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

III

TAXA FROM THE NINGBING RANGES AND NEARBY AREAS

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INTRODUCTION

This is the third report on the semi-arid zone dominant land snails of Western and central Australia, which belong to the Camaenidae, *sensu lato*. It reviews 19 species-level taxa in four new genera, *Ningbingia, Turgenitubulus, Cristilabrum* and *Prymnbriareus*. Part I (Solem, 1979) covered the genera with trans-Australian northern distributions (*Hadra* Albers, 1860; *Xanthomelon* von Martens, 1860; *Damochlora* Iredale, 1938; and *Torresitrachia* Iredale, 1939), plus some related *Chloritis*-like genera from eastern Australia. Part II (see above) revised the genus *Amplirhagada* Iredale, 1933, which is restricted to the Kimberley and has undergone extensive complex speciation.

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All specimens from the Ningbing Ranges, 3,217 adults, were collected during two short visits, the first on November 11-12, 1976 (Alan Solem and Carl C. Christensen), the second between May 16-19, 1977 (Alan Solem and Laurel E. Keller). At the time of the initial visit, we did not know if this area was indicative of east Kimberley species diversity or represented an unusual situation. The extent of both generic and specific diversity could not be recognized, since the shell structure is rather uniform. Our objective was to sample as widely as possible, so we moved onto other east Kimberley areas, which proved mostly to be dramatically less productive of land snails. Preliminary dissections in Perth early in 1977 revealed some of the diversity and a return visit during May was programmed. Unfortunately, vehicle problems on the trip up from Perth and time commitments in central Australia combined to prevent my spending more time in the Ningbings. The emphasis during the second visit had to be on: 1) obtaining live specimens from populations represented only by dead shells in the November collections; 2) sampling the previously unvisited northernmost areas of the range; 3) only then filling in a few of the wide sampling gaps. Track conditions were still bad, with the landrover getting bogged on occasion, and off-road exploration had to be limited.

Since collections are available only for November (late dry) and May (early dry season), little information can be presented on seasonality of reproduction. Where both November and May specimens were available for the same species (see discussion of *Turgenitubulus christenseni* and *Cristilabrum primum*), the sequence of development and seasonal status of organs agrees exactly with that demonstrated for *Xanthomelon* (Solem, 1979) and *Amplirhagada* (see above). Because collecting in the Ningbings has been far less intensive than that reported for the Napier Range, much less data can be offered on intra-specific variation, both in shell and genital features. The data available for *Ningbingia bulla*, for example, suggest that variation will be quite extensive, but this remains to be documented. The fact that the Napier Range is, for the most part, a continuous limestone ridge broken only occasionally by gaps, whereas the Ningbing Ranges are a series of isolated limestone islands, undoubtedly has major effects on the patterns of local distribution and variation. Isolation among the Ningbing peaks is enforced by both the annual wet season flooding and the late dry season burning. Evidence for at least an occasional flood level of 7.5 m above the plain exists. A cluster of long-dead freshwater viviparids, *Notopala essingtonensis* (Frauenfeldt, 1862), were collected from a dirt filled pocket this far above the plain at Station WA-226 (FMNH 199640). The grassy areas on the alluvial plains and in the shallow creek ravines that lie between the peaks receive now essentially annual burning in the late dry season. Prior to pastoral use, burning at irregular, but longer, intervals from natural fires would have been part of the normal ecology. Between the annual wet season flash floods and dry season fires, effective isolation exists between populations in different hills in normal years. The presumably rare catastrophic floods that inundate the entire countryside to a significant depth (and stranded the *Notopala*) would provide a rare mechanism for sporadic 'inter-island' transport. This could be particularly effective since all of the Ningbing species collected so far are 'free-sealers', that is, they lie loose in the soil during aestivation and are not sealed to an object. The actual position of the calcified epiphragm varies slightly within the aperture. The epiphragm is secreted in front of the basal lip ridge when the latter is present, up to one-third whorl posteriorly when there is no basal lip ridge.

Three genera, *Ningbingia, Turgenitubulus*, and *Cristilabrum*, are described from the Ningbing Ranges proper. They are extraordinarily similar in terms of shell morphology and patterns of variation, but differ dramatically in the genital structures. A fourth genus, *Prymnbriareus,* from El Questro Station, south-west of Wyndham, is described at the same time because of similarities in genital structure to the above taxa, although it differs rather sharply in shell features.

The Ningbing taxa are unique among currently named Australian camaenids in their development of prominent peripheral sulci on the body whorl **(Figs 78d, 88a, 89d, 98a, 99a, d)** and in many species having a high basal lip ridge that is marked externally by a deep sinus on the last part of the body whorl **(Figs 88c, f, 89c, f, 90c, f, 98c, f, 99c, f)**. To a limited degree, some of the central Australian *Semotrachia* (Solem, unpublished) have an approximation of the lip ridge, but they lack both the basal sinus and the peripheral sulcus. Only in some of the Chinese (*Traumatophora* Ancey, 1887, *Stegodera* von Martens, 1876, and *Moellendorffia* Ancey, 1887) and New World (*Pleurodonte* Fischer von Waldheim, 1807, and *Labyrinthus* Beck, 1837) camaenids are equivalent shell features a normal part of the morphology.

Detailed comparisons of the Ningbing genera's anatomy with extra-limital taxa must be deferred until after several additional genera are reviewed. Because of the many currently unanswerable questions concerning variations and distributional limits among Ningbing species and genera, discussions are abbreviated. The Ningbing radiation represents the single greatest and most interesting area of camaenid diversity discovered so far in Australia. It deserves extensive further field investigations.

Not the least of the intriguing aspects to the Ningbing region is that paralleling the limestone Ningbing Ranges on the east is a series of elevated sandstone ridges which appear to be basically snail-free, as are the extensive sandstone ranges to the south and south-west. The Weaber Rangers to the south-east contain scattered populations of *Torresitrachia weaberana* Solem (1979: 85) from Stations WA-238-9 **(Fig. 110)**. The genus *Torresitrachia* has been taken much further west at Kalumburu and on the Mitchell Plateau. It reaches the Napier Range to the south-west, but has not yet been taken in the Ningbing Ranges.

