sperm triggers female activation.

Well before the normal end of the wet season, the entire reproductive tract begins its seasonal shutdown, with February examples only slightly more **(Fig. 53,** 21 March) enlarged (except in uterus) than May-collected animals **(Fig. 53).** Even late rains apparently will trigger mating, but whether sperm transfer takes place is uncertain. The reduced ovotestis size and asence of fresh sperm packets in these individuals suggest recreational rather than procreational sex. Foreign sperm and transferred material is accumulated in the spermathecal head and held **(Fig. 53)** through the normal mid-dry season period. It is thus readily available for use as a source of complex chemicals to build the new sperm during the last portion of the dry season. The same pattern was suggested for *Xanthomelon prudhoensis* (Smith, 1894) (Solem, 1979: 33-4), and offers a contrast to the relatively quick destruction of stored sperm material in the European *Helix pomatia* Linné, 1758 (Lind, 1973).

Egg-laying was not observed in *Amplirhagada,* and no dissected specimens had recognizable eggs within the uterine tract. Neither were formed embryos observed. Thus the pattern and timing of egg-laying remains unknown. In their studies of Puerto Rican camaenids, Heatwole & Heatwole (1978: 278-283) also failed to detect uterine eggs or see oviposition, but did locate numbers of egg clutches in the soil of their study areas. The same authors report a clear seasonal variation in albumen gland size. This was not detected in the *Amplirhagada* material. Individual variation in total length of the albumen gland was moderately large, and individuals whose stomachs were gorged with food would have the albumen gland squashed flatter than normal, but whether this decrease (temporary?) in volume was accompanied by a change in weight is unknown.

The net effect on systematic observations as a result of this seasonal cycle is that materials collected in April through September or October, depending on the area, will be in an inactive reproductive state; materials taken in the late part of the local dry season will be male active, but female inactive; early wet season materials will be variably active; and late wet season samples will be in the process of shutting down for the next dry season. Much of the readily observed structural variation relates to seasonal variation. The size of the ovotestis lobes, thickness and coiling of the hermaphroditic duct, relative sizes of the prostate and uterus, size of and amount of material in the spermathecal head and shaft, and coiling of the vas deferens within the apical portion of the penial sheath are seasonal. The size of the albumen gland is age correlated.

The position and number of lobes in the ovotestis does not appear to vary significantly. The number of lobes figured for the several species ranges from five to eight. In part this is simply whether a single duct splits in two immediately after coming off the main collecting tubule or two collecting ducts emerge separately. The dissected material of *A. burnerensis* showed a range of six to eight main clumps, thus essentially equalling the range for the entire genus. All of the lobes are separately buried in the digestive gland above the stomach apex.

The talon (GT) is uniform in basic structure, so far as could be studied by gross observation. Lateral entry of the hermaphroditic duct is the rule, with only *A.*

questroana **(Fig. 40a)** of the male active taxa showing a variation—the hermaphroditic duct entering laterally almost on the tip. The situation in *A. alta alta* **(Fig. 60a)** is typical. The hermaphroditic duct reflects to the apex of the prostate-uterus and is bound to this in a sheath also containing vascular tissue. Material fixed in formalin normally has the albumen gland so hardened, that the talon can be viewed only by transparency. Thus in the species from the Prince Regent and Carson River areas, I have less confidence as to its exact shape. In the early to mid-dry season material, the talon **(Figs 57a, b; 65a)** will be noticeably more slender than in wet season materials.

When first dissected out, a very characteristic feature of specimens is for the head of the spermatheca (S) to be bound to the lower prostate (DG) and uterus (UT). Either a loop of the free oviduct (UV) twists around the spermathecal shaft, as in *A. mitchelliana* **(Fig. 62a)**, or, more frequently, the free oviduct and part of the spermathecal shaft are folded back on themselves as in *A. varia* **(Fig. 65b)** and *A. castra* **(Fig. 63a)**. In most of the illustrations, the spermathecal head, which is normally firmly bound in by connective tissue, has been pulled to one side so that the origins and insertions of tubes can be shown more clearly. Some evidence suggests that this folding may be a normal artifact when the genital system becomes active. In non-activated material, whether just becoming adult (*A. castra,* **Fig. 68a**) or seasonally inactive (*A. wilsoni,* **Fig. 57a,** *A. elevata,* **Fig. 57b,** *A. katerana,* **Fig. 41a**), there is little or no trace of this loop. Seasonal enlargement of the prostate and uterus leads to a space problem, and a slight to moderate anterior shift would result in such a looping arrangement. Thus I place little systematic importance on the extent of this loop. In *A. pusilla* **(Fig. 41b)** and *A. questroana* **(Fig. 40a)**, the expansion of the upper vagina (V) and spermathecal shaft (S) is greater than in other species. The free oviduct in these taxa is tightly bound to the spermathecal shaft and thus the opportunity for such bending is lessened.

Proportionate lengths of the terminal female organs vary both within and among species. Because of loopings, different ages and activity states, differential contraction of the preserved animal into the shell, differential shrinkage depending on the relaxant and preservative used, and the lack of easily measured reference points, such comparisons can only be approximate. The internal fusion of the free oviduct and spermatheca to form the vagina normally is through a large, 'U' or 'Y' shaped pad **(Fig. 64a)**. This pad extends up into the spermathecal shaft and tapers down into the vaginal region. It is varyingly and complexly sculptured, as are the walls of the vagina **(Fig. 64)**, thus providing species recognition surfaces (see below). In effect the vagina and spermathecal shaft form a continuous chamber with the free oviduct entering through a pore (UVO). For purposes of external measurement, the free oviduct (UV) is defined as the distance from the origin of the vas deferens to the end of the angle between the spermatheca (S) and free oviduct; the vagina (V) is the distance from the same angle to the peni-oviducal angle; the spermathecal length is from the angle between the spermatheca and free oviduct to the head of the spermatheca; and the penis sheath (PS) length is from the peni-oviducal angle to the insertion of the penial retractor muscle. These landmarks do not correspond exactly with functional anatomy, but are the only externally measurable features.

Comparing the vagina/penial sheath lengths, the standard pattern seems to be about 33-45% (*A. alta, A. burnerensis, A. carinata, A. castra, A. katerana, A. napierana, A. percita, A. varia*); slightly higher (57-72%) for *A. confusa, A. elevata, A. wilsoni,* and *A. mitchelliana;* and very long vaginae (90%) in *A. kalumburuana* and *A. drysdaleana.* In *A. pusilla* (19%) and *A. questroana* (27%), the vaginal region is noticeably shortened. Relative lengths of the free oviduct/spermatheca vary more continuously, but normally the free oviduct is half to a third the length of the spermatheca (*A. carinata, A. castra, A. drysdaleana, A. pusilla, A. questroana, A. wilsoni*). Only *A. varia* and *A. mitchelliana* have the lengths approach unity. The remaining species cluster in the 55-80% range. Similarly, the ratio between the spermatheca/penial sheath lies mostly in the 33-60% range. *A. castra* is unique in having the spermatheca significantly exceed the length of the penis (120%), while in *A. alta, A. burnerensis,* and *A. wilsoni,* it is roughly 65-80% of the length. The above measurements are not means of dissected materials, but based on the illustrated specimens. Variation within species blurred the differences among groups and erased differences within cited groups. Insufficient material for statistical analysis was available and the differences are, in general, minor.

Internal surfaces of the terminal male and female tracts provide substantial differences among species. Here measurements can be made with greater accuracy and, since the surfaces are involved in species recognition by the snails, the structural variations are sharp and clearly definable. Those on the male side are more easily quantified and are discussed first.

The penis sheath extends from at (*A. castra,* **Fig. 63b**, *A. confusa,* **Fig. 66b**) or slightly above (*A. burnerensis,* **Fig. 54a**) the peni-oviducal angle to the insertion of the penial retractor muscle (PR) on the vas deferens (VD). The muscle insertion in *Amplirhagada,* unlike in some other genera, occurs right at the top of the sheath and does not extend down inside the sheath to a lower point. The sheath itself usually is moderately thick-walled near the base, but becomes very thin and highly expandable apically. The total length of the sheath changes dramatically as a result of mating (see *A. b. burnerensis,* **Figs. 54a-b**). The vas deferens straightens out instead of being coiled inside the upper part of the sheath. The nearly straight vas deferens seen in *A. questroana* **(Fig. 40a)** also is interpreted as resulting from mating activity, since a 33 mm rain had hit the area the night before they were collected. The straight vas deferens found in *A. elevata* **(Fig. 58a)** is not interpretable in the same way, since these specimens were collected in the middle of the dry season. Activation prior to preservation frequently happened under normal WAM field procedures, and I suspect these snails had one last mating prior to preservation. The pattern of vas deferens coiling is somewhat different in each species, but not easily communicated and variable. Differences are discussed under the individual taxa, but no analysis of the folding pattern is presented.

The point at which the ascending portion of the vas deferens enters the penis sheath varies from apparently very near the apex in some species, *A. alta alta* **(Fig. 60a)** and *A. kalumburuana* **(Figs 44a, b)**, to between one-third and two-fifths of the way toward the atrium in *A. carinata, A. napierana, A. wilsoni, A. confusa,* and *A. mitchelliana* **(Figs 45a, 50a, 57a, 62a, 65a)**. It is then very loosely held to the inside wall of the sheath by connective tissue up to the retractor insertion. When the vas deferens is straightened during mating, the apparent entering point relative to the penis will change dramatically (compare *A. burnerensis,* **Figs 54a, b**), caused by the straightening of the vas deferens descending portion. While apparently there are species-specific differences in the point at which the sheath is entered by the vas deferens, considerable variability among specimens does exist and I have not been able to quantify satisfactorily the differences. In comparison with most other Kimberley and Pilbara genera, the entrance of the vas deferens lies clearly above the middle of the penis sheath and the direct apical union of the vas and the penial retractor muscle insertion have systematic importance.

After reflexing from the muscle insertion, the vas deferens coils and runs anteriorly to expand into a broader, tapered tube that then enters the penis chamber in the form of a true verge (PV) with terminal pore. The portion of the vas deferens just above the penis chamber and the vergic chamber undoubtedly function as an epiphallus, since sperm packets are exchanged during mating. The shape of an excised packet is shown in **Fig. 52e**. Its narrow end lies up the spermethecal shaft and the thin walled, open end extends up into the free oviduct. Presumably the narrow end is formed in the vergic chamber with the other portions in the vas deferens.

Within the penis chamber there are variations in proportions, sculpture of the walls, thickness of the walls, main pilaster size and ornamentation, plus the development of a 'sperm channel' in several species. Evidently the main pilaster and, to a lesser extent, the wall ornamentation, are involved directly in species recognition by the snails.

Differences in proportion are given as ratios to the actual penis length, which is defined here as the distance from the emergence of the verge base into the penis chamber down to the point of attachment of the penis sheath to the penis wall. This distance normally is less than the length of the penis sheath, but in three species, *A. kalumburuana* **(Fig. 44b)**, *A. pusilla* **(Fig. 41b)**, and *A. drysdaleana* **(Figs 39a, b)**, the penis length substantially exceeds the sheath length, with the retracted penis variously coiled **(Figs 39a, 44b)** inside the sheath. In other taxa, it is the descending arm of the vas deferens that lies coiled in the sheath.

The verge (PV) normally is conical and gradually tapers to a narrow tip with either terminal or barely subterminal pore. Variation in shape includes a shift to a more broadly triangular profile in *A. castra* **(Fig. 63b)**, *A. carinata* **(Fig. 45b)**, and to a lesser extent, *A. questroana* **(Fig. 40b)**. *A. napierana* **(Fig. 51a)** has a blunter tip and *A. percita* has a lateral extension to the tip **(Fig. 51b)**, which differentiates these two species from other *Amplirhagada*. In two species, *A. kalumburuana* **(Fig. 44c)** and

A. wilsoni **(Fig. 58b)**, the verge is noticeably reduced in size. In most species, the verge is 13-21% the length of the penis chamber. In both races of *A. varia* **(Figs 66a, 69d-e)** and *A. confusa* **(Fig. 66b)** the verge is greatly elongated, extending up to two-thirds the length of the penis chamber, although this is lessened in *A. varia depressa* which has a shorter verge. The verge in *A. castra* **(Fig. 63b)** appears to be half the length of the chamber, but this is a function of the compacted, shortened chamber rather than the verge itself. Similarly, the verge in *A. drysdaleana* is proportionately very short (7%), but this is a factor of chamber elongation rather than reduction in verge size.

Wall thickness of the penis chamber partly depends on the complexity and size of the basic sculpture. Species with reduced or very fine sculpture, such as *A. elevata* **(Fig. 58a)**, *A. varia varia* **(Fig. 66a)**, and *A. kalumburuana* **(Fig. 44c)**, have noticeably thinner walls than do heavily sculptured species such as *A. questroana* **(Fig. 40b)**, *A. wilsoni* **(Fig. 58b)**, and *A. b. burnerensis* **(Fig. 54a)**. I could detect no seasonal differences within a species on gross examination. Generally there are two rather distinct regions of sculpture in the penis chamber. The lower portion will have a series of longitudinal pressure folds or ridges, usually extending up from the atrium (Y) without change in pattern. This pattern extends above the penis sheath insertion for a variable distance. In most taxa these are simple folds, but in *A. carinata* **(Fig. 45b)**, *A. castra* **(Fig. 63b)**, and *A. mitchelliana* **(Fig. 62b)** there is an immediate corrugated pattern that matches the typical lower female tract **(Fig. 64a)**. The portion of the penis chamber that is sculptured longitudinally varies greatly. The average pattern is for the ridges to occupy one-quarter to one-third of the chamber length. There are shifts resulting in both reduction and extension of this sculpture. *A. castra* **(Fig. 63a)** has the ridges restricted to the atrium, probably as a general result of penis chamber shortening; *A. varia varia* **(Fig. 66a)**, *A. carinata* **(Fig. 45b)**, *A. drysdaleana* **(Fig. 39b)**, and *A. questroana* **(Fig. 40b)** have the ridge extension noticeably shortened; while in *A. kalumburuana* **(Fig. 44c)** and *A. pusilla* **(Fig. 42)** the ridges extend much further apically. *A. elevata* **(Fig. 58a)** has a modified form of ridging covering the entire surface of the penis chamber. The upper part of the ridges may be corrugated and gradually shift into the separate pustules, or there may be a sharp transition.

The upper part of the penis chamber has a series of small to large pustules that may or may not be arranged in distinct rows. Many of the larger pustules in such species as *A. drysdaleana* **(Fig. 39b)** and *A. questroana* **(Fig. 40b)** will have single sharp chitinized-appearing points or blunt tips on their anterior edges or top. The same type of structures are found on the upper penis chamber walls of *Torresitrachia* (Solem, 1979: Figs 16a-c). Species with smaller and more crowded pustules lacked such points on the pustules. Great care has been taken to render the patterning of the pustules accurately, as their arrangements were found to be stable within examined material of a given species. *A. wilsoni* **(Fig. 58b)**, *A. pusilla* **(Fig. 42)** and *A. carinata* **(Fig. 45)** have a very strong gutter extending from just below the tip of the verge through the pustule pattern and to the area of longitudinal ridging.

This apparent 'sperm channel' is less developed in *A. kalumburuana* **(Fig. 44c)** and *A. drysdaleana* **(Fig. 39b)**, and very weakly developed in *A. mitchelliana* **(Fig. 62b)**. It was not found in other species of *Amplirhagada*.

The presence of a large main pilaster (PT) on the upper wall of the penis chamber is diagnostic of *Amplirhagada*. It begins lateral to the verge, immediately (except in *A. elevata*, **Fig. 58a**) becomes quite high and usually quickly reaches its broadest width. In *A. drysdaleana* **(Figs 36a, 39b)** it is at its simplest, a row of broadened pustules, each with a single central point **(Fig. 36a)**. In other species it becomes more complex, with a large number of narrow to wide corrugations forming the mass of the pilaster. Generally the enlarged, corrugated section of the pilaster extends one-third to one-half the length of the penis chamber (three-quarters in *A. castra*, **Fig. 63b**). It then either abruptly (*A. castra, A. mitchelliana*), to very gradually (*A. wilsoni, A. napierana, A. alta*) tapers, lowers, and blends into the pustuled surface of the chamber walls. In *A. elevata* **(Fig. 58a)** the pattern is changed in that the main pilaster is very narrow, without points **(Fig. 36f)**, increases in height and width greatly near its midpoint and then tapers gradually. In both *A. confusa* **(Fig. 66b)** and *A. varia* **(Fig. 66a)**, the two species with greatly lengthened verges, the pilaster is reduced to a remnant composed of slightly more elevated and tightly packed pustules **(Figs 36d, e)**. It is highly significant that all of the species showing these major changes in pilaster and verge pattern occur sympatrically with other species.

On a macroscopic level, the shape of the pilaster, number and width of the corrugations, all are good species identification features for the malacologist. The surface armature on the corrugation edges serves the snail as a species recognition character. A few specimens were preserved with the penis partially everted as a reaction to the relaxing process. While the typical basal longitudinal folds disappeared, the pustules remained erect, and the main pilaster itself appeared as a strong projection on the everted surface. The points on the anterior edge of each corrugation are semi-erect and thus would serve a stimulatory function.

Each species had a clearly distinctive pattern to the points. For ease in comparison, these have been grouped into two illustrations **(Figs 36, 37)**. The simple pattern found in *A. drysdaleana* **(Fig. 36a)** is for a row of the pustules to widen, retaining the single central point, perhaps adding a lateral point, and to be slightly elevated above the rest of the pointed pustules **(Fig. 39b)**. Three highly specialized situations somewhat mimic this in appearance. *A. confusa* **(Fig. 36d)** and *A. varia* **(Fig. 36e)** have enormously enlarged verges (see **Figs 66a, b**), and the pilasters are greatly reduced in prominence. In *A. varia* there is a compression and flattening of the pustules that is not present in *A. confusa*. In both species the pilaster corrugations have broken up into a series of independent pustules that only vaguely retain row formation. In *A. elevata* **(Fig. 36f)** the pilaster has narrowed, the corrugations are partly merged, and there is no trace of points on the pilaster surface.

A different form of specialization is seen in *A. napierana* **(Fig. 36b)**, where the broadened corrugations have an irregular set of blunt tipped triangular points of varying size. Exactly the same pattern of points was found in *A. percita,* which has an interdigitating distribution pattern with *A. napierana.* In *A. burnerensis* (Smith, 1894) **(Fig. 36c)** the anterior edges of the corrugations are much smoother in outline, and the smaller blunt triangular points are usually four or five in number and confined to the upper edge and just around the side of each corrugation. A variation on the same theme is seen in *A. questroana* **(Fig. 37a)**. The corrugations in this species are wider and shorter. The very short and bluntly triangular points are restricted to near the center of each corrugation and number only two or three.

The most frequent pattern of development is for a row of sharp chitinized-appearing points to line the anterior edge of each corrugation **(Figs 37b-i)**. These points vary in number, prominence, and portion of each corrugation edged. In *A. pusilla* **(Fig. 37c)** there are two large points on more anterior sections of the pilaster and three to four near the very top. A few of the wall pustules in this species show single sharp points on their anterior edge. *A. kalumburuana* **(Fig. 37b)** has five to six

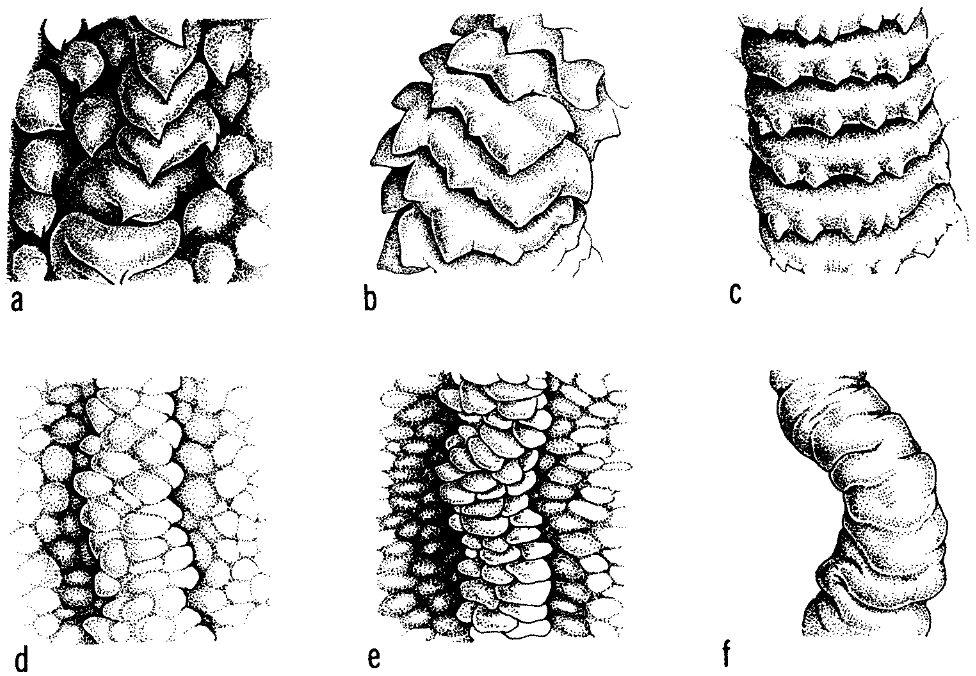


Fig. 36: Surface armature of major penial pilaster in *Amplirhagada,* a) *A. drysdaleana,* Sta. B1 (7), Drysdale Reserve, 15 August 1975, WAM 627.77, Dissection A; b) *A. napierana,* Sta. WA-321, Napier Range, 16 December 1976, FMNH 200140, Dissection C; c) *A. burnerensis* (Smith, 1894), Sta. WA-193, Napier Range, 5 December 1976, FMNH 199872, Dissection B; d) *A. confusa,* Sta. WA-221, Mitchell Plateau, 29-30 October 1976, WAM 611.77, Dissection D; e) *A. varia varia,* Sta. WA-212, Mitchell Plateau, 21-23 October 1976, WAM 615.77, WAM 616.77, composite of Dissections A and B; f) *A. elevata,* Sta. W6 (1), Prince Regent River Reserve, 21 August 1974, WAM 623.77 ex WAM 1232.75, Dissection C. Drawings not to exact scale, enlarged from penis chamber dissections of same specimens.

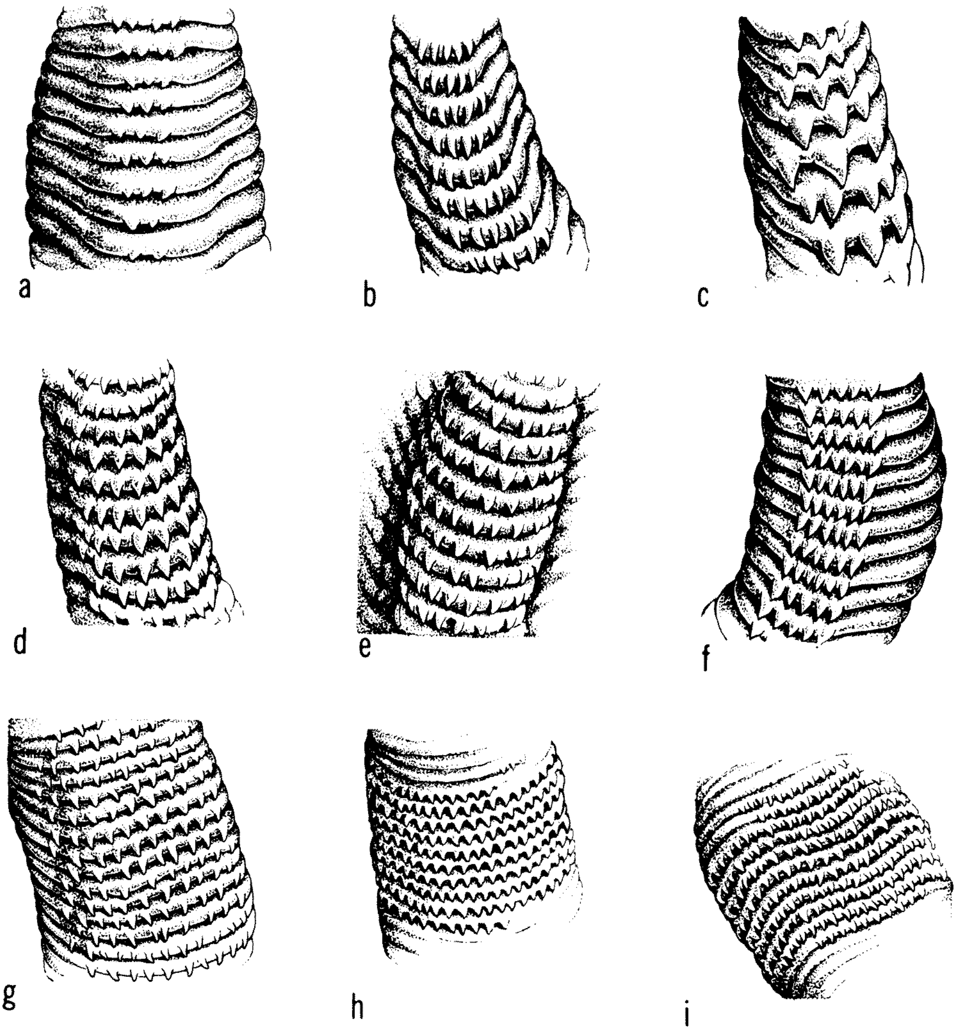


Fig. 37: Surface armature of major penial pilaster in *Amplirhagada,* a) *A. questroana,* Sta. WA-222, El Questro Station, 8 November 1976, WAM 608.77, Dissection B; b) *A. kalumburuana,* Sta. WA-220, Kalumburu Mission, 28 October 1976, WAM 618.75, Dissection A; c) *A. pusilla,* Pitta Creek, Prince Regent River, 22 August 1974, WAM 628.77 and WAM 629.77, both ex WAM 1356.75, composite of Dissections A and B; d) *A. katerana,* Katers Island, Bonaparte Archipelago, 10 June 1972, WAM 643.77 ex WAM 1285.75, composite of rehydrated materials; e) *A. alta alta,* Corneille Island, Admiralty Gulf, 16-18 August 1976, WAM 1266.75, Dissection B; f) *A. wilsoni,* Sta. E5 (7), Prince Regent River Reserve, 17 August 1974, WAM 622.77 ex WAM 316.75, Dissection A; g) *A. carinata,* Sta. WA-317, Mt Hart, King Leopold Ranges, 14 December 1976, WAM 1331.75, holotype, Dissection B; h) *A. castra,* Sta. WA-206, Mitchell Plateau, 18 October 1976, WAM 1222.75, holotype, Dissection A; i) *A. mitchelliana* Sta. WA-201, Mitchell Plateau, 15-16 October 1976, WAM 599.77, Dissection C. Drawings not to exact scale, enlarged from penis chamber dissections of same specimens.

narrow sharp points clustered right on top of each corrugation, which has distinctly concave sides. *A. katerana* **(Fig. 37d)**, *A. alta alta* **(Fig. 37e)**, and *A. wilsoni* **(Fig. 37f)** are variations on the theme, differing in size, spacing and number of points. *A. wilsoni* has the sides of the pilaster rounded rather than slightly concave and the points restricted to the upper edge. From this pattern to the situation found in *A. carinata* **(Fig. 37g)** requires only increasing the number of points, shortening the individual points and corrugations, and enlarging the pilaster itself. The logical culmination of this trend occurs in *A. mitchelliana* **(Fig. 37i)** and *A. castra* **(Fig. 37h)**, where the points are extremely small and extend all the way around the pilaster edges.

Complementing these patterns of variation in the terminal male genitalia are a few changes in surface texture on the walls of the lower female tract. Since these sections are not everted during mating, the patterns are to be interpreted as structures rather than folds as are the basic longitudinal ridges on the lower part of the penis chamber and in the atrium.

Considerable variability exists from specimen to specimen in the appearance of these internal surfaces. This probably reflects changes during mating (individuals with sperm packets inside were swollen and with the surface sculpture reduced), differential reaction to the relaxation and fixing process (a few were so thickened that all surface texture was absent), and individual variation. It is very difficult to decide how much of the observed variation is artificial. I suspect that much of it is due to the above factors, but in a few situations involving sympatry, the differences in the lower female tract are dramatic and constant.

The basic pattern **(Fig. 64a)** is for a series of weakly to strongly reticulated, fine longitudinal ridges to line the vagina up to the spermathecal-free oviduct junction. These ridges may then become simple in outline and continue up into the spermatheca on the walls opposite the free oviduct entrance, or continue as corrugated ridges up into the spermatheca. Most species have a large 'U' to 'Y'-shaped raised pad that cups the free oviduct pore. The surface of this structure may have numerous obliquely longitudinal folds in resting condition, or become swollen and thus smooth surfaced in other situations. Whether there is a clear upper vaginal ridge rising to join the basic 'U' around the free oviduct pore or no ridge may vary between species, but I am not certain how much this varies individually. The arms of the 'U' continue up into the spermatheca and gradually descend to the level of the other texture, gradually merging with it. In a few specimens collected shortly after mating, a 'sperm packet' was found within the arms of the pad. A tapered closed end **(Fig. 52e)** extended up into the spermatheca, and the thinner, open end curved into the free oviduct.

Allowing for individual variation in ridge reticulation and prominence, changes in the prominence or presence of a vaginal ridge to the 'U', and changes in the folds on the pad surface, *A. alta alta, A. burnerensis* (Smith, 1894), *A. carinata, A. drysdaleana, A. mitchelliana A. napierana, A. percita* (Iredale, 1939), *A. pusilla, A.*

questroana, and *A. wilsoni* have the basic pattern. *A. elevata* shows what may be only a minor variation, in reducing the size of the pad. The folds on the pad and reticulations were sharply outlined, possibly intensified, in *A. mitchelliana,* and this species has been illustrated for that reason **(Fig. 64a)**. The other species show the same basic structures, but have less sharply outlined folds and reticulations.

The only significant changes that I detected were under conditions of sympatry. Non-sympatric but interdigitating species such as *A. napierana* and *A. percita* (Iredale, 1939) did not show differences. *A. wilsoni* was fairly typical, with a large 'Y' pad, but the vagina had only a few low and rather amorphous ridges. *A. elevata* had fine and narrow ridges with a low 'U' pad that had longitudinal folds on its surface rather than the typical oblique folds. The low number of specimens involved, shrinkage in the formalin fixative, and inactive state of the genitalia (August samples) may have combined to cause artifacts, but the differences are accepted as probably real. *A. kalumburuana,* although not occurring with another *Amplirhagada,* was unusual in having no trace of the pad around the free oviduct pore.

In the Mitchell Plateau area, several differences were noted. The most dramatic change involves *A. castra* **(Fig. 64b)**. The basal reticulated folds are absent, the pad around the free oviduct opening is gone, and there are a few very high simple folds on the wall of the spermatheca opposite the free oviduct opening. Since *A. castra* and *A. mitchelliana* occur essentially 'on different sides of the same rock' near the Camp Creek vine thicket fringes, have very similar penis chambers **(Figs 62b, 63b)** aside from the shortening of the penis chamber in *A. castra,* and quite similar pilaster armature **(Figs 37h-i)**, the development of sharp differentiating features in the lower female tract is logical. The surface of the lower tract in *A. castra* **(Fig. 64b)** is the most modified in the genus. *A. alta crystalla* retains the typical pad, but in October has the very peculiar bulge in the vagina **(Fig. 61a)** and lacks longitudinal ridges in the lower vagina. It is possibly sympatric with both *A. mitchelliana* and *A. varia. A. confusa* and *A. varia* both lack the large pad, thus immediately differentiating them from the sympatric *A. mitchelliana. A. varia* seems to have reticulated ridges all the way up into the spermatheca, while *A. confusa* has reticulated ridges on the lower half of the vagina that then become simple ridges around the free oviduct pore and in the spermatheca.

In summary, the greatest differences in anatomical structures are found between sympatric species. Increased verge size in *A. varia* and *A. confusa* correlates with gross reduction in the main pilaster and loss of the pad around the free oviduct opening. *A. mitchelliana* and *A. castra* in the same general area have normal sized verges and a huge pilaster with many tiny points on the corrugation edges, but differ from each other dramatically in structures of the spermathecal-vaginal chamber **(Figs 64a-b)**. *A. wilsoni, A. pusilla,* and *A. elevata* apparently are sympatric in the Prince Regent River Reserve. The latter has changed penial wall sculpture, a reduced pilaster, and slightly altered lower female tract, while *A. pusilla* and *A. wilsoni* have large pilasters, well developed 'sperm gutters', but quite different **(Figs 37c, f)** armature on the surface of their pilasters. Particularly in the lower female tract, the only significant differences observed were those involving sympatric species. In the one situation where there is a linear interdigitation of two species, *A. percita* (Iredale, 1939) and *A. napierana* in the Napier Range north of Yammera Gap, the differences seem to be restricted to the form of the verge tip and the pattern of tapering by the main pilaster **(Figs 51a-b)**.

Except for these secondary differences, the species of *Amplirhagada* demonstrate a series of minor genital variations around a simple pattern.

It is not possible to make satisfactory outgroup comparisons at this time and to discuss the phylogeny of or within *Amplirhagada*. On the basis of this review, it is possible to indicate rough outlines of what are generalized and specialized character states or complexes within *Amplirhagada* and to tabulate their distribution within the genus. **Table 15** lists 16 features and designates generalized and specialized conditions. It must be emphasized that some of the specialized conditions may be arrived at in two or more ways. In no case do I claim that a specialized state must have been arrived at only once. This is a preliminary compilation to aid in understanding diversity patterns and has been simplified for purposes of this systematic review.

Table 16 tabulates the situation for each of the species. In this listing, 'G' means generalized, 'S' specialized, 'I' intermediate, and '*' or '?' unknown because of shell wear or absence of anatomical data. Since no anatomical data are available for many species, calculating the number of 'generalized' and 'specialized' states for each species has little meaning. Nor do I claim that the features are of equal importance in assessing relationships.

Considering just those species for which all sixteen features could be recorded, those with the greatest number of generalized states (11-12) are *A. alta alta, A. burnerensis* (Smith, 1894), *A. b. umbilicata, A. napierana, A. percita* (Iredale, 1939), and *A. questroana. A. questroana* with two and *A. alta alta* with three have the lowest number of specialized states. The species with the fewest generalized states, *A. elevata* with six, also has the highest number of specialized states (8). Of the several species with seven to eight specialized states, *A. elevata, A. wilsoni, A. varia varia, A. v. depressa, A. confusa* and *A. castra* are involved in sympatric occurrences, while only *A. carinata* and *A. kalumburuana* occur in congeneric isolation.

There is no concordance between specialized shell and anatomy features. For example, the generalized-specialized ranking for *A. castra* are 4-1 for shell and 4-6 for anatomy; for *A. varia varia* they are 5-1 for shell and 4-6 for anatomy. *A. alta alta* is 2-2 for shell, 9-1 for anatomy; *A. elevata* 1-4 for shell and 5-4 for anatomy.

These compilations do indicate that evolution within *Amplirhagada* involves differential patterns and multiple minor shifts, with sympatry showing marked differentiation compared with allopatric situations.

Table 15: Generalized and Specialized Features in *Amplirhagada*

Feature	Generalized Condition(s)	Specialized Condition(s)
SHELL STRUCTURES		
Spire shape	Evenly elevated	Dome-shaped
Mean whorl count	Under 6¾	6¾ or more
Peripheral contour	Rounded	Strongly angled or carinated
Umbilicus	Open	Closed
Color pattern	Complete	Reduced
Radial sculpture	Present	Strong, reduced, or absent
ANATOMICAL STRUCTURES		
Penis complex		
Penis/penis sheath length	Sheath longer	Penis longer
Penis chamber		
Verge	'normal'	Reduced or elongated
Sperm gutter	Absent	Present
Pustules	Some with points	None with points or absent
Basal ridges	'normal'	Longer or shorter, form altered
Main pilaster		
Size	Large	Reduced
Points on corrugations	Few sharp	Few dull, many sharp, absent
Shape	Concave sides	Rounded sides
Lower female tract		
Free oviduct pore pad	Present	Absent or reduced
Vagina-spermatheca ridges	Many reticulated	Few simple

Systematic review

Amplirhagada is in an exuberant phase of speciation and shows mosaic patterns of variation. Thus ordering the species into a logical linear systematic sequence proved impossible. An unsatisfactory compromise among conchological similarity, geographic proximity, and anatomical specializations has led to the following arrangement. *A. drysdaleana* appears to have the most generalized penial chamber features **(Figs 36a, 39b)** and is listed first. Other umbilicated and/or inland taxa, *A. questroana, A. pusilla, A. kalumburuana* and *A. carinata,* plus *A. astuta* (Iredale, 1939), known by a few shells from Koolan Island, and the unusual *A. katerana* from offshore islands, show similar shell and colour features, although differing greatly from each other in penial surface features. They are followed by the several Napier Range taxa, *A. percita* (Iredale, 1939), *A. napierana, A. burnerensis burnerensis* (Smith, 1894), and *A. burnerensis umbilicata.* The two large and brightly coloured

Table 16: Character State Conditions in *Amplirhagada*

	alta alta	*a. crystalla*	*a. intermedia*	*a.* subsp.	*burnerensis*	*b. umbilicata*	*carinata*	*castra*	*combeana*	*confusa*	*drysdaleana*	*elevata*	*herbertena*	*imitata*	*kalumburuana*	*katerana*	*mitchelliana*	*montalivetensis*	*napierana*	*novelta*	*percita*	*pusilla*	*questroana*	*sykesi*	*v. varia*	*v. depressa*	*wilsoni*
Spire shape	S	S	S	S	G	G	G	G	G	S	G	S	S	G	G	I	I	G	G	G	G	G	G	G	G	G	I
Mean whorl count	I	S	S	G	G	G	G	G	G	G	G	S	G	G	G	G	I	G	G	G	G	G	G	S	G	G	G
Periphery angulation	G	G	G	G	G	G	S	G	G	G	I	I	G	G	G	S	G	G	G	G	I	S	G	I	G	G	I
Umbilicus	S	S	S	S	S	G	G	S	S	S	S	S	S	S	I	S	S	S	S	S	G	G	G	S	S	S	S
Color pattern	G	G	G	*	S	S	S	I	*	G	I	G	*	I	S	S	G	G	S	*	S	I	I	G	G	G	G
Radial sculpture	I	I	*	*	S	S	I	G	G	G	G	S	?	G	I	I	I	S	S	S	S	G	I	G	G	G	S
Penis/penis sheath ratio	G	G	*	*	G	G	G	G	*	G	S	G	*	*	S	G	G	*	G	*	G	S	G	*	G	G	G
Verge length	G	G	*	*	G	G	G	G	*	S	G	G	*	*	S	G	G	*	G	*	G	G	G	*	S	S	S
Sperm gutter	G	G	*	*	G	G	S	G	*	G	S	G	*	*	S	*	I	*	G	*	G	S	G	*	G	G	S
Wall pustules	S	S	*	*	S	S	S	S	*	S	G	S	*	*	S	*	S	*	S	*	S	S	G	*	S	S	S
Basal ridges	G	G	*	*	G	G	S	S	*	G	S	S	*	*	S	*	I	*	G	*	G	S	S	*	S	S	G
Main pilaster size	G	G	*	*	G	G	G	G	*	S	I	S	*	*	G	*	G	*	G	*	G	G	G	*	S	S	G
Corrugation points	G	G	*	*	S	S	S	S	*	S	G	S	*	*	G	G	S	*	S	*	S	G	S	*	S	S	G
Sides of pilaster	G	G	*	*	G	G	S	S	*	G	G	G	*	*	G	G	S	*	G	*	G	G	G	*	G	G	S
Free oviduct pad	G	I	*	*	G	G	G	S	*	S	G	I	*	*	S	*	G	*	G	*	G	G	G	*	S	S	G
Vaginal ridges	G	S	*	*	G	G	G	S	*	I	G	G	*	*	G	*	G	*	G	*	G	G	G	*	G	G	S
TOTAL "G"	11	9	2	2	11	12	8	8	4	8	9	6	2	4	7	5	7	4	11	3	11	10	12	3	9	9	7
TOTAL "I"	2	2	0	0	0	0	1	1	0	1	3	2	0	1	2	2	5	0	0	0	1	1	2	1	0	0	2
TOTAL "S"	3	5	3	2	5	4	7	7	1	7	4	8	2	1	7	3	4	2	5	2	4	5	2	2	7	7	7

Prince Regent River Reserve taxa, *A. wilsoni* and *A. elevata,* are followed by the complex of taxa from the Mitchell Plateau and Admiralty Gulf that have been dissected: *A. alta* with its several subspecies, *A. mitchelliana, A. confusa, A. castra, A. varia varia* and *A. varia depressa.* Following these are the probably related *A. sykesi* (Smith, 1894) and *A. montalivetensis* (Smith, 1894), then *A. imitata* (Smith, 1894) and *A. combeana* Iredale, 1938 from the Admiralty Gulf, both of which have greatly accentuated radial shell sculpture. None of these have been dissected. *A. novelta* Iredale, 1939, based on a single badly worn and often repaired shell from Napier-Broome Bay, plus the unlocalized *A. herbertena* Iredale, 1939 from the Buccaneer Archipelago, complete the roster of named taxa.

The geographic range of individual species is relatively restricted **(Fig. 73)**. Undoubtedly many more remain to be discovered and described. Four such are indicated in **Fig. 73.** No key based on conchological criteria has been prepared, but comments on differentiating taxa within several loosely defined geographic areas are presented at the end of the systematic review. On the basis of the work done for this review, the most useful single feature for species recognition is the structure of the main pilaster in the penis. Without dissection and illustration of this species recognition feature and comparison with those previously known **(Figs 36-37)**, description of new taxa will be at best incomplete and at worst both meaningless and useless.

Some aid in species recognition is given by use of the mean measurements listed in **Table 17,** but the range of variation is large enough that this is not sufficient to permit identification of isolated individuals with any degree of confidence.

Table 17: Size and Shape Variation in *Amplirhagada*

Taxon	Number of Adults Measured	Mean and Range of: Shell Height		Shell Diameter		H/D Ratio	
A. drysdaleana	19	10.51	(9.3-11.7)	16.73	(14.15-19.1)	0.630	(0.594-0.665)
A. questroana	5	13.21	(12.4-14.4)	20.02	(18.9-21.15)	0.660	(0.631-0.688)
A. pusilla	59	9.93	(8.05-12.95)	16.73	(14.45-20.2)	0.590	(0.532-0.665)
A. katerana	30	15.27	(12.6-17.4)	21.56	(19.2-25.0)	0.708	(0.627-0.790)
A. kalumburuana	11	12.84	(11.8-13.7)	18.19	(17.0-19.4)	0.706	(0.676-0.792)
A. carinata	60	11.54	(10.1-15.1)	19.98	(17.9-22.5)	0.578	(0.530-0.674)
A. astuta	5	11.68	(10.7-12.5)	19.45	(18.7-20.85)	0.600	(0.572-0.621)
A. percita	934	10.90	(7.3-14.5)	17.15	(11.5-20.4)	0.630	(0.492-0.814)
A. napierana	1,261	13.41	(9.95-16.25)	18.71	(13.1-21.85)	0.714	(0.572-0.901)
A. burnerensis burnerensis	1,371	13.12	(9.0-15.0)	18.65	(14.0-21.85)	0.686	(0.568-0.855)
A. b. umbilicata	628	10.25	(7.3-14.15)	16.75	(12.8-19.8)	0.614	(0.510-0.783)
A. elevata	44	16.49	(14.5-18.50)	20.79	(18.7-22.2)	0.793	(0.725-0.881)
A. wilsoni	76	15.09	(13.4-17.25)	21.57	(18.85-25.55)	0.700	(0.599-0.840)
A. alta alta	9	15.43	(13.55-17.65)	20.06	(19.1-21.9)	0.769	(0.684-0.887)
A. a. crystalla	34	20.64	(17.0-22.7)	21.67	(19.6-24.2)	0.953	(0.865-1.044)
A. a. intermedia	21	19.31	(16.3-22.2)	22.05	(21.1-23.0)	0.875	(0.734-0.971)
A. a. subsp.	1	20.4		22.0		0.927	

Table 17: Size and Shape Variation in *Amplirhagada* (continued)

Taxon	Number of Adults Measured	Mean and Range of: Shell Height		Shell Diameter		H/D Ratio	
A. mitchelliana	561	16.09	(12.8-19.7)	21.98	(17.1-25.1)	0.732	(0.643-0.861)
A. confusa	375	16.44	(13.0-20.2)	20.10	(16.3-23.7)	0.820	(0.702-0.957)
A. castra	150	13.65	(11.7-16.6)	18.09	(15.6-21.7)	0.755	(0.668-0.874)
A. varia varia	703	13.98	(10.1-18.5)	17.32	(13.6-20.3)	0.804	(0.670-1.040)
A. v. depressa	34	11.07	(8.75-14.2)	16.27	(13.55-19.8)	0.679	(0.585-0.772)
A. sykesi	9	17.44	(16.2-18.6)	20.56	(18.95-21.4)	0.847	(0.757-0.882)
A. montalivetensis	7	14.27	(13.0-14.8)	20.39	(18.65-21.35)	0.700	(0.656-0.726)
A. imitata	139	14.74	(11.35-18.6)	18.92	(16.2-21.9)	0.767	(0.616-0.912)
A. combeana	108	11.03	(9.4-14.0)	15.05	(13.3-17.65)	0.732	(0.660-0.861)
A. novelta	1	16.8		21.5		0.781	
A. herbertena	1	15.8		21.2		0.745	

Table 17: Size and Shape Variation in *Amplirhagada* (continued)

Taxon	Number of Adults Measured	Mean and Range of: Whorls		Umbilical Width		D/U Ratio	
A. drysdaleana	19	5 ⅜+	(5 ⅛-5¾)	1.31	(1.0-1.8)	13.0	(9.86-19.1)
A. questroana	5	5¾ –	(5 ⅝-5 ⅞)	1.34	(1.0-2.0)	15.9	(9.45-21.1)
A. pusilla	59	5½ +	(5 ⅛-6 ⅛)	1.24	(0.8-1.7)	13.9	(8.76-22.0)
A. katerana	30	6½	(5 ⅞-7)	closed		closed	
A. kalumburuana	11	6 –	(5 ⅜-6¼)	closed		closed	
A. carinata	60	5 ⅝–	(5¼-6)	1.53	(1.1-2.4)	13.4	(8.83-19.1)
A. astuta	5	5 ⅝+	(5½-5¾)	1.36	(1.1-1.5)	14.5	(12.5-17.9)
A. percita	934	5 ⅝–	(4 ⅝-6¾)	1.40	(0.3-3.1)*	12.7	(5.40-36.9)*
A. napierana	1,261	5¾ +	(5-6 ⅜)	closed		closed	
A. burnerensis burnerensis	1,371	5¾	(5-6¾)	closed		closed	
A. b. umbilicata	623	5 ⅝	(4¾-6 ⅞)	1.59	(0.6-2.75)	11.3	(5.84-29.4)
A. elevata	44	6¾ +	(6¼-7¼)	closed		closed	
A. wilsoni	76	6 ⅜–	(5 ⅞-6¾)	closed		closed	
A. alta alta	9	6½	(6 ⅛-6¾)	closed		closed	
A. a. crystalla	34	7 ⅛	(6½-7½)	closed		closed	
A. a. intermedia	21	6 ⅞	(6 ⅜-7¾)	closed		closed	
A. a. subsp.	1	7¼ +		closed		closed	
A. mitchelliana	561	6¾ –	(5¾-7 ⅜)	closed		closed	

Table 17: Size and Shape Variation in *Amplirhagada* (continued)

Taxon	Number of Adults Measured	Mean and Range of: Whorls		Umbilical Width		D/U Ratio	
A. confusa	375	6½	(5 ⅞-7¼)	closed		closed	
A. castra	150	5 ⅞	(5 ⅜-6½)	closed		closed	
A. varia varia	703	6 ⅛ –	(5 ⅜-6 ⅞)	closed		closed	
A. v. depressa	34	5¾ +	(5-6½)	closed		closed	
A. sykesi	9	6½ –	(6 ⅛-6¾)	closed		closed	
A. montalivetensis	7	6	(5 ⅜-6¼)	1.14	(0.9-1.3)	18.1	(15.6-22.1)
A. imitata	139	6 ⅛ +	(5 ⅜-6¾)	closed		closed	
A. combeana	108	5½	(5 ⅛-6¼)	closed		closed	
A. novelta	1	5¾		closed		closed	
A. herbertena	1	6 ⅜ +		1.15		18.4	

* Of 905 specimens with open umbilici.

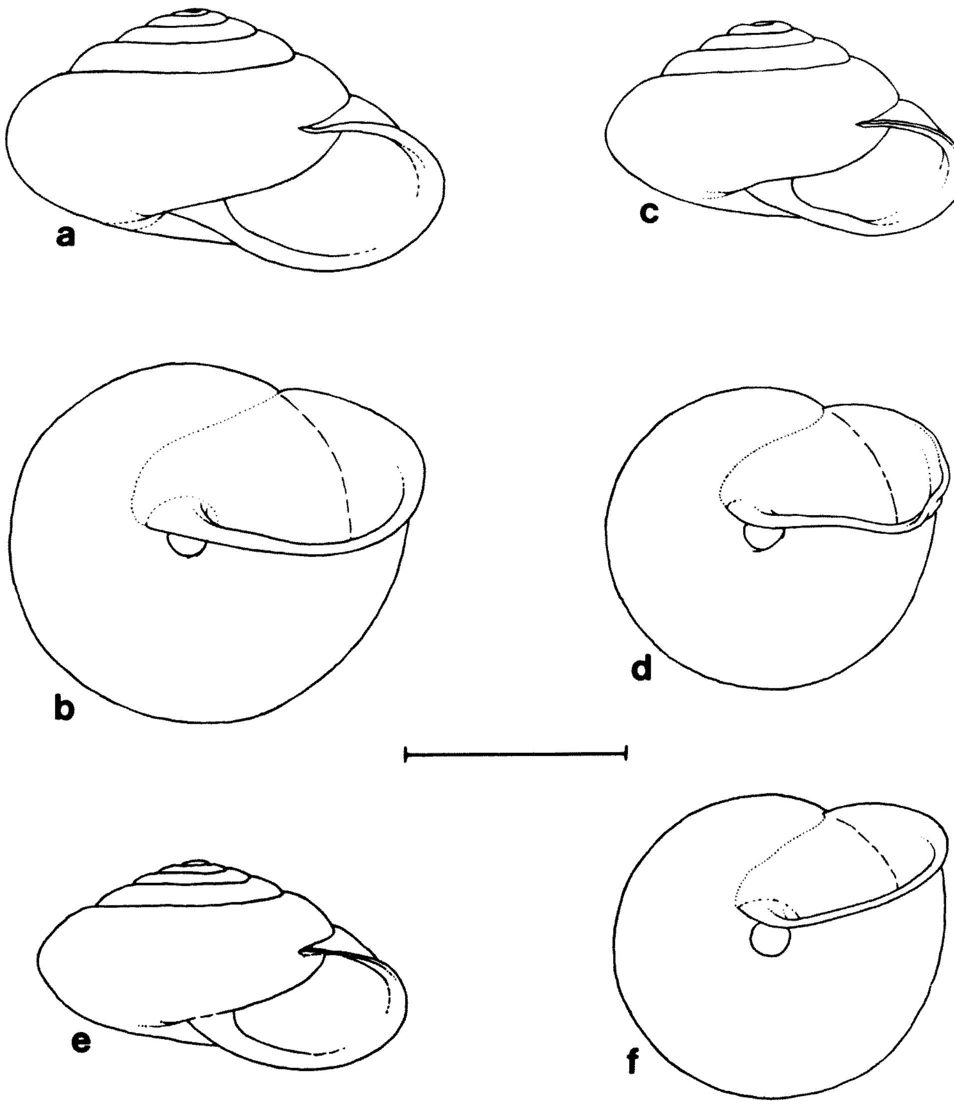


Fig. 38: Shells of *Amplirhagada,* a-b) *A. questroana,* Sta. WA-222, El Questro Station, WAM 1357.75, holotype; c-d) *A. drysdaleana,* Sta. B1 (7), Carson River, WAM 1350.75, holotype; e-f) *A. pusilla,* Pitta Creek, Prince Regent River, WAM 1356.75, holotype. Scale line equals 10 mm.

AMPLIRHAGADA DRYSDALEANA SP. NOV.

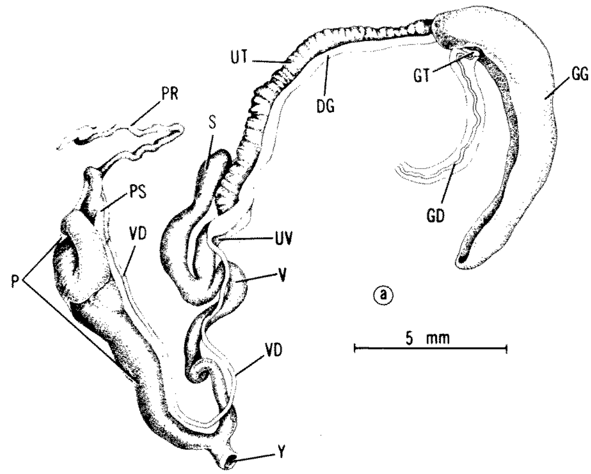
(Plate 12d; Figs 36a, 38c-d, 39a-b)

Comparative remarks

Amplirhagada drysdaleana has a slightly angled periphery **(Fig. 38c)**, is much smaller (mean diamter 16.73 mm), and slightly more depressed (mean H/D ratio 0.630), than *A. questroana* **(Figs 38a-b)** (mean diameter 20.02 mm, H/D ratio 0.660), but otherwise agrees with it in basic shape, shell sculpture, colour and umbilical features. Correlated with its smaller size is a reduced whorl count (mean whorls 5 ⅜+ and 5¾−, respectively). *A. pusilla* **(Figs 38e-f)** is noticeably more depressed (mean H/D ratio 0.587), has a more angulated periphery, and distinctly stronger radial sculpture **(Plate 12c)** than either of the other two species **(Plate 12d, e)**. *A. astuta* (Iredale, 1939) from Koolan Island is larger (mean diameter 19.45 mm), but very similar in sculpture and form. The only other described umbilicated species, *A. carinata* from the Upper Barker River drainage in the King Leopold Ranges, is much larger (mean diameter 19.98 mm), distinctly carinated **(Fig. 43a)**, and even more depressed in shape (mean H/D ratio 0.578). *A. kalumburuana* from near Kalumburu Mission is more elevated **(Fig. 43c)** (mean H/D ratio 0.706), with a rounded periphery and an umbilicus that varies from closed to moderately open. All other named *Amplirhagada* have a closed umbilicus or a narrow lateral chink, except for two taxa from the Napier Range. *A. burnerensis umbilicata* has no flare to the lip, lacks colour bands, and has a round periphery. The horn coloured, sometimes widely umbilicated *A. percita* (Iredale, 1939) has a rounded periphery and lacks radial sculpture. Anatomically, *A. drysdaleana* is distinguished by having the vagina longer than the penis sheath **(Fig. 39a)**, the penis much longer than the sheath and folded back on itself, plus a quite altered penis interior **(Fig. 39b)**. The short verge (PV) with simple terminal pore is typical. The main pilaster **(Figs 36a, 39b**, PT) consists of one row of very large pustules with single pointed tips. Neighbouring enlarged pustules **(Fig. 39b)** also have pointed tips. The basal portion of the penis is unusual **(Fig. 39b)** in having only a few very broad and weakly corrugated pilasters. All other *Amplirhagada* have either a very broad main pilaster with a few to many points on each transverse segment **(Figs 36a-c, 37a-i)**, a greatly enlarged verge with the main pilaster reduced (*A. confusa* and *A. varia,* **Figs 36d-e, 66a-b, 69b-c**), or with normal verge, reduced pilaster, and no wall pustulations (*A. elevata,* **Figs 36f, 58a**).

Holotype

WAM 1350.75, Sta. B1-7, on Carson River Escarpment about 0.5 km north of entrance to Glider Gorge, Carson River, north-west Kimberley, Western Australia (1:100:000 'Carson' map sheet 4268, grid reference 658:617). Collected by Barry R. Wilson 15 August 1975. Height of shell 11.0 mm, diameter 17.0 mm H/D ratio 0.647, whorls 5⅜+, umbilical width 1.3 mm, D/U ratio 13.1.



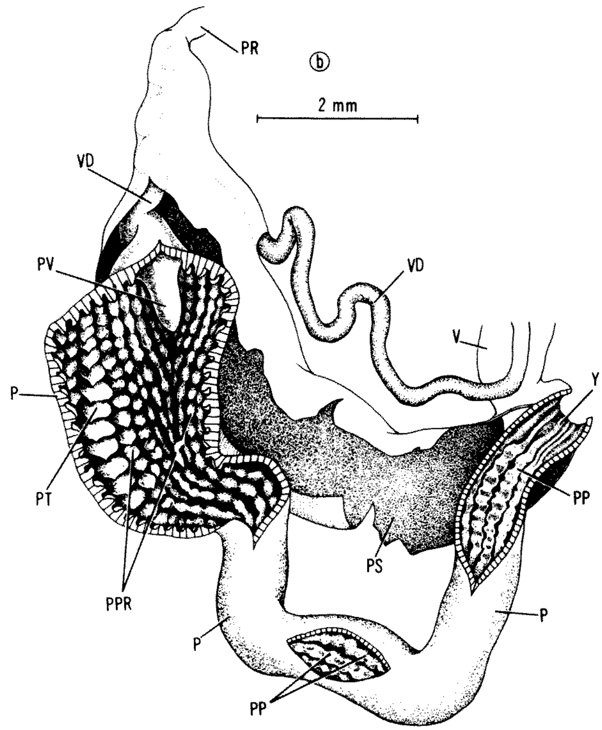


Fig. 39: Genitalia of *Amplirhagada drysdaleana,* a) whole genitalia, Sta. B1 (5), Carson River Escarpment, 14 August 1975, WAM 626.77 ex WAM 1348.75, Dissection B; b) interior of penis chamber, Sta. B1 (7), Carson River Escarpment, 15 August 1975, WAM 627.77, Dissection A. Scale lines as marked.