LIST OF THE TAXA

SYSTEMATIC REVIEW

The three new genera found in the Ningbing Ranges, *Ningbingia, Turgenitubulus,* and *Cristilabrum*, show gross differences in their terminal genitalia. In external view of the whole genitalia, *Turgenitubulus* **(Figs 91-96)** is immediately recognizable by its enormously swollen vas deferens, great elongation of the free oviduct, and positional shifting of the still short spermathecal head down from its normal position at the base of the prostate and uterus. No other dissected camaenid shows an equivalent alteration of the vas deferens. Its functional significance is unknown. Shortly before reaching the peni-oviducal angle, the vas deferens returns to normal diameter and enters the penis sheath just above its base. The penis of *Turgenitubulus* is usually very short, normally has a prominent apical plug, and typically a conical to finger-like verge.

Ningbingia **(Figs 79-87)** and *Cristilabrum* **(Figs 101-106)** both have normal sized vas deferens, shorter free oviducts, and normal positioning of the spermathecal head. In both genera the penis sheath usually is quite long, at least equalling the length of the terminal female system, whereas in *Turgenitubulus* it is distinctly shorter. Species of *Ningbingia* have the vas deferens entering the penis sheath at or above the mid-point of its length, while in all *Cristilabrum* species, except *C. bilarnium* **(Fig. 106b)**, the vas deferens enters the penis sheath basally. In *C.*

bilarnium, which is from an unnamed quite isolated set of limestone ridges **(Fig. 110)**, and whose entire genital system is somewhat unusual, the vas deferens enters the penis sheath slightly below its mid-point. Internally, differences in penis structure are gross. In *Ningbingia* and *Turgenitubulus*, there is an apical plug of varying length, but the latter has a verge **(Fig. 92b)** that is absent in the former. Below the apical plug in *Ningbingia*, there are two or at most three raised stimulatory pilasters that for at least a portion of their length (compare **Figs 79b, 80b, 81b, 82b, c, 83b, 84b, 86, 87b**) have expanded areas ornamented with partially hardened micro-ridges arranged in patterns that are species specific **(Figs 109a-e)**. The penis itself may be equal in length to the sheath **(Fig. 84b)** or considerably more than twice its length **(Figs 83b, 87b)**. The vaginal region is of only moderate length, with its upper section and the spermathecal base moderately swollen. In *Cristilabrum*, both penis and vagina are extremely long, unornamented longitudinal pilasters line the penis cavity, and there normally are stimulatory papillae (PD) flanking the vas deferens opening (DP). None of these pilasters show signs of accessory ridging. Only in the rather modified *C. bilarnium* **(Fig. 106b)** is there significant pilaster enlargement.

Prymnbriareus from the Nimberline Hills on El Questro Station, south-west of Wyndham, agrees with *Cristilabrum* in having a long penis and vagina, and has a single penial stimulator **(Fig. 108b**, PD), but also possesses three elevated stimulatory ridges that are in structure quite comparable **(Fig. 109f)** to those found in *Ningbingia. Prymnbriareus* differs significantly from the Ningbing genera sculpture **(Plate 18d-f)**. Pustuled radial ribbing is present on the spire and body whorl, while *Turgenitubulus* **(Plate 16)** and *Cristilabrum* **(Plates 17a-f, 18a-c)** have prominent radial ribs. In shape and form **(Figs 107a-c)** *Prymnbriareus* resembles more closely some of the chloritid genera in shape, the very narrow lip expansion, and lack of any basal lip ridge.

Whether the above radiation represents monophyletic endemics or is the result of separate colonizations cannot be determined at present. The exact distributional breaks between genera are not precisely known **(Fig. 110)**, although the fieldwork needed to determine this can be undertaken easily. In all probability there will be some distributional overlap between genera. In all three genera, species-level 'same rock sympatry' is known. *Ningbingia octava* and *N. laurina* from Station WA-434, *Turgenitubulus opiranus* and *T. depressus* from Station WA-227, and *Cristilabrum simplex* and *C. buryillum* from Station WA-235 are three species pairs, each found sheltering under the same rock or in the same litter pocket. Two of these pairs have been dissected. In each case, the genitalia has been markedly altered in length and internal structure, presumably to aid in species recognition. *Ningbingia laurina* **(Fig. 84b)** has the penis almost equal in length to the sheath, while the sympatric *N. octava* **(Fig. 83b)** retains the normal very long penis of the genus, if it indeed is not actually lengthened. In *N. laurina*, the penis is much thicker than usual, the apical plug is very large, and the pilaster sculpture **(Fig. 109c)** extends essentially the entire length of the pilasters. In *N. octava*, the penis is dramatically thinner, with the area of pilaster sculpture **(Figs 82c, 109b)** restricted to an extremely short section of the pilasters. The basic condition in *N. octava* also holds at the sampling station located slightly further north, Station WA-426, where it occurs without *N. laurina.*

The situation in *Turgenitubulus* is roughly comparable, in that both sympatric species show modification from the normal pattern in the genus. In *T. depressus* **(Fig. 94b)**, the penis is greatly elongated, with some corresponding elongation of the vagina, the apical plug is essentially absent, and the verge is more clearly finger-shaped than in most species. In *T. opiranus*, the penis and vagina remain short, the apical plug **(Fig. 93b)** is quite large, and there is an unusual circular ridge surrounding the verge which is drastically shortened and broadened. I suspect that an equivalent set of differences will be found between *Cristilabrum buryillum* and *C. simplex*, when the former can be dissected. *C. simplex* **(Figs 102a-b)** has by far the longest penis in the genus and what seems to be an altered penial stimulator tip.

I predict that further investigation of the patterns of genital changes among Ningbing taxa will yield vital information concerning the basic patterns of speciation within the Australian camaenids and quite possibly on the actual mechanism of speciation in this family.

GENUS *NINGBINGIA* NEW GENUS

Diagnosis

Shell of average size, spire strongly elevated, usually evenly rounded above, but sometimes **(Fig. 76e)** dome-shaped. Umbilicus narrowly to moderately open, generally regularly decoiling, partly closed by reflection of columellar lip. Apical sculpture **(Plates 15a-f)** of radially elongated pustulations initially, tending to become irregular to anastomosing radial riblets on later portions. Postapical sculpture of at most irregular radial growth wrinkles, generally macroscopically smooth. Shell base smooth or faint radial growth wrinkles. Body whorl only slightly deflected behind lip, which is moderately **(Fig. 77d)** to strongly **(Fig. 77a)** flared and expanded on palatal wall, basally reflected to partly cover umbilicus. Shell periphery rounded **(Figs 76b, d)** to angulated **(Fig. 77e)**, with (*N. octava, N. res*) or without (*N. bulla, N. laurina, N. australis*) a peripheral sulcus behind the lip that may extend up to one-half whorl apically. Basal lip with a high, deeply recessed ridge in *N. res* **(Figs 78b, d)**, which is absent in the other species. Parietal callus thin. Shell colour basically shiny light yellow horn, expanded lip and often shell base white. No colour bands or zones. Genitalia seasonally variable. Ovotestis (G) shrunken in early dry season **(Figs 81a, 82a, 84a)**, swollen near start of wet season **(Figs 85a, 87a)**, typical in structure. Hermaphroditic duct (GD) narrow and nearly unkinked early in dry season **(Figs 80a, 81a, 82a, 84a)**, varying from the same **(Fig. 87a)** to swollen and strongly kinked **(Fig. 83a)** near start of wet season. Talon (GT), albumen gland (GG), prostate (DG), and uterus (UT) without unusual features. Spermatheca (S) very short, head normally **(Fig. 83a)** bound to prostate-uterus just above free

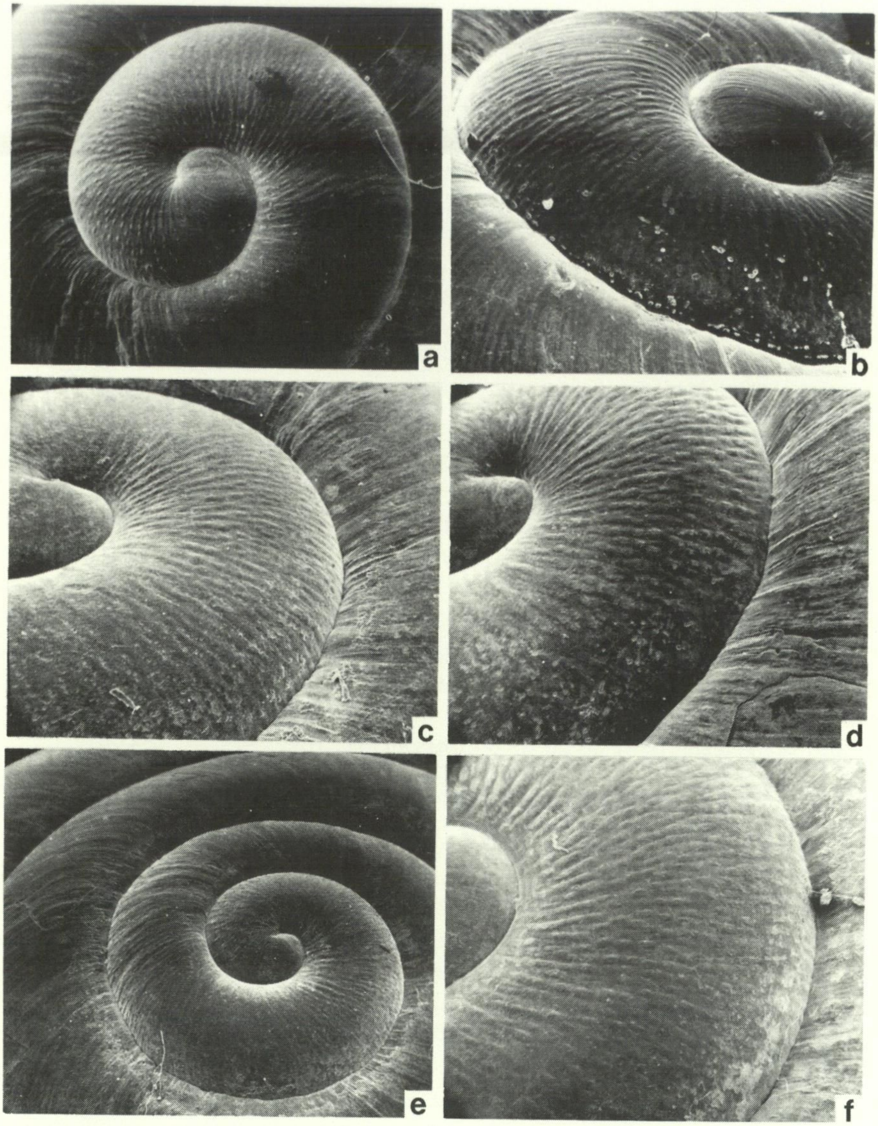


Plate 15: Shell sculpture in *Ningbingia*: (a) *N. bulla*, FMNH 199639, Dissection A, Sta. WA-427, near Knob Peak, Ningbing Ranges, apex and early spire at 11.2X; (b) *N. bulla*, FMNH 199022, Sta. WA-428, near Knob Peak, Ningbing Ranges, apex and early spire at 35.0X; (c) *N. octava*, FMNH 199635, Dissection A, Sta. WA-434, south of No. 8 Bore, Ningbing Ranges, portion of apex and early spire at 36.3X; (d) *N. laurina*, FMNH 200779, Dissection A, Sta. WA-434, south of No. 8 Bore, Ningbing Ranges, portion of apex and early spire at 37.8X; (e) *N. res*, FMNH 199571, Dissection A, Sta. WA-230, 7 km north of Tanmurra Creek, Ningbing Ranges, apex and early spire at 15.4X; (f) *N. australis*, FMNH 199054, Dissection A, Sta. WA-231, 3.5 km north of Tanmurra Creek, Ningbing Ranges, apex and early spire at 32.2X.