Paratopotype

WAM 627.77, 1 live adult from the type locality.

Paratypes

Drysdale River National Park, all collected in August 1975: Sta. B1-2, 1 km west of Glider Gorge campsite, Carson Escarpment (Carson 4268—636:603) (1 live adult, FMNH 200854); Sta. B1-3, entrance to Glider Gorge, Carson River Escarpment (Carson 4268—655:602) (7 dead adults, 5 live and 2 dead juveniles, WAM 170.76, FMNH 200853); Sta. B1-4, scree slope on south side of Glider Gorge, Carson River Escarpment (Carson 4268—657:599) (1 dead adult, WAM 171.76); Sta. B1-5, above 0.5 km up from entrance to Glider Gorge, Carson River Escarpment (Carson 4268—662:600) (2 live adults, 1 live juvenile, WAM 173.76, WAM 1348.75, WAM 1349.75); Sta. B1-7, about 0.5 km north of entrance to Glider Gorge (Carson 4268—658:617) (1 dead adult, WAM 174.76); Sta. B1-8, Carson River Escarpment about 1 km north of Glider Gorge (Carson 4268—659:611) (1 dead juvenile, WAM 175.76); Sta. C1-3, western side of Worriga Gorge on Palmoondoora Creek, about 2 km downstream from Morgan Falls (Ashton 4267—491:389) (1 live juvenile, WAM 1351.75); Sta. C2-2, east of Carson River just south of its junction with Woorakin Creek (Ashton 4267—585:340) (2 fragments, WAM 1352.75); Sta. C5-3, Forest Creek about 0.5 km upstream from Sta. C-5 campsite at Dysphania Gorge (Carson 4268—786:788) (2 fragments, WAM 183.76).

Diagnosis

Shell 14.15-19.1 mm (mean 16.73 mm) in diameter, with 5 ⅛ to 5¾ (mean 5 ⅜ +) whorls. Apex and spire moderately and evenly elevated **(Fig. 38c)**, not or only slightly rounded above, height of shell 9.3-11.7 mm (mean 10.51 mm), H/D ratio 0.594-0.665 (mean 0.630). Apical sculpture **(Plate 12d)** typical, postapical whorls with narrow, crowded, fairly prominent radial ribs, 8-10 per mm, absent on shell base which has weak incised spiral lines. Shell periphery weakly angulated to angulated **(Fig. 38c)**. Body whorl not to very slightly descending behind lip, which is strongly flared. Umbilicus narrowly open **(Fig. 38d)**, 1.0-1.8 mm (mean 1.31 mm) wide, D/U ratio 9.86-19.1 (mean 13.0). Basal lip without protrusion. Colour bands greatly reduced in prominence to absent, columellar patch absent. Based on 19 measured adults.

Genitalia **(Figs 39a-b)** in resting phase, all apical organs except albumen gland (GG) small and thin. Hermaphroditic duct (GD) entering laterally on talon (GT). Vagina (V) extremely long for genus, slightly exceeding length of penis sheath. Spermatheca (S) with longer than usual thickened basal section, head not greatly expanded, free oviduct (UV) short and slender. Vas deferens (VD) entering penis sheath (PS) near apex, coiled complexly below insertion of penial retractor muscle **(Fig. 39b, PR)**. Penis very long and tightly coiled within sheath, internally **(Fig. 39b)** with very large and widely spaced pustules, a distinct gutter leading from tip of the short conical verge, basal two-thirds of penis with highly modified wide ridging. Major pilaster (PT) a row of wider tubercles, each with one large point, some wall tubercles with single points on anterior edge **(Figs 36a, 39b)**. Based on two dissected individuals.

Discussion

All known localities for *Amplirhagada drysdaleana* are associated with the Carson Escarpment near the banks of the Carson River, a major tributary of the King Edward River that parallels the larger Drysdale River for much of its length. The nearest described species, *A. kalumburuana* from the vicinity of Kalumburu Mission on the western fringes of the Sir Frederick Hills and near the mouth of the King Edward River, agrees in having a long vagina, coiled penis, and complex folding of the vas deferens (compare **Figs. 39** and **44**), but has a much smaller verge and the major pilaster (PT) is wide and has points on the transverse corrugations **(Fig. 37b)**. The shell of *A. kalumburuana* has at most an umbilical chink **(Fig. 43d)**, has weaker and more irregular radial sculpture **(Plate 12f)**, and much brighter colouring. The two species are evidently closely related, despite the different appearing shells.

Conditions were extremely dry when the fieldwork was carried on in the Drysdale River National Park from 12-21 August 1975. Little living material was obtained. Only 5 live adults, two of which have been dissected, and 5 live juveniles were obtained. Size and shape variation in the only set of dead shells is summarized in **Table 18.**

The name *drysdaleana* has been selected in recognition of the Drysdale River National Park which includes all the known localities, rather than citing just the Carson River.

AMPLIRHAGADA QUESTROANA SP. NOV.

(Plate 12e; Figs. 37a, 38a-b, 40a-b)

Comparative remarks

Amplirhagada questroana is characterized by its narrowly open umbilicus **(Fig. 38b)**, fine radial sculpture **(Plate 12e)**, rounded periphery **(Fig. 38a)**, rather strongly elevated spire and bright colour. *A. carinata* is nearly identical in size and umbilical features **(Fig. 43b)**, but has a carinated periphery **(Fig. 43a)**, more depressed spire, and noticeably stronger sculpture **(Plate 13e)**. *A. drysdaleana* agrees in sculpture **(Plate 12d)**, umbilicus **(Fig. 38d)**, and approximate degree of spire elevation **(Fig. 38c)**, but has an angulated periphery and is noticeably smaller in size (mean diameter 16.73 mm). *A. astuta* (Iredale, 1939) from Koolan Island is more depressed and has

Table 18: Local Variation in Umbilicated *Amplirhagada*

Species and Station	Number of Adults Measured	Mean, Range, and SEM of: Shell Height	Shell Diameter	H/D Ratio
A. drysdaleana				
B1-3, Drysdale National Park	7	10.04 ± 0.218 (9.3-10.8)	16.16 ± 0.417 (14.15-17.2)	0.622 ± 0.009 (0.594-0.664)
A. pusilla				
El, Prince Regent	23	9.86 ± 0.241 (8.05-12.95)	16.77 ± 0.304 (14.45-20.2)	0.586 ± 0.005 (0.544-0.641)
Pitta Creek, dead	6	10.93 ± 0.423 (9.5-12.4)	17.53 ± 0.303 (16.7-18.65)	0.622 ± 0.016 (0.565-0.665)
Pitta Creek, live	4	9.85 ± 0.560 (8.25-10.85)	16.60 ± 0.729 (14.45-17.65)	0.592 ± 0.009 (0.571-0.615)
W4(1), Prince Regent	18	9.62 ± 0.165 (8.7-11.4)	16.43 ± 0.187 (15.0-17.8)	0.586 ± 0.007 (0.532-0.640)
W4(4), Prince Regent	4	10.23 ± 0.312 (9.6-10.9)	17.11 ± 0.356 (16.5-18.1)	0.601 ± 0.020 (0.575-0.661)
A. kalumburuana				
Mt Elizabeth Homestead	5	12.56 ± 0.337 (11.8-13.7)	17.50 ± 0.164 (17.0-17.9)	0.718 ± 0.021 (0.680-0.792)
Sta. WA.-220	6	13.07 ± 0.136 (12.7-13.6)	18.76 ± 0.155 (18.35-19.4)	0.697 ± 0.007 (0.676-0.723)
A. questroana				
Sta. 222, 224	5	13.21 ± 0.327 (12.4-14.4)	20.02 ± 0.375 (18.9-21.15)	0.660 ± 0.011 (0.631-0.688)
A. carinata				
Kongorow Pool	4	10.55 ± 0.296 (10.1-11.4)	18.80 ± 0.592 (17.9-20.5)	0.562 ± 0.008 (0.540-0.580)
Sta. WA-317, live	3	11.18 ± 0.246 (10.7-11.5)	19.53 ± 0.633 (18.3-20.4)	0.573 ± 0.009 (0.556-0.585)
Sta. WA-317 dead	12	11.69 ± 0.210 (10.9-13.5)	20.54 ± 0.207 (19.1-21.5)	0.569 ± 0.009 (0.530-0.637)
Sta. WA-318, dead	36	11.45 ± 0.088 (10.6-12.8)	19.82 ± 0.120 (18.4-21.7)	0.578 ± 0.004 (0.538-0.636)
A. astuta				
WAM 1546.70	4	11.56 ± 0.372 (10.7-12.5)	19.40 ± 0.502 (18.7-20.85)	0.596 ± 0.010 (0.572-0.621)

Table 18: Local Variation in Umbilicated *Amplirhagada* (continued)

Species and Station	Number of Adults Measured	Mean, Range, and SEM of: Whorls	Umbilical Width	D/U Ratio
A. drysdaleana				
B1-3, Drysdale National Park	7	5 ⅜ (5 ⅛-5 ⅝)	1.33 ± 0.031 (1.2-1.4)	12.2 ± 0.508 (10.1-13.7)
A. pusilla				
El, Prince Regent	23	5 ⅝+ (5 ⅛-6 ⅛)	1.36 ± 0.038 (0.95-1.7)	12.6 ± 0.387 (8.8-17.5)
Pitta Creek, dead	6	5 ⅝ (5 ⅜-5 ⅞)	1.31 ± 0.054 (1.2-1.55)	13.5 ± 0.551 (11.4-15.5)
Pitta Creek, live	4	5½ (5¼-5¾)	1.48 ± 0.048 (1.4-1.6)	11.3 ± 0.494 (10.3-12.6)
W4(1), Prince Regent	18	5 ⅜ (5 ⅛-5 ⅞)	1.10 ± 0.046 (0.8-1.15)	15.3 ± 0.608 (10.5-22.0)
W4(4), Prince Regent	4	5 ⅝– (5¼-5¾)	0.98 ± 0.048 (0.9-1.1)	17.7 ± 0.980 (15.6-20.1)
A. kalumburuana				
Mt Elizabeth Homestead	5	5 ⅞– (5 ⅝-6 ⅛)	closed	closed
Sta. WA-220	6	6+ (5 ⅞-6¼)	closed	closed
A. questroana				
Sta. 222,224	5	5¾ – (5 ⅝-5 ⅞)	1.34 ± 0.176 (1.0-2.0)	15.9 ± 1.93 (9.45-21.1)
A. carinata				
Kongorow Pool	4	5 ⅜ (5¼-5½)	1.38 ± 0.063 (1.2-1.5)	13.8 ± 0.638 (12.1-14.9)
Sta. WA-317, live	3	5 ⅝+ (5 ⅝-5¾)	1.41 ± 0.073 (1.3-1.55)	13.8 ± 0.318 (13.2-14.2)
Sta. WA-317, dead	12	5 ⅝+ (5½-6)	1.64 ± 0.120 (1.1-2.4)	13.3 ± 0.921 (8.83-19.1)
Sta. WA-318, dead	36	5 ⅝– (5 ⅜-5 ⅞)	1.51 ± 0.038 (1.1-2.0)	13.4 ± 0.311 (10.5-18.1)
A. astuta				
WAM 1546.70	4	5 ⅝ (5½-5¾)	1.43 ± 0.048 (1.3-1.5)	13.7 ± 0.578 (12.5-14.9)

an angulated periphery. *A. pusilla* has relatively strong sculpture **(Plate 12c)**, an angulated periphery **(Fig. 38e)**, depressed spire, and is the same size as *A. drysdaleana,* thus differing obviously from *A. questroana*. *A. percita* (Iredale, 1939) lacks radial sculpture **(Plate 14e)** and is unicoloured. Anatomically, *A. questroana* is distinguished by a short vaginal region **(Fig. 40a)**, very broad main pilaster **(Fig. 37a)** with only three or four blunt points on wide corrugations, and very short basal area of the penis with longitudinal pilasters **(Fig. 40b)**. *A. carinata* **(Fig. 45b)** has a very well developed gutter, finer pustulations, and the main pilaster corrugations have many fine sharp points **(Fig. 37g)**. *A. drysdaleana* has only a simplified main pilaster **(Fig. 36a)** and very different pustulose texture **(Fig. 39b)** on the walls of the penis. *A. pusilla* **(Fig. 42)** has a short verge, a narrow main pilaster (PT) with broad corrugations bearing only a few sharp points **(Fig. 37c)**, very well developed gutter, and quite altered wall sculpture inside the penis. All of the above species are very similar in shell shape and general appearance, but their penial structures are diverse.

Holotype

WAM 1357.75, Sta. WA-222, shaded talus above flood levels, east of Chamberlain River above Big Hole, El Questro Station, north-east Kimberley, Western Australia (1:100,000 'Pentecost' map sheet 4466, grid reference 332:858). Collected by Alan Solem and Carl Christensen 8 November 1976. Height of shell 13.1 mm, diameter 20.4 mm, H/D ratio 0.642, whorls 5 ⅝ –, umbilical width 1.35 mm, D/U ratio 15.1.

Paratopotypes

WAM 607.77, WAM 1358.75, FMNH 199990, FMNH 199991, 3 live adults, 14 live juveniles, 3 shell fragments, from the type locality.

Paratype

Sta. WA-224, north bank Pentecost River at El Questro Homestead (1:100,000 'Elgee' map sheet 4465, grid reference 299:909) (1 live adult, FMNH 199989, Alan Solem and Carl Christensen 8 November 1976).

Diagnosis

Shell 18.9-21.15 mm (mean 20.02 mm) in diameter, with 5 ⅝ to 5 ⅞ (mean 5 ¾ –) whorls. Apex and spire strongly and evenly elevated **(Fig. 38a)**, not rounded above, height of shell 12.4-14.4 mm (mean 13.21 mm), H/D ratio 0.631-0.688 (mean 0.660). Apical sculpture greatly reduced in prominence **(Plate 12e)**, only traces of radial lines remaining, postapical whorls with narrow, rather crowded, somewhat irregular radial ribs **(Plate 12e)**, absent on shell base which shows faint incised spiral lines. Shell periphery varying from rounded **(Fig. 38a)** to with a faint angulation. Body whorl slightly and gradually descending behind lip, which is strongly flared, although narrow. Umbilicus narrowly open **(Fig. 38b)**, 1.0-2.0 mm (mean 1.34 mm) wide, D/U ratio 9.45-21.1 (mean 15.9). Basal lip without any trace of a protrusion. Colour bands prominent, with a moderate to deep reddish suffusion on the upper spire, no columellar colour patch. Based on 5 measured adults.

Genitalia **(Fig. 40a)** in male active phase. Talon (GT) receiving hermaphroditic duct (GD) near head. Vagina (V) relatively long, spermatheca (S) base and lower shaft greatly swollen, probably indicating recent mating. Vas deferens (VD) entering penis sheath (PS) just below head, coiling pattern unknown since examples collected the day after a heavy (33 mm) rain and presumed mating. Penis complex slender, internally **(Fig. 40b)** with a normal verge (PV), no sperm gutter, a short broad pilaster that retains only three or four remnant points on the relatively narrow corrugations **(Fig. 37a)**. Walls of upper penis with complex and varying pustules, basal longitudinal ridges narrow and simple. Based on two dissected individuals.

Discussion

The soft parts of *Amplirhagada questroana* would not pull effectively, so that the shells of two paratypes had to be fragmented in order to study the anatomy. Significant differences in the stage of the reproductive cycle were seen. The specimen used for the whole genitalia (Dissection A, **Fig. 40a**) was male active, although probably just adult at the end of the previous wet season. The reduced size of the albumen gland and relatively narrow prostate-uterine area are indicative of newly mature animals. The other dissected individual, used for the penis interior (Dissection B, **Fig. 40b**), had a normal-sized albumen gland and the uterine section was much thicker. Because these differences involve the upper genital tract, which normally is not extracted when the animal breaks off, it was decided not to sacrifice any more of the three remaining adult specimens at this time. Exactly equivalent differences were seen in *Xanthomelon prudhoensis* (Smith, 1894) (see Solem, 1979: Fig. 9 and Discussion). In that species the barely adult shells collected in February and March had similarly small albumen glands and undeveloped prostate-uterine areas.

Amplirhagada questroana may have a rather wide distribution in the Durack Ranges and Elgee Cliffs region of the Chamberlain and Pentecost Rivers. Whether it inhabits the nearby Durham River and Salmond River basins is unknown, but less probable. A sudden 33 mm rainfall the night before the Sta. WA-222 examples were collected effectively prevented any exploration of upriver areas, probably triggered mating by the snails which produced the extended vas deferens and also led to active movement, so that the pattern of sealing during aestivation is unknown. All collected examples were partly extended. The type locality is a talus slope of very large boulders that mostly had the crevices silted up. A few pockets of decaying leaves and leaf mould in which the live snails were moving about were uncovered. The actual inhabitable area in the talus was quite small and the five live adults resulted from a person day of rock moving. Surprisingly, no dead specimens were obtained. The single adult from Sta. WA-224 was found under a log on the flood plain of the

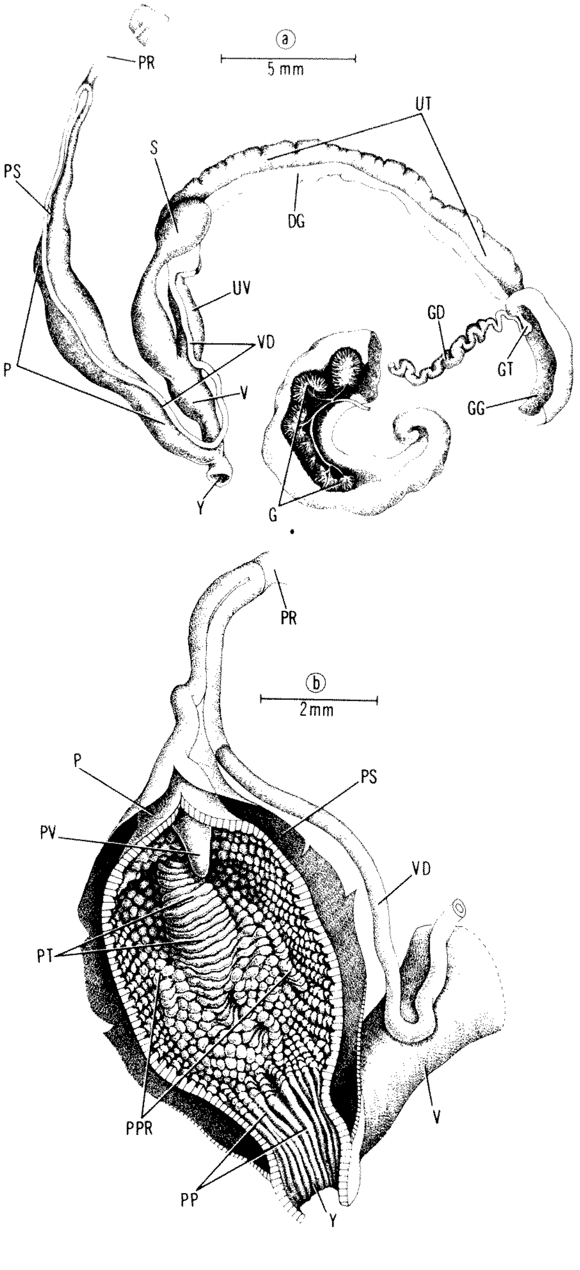


Fig. 40: Genitalia of *Amplirhagada questroana,* Sta. WA-222, El Questro Station, 8 November 1976, a) genitalia, WAM 607.77, Dissection A; b) interior of penis chamber, FMNH 199991, Dissection B. Scale lines as marked.

Pentecost River near El Questro Homestead. Despite extensive searching, no other examples were found and I suspect that this was a flood strandee from upriver.

The name *questroana* honors El Questro Station and its owners, Mr and Mrs Norman Flohr, who provided most useful advice and hospitality during fieldwork on their station in November 1976.

AMPLIRHAGADA PUSILLA SP. NOV.

(Plate 12c; Figs 37c, 38e-f, 41b, 42)

Comparative remarks

Amplirhagada pusilla is a small (mean diameter 16.73 mm), angulated **(Fig. 38e)**, relatively depressed species (mean H/D ratio 0.590) with open umbilicus **(Fig. 38f)** and rather strong radial sculpture on the shell spire **(Plate 12c)**. *A. drysdaleana* has weaker radial sculpture **(Plate 12d)**, is slightly less depressed in shape, and has a less angulated periphery **(Fig. 38c)**, but is almost identical in size, general appearance and umbilical features. *A. astuta* (Iredale, 1939) from Koolan Island is larger (mean diameter 19.45 mm) and with less sharply defined radial sculpture. *A. kalumburuana* is slightly larger (mean diameter 18.19 mm), more narrowly umbilicated **(Fig. 43d)**, with less regular sculpture **(Plate 12f)** and rounded periphery **(Fig. 43c)**. *A. carinata* is a bit more depressed (mean H/D ratio 0.578), sharply angulated **(Fig. 43a)**, and considerably larger (mean diameter 19.98 mm). *A. questroana* also is much larger (mean diamater 20.02 mm), more elevated **(Fig. 38a)**, and has a less angulated periphery. Anatomically, *A. pusilla* has a short vagina and relatively long penis **(Fig. 41b)**, which internally **(Fig. 42)** has a very small verge, distinct sperm gutter, a long zone of modified basal corrugations that resemble those seen in *A. elevata,* and a main pilaster that has very wide corrugations with only a very few large and blunt points on the surface **(Figs 37c, 42)**. *A. elevata* has a much reduced pilaster and no pustules remaining **(Figs 36f, 58a)**, and is very different conchologically. *A. drysdaleana* has an extremely long vagina, and has a very different penis interior **(Figs 39a-b)**. It has almost no features in common with *A. pusilla. A. questroana* **(Fig. 40b)** has a somewhat larger verge, no sperm gutter, a short broad pilaster with a few greatly reduced blunt points on the narrow corrugations **(Fig. 37a)** and the pustulose section of the wall much longer than the ridged area.

Holotype

WAM 1356.75, vine thicket in gorge of Pitta Creek, south of Sta. El, Upper Prince Regent River, north-west Kimberley, Western Australia (1:250,000 'Prince

Regent' map sheet SD51-16, grid reference 353:992). Collected by Barry R. Wilson 22 August 1974. Height of shell 10.25 mm, diameter 17.3 mm, H/D ratio 0.592, umbilical width 1.6 mm, D/U ratio 10.8.

Paratopotypes

WAM 230.75, WAM 1355.75, FMNH 200831, 3 live, 6 dead adults and 1 live juvenile from the type locality.

Paratypes

Prince Regent River Reserve, all collected August 1974: Sta. El, bower bird bower at base of rock cliff in gorge 0.8 km west of campsite on Upper Prince Regent River above junction with Womaramara Creek (15°49′S, 125°37′E) (23 dead adults, 3 dead juveniles, WAM 236.75, FMNH 200829, K.T. Richards, 22 August 1974); Sta. W4 (1), scree slopes below eastern face of Mt Trafalgar (Prince Regent SD51-16—291:068) (18 dead adults, 17 dead juveniles, WAM 358.75, WAM 359.75, WAM 360.75, WAM 361.75, WAM 362.75, WAM 364.75, WAM 365.75, FMNH 200830); Sta. W4 (4), scree slopes of Mt Trafalgar (Prince Regent SD51-16—291:068) (4 dead adults and 2 dead juveniles, WAM 366.75); Sta. W6, gorge of Youwanjela Creek, Upper Prince Regent River (15°34′S, 125°25′E) (2 dead adults, WAM 357.75); Sta. W6 (1), valley slope on north side of Youwanjela Creek (Prince Regent SD51-16—332:032) (1 dead juvenile, WAM 363.75).

Diagnosis

Shell 14.45-20.2 mm (mean 16.73 mm) in diameter, with 5 1/8 to 6 1/8 (mean 5½ +) whorls. Apex and spire moderately and usually evenly elevated **(Fig. 38e)**, sometimes slightly rounded above, height of shell 8.05-12.95 mm (mean 9.93 mm), H/D ratio 0.532-0.665 (mean 0.590). Apical sculpture typical, postapical whorls with prominent, rather crowded radial ribs **(Plate 12c)**, 6-8 per mm, shell base with incised spiral lines. Shell periphery sharply angulated **(Fig. 38e)**. Body whorl not to very slightly descending behind lip, which is narrowly flared. Umbilicus open **(Fig. 38f)**, 0.8-1.7 mm (mean 1.24 mm) wide, D/U ratio 8.76-22.0 (mean 13.9). Basal lip without protrusion. Colour bands narrow, reduced in prominence, no columellar colour patch. Based on 59 measured adults.

Genitalia **(Figs 41b, 42)** in resting phase. Hermaphroditic duct (GD) entering laterally on head of talon (GT). Vagina (V) short, spermatheca (S) and free oviduct (UV) short and thickened. Vas deferens (VD) entering penis sheath near top, slightly coiled below insertion of penial retractor muscle (PR). Penis quite long, sometimes coiled within sheath, internally **(Fig. 42)** with very short conical verge (PV), comparatively small pustules on the upper third to half of penis, lower two-thirds to half with slightly narrower ridges than those found in *A. elevata* **(Fig. 58a)**. A distinct sperm gutter between two raised secondary pilasters (PP) is developed. Main pilaster (PT) slender, rather short, with wide corrugations that have three to four large

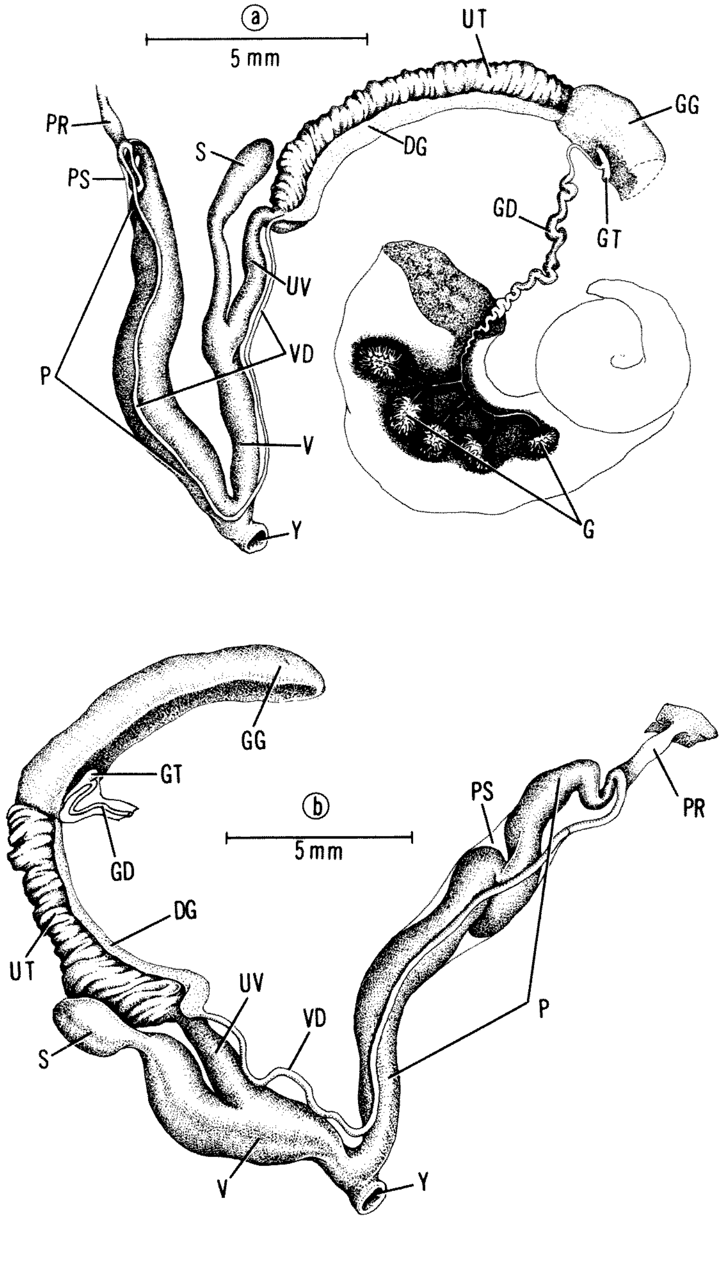


Fig. 41: Genitalia of *Amplirhagada katerana* and *A. pusilla,* a) *A. katerana,* Katers Island, Bonaparte Archipelago, 10 June 1972, WAM 643.77 ex WAM 1285.75, composite of rehydrated materials; b) *A. pusilla,* Pitta Creek, Prince Regent River, 22 August 1974, WAM 628.77, WAM 629.77, both ex WAM 1356.75, composite of Dissections A and B. Scale lines equal 5 mm.

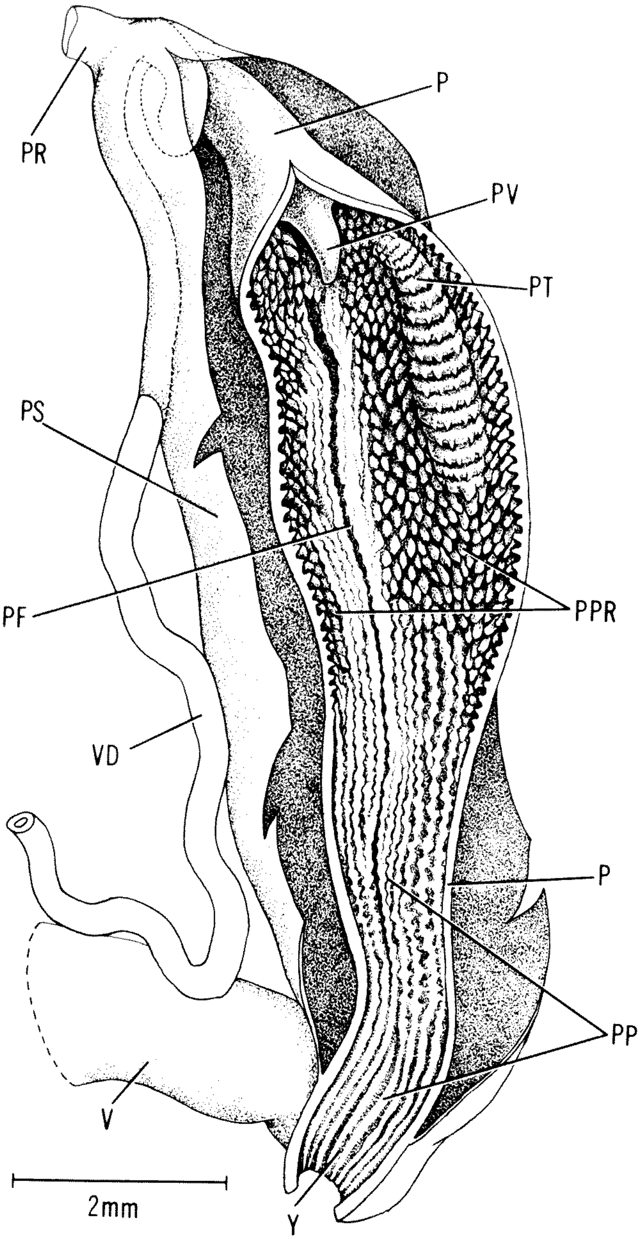


Fig. 42: Penis chamber of *Amplirhagada pusilla,* Pitta Creek, Prince Regent River, 22 August 1974, WAM 628.77, WAM 629.77, both ex WAM 1356.75, composite of Dissections A and B. Scale line equals 2 mm.

points **(Fig. 37c)**. At anterior margin, it abruptly descends into typical pustules as the profile lowers. Based on two dissected individuals.

Discussion

Live material of *Amplirhagada pusilla* was obtained on Pitta Creek during the last day of the Prince Regent River Survey. Dead shells had been taken previously at five other stations. Only slight size and shape differences could be found among the several populations sampled **(Table 18)**. Compared with the other Prince Regent River Reserve species, *Amplirhagada wilsoni* and *A. elevata, A. pusilla* is much smaller, more heavily sculptured **(Plate 12c, Plate 14a-b)**, has an open umbilicus, is more depressed, and has a much lower whorl count. *A. wilsoni* and *A. pusilla* were taken at Station W6, although on different sides of Youwanjela Creek. *A. elevata* and *A. pusilla* were collected at Station W6 (1). None were taken in quantity, so that the question of dominance cannot be answered.

Although *A. pusilla* is very similar in shell form and size to *A. drysdaleana* from the Carson River Escarpment **(Table 18)**, the genitalia shows much greater similarity to the structures seen in *A. elevata.* It proved impossible to extract the animal, and two of the four live collected adults were smashed in order to obtain anatomical details.

The name *pusilla* refers to the small size of the shell compared with other *Amplirhagada* from the north-west Kimberley region. *A. pusilla* includes both Camaenid sp. A. and Camaenid sp. B of the Prince Regent River Reserve Survey (Wilson & Smith, 1975: 99).

AMPLIRHAGADA KATERANA SP. NOV.

(Figs 37d, 41a, 43e-f)

Comparative remarks

Amplirhagada katerana is a relatively low spired shell with angulated periphery **(Fig. 43e)**, weak radial sculpture above that generally is overpowered by the incised spiral lines on the body whorl, has the umbilicus slightly open in most examples **(Fig. 43f)**, and has the supraperipheral colour band extended up to or almost to the suture. In shape and size, *A. katerana* is nearest to *A. wilsoni* from the Prince Regent River Reserve, but that species differs in being less angulated, having a more regularly elevated (rather than dome-shaped) spire **(Fig. 54e)**, the umbilical chink more nearly closed, and the colour bands are both narrow. The two species are very similar in radial sculpture, but the incised spiral sculpture is much stronger in *A. katerana.* The colour pattern is nearly identical to that of *A. kalumburuana,* which

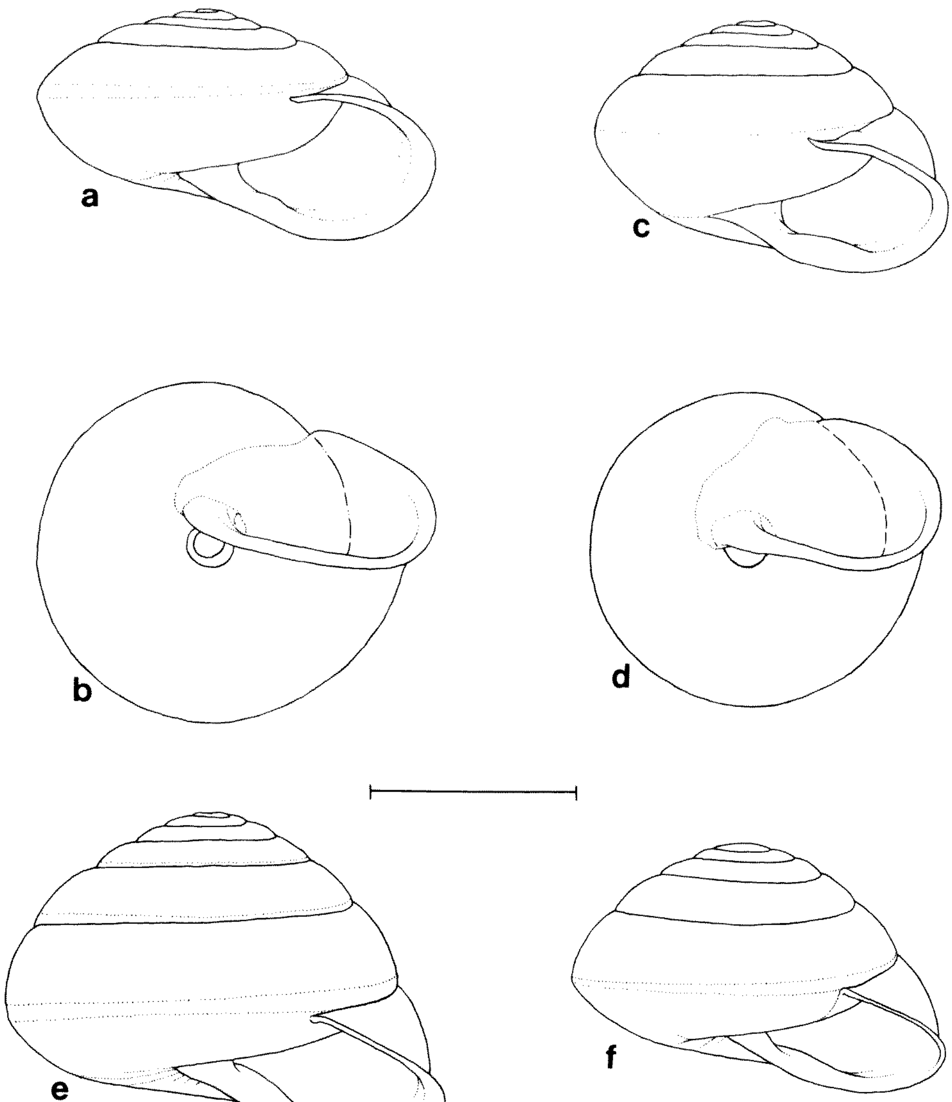


Fig. 43: Shells of *Amplirhagada*, a-b) *A. carinata*, Sta. WA-317, Mt Hart Station, King Leopold Ranges, WAM 1331.75, holotype; c-d) *A. kalumburuana*, Sta. WA-220, Kalumburu Mission, WAM 1226.75, holotype; e-f) *A. katerana*, Katers Island, Bonaparte Archipelago, e is WAM 1241.75, holotype, f is WAM 1285.75, paratopotype. Scale line equals 10 mm.

is a much smaller shell (mean diameter 18.19 mm) with an average of only 6 – whorls. Anatomically, *A. katerana* has widely spaced, rather large points on a prominent main pilaster **(Fig. 37d)**, the pustules on the penis wall are arranged in distinct rows, and there is simple coiling of the vas deferens **(Fig. 41a)**. *A. wilsoni* has a longer vagina **(Fig. 57a)** and the main pilaster (PT, **Fig. 58a)** is longer, with the points on the corrugations **(Figs 37d, f)** smaller and crowded onto the centre rather than spaced out as in *A. katerana*. Comparisons in detail with other species are not possible because only reconstructed observations based on dried specimens could be made.

Holotype

WAM 1241.75, Katers Island, Bonaparte Archipelago, Western Australia (1:250,000 'Montague Sound' map sheet SD51-12, grid reference approximately 166:344). Collected by WAM Survey team 10 June 1972. Shell height 17.0 mm, diameter 21.95 mm, H/D ratio 0.774, whorls 6¾.

Paratopotypes

WAM 1240.75, WAM 1285.75, FMNH 200850, 27 dead adults and 6 broken individuals from the type locality.

Paratypes

Bigge Island, Bonaparte Archipelago (Montague Sound SD51-12—155:300) (2 dead adults, WAM 1259.75, L.A. Smith, 6 June 1972).

Other material

Augustus Island (Prince Regent SD51-16—*ca.* 060:230) (1 dead juvenile, WAM 1254.75, N. McKenzie and L.A. Smith, 17 August 1971); 17.6 km east of Kuri Bay (1 dead adult, WAM 1260.75, L. Smith, 25-26 August 1971).

Diagnosis

Shell 19.2-25.0 mm (mean 21.56 mm) in diameter, with 5 ⅞ to 7 (mean 6 ⅛ +) whorls. Apex and spire strongly elevated, rounded to dome-shaped, height of shell 12.6-17.4 mm (mean 15.27 mm), H/D ratio 0.627-0.790 (mean 0.708). Apical sculpture unknown, postapical sculpture of very fine and crowded radial ribs, 12-15/mm, on upper spire, fading out by body whorl and replaced by fine incised spiral lines on body whorl and shell base. Shell periphery acutely to obtusely angulated **(Fig. 43e)**, rarely appearing almost rounded. Body whorl not to very slightly descending behind lip, which is slightly to moderately flared, reflexing to cover most of umbilicus, but with a narrow opening usually visible **(Fig. 43f)**. Basal lip normally without, sometimes with a faint protrusion. Subsutural colour band and columellar patch weak or absent. Supraperipheral colour normally extended upwards, only slightly reduced in intensity, almost reaching to next suture. Based on 30 measured adults.

Genitalia **(Fig. 42a)** in inactive stage, most organs reduced in size. Vagina (V) about one-third length of penis, free oviduct (UV) and spermatheca (S) long. Vas deferens (VD) with simple apical coiling. Penis interior with typical verge length, pustules arranged in rows, and a fairly short main pilaster with narrow corrugations edged by several rather large, widely spaced points **(Fig. 37d)**. Based on two mummified specimens softened with trisodium phosphate and then partially cut into serial sections to reconstruct anatomy.

Discussion

The two adults from Bigge Island (WAM 1259.75) are at the small end of the size range for the Katers Island populations and have a little more open umbilicus, but do not show any major conchological differences. The juvenile from Augustus Island (WAM 1254.75) has reduced radial sculpture and may belong to another taxon, but is provisionally assigned here. The very worn, large (diameter 23.75 mm) adult from 17.6 km east of Kuri Bay is too worn for certain identification, but agrees in form and size more with this species than any other. Neither of the last two specimens are considered to be paratypes.

Thus, the potential range of *Amplirhagada katerana* is from Camden Sound north almost to Admiralty Gulf, but the actual range is uncertain.

The Katers Island sample contained what I am interpreting as two year classes. Worn individuals had a thicker shell, were larger, and with slightly more whorls, than several smaller, thinner shells. Several of the latter had been collected alive, but not preserved, or preserved and subsequently allowed to mummify. Size and shape comparisons of the two morphs are:

	Number of Specimens	Height	Diameter	Whorls
Young	7	14.05 (12.7-15.5)	19.96 (19.2-20.7)	6 3/8 – (6 1/4 - 6 1/2)
Old	21	15.93 (12.8-17.4)	22.28 (20.3-25.0)	6 5/8 (5 7/8 -7)

Since their H/D ratios were essentially identical, this has been omitted from the comparison.

Attempted resurrection of the mummified remains with trisodium phosphate was only partly successful. On the basis of knowledge from other species, it was possible to diagram the basic genital tract **(Fig. 41a)**, including such details as the vas deferens (VD) coiling pattern and underdeveloped state of the ovotestis (G). In one specimen, the upper half of the penis interior could be examined by slicing the penis into short segments and then opening them. This was not successful enough to permit illustration of the full interior, but only to prepare a diagram of the main pilaster surface **(Fig. 37d)** and present the few details given in the species diagnosis. The shell of *A. katerana* is very distinctive, and I have no doubt as to its validity despite the inadequate anatomical presentation.

AMPLIRHAGADA KALUMBURUANA SP. NOV.

(Plate 12f; Figs 37b, 43c-d, 44a-c)

Comparative remarks

Amplirhagada kalumburuana is relatively small, mean diameter 18.19 mm, with fine radial sculpture **(Plate 12f)**, a variable umbilical chink **(Fig. 43d)**, weakly angulated periphery **(Fig. 43c)**, and a somewhat unusual colour pattern in that the supraperipheral band tends to extend upwards on the body whorl and spire, sometimes reaching the next suture. *A. combeana* Iredale and *A. imitata* (Smith) differ immediately in their very strong radial sculpture **(Plate 12a-b)** and higher spires **(Figs 71e-h)**. Taxa with similar colour pattern, *A. katerana* and *A. alta intermedia,* are larger (mean diameter 21.56 mm and 22.05 mm, respectively), with a reduced radial sculpture and more angulated periphery **(Figs 43e-f,** ***A. katerana*****)** or very much higher spire **(Fig. 59e)** and H/D ratio (*A. alta intermedia,* mean 0.875). Anatomically, *A. kalumburuana* has an extremely long vagina **(Fig. 44a)**, the long penis tightly coiled within the sheath **(Fig. 44b)**, the longitudinal ridge zone inside the penis much longer **(Fig. 44c)** than in any species except *A. elevata* **(Fig. 58a)**, a very short verge **(Fig. 44c)**, reduced main pilaster (PT) with wide corrugations and prominent sharp points **(Fig. 37b)**, and weak accessory pilasters forming a slight sperm gutter **(Fig. 44c)**. No other *Amplirhagada* comes close to matching this combination of features. *A. drysdaleana* **(Figs 39a-b)** has an equally long vagina and coiled penis, but very different wall sculpture and main pilaster, more regular shell sculpture **(Plate 12d)**, and reduced colour pattern. *A. pusilla* has strong shell sculpture **(Plate 12c)**, a more angulated periphery **(Fig. 38e)**, much shorter vagina **(Fig. 41b)**, altered main pilaster **(Fig. 37c)**, and different pustulation **(Fig. 42)**.

Holotype

WAM 1226.75, Sta. WA-220, north-east facing cove, 6.5 km south of Kalumburu Mission headquarters, north-west Kimberley, Western Australia (1:100,000 'Drysdale' map sheet 4269, grid reference 132:474). Collected by Alan Solem and John Kethley, 28 October 1976, under rocks and in talus on steep slopes in a modified vine thicket. Height of shell 12.7 mm, diameter 18.35 mm, H/D ratio 0.692, whorls 5 $\frac{7}{8}$.

Paratopotypes

WAM 617.77, WAM 1227.75, FMNH 200021, FMNH 200022, FMNH 200674, 2 live and 2 dead adults, 3 live juveniles, 1 fragment from the type locality.

Paratypes

WAM 1307.75, FMNH 200832, 5 dead adults, 32 km east of Mt Elizabeth homestead, among rocks, Ian Crawford, 5 August 1966.

Diagnosis

Shell 17.0-19.4 mm (mean 18.19 mm) in diameter, with 5 5/8 to 6 1/4 (mean 6 –) whorls. Apex and spire evenly or almost evenly elevated, at most slightly rounded above **(Fig. 43c)**, height of shell 11.8-13.7 mm (mean 12.84 mm), H/D ratio 0.676-0.792 (mean 0.706). Apical structure typical **(Plate 12f)**, postapical whorls with low, somewhat irregular radial ribs, 7-10/mm above body whorl periphery, base of shells nearly smooth, with faint traces of very fine spiral incised lines visible in oblique lighting. Shell periphery weakly angulated to rounded. Body whorl gradually but distinctly deflected behind narrow flared lip **(Fig. 43c)**, which has a weak to moderate basal protrusion. Umbilicus open in juveniles, lip reflexing to partly to almost completely cover opening in adults **(Fig. 43d)**. Subsutural colour band absent, supraperipheral colour band extending upwards toward suture to a variable extent. No columellar colour patch present. Based on 11 measured adults.

Genitalia **(Fig. 44a)** in male active phase, only uterus (UT) unexpanded. Prostate (DG), ovotestis (G), and hermaphroditic duct (GD) greatly enlarged. Free oviduct (UV) and spermatheca (S) very short, sperm packet in head of spermatheca. Vagina (V) very long, exceeding length of penis sheath, without unusual internal features. Vas deferens (VD) entering penis sheath (PS) less than one-quarter of way from top, coiled below insertion of penial retractor muscle (PR). Penis complex slightly swollen, caused by tight coiling of long penis **(Fig. 44b)**. Penis (P) internally **(Fig. 44c)** with basal longitudinal ridge area occupying almost two-thirds of length, individual ridges narrow and only weakly corrugated. Verge (PV) very small, main pilaster (PT) small, rather short, with slender, sharp points and corrugations wide at base, narrowed on top **(Fig. 37b)**. Small accessory pilasters (PP) form a faint sperm gutter. Based on one adult specimen.

Discussion

The type locality is a patch of vine thicket clustering around the base of several large figs and other big trees. This lies on the east facing slope of a gully leading to a small falls and several permanent pools in an unnamed creek. The thicket is more open than the vine thicket patches investigated on the Mitchell Plateau, but many of the same thorny plant species were tangled with. Edges of the patch had been badly charred by recent fires, but apparently much of this particular thicket escapes the annual burn. Thunderstorms in the area on the two previous days evidently had resulted in snail activity, accounting for the sperm packet.

Because the differences from other species were so obvious, and such limited anatomical material was available, only the one example was dissected. The remaining two live collected adult specimens are reserved for future studies when the genus is better understood. In the dissected adult, both esophagus and stomach were greatly distended but empty, and the intestine contained little fecal material. This suggests that digestion of food and elimination of indigestible material must take place quite rapidly.

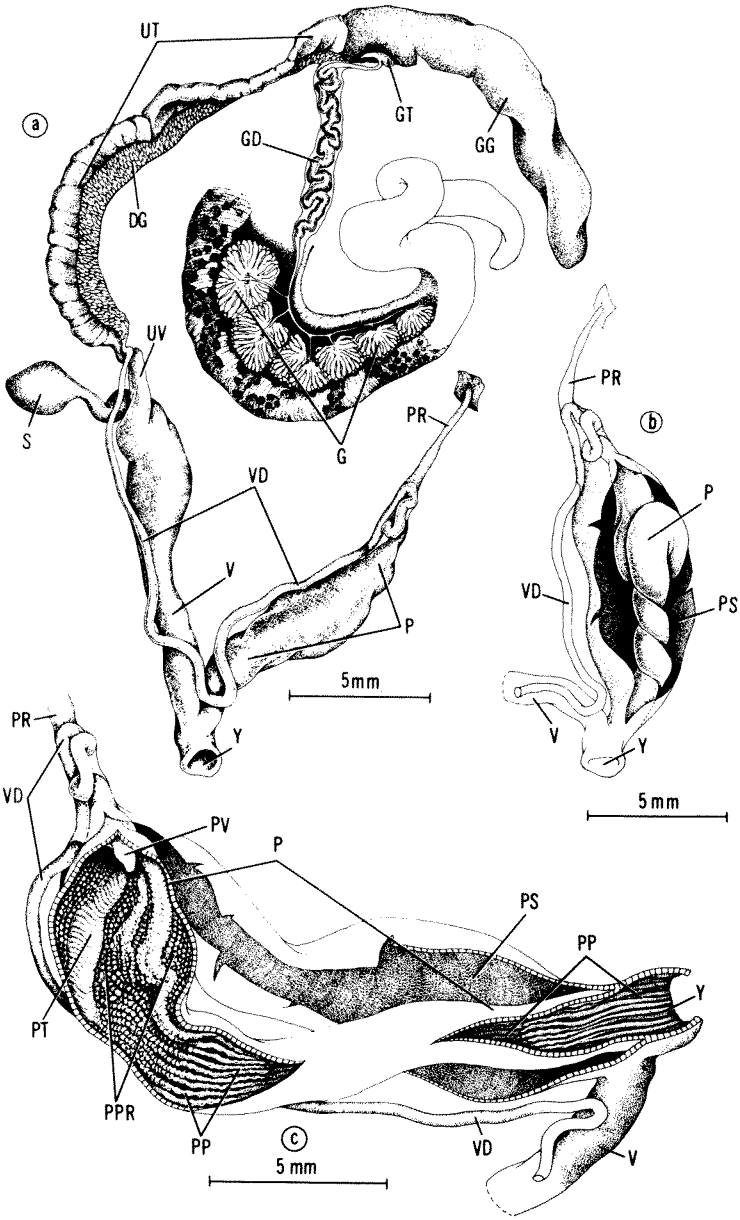


Fig. 44: Genitalia of ***Amplirhagada kalumburuana,*** Sta. WA-220, Kalumburu Mission, 28 October 1976, WAM 618.75, a) genitalia; b) penis coiled inside penis sheath; c) interior of penis chamber. Scale lines equal 5 mm.

Two large, bleached bones (WAM 1258.75) collected at Kalumburu by Harry Butler on 7 December 1965, probably are this species, but are not considered to be paratypes, nor included in the range of variation. They are 19.3 and 21.2 mm in diameter, H/D ratios 0.686 and 0.707, with 6¼ and 6¼ – whorls, respectively.

The five adult shells from 32 km east of Mt Elizabeth homestead **(Table 18)** averaged about 1 mm smaller in diameter although having ¼ whorl more, and tended to be slightly more angulated. These differences are not large enough and the material is too limited to warrant description, although the two populations may not be the same species. The approximately 240 km distance between the two known colonies is the longest range yet suggested for an inland species of *Amplirhagada.*

The name *kalumburuana* is from the nearby settlement and mission headquarters in token of thanks for hospitality extended during late October 1976.

AMPLIRHAGADA CARINATA SP. NOV.

(Plate 13e; Figs 37g, 43a-b, 45a-b)

Comparative remarks

Amplirhagada carinata has the most strongly angulated periphery **(Fig. 43a)** of any known species, relatively prominent postapical radial sculpture **(Plate 13e)**, a consistently open umbilicus **(Fig. 43b)**, usually prominent colour bands, but no umbilical colour patch, moderately large size (mean diameter 19.98 mm), and a relatively depressed shape (mean H/D ratio 0.578). *A. astuta* (Iredale, 1939) from Koolan Island is less sharply angulated **(Fig. 46b)** and with stronger radial sculpture. Of the other umbilicated species, only the much smaller (mean diameters 16.73 mm) *A. drysdaleana* and *A. pusilla* have any noticeable peripheral angulations **(Fig. 38c, e)**, while *A. questroana* **(Fig. 38a)** and the occasionally umbilicated *A. kalumburuana* **(Fig. 43c)** have rounded peripheries. *A. percita* (Iredale, 1939) from the Napier Range is variably umbilicated, but lacks any radial sculpture **(Plate 14e-f)**, is unicoloured, sometimes has a slightly angulated periphery, and generally is much smaller in size. Anatomically, the vagina (V) is very short and the spermatheca (S) relatively long with swollen base **(Fig. 45a)**, and the penis (P) relatively short and thick. Internally **(Fig. 45b)** the shortened region of basal longitudinal ridges in the penis, normal-sized verge (PV), thick and rather short main pilaster (PT) whose narrow corrugations have 8-12 fine, sharp points on their edges **(Fig. 37g)**, very fine wall pustulations and well developed sperm gutter are distinctive. None of the umbilicated *Amplirhagada* have similar points on the main pilaster, with only the patterns in *A. alta alta* **(Fig. 37e,** fewer and more widely spaced points), *A. mitchelliana* **(Fig. 37i,** finer and more crowded points), and *A. castra* **(Fig. 37h,** finer and more crowded points) coming close to that of *A. carinata.* Shells in all of these Mitchell Plateau region species have rounded peripheries, a closed umbilicus, much higher spire, brighter colour patterns with umbilical colour patches, and different radial sculpture.

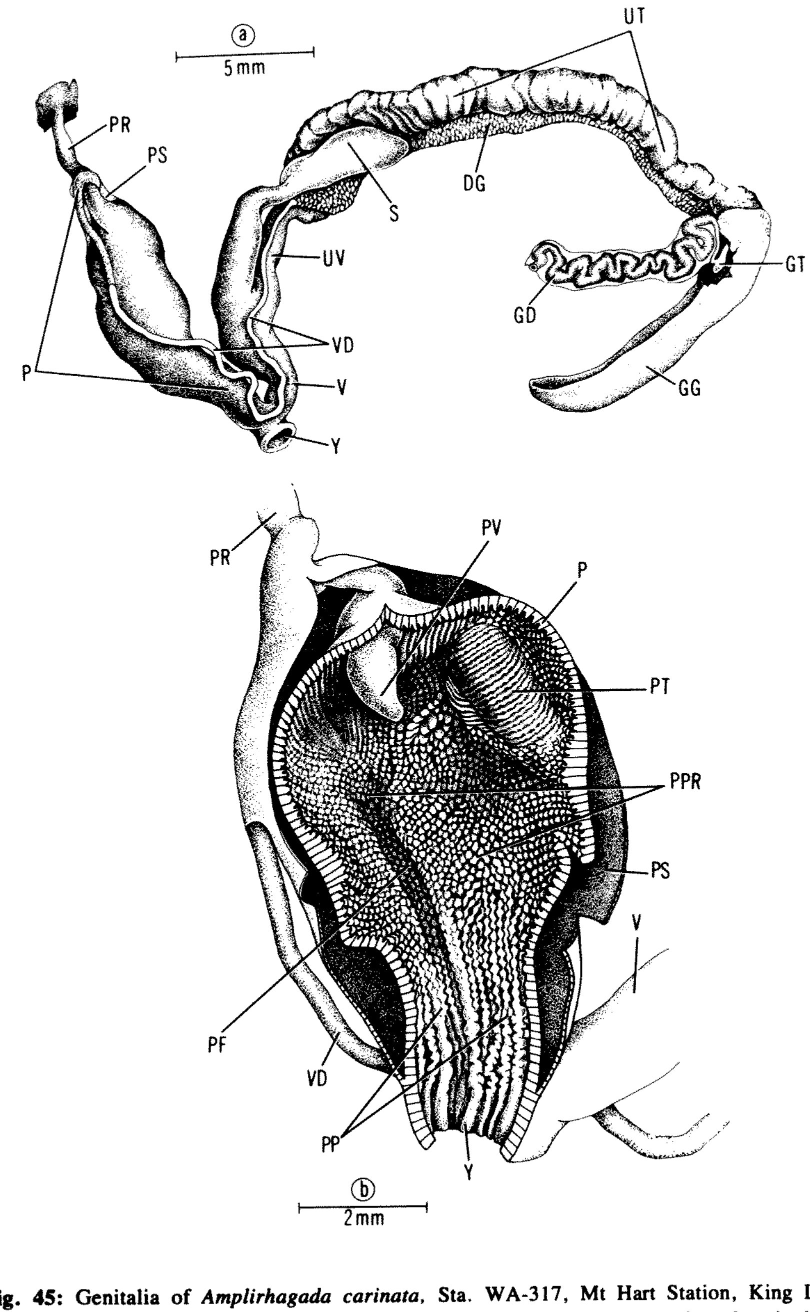


Fig. 45: Genitalia of ***Amplirhagada carinata***, Sta. WA-317, Mt Hart Station, King Leopold Ranges, 14 December 1976, a) genitalia, WAM 610.77, Dissection A; b) interior of penis chamber, WAM 1331.75, holotype, Dissection B. Scale line as marked.