oviduct (UV) and vas deferens (VD) origin, internally **(Fig. 80c)** with at most weak longitudinal folds. Base of spermatheca and vagina (V) with corrugated longitudinal ridges **(Fig. 80c)**. Combined spermathecal base and vagina frequently **(Figs 80a, 84a, 85a, 87a)** greatly swollen, vagina generally short, noticeably longer in *N. octava* **(Figs 82a, 83a)** and *N. australis* **(Fig. 87a)**. Penis complex with a thin **(Fig. 86)** to moderately thick walled **(Fig. 82b)** sheath starting just above atrium and extending to insertion of penial retractor muscle (PR) onto the vas deferens. Vas deferens (VD) a slender tube for its entire length, passing through sheath at or above midpoint, reflexing down from insertion of penial retractor either as a thin tube **(Fig. 82b)** or through a small **(Fig. 81a)** to large **(Figs 80b, 84b, 86b)** apical plug in the penis. No epiphallus or caeca on male system. Penis variable in shape and length, ranging from essentially equal in length to the sheath **(Fig. 79a)** to more than twice the sheath length **(Figs 83b, 87b)**. No verge, but several species (*N. bulla, N. laurina, N. res*) with a thick apical plug **(Fig. 84b)** through which the vas deferens passes. In *N. australis* and *N. octava*, which have long, slender penes, apical plug absent **(Figs 82b, 87b)**, and it is reduced in some *N. bulla* **(Fig. 79b)**. Upper portion of penis interior with few (*N. octava*, **Fig. 82b**, *N. australis*, **Fig. 87b**) to many (*N. bulla*, **Fig. 79a**) simple longitudinal pilasters, corrugated longitudinal pilasters (*N. laurina*, **Fig. 84b**), or narrow circular ridges (*N. res*, **Fig. 86**, *N. australis*, **Fig. 87b**). All species agree in having two very high pilasters extending from plug to atrium (shortened in *N. bulla*), that have a portion of their length with corrugated upper edges. The corrugated section can be very short (*N. octava*, **Fig. 82c**), very long (*N. res*, **Fig. 86**, *N. laurina*, **Fig. 84b**, *N. australis*, **Fig. 87b**), or intermediate (*N. bulla*, **Figs 79b, 80b, 81b**), and differ greatly in detail of sculpture **(Fig. 109)**.

Type species: *Ningbingia bulla* sp. nov.

Comparisons

Ningbingia is very similar in shell structure to *Turgenitubulus* and *Cristilabrum*, differing primarily by its absence of postapical radial sculpture and, except for *N. res*, in lacking the basal lip protrusion seen in most species of these genera. *Cristilabrum simplex* **(Fig. 97e)** comes closest to matching the shell of *Ningbingia*, but has prominent radial ribbing on the body whorl. *Prymnbriareus* is somewhat similar in size, shape and aperture **(Table 39, Figs 107a-c)**, but differs in its pustulose postapical sculpture **(Plate 18d-f)**. The lack of colour zones and either incised spiral or radial ribbing sculpture easily separate specimens of *Ningbingia* from both *Torresitrachia* and *Amplirhagada*. The latter genus normally has a much narrower or closed umbilicus.

The main features characterizing *Ningbingia* are in the genitalia. The entrance of the vas deferens is at or above the midpoint of the sheath; there are no penial stimulators (PD) by the entrance of the vas deferens into the penis (DP); the two elevated pilasters have at least a short section of corrugated ridging **(Figs 109a-e)**; and the typical position of the short spermatheca combine to separate it from the other Ningbing area genera. *Xanthomelon obliquirugosa* (Solem, 1979, **Figs 11a-d)** has a short penis sheath with apical coiling of the penis, which totally lacks internal wall sculpture. Otherwise it is very similar in genital anatomy, although conchologically (Solem, 1979, Figs 2a-b, Plate 1a) immediately separable from any other Ningbing species by its globose shell with obliquely anastomosing sculpture and high H/D ratios (0.846-1.052). *Turgenitubulus* **(Figs 91-96)** is immediately recognizable by its enormously swollen vas deferens accompanied by elongation of the free oviduct and removal of the spermathecal head from its position by the prostate-uterus base. The penis sheath is greatly reduced in relative size, has near basal entrance of the vas deferens through the penis sheath, and the penis has an apical verge. *Cristilabrum* **(Figs 101-106)**, except for *C. bilarnium* **(Figs 106a-b)**, presents a uniform appearance of basal entrance of the vas deferens through the penis sheath, a long slender, folded penis that internally has simple longitudinal pilasters, and usually has prominent penial stimulators (PD) by the vas opening (DP). *Cristilabrum bilarnium* is somewhat aberrant in structure, having a short penis that internally is very similar to that of *Turgenitubulus* and has a mid-penis sheath entrance of the vas deferens equivalent to that seen in *Ningbingia*, but lacks the vas deferens specialization of *Turgenitubulus* and conchologically is nearer to *Cristilabrum. Prymnbriareus* **(Fig. 108)** has a long penial stimulator near the vas deferens opening, three raised pilasters with peculiarly corrugated edges **(Fig. 109f)**, mid-area entrance of the vas deferens into the penial sheath, and a very long vagina with comparatively minor swelling of the spermathecal base.

Perhaps the most unusual feature of the genital system in *Ningbingia* is the 'corrugated section' on the two main pilasters. At the low magnification used in the general penis chamber illustrations, these corrugated areas look quite similar in structure, with the obvious exception of *N. octava* **(Figs 82c, 83b)**. Closer inspection shows that they are sculptured in a quite diverse manner **(Figs 109a-e)**. The raised micro-areas on the pilaster have an obviously harder consistency, although not as clearly chitonized as some of the structures found in *Torresitrachia* (Solem, 1979: Fig. 16a), and are in the form of varying shaped ridgelets, rather than simple elevated points. The pattern of these ridgelets is distinctive for each species. In *N. bulla* **(Fig. 109a)** which has only a short elevated section of each pilaster, the ridgelets tend to be most prominent near the upper edge and on the outer side of the pilaster. Both pilasters are extensively interrupted by folds and partial breaks. In *N. laurina* **(Fig. 109c)**, the ridgelets are far narrower, more numerous, restricted to the outer side of each pilaster, and tend to blend into the low corrugated wall pilasters that eventually extend longitudinally **(Fig. 84b)**. In the sympatric *N. octava* **(Fig. 109b)**, in which the corrugated area is restricted to a very small section of the pilaster **(Figs 82b-c, 83b)**, the individual ridgelets are short, relatively wide, vertical, and end in a blunt point. *Ningbingia res* **(Fig. 109d)** is unusual in that relatively large ridgelets are present on both sides of both pilasters, in the lower section of the penis chamber there is a single row of pustulated points in the gutter between the two main pilasters (see centre bottom of **Fig. 109d**), and the ridgelets continue onto the chamber walls in spiral fashion **(Fig. 86)**. *Ningbingia australis* **(Fig. 109e)** has a very

Table 34: Structural Variations in *Ningbingia*

Species	SHELL: Peripheral Sulcus	Basal Lip Ridge	PENIS STRUCTURES: Penis much Longer than Sheath	Lower Sheath Wall Thick	Apical Plug	Corrugated Ridge Area	Penis Chamber Wall Sculpture
N. bulla	−	−	−	+	+	short	long, simple
N. octava	+(−)	−	+	+	−	very short	long, simple
N. laurina	−	−	−	+ −	+	long	long, corrugated
N. res	+	+	+	−	+	very long	spiral
N. australis	−	−	+	−	−	very long	spiral

high and slender pilaster, smooth on the inside, with interrupted partially anastomosing ridgelets that carry onto the wall in at least the upper portion of the penis chamber **(Fig. 109e)**. All dissected individuals of each species were checked for the above features and found to be consistent with the illustrated pattern for that species.

The combination of slightly hardened raised ridgelets on the stimulatory pilasters and the microscopic differences in penis chamber wall corrugations are comparable

Table 35: Range of Variation in *Ningbingia* and *Turgenitubulus*

Taxon	Number of Adults Measured	Mean and Range of: Shell Height	Shell Diameter	H/D Ratio
N. bulla	364	11.35 (9.2-13.5)	17.96 (14.6-21.3)	0.615 (0.508-0.815)
N. octava	294	11.44 (9.6-13.4)	15.82 (14.1-18.8)	0.724 (0.633-0.844)
N. laurina	19	11.70 (10.8-13.8)	17.52 (16.5-18.7)	0.667 (0.617-0.738)
N. res	170	12.80 (10.9-16.6)	19.48 (17.8-21.5)	0.657 (0.567-0.860)
N. australis	128	11.61 (9.9-13.6)	17.96 (15.6-19.1)	0.647 (0.558-0.741)
T. christenseni	335	9.83 (8.0-11.4)	16.13 (14.3-18.0)	0.591 (0.493-0.725)
T. opiranus	111	9.32 (6.4-11.05)	16.19 (13.3-17.8)	0.576 (0.476-0.656)
T. depressus	189	7.29 (6.5-8.6)	14.27 (12.9-16.6)	0.511 (0.453-0.596)
T. foramenus	221	9.62 (8.3-11.5)	16.28 (14.6-18.4)	0.593 (0.503-0.688)
T. costus	77	8.93 (8.2-10.5)	15.22 (14.2-16.5)	0.587 (0.531-0.659)

Table 35: Range of Variation in *Ningbingia* and *Turgenitubulus* (continued)

Taxon	Number of Adults Measured	Mean and Range of: Whorls	Umbilical Width	D/U Ratio
N. bulla	364	5 1/8 + (4 7/8-6 1/4)	3.11 (2.2-4.5)	5.86 (4.16-8.55)
N. octava	294	6 1/8 (5-6 7/8)	1.70 (1.0-2.8)	9.60 (6.67-16.7)
N. laurina	19	5 (4 3/4-5 1/8)	2.07 (1.6-2.8)	8.64 (5.96-10.4)
N. res	170	5 3/8 (5-5 3/4)	3.29 (1.9-4.3)	6.04 (4.78-12.0)
N. australis	128	5 1/4 (4 7/8-5 3/4)	3.07 (1.4-4.2)	5.94 (4.41-12.9)
T. christenseni	335	5 3/8 − (4 1/2-6 1/8)	1.64 (0.6-2.6)	10.30 (5.98-24.6)
T. opiranus	111	5 3/8 − (5-5 3/4)	1.68 (0.8-2.4)	10.51 (7.02-14.4)
T. depressus	189	5 1/4 (5-5 5/8)	1.86 (1.1-2.6)	7.93 (5.11-11.8)
T. foramenus	221	5 3/8 (4 7/8-5 7/8)	1.78 (1.0-2.6)	9.41 (6.10-16.5)
T. costus	77	5 1/8 (4 5/8-5 5/8)	1.78 (1.1-2.4)	8.77 (6.54-13.0)

in their effect to the main pilaster micro-points found in *Amplirhagada* **(Figs 36, 37)**, and the relatively simple raised triangular projections seen in *Torresitrachia* (Solem, 1979: Figs 12b, 14a, b, 16a-c, 17b). All would function effectively in species recognition by the snails.

The species of *Ningbingia* thus show contrasting character states in several shell and penis features **(Table 34)**. This chart simplifies the presentation for ease of contrast. The presence or absence of a character cannot be assumed to be monophyletic. Since many hills within the range of *Ningbingia* have not been sampled yet, no formal key is presented. Dissection of the terminal genitalia (including opening of the penis chamber) is required for certain identification, although comparison of mean shell measurements with summed variation limits **(Table 35)** and inspection of the outline drawings of holotypes **(Figs 74-78)** should enable deciding if material represents a known species, or is yet another new species.