Holotype

WAM 1331.75, Sta. WA-317, 5 km north of Mt Hart Station homestead, in rock pile on west side of small stream immediately west of Mt Matthew, Upper Barker Drainage, King Leopold Ranges, Western Australia (1:100,000 'Matthew' map sheet 3864, grid reference 443:046). Collected by Laurie Price and Carl Christensen 14 December 1976. Height of shell 11.35 mm, diameter 20.4 mm, H/D ratio 0.556, whorls 5 ⅝+, umbilical width 1.55 mm, D/U ratio 13.2.

Paratopotypes

WAM 610.77, WAM 358.79, WAM 359.79, WAM 361.79, WAM 363-364.79, FMNH 200328, FMNH 200331, FMNH 199325, FMNH 200326, FMNH 200330, FMNH 200372, FMNH 200504, 2 live, 14 dead adults, 7 live, 14 dead juveniles from the type locality.

Paratypes

King Leopold Ranges: Sta. WA-314, 9.4 km south-east Mt Hart outcamp, Gibb River Road, south-west of Fern Creek, valley south-west of Mt Vincent (Richenda 3963—041:406) (1 dead adult, FMNH 199282, L. Price and C. Christensen, 13 December 1976); Sta. WA-318, 14.5 km north-west of Mt Hart Homestead, Humbert Creek Road, north-east slope (Matthew 3864—970:495) (1 live, 36 dead adults, 9 dead juveniles, WAM 360.79, FMNH 200752, FMNH 200504, FMNH 199308, L.P. and C.C., 14 December 1976); Sta. WA-319, south slope of valley, 22.0 km south-east of Mt Hart Homestead, access road (Isdell 3964—210:190 estimated) (3 dead juveniles, WAM 362.79, FMNH 199320, L.P. and C.C., 15 December 1976); Kongorow Pool, west side Barker River, north-north-east of Old Napier Downs Homestead (Lennard 3863—037:892) (4 dead adults, 4 dead juveniles, WAM 1330.75, B.R. Wilson and S. Slack-Smith, 16 May 1976).

Diagnosis

Shell 17.9-22.5 mm (mean 19.98 mm) in diameter, with 5¼ to 6 (mean 5⅝−) whorls. Apex and spire slowly and evenly elevated **(Fig. 43a)**, height of shell 10.1-15.5 mm (mean 11.54 mm), H/D ratio 0.530-0.674 (mean 0.578). Apical sculpture **(Plate 13e)** rather coarse, postapical whorls with prominent low, rounded radial ribs **(Plate 13e)**, about 15/mm on the penultimate whorl, shell base with traces of incised spiral lines. Shell periphery strongly angulated **(Fig. 43a)**, almost carinated at times, usually with a distinct white band below the prominent colour band. Umbilicus only partly covered by reflected lip, umbilical width 1.1-2.4 mm (mean 1.53 mm), D/U ratio 8.83-19.1 (mean 13.5). Subsutural colour band present or absent, columellar colour patch absent. Supraperipheral colour band faint to prominent, upper spire in some examples with a faint colour suffusion. Based on 60 measured adults.

Genitalia **(Fig. 45a)** in active reproductive phase, hermaphroditic duct (GD), uterus (UT) and prostate (DG) swollen. State of ovotestis not known. Hermaphroditic duct (GD) entering laterally on talon (GT). Vagina (V) short, free oviduct (UV) and spermatheca (S) comparatively long. Penis (P) rather short and thick. Vas deferens (VD) entering penis sheath (PS) slightly above mid-point, coiled and twisted **(Fig. 45b)** below insertion of penial retractor muscle (PR). Interior of penis chamber **(Fig. 45b)** with normal verge (PV), very short area of basal pilasters, a well developed sperm gutter between two secondary pilasters (PP), the main pilaster (PT) very wide with narrow corrugations on which are 8-12 fine and sharp points **(Fig. 37g)**. Wall pustules densely crowded and arranged in rows. Based on three dissected individuals.

Discussion

All known localities of *Amplirhagada carinata* are in the upper reaches of the Barker River and its tributary Wombarella Creek, or the adjacent Lennard River. All lie on the southern fringes of the King Leopold Ranges. The Kongorow Pool locality probably represents a flood strandee population or accumulation of dead shells washed down the Barker River during the previous wet season. All known specimens were taken from talus or rock piles near streams. Undoubtedly a number of additional colonies will be located in suitable habitats of the King Leopold Ranges. All specimens taken alive were free sealers with recessed epiphragms.

Variation among the sampled populations was quite minor **(Table 18)**, lying well below the level of statistical significance. The single shell from Sta. WA-314 (FMNH 199282) is very worn. It is the largest and one of the highest spired examples seen, but shares the angulated periphery. Sta. WA-317 was sampled in mid-December, late January, and mid-February. The three live adults taken in mid-December probably had mated, since a number of thunderstorms had occurred near Mt Hart in the previous three weeks. On 27 January 1977, a nearly adult live specimen, diameter 21.2 mm, with the umbilical lip reflected, but the palatal lip not yet reflected, plus a large juvenile, diameter 16.2 mm with 5 whorls, were taken. The two live juveniles collected in mid-February were 15.2 mm in diameter with 4 ⅞ whorls, and 17.35 mm with 5¼ whorls. The latter showed a slight trace of thickening to the columellar lip. These all probably represent young born in the previous wet season.

Attempts to pull two examples were only partly successful, and in the one adult whose shell was crushed, extraction of the ovotestis was not successful. Thus the ovotestis of *Amplirhagada carinata* was neither observed nor illustrated. All three examples agreed in the unusual main pilaster in the penis.

The name *carinata* refers to the extreme angulation of the shell periphery **(Fig. 45a)** in comparison with the other species of *Amplirhagada*.

AMPLIRHAGADA ASTUTA (IREDALE, 1939)

(Figs 46a-c)

Rhagada astuta Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 63, pl. IV, fig. 17—Koolan Island (16°08′S, 123°45′E), Yampi Sound, Western Australia.

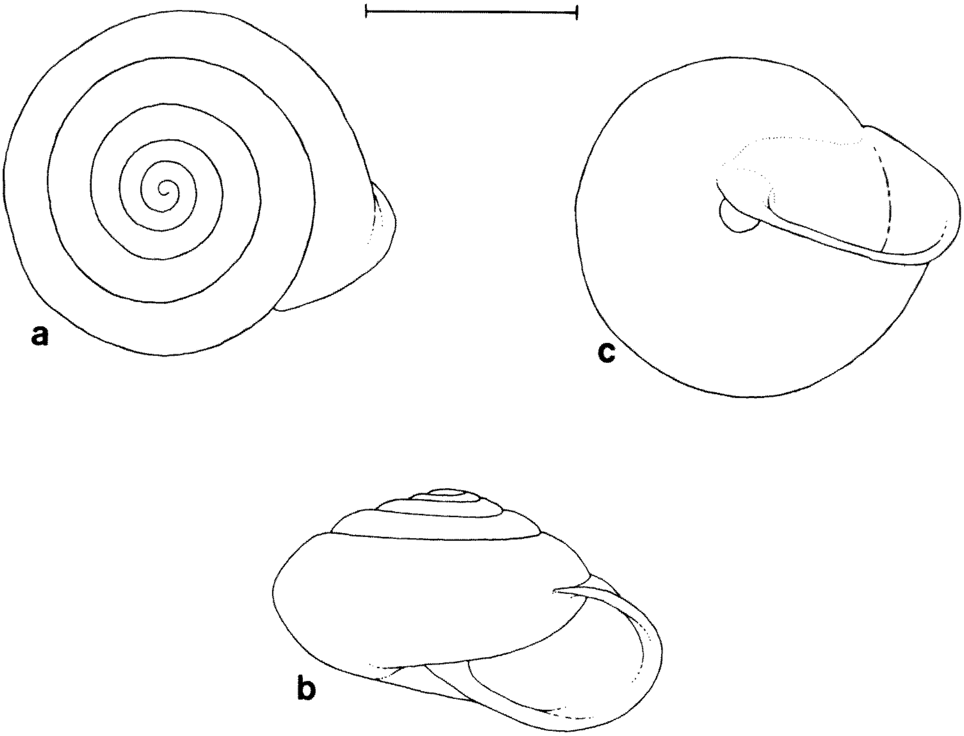


Fig. 46: Shell of *Amplirhagada astuta* (Iredale, 1939), Koolan Island, Yampi Sound, AMS C.64857, holotype of *Rhagada astuta* Iredale, 1939. Scale line equals 10 mm.

Comparative remarks

Amplirhagada astuta (Iredale, 1939) has a depressed shape **(Fig. 46b,** mean H/D ratio 0.600), slightly angulated periphery, moderately open umbilicus **(Fig. 46c,** mean D/U ratio 14.5), and radial sculpture above the periphery equivalent to that found in *A. drysdaleana* **(Plate 12d)**. *A. pusilla* has similar shape, but a more angulated periphery **(Fig. 38e)**, stronger radial sculpture **(Plate 12c)**, and is noticeably smaller (mean diameter 16.73 mm) than *A. astuta* (mean diameter 19.45 mm). *A. questroana* is very similar in size (mean diameter 20.02 mm), but is much more elevated (mean H/D ratio 0.660), and has weaker radial sculpture **(Plate 12e)**. *A. drysdaleana* is smaller (mean diameter 16.73 mm), but otherwise very similar in form, colour, and general appearance. *A. carinata* from the King Leopold Ranges is nearly identical in size and shape, but has a much more strongly angulated periphery **(Fig. 43a)** and weaker radial sculpture **(Plate 13e)**. The other umbilicated *Amplirhagada*, *A. percita* (Iredale, 1939) and *A. burnerensis umbilicata* from the Napier Range, have much less angulated peripheries and almost no trace of radial ribbing **(Plate 14c, e)**. The anatomy of *Amplirhagada astuta* (Iredale, 1939) is unknown.

Holotype

AM C.64857, Koolan Island, Yampi Sound, Western Australia (16°08′S, 123°45′E). Height of shell 12.15 mm, diameter 19.65 mm, H/D ratio 0.618, whorls 5¾, umbilical width 1.1 mm, D/U ratio 17.9.

Other material studied

Koolan Island (4 dead adults, WAM 1546.70, FMNH 200780, D. Milton, 9 August 1966).

Diagnosis

Shell 18.7-20.85 mm (mean 19.45 mm) in diameter, with 5½ to 5¾ (mean 5⅝+) whorls. Apex and spire moderately and evenly elevated, not rounded above **(Fig. 46c)**, height of shell 10.7-12.5 mm (mean 11.68 mm), H/D ratio 0.572-0.621 (mean 0.600). Apical sculpture typical, postapical whorls with prominent, somewhat irregular, rather sharply defined radial ribs equivalent to the ribbing in *A. drysdaleana* **(Plate 12d)**. Ribbing stops at periphery, shell base with weak radial growth lines and incised spiral lines. Shell periphery noticeably angulated **(Fig. 46c)**. Body whorl not descending behind lip, which is sharply reflexed and strongly expanded. Umbilicus narrowly open **(Fig. 46c)**, width 1.1-1.5 mm (mean 1.36 mm), D/U ratio 12.5-17.9 (mean 14.5). Basal lip without protrusion. Peripheral colour band moderately prominent, subsutural colour band weak to nearly absent, shell periphery with a white zone, no columellar colour patch. Based on 5 measured adults.

Anatomy unknown.

Discussion

The holotype (AM C.64857) is a very worn, colourless shell that Iredale (1939: 63) misclassified as a *Rhagada*. In usual fashion, he created a subgeneric name, *Thetagada*, without describing it. I consider this to be a *nomen nudum*.

The four adult shells collected by D. Milton in 1966 **(Table 18)** show that this is an *Amplirhagada* of the same group as *A. drysdaleana, A. pusilla, A. questroana,* and *A. carinata*. Despite their conchological similarities, the latter four show major anatomical differences, and I have no doubt but that the anatomy of *A. astuta* (Iredale, 1939) will show equivalent differences.

AMPLIRHAGADA PERCITA (IREDALE, 1939)

(Plate 14e-f; Figs 47a-j, 50c, 51b-c)

Tenuigada percita Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 68, pl. V, fig. 14—in rocks at the Limestone Caves, north end of Napier Range, Western Australia.

Tenuigada ignara Iredale, 1939, *op. cit.,* **25:** 68, pl. V, fig. 13—in rocks at the Limestone Caves, north end of Napier Range, Western Australia.

Nomenclature and type localities

The type specimens of both taxa were shells selected from a large sample that **(Table 20)** shows the same or even slightly less variation than other sets with equivalent specimen numbers. I thus have no hesitation in synonymizing the two taxa under the name with priority on the page (Iredale, 1939: 68).

Designation of an exact type locality is not done, although restriction to a small area of the Napier Range is made. According to Basedow (1918: 139-140), his party left the Original Napier Downs Homestead on 15 April and travelled 12.8 km north-west to Barnett Spring. They then 'followed the brink of the range around in a NNE direction. A short three-quarter mile brought us to the opening of a cave.' After exploring portions of this first cavern, they (p. 141) continued north-west. 'We had not proceeded far ere we reached another cave...The opening was hemispherical, and might well have been a natural stage depicting Fairyland...The arch in front was quite fifty feet high, and about 115 in length.' If the base of the range was followed, then the area that Wilson and Slack-Smith located as Barnett Cave is highly probable (1:100,000 'Lennard' map sheet 3863, grid reference 095:655). It would then follow logically that Wangalinnya Cave would be on the slopes north of the headland area, somewhere between grid reference 100:653 and 112:665, not far south-west of Sta. WA-300. The exact caves visited by Basedow were not found by any of the recent collectors, but almost certainly are in that general area. Although the material from NR IX almost exactly matches the proportions of the types **(Table 20)**, I prefer to restrict the type locality only to the north-west facing slopes of the

Table 19: Geographic Variation in *Amplirhagada percita* (Iredale, 1939)

Area	Number of Adults Measured	Mean and Range of: Shell Height	Shell Diameter	H/D Ratio
Northwest Napier, Stumpy's Well & north	156	10.64 (7.9-13.95)	16.12 (13.25-18.7)	0.659 (0.566-0.780)
Wagon Pass	48	12.52 (10.7-14.15)	17.43 (15.25-19.1)	0.718 (0.656-0.814)
WA-322, S of Wagon Pass	103	10.95 (7.3-12.2)	15.65 (12.4-17.9)	0.642 (0.548-0.739)
WA-355, NW of Barker Gorge	42	11.86 (10.15-13.70)	18.52 (17.30-20.15)	0.640 (0.570-0.700)
WA-330, SE of Barker Gorge	38	9.59 (8.1-11.2)	17.30 (15.2-18.5)	0.554 (0.492-0.636)
WA-190, WA-357, NE of Barker Gorge	143	11.23 (9.55-13.1)	17.93 (15.6-20.1)	0.626 (0.555-0.716)
W of Barker Gorge to Wombarella Gap	130	11.27 (8.25-13.6)	17.87 (15.3-20.4)	0.630 (0.539-0.732)
WA-329	40	9.10 (7.85-10.1)	16.11 (14.1-17.6)	0.565 (0.513-0.643)
Yammera Gap to 1.6 km. W	210	10.55 (7.6-12.8)	17.39 (11.5-20.0)	0.606 (0.521-0.811)

Area	Number of Adults Measured	Whorls	Umbilical Width	D/U Ratio
Northwest Napier, Stumpy's Well & north	156	5¼ − (4 ⅝-5 ⅞)	1.42 (0.7-2.3)	12.1 (6.74-20.8)
Wagon Pass	48	6 − (5 ⅜-6½)	1.02 (0.6-1.3)	18.0 (13.0-29.2)
WA-322, S of Wagon Pass	103	5 ⅝ (4¾-6½)	1.08 (0.6-1.75)	15.2 (9.09-26.6)
WA-355, NW of Barker Gorge	42	5 ⅝+ (5¼-6 ⅛)	closed-1.30	13.7-closed

Table 19: Geographic Variation in *Amplirhagada percita* (Iredale, 1939) (continued)

Area	Number of Adults Measured	Mean and Range of: Whorls		Umbilical Width		D/U Ratio	
WA-330, SE of Barker Gorge	38	5½	(5-5 ⅞)	1.62	(1.0-2.75)	11.5	(6.44-18.5)
WA-190, WA-357, NE of Barker Gorge	143	5 ⅝+	(5-6½)	1.20	(0.55-2.6)[1]	16.1	(7.16-29.8)[1]
W of Barker Gorge to Wombarella Gap	130	5 ⅝−	(5-6 ⅜)	1.20	(0.55-2.65)	16.7	(6.38-36.9)
WA-329	40	5 ⅝	(5-5 ⅞)	2.18	(1.7-2.8)	7.60	(5.59-10.8)
Yammera Gap to 1.6 km. W	210	5¾ −	(5-6¾)	2.00	(0.65-3.1)	9.33	(5.40-29.1)

[1] Of 123 with open umbilici.

Table 20: Local Variation in *Amplirhagada percita* (Iredale, 1939)

Set	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
Types AMS C.42216	57	11.51 ± 0.145 (9.35-13.95)	16.60 ± 0.138 (13.85-18.7)	0.693 ± 0.005 (0.609-0.780)
NR VIII, WAM 979.76	8	9.79 ± 0.362 (8.45-11.05)	14.86 ± 0.447 (13.3-16.4)	0.658 ± 0.007 (0.635-0.684)
NR VII, WAM 972.76	23	10.43 ± 0.207 (8.3-12.25)	15.69 ± 0.223 (14.0-17.65)	0.664 ± 0.006 (0.593-0.722)
NR IX, WAM 1342.75	10	11.43 ± 0.225 (10.45-12.65)	16.78 ± 0.222 (15.75-17.9)	0.681 ± 0.010 (0.633-0.717)
NR VI, WAM 968.76	16	9.90 ± 0.213 (8.3-11.4)	16.09 ± 0.228 (14.7-17.8)	0.615 ± 0.008 (0.569-0.671)

Table 20: Local Variation in *Amplirhagada percita* (Iredale, 1939) (continued)

Set	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
NR V, WAM 967.76	20	9.66±0.165 (8.3-10.9)	15.66±0.198 (14.5-17.35)	0.616±0.006 (0.566-0.675)
NR IV, WAM 904.76	22	10.00±0.202 (7.9-11.4)	15.95±0.258 (13.25-17.8)	0.626±0.006 (0.579-0.678)
NR II, WAM 1339.75, WAM 1343.75,	48	12.52±0.122 (10.7-14.15)	17.43±0.108 (15.25-19.1)	0.718±0.005 (0.656-0.814)
WA-322, FMNH 199332, dead	92	11.19±0.092 (8.35-12.2)	15.84±0.086 (14.2-17.9)	0.643±0.004 (0.548-0.739)
FMNH 200145, live	11	8.93±0.317 (7.3-10.9)	14.07±0.264 (12.4-15.2)	0.634±0.013 (0.576-0.732)

Set	Number of Adults Measured	Whorls	Umbilical Width	D/U Ratio
Types AMS C.42216	57	5 3/8− (4 7/8-5 7/8)	1.28±0.028 (0.85-1.8)	13.3±0.341 (9.2-18.9)
NR VIII, WAM 979.76	8	5+ (4 7/8-5 1/4)	1.36±0.096 (1.1-1.8)	11.4±0.882 (7.39-14.7)
NR VII, WAM 972.76	23	5 1/8 (4 3/4-5 5/8)	1.37±0.066 (0.7-1.9)	12.2±0.710 (7.95-20.8)
NR IX, WAM 1342.75	10	5 1/4 + (5 1/8-5 5/8)	1.25±0.058 (0.8-1.3)	16.8±0.896 (12.8-20.3)
NR VI, WAM 968.76	16	5 1/8+ (4 7/8-5 1/2)	1.63±0.067 (1.3-2.15)	10.1±0.399 (7.12-12.3)
NR V, WAM 967.76	20	5 1/8 (4 5/8-5 3/8)	1.70±0.065 (1.2-2.3)	9.49±0.408 (6.74-12.4)
NR IV, WAM 904.76	22	5 1/4 (4 5/8-5 5/8)	1.52±0.063 (0.9-2.1)	10.9±0.584 (7.53-16.2)
NR II, WAM 1339.75, WAM 1343.75	48	6− (5 3/8-6 1/2)	1.02±0.051 (0.6-1.3)	18.0±1.075 (13.0-29.2)

Table 20: Local Variation in *Amplirhagada percita* (Iredale, 1939) (continued)

Set	Number of Adults Measured	Mean, Range and SEM of: Whorls	Umbilical Width	D/U Ratio
WA-322				
FMNH 199332, dead	92	5 ⅝ (5-6½)	1.08 ± 0.024 (0.60-1.75)	15.4 ± 0.378 (9.09-26.6)
FMNH 200145, live	11	5 ⅛ (4¾-5½)	1.08 ± 0.056 (0.8-1.3)	13.4 ± 0.940 (9.5-18.2)

Set	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
WA-355, dead FMNH 199108	42	11.86 ± 0.130 (10.15-13.70)	18.52 ± 0.124 (17.30-20.15)	0.640 ± 0.004 (0.570-0.700)
WA-330, dead FMNH 199261	38	9.59 ± 0.124 (8.1-11.2)	17.30 ± 0.147 (15.2-18.5)	0.554 ± 0.006 (0.492-0.636)
WA-190,				
17-V-76, live	14	11.41 ± 0.256 (9.7-13.1)	17.84 ± 0.233 (16.1-19.15)	0.639 ± 0.008 (0.588-0.684)
17-V-76, dead	35	11.38 ± 0.131 (9.7-13.1)	17.88 ± 0.150 (15.9-19.95)	0.636 ± 0.005 (0.582-0.690)
8-X-76, dead	48	11.24 ± 0.122 (9.85-13.1)	17.95 ± 0.128 (15.6-19.7)	0.627 ± 0.004 (0.569-0.716)
WA-331, dead FMNH 199089	31	10.46 ± 0.145 (8.25-11.8)	17.45 ± 0.170 (15.3-19.3)	0.599 ± 0.005 (0.539-0.634)
WA-191, dead FMNH 199442	19	10.73 ± 0.226 (9.51-12.9)	17.58 ± 0.229 (16.0-19.4)	0.610 ± 0.007 (0.565-0.686)
WA-326, dead FMNH 199076	37	11.58 ± 0.113 (10.05-13.0)	18.11 ± 0.155 (16.2-20.4)	0.640 ± 0.004 (0.586-0.694)
WA-332, dead FMNH 199096	19	11.56 ± 0.194 (9.7-12.9)	18.01 ± 0.230 (16.0-19.8)	0.642 ± 0.008 (0.594-0.709)
WA-329, dead FMNH 199272	36	9.11 ± 0.103 (7.85-10.1)	16.16 ± 0.123 (15.1-17.6)	0.564 ± 0.005 (0.513-0.632)

Table 20: Local Variation in *Amplirhagada percita* (Iredale, 1939) (continued)

Set	Number of Adults Measured	Mean, Range and SEM of: Whorls	Umbilical Width	D/U Ratio
WA-355, dead FMNH 199108	42	5 ⅝+ (5¼-6 ⅛)	closed-1.30[4]	13.7-closed[4]
WA-330, dead FMNH 199261	38	5½ (5-5 ⅞)	1.62±0.068 (1.0-2.75)	11.5±0.537 (6.44-18.5)
WA-190,				
17-V-76, live	14	5 ⅝− (5 ⅛-5 ⅞)	1.03±0.089[1] (0.6-1.65)	18.38±1.739[1] (9.94-29.8)
17-V-76, dead	35	5 ⅝ (5¼-6)	1.02±0.059[2] (0.55-2.1)	18.2±0.863[2] (8.8-29.8)
8-X-76, dead	48	5 ⅝ (5 ⅛-6)	1.13±0.038[3] (0.6-1.8)	16.7±0.617[3] (9.56-29.2)
WA-331, dead FMNH 199089	31	5 ⅜+ (5-5 ⅞)	1.57±0.63 (1.0-2.3)	12.1±0.529 (6.95-18.9)
WA-191, dead FMNH 199442	19	5¾ (5-6¼)	1.35±0.079 (0.8-1.9)	14.1±1.039 (9.02-26.6)
WA-326, dead FMNH 199076	37	5 ⅝− (5¼-5 ⅞)	0.94±0.063 (0.55-1.4)	20.7±1.075 (12.4-36.9)
WA-332, dead FMNH 199096	19	5 ⅝− (5-6 ⅜)	1.01±0.064 (0.8-1.4)	19.1±1.254 (9.41-32.0)
WA-329, dead FMNH 199272	36	5 ⅝+ (5-5 ⅞)	2.21±0.050 (1.7-2.8)	7.5±0.187 (5.59-10.8)

Set	Number of Adults Measured	Shell Height	Shell Diameter	H/D Ratio
WA-306, dead FMNH 199170	35	11.32±0.112 (9.55-12.8)	17.86±0.112 (16.7-19.4)	0.634±0.006 (0.558-0.707)
WA-402, dead FMNH 199359	17	10.78±0.214 (8.7-11.9)	17.98±0.270 (15.8-19.8)	0.599±0.007 (0.534-0.652)
WA-199, dead FMNH 199401	27	10.71±0.152 (9.24-12.4)	17.63±0.200 (16.0-20.0)	0.608±0.006 (0.537-0.697)
WA-400, dead FMNH 199302	23	10.48±0.210 (8.63-12.4)	17.43±0.219 (15.3-19.6)	0.601±0.007 (0.547-0.670)

Table 20: Local Variation in *Amplirhagada percita* (Iredale, 1939) (continued)

Set	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
WA-301				
FMNH 199185, dead, 9-XII-76	57	10.13±0.122 (7.6-11.7)	17.03±0.139 (15.2-19.2)	0.594±0.004 (0.521-0.691)
FMNH 200296, live, 19-II-76	10	9.95±0.181 (9.1-10.7)	16.24±0.577 (11.5-17.7)	0.619±0.023 (0.566-0.811)
NW side of Yammera Gap, WAM	14	10.14±0.753 (8.75-10.9)	16.92±1.056 (14.7-18.6)	0.597±0.022 (0.556-0.639)

Set	Number of Adults Measured	Whorls	Umbilical Width	D/U Ratio
WA-306, dead FMNH 199170	35	5 5/8− (5-6½)	1.48±0.060 (0.7-2.1)	12.8 ±0.559 (8.67-23.5)
WA-402, dead FMNH 199359	17	5 3/8 (5-6 1/8)	2.30±0.084 (1.8-3.0)	8.01±0.337 (5.43-10.4)
WA-199, dead FMNH 199401	27	5 7/8 (5¾-6 3/8)	2.02±0.095 (0.9-2.9)	9.36±0.567 (6.32-20.1)
WA-400, dead FMNH 199302	23	5 7/8− (5-6½)	2.08±0.264 (1.40-2.5)	8.55±0.310 (7.09-13.2)
WA-301				
FMNH 199185, dead, 9-XII-76	57	6− (5½-6 5/8)	2.12±0.047 (1.4-3.0)	8.28±0.233 (6.13-15.9)
FMNH 200296, live, 19-II-77	10	5½+ (5-5 7/8)	2.00±0.121 (1.35-2.45)	8.41±0.652 (5.90-12.7)
NW side Yammera Gap, WAM	14	5½− (5 1/8-5¾)	1.81±0.217 (1.55-2.2)	9.34±1.500 (6.65-11.1)

[1] Plus 4 with closed umbilici.

[2] Plus 11 with closed umbilici.

[3] Plus 5 with closed umbilici

[4] Nine have closed, 33 have barely open, umbilici.

Napier Range fronting Hawkstone Creek between grid references 096:653 and 153:680, to allow for errors in mileage as reported by Basedow. The actual cavern pictured by Basedow (1918: Plate XII, Fig. 2, facing p. 140) and named Wangalinnya Caves should be readily recognizable. The exact habitat of the snails was reported as: 'The rocky walls which stood on either side of the cave were honeycombed with pits and cavities, which all contained a number of heliform land-snails' (Basedow, 1918: 142). A frequently observed shelter niche of *A. percita* elsewhere in the Napier Range is in fissures or on cave roofs.

Comparative remarks

Amplirhagada percita (Iredale, 1939) is a normally umbilicated **(Figs 47c, g)**, relatively low spired (mean H/D ratio 0.630, **Figs 47f, i**), unicoloured brownish, rather thin shell, with sharply reflected and moderately expanded lip **(Figs 47d, i, j)**. The complete lack of colour bands and patches, plus the almost total absence of radial sculpture **(Plate 14e-f)** and stronger incised spiral lines serve to differentiate it from other *Amplirhagada*. *A. napierana,* which has an interdigitated distribution from Yammera Gap to the north-west end of the Napier Range, normally has a closed umbilicus, higher spire (mean H/D ratio 0.714, **Fig. 48a**), thicker shell that is dead white in adults, and is slightly larger. *A. burnerensis umbilicata* from east of Yammera Gap is similar in size and shape, but has the lip only very slightly, if at all, expanded, plus a prominent columellar colour patch that extends onto and behind the lip. Umbilicated *Amplirhagada* of similar size and shape, such as *A. pusilla* and *A. drysdaleana,* have prominent radial sculpture **(Plate 12c-d)**, angulated peripheries **(Figs 38c, e)**, and prominent spiral colour bands. Anatomically, *A. percita* (Iredale, 1939) is most readily recognized by its verge with a lateral extension to the blunt tip **(Fig. 51b)** and the main pilaster, which has the same unusual irregular projections on the corrugations as in *A. napierana* **(Figs 36b, 51a)**. The main pilaster in *A. percita* differs in lacking the tapering anterior extension with its sculpture of wall pustules. *A. napieriana* **(Fig. 51a)** has a blunt tip to the verge without any lateral extension. No other *Amplirhagada* have equivalent main pilaster armature or a blunt tipped verge.

Holotype of *percita*

AM C.64878, Limestone Caves, north end of Napier Range, Western Australia. Type locality here restricted to that section of the Napier Range facing Hawkstone Creek (1:100,000 'Lennard' map sheet 3863, between grid references 096:653 and 153:680). Height of shell 13.8 mm, diameter 17.9 mm, H/D ratio 0.771, whorls 5 7/8 –, umbilical opening a lateral crack.

Holotype of *ignara*

AM C.64879, Limestone Caves, north end of Napier Range, Western Australia. Type locality here restricted to the same as for *Tenuigada percita* Iredale, 1939 (see above). Height of shell 10.25 mm, diameter 15.3 mm, H/D ratio 0.670, whorls 5 +, umbilical width 1.55 mm, D/U ratio 9.87.

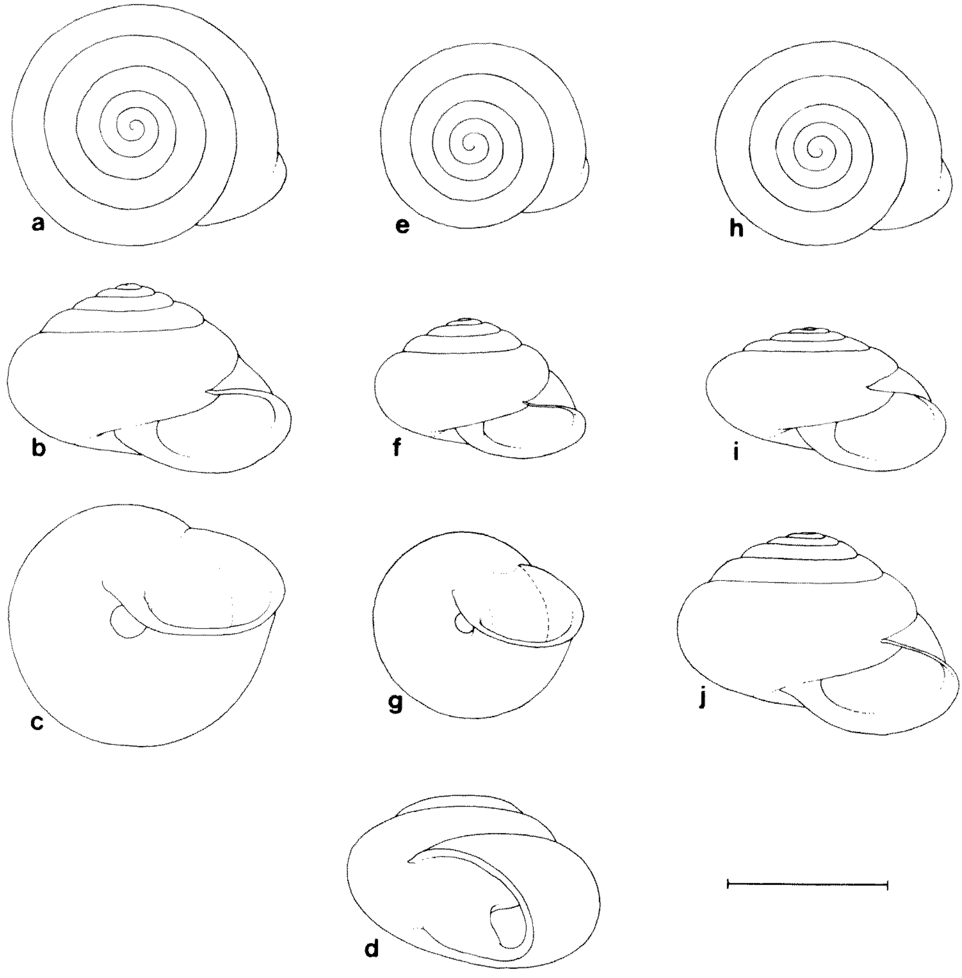


Fig. 47: Shells of *Amplirhagada percita* (Iredale, 1939), a-d) north end of Napier Range, WAM 69.40, paratype of *percita;* e-g) north end of Napier Range, WAM 70.40, paratype of form *ignara* (Iredale, 1939); h-i) Sta. WA-199, Napier Range, FMNH 199401; j) Sta. NR II, Wagon Pass, Napier Range, WAM 1339.75. Scale line equals 10 mm.

Paratopotypes of *percita* and *ignara*

WAM 69.40, WAM 70.40, 5 dead adults from the type locality:

Type lot of both taxa

AM C.42216, FMNH 198494, 55 dead adults from the type locality.

Measured materials

Napier Range, ordered west to east geographically, unless specified otherwise collected by Solem, Price or Christensen between October 1976 and May 1977: Sta. NR VII, north side of gully, north of Barnett Cave (Lennard 3863—*ca.* 119:674) (23 dead adults, WAM 972.76, FMNH 200833, B.R. Wilson and S. Slack-Smith, 29 August 1975); Sta. NR VIII, north side of embayment, north of entrance to Barnett Cave (Lennard 3863—098:653) (8 dead adults, WAM 979.76, B.R.W. and S.S.-S., 29 August 1975); Sta. NR IX, entrance to Barnett Cave (Lennard 3863—096:655) (10 dead adults, WAM 978.76, WAM 1342.75, FMNH 200839, B.R.W. and S.S.-S., 30 August 1975); Sta. NR VI, north-west of Sta. NR V, north-west of Stumpy's Well (Lennard 3863—*ca.* 082:695)(16 dead adults, WAM 968.75, FMNH 200835, B.R.W. and S.S.-S., 29 August 1975); Sta. NR V, bluff north-west of Stumpy's Well (Lennard 3863—057:708) (20 dead adults, WAM 967.76, FMNH 200836, B.R.W. and S.S.-S., 29 August 1975); Sta. NR IV, *ca.* 4.5 km north of Original Napier Downs Homestead ruins (Lennard 3863—*ca.* 045:702) (22 dead adults, WAM 904.76, WAM 965.76, FMNH 200838, B.R.W. and S.S.-S., 29 August 1975); Sta. NR II, north-east corner of Wagon Pass (Lennard 3863—*ca.* 005:723) (48 dead adults, WAM 1339.75, WAM 1343.75, FMNH 200837, B.R. Wilson and S. Slack-Smith, 21 May 1976); Sta. WA-322, 0.6 km east of road, 3 km south-east Original Napier Downs Homestead (Lennard 3863—985:719) (11 live, 92 dead adults, 16 live, 1 dead juveniles, FMNH 199332, FMNH 200145, WAM 327.79, WAM 332.79); Sta. WA-355, cliff base north of Barker Gorge, 1.4 km west of Barker River, north side (Lennard 3863—928:829) (40 dead adults, FMNH 199108, WAM 331.79); Sta. WA-330, 0.2 km south-east of Barker Gorge, south side (Lennard 3863—904:833) (1 live, 38 dead adults, 1 live, 1 dead juveniles, FMNH 199261, FMNH 199947, WAM 336.79); Sta. NR II-1, east corner Barker Gorge, east of Barker River-Wombarella Creek junction (14 live, 35 dead adults, WAM 1346.75-1347.75, B.R.W. and S.S.-S., 17 May 1976); Sta. WA-190, north-east side Barker Gorge, north side (Lennard 3863—914:841) (5 live, 63 dead adults, 27 live, 9 dead juveniles, FMNH 199412, FMNH 199436, FMNH 199717, FMNH 200068, FMNH 200363, FMNH 200736, WAM 322.79, WAM 324.79, WAM 326.79, WAM 335.79, WAM 344-345.79); Sta. WA-357, cliffs and caves 0.2 km south of Wombarella Creek crossing, north side (Lennard 3863—914:841) (41 live adults, 42 live juveniles, FMNH 199794-5, FMNH 200313, FMNH 200315, FMNH 200319, FMNH 200321, FMNH 200323, WAM 314-316.79, WAM 321.79, WAM 325.79, WAM 330.79); Sta. WA-331, 1.6 km south-east Barker Gorge, south side (Lennard 3863–893: 844) (1 live, 2 dead adults, FMNH 199089, FMNH 199864); Sta. WA-191, 3.4 km east of Wombarella Creek crossing, north side (Lennard 3863–890:861) (25 dead adults, FMNH 199442, WAM 338.79); Sta. WA-326, 1.5 km north-west of Wombarella Gap, south side (Lennard 3863–878:862) (37 dead adults, FMNH 199076, WAM 346.79); Sta. WA-332, north-west side of Wombarella Gap, south side (Lennard 3863–872:872) (8 live, 19 dead adults, 5 live juveniles, FMNH 199096, FMNH 199921, FMNH 200166, WAM 318.79, WAM 339.79, WAM 347.79); Sta. WA-329, 6.9 km south-east of Wombarella Gap, south side (Lennard 3863–828:921) (4 live, 35 dead adults, 2 live, 4 dead juveniles, FMNH 199272, FMNH 199928, WAM 313.79, WAM 343.79); Sta. WA-306, 1.6 km north-west of Yammera Gap, north side (Lennard 3863–831:922) 40 dead adults, FMNH 199170, WAM 334.79); Sta. WA-360, 1.5 km west of Yammera Gap, north side (Lennard 3863–831:923) (1 live adult, 4 live juveniles, FMNH 200287, WAM 328.79); Sta. 402, 1.5 km west of Yammera Gap, north side (Lennard 3863–925:830) (21 dead adults, FMNH 199359); Sta. WA-281, 1.3 km west of Yammera Gap, above stockmen's huts, north side (Lennard 3863–827:928) (20 live, 6 dead adults, 16 live, 1 dead juveniles, 199799, FMNH 199870, FMNH 200267-8, WAM 312.79, WAM 317.79, WAM 320.79, WAM 342.79); Sta. WA-199, 1.2 km west of Yammera Gap, above workshop, north side (Lennard 3863–826:928) (30 dead adults, 1 live, 5 dead juveniles, FMNH 199401, FMNH 200107, WAM 340.79); Sta. WA-400, 0.5 km north-west of Yammera Gap, north side (Lennard 3863—822:932) (1 live, 28 dead adults, 1 live, 3 dead juveniles, FMNH 199302, FMNH 199824, WAM 341.79); Sta. WA-301, north side of Yammera Gap, south-west corner (Lennard 3863—819:933) (15 live, 57 dead adults, 15 live, 16 dead juveniles, FMNH 199185, FMNH 199940, FMNH 200296, WAM 319.79, WAM 329.79, WAM 348.79).

Distribution limits in Napier Range

Amplirhagada percita is the common species from just south of Wagon Pass (Sta. WA-322) north to Barnett Cave, where it is replaced momentarily by *A. napierana* 'near Barnett Cave' and at Sta. WA-300. *A. napierana* extends from the Chedda Cliffs (Sta. WA-321) to the west bank of Barker Gorge (Sta. WA-354), except for one colony of apparent *A. percita* just north-west of Barker Gorge (Sta. WA-355). *A. percita* ranges from the east side of Barker Gorge to the west of Wombarella Gap. It is then replaced by *A. napierana* from the east side of Wombarella Gap to a point about 1.5-1.6 km west of Yammera Gap (Sta. WA-306, WA-360) on the north side of the range and WA-329 on the south side. From there to the west side of Yammera Gap, *A. percita* is present in abundance. *A. percita* thus shows four areas of occurrence, interrupted by three zones of *A. napierana.*

Diagnosis

Shell 11.4-20.4 mm (mean 17.15 mm) in diameter, with 4 ⅝ to 6¾ (mean 5 ⅝ –) whorls. Apex and spire moderately to strongly elevated **(Figs 47b, f, i, j)**, usually not rounded above, height of shell 7.3-14.5 mm (mean 10.90 mm), H/D ratio

0.492-0.814 (mean 0.630). Apical sculpture **(Plate 14e)** of fine elongated pustules, postapical sculpture of very weak radial growth lines **(Plate 14e)**, shell base and much of spire with relatively prominent incised spiral lines **(Plate 14f)**. Shell periphery evenly rounded **(Figs 47b, d, f, i, j)**, body whorl moderately descending behind lip **(Fig. 47d)**, which is thin and rather strongly expanded and flared **(Fig. 47j)**. Umbilicus normally (96.9%) open **(Figs 47c, g)**, occasionally (3.1%) only a lateral crack, umbilical width 0.3-3.1 mm (mean 1.40 mm), D/U ratio 5.40-36.9 (mean 12.7). Basal lip without trace of protrusion. No colour bands or patches, both adult and juveniles a uniform light horn colour with white lip. Based on 934 measured adults.

Genitalia externally agreeing with that of *A. napierana* **(Fig. 50)**, equally variable seasonally (see Discussion). Internally **(Fig. 51b)** with wall pustules (PPR) and basal longitudinal ridges (PP) as in *A. napierana* **(Fig. 51a)**, but verge with a blunt tip having a lateral extension and the main pilaster (PT) shorter than that of *A. napierana* and lacking the long anterior extension found in that species. Armature of the main pilaster corrugations identical to those found in *A. napierana* **(Fig. 36b)**. Based on 15 dissections and many checked individuals.

Discussion

Unlike its interdigitated neighbour *A. napierana,* the separate geographic zones of *A. percita* show distinct average differences in shell form and shape. Zonal averages and variation in certain edge populations are presented in **Table 21,** while **Table 20** gives details of individual populations and contrasts living and dead material collected simultaneously. Not all measured populations are listed individually in **Table 20,** but those omitted do not depart from the pattern shown for that particular area.

In the north-west part of the Napier Range opposite Hawkstone Creek (types) and at the entrance to Barnett Cave (Sta. NR IX), the shells are higher spired than those from the area further south up to Wagon Pass **(Table 19)**. The material from Sta. NR VII, the northernmost known locality, is almost as high as the types, but those from Sta. NR IV, V, and VI are distinctly more depressed. All of them agree in having a moderately narrow umbilicus **(Figs 47c, g)**, and a reduced whorl count. At Wagon Pass (Sta. NR II, **Fig. 47j, Tables 19, 20)** the shells are somewhat larger, with an increased whorl count, more elevated spire, and narrow umbilicus. At Sta. WA-322, south of Wagon Pass, in size, shape and whorl count, the shells agree with those from north of Wagon Pass (see **Tables 19, 20)**.

On the west side of Barker Gorge, at Stas. WA-354 and WA-355, there are populations which are typical of neither species. The specimens from WA-354 have been classified as *A. napierana,* and those from WA-355 as *A. percita.* Their characteristics are discussed under the former species. On the east side of Barker Gorge there is a low spired, rather widely umbilicated form at Sta. WA-330 **(Table 19)**, while at Sta. WA-190 there is a population that is typical of the Barker Gorge to

Table 21: Size and Shape of *Amplirhagada percita* (Iredale, 1939) and *A. napierana* at Contact Zones

Population	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
A. percita, all	934	10.90 (7.3-14.5)	17.15 (11.5-20.4)	0.630 (0.492-0.814)
A. napierana, all	1,261	13.41 (9.95-16.25)	18.71 (13.1-21.85)	0.714 (0.572-0.901)
Barnett Cave				
'entrance' *(percita)*	10	11.43 ± 0.225 (10.45-12.65)	16.78 ± 0.222 (15.75-17.9)	0.681 ± 0.010 (0.633-0.717)
'near to' *(napierana)*	15	14.16 ± 0.269 (12.6-16.0)	19.31 ± 0.229 (17.5-21.05)	0.733 ± 0.010 (0.679-0.829)
West side of Barker Gorge				
WA-355 *(percita)*	41	11.86 ± 0.130 (10.15-13.70)	18.52 ± 0.124 (17.3-20.15)	0.640 ± 0.004 (0.570-0.700)
WA-354 *(napierana)*	40	12.34 ± 0.143 (10.1-13.6)	18.55 ± 0.135 (16.85-20.25)	0.665 ± 0.006 (0.580-0.728)
Wombarella Gap				
W side, WA-332, live *percita*	7	11.59 ± 0.317 (10.1-12.4)	18.30 ± 0.417 (17.0-20.1)	0.633 ± 0.012 (0.594-0.678)
W side, WA-332, dead *percita*	19	11.56 ± 0.194 (9.7-12.9)	18.01 ± 0.230 (16.0-19.8)	0.642 ± 0.008 (0.594-0.709)
E side, WA-333, dead *napierana*	17	13.73 ± 0.192 (12.0-14.8)	19.47 ± 0.176 (18.2-20.8)	0.705 ± 0.007 (0.659-0.762)
E side, WA-376, dead *napierana*	24	13.98 ± 0.170 (12.4-15.5)	19.28 ± 0.158 (18.0-20.6)	0.725 ± 0.007 (0.648-0.790)
W of Yammera Gap				
WA-382, *napierana*	41	13.17 ± 0.138 (11.1-14.85)	18.30 ± 0.098 (17.15-20.2)	0.720 ± 0.006 (0.618-0.784)
WA-360, *napierana*	27	12.84 ± 0.149 (11.2-14.2)	18.62 ± 0.130 (17.5-20.85)	0.689 ± 0.006 (0.625-0.731)
WA-306, *percita*	39	11.54 ± 0.130 (10.05-14.5)	17.61 ± 0.106 (16.45-19.25)	0.654 ± 0.006 (0.591-0.739)
WA-402, *percita*	17	11.02 ± 0.215 (8.9-11.9)	17.69 ± 0.240 (15.7-19.1)	0.622 ± 0.007 (0.567-0.675)

Table 21: Size and Shape of *Amplirhagada percita* (Iredale, 1939) and *A. napierana* at Contact Zones (continued)

Population	Number of Adults Measured	Mean, Range and SEM of: Whorls	Umbilical Width	D/U Ratio
A. percita, all	934	5 ⅝ – (4 ⅝-6 ¾)	1.40 (0.3-3.1)[1]	12.7 (5.40-36.9)[1]
A. napierana, all	1,261	5 ¾ + (5-6 ⅜)	closed	closed
Barnett Cave				
'entrance' *(percita)*	10	5 ¼ + (5 ⅛-5 ⅝)	1.03 ± 0.058 (0.8-1.3)	16.8 ± 0.89 (12.8-20.3)
'near to' *(napierana)*	15	5 7/8 + (5½-6 ⅜)	closed	closed
West side of Barker Gorge				
WA-355 *(percita)*	41	5 ⅝ + (5¼-6 ⅛)	22% closed (rest 0.55-1.3)	22.3 ± 0.854 (13.7-32.5)
WA-354 *(napierana)*	40	5 ¾ (5¼-6 ⅛)	75% closed (rest 0.5-0.95)	
Wombarella Gap				
W side, WA-332, live *percita*	7	5½ (5-6 ⅜)	1.26 ± 0.119 (0.8-1.6)	15.5 ± 1.81 (10.8-23.4)
W side, WA-332, dead *percita*	19	5 ⅝ – (5-6 ⅜)	1.01 ± 0.064 (0.8-1.4)	19.1 ± 1.25 (9.41-32.0)
E side, WA-333, dead *napierana*	17	6 – (5¾-6¼)	closed	closed
E side, WA-376, dead *napierana*	24	6 (5½-6¼)	closed	closed
W of Yammera Gap				
WA-382, *napierana*	41	5¾ + (5¼-6¼)	closed	closed
WA-360, napierana	27	5¾ + (5½-6 ⅛)	1.11 ± 0.078[2] (0.8-1.45)	17.4 ± 1.280[2] (12.3-23.5)
WA-306, *percita*	39	5 ⅝ (5 ⅛-6)	1.16 ± 0.053 (0.55-1.75)	16.8 ± 0.890 (10.1-32.5)
WA-402, *percita*	17	5½ + (5-5 ⅞5 7/8)	1.93 ± 0.082 (1.5-2.5)	9.44 ± 0.438 (6.98-12.4)

[1] Of 905 (96.9%) with open umbilicus.

[2] Of 8 (29.6%) with open umbilicus.

Wombarella Gap morph, except that a few individuals (20 of 143) have a closed or nearly closed umbilicus. The populations from Barker Gorge to Wombarella Gap again appear uniform and narrowly umbilicated.

About 1.5-1.6 km west of Yammera Gap, populations from Sta. WA-306, WA-360 and WA-402 show mixtures of species characters. Populations nearer to Yammera Gap on the north side of the range and at Sta. WA-329 on the south side **(Table 19)** are the most widely umbilicated shells of *A. percita* yet seen, and have a somewhat lower spire **(Figs 47h-i)**. There is very little difference between populations in this area **(Table 20)**.

To summarize the above, at the north-west end of the Napier Range the shells are high spired with a narrow umbilicus and reduced whorl count, except for a very high spired, high whorl count population at Wagon Pass, and a tendency for a lower spire and slightly wider umbilicus near Stumpy Creek. Below Wagon Pass and continuing to Wombarella Gap, the shells show a distinctly higher whorl count, are narrowly umbilicated and moderately high spired, despite the interrupted distribution and a few local unusual morphs. The material from Yammera Gap to 1.6 km west is much more widely umbilicated, with a lower spire, and normal whorl count.

Specimens of *Amplirhagada percita* collected in October, December, January through March, and May were dissected, although not from a single station. The patterns of seasonal variation are the same reported in *A. burnerensis burnerensis*. No geographic variation was noted in the anatomy.

AMPLIRHAGADA NAPIERANA SP. NOV.

(Plate 14d; Figs 36b, 48a-b, 50, 51a)

Comparative remarks

Adult examples of *Amplirhagada napierana* are immediately recognizable by their closed umbilicus, white colour without trace of reddish bands or patches, almost complete absence of radial sculpture **(Plate 14d)**, reflected lip, and relatively high spire (mean H/D ratio 0.714, **Fig. 48a**). *A. percita* (Iredale, 1939) has an interdigitated distribution with *A. napierana* and shows some indication of hybridization in zones of contact, but is usually recognizable by its open umbilicus **(Figs 47c, g)**, pale horn colour, thinner shell, lower spire (mean H/D ratio 0.630), and slightly smaller size. *A. burnerensis burnerensis* (Smith, 1894) replaces *A. napierana* east of Yammera Gap, and is almost identical in size and shape, but differs immediately in having a less reflected lip with a strong columellar colour patch that extends on and behind the shell lip. *A. b. umbilicata* is similar in colour to the nominate subspecies,

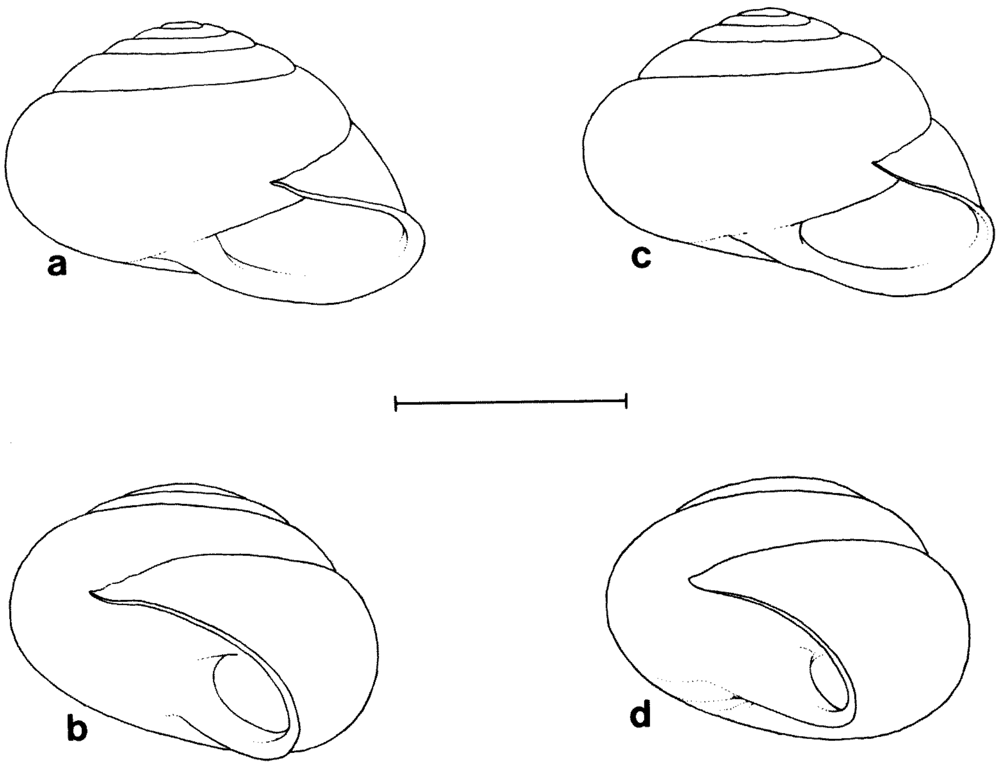


Fig. 48: Shells of *Amplirhagada,* a-b) *A. napierana,* Sta. WA-313, Napier Range, WAM 326.77, holotype; c-d) *A. burnerensis* (Smith, 1894), Windjana Gorge, Napier Range, WAM 101.68. Scale line equals 10 mm.

but has an open umbilicus and lower spire, with almost no reflection to the shell lip. All other *Amplirhagada* with closed umbilici have very strong radial sculpture and/or prominent spiral colour bands. Anatomically, *A. napierana* has a long vagina (V, **Fig. 50**) and elongated penis complex. Internally the verge is rather large and blunt-tipped **(Fig. 51a)**, the area of longtudinal ridges is short, extending barely above the start of the penis sheath, which is just above the vagina, the wall pustules are as in *A. b. burnerensis* **(Fig. 54a)**, and the main pilaster is altered from that of *A. b. burnerensis.* In *A. napierana* it is quite elongated **(Fig. 51a)**, extending two-thirds the length of the penis, the upper portion **(Fig. 36b)** with very broad corrugations that have a variable number of triangular extensions on the anterior edge, and the lower two-thirds tapering gradually and surmounted with wall pustules. *A. percita* (Iredale, 1939) agrees in basic structures with *A. napierana,* but normally there is a lateral extension to the blunt-tipped verge **(Fig. 51b)** and the main pilaster is without the tapered section surmounted with wall pustules. No other *Amplirhagada* have similar structures on the main pilaster corrugation edges.

Holotype

WAM 326.77, Sta. WA-313, among roots of a boab tree 3.2 km west of Barker Gorge, south side Napier Range, Western Australia (1:100,000 'Lennard' map sheet 3863, grid reference 914:808). Collected by Laurie Price and Carl Christensen 12 December 1976. Height of shell 13.65 mm, diameter 18.9 mm, H/D ratio 0.722, whorls 6.

Paratopotypes

WAM 327.77, WAM 241.79, WAM 289.79, FMNH 199322, FMNH 200161, 14 live, 26 dead adults, 8 live juveniles from the type locality.