Size and shape variation is summarized in **Table 35**. Overlap among species is sufficient that measurements alone from isolated specimens or small samples would be inadequate for identification. In particular, the shells of *N. bulla* and *N. australis* are very similar in most measurements. Since the variation among populations of the

Table 36: Local Variation in *Ningbingia*

Taxon	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
N. bulla				
WA-427, FMNH 199048	97 (D)	10.84 ± 0.076 (9.6-12.9)	17.45 ± 0.091 (14.6-19.4)	0.621 ± 0.004 (0.545-0.735)
WA-428, FMNH 199022	155 (D)	11.47 ± 0.068 (9.2-12.4)	17.81 ± 0.057 (16.0-19.9)	0.602 ± 0.003 (0.508-0.717)
WA-429, FMNH 199054	42 (D)	11.86 ± 0.090 (10.0-12.8)	18.78 ± 0.096 (17.5-20.3)	0.632 ± 0.004 (0.562-0.697)
WA-430, FMNH 199042	19 (D)	11.32 ± 0.102 (10.6-12.1)	18.34 ± 0.256 (14.6-19.6)	0.620 ± 0.011 (0.586-0.815)
WA-431, FMNH 199041	30 (D)	12.05 ± 0.096 (11.2-13.5)	18.75 ± 0.163 (17.7-21.3)	0.643 ± 0.004 (0.601-0.687)
N. octava				
WA-426, FMNH 199633	71 (L)	11.14 ± 0.057 (9.9-12.4)	15.29 ± 0.059 (14.1-16.6)	0.729 ± 0.004 (0.665-0.800)
WA-426, FMNH 199028	122 (D)	11.22 ± 0.052 (9.6-12.6)	15.82 ± 0.046 (14.4-17.3)	0.709 ± 0.003 (0.639-0.788)
WA-434, FMNH 199635	17 (L)	12.31 ± 0.132 (11.2-13.0)	15.96 ± 0.120 (15.2-16.9)	0.772 ± 0.010 (0.707-0.844)
WA-424, FMNH 199032	84 (D)	11.84 ± 0.069 (10.2-13.4)	16.23 ± 0.062 (15.1-18.8)	0.730 + 0.004 (0.633-0.843)
N. laurina,				
WA-434, FMNH 199051	16 (D)	11.75 ± 0.212 (10.8-13.8)	17.56 ± 0.134 (16.6-18.7)	0.669 ± 0.010 (0.617-0.738)
N. res				
WA-230, FMNH 199957	19 (L)	12.74 ± 0.165 (11.7-14.3)	19.32 ± 0.140 (18.5-20.9)	0.660 ± 0.008 (0.602-0.726)
WA-230, FMNH 199008	42 (D)	13.28 ± 0.147 (11.5-16.6)	19.82 ± 0.103 (17.9-21.5)	0.671 ± 0.008 (0.572-0.860)
WA-229, FMNH 199007	109 (D)	12.63 ± 0.085 (8.6-14.4)	19.38 ± 0.081 (13.6-21.1)	0.651 ± 0.003 (0.567-0.728)
N. australis				
WA-231, FMNH 199954	17 (L)	12.41 ± 0.148 (11.4-13.6)	18.41 ± 0.093 (17.7-18.9)	0.675 ± 0.008 (0.613-0.741)
WA-231, FMNH 199004	111 (D)	11.49 ± 0.051 (9.9-13.0)	17.89 ± 0.060 (15.6-19.1)	0.643 ± 0.003 (0.558-0.733)

Table 36: Local Variation in *Ningbingia* (continued)

Taxon	Number of Adults Measured	Mean, Range and SEM of: Whorls	Umbilical Width	D/U Ratio
N. bulla,				
WA-427, FMNH 199048	97 (D)	5 + (4⅞-5⅜)	3.07 ± 0.045 (2.3-4.5)	5.78 ± 0.075 (4.16-8.02)
WA-428, FMNH 199022	155 (D)	5¼ − (4⅞-5½)	3.09 ± 0.027 (2.2-4.4)	5.83 ± 0.051 (4.18-8.55)
WA-429, FMNH 199054	42 (D)	5¼ (5-5½)	3.18 ± 0.052 (2.6-4.1)	5.96 ± 0.088 (4.73-7.37)
WA-430, FMNH 199042	19 (D)	5¼ + (5-5¾)	—	—
WA-431, FMNH 199041	30 (D)	5¼ + (5-5⅜)	2.97 ± 0.099 (1.8-3.9)	6.58 ± 0.287 (4.68-10.6)
N. octava				
WA-426, FMNH 199633	71 (L)	6 (5¾-6¼)	1.73 ± 0.029 (1.1-2.25)	9.00 ± 0.158 (7.02-13.9)
WA-426, FMNH 199028	122 (D)	6 (5-6½)	1.76 ± 0.025 (1.2-2.3)	9.22 ± 0.131 (6.70-13.8)
WA-434, FMNH 199635	17 (L)	6½ − (6⅛-6⅞)	1.47 ± 0.054 (1.0-2.0)	11.13 ± 0.480 (8.67-16.7)
WA-434, FMNH 199032	84 (D)	6⅜ − (5⅜-6¾)	1.62 ± 0.033 (1.0-2.8)	10.35 ± 0.203 (6.67-16.0)
N. laurina				
WA-434, FMNH 199051	16 (D)	5 − (4¾-5⅛)	2.05 ± 0.084 (1.6-2.8)	8.75 ± 0.324 (5.96-10.4)
N. res				
WA-230, FMNH 199957	19 (L)	5½ (5¼-5¾)	2.71 ± 0.097 (2.2-3.8)	7.26 ± 0.201 (5.56-8.77)
WA-230, FMNH 199008	42 (D)	5⅜ (5⅛-5¾)	3.28 ± 0.088 (1.7-4.3)	6.28 ± 0.225 (4.78-12.0)
WA-229, FMNH 199007	109 (D)	5¼ + (5-5⅝)	3.39 ± 0.032 (2.4-4.1)	5.73 ± 0.077 (3.54-8.26)
N. australis				
WA-231, FMNH 199954	17 (L)	5½ (5¼-5¾)	3.19 ± 0.088 (2.7-3.8)	5.83 ± 0.148 (4.91-6.80)
WA-231, FMNH 199004	111 (D)	5¼ (4⅞-5⅝)	3.05 ± 0.035 (1.4-4.2)	5.95 ± 0.085 (4.41-12.9)

same species (*N. bulla*, **Table 36**) is as great as the mean differences among species, the problem of shell identification becomes even more chancy and difficult, except where there are prominent features such as sulci and basal ridges.