Paratypes

Napier Range, ordered geographically from west to east, unless otherwise stated collected by Solem, Price or Christensen between October 1976 and May 1977: Sta. WA-300, cliffs at north-west end of range, west of Van Emmerick (=Patterson) Range, *ca.* 18.3 km by track from Red Bull Bore (Lennard 3863—110:660) (16 dead adults, FMNH 199254, WAM 291.79); Sta. NR IX, near Barnett Cave (Lennard 3863—*ca.* 096:655) (15 dead adults, WAM 964.76, B.R. Wilson and S. Slack-Smith, 30 August 1975); Sta. WA-321, 12.7 km west of Barker Gorge, south side (Lennard 3863—955:719) (18 live, 34 dead adults, 2 live juveniles, FMNH 199312, FMNH 200140, WAM 254.79); Sta. WA-192, near Chedda Cliffs, 9.1 km from Barker River Gorge Bank, south side (Lennard 3863—945:757) (32 live, 157 dead adults, 30 dead juveniles, FMNH 199416, FMNH 199419, FMNH 199862, WAM 255.79, WAM 265.79, WAM 270.79, WAM 286.79); Sta. WA-324, 7.1 km west of Barker Gorge, south side (Lennard 3863—935:765) (20 live, 23 dead adults, 4 live juveniles, FMNH

199085, FMNH 200047, WAM 242.79, WAM 268.79, WAM 273.79); Sta. WA-320, 4.7 km west of Barker Gorge, south side (Lennard 3863—921:788) (12 live, 35 dead adults, 4 dead juveniles, FMNH 199341, FMNH 200045, WAM 243.79, WAM 271.79); Sta. WA-312, crevices in rock walls 3.2 km west of Barker Gorge, south side (Lennard 3863—914:808) (31 live, 47 adults, 4 live juveniles, FMNH 199340, FMNH 200186, FMNH 200192, WAM 240.79, WAM 246.79, WAM 276.79); Sta. WA-354, north-west side Barker Gorge, 0.7 km south of Barker River Ford, north side (Lennard 3863—913:832) (2 live, 40 dead adults, FMNH 199112, FMNH 200298, WAM 245.79); Sta. WA-333, south-east side Wombarella Gap, south side (Lennard 3863—870:874) (17 dead adults, FMNH 199090, WAM 275.79); Sta. WA-376, north-east side Wombarella Gap, north side (Lennard 3863—871:878) (3 live, 24 dead adults, 2 live juveniles, FMNH 199305, FMNH 200150, WAM 247.79, WAM 284.79); Sta. WA-327, 1.6 km south-east Wombarella Gap, south side (Lennard 3863—863:885) (18 live, 37 dead adults, 4 live, 9 dead juveniles, FMNH 199078, FMNH 199911, FMNH 199913, WAM 264.79, WAM 278.79); Sta. WA-325, 0.6 km south-west of road, 3.9 km north-west of Yammera Gap, north side (Lennard 3863—862:891) (120 live, 42 dead adults, 93 live juveniles, FMNH 199216, FMNH 199264, FMNH 199718, FMNH 199856, FMNH 199858, FMNH 199860, FMNH 200102, FMNH 200104, FMNH 200241, FMNH 200243, FMNH 200245-8, FMNH 200252, FMNH 200257, FMNH 200768, WAM 237.79, WAM 248-251.79, WAM 253.79, WAM 258-259.79, WAM 261.79, WAM 263.79, WAM 267.79, WAM 269.79, WAM 274.79, WAM 285.79); Sta. WA-377, 5.5 km west of Yammera Gap, north side (Lennard 3863—857:893) (7 live adults, 1 live juvenile, FMNH 199855, WAM 266.79), Sta. WA-311, 5.3 km north-west of Yammera Gap, north side (Lennard 3863—855:902) (11 live, 43 dead adults, 8 live juveniles, FMNH 199344, FMNH 200141, WAM 239.79, WAM 283.79); Sta. WA-328, 4.0 km south-east Wombarella Gap, south side (Lennard 3863—847:904) (36 dead adults, FMNH 199273, WAM 277.79); Sta. WA-401, 3.4 km north-west Yammera Gap, north side (Lennard 3863—843:913 estimated) (6 live, 51 dead adults, 7 live juveniles, FMNH 199372, FMNH 199841, FMNH 200778, WAM 252.79, WAM 272.79, WAM 209.79); Sta. WA-200, 2.7 km west of Yammera Gap, north side (Lennard 3863—840:917) (18 live, 48 dead adults, 24 live, 4 dead juveniles, FMNH 199217, FMNH 199381, FMNH 199399, FMNH 199888, FMNH 199936, FMNH 200024, WAM 328.79, WAM 244.79, WAM 280-281.79, WAM 287.79, WAM 290.79); Sta. WA-358, 2.6 km north of Yammera Gap, north side (Lennard 3863—828:918) (25 live adults, 35 live juveniles, FMNH 199812, FMNH 200080, FMNH 200277, WAM 256-257.79, WAM 260.79); Sta. WA-381, 2.4 km north-west of Yammera Gap (Lennard 3863—826:918) (3 live, 40 dead adults, 1 live juvenile, FMNH 199142, FMNH 199823, WAM 262.79, WAM 288.79); Sta. WA-380, 2.3 km north-west of Yammera Gap, north side (Lennard 3863—825:920) (1 live, 39 dead adults, 2 live, 1 dead juvenile, FMNH 199144, FMNH 199836, WAM 434.79); Sta. WA-382, 2.1 km north-west Yammera Gap, north side (Lennard 3863—835:921) (41 dead adults, FMNH 199347, WAM 279.79); Sta. WA-360, 1.5 km west of Yammera Gap, north side (Lennard 3863—821:923) (27 dead adults, FMNH 199150, WAM 282.79).

Distribution limits in Napier Range

Amplirhagada napierana has a small pocket of occurrence in the north-west part of the Napier Range at 'near Barnett Cave' and Sta. WA-300. It is replaced by *A. percita* from Barnett Cave to somewhere north of the Chedda Cliffs (Sta. WA-321), from which point to the west side of Barker Gorge it is present in abundance, except for an isolated colony of apparent *A. percita* just north-west of Barker Gorge at Sta. WA-355. *A. napierana* does not occur in the area between Barker Gorge and Wombarella Gap, but reappears from the east side of Wombarella Gap to a point 1.5-1.6 km west of Yammera Gap, at which point it is suddenly replaced by *A. percita,* which extends to the west side of Yammera Gap. *A. napierana* thus has a three area distribution pattern in the Napier Range.

Diagnosis

Shell 13.1-21.85 mm (mean 18.71 mm) in diameter, with 5 to 6⅜ (mean 5¾ +) whorls. Apex and spire strongly and almost evenly elevated, sometimes rounded above, height of shell 9.95-16.25 mm (mean 13.41 mm), H/D ratio 0.572-0.901 (mean 0.714). Apical sculpture **(Plate 14d)** typically reduced in prominence, postapical sculpture of weak radial growth ridges, shell base with weak incised spiral lines. Shell periphery rounded **(Fig. 48a)**, body whorl descending gradually behind lip **(Fig. 48b)**, which is moderately expanded and flared. Lip reflected over umbilical opening leaving at most a narrow chink, except in a few populations apparently hybridizing with *A. percita* (Iredale, 1939). Basal lip without any trace of a protrusion. Juvenile shells light horn colour, adults becoming dead white, sometimes with a horn tone to the apical whorls, no trace of colour bands or patches at any growth stage. Based on 1,261 measured adults.

Gentalia **(Figs 50, 51a)** seasonally variable (see Discussion). Ovotestis typical, hermaphroditic duct (GD, **Fig. 50**) entering laterally on talon (GT). Free oviduct (UV) and vagina (V) rather long, spermatheca (S) with bulbous head, base of shaft expanded. Vas deferens (VD) entering penis sheath (PS) about one-third of way from apex, tightly coiled below insertion of penial retractor muscle (PR). Penis complex more elongated than in *A. burnerensis* (Smith, 1894), internally **(Fig. 51a)** very similar to *A. burnerensis* **(Fig. 54a)**, except that the area of basal longitudinal ridges is shorter, the verge is noticeably longer and blunt-tipped **(Fig. 51a)**. The main pilaster (PT) is very long **(Fig. 51a),** extending two-thirds the length of the penis chamber, with its lower two-thirds tapering gradually and having a sculpture of typical wall pustules. The upper third of the main pilaster is rather narrow, and has wide corrugations that have irregularly sized triangular projections on their anterior edges **(Fig. 36b)**. Based on 20 dissections and many checked individuals.

Discussion

Conchological variation in *Amplirhagada napierana* is minor over much of its range. **Table 22** summarizes variation at 11 stations, in some cases including live collected and dead individuals separately. The differences in H/D ratio and whorl

Table 22: Local Variation in *Amplirhagada napierana*

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
WA-300, dead	16	13.97±0.102 (13.3-14.6)	19.68±0.147 (18.7-20.6)	0.710±0.005 (0.672-0.750)	5 7/8 − (5 3/8-6 1/8)
NR IX, dead	15	14.16±0.269 (12.6-16.0)	19.31±0.229 (17.5-21.05)	0.733±0.010 (0.679-0.829)	5 7/8 + (5½-6 3/8)
WA-321					
live	18	13.32±0.216 (12.05-15.2)	18.23±0.230 (15.55-19.55)	0.734±0.010 (0.670-0.804)	5 7/8 (5 5/8-6 3/8)
dead	31	13.36±0.202 (10.45-15.7)	18.54±0.203 (16.6-20.6)	0.720±0.007 (0.630-0.803)	5 7/8 − (5¼-6¼)
WA-192, live	32	13.05±0.129 (11.1-14.2)	17.55±0.143 (15.9-19.2)	0.744±0.006 (0.651-0.805)	5 7/8 − (5 5/8-6)
WA-324, live	20	11.91±0.128 (10.7-13.0)	17.21±0.139 (16.0-18.1)	0.692±0.006 (0.629-0.727)	5 5/8 + (5 3/8-6)
WA-320, live	10	14.01±0.334 (12.5-15.7)	19.28±0.261 (18.1-20.25)	0.725±0.010 (0.691-0.785)	5 7/8 + (5½-6 1/8)
WA-312					
live	21	13.68±0.205 (11.1-15.1)	19.22±0.207 (16.75-21.1)	0.712±0.007 (0.663-0.771)	5 7/8 − (5 3/8-6 1/8)
dead	45	13.35±0.121 (11.7-15.05)	19.19±0.215 (14.5-21.35)	0.698±0.007 (0.627-0.900)	5¾ (5-6 1/8)
WA-313, live	15	13.62±0.253 (12.0-15.3)	18.85±0.233 (17.1-20.1)	0.723±0.010 (0.654-0.771)	5¾ (5 3/8-6 1/8)
WA-327, live	18	13.94±0.189 (12.15-15.25)	18.72±0.163 (17.85-19.8)	0.745±0.007 (0.671-0.787)	5¾ (5 3/8-6¼)
WA-325, dead	42	13.51±0.145 (11.65-15.2)	18.70±0.141 (17.1-21.5)	0.722±0.006 (0.638-0.809)	5¾ (5 3/8-6 1/8)
WA-311, dead	41	14.04±0.119 (11.95-15.8)	19.45±0.119 (17.6-20.85)	0.722±0.006 (0.639-0.797)	5¾ + (5 3/8-6 1/8)

count are trivial, and there is a maximum difference of 2.47 mm in mean diameter and 2.24 mm in mean height. Data on the other sampled populations was recorded and analyzed, but is not published as it only confirms the conservative pattern of variation. Typical populations are readily separable from *A. percita* (Iredale, 1939) in having the umbilicus closed instead of narrowly open, possessing a thicker, white coloured shell, and generally with a greater H/D ratio and significantly greater shell height.

The two species show an interesting pattern of multiple replacements between Hawkstone Creek and Yammera Gap, with four zones occupied by *A. percita* and three by *A. napierana.* Despite the delayed and relatively dry wet season of 1976-1977 in the Napier Range, many portions of the range became inaccessible by late December 1976 and had not become accessible when fieldwork was terminated in May 1977. Thus only some of the zones of transition could be collected from intensively, with others narrowed to a comparatively great distance of 2-3 km. Intensive early dry season collecting in the zones of transition will be required in order to test the question of hybridization or step cline variation. Available data on the populations from the zones of transition are summarized in **Table 21.** Each zone is discussed separately, from west to east.

At the 'entrance' of Barnett Cave (Sta. NR IX), the shells of *A. percita* are slightly higher and a little more narrowly umbilicated than examples from other parts of the same zone **(Table 21)**. In contrast, the *A. napierana* from 'near to' Barnett Cave (Sta. NR IX) are typical in size, shape, and closed umbilicus.

Typical *A. percita* **(Table 20)** were taken from Barnett Cave continuously to Sta. WA-322, just south of Wagon Pass (Lennard 3863–985: 719), while typical *A. napierana* **(Table 22)** were found at the Chedda Cliffs, Sta. WA-321 (Lennard 3863—955:719). I suspect that this transition zone will be found at or near the small tributary of Station Creek shown bisecting the Napier Range at Lennard 3863—970:718, but no intermediate area collections are known.

A. napierana extends from the Chedda Cliffs essentially up to the west side of Barker Gorge. Two of the few populations showing possible intergradation, Sta. WA-354 and WA-355, were sampled 31 December 1976, but the flooding of Wombarella Creek and the Barker River prevented later work in this area. The material from Sta. WA-354, located within the gorge below the main ford, has **(Table 21)** the size, colour, and whorl count of *A. napierana,* but has the spire elevation of *A. percita* and 25% of the specimens have the umbilicus narrowly open, rather than being closed. These have been classified as *A. napierana,* but do show some *percita* features. Material from Sta. WA-355, located on the north side of the range, 1.4 km from the Barker River ford, have 22% with a closed umbilicus, the rest with a very narrow opening, a low spire, thinner shell, and low H/D ratio, but the size of *A. napierana.* They have been classified as *A. percita,* although tending toward *A. napierana* in some features. Abundant materials from the east side of Barker Gorge, both north and south facies of the range, are typical *A. percita* **(Table 20)**, which continues without major variability to the west edge of Wombarella Gap **(Table 20)**.

At Wombarella Gap, there is a sharp transition, with typical *A. percita* on the west side (Sta. WA-332) and typical *A. napierana* (Sta. WA-333 and WA-376) on the east side **(Table 21)**. None of these populations show any trace of characters typifying the other species.

A. napierana then continues in typical form to about 1.6 km west of Yammera Gap, where it is sharply replaced by *A. percita.* Possible minor errors in odometer reading and collecting on 10 December (Sta. WA-306), 21 January (Sta. WA-360), and 22 March (Sta. WA-402) prevents exact pinpointing, but restrict the transition zone to an 0.1 km stretch. At Sta. WA-382, 2.1 km west of Yammera Gap on the south side of the range, typical *A. napierana* **(Table 21)** occur. At Sta. WA-360, collected 21 January 1977 and logged as 1.5 km west of Yammera Gap, dead shells of *A. napierana* size, but with slightly lower spire and 29.6% having a slightly open umbilicus **(Table 21)** were collected. They are classified as *A. napierana,* but the occurrence of an open umbilicus in a significant portion of the sample suggests that hybridization or introgression may be occurring. Unfortunately only dead examples were taken. At Sta. WA-306, logged as 1.6 km west of Yammera Gap, and situated on the range just west of the Napier Downs Station 'Garbage Dump Valley', there is a population with the size and shape of *A. percita,* but an umbilical opening that is much narrower (mean D/U ratio 16.8) than those from Sta. WA-402 (mean D/U ratio 9.44) which was logged 22 March 1977 as 1.5 km west of Yammera Gap and on west side of valley containing Napier Downs Station garbage dump. The latter population **(Table 21)** is typical *A. percita* and characteristic of the populations collected from there to Yammera Gap. I suspect that only a 100 meters may separate Sta. WA-306, WA-360, and WA-402, with the first one located slightly to the west of the others, despite the different odometer reading. If this is correct, then the actual transition between *A. napierana* and *A. percita* may occur within less than 150 meters, and the actual area of noticeable intermediates may be much narrower than that.

Neither *A. napierana* nor *A. percita* have been collected east of Yammera Gap. They are replaced in this region by first *A. burnerensis burnerensis* (Smith, 1894) and then *A. burnerensis umbilicata.*

Samples from October, December, January through March and May were dissected, following the same trends outlined for *A. burnerensis* **(Fig. 53)**. Because Sta. WA-325 remained accessible during the wet season, more closely spaced sampling was done at this station than elsewhere, but the sampling did not begin until after the start of the wet season so that *A. burnerensis* has been used as the standard. More detailed analysis of the Sta. WA-325 samples of *A. napierana* will be presented elsewhere.

AMPLIRHAGADA BURNERENSIS (SMITH, 1894)

Two subspecies with a mosaic distribution are recognized. While they differ in shell size, shape and umbilical characteristics as much if not more than most species, in the absence of any anatomical differences, I have chosen to treat them as subspecies. Comparisons with other taxa are given separately for each subspecies.

The transition between the two subspecies on the south side of the Napier Range is abrupt. At Sta. WA-344, 3.2 km east of Yammera Gap, typical *A. b. burnerensis* has been taken. At Sta. WA-345, a hill 'just north-east of Sta. WA-344, 3.2 km east of Yammera Gap,' typical dead *A. b. umbilicata* have been collected. The other areas of change have not been that pinpointed, but currently can be narrowed down to a distance of less than 1 km. The open umbilicus, lower spire, much less reflected lip, and noticeably smaller size of *A. b. umbilicata* make field recognition easy, so that detailed studies of local distribution are quite possible.

AMPLIRHAGADA BURNERENSIS BURNERENSIS (SMITH, 1894)

(Figs 36c, 48c-d, 49a-e, 52a-f, 53, 54a-b)

Helix (Hadra) burnerensis Smith, 1894, Proc. Malac. Soc. London, **1:** 91, pl. VII, fig. 18—Burner Ranges, Derby District, north-west Australia, error for Napier Range, Western Australia.

Amplirhagada burnerensis (Smith), Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 67, pl. V, fig. 11.

Amplirhagada terma Iredale, 1939, *op. cit.,* **25:** 67, p. V, fig. 8—Barrier (= Napier) Ranges, Derby district, N.W. Australia.

Nomenclature and type localities

Iredale (1939: 57-58) copied from Etheridge (1889: 200) the localities visited by W.W. Froggatt, the collector of the type specimens. These had been sent to the British Museum (Natural History) by J.C. Cox. One of these localities is 'Lennard River Gorge, Napier Range' (= Windjana Gorge). The holotype of *Helix burnerensis* Smith, 1894 (BMNH 88.11.28.65) falls within the size range of material from Sta. WA-193 and WA-194, as does the holotype of *Amplirhagada terma* Iredale, 1939. The type locality is thus restricted, for both taxa, to the south entrance of Windjana Gorge, Napier Range. This is the region of great abundance for this species in the vicinity of Windjana Gorge. The exact date of collection for the types is unknown, although the evidence in Etheridge (1889: 199) suggests that it was in 1883 or slightly earlier. It is not possible to pick either side of the gorge entrance as a more probable location for the original collection.

The holotype of *Helix burnerensis* Smith, 1894, is a recently dead, rather high adult shell that has a slight lateral crack at the umbilicus. About half of the Windjana Gorge shells show this feature. The holotype of *Amplirhagada terma* Iredale, 1939 **(Figs 49a-b)** is a small shell with closed umbilicus and slightly angled periphery. Both can be matched by dead material from Sta. WA-193A **(Table 23)** and I have no hesitation in uniting them under the older name, particularly since Iredale (1939: 67) stated that the type was selected from a 'series of 60' collected by Froggatt. The

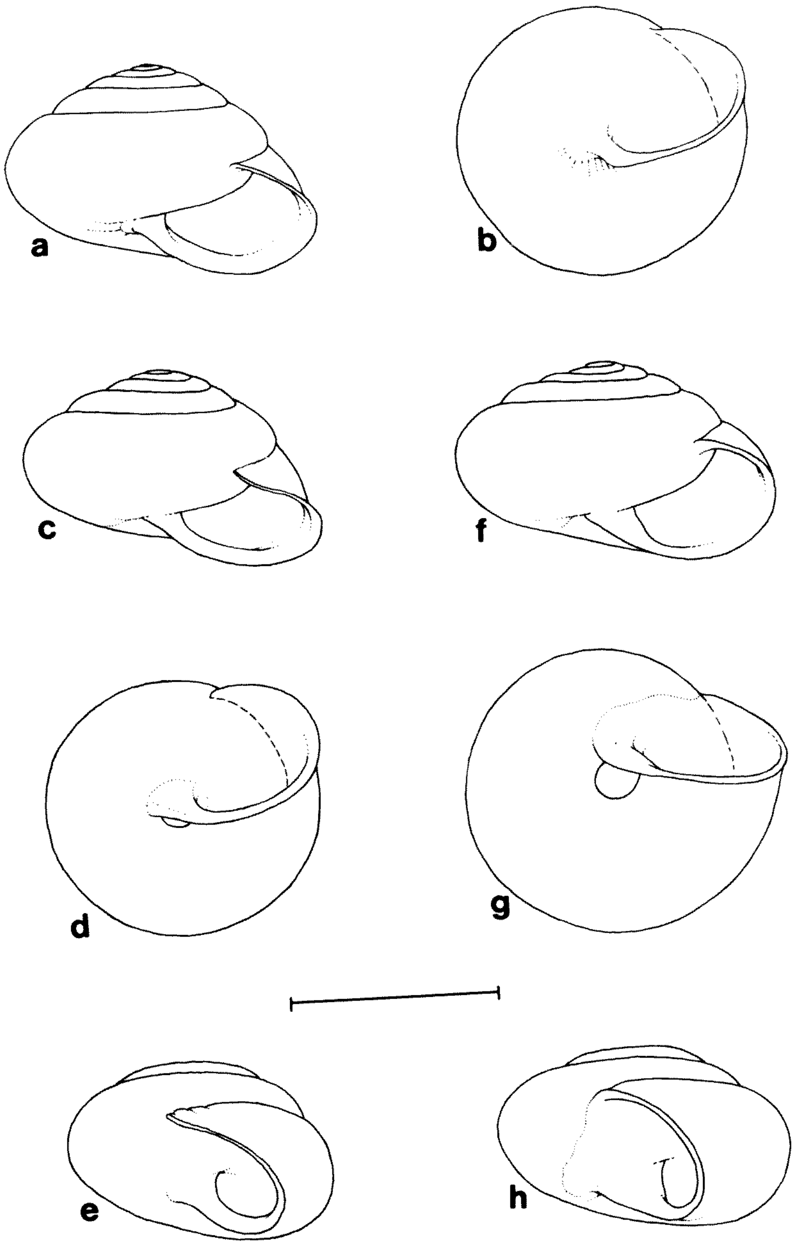


Fig. 49: Shells of *Amplirhagada*, a-e) *A. burnerensis* form *terma* Iredale, 1939, a-b are AM C.64877, holotype, c-e are WAM 68.40, paratype; f-h) *A. burnerensis umbilicata*, Sta. WA-198, Napier Range, FMNH 199446, paratype. Scale line equals 10 mm.

paratypes (WAM 68.40, **Figs. 64c-e**) are unusual only in having a wider umbilical crack and a more reflected lip, but can be matched by WA-193A materials.

Comparative remarks

Amplirhagada burnerensis burnerensis (Smith, 1894) is characterized by its closed or barely cracked umbilicus, almost total lack of radial sculpture, narrowly flared and thin lip, lack of spiral colour bands, and presence of a strong reddish suffusion behind and on the lip (fading to dull orange in collections). *A. napierana* (see **Figs 48a-d**) is nearly identical in shell form, but differs in having a more expanded lip, a slightly more abrupt columellar curve **(Fig. 48b)**, and in being dead white in colour as adults. *A. burnerensis umbilicata* is smaller and much more depressed **(Table 17)**, with a distinctly open umbilicus **(Fig. 49g)**, the lip at most slightly flared **(Fig. 49h)**, and the spire more evenly elevated **(Fig. 49f)**. *A. percita* (Iredale, 1939) also is umbilicated **(Figs 47c, g)** and is uniformly brownish-horn in colour, with a generally lower spire (mean H/D ratio 0.630), and slightly more tightly coiled whorls. All other *Amplirhagada* either have strong radial sculpture (*A. combeana* Iredale, 1938), or a combination of noticeable to strong radial sculpture plus prominent spiral colour bands. Anatomically, *A. burnerensis* has the vas deferens tightly coiled within the penis sheath **(Fig. 54b)** except after mating **(Fig. 54a)**, the verge is typical in size, but the main pilaster (PT, **Fig. 54a**) is rather short, with wide corrugations that have 4-6 bluntly triangular, short points across the upper edge of each corrugation **(Fig. 36c)**. *A. napierana* has fewer and wider corrugations with 2-4 wider and less clearly defined points on the anterior edge, and the verge **(Fig. 51a)** is blunt tipped. *A. percita* (Iredale, 1939) has the same structures as in *A. napierana,* except that the verge tip **(Figs 51b-c)** has a lateral extension. No other *Amplirhagada* has the same type of point structure on the main pilaster.

Holotype of *burnerensis*

BMNH 88.11.28.65, Burner Ranges, Derby district, N.W. Australia. Collected by W.W. Froggatt in 1883 or slightly earlier. Type locality here restricted to south entrance of Windjana Gorge, Napier Range, Western Australia. Height of shell 14.3 mm, diameter 18.7 mm, H/D ratio 0.776, whorls 6¹/₈, umbilicus with a slight lateral crack.

Paratypes of *burnerensis*

BMNH 88.11.28.66-67, two dead juveniles from the type locality.

Holotype of *terma*

AM C.64877, Burner (=Barrier) Ranges, Derby district, N.W. Australia. Collected by W.W. Froggatt in 1883 or slightly earlier. Type locality here restricted to south entrance to Windjana Gorge, Napier Range, Western Australia. Height of shell 11.4 mm, diameter 16.0 mm, H/D ratio 0.713, whorls 5¾, umbilicus closed.

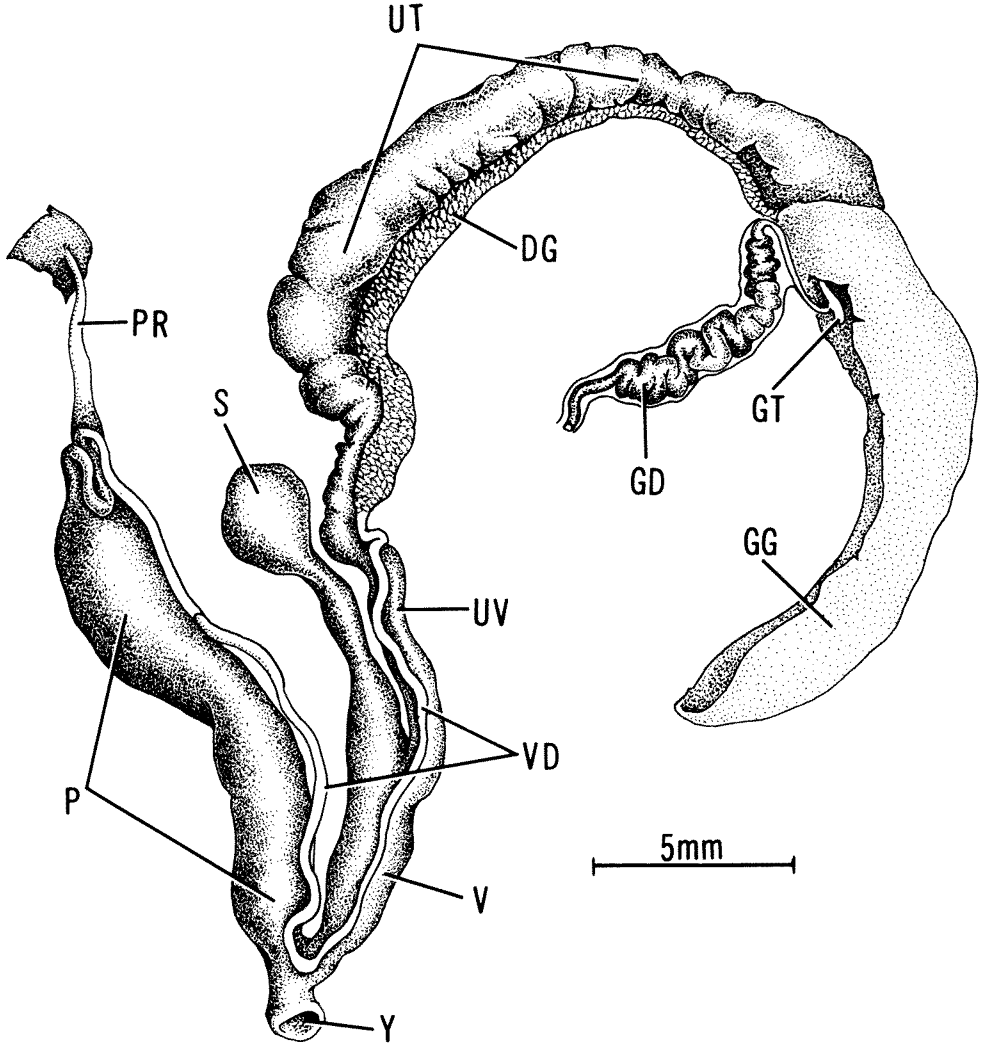


Fig. 50: Genitalia of *Amplirhagada napierana,* Sta. WA-321, Napier Range, 16 December 1976, FMNH 200140, Dissection C. Scale line as marked.

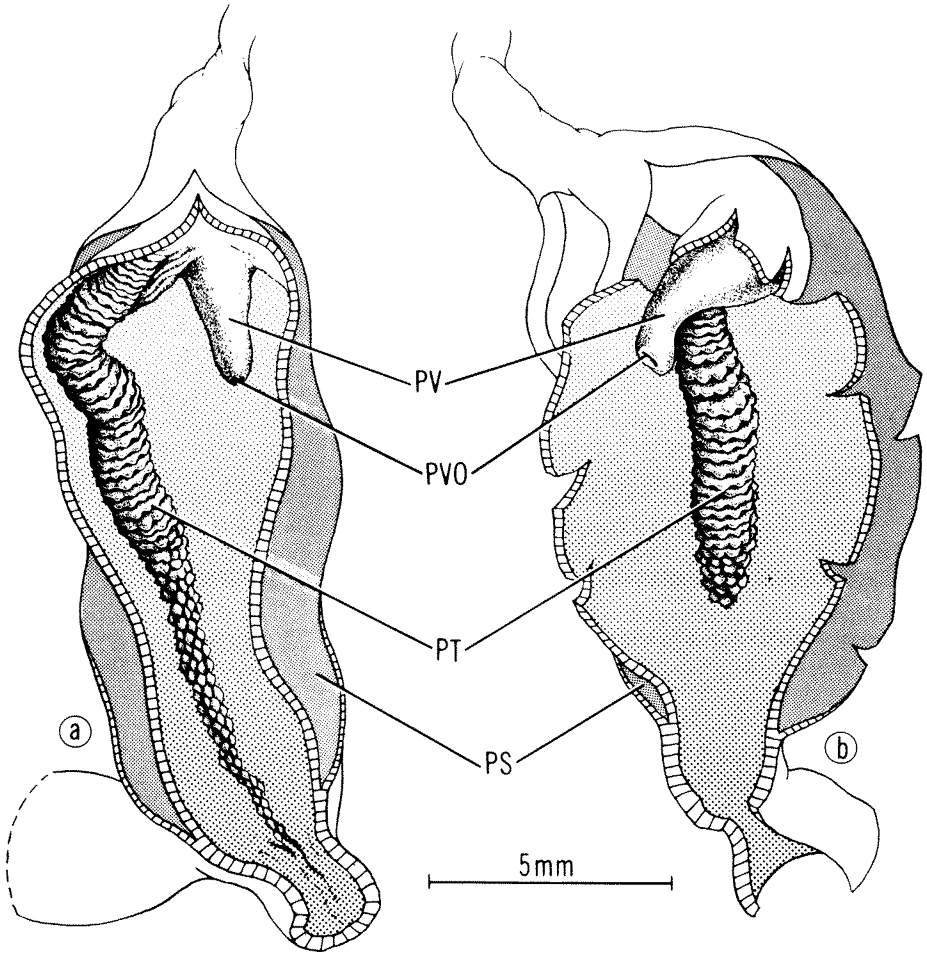


Fig. 51: Penis interiors of *Amplirhagada napierana* and *A. percita* (Iredale, 1939), a) *A. napierana,* Sta. WA-321, Napier Range, 16 December 1976, FMNH 200140, Dissection B; b) *A. percita* (Iredale, 1939), Sta. WA-190, Napier Range, 5 December 1976, FMNH 200068, Dissection C. Note lateral extension to verge tip (PV) in b and prolongation of main pilaster (PT) length in a. Scale line equals 5 mm.

Paratypes of *terma*

WAM 68.40, 2 dead shells, apparently subadult, from the type locality.

Measured materials

Napier Range, ordered west to east geographically, all collected by Solem or Price and Christensen, October 1976 to May 1977: Sta. WA-302, south-east side Yammera Gap, centre of gap (Lennard 3863—818:944) (11 live, 127 dead adults, 2 live juveniles, FMNH 199188, FMNH 199923-4, WAM 400.79, WAM 406.79); Sta. WA-305, 0.5 km east of Yammera Gap, south side (Lennard 3863—815:938) (8 live, 63 dead adults, 10 live juveniles, FMNH 199193, FMNH199246, FMNH 199825, FMNH 200061, FMNH 200109, FMNH 200263, FMNH 200266, WAM 417.79, WAM 395.79, WAM 432.79); Sta. WA-303, 1.0 km east of Yammera Gap, north side (Lennard 3863—818:944) (81 dead adults, FMNH 199181, WAM 412.79); Sta. WA-339, 1.1 km south-east of Yammera Gap, south side (Lennard 3863—812:942) (11 live, 21 dead adults, 26 live juveniles, FMNH 199089, FMNH 200156, WAM 399.79); Sta. WA-340, 1.9 km south-east Yammera Gap, south side (Lennard 3863—808:948) (1 live, 36 dead adults, FMNH 199081, FMNH 200138, WAM 409.79); Sta. WA-349, 2.0 km south-east Yammera Gap, south side (Lennard 3863—808:950) (9 live, 18 dead adults, 1 live, 1 dead juveniles, FMNH 199132, FMNH 200138, WAM 431.79, WAM 398.79); Sta. WA-348, canyon mouth 2.4 km south-east Yammera Gap, south side (Lennard 3863—807:955) (28 dead adults, FMNH 199125, WAM 433.79); Sta. WA-347, canyon 2.9 km south-east Yammera Gap, south side (Lennard 3863—806:956) (46 dead adults, FMNH 199163, WAM 408.79); Sta. WA-341, 3.1 km south-east Yammera Gap, south side (Lennard 3863—806:959) (8 live, 40 dead adults, 1 live juvenile, FMNH 199136, FMNH 200135, WAM 416.79, WAM 389.79); Sta. WA-344, north-east side low cliff, south-east side of canyon 3.2 km south-east Yammera Gap, south side (Lennard 3863—807:960) (25 dead adults, FMNH 199077, WAM 413.79); Sta. WA-352, 6.0 km east of Yammera Gap, north side (Lennard 3863—805:994) (5 live, 40 dead adults, 1 live juvenile, FMNH 199141, FMNH 200261, WAM 383.79, WAM 420.79); Sta. WA-337, cliff base 6.4 km east-southeast Yammera Gap, south side (Lennard 3863—786:991) (10 live, 37 dead adults, 4 live juveniles, FMNH 199267, FMNH 200120, WAM 415.79, WAM 390.79); Sta. WA-353, 10.0 km east of Yammera Gap, north side (Lennard 3863—787:031) (3 live, 40 dead adults, FMNH 199139, FMNH 200299, WAM 418.79); Sta. WA-193, south-west corner Windjana Gorge, first inhabitable area (Lennard 3863—743:063) (31 live adults, 13 live juveniles, FMNH 199653, FMNH 199872, WAM 396.79, WAM 397.79); Sta. WA-193A, single large fissure just west of WA-193 (Lennard 3863—743:063) (39 live, 241 dead adults, 76 live, 7 dead juveniles, FMNH 199429, FMNH 200025, WAM 405.79); Sta. WA-193B, 2nd large fissure west of WA-193 (Lennard 3863—743:063) (36 live, 3 dead adults, 21 live juveniles, FMNH 200036-7, FMNH 200041, WAM 391.79); Sta. 194, entrance and first 182 m east at south-east corner Windjana Gorge (Lennard 3863–737:065) (189 live, 37 dead adults, 114 live, 3 dead juveniles, FMNH 199199, FMNH 199724, FMNH 199852, FMNH 200016, FMNH 200020, FMNH 200055, FMNH 200057-8, FMNH 200301, FMNH 200303, FMNH 200307, FMNH 200311, FMNH 200368, WAM 423.79, WAM 426.79, WAM 428.79, WAM 550.79, WAM 555.79, WAM 559-61.79, WAM 569.79, WAM 571.79); Sta. WA-309, 3.1 km north-west Windjana Gorge, north side (Lennard 3863—758:073) (5 live, 25 dead adults, 2 live, 13 dead juveniles, FMNH 199171, FMNH 200093, WAM 410.79, WAM 394.79); Sta. WA-334, cliff base just north of Lillimilura Police Station ruins, 3 km south-east Windjana Gorge, south side (Lennard 3863—725:088) (9 live, 30 dead adults, 9 live juveniles, FMNH 199092, FMNH 200134, WAM 419.79, WAM 393.79); Sta. WA-308, north-west corner Windjana gorge, north side (Lennard 3863—740:093) (36 dead adults, 4 dead juveniles, FMNH 199174, WAM 411.79); Sta. WA-307, south-east side of Windjana Gorge at entrance (Lennard 3863—737:097) (11 dead adults, 1 dead juvenile, FMNH 199209, WAM 425.79); Sta. WA-335, cliffs and caves 0.5 km north-east of road, 3.4 km south-east Lillimilura Police Station ruins, south side (Lennard 3863—708:123) (11 live, 36 dead adults, 1 live juvenile, FMNH 199266, FMNH 200148, WAM 401.79, WAM 414.79); Sta. WA-280, 11.4 km east of Windjana Gorge turnoff, south side (1:100,000 Richenda map sheet 3963–674:142) (88 dead adults, FMNH 199228, WAM 208.79); Sta. WA-336, cliffs north-east of road, 4.3 km south-east of Carpenter Gap, south side (Richenda 3963—663:149) (14 live, 28 dead adults, 2 live juveniles, FMNH 199277, FMNH 200158, WAM 421.79, WAM 392.79).

Distribution limits in Napier Range

Amplirhagada burnerensis burnerensis has an interrupted distribution extending from the east side of Yammera Gap to at least 4.3 km south-east of Carpenter Gap. Somewhere between there and McSherry Gap, it is replaced apparently by *Quistrachia monogramma* (Ancey, 1898). Little collecting has been done in this portion of the range, which is isolated during the wet season. On the north side of the range, the nominate race extends at least 1.0 km east of Yammera Gap (WA-303), but somewhere between there and 2.0 km east (WA-196) is replaced by *A. b. umbilicata,* which extends through 5.8 km east (WA-197). *A. b. burnerensis* reappears at 6.0 km east (WA-352) and is present at 10.0 km east (WA-353), but replaced again at 10.6 km east (WA-359) and *ca.* 12.2 km east (WA-310) by *A. b. umbilicata,* but then *A. b. burnerensis* reappears at WA-309 and continues across Windjana Gorge to its southern limits. On the south side of the range, *A. b. burnerensis* extends from Yammera Gap to 3.1 km east (WA-341) and 3.2 km east (WA-344). From 3.2 km (WA-345) to 4.8 km east of Yammera Gap (WA-342, WA-338) typical *A. b. umbilicata* are found. *A. b. burnerensis* reappears at 6.4 km east (WA-337) and presumably continues to and across Windjana Gorge.

Diagnosis

Shell 14.0-21.85 mm (mean 18.65 mm), with 5 to 6¾ (mean 5¾) whorls. Apex and spire usually strongly elevated, often rounded above, height of shell 9.0-15.0

mm (mean 13.12 mm), H/D ratio 0.568-0.855 (mean 0.686). Apical sculpture of fine low pustules, post-apical whorls with faint radial growth lines at irregular intervals and a noticeable sculpture of incised spiral lines **(Plate 14f)** extending up the spire. Shell periphery normally rounded **(Fig. 48c)**, occasionally slightly angulated **(Fig. 49a)** in smaller individuals. Body whorl slightly to moderately descending behind lip **(Fig. 48d)**, which is narrowly expanded and slightly flared. Umbilicus completely or nearly completely covered by reflected lip, at most **(Fig. 49d)** with a slight lateral crack. Basal lip without any trace of a protrusion. Colour bands absent, columellar area bright orange to red in live material, fading to dull orange or purplish red in museum specimens, colour extending along and behind lip and part-way up on body whorl. Based on 1,371 measured adults.

Genitalia **(Figs 52-54)** seasonally variable (see under Discussion). Ovotestis (G) typical, hermaphroditic duct (GD) entering laterally on talon (GT, **Fig. 52a**). Vagina (V) somewhat variable in length, short **(Fig. 52a)** to moderate **(Fig. 54b)**, spermatheca (S) with base greatly swollen just after mating **(Fig. 52a)**, normally **(Fig. 54b)** fairly slender, head elongated and moderately swollen. Vas deferens (VD) entering penis sheath (PS) near top, tightly coiled below insertion of penial retractor muscle (PR) normally **(Figs 52c, 54b)** except after mating **(Fig. 52a)**. Penis complex of normal width, slightly bulbous medially, internally **(Fig. 54a)** with slightly enlarged verge (PV), basal area of longitudinal ridges (PP) normal, wall pustules (PPR) partly arranged in rows, no sperm groove present. Main pilaster (PT) confined usually to upper third to half of penis chamber, tapering abruptly above and below, surface **(Fig. 36c)** with rather wide corrugations, each bearing four to six broadly triangular, short points with rounded tips. Based on 35 dissected and many checked individuals.

Discussion

There is no clear pattern of local variation in the populations of *Amplirhagada burnerensis burnerensis* (Smith, 1894) in regard to conchological features. Measurements of some of the larger samples are given in **Table 23.** Materials from the comparatively narrow rock crevices at Sta. WA-193 and WA-193A are among the smaller sized shells, while those from east of Windjana Gorge (WA-335, WA-336, WA-280) are among the largest in size. Yet the westernmost sample from the east margin of Yammera Gap (Sta. WA-302) is very close in size to the eastern samples. There is more variation in H/D ratio, relating to the doming of the spire, but again there is no geographic basis to the variability.

Considerably greater variation is found in the genitalia, much of it relating to seasonal samples. Available preserved materials covered mid-dry season (July), late dry season (October), normal wet season start (early December), several mid to late wet season samples (late December, January, February, mid-March), and early dry season (May). The significant seasonal variations in several organs are summarized in **Fig. 53.** The general pattern is to become male active just prior to the normal start of the wet season, female active after copulation, multiple matings occur during the

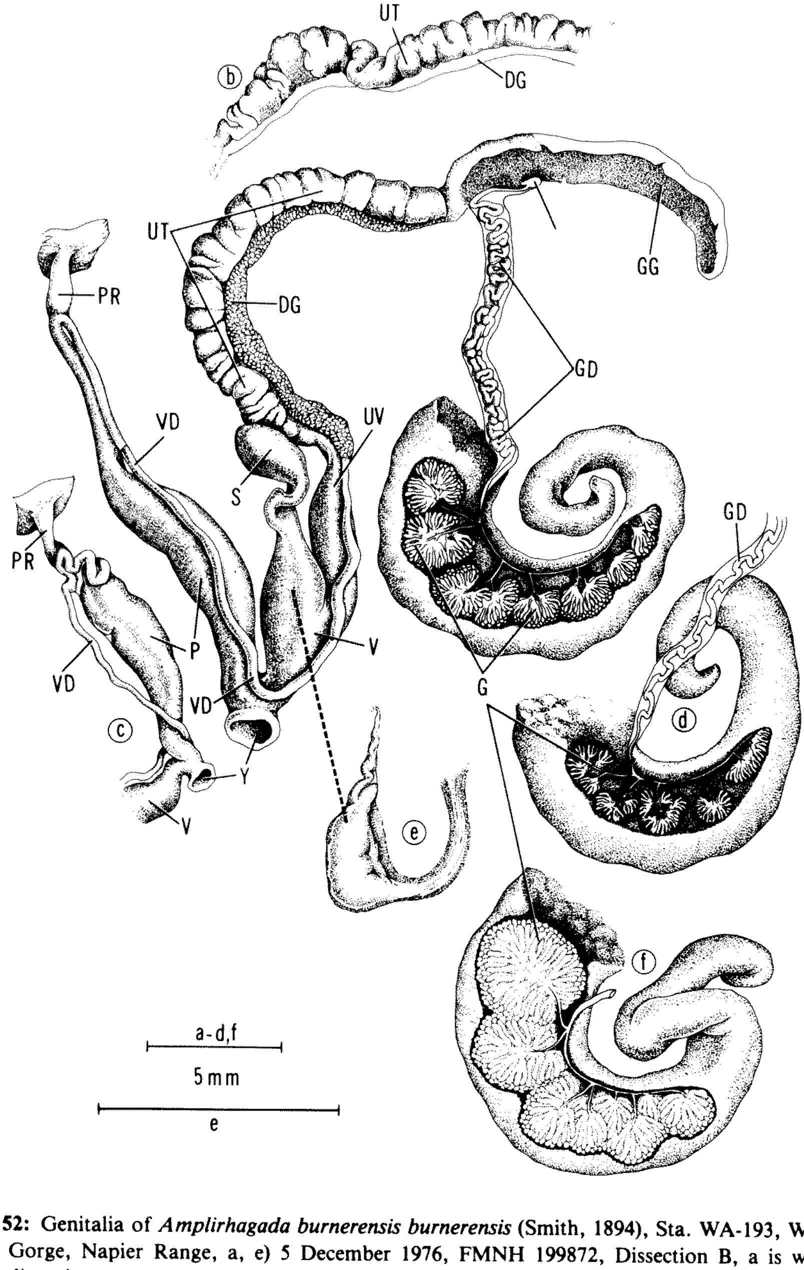
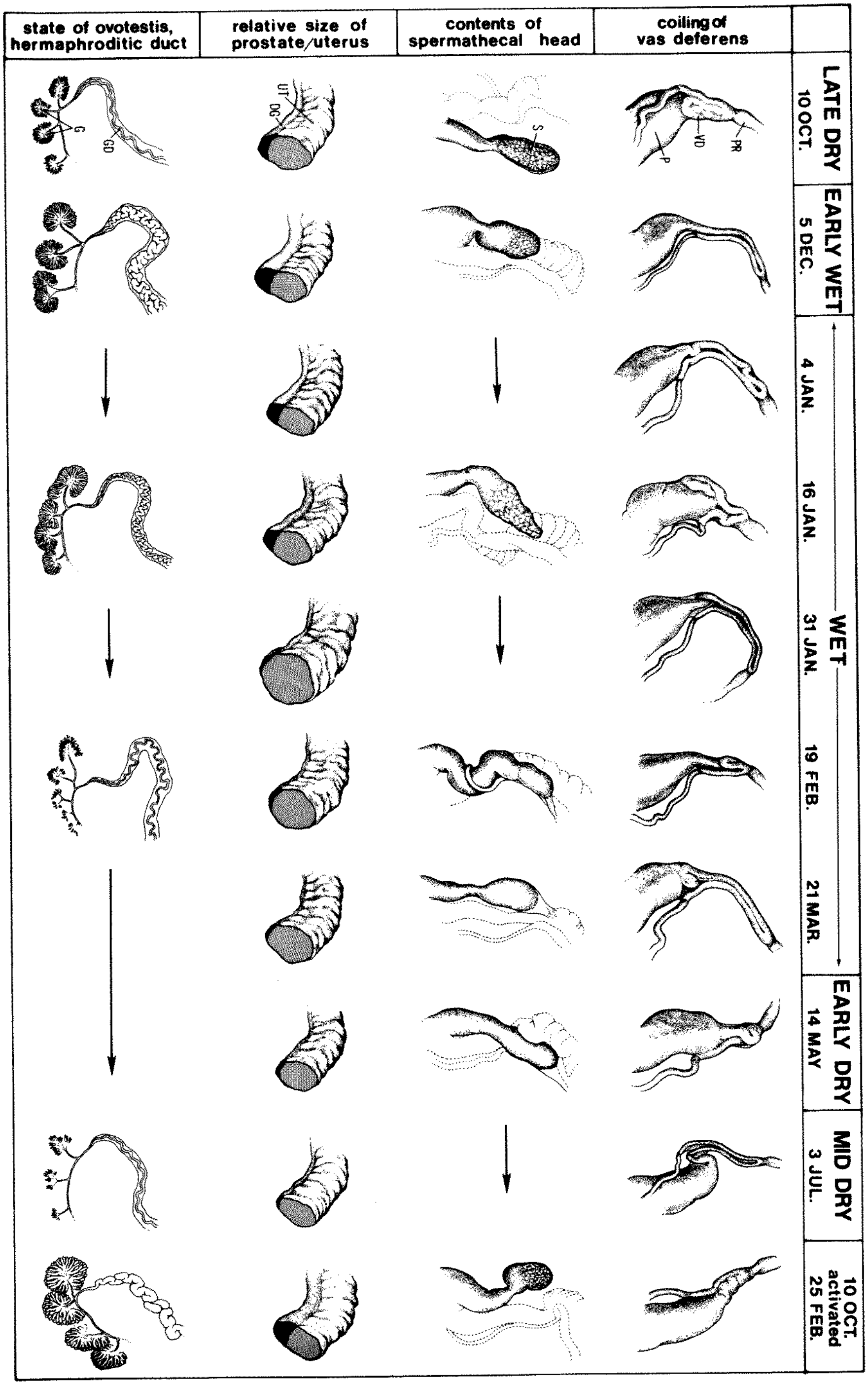


Fig. 52: Genitalia of ***Amplirhagada burnerensis burnerensis*** (Smith, 1894), Sta. WA-193, Windjana Gorge, Napier Range, a, e) 5 December 1976, FMNH 199872, Dissection B, a is whole genitalia, e is sperm packet removed from base of spermatheca and free oviduct; b-d) 10 October 1976, Sta. WA-193A, FMNH 200025, Dissection B, b is prostate (DG) and uterus (UT), c is penis complex (P), d is ovotestis (G) and hermaphroditic duct (GD); f) is ovotestis (G) from individual collected 10 October 1976 and kept in aestivation until 25 February 1977, Sta. WA-193A, Windjana Gorge, Napier Range. Scale lines equal 5 mm.


state of ovotestis, hermaphroditic duct
relative size of prostate/uterus
contents of spermathecal head
coiling of vas deferens
LATE DRY
10 OCT.
EARLY WET
5 DEC.
WET
4 JAN.
16 JAN.
31 JAN.
19 FEB.
21 MAR.
EARLY DRY
14 MAY
MID DRY
3 JUL.
10 OCT.
activated
25 FEB.
G
GD
UT
DG
S
PR
VD
P

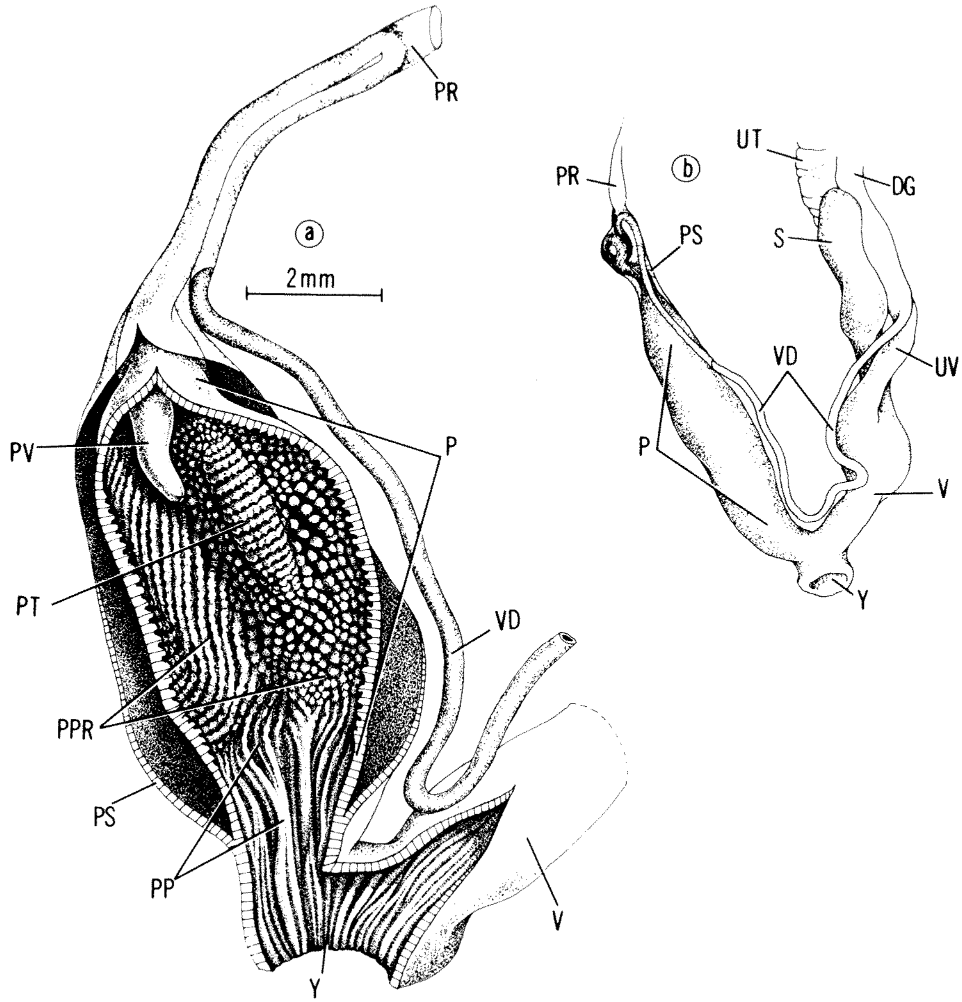


Fig. 54: Genitalia of *Amplirhagada burnerensis* (Smith, 1894), a) interior of penis chamber, Sta. WA-193, Windjana Gorge, Napier Range, 5 December 1976, FMNH 199872, Dissection B; b) terminal genitalia with elongated vagina (V), Sta. 194, Windjana Gorge, Napier Range, 4 January 1977, FMNH 200055, Dissection A. Scale lines as marked.

Fig. 53: Seasonal variation in the genitalia of *Amplirhagada burnerensis burnerensis* (Smith, 1894). Sta. WA-193 and WA-194, Windjana Gorge, Napier Range. Partly diagrammatic, not to exact scale. Specimens collected on 5 December were taken the morning after first thunderstorms of season (much later than usual). No heavy rains came until mid-January, but there were local thunderstorms and under one inch rains before then. Cyclones 'Leo' and 'Karen' in early March produced rainfall that undoubtedly led to mating and the elongated vas deferens seen in the 21 March individuals.

Table 23: Local Variation in *Amplirhagada burnerensis burnerensis* (Smith, 1894)

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
WA-302					
live	11	12.60 ± 0.260 (11.5-14.4)	19.40 ± 0.302 (18.2-21.6)	0.649 ± 0.008 (0.598-0.687)	5¾ + (5½-6⅛)
dead	125	12.67 ± 0.072 (10.3-14.8)	18.85 ± 0.091 (16.1-21.5)	0.673 ± 0.003 (0.576-0.758)	5¾ (5⅜-6⅜)
WA-305, dead	62	12.45 ± 0.109 (10.6-14.2)	18.69 ± 0.013 (16.4-20.8)	0.667 ± 0.013 (0.594-0.731)	5¾ − (5¼-6½)
WA-303, dead	80	12.59 ± 0.088 (11.0-14.9)	18.54 ± 0.106 (17.0-21.2)	0.680 ± 0.003 (0.600-0.741)	5⅝ + (5⅜-6¼)
WA-339, dead	21	13.33 ± 0.156 (12.2-14.85)	18.65 ± 0.112 (17.45-19.55)	0.715 ± 0.008 (0.655-0.801)	5⅝ + (5¼-6)
WA-340, dead	36	13.11 ± 0.122 (11.6-15.0)	19.21 ± 0.180 (17.2-21.9)	0.683 ± 0.006 (0.633-0.767)	5⅝ + (5⅜-6⅛)
WA-349					
live	9	14.37 ± 0.121 (13.7-14.8)	18.44 ± 0.147 (17.8-19.1)	0.779 ± 0.008 (0.762-0.811)	5⅞ (5¾-6⅛)
dead	19	13.63 ± 0.187 (12.1-14.75)	18.51 ± 0.253 (16.4-20.5)	0.737 ± 0.008 (0.650-0.794)	5⅞ − (5⅝-6⅛)
WA-348, dead	28	13.46 ± 0.139 (11.55-14.90)	19.44 ± 0.174 (16.75-20.85)	0.693 ± 0.005 (0.652-0.739)	5¾ (5½-6)
WA-347, dead	45	13.59 ± 0.136 (12.2-15.8)	19.41 ± 0.125 (17.9-21.6)	0.700 ± 0.005 (0.642-0.772)	6⅛ − (5⅛-6¾)
WA-341, dead	40	12.25 ± 0.100 (10.9-13.7)	18.00 ± 0.108 (16.9-19.6)	0.680 ± 0.004 (0.624-0.741)	5⅝ − (5-6½)
WA-344, dead	25	12.81 ± 0.169 (11.5-14.6)	18.92 ± 0.186 (17.2-21.1)	0.677 ± 0.007 (0.610-0.772)	5⅞ + (5-6¾)
WA-352, dead	36	13.02 ± 0.174 (11.1-15.6)	18.74 ± 0.141 (16.9-20.4)	0.693 ± 0.006 (0.636-0.785)	5⅝ + (5¼-6¾)
WA-337					
live	10	13.41 ± 0.253 (12.2-14.9)	18.32 ± 0.385 (16.8-20.4)	0.732 ± 0.008 (0.681-0.773)	6 − (5¾-6⅛)
dead	36	13.07 ± 0.161 (11.2-15.4)	19.38 ± 0.236 (14.2-21.7)	0.674 ± 0.007 (0.615-0.817)	5¾ + (5⅜-6¼)
WA-353, dead	40	13.24 ± 0.117 (11.35-14.9)	18.76 ± 0.136 (16.2-21.0)	0.706 ± 0.004 (0.638-0.784)	5⅞ − (5½-6⅛)

Table 23: Local Variation in *Amplirhagada burnerensis burnerensis* (Smith, 1894) (continued)

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
WA-193					
live, 10-X-76	29	12.59 ± 0.155 (11.1-14.15)	18.11 ± 0.160 (16.7-20.1)	0.696 ± 0.006 (0.648-0.765)	5¾ (5¼-6⅛)
live, 5-XII-76	12	12. 57 ± 0.276 (11.5-15.0)	17.62 ± 0.254 (15.75-18.8)	0.714 ± 0.012 (0.656-0.798)	5¾ (5¼-6⅛)
dead, 10-X-76	39	12.14 ± 0.133 (10.7-14.2)	18.10 ± 0.141 (16.5-20.0)	0.670 ± 0.005 (0.614-0.739)	5¾ − (5⅜-6⅛)
WA-193A, dead	231	11.74 ± 0.055 (9.05-15.9)	17.75 ± 0.056 (15.8-21.5)	0.661 ± 0.004 (0.568-0.855)	5⅝ (5-6⅛)
WA-194					
live, 21-III-77	26	13.23 ± 0.218 (11.1-15.5)	19.18 ± 0.222 (17.1-21.7)	0.689 ± 0.007 (0.634-0.789)	5⅞ − (5¼-6⅜)
live, 14-V-77	32	13.01 ± 0.124 (11.5-14.4)	18.79 ± 0.154 (17.5-20.8)	0.693 ± 0.005 (0.644-0.770)	5⅝ + (5⅜-6)
WA-309, dead	24	13.21 ± 0.150 (11.4-16.8)	18.36 ± 0.159 (16.4-20.6)	0.719 ± 0.005 (0.684-0.816)	6 − (5½-6⅛)
WA-308, dead	40	12.75 ± 0.123 (11.4-14.5)	18.35 ± 0.090 (17.4-19.55)	0.695 ± 0.005 (0.655-0.772)	5⅞ − (5½-6¼)
WA-334					
live	9	13.27 ± 0.294 (11.8-14.7)	18.33 ± 0.353 (17.0-20.05)	0.725 ± 0.012 (0.677-0.783)	5¾ (5½-6)
dead	28	13.58 ± 0.127 (12.5-14.8)	19.05 ± 0.116 (17.9-20.2)	0.713 ± 0.006 (0.652-0.771)	5⅝ + (5½-6)
WA-307, dead	11	13.34 ± 0.132 (12.55-13.8)	18.85 ± 0.105 (18.3-19.5)	0.708 ± 0.006 (0.671-0.738)	5⅞ (5⅝-6)
WA-335					
live	11	14.20 ± 0.223 (12.75-15.0)	19.58 ± 0.255 (18.35-20.5)	0.726 ± 0.012 (0.670-0.807)	5⅞ (5⅝-6⅛)
dead	37	13.96 ± 0.139 (12.0-15.8)	19.98 ± 0.150 (18.6-21.8)	0.699 ± 0.005 (0.645-0.775)	5¾ (5¼-6⅛)
WA-280, dead	17	12.85 ± 0.134 (12.4-13.9)	19.06 ± 0.192 (17.4-20.45)	0.675 ± 0.006 (0.633-0.710)	5¾ (5½-6)
WA-336					
live	14	13.98 ± 0.149 (13.0-14.8)	19.93 ± 0.152 (18.75-20.75)	0.702 ± 0.007 (0.660-0.758)	5⅞ + (5¾-6⅛)
dead	28	13.19 ± 0.117 (12.3-15.0)	20.33 ± 0.146 (19.1-21.8)	0.649 ± 0.006 (0.590-0.711)	5¾ (5⅝-6⅛)

first half of the wet, then deactivation of the reproductive tract in the late wet season is accompanied by extreme shrinking of the ovotestis and filling of the digestive gland with stored food. This sequence was derived from study of samples from Sta. WA-193 and WA-194, which are at the south-west and south-east sides of the entrance to Windjana Gorge. Data from other species of *Amplirhagada* conform to the same patterns, although none were documented by such extensive data.

The basic gross changes in the genitalia were determined by dissection. Time did not permit histological study. With the outline developed here, a sampling program to study the microscopic changes within organs can be devised simply and would be an appropriate thesis project.

At the middle of the dry season, the ovotestis (**Fig. 53**) is miniscule in terms of lobe length and volume, and the hermaphroditic duct is very slender with 'waved' coiling. Essentially the same pattern is seen in material collected 10 October (**Fig. 52d**), which is well before the normal start of the wet season in the Napier Range (in only 3 of 17 years with available October records has there been more than 10 mm of October rain recorded at Napier Downs, the rainfall station nearest to Windjana Gorge). On 5 December (**Fig. 52a**), the morning just following the first shower of the wet season at Windjana Gorge (abnormally late), the ovotestis (G) is greatly enlarged and the hermaphroditic duct (GD) is thicker and much more tightly coiled than in October. The presence of the spermatophore (**Fig. 52e**) is evidence that the mating had just occurred. Individuals collected at various dates in January showed variation in the thickness of the ovotestis lobes, probably indicating different times of mating, but with the hermaphroditic duct very thick and tightly kinked. By mid-February, the ovotestis has drastically shrunken in size, the hermaphroditic duct is much thinner and less tightly coiled. From then until August there is slight variation in the ovotestis lobe size and shape, but the pattern of greatly reduced size is clear, and the thin, relatively uncoiled hermaphroditic duct is constant.

The pattern of change in the prostate (DG) and uterus (UT) also is illustrated in **Fig. 53.** The normal dry season condition is for a thin prostate and a small, almost circular uterus (mid-February to October). In early December the prostate is significantly thickened and continues in that pattern of increased size through January, after which it apparently shrinks quickly. The uterus did not enlarge until January in the 1976-1977 wet season, probably because of the very late and light start to that wet season, coupled with a collecting artifact. At Sta. WA-194, collections in early December were of snails at the surface of crevices that had been activated by a light shower. Collections from then until late January were obtained by progressively deeper 'quarrying' of talus and included individuals increasingly sheltered from the early light showers, and thus activated progressively later in the wet season. Heavy, general soaking rains did not come until late January or February. I would anticipate that the reduced uterus size in the samples of 4 January through 16 January represent a delayed activation rather than a normal pattern and that the enlarged uterus seen on 31 January would have occurred in late December or early January under more normal wet season regime. The increased size of the prostate indicates male activity, while the increased size of the uterus indicates female activity of the tract.

Changes in two areas are immediately indicative of recent mating. The tight coiling of the vas deferens (VD) inside the sheath seen in October **(Fig. 52c)** contrasts immediately with the elongated state found just after mating **(Fig. 52a)**. The recoiling procedure after mating probably takes several days, and the partial recoiling seen in **Fig. 54b** (4 January), followed by tight coiling on 16 January, then straightening on 31 January, variable coiling on 19 February, straight on 21 March (shortly after a heavy dousing by a cyclone fringe storm), heavy coiling in May and August, suggest strongly that multiple matings do occur. The presence of a spermatophoral mass in the lower spermatheca, with its open end pointing up into the free oviduct **(Fig. 52e)**, on 5 December is direct evidence of mating. Externally this is indicated by the swollen spermathecal base (compare **Figs 52a** and **54b** for width of this area). Throughout the year the head of the spermatheca contains material that is very loosely packed during the early wet season, very tightly packed during the late wet and early dry season. The significance of this has been discussed in the general discussion above.

Important evidence concerning the timing and sequence of changes came from specimens collected 10 October 1976 and shipped live to Perth for electrophoretic work. On 25 February 1977, several of these individuals were drowned, preserved, and then dissected. In the interim they had been inside a collecting bag, inside a closed cardboard box as wrapped in paper for mailing, sitting on a shelf in the basement specimen lab of the Western Australian Museum in Perth. The room was in the middle of the building with controlled climate. Thus the specimens had not been given the normal opportunity to activate at the start of the wet season. When dissected, the ovotestis (G, **Fig. 52f**) was enormous, almost filling the entire digestive gland lobe, the hermaphroditic duct was swollen and tightly kinked **(Fig. 53)**, the prostate was greatly enlarged and the uterus still very small. The spermathecal head still contained a small quantity of material, but the base was very slender. The vas deferens was tightly coiled **(Fig. 53)**. The large size of the hermaphroditic duct and prostate indicate that the specimen was still male active, which is confirmed by the enormous size of the ovotestis. The animals simply had continued to produce sperm in anticipation of mating upon activation, but the small size of the uterus (comparable to the August and October, not the January or February field samples) indicates that female activation had not occurred. Since late February and March field samples had undergone shrinkage of both ovotestis *and* hermaphroditic duct **(Fig. 53)**, this sequence is not a simple endogenous rhythm. The triggering of male development prior to the normal start of the wet season may well be controlled by either an endogenous cycle or by some environmental trigger, but the absence of female activation in those specimens kept inactive from October to February strongly suggests that it is mating that triggers the female system activation.

Other parts of the genitalia showed no obvious changes in gross structure through the seasons. The albumen gland does not change in size or shape once adult size is reached. In newly adult shells it is extremely small, usually only a quarter to third the normal length, reaching full size sometime during the next wet season. Subsequent to that point there is no evidence as to any change in length or volume, allowing for variability in preservation and the amount of food in the stomach. The penis complex showed no gross changes and the main pilaster does not seem to change at all during the seasons, unlike the situation in at least some *Torresitrachia* (Solem, 1979: 59-60).

Unfortunately, no examples of *Amplirhagada burnerensis* (Smith, 1894) were observed copulating.

AMPLIRHAGADA BURNERENSIS UMBILICATA SUBSP. NOV.

(Plate 14c; Figs 49f-h)

Comparative remarks

Amplirhagada burnerensis umbilicata is characterized by its open umbilicus **(Fig. 49g)**, lack of expansion and flare to the lip **(Fig. 49h)**, relatively low spire (mean H/D ratio 0.614), absence of spiral colour bands combined with a reddish columellar patch that extends along and behind the lip, reduced apical and near total lack of postapical radial sculpture **(Plate 14c)**, and relatively small size (mean diameter 16.75 mm). *A. b. burnerensis* has a closed or slightly cracked umbilicus, averages almost 2 mm more in diameter, and usually has a moderately reflected lip. *A. pusilla* is very similar in size and shape, but has a clearly angulated periphery **(Fig. 38e)**, flàtter whorls and thinner body whorl, much more strongly reflected lip, spiral colour bands, and very prominent sharply defined radial sculpture **(Plate 12c)**. *A. drysdaleana* also is sharply angulated **(Fig. 38c)** with a strongly reflected lip, prominent colour bands, and prominent radial sculpture **(Plate 12d)**. Other umbilicated species are much larger and with strongly reflected lips. The horn-coloured *A. percita* (Iredale, 1939) from west of Yammera Gap in the Napier Range has a reflected lip, no red coloration, usually a less prominently elevated spire, no trace of radial sculpture **(Plate 14e)**, and a thinner shell. Anatomically, dissected material of *A. b. umbilicata* showed no differences from the nominate subspecies.

Holotype

WAM 310.79, Sta. WA-196, 2 km east of Yammera Gap, north side of Napier Range, Western Australia (1:100,000 'Lennard' map sheet 3863, grid reference 815:954). Collected by Alan Solem, Laurie Price and Carl Christensen, 9 December 1976. Height of shell 10.55 mm, diameter 16.7 mm, H/D ratio 0.632, whorls 5 ⅜, umbilical width 1.3 mm, D/U ratio 12.8.

Paratopotypes

WAM 301.79, WAM 306.79, FMNH 199191-2, FMNH 199422, FMNH 199945, 1 live, 74 dead adults, 24 dead juveniles from the type locality.

Paratypes

Napier Range, ordered west to east geographically, unless specified otherwise all collected by Solem, Price and Christensen between October 1976 and May 1977: Sta. WA-344, 3.2 km south-east Yammera Gap, south side (Lennard 3863–807:960) (17 live, 29 dead adults, 11 live, 14 dead juveniles, FMNH 199135, FMNH 200111, FMNH 200115, WAM 294.79, WAM 308.79); Sta. WA-345, hill just north-east of WA-344, 3.2 km south-east Yammera Gap south side (Lennard 3863–807:960) (17 dead adults, 7 dead juveniles, FMNH 199130); Sta. WA-350, 2.4 km south-east Yammera Gap, north side (Lennard 3863—814:960) (1 live, 11 dead adults, 8 live, 27 dead juveniles, FMNH 199127, FMNH 200169, WAM 297.79, WAM 307.79); Sta. WA-346, north-east slope of canyon, *ca.* 0.2 km from WA-344, 3.4 km south-east Yammera Gap, south side (Lennard 3863—808:962) (13 dead adults, 8 dead juveniles, FMNH 199147, WAM 302.79); Sta. WA-343, 3.6 km south-east Yammera Gap, south side (Lennard 3863—807:964) (27 dead adults, 14 dead juveniles, FMNH 199115, WAM 305.79); Sta. WA-304, 3.2 km east of Yammera Gap, north side (Lennard 3863—815:969) (79 dead adults, 9 live, 78 dead juveniles, FMNH 199250, FMNH 200105, WAM 292.79, WAM 299.79); Sta. WA-198, 4.25 km east of Yammera Gap, north side (Lennard 3863—811:978) (1 dead adult, 1 dead juvenile, FMNH 199446); Sta. WA-338, 4.3 km east-south-east Yammera Gap, south side (Lennard 3863—808:977) (2 live, 20 dead adults, 4 live, 19 dead juveniles, FMNH 199275, FMNH 200155, WAM 433.79, WAM 293.79); Sta. WA-342, 4.8 km south-east Yammera Gap, south side (Lennard 3863—807:973) (2 live, 28 dead adults, 1 live, 4 dead juveniles, FMNH 199100, FMNH 200116, WAM 300.79, WAM 311.79); *ca.* 5 km south-east Yammera Gap, north side (12 dead adults, WAM, B.R. Wilson and S. Slack-Smith, 24 May 1976); *ca.* 5.3 km south-east Yammera Gap (15 dead adults, WAM, B.R. Wilson and S. Slack-Smith, 22 May 1976); Sta. WA-197, 5.8 km east of Yammera Gap, north side (Lennard 3863—807:991) (54 dead adults, 1 live, 12 dead juveniles, FMNH 199391, FMNH 200010); Sta. WA-359, 10.5 km east of Yammera Gap, north side (Lennard 3863—782:033) (9 live, 22 dead adults, 10 live, 4 dead juveniles, FMNH 199117, FMNH 200152, FMNH 200285-6, WAM 295.79, WAM 298.79, WAM 304.79); Sta. WA-310, 8.5 km north-west Windjana Gorge, north side (Lennard 3863—778:050) (1 live, 35 dead adults, 1 live, 3 dead juveniles, FMNH 199336, FMNH 200095).

Distribution limits in Napier Range

Amplirhagada burnerensis umbilicata shows slightly different distributions on the north and south sides of the Napier Range. On the north side, it replaces the nominate race somewhere between 1.0 km (WA-303) and 2.0 km (WA-196) east of Yammera Gap, then extends through 5.8 km east (WA-197) with the nominate race reappearing at 6.0 km east (WA-352). *A. b. umbilicata* reappears at 10.6 km east (WA-359) and about 12.2 km east (WA-310), but elsewhere the nominate race is present. On the south side, the transition between the subspecies occurs abruptly, with Sta. WA-344 at 3.2 km east having typical *A. b. burnerensis,* and WA-345, 'hill just north-east of WA-344', at 3.2 km east having *A. b. umbilicata*, which then extends east to 4.8 km east (Sta. WA-338, WA-342). The nominate race occurs at the next sampling station, WA-337, which is 6.4 km east of Yammera Gap. *A. b. umilicata* thus has a somewhat mosaic distribution pattern.

Diagnosis

Shell 12.8-19.8 mm (mean 16.75 mm) in diameter, with 4¾ to 6⅞ (mean 5⅝) whorls. Apex and spire moderately and almost evenly elevated, height of shell 7.3-14.15 mm (mean 10.25 mm), H/D ratio 0.510-0.783 (mean 0.614). Apical sculpture **(Plate 14c)** reduced in prominence, composed of fine elongated pustulations, postapical whorls with very weak and irregular radial growth lines. Shell base and part of upper spire showing typical weak spiral incised lines **(Plate 14f)**. Shell periphery rounded **(Fig. 49f)**, body whorl at most slightly descending behind lip **(Fig. 49h)**, only rarely with any flare or expansion. Umbilicus narrowly open **(Fig. 49g)**, 0.6-2.75 mm (mean 1.59 mm) wide, D/U ratio 5.84-29.4 (mean 11.3). Basal lip without any trace of a protrusion. Colour bands absent, columellar colour patch extends onto and behind lip, often continuing along body whorl suture for a distance, usually lighter in tone than for nominate subspecies. Based on 628 measured adults.

Genitalia (not illustrated) agreeing with that of the nominate subspecies. Based on 8 dissections.

Discussion

Local variation in *Amplirhagada burnerensis umbilicata* is summarized in Table 24. There is no obvious geographic pattern to the variations, and no distinction between those from the south and north sides of the range. In the area where the abruptness of the transition between the two subspecies is documented, Sta. WA-345 has one of the largest and most widely umbilicated populations of *A. b. umbilicata* **(Table 24)**, while at Sta. WA-344 the population of *A. b. burnerensis* (Smith, 1894) shows no unusual features.

Since the dissections of several examples showed no differences in anatomy from the structures found in *A. b. burnerensis,* no illustrations were prepared.

AMPLIRHAGADA ELEVATA SP. NOV.

(Plate 14a; Figs 36f, 55f, 57b, 58a)

Comparative remarks

Amplirhagada elevata is a quite high (mean H/D ratio 0.796), dome-shaped **(Fig. 55f)** shell with rather flat whorls, noticeably angled periphery, no basal lip protrusion, reduced radial sculpture **(Plate 14a)**, and relatively pale colour. The partly sympatric *A. wilsoni* has a distinctly lower spire (mean H/D ratio 0.700, **Fig. 55e**),

Table 24: Local Variation in *Amplirhagada burnerensis umbilicata*

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
North Side of Range				
WA-196				
11-X-76, dead	32	10.79 ± 0.167 (8.5-12.6)	16.73 ± 0.142 (15.1-18.6)	0.644 ± 0.007 (0.563-0.733)
9-XII-76, live	16	10.78 ± 0.168 (9.7-12.0)	16.68 ± 0.248 (15.0-19.0)	0.647 ± 0.009 (0.584-0.758)
9-XII-76, dead	41	10.38 ± 0.159 (8.5-13.1)	16.54 ± 0.143 (14.6-18.4)	0.627 ± 0.006 (0.563-0.712)
WA-351				
live	14	11.58 ± 0.189 (10.5-12.9)	17.01 ± 0.257 (15.45-18.75)	0.682 ± 0.009 (0.610-0.727)
dead	43	11.02 ± 0.166 (7.30-13.1)	17.52 ± 0.159 (14.9-19.5)	0.629 ± 0.007 (0.415-0.701)
WA-350, dead	33	9.99 ± 0.188 (8.3-14.1)	16.61 ± 0.189 (13.9-19.1)	0.602 ± 0.009 (0.538-0.783)
WA-304, dead	147	9.35 ± 0.065 (7.4-11.7)	16.01 ± 0.079 (12.8-18.7)	0.583 ± 0.003 (0.510-0.696)
5 km E of Yammera Gap	12	10.33 ± 0.198 (9.15-11.5)	16.81 ± 0.298 (15.35-19.3)	0.615 ± 0.009 (0.575-0.665)
5.3 km E of Yammera Gap	15	10.84 ± 0.280 (8.95-12.25)	16.50 ± 0.352 (14.05-18.05)	0.656 ± 0.005 (0.611-0.679)
WA-197, dead	66	10.83 ± 0.169 (9.2-12.9)	17.33 ± 0.114 (14.6-19.8)	0.633 ± 0.003 (0.554-0.694)
WA-359				
dead	15	10.08 ± 0.266 (8.7-11.5)	16.49 ± 0.198 (15.7-17.8)	0.611 ± 0.11 (0.539-0.714)
live	5	9.84 ± 0.347 (8.5-10.5)	16.06 ± 0.218 (15.6-16.7)	0.613 ± 0.019 (0.545-0.656)
WA-310, dead	37	9.90 ± 0.125 (8.5-12.6)	16.76 ± 0.153 (15.2-18.9)	0.590 ± 0.005 (0.535-0.666)
South Side of Range				
WA-345, dead	20	10.75 ± 0.199 (9.5-12.1)	17.62 ± 0.186 (16.2-18.8)	0.610 ± 0.007 (0.564-0.672)

Table 24: Local Variation in *Amplirhagada burnerensis umbilicata* (continued)

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
WA-346, dead	16	10.61 ± 0.174 (9.4-11.7)	17.24 ± 0.157 (15.6-18.2)	0.615 ± 0.008 (0.571-0.680)
WA-343, dead	41	10.55 ± 0.116 (8.87-11.9)	17.64 ± 0.160 (15.8-19.4)	0.598 ± 0.004 (0.529-0.646)
WA-342, dead	33	9.71 ± 0.144 (8.15-11.7)	16.22 ± 0.199 (14.1-18.7)	0.599 ± 0.005 (0.533-0.658)
WA-338, dead	29	10.07 ± 0.133 (8.6-11.4)	16.40 ± 0.172 (14.6-18.0)	0.614 ± 0.005 (0.558-0.661)

Station	Number of Adults Measured	Whorls	Umbilical Width	D/U Ratio
North Side of Range				
WA-196				
11-X-76, dead	32	5½ + (5-6 ⅜)	1.53 ± 0.044 (1.1-2.0)	11.3 ± 0.364 (8.45-15.6)
9-XII-76, live	16	5 ⅝ + (5-6¼)	1.50 ± 0.065 (1.1-1.9)	11.4 ± 0.477 (8.54-15.1)
9-XII-76, dead	41	5 ⅝ (5-6¾)	1.53 ± 0.052 (0.95-2.3)	11.4 ± 0.433 (6.96-18.7)
WA-351				
live	14	5¾ (5¼-6 ⅛)	1.06 ± 0.062 (0.8-1.5)	16.6 ± 0.834 (11.7-22.0)
dead	43	6 + (5½-6¾)	1.41 ± 0.045 (0.8-2.0)	13.1 ± 0.533 (7.45-24.0)
WA-350, dead	33	5 ⅝ (5-6¾)	1.85 ± 0.054 (1.25-2.3)	9.23 ± 0.297 (7.50-13.7)
WA-304, dead	147	5½ (4¾-6 ⅛)	1.94 ± 0.027 (1.1-2.7)	8.50 ± 0.140 (5.84-14.3)
5 km E of Yammera Gap	12	5½ + (5 ⅜-5 ⅞)	1.65 ± 0.186 (1.05-2.1)	11.6 ± 0.689 (7.43-15.6)
5.3 km E of Yammera Gap	15	5¾ − (5 ⅜-6 ⅛)	1.09 ± 0.045 (0.8-1.4)	15.6 ± 0.807 (10.8-21.9)

Table 24: Local Variation in *Amplirhagada burnerensis umbilicata* (continued)

Station	Number of Adults Measured	Mean, Range and SEM of: Whorls	Umbilical Width	D/U Ratio
WA-197, dead	66	5⅝+	1.20 ± 0.029	15.1 ± 0.436
		(5¼-6¼)	(0.6-1.9)	(9.05-29.4)
WA-359				
dead	15	5¼ +	1.52 ± 0.070	11.2 ± 0.587
		(4⅞-5½)	(0.95-1.95)	(8.59-17.5)
live	5	5⅛	1.30 ± 0.248	12.6 ± 0.082
		(4⅞-5¼)	(1.05-1.50)	(10.4-15.2)
WA-310, dead	37	5⅝	1.34 ± 0.041	12.9 ± 0.467
		(5¼-6⅛)	(0.75-2.0)	(8.87-25.2)
South Side of Range				
WA-345, dead	20	5¾ −	1.82 ± 0.067	9.94 ± 0.416
		(5⅛-6½)	(1.35-2.3)	(7.04-13.7)
WA-346, dead	16	6+	1.59 ± 0.049	11.1 ± 0.426
		(5¼-6⅞)	(1.2-1.95)	(8.00-15.2)
WA-343, dead	41	5⅝	1.75 ± 0.039	10.2 ± 0.239
		(5¼-6)	(1.4-2.4)	(7.03-13.9)
WA-342, dead	33	5⅜+	1.58 ± 0.045	10.6 ± 0.277
		(5-5⅞)	(1.2-2.15)	(7.46-14.2)
WA-338, dead	29	5½ +	1.32 ± 0.041	12.7 ± 0.402
		(5⅛-6)	(1.0-1.8)	(9.32-16.3)

stronger radial sculpture **(Plate 14b),** and a reduced whorl count (mean whorls 6⅜− for *wilsoni*, 6⅞− for *elevata*). *A. alta* from the Admiralty Gulf and Mitchell Plateau fringes is generally even higher spired **(Figs 59a-f)** with a greater mean whorl count **(Table 17),** has slightly stronger sculpture **(Plate 13f),** and is more brightly coloured. *A. varia varia* from the Mitchell Plateau is equally high (mean H/D ratio 0.804), but averages only 6⅛- whorls, has a strong basal lip protrusion **(Fig. 67b),** generally has a strong colour suffusion on the spire, and is smaller in size (mean diameter 17.32 mm). *A. confusa* from the Mitchell Plateau has much stronger radial sculpture **(Plate 13a),** more rounded whorls **(Fig. 55a)** with a moderately prominent basal lip protrusion, and is more brightly coloured, with fewer whorls (mean whorls 6½). *A. mitchelliana* is much more depressed (mean H/D ratio 0.732, **Fig. 55c),** more brightly coloured, has more rounded whorls, and retains traces of a basal lip protrusion. Anatomically, the penis interior **(Fig. 58a)** is quite altered. The basal longitudinal ridges (PP) extend the

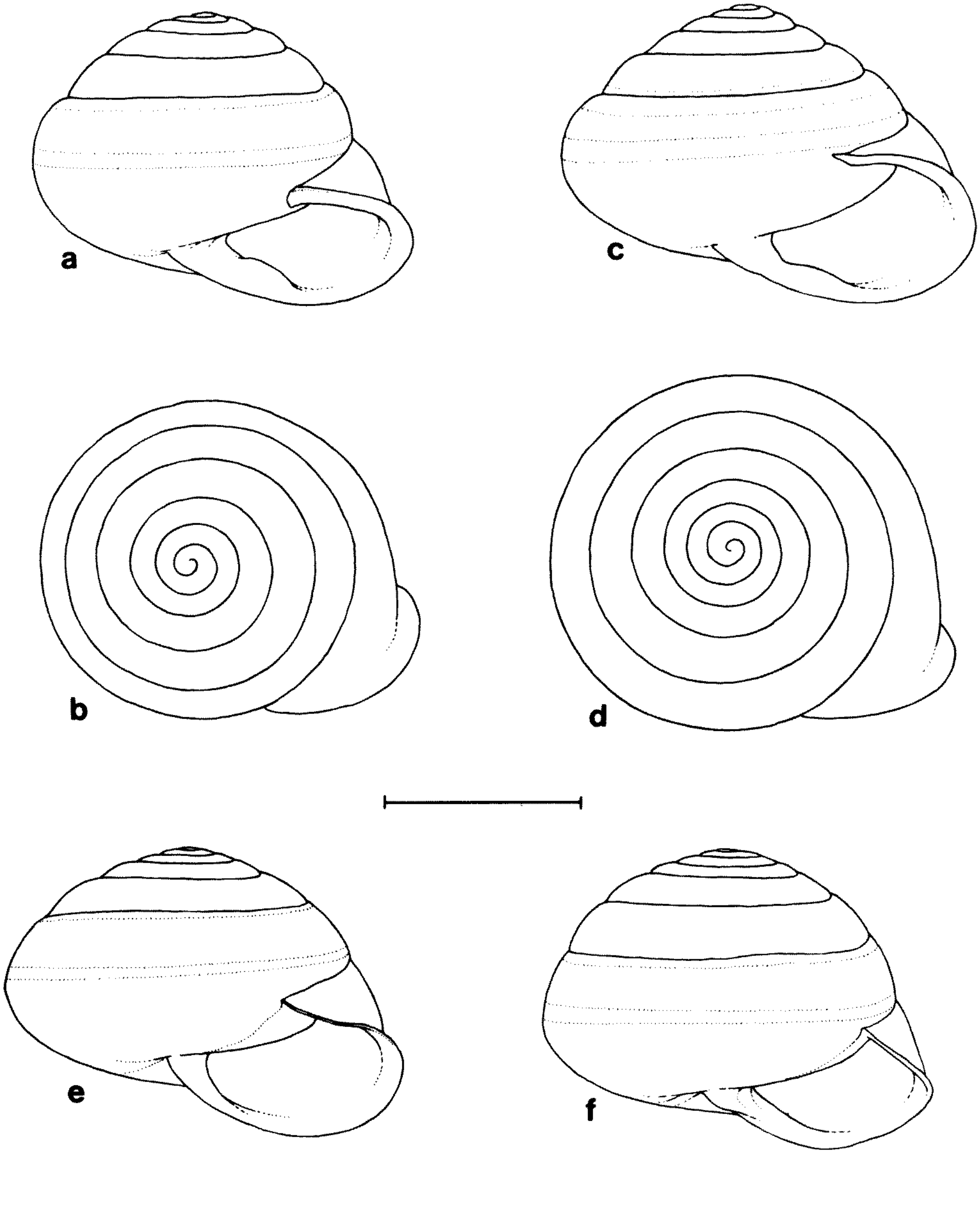


Fig. 55: Shells of *Amplirhagada*, a-b) *A. confusa*, Sta. WA-221, Mitchell Plateau, WAM 1224.75, holotype; c-d) *A. mitchelliana*, Sta. WA-201, Mitchell Plateau, WAM 1223.75, holotype; e) *A. wilsoni*, Sta. E5 (7), Prince Regent River Reserve, WAM 1239.75, holotype; f) *A. elevata*, Sta. W6 (1), Prince Regent River Reserve, WAM 1234.75, holotype. Scale line equals 10 mm.

length of the penis instead of breaking up into pustules in the upper section, the main pilaster (PT) is reduced to a single corrugated ridge without points on the corrugations **(Fig 36f)**, the verge is normal sized, and there is no sperm groove. *A. wilsoni* has the normal coiling of the vas deferens in the sheath **(Fig. 57a)**, the verge (PV, **Fig. 58b**) is reduced, the main pilaster (PT) is large and with a short row of crowded points **(Fig. 37f)** on each upper corrugation, and there is a prominent sperm groove and typical wall pustulations (PPR). The other species with reduced main pilasters, *A. varia* and *A. confusa*, are immediately recognizable by their very long verges **(Figs 66a-b)** and different pattern of pilaster reduction **(Figs 36d-e)**. All other *Amplirhagada* have a large main pilaster.

Holotype

WAM 1234.75. Sta. W6 (1), valley slope on north side of Youwanjela Creek near main campsite, Prince Regent River Reserve, Western Australia (1:250,000, 'Prince Regent' map sheet SD51-16, grid reference 332:032). Collected by Barry R. Wilson and Peter Smith 21 August 1974. Height of shell 16.9 mm, diameter 21.2 mm, H/D ratio 0.797, whorls 7⅛.

Paratopotypes

WAM 325.75-327.75, WAM 331.75, WAM 1231.75-1233.75, WAM 1236.75, FMNH 200852, 10 live and 28 dead adults, 2 live and 2 dead juveniles from the type locality.

Paratypes

Prince Regent River Reserve, collected August, 1974: Sta. W6 (2), V-shaped gully about 300 metres east of main campsite, Youwanjela Creek (2 dead adults, 3 dead juveniles, WAM 323.75, WAM 327.75); Sta. W6 (5), valley slopes on south side of Youwanjela Creek (2 live, 1 dead adults, WAM 324.75, WAM 1271.75).

Diagnosis

Shell 18.7-22.2 mm (mean 20.79 mm) in diameter, with 6¼ to 7¼ (mean 6¾ +) whorls. Apex and spire strongly elevated, rounded above producing a dome-shaped shell **(Fig. 55f)**, height of shell 14.5-18.5 mm (mean 16.49 mm), H/D ratio 0.725-0.881 (mean 0.793). Apical and postapical sculpture greatly reduced **(Plate 14a)**, base of shell with incised spiral lines. Shell periphery slightly angled, whorls relatively flattened laterally **(Fig. 55f)**. Body whorl very slightly descending behind lip, which is moderately expanded and without trace of basal protrusion. Umbilicus usually a very narrow lateral chink, too narrow for accurate measurement. Colour bands and columellar patch narrow, often reduced in prominence. Most examples with a very weak colour suffusion on the upper spire, often a partial suffusion behind the lip or on the lip edge itself. Based on 44 measured adults.

Genitalia **(Fig. 57b)** in resting phase, with moderately developed ovotestis (G), hermaphroditic duct (GD) slender and not kinked, entering laterally on head of talon (GT), prostate (DG) and uterus (UT) very slender. Spermatheca (S) short, head slightly expanded, free oviduct (UV) short and rather thick. Vagina (V) relatively long, slender. Vas deferens (VD) entering penis sheath (PS, **Fig. 58a**) three-quarters of way up, not coiled below insertion of penial retractor muscle (PR). Penis sheath very thin. Interior of penis chamber **(Fig. 58a)** with small conical verge (PV), longitudinal ridges (PP) continuous from base to apex, partly corrugated above middle zone, no wall pustules developed. Main pilaster (PT) slender, rather high in mid-section, having incomplete corrugations across its surface **(Fig. 36f)**, no points on anterior edges of corrugations. No trace of a sperm gutter. Based on 4 dissected adults, several other individuals checked.

Discussion

The shell of *Amplirhagada elevata* has the same size and shape relationship to *A. wilsoni* that *A. confusa* does to *A. mitchelliana*, the elevated member of the pair having a reduced diameter. They differ in that the increased whorl count and reduced sculpture of *A. elevata* are matched by *A. mitchelliana,* the less elevated member of the Mitchell Plateau pair. In the genitalia, both elevated shells have the main pilaster reduced, but in different ways **(Figs 36d, f)**, and they show other alterations. The verge in *A. confusa* is greatly enlarged, but the wall pustulations remain **(Fig. 66b)**, while in *A. elevata* the verge is of normal size, but there are no wall pustulations **(Fig. 58a)**. Despite their very similar shell shape and size, it is evident that *A. elevata* and *A. confusa* are convergent rather than monophyletic.

Both *A. elevata* and *A. wilsoni* have been taken at Sta. W6 (2) and W6 (5), but in very limited quantity. The great modifications in the penis interior of *A. elevata* **(Fig. 58a)** and *A. wilsoni* **(Fig. 58b)** in regard to sperm gutter (PF), main pilaster (PT), wall pustulations (PPR), and longitudinal ridges (PP) are adjustments by the former for species recognition under conditions of microsympatry. *A. wilsoni,* except for the intensified sperm gutter, retains generalized structures in the penis chamber.

A. elevata seemed to be unique among dissected *Amplirhagada* in having the vas deferens uncoiled normally during the resting phase. In several taxa, dissection of material subsequent to mating activity showed an uncoiled vas deferens in an elongated penis sheath. The August date of collection for *A. elevata* normally would rule out that possibility, but the habit of WAM staff to wait several days for preservation to be done, permits activation in field containers and out of season mating to occur. I assume this took place in these specimens.

The name *elevata* refers to the very high, dome-shaped spire that characterizes this species.

AMPLIRHAGADA WILSONI SP. NOV.

(Plate 14b; Figs 37f, 55e, 56, 57a, 58b)

Comparative remarks

Amplirhagada wilsoni is approximately the same size and shape as *A. mitchelliana,* but has flatter whorls, a more rounded spire **(Figs 55c, e)**, no trace of a basal lip protrusion, slightly more prominent radial sculpture **(Plate 13b, Plate 14b)**, often an angulated periphery **(Fig. 56)**, and usually more noticeable deflection of the body whorl behind the lip. The sympatric *A. elevata* is much more elevated (mean H/D ratio 0.793) with an increased whorl count, reduced radial sculpture **(Plate 14a)**, and a dome-shaped appearance **(Fig. 55f)**. *A. confusa* **(Fig. 55a)** is much more elevated (mean H/D ratio 0.820), has strong radial sculpture **(Plate 13a)**, and a strong basal lip protrusion. *A. katerana* is more strongly angulated **(Fig. 43e)**, with a generally slightly open umbilicus, weaker radial sculpture and a more regularly elevated spire. Other species of comparable size and shape have a noticeably open umbilicus. Anatomically, *A. wilsoni* has a relatively long vagina (V, **Fig. 57a**) and spermatheca (S), and the vas deferens (VD) is tightly coiled within the penis sheath. Internally **(Fig. 58b)**, the penis chamber has a very prominent sperm groove (PF), the verge (PV) is small, the main pilaster (PT) is tapered over its lower half and the relatively narrow corrugations have 5-6 points clustered in the center of each **(Fig. 37f)**, and the wall pustulations are very prominent (PPR, **Fig. 58b**). *A. elevata* **(Fig. 58a)** lacks wall pustulations and a sperm groove, has the main pilaster drastically reduced in size and without points, and the verge is slightly larger. *A. confusa* and *A. varia* **(Figs 66a-b)** differ in their large verges and reduced main pilasters, while *A. mitchelliana* and *A. castra* have the main pilaster enlarged and with many very tiny and closely crowded points **(Fig. 37h-i)** across the entire front edge of each corrugation. *A. katerana* **(Fig. 37d)** is somewhat intermediate in main pilaster armature, but has more points than in *A. wilsoni.*

Holotype

WAM 1239.75, Sta. E5 (7), below opening of deep gully about 2 km due west of Enid Falls campsite, Rufous Creek, Roe River, Prince Regent River Reserve, Western Australia (1:250,000 'Prince Regent' map sheet SD51-16, grid reference 343:085). Collected by Barry R. Wilson and Peter Smith 17 August 1974. Height of shell 15.45 mm, diameter 21.5 mm, H/D ratio 0.719, whorls 6¼.

Paratopotypes

WAM 316.75, WAM 1237.75-1238.75, 6 live adults, 9 live juveniles from the type locality.

Paratypes

Prince Regent River Reserve, collected August 1974: Sta. E5 (1), small gully at north-east corner of main gorge below Enid Falls (12 live, 4 dead adults, WAM

318.75, WAM 320.75, WAM 1274.75, WAM 1281.75-1282.75, FMNH 200842); Sta. E5 (2), east side of main gorge below Enid Falls (6 live, 3 dead adults, 3 live juveniles, WAM 322.75, WAM 1273.75, FMNH 200840); Sta. E5 (3), at top of Enid Falls (8 live, 1 dead adults, WAM 321.75, WAM 1275.75, WAM 1278.75-1279.75); Sta. E5 (6), eastern side of big gully about 2 km due west of Enid Falls campsite (Prince Regent SD51-16—344:085) (27 dead adults, WAM 332.75, FMNH 200841); Sta. E5 (9), west slope of valley of northern tributary of Rufous Creek about 1.5 km north of Enid Falls campsite (Prince Regent SD51-16—346:088) (3 live, 2 dead adults, WAM 315.75, WAM 1280.75); Sta. W3, Fern gully, just west of Gariyeli Creek, Prince Regent River (15°31'S, 125°13'E) (1 dead adult, WAM 328.75); Sta. W6 (2), V-shaped gully about 300 metres east of main campsite, Youwanjela Creek (Prince Regent SD51-16—332:033) (1 live adult, WAM 1276.75); Sta. W6 (5), valley slopes on south side of Youwanjela Creek near main campsite (Prince Regent SD51-16—332:032) (1 live adult, WAM 1272.75).

Diagnosis

Shell 18.85-25.55 mm (mean 21.57 mm) in diameter, with 5 7/8 to 6 3/4 (mean 6 3/8-whorls). Apex and spire moderately and almost evenly elevated, somewhat rounded above, height of shell 13.4-17.25 mm (mean 15.09 mm), H/D ratio 0.599-0.840 (mean 0.700). Apical sculpture typical, postapical whorls **(Plate 14b)** with low, somewhat irregular radial ribs above periphery, shell base and lower spire showing incised spiral lines **(Plate 14f)**. Shell periphery normally **(Fig. 56b)** slightly angled, sometimes **(Fig. 56a)** fairly sharply angled, occasionally **(Fig. 56c)** rounded.

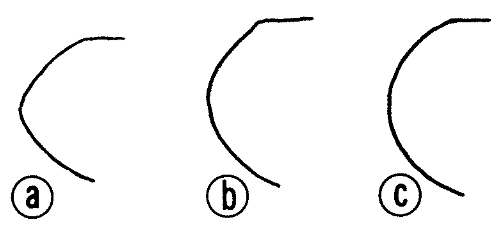


Fig. 56: Variation in peripheral angulation in shells of *Amplirhagada wilsoni*, Prince Regent River Reserve, a) Sta. E5 (6), WAM 332.75; b) Sta. E5 (2), WAM 322.75; c) Sta. E5 (3), WAM 1278.75.

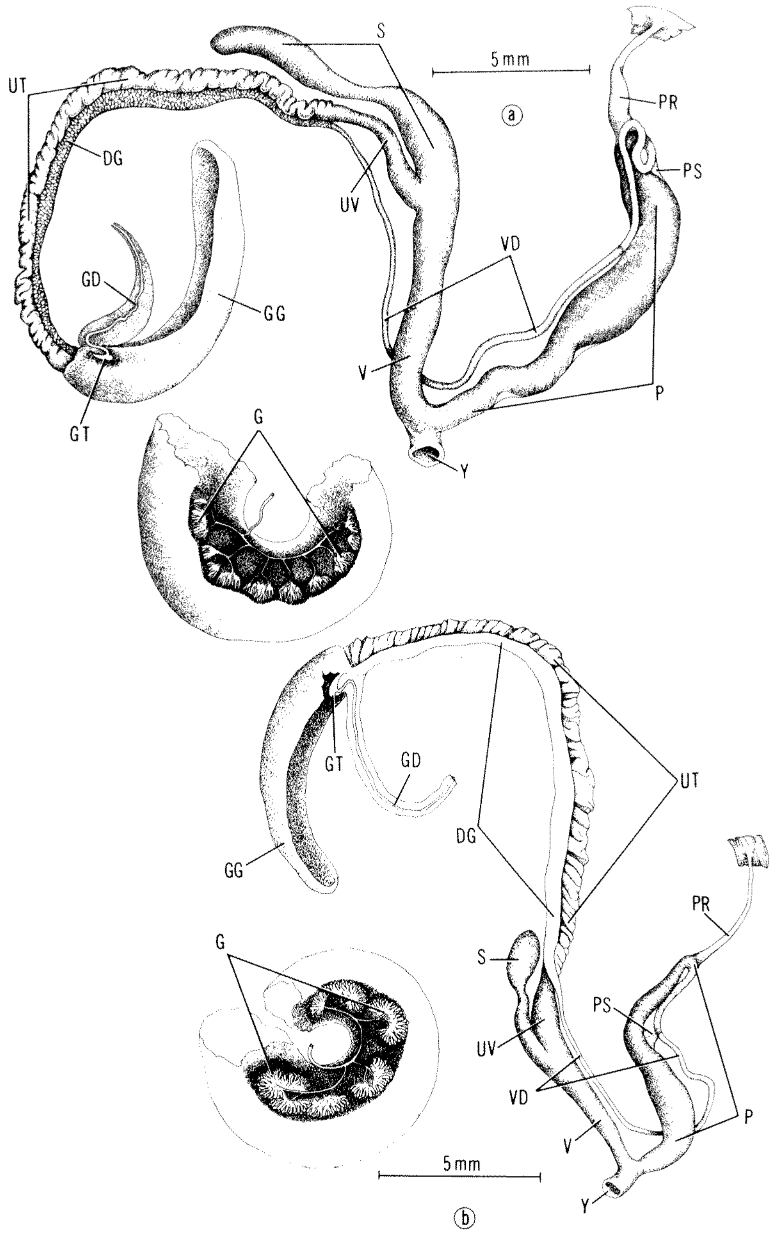


Fig. 57: Genitalia of *Amplirhagada wilsoni* and *A. elevata*, a) *A. wilsoni*, Sta. E5 (7), Prince Regent River Reserve, 17 August 1974, WAM 622.77 ex WAM 1237.75, Dissection A; b) *A. elevata*, Sta. W6 (1), Prince Regent River Reserve, 21 August 1974, WAM 623.77 ex WAM 1232.75, Dissection C. Scale lines equal 5 mm.

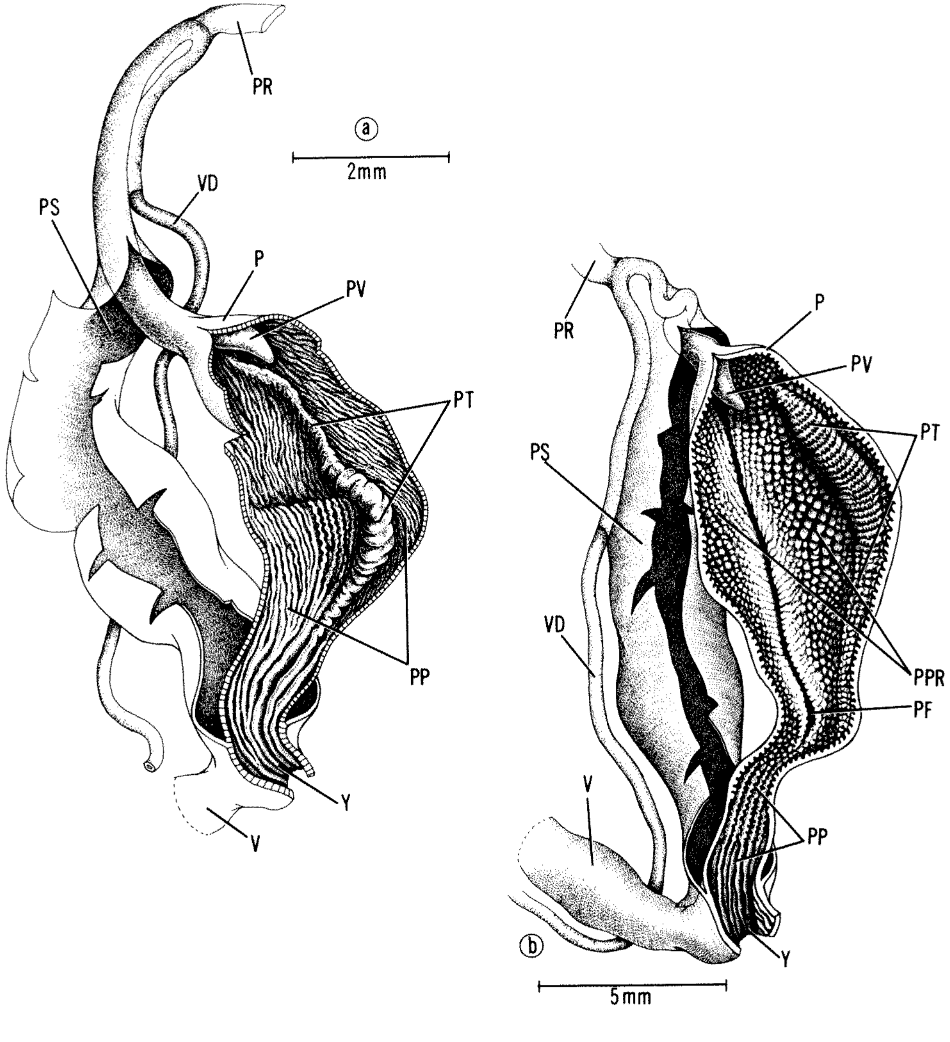


Fig. 58: Penis chamber interiors of *Amplirhagada wilsoni* and *A. elevata,* a) *A. elevata,* Sta. W6 (1), Prince Regent River Reserve, 21 August 1974, WAM 623.77 ex WAM 1232.75, Dissection C; b) *A. wilsoni,* Sta. E5 (7), Prince Regent River Reserve, 17 August 1974, WAM 622.77 ex WAM 1237.75, Dissection A. Scale lines as marked.

Body whorl slowly deflected behind lip, which is moderately flared and expanded, without trace of basal lip protrusion **(Fig. 55e)**. Umbilicus variable, from a narrow lateral crack to completely closed. Narrow subsutural and supraperipheral colour bands present in all examples, columellar colour patch rarely absent, a few examples with a weak reddish suffusion on the upper spire. Based on 76 measured adults.

Genitalia **(Fig. 57a)** in resting phase, ovotestis (G), prostate (DG), and uterus (UT) reduced in size. Hermaphroditic duct (GD) slender and unkinked, entering laterally on head of talon (GT). Spermatheca (S) with long shaft and elongated, slender head, basal portion moderately swollen, free oviduct (UV) slender and not kinked, vagina (V) long and slender. Vas deferens (VD) entering penis sheath about two-thirds way up, tightly coiled below insertion of penis retractor muscle (PR). Penis (P) slender, tapering from above, penis sheath (PS) very thin. Internally **(Fig. 58b)**, penis chamber with a very small verge (PV), quite large sperm groove (PF), short area of basal longitudinal ridges (PP), very prominent wall pustules (PPR), and a prominent main pilaster (PT) that tapers gradually over lower three-fifths. Surface of main pilaster **(Fig. 37f)** with narrow corrugations, each bearing five to six elongately triangular points clustered on the middle third to quarter of the corrugation edge. Based on 7 dissected adults and several checked examples.

Discussion

Except for the single shell from Gariyeli Creek (Sta. W3) and the two live adults taken sympatrically with *Amplirhagada elevata* along Youwanjela Creek (Sta. W6) on the Prince Regent River, all specimens of *A. wilsoni* came from a tributary of the Roe River, which empties into Prince Frederick Harbour. This is the first drainage basin south of the Mitchell Plateau region, with its great assemblage of *Amplirhagada*. Despite the general conchological similarity of *A. wilsoni* and *A. mitchelliana,* they are anatomically quite distinct.

Only minor variation was found among populations sampled **(Table 25)**, with the differences in peripheral angulation **(Fig. 56)** not being restricted to single populations. Unlike the situation on the Mitchell Plateau, where there is very extensive conchological overlap between sympatric species, *A. elevata* and *A. wilsoni* can be readily separated. No example of *A. wilsoni* has more than 6¾ whorls, and only 9 of 31 adult *A. elevata* had less than 6¾ whorls. Only 5 of 76 adult *A. wilsoni* had an H/D ratio of more than 0.760, while only 7 adult *A. elevata* had an H/D ratio of less than 0.760. Conchologically borderline live collected examples were checked as to penis structure, since there are major differences in this region between the species.

Seven long dead examples from Sta. E6, Garimbu Creek, an upper tributary of the Roe River (WAM 329.75) are broken and almost completely bleached. They are probably *A. wilsoni,* but are not listed as such or considered to be paratypes.

Great pleasure is taken in naming this species after Barry R. Wilson, formerly Head, Division of Natural Sciences, Western Australian Museum, in recognition of his many contributions to the success of this project and to knowledge of the Australian mollusc faunas.

Table 25: Local Variation in *Amplirhagada elevata* and *A. wilsoni*

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
A. elevata					
W6(1), dead	13	16.39 ± 0.277 (15.3-18.2)	20.78 ± 0.180 (19.75-21.9)	0.789 ± 0.011 (0.728-0.845)	6⅞ – (6½-7¼)
W6(1), live	13	16.90 ± 0.343 (14.5-18.5)	21.15 ± 0.208 (19.75-22.2)	0.799 ± 0.012 (0.725-0.881)	6⅞ (6½-7⅛)
W6(5)	3	16.07 ± 0.566 (15.15-17.1)	19.33 ± 0.491 (18.7-20.3)	0.831 ± 0.017 (0.797-0.853)	6⅞ (6⅞-7)
A. wilsoni					
E5(1)	10	15.34 ± 0.330 (14.1-16.8)	21.61 ± 0.266 (20.0-22.3)	0.711 ± 0.020 (0.632-0.840)	6⅜ + (6⅛-6¾)
E5(1)	6	15.26 ± 0.317 (14.55-16.65)	21.98 ± 0.384 (21.0-23.6)	0.695 ± 0.009 (0.666-0.729)	6⅜ (6⅛-6¾)
E5(2)	9	14.92 ± 0.170 (14.2-15.8)	21.91 ± 0.214 (21.1-23.2)	0.682 ± 0.010 (0.612-0.720)	6⅜ + (6⅛-6⅝)
E5(3)	7	15.98 ± 0.286 (15.2-17.25)	22.10 ± 0.309 (20.5-22.8)	0.723 ± 0.011 (0.671-0.757)	6½ – (6¼-6½)
E5(6)	27	14.60 ± 0.118 (13.4-15.9)	21.43 ± 0.264 (18.85-25.55)	0.683 ± 0.008 (0.599-0.772)	6¼ – (5⅞-6⅝)
E5(7)	7	15.43 ± 0.323 (14.3-16.5)	20.70 ± 0.393 (19.6-22.6)	0.746 ± 0.013 (0.715-0.796)	6¼ + (6⅛-6½)
E5(9)	5	16.21 ± 0.306 (15.25-16.95)	22.44 ± 0.373 (21.5-23.65)	0.723 ± 0.011 (0.693-0.749)	6½ + (6½-6⅝)

AMPLIRHAGADA ALTA SP. NOV.

Four morphologically separable taxa, two of which have been dissected, are grouped as this species. Three are given nomenclatural recognition, but the fourth, from Wollaston Island, is represented by insufficient material to permit naming. In all probability it will prove to be subspecifically distinguishable, but naming at this time is premature.

Their exact relationship to the previously named *Amplirhagada sykesi* (Smith, 1894) and *A. montalivetensis* (Smith, 1894) cannot be determined until the latter have been dissected. The conchological differences among these taxa are equivalent to those found between mainland species that are anatomically very distinct, but the shell differences between *A. alta alta* and *A. alta crystalla,* which anatomically show only minor differences, are even greater in degree. Under the circumstances, giving specific level recognition to the taxa whose anatomy have been investigated is preferred over synonymization with poorly known taxa.

Distinguishing features for the species are given under the comparative remarks and diagnosis for the nominate subspecies.

AMPLIRHAGADA ALTA ALTA SP. ET SUBSP. NOV.

(Figs 37e, 59a-b, 60a-b)

Comparative remarks

Amplirhagada alta alta is much more depressed (mean H/D ratio 0.769) and has a significantly lower whorl count (mean 6½ –) than either *A. alta crystalla* (mean H/D ratio 0.953, mean whorl count 7 ⅛) or *A. alta intermedia* (mean HD ratio 0.875, mean whorl count 6 ⅞). *A. sykesi* (Smith, 1894) differs in having greatly accentuated spiral sculpture, almost no trace of radial sculpture, a higher spire (mean H/D ratio 0.847) with the same whorl count, a closed umbilicus, and usually no trace of a protrusion on the basal lip. *A. alta alta* has little trace of spiral sculpture, radial sculpture of about the same intensity as that found in *A. mitchelliana* **(Plate 13b)**, a prominent basal protrustion **(Figs 59a-b)**, and a very slight umbilical crack. *A. confusa* has a much heavier radial sculpture **(Plate 13a)**, higher spire **(Fig. 55a)**, and lower whorl count, while *A. elevata* has an angled periphery **(Fig. 55f)** and much lower radial sculpture **(Plate 14a)**. The very heavily sculptured **(Plate 12a)** *A. imitata* (Smith, 1894) averages less than 6¼ whorls, has a reduced to absent basal lip protrusion **(Figs 71e-f)**, and generally more open umbilical chink. *A. alta alta* differs anatomically from *A. mitchelliana* **(Fig. 62b)** most obviously in the structure of its main pilaster, which is narrower **(Fig. 60b)**, has wider corrugations with only a few points **(Figs 37e, i)**, the same simple vas deferens coiling **(Fig. 60a)** seen in *A. confusa* **(Fig. 65a)** and *A. wilsoni* **(Fig. 57a)** rather than the complex coiling seen in *A. mitchelliana* **(Fig. 62a)**. The general appearance of the terminal male genitalia is the same as in *A. burnerensis* (Smith, 1894) **(Fig. 52)** and *A. kalumburuana* **(Fig. 44a)**, species that differ radically in shell features from *A. alta*.