The generic name *Ningbingia* obviously recognizes the Ningbing Ranges radiation of camaenids. Despite a number of inquiries in both Kununurra and Perth, I have not been able to find out the origin of the name Ningbing itself.

NINGBINGIA BULLA SP. NOV.

(Plate 15a-b; Figs 74a-f, 75a-f, 79a-b, 80a-b, 81a-b, 109a)

Comparative remarks

Ningbingia bulla is very similar to *N. australis* **(Figs 77d-f)**, differing primarily in having a lower mean H/D ratio (0.615) than that of *N. australis* (0.647). There is so much overlap **(Table 35)** that this ratio cannot be used to separate small series or individual specimens. The lack of noticeable radial sculpture on the spire and body whorl of both species easily separate them from the generally heavily sculptured species of *Turgenitubulus* and *Cristilabrum*, many of which also have a conspicuous basal lip knob. Only *C. simplex* **(Figs 97d-f)** could be confused, and its more expanded lip, deeper sutures, and retention of prominent radial sculpture on at least the body whorl permit shell identification. *Ningbingia laurina* has more rapidly decoiling whorls **(Fig. 77a)**, a distinctly narrower umbilicus **(Fig. 77b)** and a higher spire; *N. octava* **(Figs 76a-f)** has much tighter coiling, more whorls (mean whorl count 6 ⅛), and a peripheral sulcus on the body whorl; and *N. res* **(Figs 78a-d)** has a very characteristic, deeply recessed basal ridge inside the aperture and a prominent peripheral sulcus. Anatomically, the relatively short penis **(Figs 79b, 80b, 81b)** that is little longer or the same length as its sheath, and the short section of the main pilasters that has corrugated ridging in *N. bulla* contrast with the very long penis **(Fig. 87a)** folded upon itself within the sheath and the very long section of the main pilasters **(Fig. 87b)** with corrugated edges found in *N. australis*. Other *Ningbingia* species show gross differences in penis length and the pattern of pilaster corrugations **(Figs 82, 83, 84, 86, 109a-e)**. The very coarse pilaster corrugations in *N. bulla* **(Fig. 109a)** are very different from those of other *Ningbingia* and most similar to those of *Prymnbriareus*.

Holotype

WAM 535.79, Sta. WA-427, east face of ridge 5.7 km north of No. 8 Bore, north end of Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Knob Peak' map sheet 4668–544:501). Collected by Alan Solem, 17 May 1977. Height of

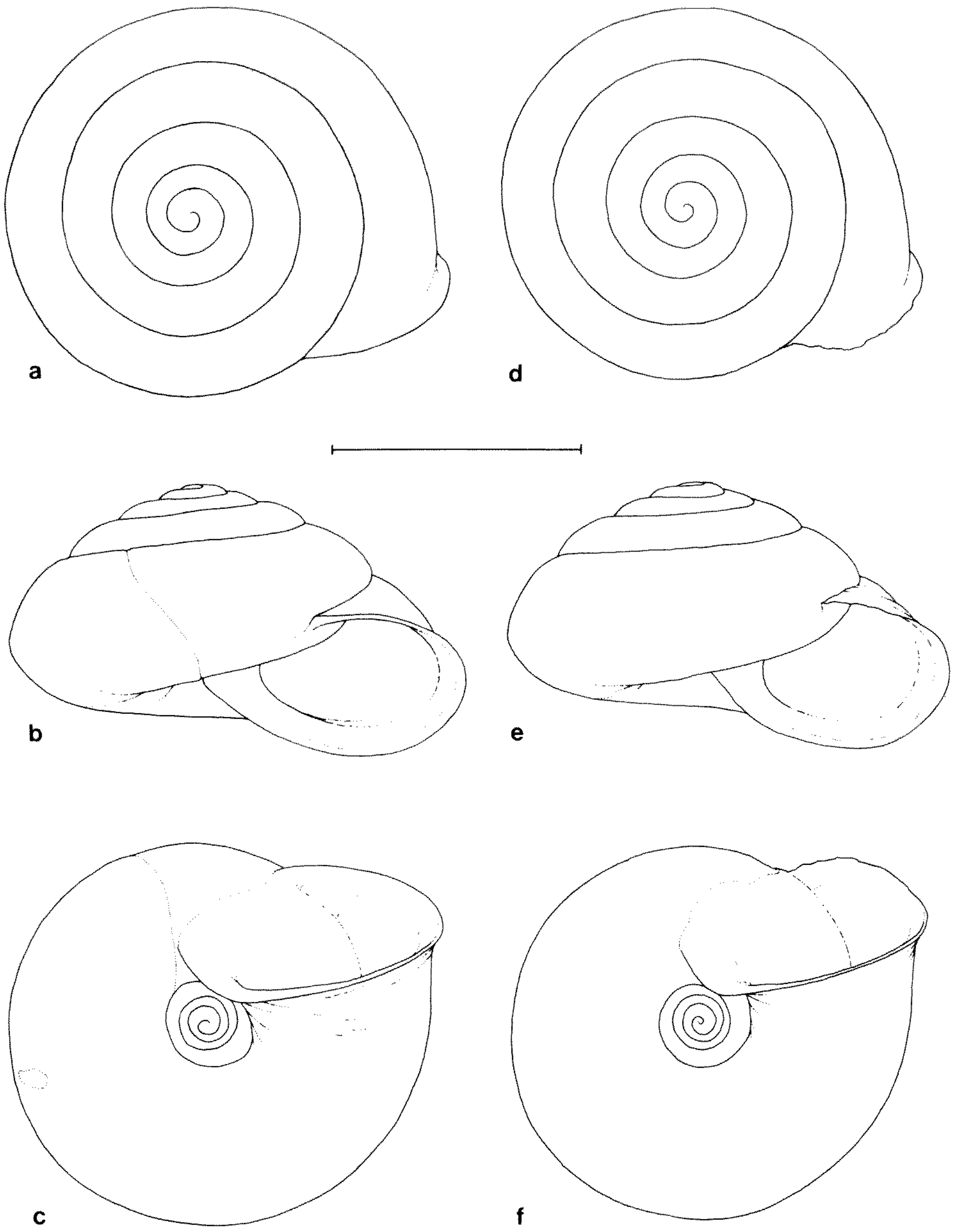


Fig. 74: Shells of *Ningbingia bulla*: (a-c) Sta. WA-427, near Knob Peak, Ningbing Ranges, WAM 535.79, holotype; (d-f) Sta. WA-428, near Knob Peak, Ningbing Ranges, WAM 498.79, paratype. Scale line equals 10 mm.