Holotype

WAM 1269.76, under rock in gully, stream bed up from north-west corner of bay on south side, Corneille Island, Admiralty Gulf, north-west Kimberley, Western Australia (1:100,000 'Admiralty Gulf' map sheet 4069, grid reference 296:944). Collected by Fred Wells, 16-18 August 1976. Shell height 15.2 mm, diameter 19.55 mm, H/D ratio 0.777, whorls 6 ⅜.

Paratopotypes

WAM 1266.75, WAM 1267.75, WAM 1268.75, FMNH 200860, 10 live and 1 dead adult, 35 live juvenile specimens from the type locality.

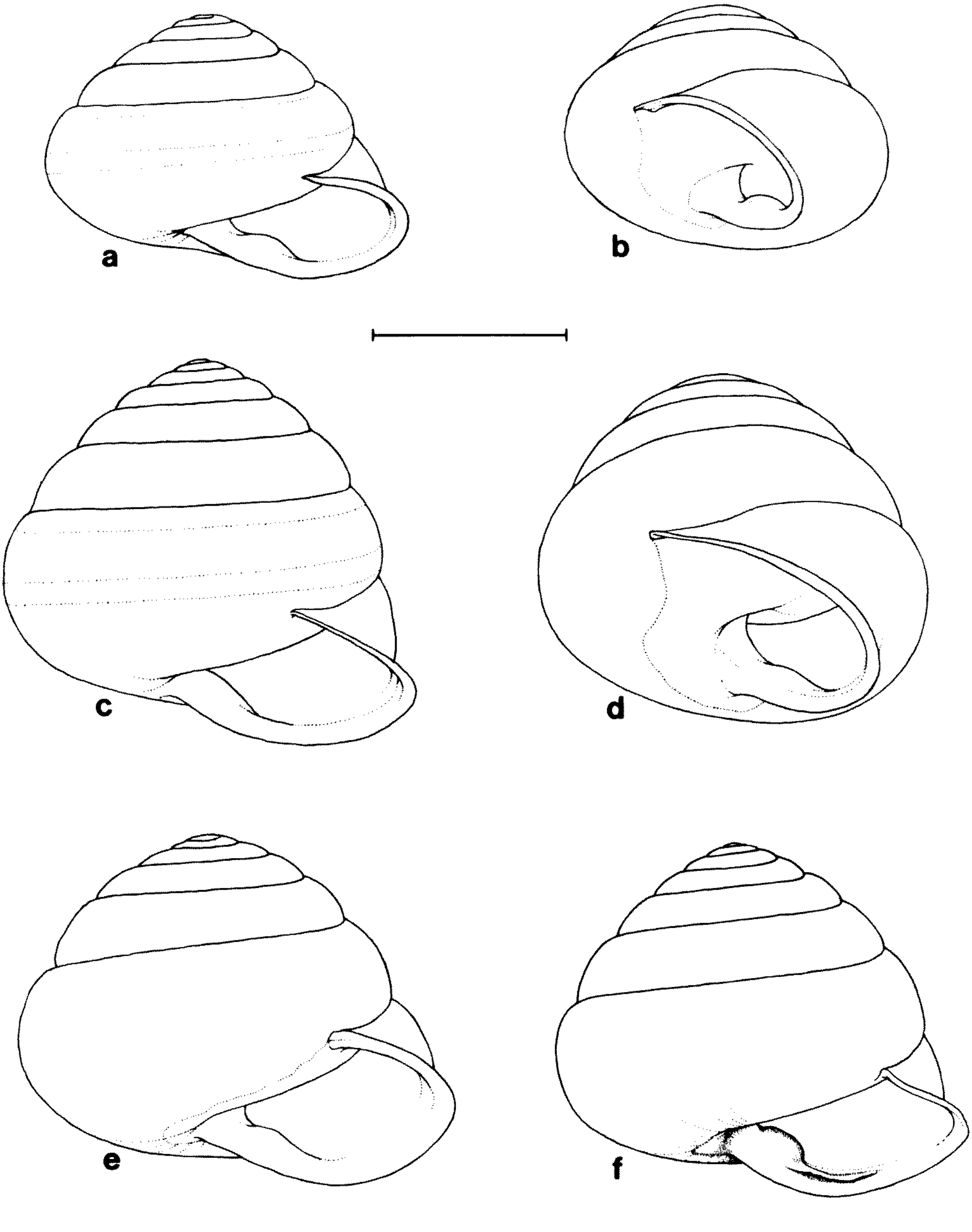


Fig. 59: Shells of *Amplirhagada alta,* a-b) *A. alta alta,* Corneille Island, Admiralty Gulf, WAM 1269.75, holotype; c-d) *A. alta crystalla,* Sta. 3, Crystal Creek, Mitchell Plateau, WAM 1284.75, holotype; e) *A. alta intermedia,* South Maret Island, Bonaparte Archipelago, WAM 1244.75, holotype; f) *A.* subsp., Wollaston Island, Montague Sound, WAM 1253.75. Scale line equals 10 mm.

Diagnosis

Shell 19.1-21.9 mm (mean 20.06 mm) in diameter, with 6 ⅛ to 6¾ (mean 6½ –) whorls. Apex and spire strongly and almost evenly elevated **(Fig. 59a)**, at most slightly rounded above, height of shell 13.55-17.65 mm (mean 15.43 mm), H/D ratio 0.684-0.887 (mean 0.769). Apical sculpture typical, postapical whorls with radial sculpture of the same intensity as in *A. mitchelliana* **(Plate 13b)**, but more widely spaced, about 6-8/mm, shell base with weak spiral incised lines **(Plate 14f)**. Shell periphery rounded **(Fig. 59a)**, without angulation in adults, juveniles strongly angled. Body whorl descending significantly, but slowly, behind lip **(Fig. 59b)**, which flares and reflexes to nearly cover the umbilical opening, only a very narrow chink remaining. Basal lip with a moderate to strong protrusion **(Figs 59a-b)** in all adults except one badly deformed example resulting from a repaired break. Colour variable, bands very narrow to usually prominent, occasionally base with reddish suffusion, more often spire and even body whorl with heavy supraperipheral colour suffusion. Columella with red colour patch. Based on 9 measured adults.

Genitalia **(Figs 60a-b)** in resting phase, hermaphroditic duct (GD) entering laterally on head of talon (GT). Ovotestis (G) intermediate in size, prostate (DG) and uterus (UT) clearly underdeveloped. Vagina (V) about one-third length of penis, spermatheca (S) with long shaft and swollen head, free oviduct (UV) slightly longer than vagina, very slender. Vas deferens (VD) entering penis sheath near top, with a simple 'S'-loop below insertion of penial retractor muscle (PR). Penis complex slender, internally **(Fig. 60b)** with normal verge (PV) having terminal pore (EP). Main pilaster (PT) tapering basally, corrugations wider than in *A. mitchelliana* **(Fig. 62b)**, each with five to six fine points on anterior edge of upper section **(Fig. 37e)**, reduced to three or four shortly after tapering begins. Walls of penis thick, pustules large and prominent, length of section with longitudinal ridges varying from one-quarter to one-third total length of penis. Based on 3 dissected adult individuals.

Discussion

All material of *Amplirhagada alta alta* was found under a large rock in a gully, sealed to the rock face against which the rock was resting, or to other shells (Fred Wells, personal communication). One dead shell, WAM 1268.75, was excluded from the measured range because a repaired injury about one whorl behind the aperture had caused a noticeable increase in the rate of whorl descension, thus producing an extremely high spired individual (H/D ratio 0.933).

The radial shell sculpture of *A. alta alta* is stronger than that of the other subspecies **(Plate 13f)**, approaching that of *A. mitchelliana* **(Plate 13b)**, although more widely spaced. The very heavily sculptured *A. confusa* **(Plate 13a)** and *A. imitata* (Smith, 1894) **(Plate 12a)** represent a different level of sculptural intensity and specimens cannot be confused with *A. alta*.

The name *alta* refers to the very high spire that is characteristic of this species.

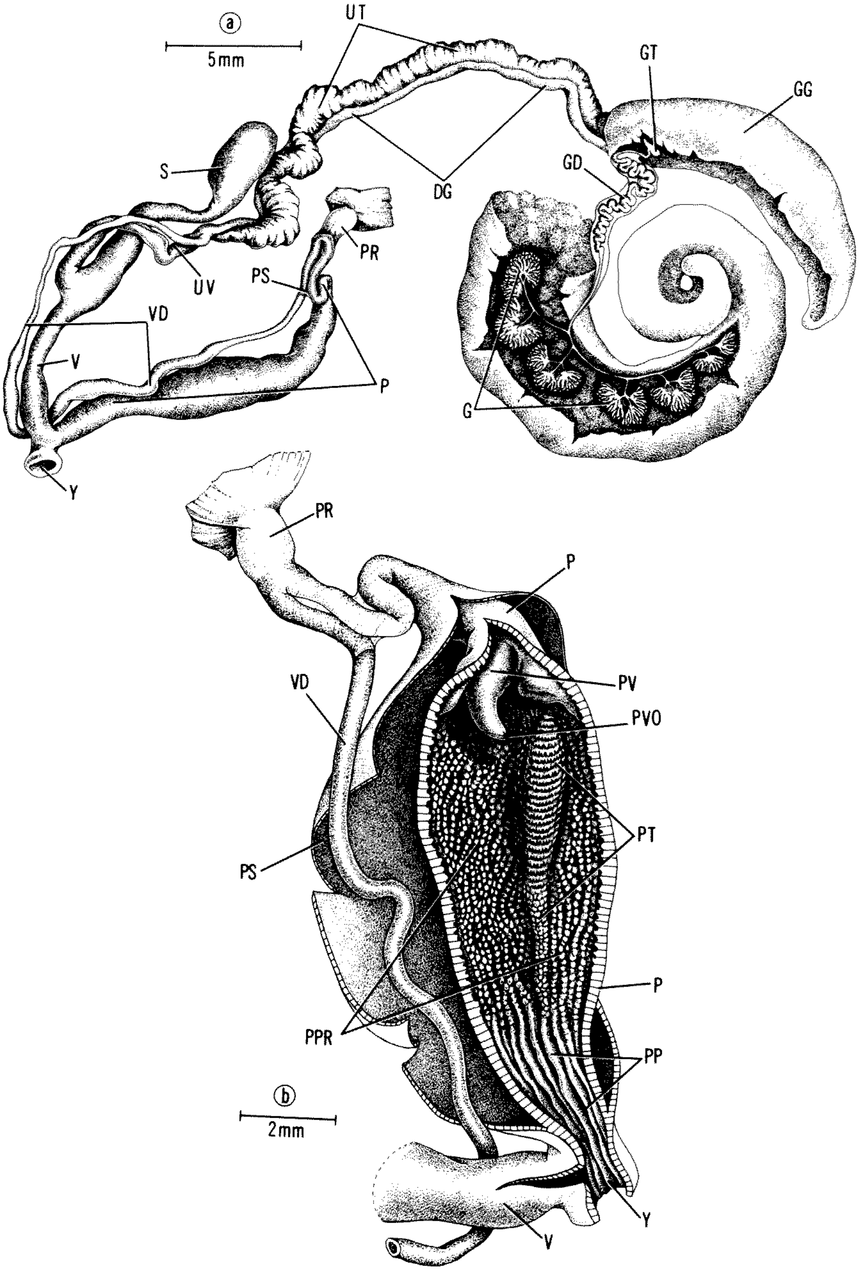


Fig. 60: Genitalia of *Amplirhagada alta alta,* Corneille Island, Admiralty Gulf, 16-18 August 1976, FMNH 200860, Dissection B, a) genitalia; b) interior of penis chamber. Scale lines as marked.

AMPLIRHAGADA ALTA CRYSTALLA SUBSP. NOV.

(Plate 13f; Figs 59c-d, 61a-b)

Comparative remarks

Amplirhagada alta crystalla has the highest spire (mean H/D ratio 0.953) of any known member of the genus. The completely closed umbilicus, reduced prominence of the basal protrusion **(Figs 59c-d)**, and reduced radial sculpture **(Plate 13f)** are other features separating it from *A. alta alta. A. alta intermedia* has a slightly open umbilicus, more prominent basal protrusion **(Fig. 59e)**, is lower in height (mean H/D ratio 0.875) and has a slightly reduced whorl count (mean 6 ⅞). *A. confusa* is smaller, averages only 6½ − whorls, and has very prominent radial sculpture **(Plate 13a)**. *A. alta crystalla* differs anatomically from the nominate subspecies only in having a different coiling pattern to the vas deferens **(Fig. 61a)** and the lower walls of the vagina thickened to form a large bulge **(Figs 61a-b)**. The penis interiors of the two taxa are the same, and hence only subspecific differentiation is proposed.

Holotype

WAM 1284.75, Sta. 3, collected under sandstone rocks at the base of a boab tree, above gauging station pool, Crystal Creek, Mitchell Plateau, north-west Kimberley, Western Australia (1:100,000 'Admiralty Gulf' map sheet 4069, grid reference 965:013). Collected by Barry R. Wilson and Clayton Bryce 2 November 1976. Shell height 21.85 mm, diameter 22.3 mm, H/D ratio 0.980, whorls, 7¼.

Paratopotypes

WAM 1261.75-WAM 1264.75, WAM 1283.75, FMNH 200861, 6 live, 4 dead adults, 9 live, 3 dead juveniles, 30 October and 2 November 1976 from the type locality.

Paratypes

Mitchell Plateau: Sta. 1, west side Crystal Creek, King Leopold sandstones (Admiralty Gulf 4069-968:011) (2 live, 1 dead adults, 1 live juvenile WAM 1265.75, B.R. Wilson and C. Bryce 2 November 1976); Sta. WA-394, sandstone boulders south-east side of Crystal Creek, north-east of road, 8.2 km from Walsh Point Road (Warrender 4068—946:001) (9 live and 7 dead adults, 17 live and 2 dead juveniles, FMNH 199351, FMNH 200013, FMNH 200774, WAM 349.79, WAM 351.79, L. Price and C. Christensen 15 March 1977); Sta. WA-399, sandstone rocks and boab tree above gauging station pool, Crystal Creek (Admiralty Gulf 4069—965:013) (2 live and 2 dead adults, 2 live juveniles, FMNH 199356, FMNH 199818, WAM 350.79, WAM 352.79, L. Keller 18-19 March 1977).

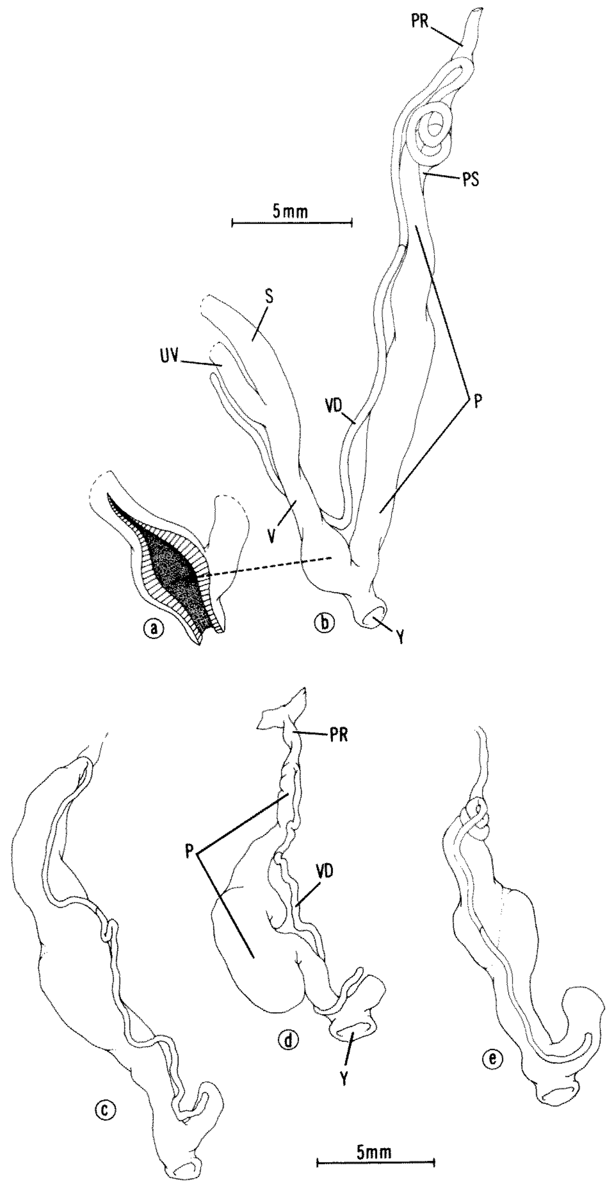


Fig. 61: Genital details of *Amplirhagada alta crystalla* and *A. mitchelliana,* a-b) terminal genitalia of *A. alta crystalla* showing vaginal bulge, Sta. 3, Crystal Creek, Mitchell Plateau, 2 November 1976, WAM 624.77 ex WAM 1261.75, Dissection B, a is terminalia, b is vaginal wall with unusual thickening; c-e) *A. mitchelliana,* variation in penis length and contraction, c is Crystal Creek track, 31 October 1976, WAM 1291.75, d is Sta. WA-205, Camp Creek, Mitchell Plateau, 18 October 1976, FMNH 200069, Dissection B, e is Sta. WA-205, 18 October 1976, FMNH 200069, Dissection C. Scale lines as marked.

Table 26: Local Variation in *Amplirhagada alta*

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
A. alta alta					
Corneille Island	9	15.43 ± 0.486 (13.55-17.65)	20.06 ± 0.315 (19.1-21.9)	0.769 ± 0.019 (0.684-0.887)	6½ – (6⅛-6¾)
A. a. intermedia					
North Maret	4	17.74 ± 0.553 (16.3-18.9)	21.81 ± 0.205 (21.25-22.2)	0.814 ± 0.033 (0.734-0.889)	6½ – (6⅜-6⅝)
South Maret	5	19.44 ± 0.466 (18.6-21.15)	22.20 ± 0.315 (21.1-23.0)	0.876 ± 0.063 (0.838-0.946)	6¾ (6⅝-7)
East Montalivet	11	19.99 ± 0.391 (17.3-21.6)	22.15 ± 0.179 (21.15-22.85)	0.902 ± 0.014 (0.805-0.971)	7⅛ (6⅞-7¾)
A. alta subsp.					
Wollaston	1	20.4	22.0	0.927	7¼ +
A. a. crystalla					
WA-394, dead	7	20.15 ± 0.314 (18.8-20.85)	21.59 ± 0.225 (20.85-22.2)	0.934 ± 0.014 (0.865-0.974)	7 + (6¾-7¼)
WA-394, live	9	19.71 ± 0.528 (17.0-22.7)	20.84 ± 0.360 (19.6-22.6)	0.946 ± 0.020 (0.867-1.042)	7 (6½-7½)
WA-399, all	4	21.33 ± 0.501 (19.85-22.0)	21.89 ± 0.593 (20.65-23.0)	0.978 ± 0.042 (0.871-1.044)	7¼ – (6⅞-7½)
#3, 2 Nov. 1976, all	9	21.43 ± 0.247 (20.0-22.5)	22.42 ± 0.304 (20.9-24.2)	0.956 ± 0.010 (0.913-1.018)	7¼ (7-7½)

Diagnosis

Shell 19.6-24.2 mm (mean 21.67 mm) in diameter, with 6½ to 7½ (mean 7⅛) whorls. Apex and spire strongly elevated, dome-shaped **(Fig. 59c)**, slightly more angled above, height of shell 17.0-22.7 mm (mean 20.64 mm). H/D ratio 0.865-1.044 (mean 0.953). Apical sculpture typical, postapical whorls with vague traces of irregular radial ridges **(Plate 13f)**, lower spire with faint traces of incised spiral lines **(Plate 14f)**. Shell periphery rounded. Body whorl usually descending very slightly, if at all, for a considerable distance behind the lip **(Fig. 59d)**, which is narrowly, but sharply reflexed, completely covering umbilicus. Basal lip with an angled, fairly prominent protrusion **(Fig. 59d)**. Colour typical in banding and columellar colour patch, all but two examples with heavy colour suffusion on the spire and upper body whorl. Based on 32 measured adults.

Genitalia (**Figs 61a-b**) agreeing with that of *A. alta alta,* allowing for seasonal differences in development, except for more complex coiling pattern of the vas deferens (**Fig. 61a,** VD) and lower entry of the penis sheath, and the very conspicuous enlargement of the vagina (V) just above the atrium (Y). The enlargement is caused by thickening of the vaginal wall at this point (**Fig. 61b**). The size of the swollen area varied considerably among dissected individuals. Based on 3 dissections and checking 4 other individuals.

Discussion

The type locality of *Amplirhagada alta crystalla* is from the rocks in the roots of a boab tree on the east bank of Crystal Creek above the gauging station pool, and the paratypes came from the series of sandstone ridges above the gauging station pool. At the same time, specimens were taken on the west side of Crystal Creek. The latter were collected over perhaps a one mile radius from the creek bank, and thus the cited grid reference is only an approximation. In March, 1977, material was taken further upstream (WA-394) and possibly from the type locality (WA-399).

The very high spire and collecting notes of occurrence among large rocks suggest that *A. alta crystalla* may be a rock sealer, as are *A. alta alta* and *A. confusa.* One of the collectors (Clayton Bryce, personal communication) remembers that at least some were sealed to tree roots or rock faces when collected.

The extremely high spire of *A. alta crystalla* has the shell height at times exceeding the diameter (**Table 26**). Except for the possibility of the type locality being developed, selection of this form as the nominate race would have been appropriate. The name *crystalla* refers to its distribution along Crystal Creek, a small river that empties into the Admiralty Gulf in an unnamed bay to the west of Crystal Head.

AMPLIRHAGADA ALTA INTERMEDIA SUBSP. NOV.

(Fig 59e)

Helix (Hadra) imitata Smith, 1894, Proc. Malac. Soc. London, **1:** 92 (part)—North Maret Island (14°25′S, 124°58′E), Bonaparte Archipelago, Western Australia.

Comparative remarks

Amplirhagada alta intermedia is midway in shell form between *A. alta alta* and *A. alta crystalla,* with a mean H/D ratio of 0.875 and mean whorl count of 6⅞ (see **Table 26**). The slightly open umbilical chink, weak to moderate (**Fig. 59e**) basal lip protrusion, and more rounded whorls (**Figs 59a, c, e**) are additional minor differences from the other two races. In the few unworn examples available, the radial sculpture is nearly absent and the spiral incised lines are noticeable on the body whorl above the periphery. *A. sykesi* (Smith, 1894) is slightly less elevated (**Fig. 70b,** mean H/D ratio 0.847) and has fewer whorls (mean 6½ −), even more reduced sculpture on the spire, and a much less prominent colour pattern.

Holotype

WAM 1244.75, South Maret Island, Bonaparte Archipelago, north of York Sound, north-west Kimberley, Western Australia (1:250,000 'Montague Sound' map sheet SD51-12, grid reference approximately 169:280). Collected by WAM Survey Party 8 June 1972. Shell height 19.7 mm, diameter 23.0 mm, H/D ratio 0.857, whorls 6¾.

Paratopotypes

WAM 1245.75, FMNH 200863, 4 dead adults, 4 dead juveniles, from the type locality.

Paratypes

Bonaparte Archipelago, north of Montague Sound: East Montalivet Island (7 dead adults, 2 dead juveniles, WAM 1243.75, FMNH 200862, 8 June 1972; 4 dead adults, 1 fragment, WAM 1255.75, 8 June 1972; 1 dead adult, 2 fragments, WAM 1547.70, R. W. George 21 October 1962); North Maret Island (4 dead adults, BMNH 92.1.29.162-4, J. J. Walker, paratypes of *Helix imitata* Smith, 1894).

Diagnosis

Shell 21.1-23.0 mm (mean 22.05 mm) in diameter, with 6⅜ to 7¾ (mean 6⅞) whorls. Apex and spire strongly elevated, slightly rounded above **(Fig. 59e)**, height of shell 16.3-22.2 mm (mean 19.31 mm), H/D ratio 0.734-0.971 (mean 0.875). Apical sculpture not observed, unworn examples with vague postapical radial undulations at irregular intervals, incised spiral lines visible above periphery on body whorl. Shell periphery rounded in adults **(Fig. 59e)**, moderately angled in young. Body whorl not or only slightly descending behind lip, which is normally flared and with a relatively prominent basal protrustion in Maret Islands material, slightly reduced in the East Montalivet shells. Lip reflexed to nearly cover umbilicus, which is slightly open in most examples. Colour absent from most shells because of wear, those retaining colour with normal banding and columellar patch, plus a heavy supraperipheral suffusion on the lower spire. Based on 21 measured adults.

Discussion

Despite the poor quality of most available material, the differences from *A. alta alta* and *A. alta crystalla* in proportions, umbilicus, basal protrusion, and whorl count are sufficient to warrant nomenclatural recognition for *A. alta intermedia*. The name *intermedia* indicates the position of this race in the range of variation for *A. alta*.

Specimens from East Montalivet Island had a higher shell, greater whorl count and slightly more prominent basal protrusion than did adults from North or South Maret Islands **(Table 26)**. The differences are not large enough to suggest nomenclatural separation at this time, but discovery that they differ in their anatomy would not surprise me.

AMPLIRHAGADA ALTA SUBSP.

(Fig. 59f)

Material studied

North-west Kimberley, Montague Sound: Wollaston Island ('Montague Sound' SD51-12–*ca*. 163:336) (1 dead adult, 1 broken adult, WAM 1253.75, L.A. Smith 11 June 1972).

Discussion

The two specimens of *Amplirhagada alta* subsp. are a high spired shell **(Table 26)** in which the basal protrusion has been enlarged into a distinct tubercle **(Fig. 59f)**. Both examples show this, and it is not the result of a repaired injury. In all probability this is another geographic race of *A. alta,* or represents yet another full species of *Amplirhagada,* but the available material is not sufficient to warrant naming.

Wollaston Island is on the coastal shelf of Montague Sound just west of Katers Island and is from a region that should contain a number of species belonging to *Amplirhagada.*

AMPLIRHAGADA MITCHELLIANA SP. NOV.

(Plate 13b; Figs 37i, 55c-d, 61c-e, 62a-b, 64a)

Comparative remarks

Amplirhagada mitchelliana has a rather large shell (mean diameter 21.98 mm), with rounded whorls **(Fig. 55c)**, a weak basal lip protrusion, strong colour bands and a columellar patch, often a heavy spire suffusion, relatively weak radial sculpture **(Plate 13b)**, and a moderately to strongly and almost evenly elevated spire (mean H/D ratio 0.732). The sympatric *A. confusa* has a domed spire **(Fig. 55a)**, greater elevation (mean H/D ratio 0.820), stronger basal lip protrusion, much more prominent radial sculpture **(Plate 13a)**, and tends toward having a lesser degree of colour suffusion on the spire. *A. castra* has the same shape, but averages almost a whorl less and is significantly smaller (mean diameter 18.09 mm). *A. varia depressa* is much smaller (mean diameter 16.27 mm), and even more depressed (mean H/D ratio 0.679). *A. varia varia* is much smaller (mean diameter 17.32 mm) and much higher (mean H/D ratio 0.804). The most similar extralimital species is *A. wilsoni* from the Prince Regent River Reserve. It is almost identical in size and shape, but has distinctly flatter whorls **(Fig. 55e)**, and stronger radial sculpture **(Plate 14b)**. Other *Amplirhagada* differ significantly in spire elevation (*A. alta*), size or radial sculpture. Anatomically, the long vagina (V, **Fig. 62a)**, rather fat top half of the penis complex, and the large main pilaster (PT, **Fig. 62b)** with its very narrow corrugations and multitude of fine points **(Fig. 37i)** on the anterior edges immediately differentiate *A. mitchelliana* from all species except *A. castra.* The latter shows a few minor differences in pilaster armature (**Fig. 37h**) and length (**Fig. 63b**), but is recognizable primarily by the altered sculpture on the wall of the vagina (V, **Fig. 64b**) and spermathecal base (S). *A. confusa* and *A. varia* are immediately separable by their greatly enlarged verges and greatly reduced main pilasters (**Figs 66a-b**). *A. alta* has a narrower main pilaster and fewer, much larger points (**Fig. 37e**).

Holotype

WAM 1223.75, Sta. WA-201, upper slopes of cove to south of Warrender Road at drop-off camp area, Mitchell Plateau, Western Australia (1:100,000 'Warrender' map sheet 4068, grid reference 813:001). Collected by Alan Solem 19 October 1976 under medium-sized isolated rocks in open eucalypt forest. Height of shell 16.8 mm, diameter 22.5 mm, H/D ratio 0.747, whorls 6 5/8 +.

Paratopotypes

WAM 1219.75, FMNH 199378, FMNH 199387, FMNH 199555, FMNH 199560, FMNH 199838, FMNH 199987, FMNH 199995, FMNH 200028, FMNH 200375, WAM 599.77, WAM 380.79, WAM 387.79, 18 live and 51 dead adults, 40 live and 7 dead juveniles, 15-25 October 1976 and 12 March 1977 from the type locality.

Paratypes

Mitchell Plateau: Sta. WA-202, 1st and 2nd line of boulders at base of slope to north of Warrender road, open eucalypt forest under small to medium rocks (Warrender 4068—814:014) (27 live, 53 dead adults, 22 live juveniles FMNH 200791, FMNH 200789, FMNH 199366, FMNH 199829-30, FMNH 200031, FMNH 200034, WAM 1217.75, 16-17 October 1976, 13 March 1977); Sta. WA-203, large boulder fissures on side of dry creek, ca. 200 yards east of WA-202 (1 dead adult, FMNH 200091, A Solem and J. Kethley 16 October 1976); open slope near Sta. WA-203 under 2 foot diameter rock (1 live adult, FMNH 199969, A Solem 17 October 1976); Sta. WA-205, gully on track to big vine thicket above Camp Creek (Warrender 4068−520:039) (26 live, 42 dead adults, 23 live, 11 dead juveniles, FMNH 199411, FMNH 200069, WAM 1217.75, WAM 609.77, WAM 375.79, A. Solem 18 October 1976); Sta. WA-208, 3.8-5.7 km east of drop-off camp area on AMAX-Port Warrender Road (Warrender 4068−*ca*. 784:013) (15 dead adults, 1 dead juvenile, FMNH 199607, Alan Solem 21 October 1976); Sta. WA-209, 10.7-13.9 km east of drop-off camp area. AMAX-Port Warrender Road (Warrender 4068−*ca*. 696:998) (1 live, 2 dead adults, 1 dead juvenile, FMNH 199984-5, A. Solem 21 October 1976); near vine thicket south of AMAX Camp along Camp Creek (Warrender 4068−584:060) (9 live adults, 1 live juvenile, WAM 1289.75, FMNH 200859, L. Smith and R. Johnstone January 1973); Sta. WA-210, 5.0 km toward Camp Creek Quarry from AMAX-Port Warrender Road on steep slope with mixed palm-eucalypt forest under boulders (Warrender 4068−563:049) (2 dead adults, 1 live juvenile, FMNH 199616, FMNH 200065, WAM 1225.75, A. Solem 21 October

1976); Sta. WA-211, 1.5 km east of airport road toward AMAX camp (Warrender 4068–*ca.* 612:039) (3 dead adults, 1 dead juvenile, FMNH 199601, WAM 377.79, A. Solem 21 October 1976); Sta. WA-212, vine thicket at west end of valley at drop-off camp area near WA-201 (Warrender 4068–813:007) (1 live, 4 dead adults, FMNH 199598, FMNH 200079, FMNH 200088, 21-23 October 1976, 11 March 1977); Sta. WA-214, trees along WA-213 stream, drop-off camp area (Warrender 4068–813:007) (1 live adult, 2 live juveniles, FMNH 199980, A. Solem 22 October 1976); Sta. WA-221, rock pile at base of WA-201 Valley (Warrender 4068–813:007) (11 live adults, 2 live juveniles, FMNH 200123-4, FMNH 201236, WAM 1215.75, WAM 385.79, A. Solem 30 October 1976); Sta. WA-383, 10 metres uphill from WA-212, drop-off camp area (Warrender 4068–813:007) (1 live adult, FMNH 199974, L. Price and C. Christensen 11 March 1977); Sta. WA-385, 10 metres downhill from WA-384 vine thicket, west of drop-off camp area (Warrender 4068–812:006) (4 live adults, FMNH 199840, WAM 384.79, L. Price and C. Christensen 12 March 1977); Sta. WA-391, under boulders, 0.8 km south-east of AMAX Camp, main road (Warrender 4068–596:067) (32 live, 73 dead adults, FMNH 199283, FMNH 199801-2, WAM 374.79, WAM 382.79, WAM 386.79, L. Price and C. Christensen 14 March 1977); Sta. WA-392, under boulders on road to Surveyors Pool, 0.3 km west of AMAX-Port Warrender Road (Warrender 4068–769:007) (19 live, 14 dead adults, FMNH 199300, FMNH 199813, WAM 376.79, WAM 379.79, L. Price and C. Christensen 14 March 1977); Sta. WA-393, vine thicket on west slope Walsh Point Road, 1.6 km east of Crystal Creek Road junction (Warrender 4068–879:027) (1 dead adult, FMNH 199315, L. Price and C. Christensen 15 March 1977); Sta. WA-396, under basalt boulders, 1 km east-south-east of 'Crusher', 0.3 km north-west of WA-395 (Warrender 4068–543:053) (4 live adults, FMNH 199976, WAM 381.79, L. Price and C. Christensen 16 March 1977); Sta. WA-397, under boulders, 10.2 km south-east of AMAX Camp, main road (Warrender 4068–542:137) (49 live, 42 dead adults, 14 live juveniles, FMNH 199297, FMNH 199833, WAM 378.79, WAM 388.79, L. Price and C. Christensen 17 March 1977); Mitchell River Falls, Mitchell River (3 live, 19 dead adults, 14 dead juveniles, WAM 1242.75, WAM 1290.75, FMNH 200824, FMNH 200849, Fred Wells, 6 August 1976); Camp Creek track, 3.5 km south of AMAX Camp (7 live, 2 dead adults, B.R. Wilson and C. Bryce 3 November 1976); Crystal Creek track (Warrender 4068–885:004) (3 live, 2 dead adults, WAM 1279.75, WAM 1291.75, B.R. Wilson and C. Bryce, 31 October 1976), 19 km west of mouth of Lawley River (Warrender 4068–723:082) (1 dead adult, WAM 1293.75, B.R. Wilson and C. Bryce 17 October 1976).

Diagnosis

Shell quite large, 17.1-25.1 mm (mean 21.98 mm) in diameter, with 5¾ to 7⅜ (mean 6¾ –) rather tightly coiled whorls. Apex and spire moderately to strongly and evenly elevated, usually only slightly rounded above, height of shell 12.8-19.7 mm (mean 16.09 mm), H/D ratio 0.643-0.861 (mean 0.732). Apical whorls **(Plate**

13b) with relatively strong pustulations, postapical radial sculpture of very low and irregular to slightly prominent radial growth wrinkles above periphery, shell base normally with a few weak incised spiral lines. Shell periphery rounded **(Fig. 55c)**, occasionally weakly angulated in small adults. Umbilicus normally a very slight lateral crack, occasionally completely covered, but never with a smooth callus. Body whorl descending gradually just behind lip, which is rather strongly flared and has a weak to prominent basal protrusion **(Fig. 55c)**. Supraperipheral and subsutural colour bands normally wide, rarely absent, columellar colour patch prominent, sometimes entire spire heavily suffused with reddish tones that may equal in intensity the spiral bands. Based on 561 measured adults.

Gentalia **(Figs 62a-b)** seasonally variable (see under Discussion). Hermaphroditic duct (GD, **Fig. 62a**) entering laterally on talon (GT). Vagina (V) quite long and slender basally, spermatheca (S) short with rather expanded head and slender shaft. Vas deferens (VD) entering penis sheath (PS) two-thirds of way up, tightly and complexly coiled below penial retractor muscle (PR) insertion. Penis generally thickened in upper half to two-thirds, variable with degree of contraction of animal **(Figs 61c-e)**, internally **(Fig. 62b)** with small verge (PV), very small wall pustulations that are organized into rows and partly fused, a basal area of weakly corrugated ridges, and a very high and broad main pilaster (PT) that has very narrow corrugations with extremely fine and crowded triangular points along the whole anterior edge **(Fig. 37i)**. Based on 25 dissections and numerous checked individuals.

Discussion

Amplirhagada mitchelliana is the most widely distributed species on the Mitchell Plateau, ranging from south of the AMAX Camp and the Mitchell River Falls to Crystal Creek and near the Lawley River. It is the common species in open areas on the Plateau, at times occurring quite abundantly under 30-92 cm isolated rocks and boulders or larger logs in the eucalypt and *Livistona* woodlands. It is found in both flat and sloping areas. At the base of gullies where shallow (two to four layer) talus of 15-45 cm rocks occur and in the fissures of large boulders flanking seasonal creek scour channels, it generally is replaced by *A. confusa*. In the vine thickets, *A. mitchelliana* is replaced by either *A. varia* or *A. castra*. During October collections, the vine thicket taxa and *A. mitchelliana* were never found to be microsympatric. The latter was found up to the fringe of the vine thickets, but not alive within their borders, and the former came out to the fringes, but not beyond. At all seasons, small numbers of *A. mitchelliana* were taken in *A. confusa* habitats, and *vice versa*. Probably these mixings are the results of accidental washing down during the heavy rains of the wet season. The one place where both species were found in fair numbers and were field identified with certainty, Sta. 221, showed specimens of *A. confusa* sealed to rocks and grouped nearer to the surface of the talus, while *A. mitchelliana* was free sealed and generally deeper in the talus piles. Conchological differences between *A. mitchelliana* and *A. confusa* are discussed under the latter species.

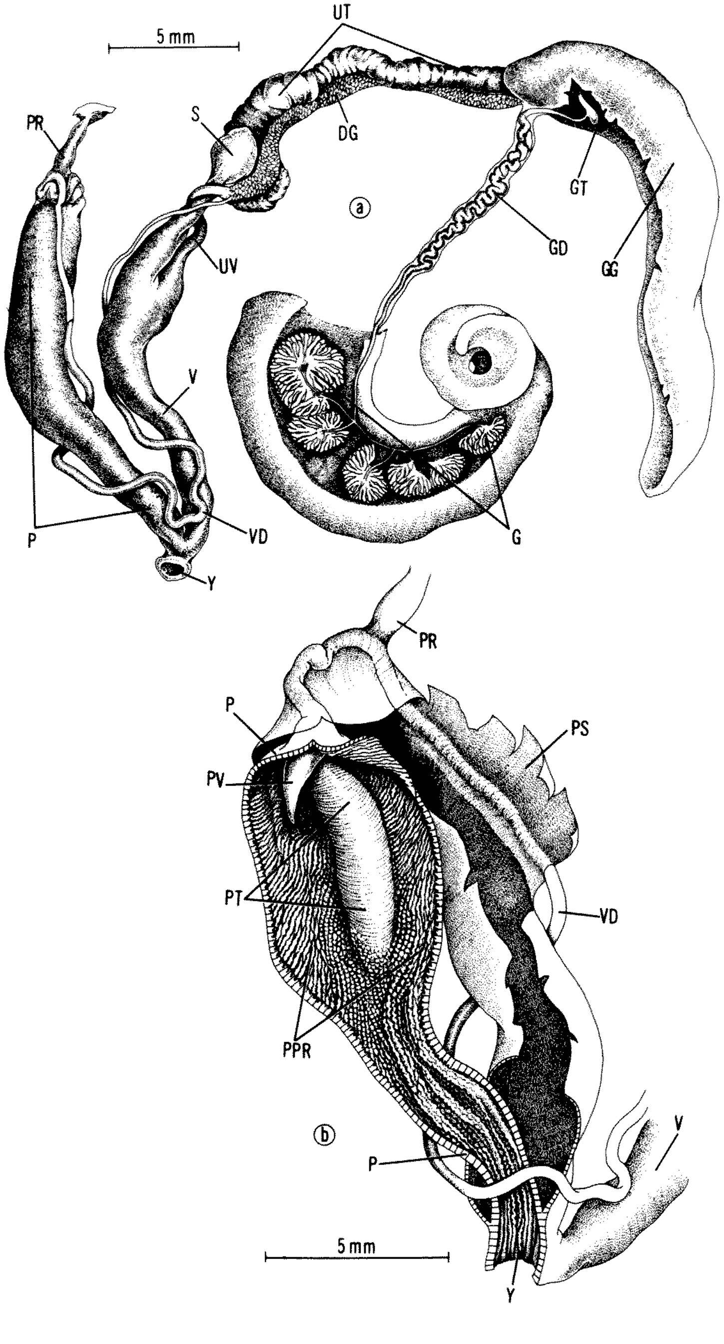


Fig. 62: Genitalia of ***Amplirhagada mitchelliana,*** Sta. WA-201, Mitchell Plateau, 15-16 October 1976, WAM 599.77, Dissection C, a) genitalia; b) interior of penis chamber. Scale lines as marked.

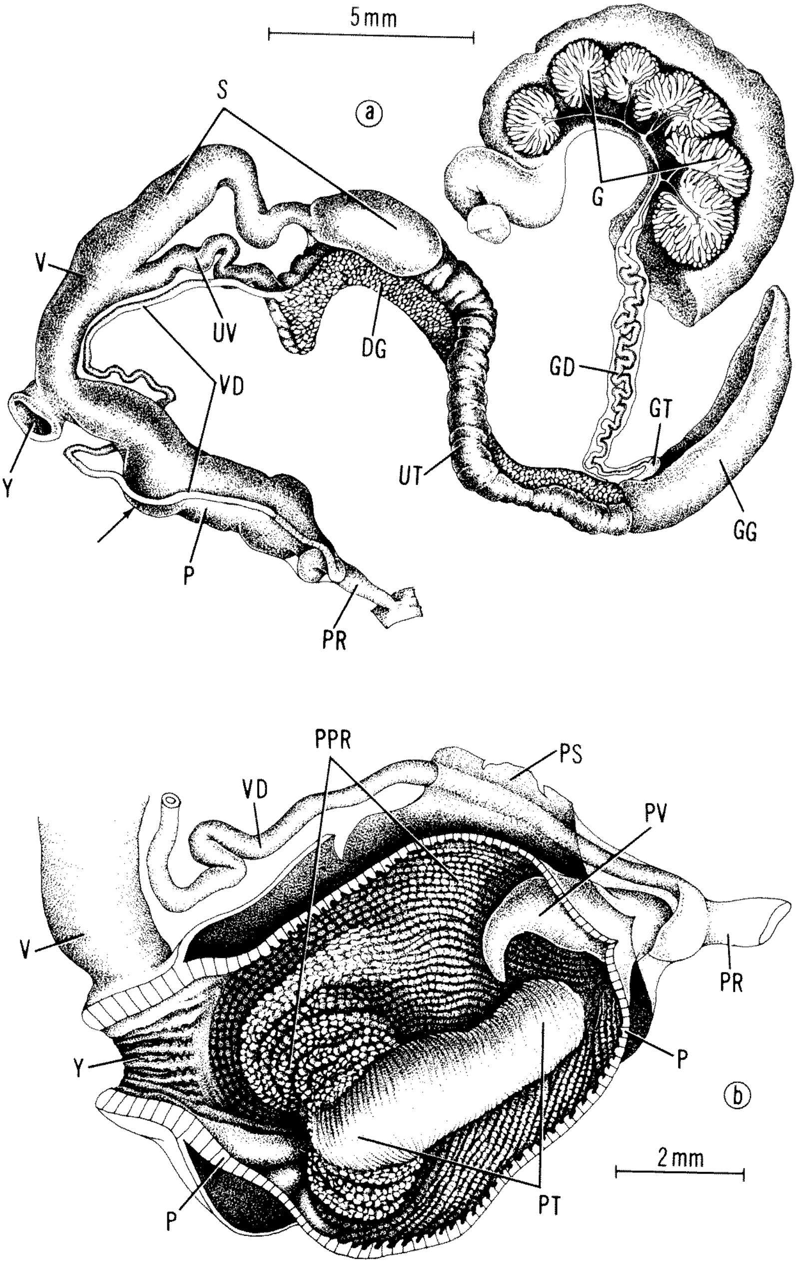


Fig. 63: Genitalia of *Amplirhagada castra,* Sta. WA-206, Camp Creek, Mitchell Plateau, 18 October 1976, WAM 1222.75, holotype, Dissection A, a) genitalia; b) interior of penis chamber. Scale lines as marked.

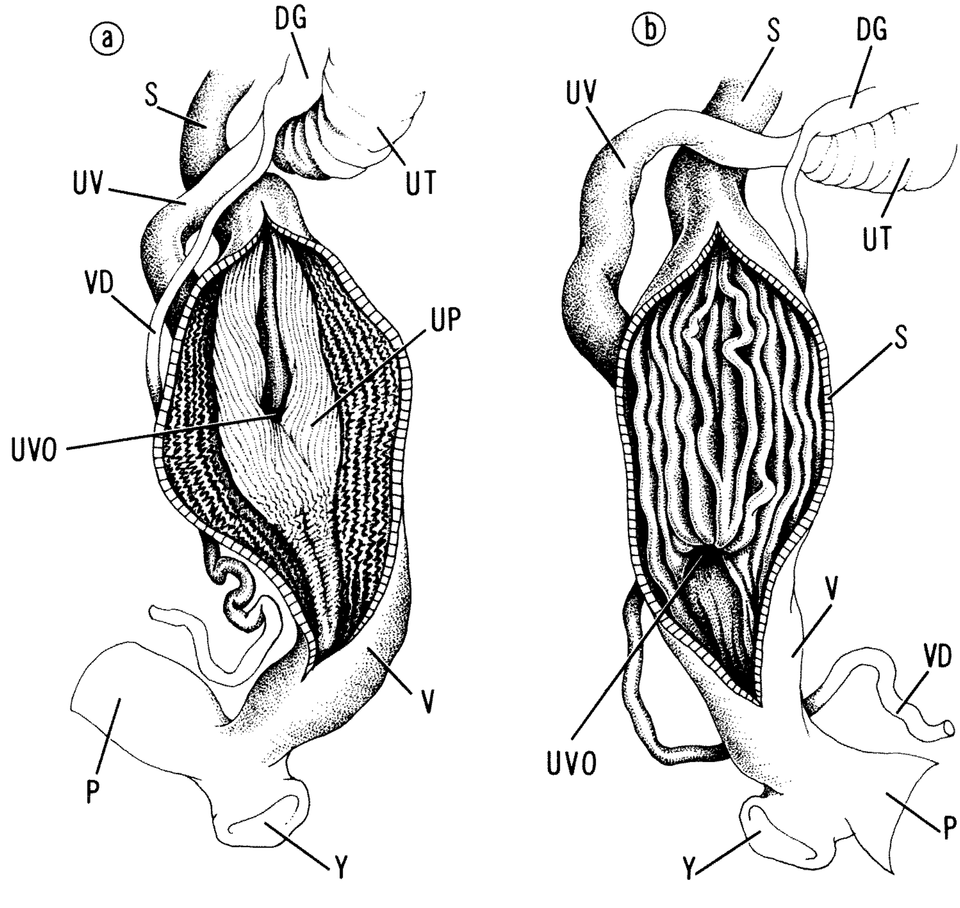


Fig. 64: Sculpture on spermathecal-vaginal walls in *Amplirhagada mitchelliana* and *A. castra,* a) *A. mitchelliana,* Sta. WA-201, Mitchell Plateau, 15-16 October 1976, FMNH 199995, Dissection A; b) *A. castra,* Sta. WA-206, Camp Creek, Mitchell Plateau, 18 October 1976, FMNH 199996, Dissection B. Greatly enlarged.

Table 27: Local Variation in *Amplirhagada napierana*

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Mitchell River Falls, dead 5-VIII-76	19	14.24 ± 0.175 (12.8-15.35)	20.75 ± 0.211 (19.4-22.35)	0.686 ± 0.006 (0.647-0.727)	6¼ + (6 -6 ⅝)
WA-201, X-76, dead	44	16.22 ± 0.145 (14.3-18.55)	21.93 ± 0.359 (18.45-24.2)	0.741 ± 0.006 (0.678-0.861)	6½ (6 ⅛-7)
WA-201, X-76, live	16	17.27 ± 0.196 (15.9-18.15)	23.26 ± 0.207 (21.8-24.9)	0.743 ± 0.010 (0.681-0.833)	6¾ − (6½-7)
WA-202, X-76, dead	53	16.38 ± 0.159 (14.0-18.4)	22.05 ± 0.194 (18.6-24.8)	0.741 ± 0.005 (0.664-0.848)	6 ⅝ + (6 ⅛-7¼)
WA-202, X-76, live	10	16.82 ± 0.219 (15.35-17.7)	22.81 ± 0.230 (22.0-24.0)	0.738 ± 0.003 (0.698-0.787)	6¾ − (6½-7)
WA-202B, III-77, live	8	17.19 ± 0.242 (15.8-18.6)	23.56 ± 0.279 (21.8-25.1)	0.729 ± 0.008 (0.697-0.762)	6¾ (6½-7)
WA-391, III-77, dead	73	16.23 ± 0.108 (13.35-18.1)	21.77 ± 0.117 (19.3-24.2)	0.746 ± 0.005 (0.656-0.839)	6¾ (6¼-7 ⅛)
WA-391, III-77, live	17	16.68 ± 0.176 (15.4-17.8)	22.62 ± 0.136 (21.7-23.55)	0.737 ± 0.007 (0.665-0.774)	6 ⅞ + (6 ⅝-7¼)
WA-391, III-77, live	15	16.08 ± 0.430 (14.5-17.7)	21.46 ± 0.228 (20.1-23.2)	0.749 ± 0.007 (0.712-0.810)	6 ⅞ (6 ⅝-7¼)
WA-392, III-77, dead	14	16.70 ± 0.205 (15.25-18.1)	22.93 ± 0.186 (21.9-24.6)	0.729 ± 0.008 (0.677-0.783)	6¾ − (6 ⅜-7)
WA-392, III-77, live	19	17.44 ± 0.203 (15.4-18.7)	23.49 ± 0.131 (22.5-24.3)	0.742 ± 0.008 (0.664-0.817)	6¾ + (6 ⅛-7)
WA-397, III-77, dead	42	15.22 ± 0.120 (12.95-16.85)	21.05 ± 0.124 (19.5-23.15)	0.724 ± 0.005 (0.647-0.798)	6 ⅝ (6-7)
WA-397, III-77, live	49	15.23 ± 0.129 (13.4-17.6)	21.16 ± 0.117 (19.65-23.0)	0.719 ± 0.004 (0.646-0.793)	6 ⅝ + (6 ⅛-7¼)
WA-205, X-76, dead	42	15.50 ± 0.125 (13.7-17.6)	21.42 ± 0.150 (19.1-23.8)	0.725 ± 0.006 (0.664-0.844)	6¾ − (6¼-7 ⅜)
WA-205, X-76, live	26	15.99 ± 0.236 (13.75-18.0)	21.70 ± 0.258 (19.55-24.8)	0.737 ± 0.007 (0.665-0.781)	6¾ − (5 ⅞-7 ⅛)
WA-221, X-76, live	11	17.49 ± 0.167 (16.8-18.4)	24.00 ± 0.199 (23.2-25.2)	0.729 ± 0.008 (0.690-0.763)	6¾ + (6½-7)

The only significant local shell variation was seen in the adults from Mitchell River Falls (WAM 1242.75, **Table 27**), which were distinctly smaller in size than other populations. At Sta. 205, all adults were taken in a very small area. Here, as well as five other stations, the live collected adults were slightly to noticeably larger than dead adults from the same station. This probably reflects recent favourable wet seasons on the Mitchell Plateau, since the consistent larger size of the live adults in six situations is not coincidental.

A single dead shell from the King Edward River bank in rock piles near a small waterfall, about 2 km west of the Mitchell Plateau access road (NMV) collected by Don Beauglehole 2 June 1976 is probably *A. mitchelliana,* but is too worn for certain identification. The shell measured 14.6 mm high, 21.8 mm in diameter, with 6 3/8 whorls.

The name *mitchelliana* has been chosen because of the species' wide distribution in open areas on the Mitchell Plateau. Most of the other species tend to have isolated foci of abundance with large areas between foci that are not regularly inhabited by the species. In contrast, *A. mitchelliana* is found in sparser numbers almost everywhere, except where replaced by the vine thicket taxa.

Seasonal variation in the genitalia is based on study of examples collected in August, October, early November, January, and March. In August the genitalia agrees exactly with that of *A. burnerensis* (Smith, 1894) in that it is in inactive condition. In mid-October **(Fig. 62a)** the ovotestis (G) and prostate (DG) are equivalent in prominence to the early December examples of *A. burnerensis* **(Fig. 53)**. This correlates with the normal start of the rainy season on the Mitchell Plateau in October, with an average of 57 mm of October precipitation from 1968-1973 (Miles and Burbidge, 1975: 17, **Table 1**). In January the uterus is grossly enlarged, while in March the same pattern of shut down and contraction of organs seen in the Napier Range taxa is underway. Thus, the limited data available suggests that the same pattern is followed by *A. mitchelliana* as for *A. burnerensis,* but that the timing is altered to adjust to the normally earlier start of the wet season on the Mitchell Plateau.

AMPLIRHAGADA CONFUSA SP. NOV.

(Plate 13a; Figs 36d, 55a-b, 65a, 66b)

Comparative remarks

Amplirhagada confusa has a very high, domed shape **(Fig. 55a,** mean H/D ratio 0.820), prominent radial sculpture on the postapical whorls **(Plate 13a)**, a usually quite prominent basal lip protrusion **(Fig. 55a)**, and quite tightly coiled whorls **(Fig. 55b)**. The sympatric *A. mitchelliana* has a generally much lower spire that is rounded above **(Fig. 55c,** mean H/D ratio 0.732), greatly reduced radial sculpture on the postapical whorls **(Plate 13b)**, and a much less prominent basal lip protrusion **(Fig. 55c)**. *A. alta crystalla,* the only mainland race of that species, has a dramatically higher spire **(Fig. 59c,** mean H/D ratio 0.953), increased whorl count (mean whorls 7 1/8), and less prominent radial sculpture **(Plate 13f)**. The other Mitchell Plateau species, *A. castra* and *A. varia,* are distinctly smaller (mean diameters

16.27-18.09 mm), with a reduced whorl count (mean whorls 5¾+ to 6⅛), and basically confined to vine thickets. Of extralimital species, the most similar is *A. elevata* from the Prince Regent River Reserve. It differs in having flatter whorls **(Fig. 55f)**, no trace of a basal lip protrusion, very weak radial sculpture **(Plate 14a)**, and usually an angulated periphery. *A. sykesi* (Smith, 1894) almost completely lacks radial sculpture, has no basal lip protrusion, and is normally much lighter in colour. *A. imitata* (Smith, 1894) and *A. combeana* Iredale, 1938 have much stronger radial sculpture **(Plates 12a-b)** and are much smaller in size. Anatomically, *A. confusa* has a very slender long penis (P) and vagina (V, **Fig. 65a**), which internally is immediately recognizable by its very long verge (PV, **Fig. 66b**) and reduced main pilaster (PT). *A. varia* has a very similar penis interior **(Fig. 66a)**, but the main pilaster (PT) is much longer and has more elongated pustules on the pilaster **(Fig. 36e)** than does the main pilaster in *A. confusa* **(Figs 36d, 66b)**. In *A. elevata* the main pilaster is reduced to a single ridge **(Fig. 36f)**, but the verge (PV, **Fig. 58a**) is much smaller and the basal longitudinal ridges extend the length of the penis chamber. All other *Amplirhagada* have a very large main pilaster with complex armature **(Figs 36-37)**.

Holotype

WAM 1224.75, Sta. WA-221, shallow rock talus at base of cove at WA-201 drop-off camp area, south of AMAX-Port Warrender Road, Mitchell Plateau, Western Australia (1:100,000 'Warrender' map sheet 4068, grid reference 811:011). Collected by Alan Solem 30 October 1976. Height of shell 16.4 mm, diameter 20.2 mm, H/D ratio 0.812, whorls, 6⅜+.

Paratopotypes

WAM 1218.75, FMNH 200121-2, WAM 370.79, FMNH 200128, 76 live, 7 dead adults from the type locality.

Paratypes

Mitchell Plateau: Sta. WA-201, drop-off camp area cove, AMAX-Port Warrender Road (Warrender 4068—813:011) (11 dead adults, FMNH 199377, FMNH 199386, A. Solem 15-19 October 1976); Sta. WA-202A, east of AMAX-Port Warrender Road, near drop-off camp (Warrender 4068—814:014) (5 live adults, FMNH 199831, L. Price and C. Christensen 13 March 1977); Sta. WA-202B, 2nd line of boulders east of AMAX-Port Warrender Road, drop-off camp area (Warrender 4068—814:014) (2 live adults, FMNH 199828, L. Price and C. Christensen 13 March 1977); Sta. WA-203, fissures in creek boulders east of AMAX-Port Warrender Road near drop-off (Warrender 4068—811:016) (32 live, 3 dead adults, 18 live juveniles, WAM 1220.75, WAM 366.79, FMNH 199835, FMNH 200089, FMNH 200092, 16 October 1976, 13 March 1977); Sta. WA-204, vine thicket 1.6 km toward Crystal Creek from AMAX-Port Warrender Road (Warrender 4068—887:005) (1 dead adult, FMNH 199395, A. Solem 17 October 1976);

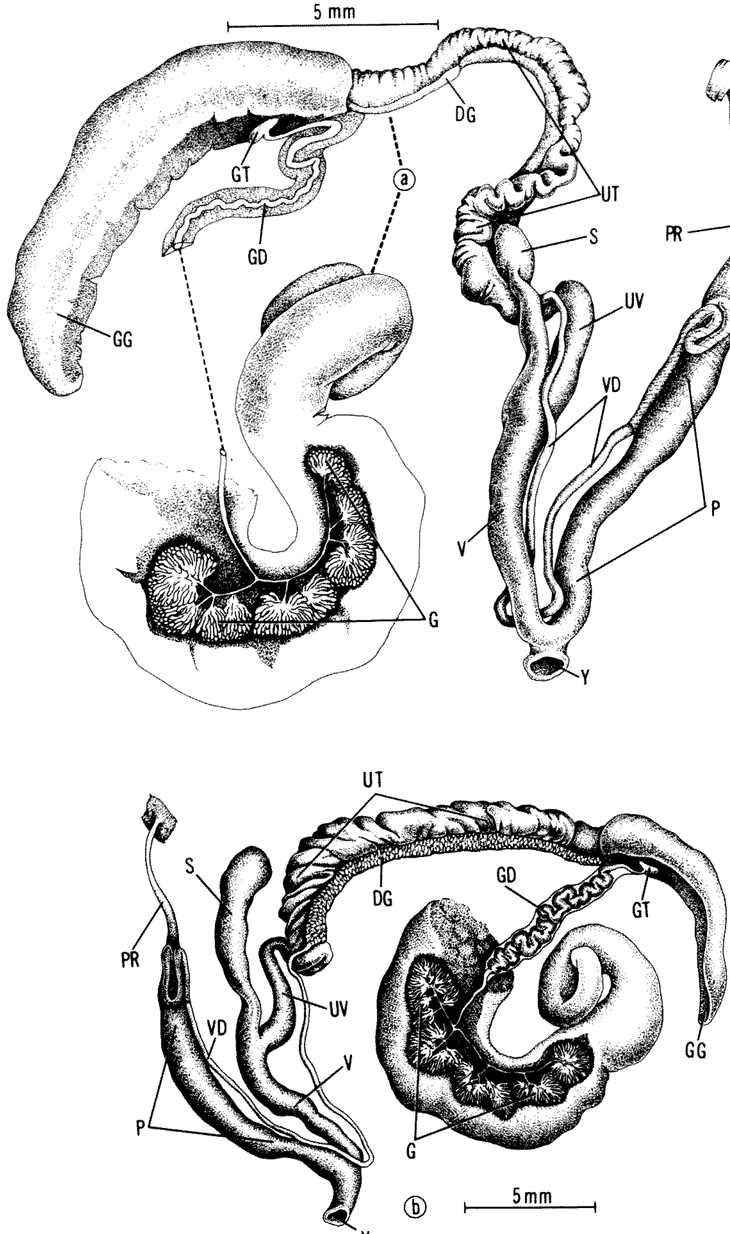


Fig. 65: Genitalia of *Amplirhagada confusa* and *A. varia varia,* a) *A. confusa,* Sta. WA-221, Mitchell Plateau, 29-30 October 1976, FMNH 200122, Dissection A; b) *A. varia varia,* Camp Creek near AMAX camp, Mitchell Plateau, January 1973, WAM 625.77 ex WAM 1326.75, Dissection A. Scale lines equal 5 mm.

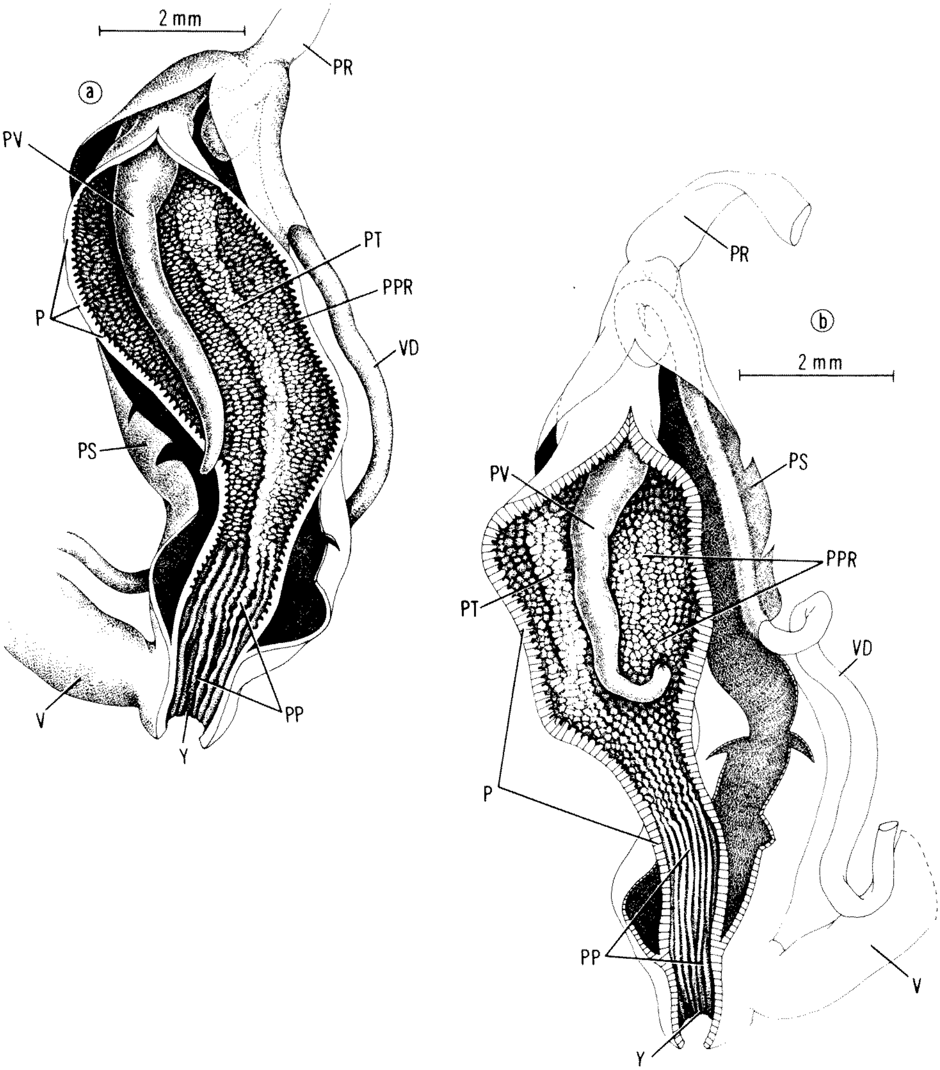


Fig. 66: Interior of penis chambers in *Amplirhagada confusa* and *A. varia varia,* a) *A. varia varia,* Sta. WA-212, Mitchell Plateau, 21-23 October 1976, WAM 615.77 and WAM 616.77, composite of Dissections A and B; b) *A. confusa,* Sta. WA-221, Mitchell Plateau, 29-30 October 1976, WAM 611.77, Dissection D. Scale lines equal 2 mm.

Sta. WA-205, weak gully above Camp Creek on track to big vine thicket (Warrender 4068—520:039) (3 dead adults, FMNH 199410, WAM 373.79, A. Solem, 18 October 1976); Sta. WA-214, trees along WA-213 stream, drop-off area (Warrender 4068–813:007) (1 live adult, FMNH 199411, A. Solem 22 October 1976); Sta. WA-215, rocky hillside at cycad patch, AMAX-Port Warrender Road (Warrender 4068—834:011) (25 live, 6 dead adults, FMNH 199574, FMNH 199847, FMNH 200788, WAM 367.79, 24 October 1976, 13 March 1977); Sta. WA-386, near waterfall on stream bank, A—found under small rock overhangs in shade, B—sealed to small rocks under and between boulders, C—under small boulders north-east of stream in exposed and unshaded area (81 live, 6 dead adults, 2 live juveniles, FMNH 199800, FMNH 199998-200000, FMNH 200209, FMNH 200211, WAM 353.79, WAM 368.79, WAM 369.79, WAM 372.79, L. Price and C. Christensen 12 March 1977); Sta. WA-389, boulders near vine thicket, 300 metres east of WA-215, AMAX-Port Warrender Road (Warrender 4068—832:013) (7 live adults, FMNH 199982, WAM 372.79, L. Price 13 March 1977); Sta. WA-394, sandstone boulders on south-east side of Crystal Creek, north-east of road, 8.2 km from Walsh Point Road (Warrender 4068—946:001) (2 live, 1 dead adults, FMNH 199355, FMNH 200790, L. Price and C. Christensen 15 March 1977); Sta. WA-395, vine thicket on south-west slope, ca. 1.3 km south-east of 'Crusher' (Warrender 4068—541:056) (1 dead adult, FMNH 200792, L. Price and C. Christensen 16 March 1977); Sta. WA-398, sealed to boulders at south margin of vine thicket immediately east of road, 1.0 km north of drop-off camp area (Warrender 4068—812:015) (102 live adults, 12 live juveniles, FMNH 199787, WAM 365.79, L. Price and C. Christensen 18 March 1977); boulders at Walsh Point, Port Warrender (Warrender 4068—ca. 873:065) (1 live, 5 dead adults, 7 dead juveniles, WAM 1228.75-1230.75, FMNH 200847, B. Wilson and S. Slack-Smith 29 October 1976).

Diagnosis

Shell 16.3-23.7 mm (mean 20.10 mm) in diameter, with 5 ⅞ to 7¼ (mean 6¾ –) very tightly coiled whorls **(Fig. 55b)**. Apex and spire very strongly elevated, dome-shaped **(Fig. 55a)**, height of shell 13.0-20.2 mm (mean 16.44 mm), H/D ratio 0.702-0.957 (mean 0.820). Apical sculpture **(Plate 13a)** of very prominent pustulations, postapical whorls with prominent, closely spaced radial riblets, 5-8 per mm, shell base smooth except for faint spiral incised lines. Shell periphery evenly rounded, without trace of angulation. Body whorl descending moderately to rather sharply behind lip, which is sharply flared and almost completely covers the umbilicus. Basal lip protrusion variable in size, usually prominent, but sometimes very weak. Subsutural and supraperipheral colour bands dark, usually wide, sometimes extending upwards to suffuse the entire whorl profile with red, columellar colour patch prominent. Spire and apex sometimes suffused with reddish tones. Based on 375 measured adults.

Genitalia **(Figs 65a, 66b)** in male active, but pre-mating phase. Ovotestis (G) large, hermaphroditic duct (GD) slender and relatively decoiled, entering well down side of talon (GT). Prostate (DG) prominent, uterus (UT) still in resting phase. Free oviduct (UV) long and slender, partly kinked, spermatheca (S) with slender base and oval expanded head. Vas deferens (VD) entering penis sheath (PS) about two-thirds of way up, forming a simple S-loop just below insertion of penial retractor muscle (PR). Penis (P) quite slender, internally **(Fig. 66b)** with a very long tapering verge (PV), the main pilaster (PT) is reduced to a short, rather broad ridge, the wall pustules (PPR) are prominent, the area of basal longtudinal ridges (PP) extends well above the point of origin of the penis sheath (PS) and the walls of the penis chamber are relatively thick. Based on 23 dissected and several checked individuals.

Discussion

Amplirhagada confusa is so named because specimens can be confounded with both the sympatric *A. mitchelliana* and the vine thicket inhabiting *A. varia varia.* In the area of known sympatry, roughly the western third of the Mitchell Plateau down to Port Warrender, specimens of *A. mitchelliana* and *A. confusa* from a single valley or talus normally can be separated conchologically. *A. confusa* has a higher spire, stronger radial sculpture, greater body whorl descension behind the lip, and a stronger basal lip protrusion than does *A. mitchelliana.* Ecologically, *A. confusa* normally aestivates sealed to a rock or another shell, while *A. mitchelliana* lies on the soil surface in talus or under boulders with a calcified seal across the aperture, but does not normally seal itself to a surface. Anatomically, the thin penis **(Fig. 65a)**, very long verge and reduced main pilaster **(Fig. 66b)** of *A. confusa* are very different from the fat penis **(Fig. 62a)**, small verge and huge main pilaster **(Fig. 62b)** of *A. mitchelliana. A. varia varia* and *A. confusa* differ conchologically primarily in shell diameter (mean diameters 17.32 mm and 20.10 mm, respectively). Anatomically, the longer main pilaster **(Fig. 66a)**, thinner penis walls, and slightly different pustule pattern of *A. varia varia* are the main distinguishing features. Ecologically, *A. confusa* has been found primarily in boulder areas or talus, sometimes (Sta. WA-389, WA-398) on the fringes of or near vine thickets, while *A. varia varia* has been taken, with one exception, only in vine thickets. A detailed study of their distribution near and in vine thickets would be an interesting project.

The building of multiple apertural seals is common in *A. confusa.* Specimens from Sta. WA-221 frequently showed three or four seals, and one individual had 11 separate seals situated right behind each other for almost one-eighth whorl.

Local variation in *A. confusa* is summarized in **Table 28.** There is no clear pattern of variation, with specimens from Sta. WA-215 being slightly larger than the remaining populations. This was one of the few 'open woodland' situations in which *A. confusa* was collected. Possibly because of the presence of cycads, this was a somewhat wetter area, hence the slightly larger size. Most populations sampled involved more sheltered areas that would tend toward a greater degree of moisture retention.

Seasonal variation in the genitalia follows the patterns seen in *A. mitchelliana* and *A. castra.*

Table 28: Local Variation in *Amplirhagada confusa*

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
WA-201, X-76, dead	11	16.16±0.331 (14.6-18.05)	20.42±0.333 (18.35-22.15)	0.792±0.013 (0.723-0.889)	6½ + (6⅛-7)
WA-203, X-76, live	12	16.65±0.307 (14.75-18.3)	20.47±0.249 (19.1-22.6)	0.814±0.013 (0.743-0.886)	6½ (6¼-6⅞)
WA-203, III-77, live	20	17.09±0.189 (15.6-18.5)	20.63±0.234 (19.05-23.01)	0.829.±0.009 (0.755-0.910)	6⅝ − (6¼-7)
WA-215, III-77, live	24	17.79±0.544 (16.0-20.2)	22.25±0.269 (21.0-23.7)	0.800±0.008 (0.736-0.882)	6⅞ − (6⅜-7⅛)
WA-221, X-76, dead	7	16.11±0.361 (14.5-17.5)	18.51±0.596 (17.6-20.75)	0.848±0.011 (0.803-0.890)	6⅜ (6¼-6⅞)
WA-221, X-76, live	14	16.54±0.273 (13.8-17.5)	19.58±0.308 (16.3-20.75)	0.845±0.008 (0.798-0.920)	6½ − (6-6¾)
WA-221, X-76, live	63	15.89±0.265 (13.9-18.5)	19.35±0.106 (17.8-21.3)	0.835±0.004 (0.760-0.921)	6⅜ (6-7)
WA-386, III-77, live	16	15.74±0.214 (14.1-16.75)	19.95±0.295 (18.8-23.35)	0.790±0.008 (0.711-0.834)	6⅜ (5⅞-6⅞)
WA-386A, III-77, live	12	16.35±0.334 (14.2-17.9)	20.29±0.256 (18.2-21.5)	0.808±0.013 (0.746-0.869)	6½ (6⅛-7)
WA-386A, III-77, live	39	16.93±0.146 (14.8-18.5)	20.39±0.107 (18.9-21.7)	0.830±0.006 (0.734-0.923)	6⅝ + (6¼-7)
WA-386C, III-77, live	14	16.73±0.305 (15.2-18.65)	20.09±0.187 (19.0-21.15)	0.833±0.011 (0.776-0.905)	6½ + (6¼-6⅞)
WA-398, III-77, live	102	16.34±0.104 (14.1-19.1)	19.77±0.078 (17.8-21.7)	0.826±0.004 (0.742-0.957)	6½ − (6-7⅛)

AMPLIRHAGADA CASTRA SP. NOV.

(Plate 13d; Figs 37h, 63a-b, 64b, 67e-f, 68)

Comparative remarks

Amplirhagada castra usually has a lower basal lip protrusion **(Fig. 67f)** and a lower spire **(Fig. 67e,** mean H/D ratio 0.755) than does *A. varia varia* **(Figs 67a-b,** mean H/D ratio 0.804). Frequently, *A. castra* has such a heavy spire colour suffusion that it appears almost monochrome, while *A. varia,* even when it has a heavy

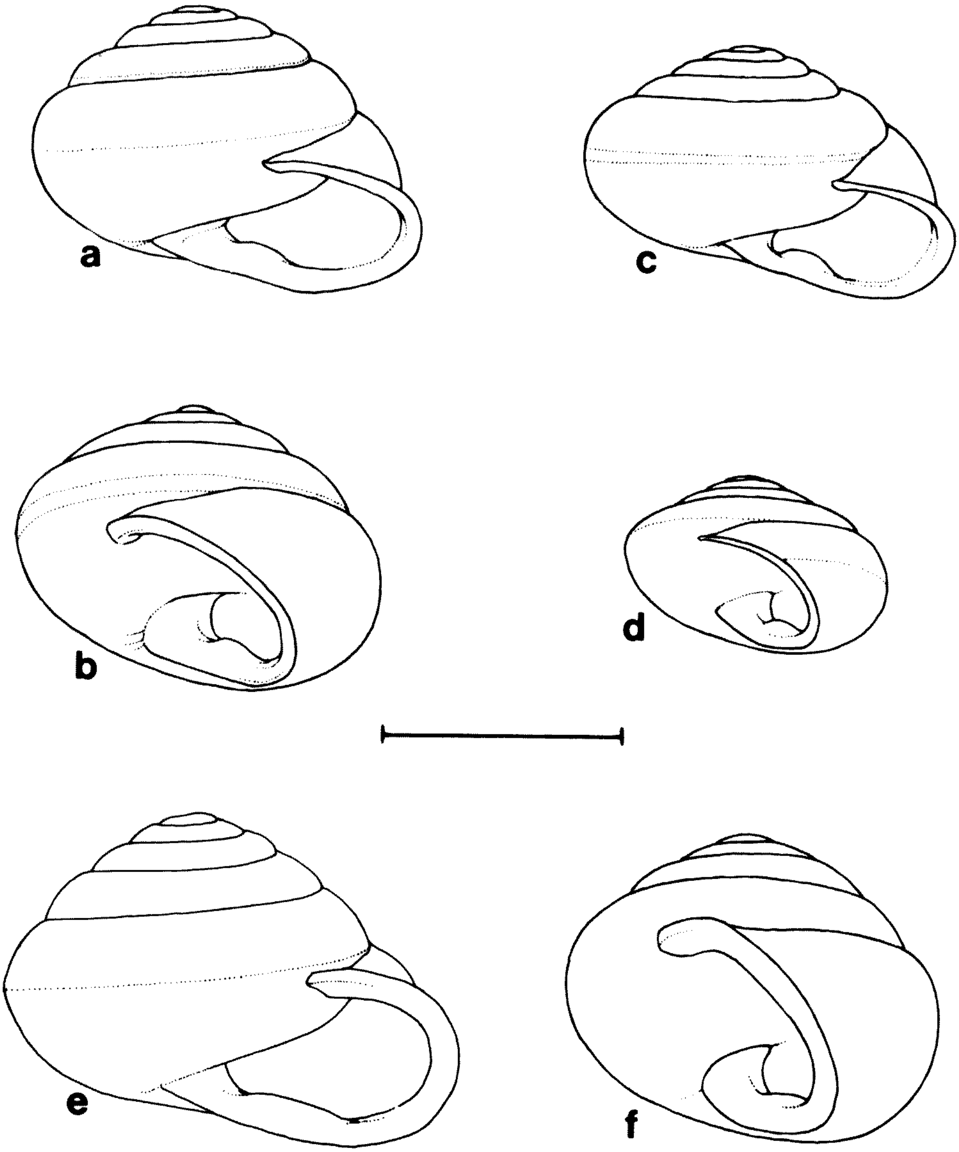


Fig. 67: Shells of *Amplirhagada varia* and *A. castra,* a-b) *A. varia varia,* Sta. WA-212, Mitchell Plateau, a is WAM 1221.75, holotype, b is FMNH 200087, paratopotype; c-d) *A. varia depressa,* Sta. 2, Warrender Hill, Admiralty Gulf, c is WAM 1324.75, holotype, d is WAM 1323.75, paratopotype; e-f) *A. castra,* Sta. WA-206, Camp Creek, Mitchell Plateau, WAM 1222.75, holotype. Scale line equals 10 mm.

suffusion, retains bright colour bands with less supplementary colour. The radial sculpture on the spire is very similar in the two species **(Plate 13c-d)**, but the tendency is for the individual ribs to be narrower and more sharply defined in *A. varia.* Overlap in all these features is extensive enough that worn examples and short sets would be extremely difficult to identify with certainty. *A. confusa* is distinctly larger (mean diameter 20.10 mm), averages nearly one-half whorl more (mean whorls 6½) than *A. castra* (mean diameter 18.09 mm, mean whorls, 5 ⅞), generally has a much higher spire (mean H/D ratio 0.820), somewhat stronger radial sculpture **(Plate 13a)**, a more rounded shell periphery **(Fig. 55a)** and usually less secondary coloration. *A. mitchelliana* is similar in shape and shell height (mean H/D ratio 0.732), with rounded periphery **(Fig. 55c)**, a greatly reduced basal lip protrusion **(Fig. 55c)**, very weak radial sculpture **(Plate 13b)**, is much larger (mean diameter 21.98 mm), and averages 6¾ – whorls. *A. alta crystalla* **(Figs 59c-d)** is much larger (mean diameter 21.67 mm), with a much higher spire (mean H/D ratio 0.953), an increased whorl count (mean whorls 7 ⅛), and very reduced radial sculpture **(Plate 13f)**. *A. imitata* (Smith, 1894) is very similar in size and shape, but has quite characteristic prominent and sharply defined radial sculpture **(Plate 12a)**. Anatomically, *A. castra* has a short vagina (V, **Figs 63a, 68**), long free oviduct (UV) and spermatheca (S), plus a very characteristic lateral bulge near the base of the penis (indicated by arrow). Internally **(Fig. 63b)** the verge (PV) is larger than average, the main pilaster (PT) is extremely large and its base causes the lateral outpocketing of the penis. The wall pustulations are small and organized into many rows. The area of longitudinal ridges inside the penis is drastically reduced, being restricted to the atrium (Y) and below the penis sheath (PS). The sculpture on the main pilaster **(Fig. 37h)** consists of short, broadly triangular points that extend from edge to edge of the narrow corrugations. *A. mitchelliana* is very similar in genital structure **(Figs 37i, 62a-b)**, but has a longer vagina, the main pilaster (PT) is shorter, and has narrower, slightly more widely spaced points **(Fig. 37i)** on equally narrow corrugations. The most striking difference, however, is that *A. castra* has the sculpture in the lower female tract **(Fig. 64b)** dramatically altered from that seen in *A. mitchelliana* **(Fig. 64a)**. Both *A. varia* and *A. confusa* differ **(Figs 66a-b)** from *A. castra* in their greatly enlarged verges and reduced main pilasters **(Figs 36d-e)**, while *A. alta* **(Fig. 37e)** has wider corrugations with a reduced number of triangular points on the main pilaster. An ecological difference is that *A. castra* and *A. mitchelliana* are both free sealers that aestivate on the soil surface or slightly buried, while *A. varia, A. confusa* and *A. alta* seal themselves to rocks or another shell during aestivation.

Holotype

WAM 1222.75, Sta. WA-206, under rocks and logs in large vine thickets above Camp Creek, south of 'Crusher', Mitchell Plateau, Western Australia (1:100,000 'Warrender' map sheet 4068, grid reference 520:040). Collected by Alan Solem 18 October 1976. Height of shell 15.5 mm, diameter 19.8 mm, H/D ratio 0.783, whorls 6 ⅛+.

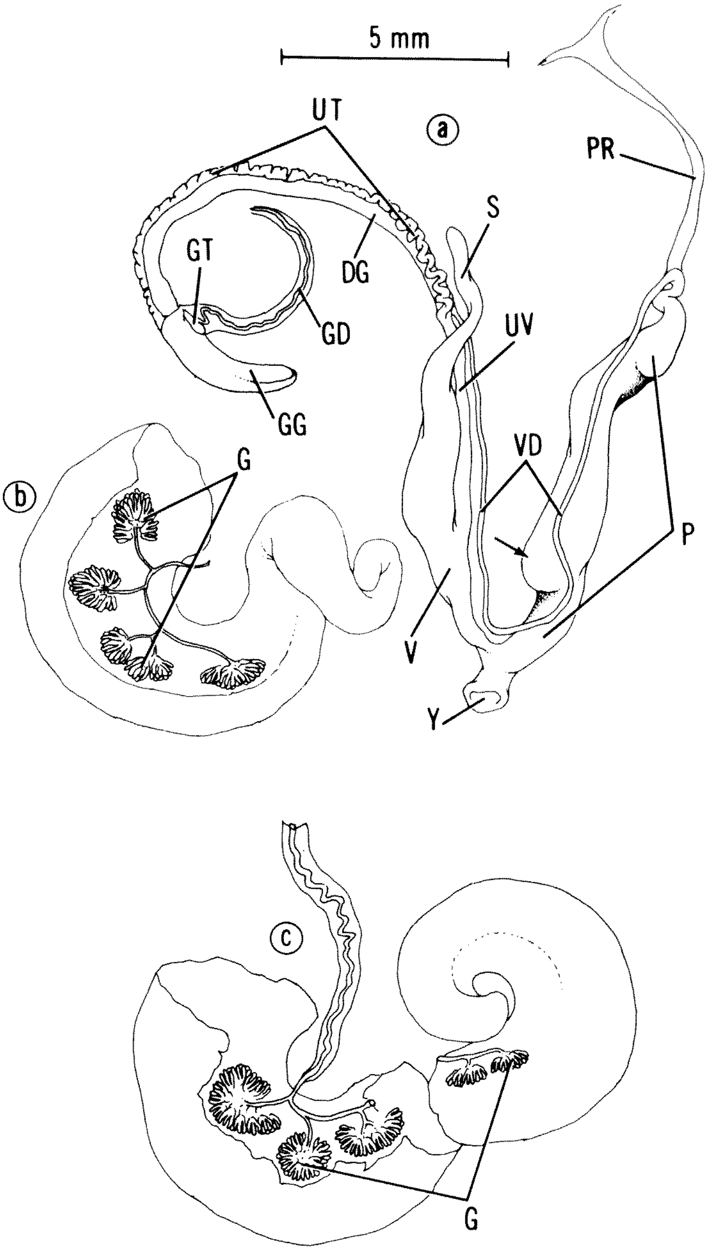


Fig. 68: Genitalia of *Amplirhagada castra,* a-b) Sta. WA-206, Camp Creek, Mitchell Plateau, 20 June 1975, WAM 1317.75, composite of Dissections A and B, genitalia of newly adult specimen, a is genitalia, b is ovotestis; c) Sta. MP-4 (= WA-206), 23 August 1975, WAM 1314.75, ovotestis in resting phase. Scale lines equal 10 mm.

Paratopotypes

WAM 1213.75, WAM 356.79, WAM 357.79, FMNH 199326, FMNH 199994, FMNH 200440, FMNH 200442, FMNH 200446, 24 live, 31 dead adults, 11 live, 4 dead juveniles. A. Solem 18 October 1976: WAM 1317.75, FMNH 200851, 23 live adults, 12 live juveniles, L.C. Smith and R. Johnstone 20 June 1975; WAM 1235.75, 5 live, 1 dead adults, 7 live juveniles, B.R. Wilson and S. Slack-Smith 23 August 1975; WAM 1314.75, WAM 1315.75, 9 live, 1 dead adults, 4 live juveniles, B.R. Wilson, C. Bryce 2-3 November 1976.

Paratypes

Sta. WA-395, vine thickets on south-west slope, ca. 1.3 km east-south-east of 'Crusher', Mitchell Plateau (Warrender 4068—541:056) (29 live, 18 dead adults, 3 live juveniles, FMNH 199299, FMNH 199281, WAM 354.79, WAM 355.79, L. Price and C. Christensen 16 March 1977).

Other material

Vine thicket near Camp Creek, ca. 14°53′S, 125°49′E (27 live and dead adults, 7 broken specimens, WAM 1319.75, FMNH 200826, W.H. Butler 2 August 1973).

Diagnosis

Shell 15.6-21.7 mm (mean 18.09 mm) in diameter, with 5 3/8 to 6½ (mean 5 7/8) whorls. Apex and spire moderately to very strongly elevated, usually rounded above **(Fig. 67e)**, height of shell 11.7-16.6 mm (mean 13.65 mm), H/D ratio 0.668-0.874 (mean 0.755). Apical sculpture typical, postapical whorls **(Plate 13d)** with prominent, relatively regularly spaced radial ribs, about 8-11/mm on upper spire, becoming reduced and irregular on lower spire and body whorl, shell base with weak incised spiral lines. Shell periphery rounded to weakly angled **(Fig. 67e)**. Body whorl very slightly and gradually to not deflected behind lip **(Fig. 67f)**, which is narrowly flared and expanded. Basal lip with a weak to moderate protrusion **(Figs 67e-f)**, lip reflexed to almost completely cover the umbilicus or leaving a narrow chink open. Subsutural colour band weak to absent, occasionally faint trace of columellar colour in umbilical chink. Supraperipheral colour band variable in intensity, spire and body whorl usually with a heavy colour suffusion tending toward dark brown, shell periphery white or slightly yellow in tone. Based on 150 measured adults.

Genitalia **(Figs. 63a-b, 64b, 68a-c)** seasonally variable. Ovotestis (G) enlarged greatly, hermaphroditic duct (GD) entering laterally on talon (GT). Vagina (V) very short, free oviduct (UV) and shaft of spermatheca (S) long. Vas deferens (VD) entering penis sheath at upper quarter, complexly coiled just below insertion of penial retractor muscle (PR). Lateral bumps visible on penis exterior (arrows in **Figs. 63a, 68a**) caused by very large main pilaster **(Fig. 63b**, PT). Penis internally **(Fig. 63b)** with very short area of longitudinal ridging (PP) at base, average sized verge (PV), prominent pustules (PPR) clearly arranged in rows, and a huge main pilaster (PT) that basally and sometimes apically causes lateral bulges on the penis exterior. Surface of main pilaster **(Fig. 37h)** with very narrow corrugations that are edged with numerous broadly triangular, closely spaced points, lower portion of pilaster gradually blending into pustule area. Lower portion of spermathecal shaft **(Fig. 64b)** highly unusual in lacking the typical elevated U-shaped pad (UP, **Fig. 64a**), instead showing a few very high longitudinal ridges that extend into the very short vagina (V). Based on 9 dissected adults, 3 juveniles, several checked individuals.

Discussion

The type locality for *Amplirhagada castra* (Sta. WA-206, MP-4) is the largest known patch of vine thicket on the Mitchell Plateau. It is located just across a ridge south of the Camp Creek 'Crusher', hence the selection of the name *castra,* referring to Camp Creek. A number of WAM staff members have worked this thicket in recent years and several samples were available for study. The material collected by Harry Butler in 1973 (WAM 1319.75) almost certainly is from the same colony, but because of problems with preservation has not been listed as paratypic. The only other known colony, Sta. WA-395, is located approximately 2.7 km north-east on the opposite side of the main tributary to Camp Creek.

Conchological variation in the available samples is summarized in **Table 29.** Despite the different years, collectors, and sample sizes, the Sta. WA-206 material is uniform in size and shape, with the WA-395 material about 1.5 mm larger in diameter and a quarter whorl more.

Seasonal variation could be studied on the basis of samples from March 1977 (Sta. WA-395), June 1975 (WAM 1317.75), August 1975 (WAM 1314.75) and October 1976 (Sta. WA-206). In March, the reproductive system is shutting down for the dry season. The ovotestis is greatly shrunken, the hermaphroditic duct very slender, but still coiled, the spermatheca is filled and swollen, the uterus is still rather enlarged. In June **(Fig. 68b)**, the ovotestis is shrunken, the hermaphroditic duct is much less coiled and even slenderer, the uterus is very greatly reduced, the spermatheca still contains some material, but is noticeably less swollen. A specimen that reached adult shell size at the end of the previous wet season and was collected in June is illustrated **(Figs 68a-b)**. The short albumen gland (GG), empty spermathecal head (S), very thin uterus (UT) and prostate (DG), and small hermaphroditic duct (GD) and ovotestis **(Fig 68b,** G) are characteristic of newly adult examples. The penis (P) shows the normal large bulge (arrow in **Fig. 68a)** near the base, and the internal structures are fully developed. In August, the ovotestis **(Fig. 68c)** has begun to thicken but not elongate, and the hermaphroditic duct is still slender. The spermatheca is empty and the uterus is still reduced. In mid-October **(Figs 63a-b)** the ovotestis (G) is enormously swollen, the hermaphroditic duct (GD) tightly coiled, but not yet swollen (compare with **Fig. 65b** of *A. varia varia* collected in January), the prostate (DG) is clearly enlarged while the uterus (UT) is still relatively small in size. A mild shower, the first recorded for the season, had hit Sta. WA-206 the night prior to the sample being taken, but there

Table 29: Local Variation in *Amplirhagada castra*

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
WA-206					
2-VIII-1973, live	7	13.75 ± 0.222 (13.1-14.65)	17.79 ± 0.278 (16.9-19.05)	0.773 ± 0.012 (0.734-0.835)	5 7/8 − (5 5/8-6)
20-VI-1975, live	23	13.54 ± 0.128 (12.3-14.65)	17.34 ± 0.148 (15.6-18.4)	0.782 ± 0.008 (0.668-0.857)	5¾ (5 3/8-6½)
23-VIII-1975, live	5	13.21 ± 0.346 (12.35-13.9)	17.41 ± 0.265 (16.7-18.25)	0.760 ± 0.045 (0.705-0.832)	5¾ (5 5/8-5 7/8)
18-X-1976, live	25	13.62 ± 0.151 (12.5-15.5)	17.88 ± 0.184 (16.65-20.1)	0.763 ± 0.008 (0.693-0.874)	5 7/8 (5½-6½)
18-X-1976, dead	31	13.10 ± 0.116 (11.7-14.6)	17.66 ± 0.118 (16.25-18.95)	0.741 ± 0.007 (0.680-0.830)	5¾ + (5½-6)
3-XI-1976, live	11	13.25 ± 0.273 (11.9-14.6)	17.70 ± 0.184 (16.85-18.85)	0.748 ± 0.011 (0.697-0.807)	5 7/8 (5 5/8-6 1/8)
WA-395					
FMNH 199821, live	29	14.41 ± 0.173 (12.8-16.6)	19.19 ± 0.195 (17.0-21.7)	0.751 ± 0.006 (0.681-0.817)	6 + (5½-6 5/8)
FMNH 199299, dead	18	13.85 ± 0.255 (12.0-15.7)	18.88 ± 0.204 (17.5-20.4)	0.733 ± 0.007 (0.678-0.809)	6 + (5 5/8-6½)

was no indication that the aestivating *Amplirhagada* had been activated as the sheltered microhabitats of the sealed snails were still bone dry.

The penis interior of the holotype **(Fig. 63b)** is unusual in that the lateral bulge was greatly pronounced and the main pilaster (PT) twisted down into the pocket. Compared with other examples dissected, this penis seems shortened (compare **Fig. 63a**) and the main pilaster shorter than it actually is. The pattern of the pustule rows and shortening of the longitudinal ridge area is constant in all dissected material

One set, WAM 1319.75, contained 7 adult specimens taken from the stomach of a Scrub Fowl (*Megapodius freycinet* [Gaimard, 1823], field number BB833, W.H. Butler, 2 August 1973, now AMNH 810980). Two of these had started to push the epiphragm aside, but the other five were fully sealed. The shell surface showed no traces of erosion from the digestive juices in the bird's stomach, but there is no data as to when they had been consumed.

Specimens of *Amplirhagada mitchelliana* have been collected on the fringes of both known stations for *A. castra* (WA-205 and WA-206 are less than 100 metres apart, while WA-395 and WA-396 are 0.3 km apart), and, while they are conchologically quite dissimilar in size, shape and sculpture **(Table 17, Plate 13b, d)**, their male anatomy is very similar. They share the habit of closing off the aperture with a seal rather than attaching to a rock or other shell. Most *A. castra* **(Figs 63a, 68a)** have a conspicuous bulge near the base of the penis (arrow) caused by the very large and long main pilaster (PT, **Fig. 63b**), which is lacking in *A. mitchelliana* **(Fig. 62a)** unless the animal has died in a severely retracted position **(Fig. 61d)**. The penis interiors of *A. castra* **(Fig. 63b)** and *A. mitchelliana* **(Fig. 62b)** differ in the length of the longitudinal ridge area, length of the main pilaster (PT), and actual size of the verge. The gross appearance of the main pilaster is the same in the two species, but there are consistent differences in the sculpture on the corrugations of the main pilaster. In *A. castra* **(Fig. 37h)** the points are broadly triangular and with narrow spaces between, while in *A. mitchelliana* **(Fig. 37i)** the points are more narrowly triangular with wider spaces between them. This difference is quite small compared with the normal range of differences in *Amplirhagada* **(Figs 36-37)**, but is placed into context by examining the wall sculpture in the lower female tract **(Figs 64a-b)**. The loss of the pad (UP) around the free oviduct opening (UVO) and development of high ridges on the walls of the lower free oviduct in *A. castra* **(Fig. 64b)** are the only specializations found in this area of the genitalia in *Amplirhagada* examined to date. They are quite sufficient to permit species recognition by individuals and provide a contrast to the situation seen in most other sympatric species where it is the armature on the main pilaster or a change in the verge that enables species recognition.

AMPLIRHAGADA VARIA SP. NOV.

Two morphological series are grouped under this name. Although they differ significantly in shell proportions, colour pattern, and verge length, they are considered to be one species. Except for a few examples (WAM 1321.75, WAM 1322.75) taken nearby one of the smallest vine thickets, all materials have been found in the vine thickets themselves. The populations are thus allopatric and sharply isolated from each other. Most vine thickets near the Mitchell Plateau have not been sampled yet. Further collecting and study may indeed result in changing the concept of this species.

In the field, *A. castra* and *A. varia varia* were confused, although they differ radically in male genitalia (compare **Figs 63b** and **66a**), while *A. varia depressa* can be taken for a dwarf race of *A. mitchelliana* on shell shape and colour, but is readily separable on the very different penis interior (compare **Figs 62b** and **66a**) and strong radial sculpture on the shell **(Plates 13b, c)**. Full comparative comments are given under the two subspecies.

AMPLIRHAGADA VARIA VARIA SP. ET SUBSP. NOV.

(Plate 13c; Figs 36e, 65b, 66a, 67a-b, 69a-d)

Comparative remarks

Amplirhagada varia varia averages 1.05 mm larger in diameter, 2.91 mm higher, and 0.125 greater in H/D ratio than does *A. v. depressa*. The latter generally has a much lighter background colour and only the prominent two red bands, while *A. v. varia* mostly has the spire with a heavy colour suffusion. The verge of *A. v. varia* is 2.48-5.62 mm (mean 3.97 ± 0.225 mm) long, while in *A. v. depressa* the verge length is 1.18-1.57 mm (mean 1.45 ± 0.072 mm). There is sufficient overlap in shell measurements, that dissection is required to confirm the identity of isolated specimens, although the averages of populations seem quite consistently different. *A. castra* differs conchologically in having a slightly angled periphery **(Fig. 67e)**, reduced radial shell sculpture **(Plate 13d)** and less body whorl descension **(Fig. 67f)**. Anatomically it has a short verge and a huge main pilaster **(Fig. 63b)**. Species such as *A. imitata* (Smith) have even stronger radial sculpture **(Plate 12a)**, a weaker basal protrusion **(Fig. 71)**, and usually a more evenly elevated spire. The reduced main pilaster and very long verge of *A. varia varia* **(Fig. 66a)** are comparable to the situation found in *A. confusa* **(Fig. 66b)**, but the very different coiling pattern, shell sculpture **(Plate 13a)**, and method of main pilaster reduction separate them easily. These two species do share the pattern of sealing to an object during aestivation, rather than free sealing. Their enlarged verges and reduced main pilasters **(Figs 36d, e)** are unique in *Amplirhagada*.

Holotype

WAM 1221.75, Sta. WA-212, vine thicket at west end of WA-201 gully, west of AMAX-Port Warrender Road at drop-off camp area, Mitchell Plateau, Western Australia. (1:100,000 'Warrender' map sheet 4068, grid reference 813:007). Collected by Alan Solem 23 October 1976. Height of shell 13.15 mm, diameter 17.1 mm, H/D ratio 0.769, whorls 5 ⅞.

Paratopotypes

WAM 1214.75, WAM 219.79, WAM 221.79, WAM 222.79, WAM 225.79, WAM 230.79, WAM 234.79, WAM 235.79, FMNH 199599, FMNH 200072, FMNH 200078, FMNH 200083-7, FMNH 200449, FMNH 200456, FMNH 200461, FMNH 200472-3, 126 live and 178 dead adults, 36 live and 3 dead juveniles from the type locality, 21-30 October 1976 and 11 March 1977.

Paratypes

Mitchell Plateau: Sta. WA-204, vine thicket 1.6 km toward Crystal Creek from AMAX-Port Warrender Road (Warrender 4068—887:005) (77 live and 157 dead adults, 59 live and 12 dead juveniles, WAM 1325.75, WAM 217.79, WAM 1212.75,

WAM 218.79, WAM 223.79, WAM 226.79, WAM 232.79, FMNH 199963-7, FMNH 199392, FMNH 199810, FMNH 200402, FMNH 200406, various collectors, 17-31 October 1976, 17 March 1977); Crystal Creek track above Sta. WA-204 vine thicket in open eucalypt woodland (7 dead adults, WAM 1321.75, WAM 1322.75, B.R. Wilson and C. Bryce 31 October 1976); Sta. WA-384, vine thicket south-west of WA-213 stream, west of drop-off camp area (Warrender 4068—812:006) (42 live adults, 10 live juveniles, FMNH 200001, FMNH 200005, WAM 227.79, L. Price and C. Christensen 12 March 1977); Sta. WA-388A, liana patch west of drop-off camp area (62 live adults, 7 live juveniles, FMNH 199832, WAM 229.79, L. Price and C. Christensen 12 March 1977); Sta. WA-388B, under boulders, liana patch west of drop-off camp area (18 live adults, 1 live juvenile, FMNH 199798, WAM 231.79, L. Price and C. Christensen 12 March 1977); Sta. WA-393, vine thicket on west slope Walsh Point Road, 1.6 km east of Crystal Creek road junction (Warrender 4068—879:027) (76 live and 29 dead adults, 17 live and 2 dead juveniles, FMNH 199313-4, FMNH 199805, FMNH 199809, L. Price and C. Christensen 15 March 1977); headland south-south-east of Walsh Point, Port Warrender Bay, Admiralty Gulf (Warrender 4068—831:088) (3 live and 1 dead adults, 3 live juveniles, WAM 1309.75, WAM 1310.75, B.R. Wilson 17 October 1976); vine thicket along Camp Creek near AMAX Camp (Warrender 4068—583:060) (12 live adults, 12 live juveniles, WAM 1326.75, FMNH 200858, L. Smith and R. Johnstone January 1973).

Diagnosis

Shell 13.6-20.3 mm (mean 17.32 mm) in diameter, with 5 3/8 to 6 7/8 (mean 6 1/8 −) whorls. Apex and spire strongly elevated, moderately rounded above, height of shell 10.1-18.5 mm (mean 13.98 mm), H/D ratio 0.670-1.040 (mean 0.804). Apical sculpture **(Plate 13c)** typical, postapical sculpture of prominent, rather well defined radial ribs, 5/mm on the spire, often becoming somewhat irregular by body whorl, shell base with incised spiral lines. Periphery rounded **(Figs 67a-b)**, without trace of angulation in most adults, smallest individuals often with weak angulation. Body whorl normally descending sharply behind lip **(Figs 67a-b)**, which is moderately flared and reflexes to nearly completely cover umbilicus, leaving only a narrow chink. Basal lip normally with a rather prominent protrusion **(Fig. 67b)**. Colour bands and columellar patch prominent, frequently lip edge with a weak purplish suffusion, periphery light in colour, spire normally with a heavy to overriding colour suffusion turning spire as dark as main bands, shell base light except for columellar patch which frequently is confined to the lip itself. Based on 703 measured adults.

Genitalia **(Figs 65b, 69a-d)** seasonally variable. Hermaphroditic duct (GD) entering laterally on talon (GT), greatly enlarged and swollen in January **(Fig. 65b)**, narrow and relatively uncoiled in October **(Fig. 69a)** and March **(Fig. 69c)**. Ovotestis (G) enormous in October **(Fig. 69b)**, partly reduced in January **(Fig. 65a)**, greatly shrunken in March **(Fig. 69c)**. Prostate (DG) large in October **(Fig. 69a)**, reduced greatly in March **(Fig. 69c)**, uterus (UT) large in January **(Fig. 65b)** reduced in

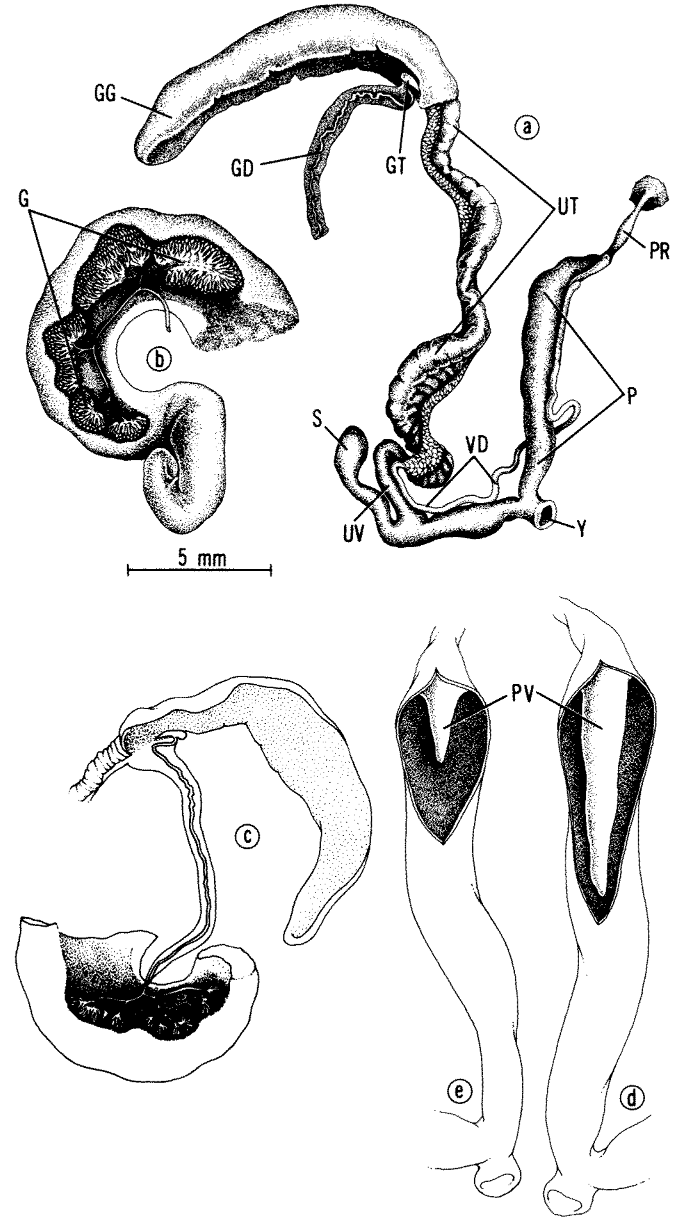


Fig. 69: Genitalia of ***Amplirhagada varia*****,** **a-d)** *A.* ***varia varia*****,** **a-b, d, Sta. WA-212,** Mitchell Plateau, 21-23 October 1976, WAM 616.77, Dissection C, a is whole genitalia, b is ovotestis, d is diagram of verge length relative to penis sheath length, c is ovotestis of Sta. WA-393, Mitchell Plateau, 17 March 1977, FMNH 200072, Dissection B; e) diagram of verge length in *A. varia depressa*, Sta. 2, Warrender Hill, Admiralty Gulf, 1 November 1976, WAM 1323.75, Dissection B. Scale line for a-c, d-e diagrammatic and not to scale.

October (**Fig. 69a**) and March (**Fig. 69c**). Vagina (V) somewhat variable in length, 2.48-7.06 mm (mean 4.61 ± 0.28 mm) long, penis sheath 1.76-3.43 times (mean 2.45 ± 0.11) vagina length. Vas deferens (VD) entering penis sheath (PS) near top, S-coiled (**Fig. 65b**) below insertion of penial retractor muscle (PR). Basal portion of prostate-uterus and upper portion of free oviduct (UV) kinked. Penis complex very slender, internally (**Fig. 66a**) with a long verge (PV), length 2.48-5.62 mm (mean 3.97 ± 0.22 mm), that tapers very gradually. The ratio of verge to penis length is 1.65-4.17 (mean 2.68 ± 0.14). Walls of penis thin, longitudinal ridge section short, main pilaster (PT) reduced to a raised row of broad ovate pustules (**Fig. 36e**), with the wall pustules also distinctly ovate. Based on 18 dissected and measured individuals; many additional examples checked.

Discussion

Without careful examination of the penis interior, examples of *Amplirhagada varia varia* (**Fig. 66a**) can be mistaken for *A. confusa* (**Fig. 66b**). The latter has thicker walls to the penis, the wall pustules are irregularly circular rather than clearly ovate, the main pilaster is shorter and broader with quite different shape to the pustules (**Figs 36d-e**). Conchologically, *A. confusa* is a distinctly larger (mean diameter 20.10 mm) shell with higher mean whorl count (6½), has generally flatter whorl contours (**Fig. 55a**), and a somewhat less prominent basal lip protrusion. Nowhere have the two species been taken microsympatrically, although their known geographic ranges extensively overlap on the Mitchell Plateau. While the anatomical differences are relatively minor, treatment as full species seems prudent at this time.

Amplirhagada varia varia has been collected in seven different vine thickets to date, which range from a shore side situation near Walsh Point to an area near the AMAX Camp on the Mitchell Plateau proper. There are distinct minor size and shape differences among the populations from the various thickets, those from the Crystal Creek track area (Sta. WA-204 and WA-393) being distinctly less elevated (**Table 30**) than those from near the drop-off camp area (Sta. WA-212, WA-384, WA-388). The small size of the WA-204 and Camp Creek populations may relate to the smaller size of these vine thickets. There are no significant differences between live and dead examples collected simultaneously (**Table 32**), or between October 1976 and March 1977 samples from the same populations. The few dead examples taken in open eucalypt woodland and south-south-east of Walsh Point (**Table 32**) are partly intermediate between *A. varia* and *A. confusa*. They have been classified as *A. varia* because of their low whorl count (Walsh Point) and shell sculpture (above WA-204). Careful study of additional vine thickets and their fringes will be required to determine the exact relationship of the two species.

For nineteen examples dissections were carried far enough so that the length of the terminal genitalia could be measured. Nearly all of these were from expanded individuals, so that the factor of differences due to contraction upon withdrawal into the shell was not present. In one new adult collected 17 March 1977 (WA-393) the verge was only 0.78 mm long and the penis 6.14 mm long. The other eighteen were

Table 30: Variation in *Amplirhagada varia varia* from each vine thicket

Station	Number of Adults Measured	Mean and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
WA-388	80	15.07 (12.8-17.2)	18.23 (16.25-20.0)	0.827 (0.708-0.902)	6¼ (5⅜-6¾)
WA-384	42	15.28 (12.8-17.1)	18.40 (16.85-20.1)	0.830 (0.750-0.922)	6⅜ − (5¾-6½)
WA-212	303	14.48 (11.0-18.5)	17.47 (14.9-19.95)	0.823 (0.691-1.040)	6⅛ (5½-6⅞)
WA-393	102	13.18 (10.8-15.9)	17.61 (15.2-19.7)	0.748 (0.670-0.832)	6⅛ (5¾-6¾)
WA-204	149	12.05 (10.1-15.4)	16.07 (13.6-18.8)	0.785 (0.703-0.893)	5⅞ + (5⅜-6⅝)
Camp Creek	12	12.02 (10.2-13.9)	15.36 (14.25-16.7)	0.781 (0.689-0.851)	5⅞ + (5½-6¼)
SSE Walsh Point	4	15.13 (13.7-17.0)	19.16 (17.9-20.3)	0.787 (0.751-0.842)	6⅛ + (5⅞-6½)

fully adult, and size and proportional variation is summarized in **Table 31.** There was no significant mean difference between stations, the intrastation range approximating the total range. The difference between the new adult and fully adult examples in penis and verge length suggests that mating would not have occurred by the new adult until the next wet season. The striking difference in verge length **(Figs 69d-e)** between *A. varia varia* and *A. v. depressa* is not an artifact of seasonality, since all available material of *A. v. depressa* was taken in October and early November, a period of sexual activity for Mitchell Plateau *Amplirhagada.*

Table 31: Length and proprotions of terminal genitalia in *Amplirhagada varia*

Taxon	Number of Adults Measured	Mean, Range and SEM of: Penis Sheath Length in mm	Verge Length in mm	Vagina Length in mm	Penis/Verge Ratio
A. varia varia	18	10.24 ± 0.365 (8.5-13.46)	3.97 ± 0.225 (2.48-5.62)	4.61 ± 0.276 (2.48-7.06)	2.68 ± 0.140 (1.65-4.17)
A. varia depressa	5	8.63 ± 0.569 (6.93-10.2)	1.45 ± 0.072 (1.18-1.57)	3.14 ± 0.695 (2.09-5.88)	6.00 ± 0.451 (4.4-7.0)

Table 32: Local Variation in *Amplirhagada varia varia* and *A. v. depressa*

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
A. v. varia					
Camp Creek, WAM 1326.75, live	12	12.02 ± 0.374 (10.2-13.9)	15.36 ± 0.234 (14.25-16.7)	0.781 ± 0.014 (0.689-0.851)	5 ⅞ + (5½-6¼)
WA-384, 12-III-77, live	42	15.28 ± 0.169 (12.8-17.1)	18.40 ± 0.126 (16.85-20.1)	0.830 ± 0.007 (0.750-0.922)	6 ⅜ − (5¾-6½)
WA-212					
21-X-76, dead	170	14.46 ± 0.062 (11.5-18.5)	17.27 ± 0.093 (15.4-19.95)	0.827 ± 0.004 (0.718-1.04)	6 ⅛ + (5½-6 ⅞)
21-X-76, live	17	13.56 ± 0.287 (11.35-15.35)	16.84 ± 0.155 (15.7-17.85)	0.804 ± 0.013 (0.696-0.914)	5 ⅞ + (5½-6¼)
22-X-76, live, 1 rock	5	14.46 ± 0.299 (13.3-14.95)	17.63 ± 0.297 (16.9-18.45)	0.820 ± 0.017 (0.773-0.876)	6 − (5 ⅝-6 ⅛)
23-X-76, dead	7	14.75 ± 0.670 (11.0-16.3)	17.89 ± 0.578 (14.9-19.55)	0.829 ± 0.020 (0.738-0.899)	6 ⅛ − (5½-6 ⅜)
23-X-76, live	39	14.46 ± 0.182 (11.05-16.95)	17.77 ± 0.148 (15.55-18.95)	0.814 ± 0.007 (0.691-0.887)	6 + (5½-6 ⅜)
11-III-76, live	65	14.74 ± 0.129 (12.1-16.9)	17.90 ± 0.100 (15.5-19.95)	0.823 ± 0.004 (0.746-0.894)	6 ⅛ (5 ⅝-6 ⅝)
WA-388A	62	15.05 ± 0.128 (12.9-17.1)	18.28 ± 0.104 (16.65-20.0)	0.823 ± 0.005 (0.708-0.897)	6¼ (5 ⅞-6¾)
WA-388B	18	15.15 ± 0.275 (12.8-17.2)	18.03 ± 0.263 (16.25-19.55)	0.840 ± 0.010 (0.749-0.902)	6¼ (5 ⅜-6 ⅝)
WA-393 15-III-77, live	76	13.23 ± 0.112 (10.8-15.9)	17.62 ± 0.116 (15.2-19.7)	0.750 ± 0.004 (0.670-0.832)	6 ⅛ (5¾-6¾)
15-III-77, dead	26	13.05 ± 0.163 (11.5-14.2)	17.57 ± 0.154 (16.6-19.15)	0.743 ± 007 (0.673-0.798)	6 ⅛ + (5 ⅞-6 ⅝)
WA-204					
17-30-X-76, live	21	12.13 ± 0.261 (10.25-15.4)	15.68 ± 0.235 (13.6-18.6)	0.772 ± 0.016 (0.703-0.842)	5¾ + (5 ⅜-6 ⅝)
17-X-76, dead	55	12.86 ± 0.130 (11.4-15.05)	16.30 ± 0.117 (14.8-18.8)	0.787 ± 0.006 (0.723-0.893)	6 (5½-6½)
24-X-76, dead	6	12.82 ± 0.230 (11.65-13.8)	16.13 ± 0.322 (15.2-16.9)	0.794 ± 0.061 (0.742-0.841)	6 (5 ⅞-6¼)

Table 32: Local Variation in *Amplirhagada varia varia* and *A. v. depressa* (continued)

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
24-X-76, WAM 1325.75, dead	7	12.61 ± 0.832 (11.35-13.6)	16.14 ± 0.539 (15.1-16.9)	0.781 ± 0.041 (0.712-0.832)	5 7/8 + (5 7/8-6 1/8)
12-III-76, live	60	12.60 ± 0.143 (10.1-15.4)	15.99 ± 0.132 (14.2-18.75)	0.788 ± 0.005 (0.711-0.892)	5 7/8 + (5 3/8-6 1/2)
Above WA-204, WAM 1321.75, WAM 1322.75, dead	7	14.84 ± 0.305 (13.1-15.4)	18.45 ± 0.121 (17.9-18.9)	0.797 ± 0.017 (0.708-0.842)	6 3/8- (6- 5/8)
Headland, SSE of Walsh Point, 17-X-76, live	4	15.13 ± 0.418 (13.7-17.0)	19.16 ± 0.632 (17.9-20.3)	0.787 ± 0.020 (0.751-0.842)	6 1/8 + (5 7/8-6 1/2)
A. v. depressa					
Sta. 2, E of Crystal Creek, live	7	12.30 ± 0.621 (10.4-14.2)	17.14 ± 0.647 (15.15-19.8)	0.716 ± 0.015 (0.667-0.772)	6 1/8 (5 5/8-6 1/2)
Walsh Point, live	4	12.69 ± 0.390 (12.05-13.7)	18.13 ± 0.423 (17.45-19.2)	0.701 ± 0.017 (0.658-0.739)	6 1/8 – (6-6 3/8)
Sta. 2, live Warrender Hill	16	10.27 ± 0.179 (8.8-11.6)	15.50 ± 0.232 (13.55-17.25)	0.663 ± 0.006 (0.627-0.707)	5 1/2 + (5-5 3/4)
Sta. 3, dead Warrender Hill	7	10.74 ± 0.484 (8.75-12.3)	16.08 ± 0.313 (14.95-17.1)	0.666 ± 0.020 (0.585-0.719)	5 7/8 – (5 1/4-6 3/8)

AMPLIRHAGADA VARIA DEPRESSA SUBSP. NOV.

(Figs 67c-d, 69e)

Comparative remarks

Amplirhagada varia depressa differs from the nominate race in the features listed under 'Comparative remarks' for the latter. The very low H/D ratio (mean 0.679) is approached only by the much larger *A. wilsoni* (mean H/D ratio 0.700) and *A. questroana* (mean H/D ratio 0.660), sharply angulated *A. katerana* (mean H/D ratio 0.708), and the somewhat similar in size and shape *A. kalumburuana* (mean H/D ratio 0.706). Only the strongly carinated and depressed *A. carinata* (mean H/D ratio 0.578) and the umbilicated *A. pusilla* (mean H/D ratio 0.590) and *A. drysdaleana* (mean H/D ratio 0.630) have a lower spire. In colour and general appearance, *A. varia depressa* closely resembles a miniature *A. mitchelliana*, but that species is generally much larger (mean diameter 21.99 mm), averages almost a whorl more (mean whorls 6 ⅝), although with some overlap, and has much less regular and weaker radial sculpture on the postapical whorls **(Plate 13b)**. Anatomically, the long verge and reduced pilaster of *A. v. depressa* **(Figs 36e, 69e)** agree at least superficially with the condition in *A. confusa* **(Figs 36d, 66b)**, but that species is very high spired **(Fig. 55b**, mean H/D ratio 0.820) and has not been collected in vine thickets. All other Mitchell Plateau region *Amplirhagada* have a small to medium-sized verge and a very highly developed pilaster.

Holotype

WAM 1324.75, Sta. 2, vine thicket on basalt, slopes of Warrender Hill, inland from MacGregor Point, Port Warrender, Admiralty Gulf, north-west Kimberley, Western Australia (1:100,000 'Warrender' map sheet 4068, grid reference *ca.* 918:041). Collected by B.R. Wilson and C. Bryce 1 November 1976. Height of shell 11.1 mm, diameter 16.75 mm, H/D ratio 0.663, whorls 5⅝ –.

Paratopotypes

WAM 1323.75, FMNH 200856, 15 live and 1 dead adults, 8 live juveniles, from the type locality.

Paratypes

Sta. 3, Warrender Hill, inland from Point MacGregor, Admiralty Gulf (2 live and 5 dead adults, 1 live juvenile, WAM 1328.75, FMNH 200855, B.R. Wilson and C. Bryce 1 November 1976); Walsh Point, gully in hill above shore (Warrender 4068 – *ca.* 875:063) (3 live and 1 dead adults, 11 live juveniles, WAM 1329.75, FMNH 200857, B.R. Wilson and C. Bryce 28 October 1976); Sta. 2, basalt ridge on steep hillside, open grassy eucalypt woodland east of Crystal Creek Pools, inland from Port Warrender (Admiralty Gulf 4069—953:013) (7 live, 1 dead adults, 11 live juveniles, WAM 1327.75, FMNH 200827, B.R. Wilson and C. Bryce 2 November 1976).

Diagnosis

Shell 13.55-19.8 mm (mean 16.27 mm) in diameter, with 5 to 6½ (mean 5¾ +) whorls. Apex and spire moderately and evenly elevated, very slightly rounded above, height of shell 8.75-14.2 mm (mean 11.07 mm), H/D ratio 0.585-0.772 (mean 0.679). Apical sculpture typical, postapical whorls with rather prominent radial ribs, 5-7/mm on upper spire, more widely spaced on body whorl, shell base retaining traces of radial ribs plus weak incised spiral lines. Shell periphery rounded **(Fig. 67d)**, normally without trace of angulation, sometimes moderately angulated. Body whorl descending sharply behind lip, which is moderately flared, with a relatively prominent basal protrusion **(Fig. 67c)**. Lip reflexion partly covers umbilicus, usually a prominent chink remaining. Colour bands and umbilical patch usually present, narrow, spire only rarely with a darker suffusion, normally pale yellow-white in tone. Rarely colour bands faded or even absent. Based on 34 measured adults.

Genitalia **(Fig. 69e)** agreeing with that of *A. varia varia* except for length of verge, which is noticeably shorter, 1.18-1.70 mm (mean 1.45 ± 0.072 mm) long in 5 measured examples. Interior of penis with a tendency toward a secondary weak pilaster more frequently than in *A. varia varia*. Based on 7 dissections plus several other checked individuals.

Discussion

Although the Walsh Point and Crystal Creek pools populations of *Amplirhagada varia depressa* average ¼ to ⅝ whorl more, 1.5-2.5 mm larger in diameter, and are more elevated than the Warrender Hill populations **(Table 32)**, the shells show no differences in structure that would suggest separation of these populations. Three of the four localities are vine thickets, while the other is open eucalypt woodland near Warrender Hill.

The shorter verge **(Figs 69d-e)** of *A. v. depressa* compared with that of the nominate race **(Table 31)** is diagnostic, while the size, colour, and shape differences in the shell are good recognition features. The name *depressa* refers to the low spire of this taxon in relation to the other species of *Amplirhagada* found on the Mitchell Plateau.

AMPLIRHAGADA SYKESI (SMITH, 1894)

(Figs 70a-c)

Helix (Hadra) sykesi Smith, 1894, Proc. Malac. Soc. London, **1:** 92, pl. VII, fig. 8—Parry Island (14°19′S, 125°46′E), Admiralty Gulf, north-west Australia.

Amplirhagada sykesi (Smith), Iredale, 1933, Records Australian Mus., **19** (1): 52; Iredale, 1938, Australian Zool., **9** (2): 113; Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 65-66, pl. V, fig. 3.

Comparative remarks

Amplirhagada sykesi (Smith, 1894) is a very high spired shell **(Fig. 70b,** mean H/D ratio 0.847) in which the radial sculpture is almost absent, a secondary sculpture of incised spiral lines extends well up onto the spire, there is normally no basal protrusion on the lip, and the umbilical region shows a slight lateral crack. The increased whorl count (mean whorls 6½ –) and elevated spire are exceeded only by some of the races of *A. alta,* which differ in having a prominent basal protrusion on the lip and traces of radial sculpture on the spire **(Plate 13f)**. *A. montalivetensis* (Smith, 1894) has a distinctly lower spire **(Fig. 70e,** mean H/D ratio 0.700), noticeable protrusion on the basal lip, more deeply impressed sutures and more strongly rounded whorls, and a more expanded lip. *A. confusa* and *A. mitchelliana* from the Mitchell Plateau have much to moderately stronger radial sculpture **(Plates 13a-b)** and usually a prominent basal lip protrusion **(Figs 55a, c)**. *A. elevata* from the Prince Regent River Reserve is less elevated (mean H/D ratio 0.802) with a greater whorl count (mean 6 ⅞), but is much more strongly rounded above **(Fig. 55f)**, has shallow sutures and flatter whorls, and weaker sculpture **(Plate 14b)**. *A. wilsoni* almost completely lacks radial sculpture **(Plate 14a)**, is much less elevated **(Fig. 55e**, mean H/D ratio 0.700), and has stronger colour bands. The anatomy of *Amplirhagada sykesi* (Smith, 1894) is unknown.

Lectotype

BMNH 92.1.29.144, Parry Island (14°19′S, 125°46′E), Admiralty Gulf, Western Australia. Collected by J.J. Walker. Height of shell 18.4 mm, diameter 20.85 mm, H/D ratio 0.882, whorls 6 ⅛.

Paralectotypes

BMNH 92.1.29.145-148, AM C.64874, SMF 27552, 6 dead adults from the type locality.

Other material studied

Admiralty Gulf (1 dead adult, IRSB); Parry Island (2 dead adults, 2 dead juveniles, WAM 1251.75, FMNH 200848, I.M. Crawford, 13 August 1974).

Diagnosis

Shell 18.95-21.4 mm (mean 20.56 mm) in diameter, with 6 ⅛ to 6¾ (mean 6½ –) whorls. Apex and spire strongly and almost evenly elevated, only slightly rounded above, height of shell 16.2-18.6 mm (mean 17.44 mm), H/D ratio 0.757-0.882 (mean 0.847). Apical sculpture typical, early spire with very low and irregular radial undulations, about equivalent to that found in *A. alta crystalla* **(Plate 13f)**, lower spire with incised spiral lines as in *A. percita* (Iredale, 1939) **(Plate 14f)**. Shell periphery at most slightly angulated **(Fig. 70b)**, body whorl not to slightly descending behind moderately flared lip. Basal lip without **(Fig. 70b)** to occasionally with a very strong protrusion. Umbilical area closed by reflection of lip, only a slight lateral crack visible **(Fig. 70c)**. Subsutural and peripheral colour bands prominent, columellar colour patch light in tone. Some specimens with a weak colour suffusion on the spire. Based on 9 measured adults.

Anatomy unknown.

Discussion

The lectotype (BMNH 92.1.29.144) is unusual in having a fairly prominent basal protrusion on the lip. One of the paralectotypes has a weak protrusion, while the

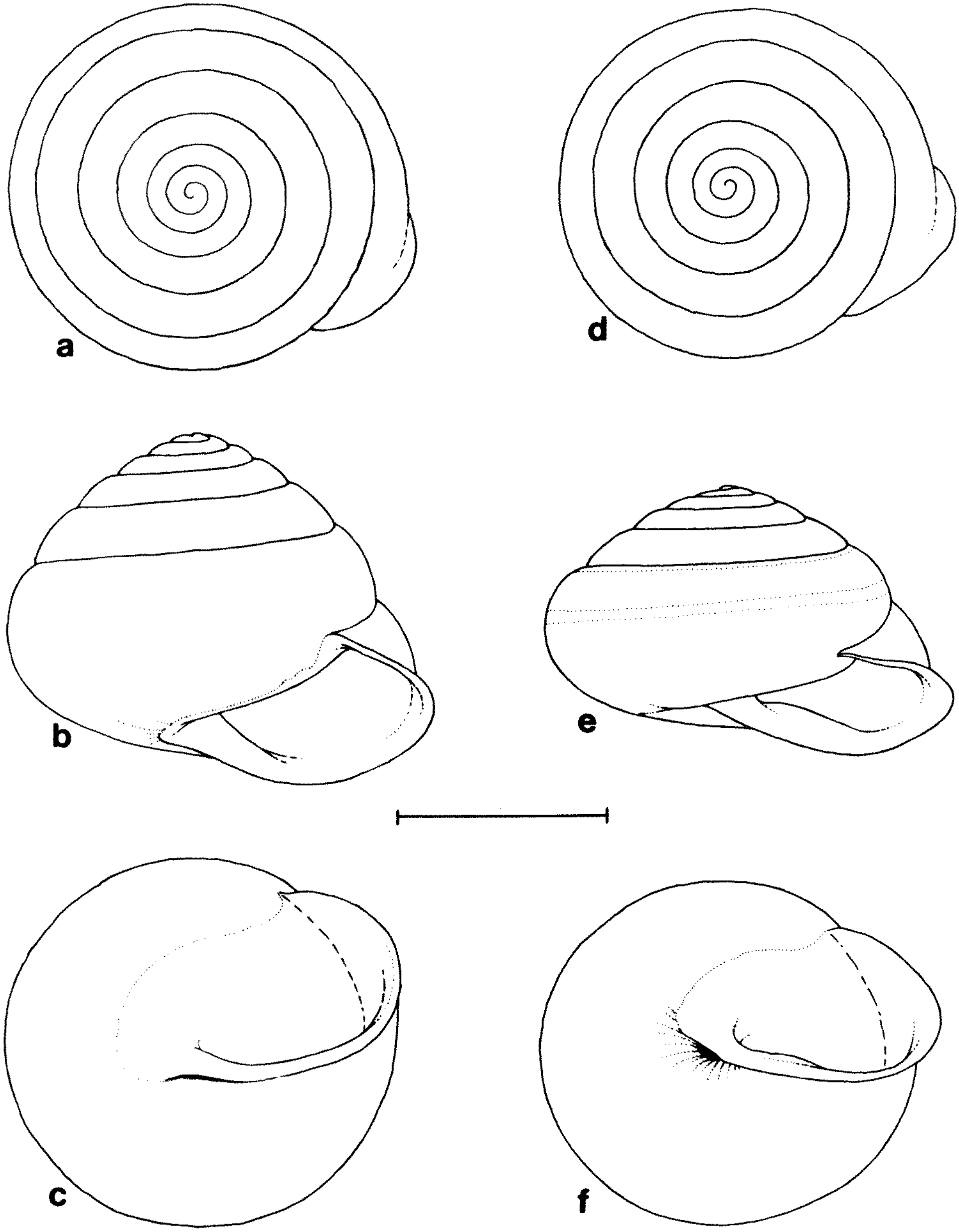


Fig. 70: Shells of *Amplirhagada sykesi* (Smith, 1894) and *A. montalivetensis* (Smith, 1894), a-c) *A. sykesi* (Smith, 1894), Parry Island, Admiralty Gulf, FMNH 200848, topotype; d-f) *A. montalivetensis* (Smith, 1894), Montalivet Island, Montague Sound, AM C.33896, syntype. Scale line equals 10 mm.

others have at most a faint swelling and generally agree with the figured shell **(Fig. 70b)**. All examined shells have the weak lateral crack at the umbilicus **(Fig. 70c)**. Two of the six paralectotypes have a weak colour suffusion on the spire, three lack the suffusion, and the remaining examples are too worn or faded for such suffusion to be detected.

The strong development of the spiral sculpture on the spire and the general lack of a basal protrusion on the lip are the main features separating *Amplirhagada sykesi* (Smith, 1894) from *A. alta* and its various subspecies. Since even smaller conchological differences separate such anatomically diverse taxa as *A. wilsoni* and *A. elevata,* specific separation of *A. sykesi* is maintained despite the lack of anatomical material.

AMPLIRHAGADA MONTALIVETENSIS (SMITH, 1894)

(Figs 70d-f)

Helix (Hadra) montalivetensis Smith, 1894, Proc. Malac. Soc. London, **1:** 91-92, pl. VII, fig. 21—Montalivet Island, Western Australia. Here restricted to West Montalivet Island (14°18′S, 125°13′E).

Amplirhagada montalivetensis (Smith), Iredale, 1938, Australian Zool., **9** (2): 113; Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 66, pl. V, fig. 5.

Comparative remarks

Amplirhagada montalivetensis (Smith, 1894), has a relatively depressed shell **(Fig. 70e,** mean H/D ratio 0.700), slightly open umbilical crack **(Fig. 70f)**, relatively loose whorl coiling pattern **(Fig. 70d)** compared with *A. sykesi* (Smith, 1894) **(Fig. 70a)**, narrow colour bands, a prominent basal lip protrusion, and reduced radial sculpture with the incised spiral lines extending far up the spire. The relatively low whorl count (mean 6) and slight umbilical opening (mean D/U ratio 18.1) immediately separate it from the *A. alta* complex. *A. sykesi* (Smith, 1894) is much more elevated **(Fig. 70b,** mean H/D ratio 0.847), with a higher whorl count (mean 6½ −), the whorls more tightly coiled **(Fig. 70a)**, and generally lacks the basal protrusion, but agrees in sculpture and colour pattern. Species from the Prince Regent River Reserve (*A. wilsoni* and *A. elevata*) and Mitchell Plateau (*A. confusa* and *A. mitchelliana*) agree in general size and colour patterns, but have much more prominent radial sculpture **(Plate 13a-b, Plate 14a-b)**, flatter whorls with shallower sutures **(Fig. 55)**, and closed umbilici. The anatomy of *A. montalivetensis* (Smith, 1894) is unknown.

Lectotype

BMNH 90.12.30.138, Montalivet Island, Montague Sound, Western Australia. Here restricted to West Montalivet Island (14°18′S, 125°13′E). Collected by J.J. Walker. Height of shell 14.0 mm, diameter 21.35, H/D ratio 0.656, whorls 6, umbilical width 1.2 mm, D/U ratio 17.8.

Paralectotypes

BMNH 90.12.30.139-142, AM C.33896, 5 dead adults from the type locality.

Other material studied

North-west Australia (1 dead adult, IRSB).

Diagnosis

Shell 18.65-21.35 mm (mean 20.39 mm) in diameter, with 5 3/8 to 6 1/4 (mean 6) whorls. Apex and spire moderately and evenly elevated **(Fig. 70e)**, sometimes slightly rounded above, height of shell 13.0-14.8 mm (mean 14.27 mm), H/D ratio 0.656-0.726 (mean 0.700). Apical sculpture mostly eroded in available material, with traces of anastomosing radial ridgelets, postapical whorls with very low and irregular radial undulations, plus incised spiral lines that predominate over the radials by the third whorl. Shell periphery weakly angulated to rounded **(Fig. 70e)**. Body whorl descending slightly to moderately behind lip, which is rather strongly flared and has an elongated basal protrusion **(Fig. 70e)**. Columellar lip expanded and reflected to almost cover the umbilicus **(Fig. 70f)**, umbilical width 0.9-1.3 mm (mean 1.14 mm), D/U ratio 15.6-22.1 (mean 18.1). Subsutural and peripheral colour bands wide and prominent, columellar colour patch lighter in tone, but present on lip and around umbilical area. Based on 7 measured adults.

Anatomy unknown.

Discussion

The lectotype (BMNH 90.12.30.138) differs from the figured paralectotype **(Figs 70d-f,** AM C.33896) in having a lower spire and a slight peripheral angulation. Otherwise the material shows very little variation.

The original description does not indicate which of the Montalivet Islands was visited, but since shells from East Montalivet Island are *Amplirhagada alta intermedia,* I am restricting the type locality to West Montalivet Island despite the lack of new collections.

Both *A. sykesi* (Smith, 1894) and *A. montalivetensis* (Smith, 1894) have unusually strong incised spiral lines that extend well up the spire. Only *A. percita* (Iredale, 1939) **(Plate 14f)** has equivalently strong sculpture. They thus provide a great contrast to the smaller, heavily sculptured *A. imitata* (Smith, 1894) **(Plate 12a)** and *A. combeana* (Iredale, 1938) **(Plate 12b)** from the Admiralty Gulf region.

AMPLIRHAGADA IMITATA (SMITH, 1894)

(Plate 12a; Figs 71a-g)

Helix (Hadra) imitata Smith, 1894, Proc. Malac. Soc. London, **1:** 92, pl. VII, fig. 15—Baudin, North Maret (error) and Condillac Islands in the Admiralty Gulf, and Cape Bougainville, north-west Australia.

Amplirhagada imitata (Smith), Iredale, 1938, Australian Zool., **9** (2): 113-114; Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 66, pl. V, fig. 7—type locality restricted to Baudin Island.

Amplirhagada burrowsena Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 68, pl. V, fig. 9—Vansittart Bay, north-west Australia.

Comparative remarks

Amplirhagada imitata (Smith, 1894) is rather variable in size and degree of spire elevation **(Figs 71b, e-g)**, but is immediately recognizable by its sculpture of sharply defined, prominent radial ribs on the spire **(Plate 12a)**, relatively thick, solid shell, normal lack of a basal lip protrusion, and tightly coiled whorls **(Fig. 71a)**. *A. combeana* Iredale, 1938 from Cassini Island is smaller than *A. imitata* (mean diameters 15.05 and 18.92 mm), with a reduced whorl count (means 5½ and 6⅛+, respectively), and has much broader, more irregular radial ribs **(Plate 12b)**. Other heavily sculptured species such as *A. pusilla* **(Plate 12c)** and *A. drysdaleana* **(Plate 12d)** are much thinner shelled, have open umbilici, and much lower spires. No other known *Amplirhagada* have nearly as prominent radial sculpture. The anatomy of *Amplirhagada imitata* (Smith, 1894) is unknown.

Lectotype of *Helix imitata* Smith, 1894

BMNH 90.12.30.61, Baudin Island, Institut Islands, Admiralty Gulf, Western Australia (14°08′S, 125°36′E). Collected by J.J. Walker. Height of shell 14.75 mm, diameter 19.1 mm, H/D ratio 0.772, whorls 6+, umbilicus with a slight lateral crack.

Paralectotypes of *Helix imitata* Smith, 1894

BMNH 90.12.30.62-68, AM C.33894, AM C.64875, 10 dead adults from the type locality; BMNH 91.11.21.113-117, Condillac Island, Institut Islands, Admiralty Gulf (14°06′S, 125°33′E), 5 dead adults; BMNH 92.1.29.162-164, North Maret Island, Bonaparte Archipelago (*ca.* 14°25′S, 124°58′E), 4 dead adults that are *Amplirhagada alta intermedia;* BMNH 91.11.21.105-108, Cape Bougainville (13°54′S, 126°06′E), 4 dead adults.

Holotype of *Amplirhagada burrowsena* Iredale, 1939

AM C.106525, Vansittart Bay, north-west Australia (14°04′S, 126°17′E). Collected by Capt. W. Burrows. Height of shell 15.35 mm, diameter 19.4 mm, H/D ratio 0.791, whorls 6⅛−.

Paratypes of *Amplirhagada burrowsena* Iredale, 1939

AM C.45121, 1 dead adult and 1 dead juvenile from the type locality.

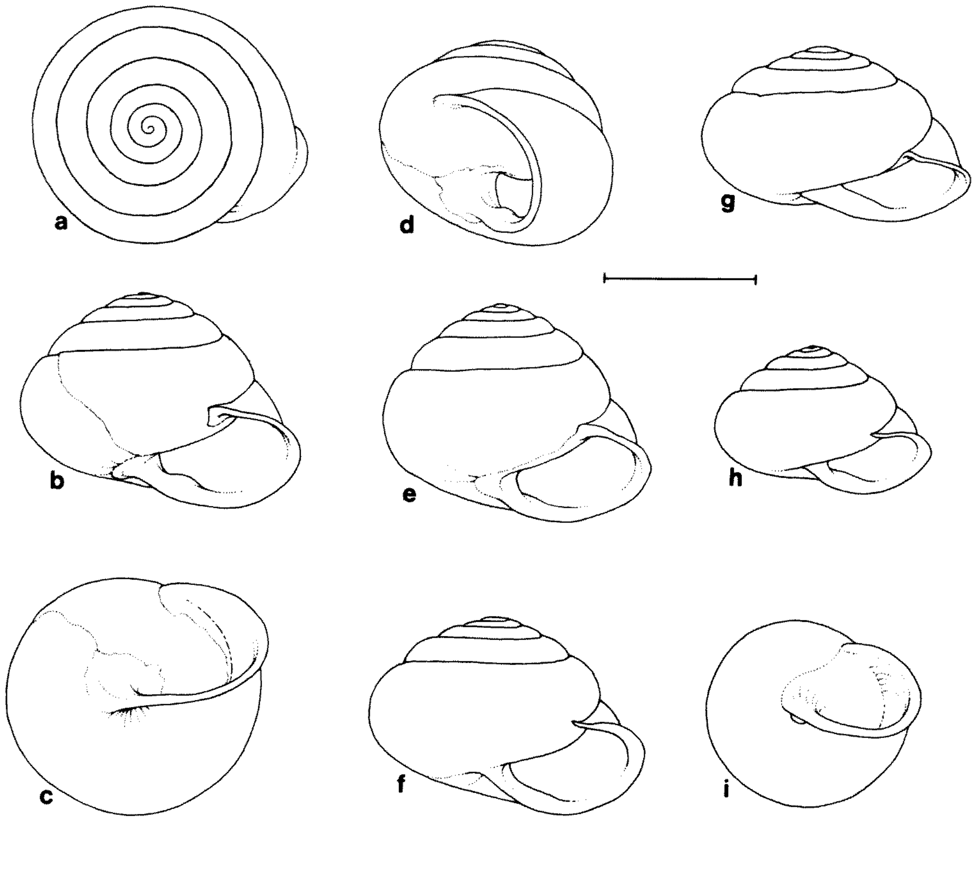


Fig. 71: Shells of *Amplirhagada imitata* (Smith, 1894) and *A. combeana* Iredale, 1938, a-g) *A. imitata* (Smith, 1894) a-d are from Vansittart Bay, AM C.106525, holotype of *A. burrowsena* Iredale, 1939, e is from Condillac Island, Institut Islands, FMNH 200846, f is from Baudin Island, Institut Islands, FMNH 200844, g is from South-west Osborne Island, Admiralty Gulf, FMNH 200845; h-i) *A. combeana* Iredale, 1938, Cassini Island, Institut Islands, FMNH 200825. Scale line equals 10 mm.

Other material studied

Admiralty Gulf: Condillac Island (1 dead adult, BMNH 91.11.21.112, J.J. Walker May 1891; 1 dead adult, WAM 1256.75, Ian Crawford 25 October 1967; 48 dead adults, 20 dead juveniles, WAM 1249.75, FMNH 200846, Fred Wells 15 August 1976); Baudin Island (4 dead adults, FMNH 41588, SMF, IRSB, ex Sowerby and Fulton in early 1900s; 44 dead adults, 15 dead juveniles, WAM 1252.75, FMNH 200844, Fred Wells 15 August 1976); South-west Osborne Island (14°22'S, 125°57'E) (16 dead adults, 11 dead juveniles, WAM 1247.75, FMNH 200845, W.K. Youngson 28 June 1973); Middle Osborne Island (14°19'S, 126°00'E) (1 dead adult, WAM 1246.75, 13 June 1973); about 18 km east of Kuri Bay along water-course (1 dead adult, WAM 1257.75, L.A. Smith 25-26 August 1971).

Diagnosis

Shell 16.2-21.9 mm (mean 18.92 mm) in diameter, with 5 3/8 to 6¾ (mean 6 1/8+) whorls. Apex and spire moderately **(Fig. 71g)** to very strongly **(Figs 71b, e)** elevated, slightly to moderately rounded above, height of shell 11.35-18.6 mm (mean 14.74 mm), H/D ratio 0.616-0.912 (mean 0.767). Apical sculpture typical, postapical whorls **(Plate 12a)** with prominent, sharply defined radial ribs, about 5/mm on mid-spire, reduced below periphery of body whorl. No trace of incised spiral lines visible. Shell periphery weakly angulated **(Fig. 71g)** to rounded **(Fig. 71e)**. Body whorl normally descending rather abruptly behind lip, which is strongly flared, usually completely covers the umbilical chink, and rarely **(Figs 71b, d)** shows a weak to knob-like basal protrusion. Colour bands narrow, reduced in prominence, a faint columellar colour patch developed on fresh specimens, occasionally a weak spire colour suffusion. Based on 139 measured adults.

Anatomy unknown.

Discussion

Amplirhagada imitata (Smith, 1894) has by far the most sharply defined and prominent radial sculpture of any member of the genus. This very striking difference is the rationale for uniting under this name several allopatric populations that have not been dissected. Material from Kuri Bay on Camden Sound; Baudin, Condillac and the Osborne Islands in Admiralty Gulf; Cape Bougainville; and Vansittart Bay all agree in basic size, shape and radial sculpture. It is quite possible that a complex of species is confused under this name, but until dissections can be made, the similarities are far greater than the differences.

The types of *A. burrowsena* Iredale, 1939 are two adults that lack any colour bands and a juvenile that retains traces of both peripheral and subsutural colour bands. The larger adult, designated as holotype **(Figs 71a-d)**, has the sculpture on the spire slightly finer and more crowded than examples from Baudin Island, but the sculpture on the body whorls is essentially identical. The basal lip protrusion in both adults is relatively prominent, but no larger than is found in a paratype from Baudin

Island (AM C.64875) figured by Iredale (1939, **Plate V, Fig. 7**). The descension of the whorl in the holotype of *A. burrowsena* **(Fig. 71d)** is slightly less than average, but falls within the observed range of variation. I have no hesitation in synonymizing this name.

The specimens from Cape Bougainville (BMNH 91.11.21.105-108) are low spired **(Table 33)**, but typical in colour pattern and sculpture.

The specimens from North Maret Island (BMNH 92.1.29.162-164) were misclassified. They belong to *Amplirhagada alta intermedia.*

Variation in allochronic sets from Baudin, Condillac and South-west Osborne Islands is summarized in **Table 33.** There is clear geographic, but not temporal, variation. The South-west Osborne Island shells are much more depressed in shape **(Fig. 71g)**, those from Baudin Island are intermediate in spire elevation **(Fig. 71f)**, and those from Condillac Island have very high spires **(Fig. 71e)**. The high spire of the Condillac population undoubtedly is caused primarily by the 3/8 whorl increase in the mean whorl count **(Table 33)**.

Despite the rather numerous collections of *Amplirhagada imitata* (Smith, 1894) over the years, no preserved material or even obviously live collected examples were seen.

AMPLIRHAGADA COMBEANA IREDALE, 1938

(Plate 12b; Figs 71h-i)

Helix (Hadra) imitata var. *cassiniensis* Smith, 1894, Proc. Malac. Soc. London, **1:** 92, pl. VII, fig. 16– Cassini Island (13°59′S, 125°36′E), north-west Australia (not *Helix millepunctata* var. *cassiniensis* Smith, 1894: 88).

Amplirhagada combeana Iredale, 1938, Australian Zool., **9** (2): 113—new name for *Helix (Hadra) imitata* var. *cassiniensis* Smith (1894: 92), not *Helix (Chloritis) millepunctata* var. *cassiniensis* Smith (1894: 88); Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 67, pl. V, fig. 10.

Comparative remarks

Amplirhagada combeana Iredale, 1938 is a small (mean diameter 15.05), very heavily but irregularly sculptured **(Plate 12b)** relative of the larger (mean diameter 18.92 mm) *A. imitata* (Smith, 1894) with its equally strong but much more sharply defined radial sculpture **(Plate 12a)**. *A. combeana* has the spire less rounded above **(Fig. 71h)** and there is a tendency for the umbilical chink to be slightly open **(Fig. 71i)**. It is the smallest known species of *Amplirhagada* and has by far the strongest radial sculpture. The anatomy of *Amplirhagada combeana* Iredale, 1938 is unknown.

Table 33: Local Variation in *Amplirhagada imitata* (Smith, 1894) and *A. combeana* (Iredale, 1938)

Station	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
A. imitata					
Cape Bougainville	4	14.06 ± 0.213 (13.8-14.7)	18.98 ± 0.230 (18.4-19.55)	0.742 ± 0.012 (0.706-0.754)	5¾ − (5⅝-5¾)
Baudin, all	59	14.30 (12.0-15.9)	18.56 (16.6-20.6)	0.770 (0.685-0.864)	6 + (5⅜-6½)
Baudin, 15-VIII-76	44	14.27 ± 0.136 (12.0-15.9)	18.49 ± 0.117 (16.6-20.15)	0.772 ± 0.007 (0.685-0.864)	6 + (5½-6½)
Baudin, types	8	14.24 ± 0.385 (11.65-15.15)	18.84 ± 0.480 (16.6-21.4)	0.756 ± 0.016 (0.675-0.817)	6 − (5⅜-6¼)
Condillac, all	56	15.82	19.36	0.818	6⅜ −
Condillac, types	6	16.38 ± 0.662 (15.2-18.5)	19.35 ± 0.634 (17.9-21.9)	0.846 ± 0.015 (0.804-0.904)	6⅜- (6-6⅝)
Condillac, 15-VIII-76	48	15.75 ± 0.164 (13.1-18.6)	19.41 ± 0.147 (16.2-21.2)	0.813 ± 0.008 (0.669-0.912)	6⅜ − (5⅞-6¾)
South-west Osborne	16	12.94 ± 0.233 (11.35-14.45)	18.70 ± 0.238 (17.25-20.4)	0.692 ± 0.011 (0.616-0.787)	6⅛ (5⅜-6½)
A. combeana					
types	9	12.28 ± 0.534 (9.9-14.0)	15.46 ± 0.473 (13.3-17.25)	0.792 ± 0.016 (0.706-0.854)	5⅝ (5¼-6⅛)
Cassini, 19-VIII-76	7	12.25 ± 0.370 (11.0-13.7)	16.95 ± 0.270 (15.8-17.65)	0.722 ± 0.013 (0.681-0.781)	5⅝ − (5⅜-5¾)
Cassini, 25-IX-67	90	10.77 ± 0.064 (9.4-12.5)	14.85 ± 0.067 (13.5-16.4)	0.725 ± 0.003 (0.660-0.807)	5½ (5⅛-6)

Lectotype

BMNH 91.11.21.188, Cassini Island, Institut Islands, Admiralty Gulf, Western Australia (13°59′S, 125°36′E). Collected by J.J. Walker. Height of shell 14.0 mm, diameter 16.4 mm, H/D ratio 0.854, whorls 5¾, umbilicus showing a slight lateral crack.

Paralectotypes

BMNH 91.11.21.189-191, BMNH 91.11.21.118-124, AM C.33898, IRSB, 10 dead adults, 2 dead juveniles from the type locality.

Other material studied

Cassini Island (91 dead adults, WAM 1248.75, FMNH 200825, Ian Crawford 25 September 1967; 7 dead adults, 4 fragments, WAM 1250.75, Fred Wells 19 August 1976).

Diagnosis

Shell 13.3-17.65 mm (mean 15.05 mm) in diameter, with 5 ⅛ to 6¼ (mean 5½) whorls. Apex and spire strongly and evenly elevated **(Fig. 71h)**, very slightly rounded above, height of shell 9.4-14.0 mm (mean 11.03 mm), H/D ratio 0.660-0.861 (mean 0.732). Apical sculpture typical, postapical whorls with broad, rounded, coarse, quite promiment radial ribs **(Plate 12b)** that become greatly reduced to absent below the periphery, shell base smooth, except for incised spiral lines. Shell periphery rounded to very weakly angulated. Body whorl abruptly deflected behind lip, which is moderately flared, basal lip occasionally with a protrusion. Umbilicus nearly covered by reflection of lip, but usually a slight lateral crack visible **(Fig. 71i)**. Fresh specimens show typical subsutural and peripheral colour bands, but columellar patch reduced to a faint trace at the parietal-columellar margin, not extending onto reflected lip. Based on 108 measured adults.

Anatomy unknown.

Discussion

Some of the smallest examples of *Amplirhagada combeana* Iredale, 1938 have moderately prominent basal lip protrusions, probably the result of gerontic shell thickening. Recognition of *A. combeana* Iredale, 1938 as a distinct species is based on the differences in quality of spacing of the radial sculpture, greatly reduced size, and more open umbilical crack. This contrasts with the treatment of *Damochlora millepunctata* (Smith, 1894), where the Cassini Island sample is smaller in size, has fewer whorls, a greater H/D ratio, and a narrower umbilicus than does material from Baudin Island (Solem, 1979: Table 9). Although Iredale (1939: 46-47) treated var. *cassiniensis* as a distinct species, the differences are in proportions and relatively minor in extent. I have treated them as local variations, in contrast to the situation in *Amplirhagada,* where the populations on Baudin (*A. imitata*) and Cassini (*A. combeana*) show the qualitative differences outlined above. These conchological differences have correlated with species level differences in anatomical features of other *Amplirhagada.* I have accepted probable species level differentiation despite the lack of anatomical evidence.

Three allochronic populations of *Amplirhagada combeana* Iredale, 1938 are listed in **Table 33**. Although the whorl count is constant, there are noticeable differences in size and proportions. Unfortunately none of the collections were accompanied by detailed notes as to where on Cassini Island the specimens were collected. It is thus impossible to know whether temporal or spatial variation is involved.

AMPLIRHAGADA NOVELTA IREDALE, 1939

(Figs 72a-c)

Amplirhagada novelta Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 67-68, pl. V, fig. 12—Drysdale River, Napier-Broome Bay, north-west Australia.

Comparative remarks

The single known specimen of *Amplirhagada novelta* Iredale, 1939 agrees quite well in size and shape with topotypic material of *A. sykesi* (Smith, 1894) from Parry Island **(Figs 70a-c)**, but has one whorl less at the same diameter and slightly larger nuclear whorls. The presence of a callus over the umbilical region is unique to *A. novelta,* but whether this is a diagnostic feature or resulted from a repaired injury to the shell that lies about one-eighth whorl back is unknown. This injury could have resulted in slightly greater deflection of the body whorl behind the aperture. Without additional material, the status of this taxon will remain unknown.

Holotype

WAM 3994, Napier-Broome Bay, north-west Kimberley, Western Australia. Collector and date of collection unknown. Height of shell 16.8 mm, diameter 21.5 mm, H/D ratio 0.781, whorls 5¾.

Diagnosis

Shell 21.5 mm in diameter, with 5¾ whorls. Apex and spire strongly and evenly elevated, height of shell 16.8 mm, H/D ratio 0.781. Apex and spire worn, only occasional traces of irregular, weak radial ribs remaining, shell base with traces of incised spiral lines. Shell periphery evenly rounded, without trace of angulation. Body whorl starting to descend moderately strongly behind lip, then ceasing to descend for last portion of growth. Lip rather narrowly flared, reflexing to completely cover umbilicus with a callus hiding the lip edge layers. Basal lip without protrusion. A repaired major shell injury one-half whorl behind the aperture and a minor repaired shell injury less than one-eighth whorl behind the aperture may have changed the growth pattern to produce the closed umbilicus and unusual lip descension pattern. Colour pattern absent, except for a vaguely translucent zone marking the location of the supraperipheral colour band, which is very narrow. Based on the holotype and only known specimen.

Anatomy unknown.

Discussion

The holotype of *Amplirhagada novelta* Iredale, 1939 is sufficiently worn that the possibility of its being an aberrant member of the *Rhagada tescorum* (Benson, 1853) complex cannot be excluded. Without further collections, its status will remain uncertain. Certainly detailed comparisons with the *A. sykesi-alta-montalivetensis* complex will be needed.

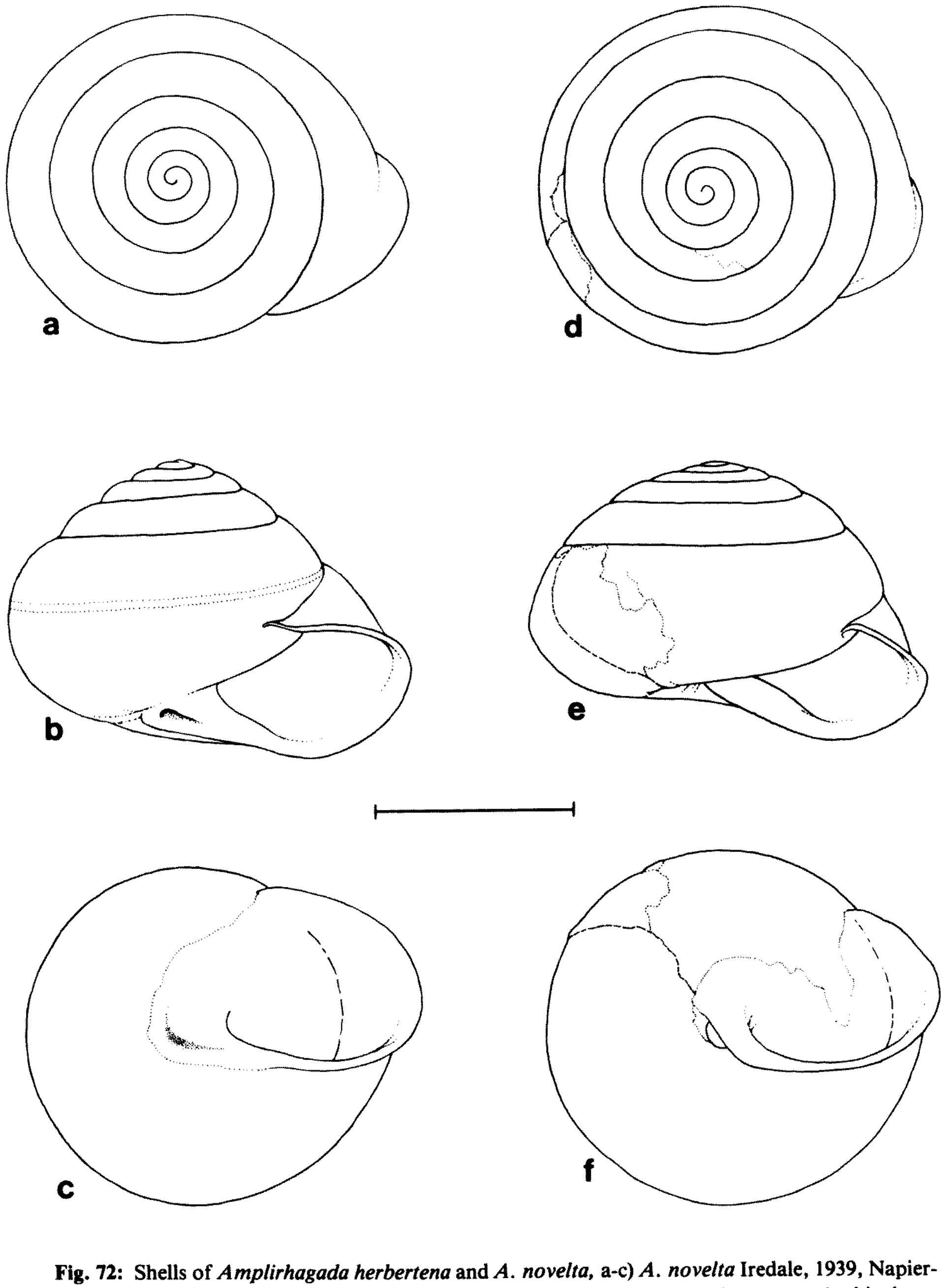


Fig. 72: Shells of *Amplirhagada herbertena* and *A. novelta*, a-c) *A. novelta* Iredale, 1939, Napier-Broome Bay, WAM 39.94, holotype; d-f) *A. herbertena* Iredale, 1939, Buccaneer Archipelago, AM C.42553, holotype. Scale line equals 10 mm.

AMPLIRHAGADA HERBERTENA IREDALE, 1939

(Figs 72d-f)

Amplirhagada herbertena Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 66, pl. V, fig. 6—Buccaneer Archipelago, Western Australia.

Comparative remarks

The single known specimen **(Figs 72d-f)** of *Amplirhagada herbertena* Iredale, 1939 has a series of major (broken line) and minor (dotted line) injuries to the shell that may have significantly altered the growth pattern, especially in regard to the open umbilicus. It has remnants of spiral lines on the spire and base, suggesting possible affinity to *A. sykesi* (Smith, 1894) and *A. montalivetensis* (Smith, 1894), a clearly angled periphery, a narrowly open umbilicus, and a rather high, domed spire **(Fig. 72e)**. It is intermediate in shape between *A. sykesi* and *A. montalivetensis* and differs from both in its open umbilicus. The absence of radial sculpture and the open umbilicus combine to separate it from any form of *A. alta*. *A. elevata* has a less angled periphery, lacks the basal protrusion, and has a higher whorl count. On the basis of its sculpture and shape, it possibly is a valid species.

Holotype

AM C.42553, Buccaneer Archipelago, Western Australia. Collected by H. Basedow. Shell height 15.8 mm, diameter 21.2 mm, H/D ratio 0.745, whorls 6 3/8 +, umbilical width 1.15 mm, D/U ratio 18.4.

Diagnosis

Shell 21.2 mm in diameter, with 6 3/8 + whorls. Apex and spire strongly elevated, dome-shaped, height of shell 15.8 mm, H/D ratio 0.745. Apex and early spire worn, faint traces of radial growth irregularities visible in areas, lower spire and shell base with fine incised spiral lines. Shell periphery noticeably angled, more so after major repaired injury. Body whorl very slightly descending behind lip, which is moderately flared and has a long, prominent basal protrusion. Umbilicus narrowly open, reflected lip only partly covering it, 1.15 mm wide, D/U ratio 18.4. No trace of colour left on shell. Based on 1 adult specimen.

Anatomy unknown.

Discussion

A single worn, badly damaged adult shell normally is inadequate material for description of a species. I would not have described *Amplirhagada herbertena* from the single known specimen, but the differences are, in the context of known variation in other species, possibly indicative of specific level differences. Until collections can be made from many islands of the Buccaneer Archipelago, *A. herbertena* will remain a problematic species, both in terms of validity and geographic location.

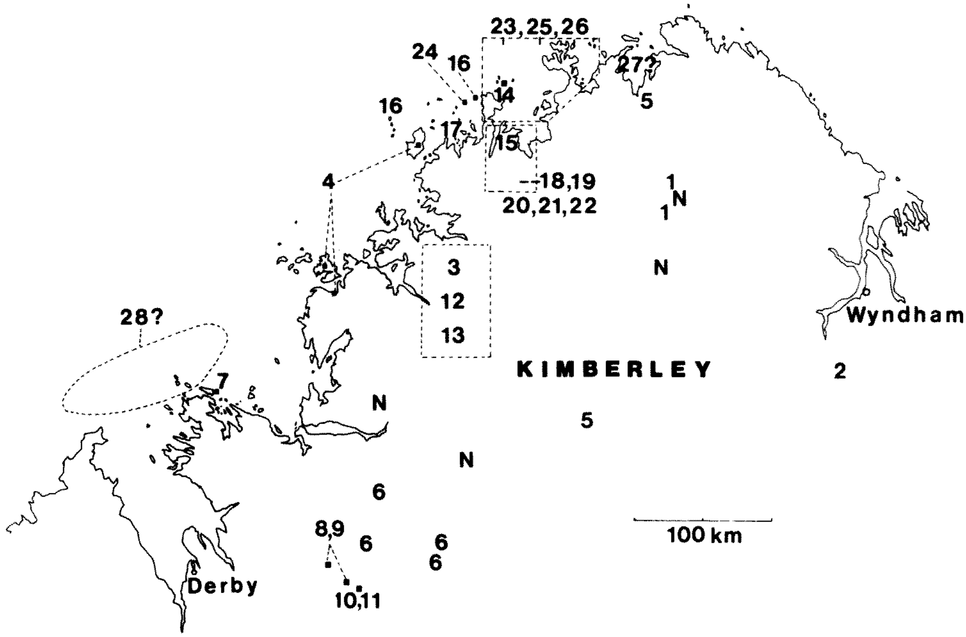


Fig. 73: Distribution of *Amplirhagada;* 1, *drysdaleana;* 2, *questroana;* 3, *pusilla;* 4, *katerana;* 5, *kalumburuana;* 6, *carinata;* 7, *astuta* (Iredale, 1939); 8, *percita* (Iredale, 1939); 9, *napierana;* 10, *b. burnerensis* (Smith, 1894); 11, *b. umbilicata;* 12, *elevata;* 13, *wilsoni;* 14, *alta alta;* 15, *a. crystalla;* 16, *a. intermedia;* 17, *a.* subsp.; 18, *mitchelliana;* 19, *confusa;* 20, *castra;* 21, *v. varia;* 22, *v. depressa;* 23, *sykesi* (Smith, 1894); 24, *montalivetensis* (Smith, 1894); 25, *imitata* (Smith, 1894); 26, *combeana* Iredale, 1938; 27, *novelta* Iredale, 1939; 28, *herbertena* Iredale, 1939. The symbol 'N' indicates localities from which worn shell material that probably represent new species have been seen.

DISTRIBUTION

The 28 taxa mentioned above, plus several sets that are in too poor condition for describing, are found **(Fig. 73)** in the areas and islands along the coast between the Buccaneer Archipelago and Koolan Island on the south to Napier-Broome Bay and Kalumburu in the north. Inland they range from the Napier Range and Harding Range through the King Leopold Ranges, Mt Elizabeth Station, the Drysdale River Reserve and with an apparently isolated occurrence south of Wyndham, (*A. questroana*). The southernmost record to date is for *Amplirhagada burnerensis burnerensis* (Smith, 1894) at about 4.3 km south-south-east of Carpenter Gap, Napier Range (*ca.* 17°29′S, 125°02′E).

No collecting has been done in the area around Walcott Inlet, and the vast inland area between the Drysdale River (see Merrifield, Slack-Smith, and Wilson, 1977) and the west shore of Cambridge Gulf is unsampled. No *Amplirhagada* have been taken in the Ningbing or Weaber Ranges in the far north-east corner of Western Australia. To what extent the genus may be found in the seasonally dry areas of the upper Durack and Chamberlain drainages is unknown. Only scattered and fragmentary collections are available from the Kimbolton area, islands of Yampi Sound, and spot collections from the inland areas between Napier Downs in the Napier Range and Kalumburu Mission. Undoubtedly many more new species remain to be discovered.

With few exceptions, the range of known species is relatively small. The supposed exceptions may result from confusing similar appearing shells that actually are the product of anatomically distinct species. Thus, *A. imitata* (Smith, 1894) has a cited range from Kuri Bay to Cape Bougainville, with intermediate records from Baudin, Condillac, South-west Osborne and Middle Osborne Islands. The Vansittart and Kuri Bay records are based on one or a few worn dead shells, and none of the island populations have been dissected. *A. katerana* is reported from Katers, Bigge and Augustus Islands, plus a single worn adult from east of Kuri Bay. Despite its quite characteristic form, the latter record needs verification by collection and dissection of living animals. The report of *A. kalumburuana* from east of Mt Elizabeth Homestead is based on dead material, and, in view of the intervening *A. drysdaleana,* probably is based on a misidentification. In the absence of new collections, I choose to let the association stand temporarily.

The unquestioned center of known diversity lies in the Montague Sound-Admiralty Gulf area. The following mainland and island species are known only from this region, or with questionable extensions beyond it:

A. varia varia—Mitchell Plateau, mining camp to Walsh Point
A. v. depressa—Mitchell Plateau, Warrender Hill and Crystal Creek area
A. castra—Mitchell Plateau, two areas near Camp Creek
A. confusa—Mitchell Plateau, down to Walsh Point

A. mitchelliana—Camp Creek, Mitchell River Falls and Lawley River to Crystal Creek
A. alta crystalla—Mitchell Plateau, area of Crystal Creek
A. alta alta—Corneille Island
A. alta intermedia—South Maret, East Montalivet Islands
A. alta subsp.—Wollaston Island
A. combeana (Iredale, 1939)—Cassini Island
A. imitata (Smith, 1894)—Baudin, Condillac, North Maret, South-west Osborne, Middle Osborne Islands, Cape Bougainville, east of Kuri Bay
A. sykesi (Smith, 1894)—Parry Island
A. montalivetensis (Smith, 1894)—West (?) Montalivet Island
A. katerana—Katers, Bigge, Augustus Islands, east of Kuri Bay

To the south-west of the Mitchell Plateau-Admiralty Gulf-Montague Sound area lies the Prince Regent drainage, with three overlapping, partly sympatric taxa—*A. pusilla, A. wilsoni,* and *A. elevata.* Additional taxa from Beverly Springs Station are not represented by enough material to warrant naming.

In the Upper Barker River drainage near Mt Hart and just north of the Napier Range, *A. carinata* is found, while in the Napier Range itself there is an interesting complex of taxa. *A. percita* (Iredale, 1939) and *A. napierana* have an interdigitating distribution from near Hawkstone Creek at the north end of the Napier's to the vicinity of Yammera Gap just east of the present Napier Downs Homestead. On the other side of Yammera Gap, *A. burnerensis* (Smith, 1894) replaces them, and in turn is interrupted by *A. b. umbilicata.*

The remaining species are isolated and known from a limited number of colonies. *A. herbertena* Iredale, 1939, from an unnamed island in the Buccaneer Archipelago, *A. astuta* (Iredale, 1939) from Koolan Island, Yampi Sound, *A. novelta* Iredale, 1939, from the Drysdale River at Napier-Broome Bay, *A. drysdaleana* from the Carson River Basin, *A. kalumburuana* from just south of Kalumburu Mission and possibly Mt Elizabeth Homestead, and *A. questroana* near the junction of the Chamberlain and Pentecost Rivers on El Questro Homestead, complete the named taxa.

Several sets of dead shells in the WAM collection unquestionably are *Amplirhagada* and in all probability represent additional undescribed species. Because of limited material, worn condition of the shells, and absence of any preserved soft parts, they are not described. The following few brief notes are intended to stimulate additional collections and to emphasize that only a portion of the extant *Amplirhagada* are known currently. A large shell from Old Doongan Homestead (WAM 167.76) is 15.4 mm high, diameter 22.7 mm, H/D ratio 0.678, with 6 5/8 whorls, umbilical width 1.2 mm, D/U ratio 18.9. Four juveniles are WAM 168.76. The radial ribbing and incised spiral lines are marked and it does not match any of the Mitchell, Drysdale, or Prince Regent shells. Four adults from near Plain

Creek Pool, Beverley Springs Station (WAM 229.75, WAM 231.75) are quite similar to the Doongan shell in sculpture and umbilicus, but are much more depressed and with a lower whorl count. Their measurements are: height 10.7-14.1 mm (mean 12.2 mm), diameter 18.55-21.75 mm (mean 20.02 mm), H/D ratio 0.563-0.648 (mean 0.609), whorls 5½ to 6⅛ (mean 5¾+), umbilical width 0.9-1.35 mm (mean 1.18 mm), D/U ratio 13.7-24.2 (mean 17.6). Another set of fire-blackened shells (WAM 1354.75) from Beverley Springs Station, taken about 5 km from the homestead on the access road to the Gibb River Road, are similar to *A. drysdaleana* and *A. pusilla* in shape and sculpture, but are larger, more elevated, have a higher whorl count and are more narrowly umbilicated. The measurements of 8 adults are: height 11.2-13.0 mm (mean 12.05 mm), diameter 18.5-20.4 mm (mean 19.52 mm), H/D ratio 0.589-0.650 (mean 0.617), whorls 5⅜ to 6 (mean 5¾+), umbilical width 0.9-1.2 mm (mean 1.09 mm), D/U ratio 16.1-21.1 (mean 18.0). A single very worn shell from Station C2-2, valley of creek running north-west into Carson River almost opposite Woorakin Creek (1:100,000 'Ashton' map sheet 4267, grid reference 585:340) (WAM 1353.75) is 14.5 mm high, diameter 20.9 mm, H/D ratio 0.694, whorls 6⅛, umbilical width 0.95 mm, D/U ratio 22.0. The round periphery, very narrow umbilicus and lack of radial sculpture differentiate it from either *A. kalumburuana* or *A. drysdaleana,* the nearest described species in terms of geography.

All of the above samples differ in enough characters from described species to suggest that they represent new taxa. Without additional material and preferably preserved soft parts, I am unwilling to name them.

In view of the many taxa collected in the Montague Sound-Admiralty Gulf area and their generally quite resticted ranges, simple inspection of 1:100,000 maps suggests that such malacologically uncollected islands as Lafontaine, Kingsmill, Fenelon, Descartes, Laplace, Moliere, Racine and Lavoisier in the Admiralty Gulf, the many islands between King Sound and Collier Bay, plus the islands off the far north coast might be expected to yield additional species. Considering also the very fragmentary and spotty collections from inland areas, an eventual doubling or even tripling of known species of *Amplirhagada* is not improbable.

This report is thus a preliminary review of a prolific generic unit.

Because of the considerable intrapopulational variability in shell size and shape, relatively minor shell sculpture and colour variations among species, and the fact that collections from new areas undoubtedly will result in finding new species, I have not attempted to prepare a key for shell identifications. For those taxa whose distributions are allopatric, geographic comparisons of shell and anatomy will be easiest. If preserved animals are available, dissection of the terminal genitalia and observation of the main pilaster at 20X to 50X (compare with **Figs 36-37**), verge size and shape, and microsculpture of the penial chamber walls at medium magnifications will permit ready separation of sympatric taxa. Under each species' 'Comparative remarks' I have attempted to indicate how the shell differs from similar and sympatric taxa, so far as they are covered in this report.

Description of new *Amplirhagada* without reference to the penis chamber structures will be a disservice to science, since this area is used by the snail in species recognition. How can we hope to recognize and name valid species without finding out and illustrating how they do?

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