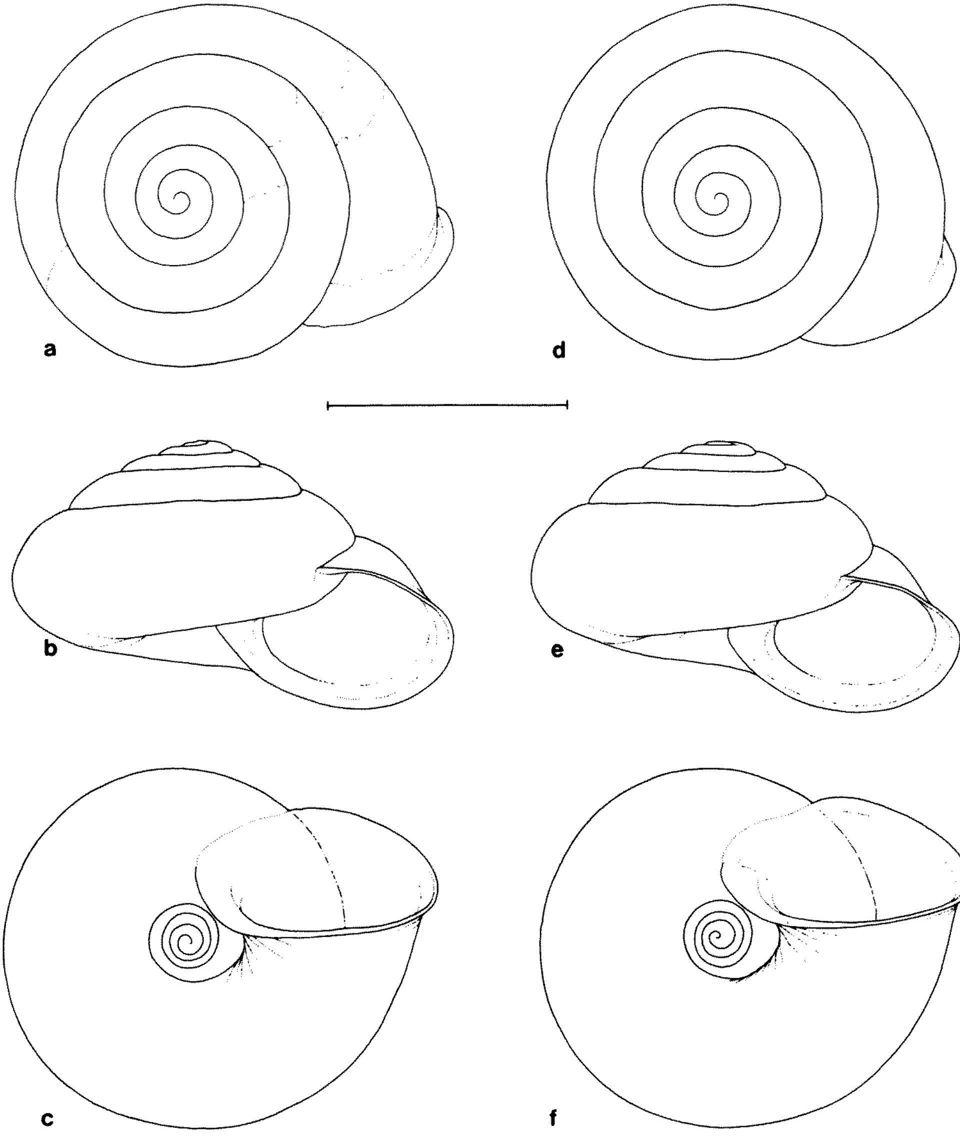


Fig. 75: Shells of *Ningbingia bulla*: (a-c) Sta. WA-429, near Knob Peak, Ningbing Ranges, WAM 497.79, paratype; (d-f) Sta. WA-431, near Knob Peak, Ningbing Ranges, WAM 523.79, paratype. Scale line equals 10 mm.

shell 11.55 mm, diameter 18.0 mm, H/D ratio 0.642, whorls 5¼, umbilical width 3.0 mm, D/U ratio 6.00.

Paratopotypes

WAM 500.79, WAM 568.79, FMNH 199048, FMNH 199639, 3 live and 97 dead adults, 6 live juveniles from the type locality.

Paratypes

Ningbing Ranges, north of Kununurra: Sta. WA-428, west and north face of small hill, 5.4 km north of No. 8 Bore ('Knob Peak' 4668–544:498) (6 live, 155 dead adults, 2 live juveniles, WAM 575.79, WAM 498.79, WAM 545.79, FMNH 199022, FMNH 199632); Sta. WA-429, south face and south-west cove of WA-427 block, 5.4 km north of No. 8 Bore ('Knob Peak' 4668–543:499) (12 live and 42 dead adults, 11 live juveniles, WAM 521.79, WAM 564.79, WAM 497.79, FMNH 199054, FMNH 199637); Sta. WA-430, isolated hill across creek, west of WA-428, 5.45 km north of No. 8 Bore ('Knob Peak' 4668–542:498) (19 dead adults, WAM 520.79, FMNH 199042); Sta. WA-431, 4.25 km north of No. 8 Bore, 0.4 km west of road, saddle between peaks ('Knob Peak' 4668–549:483) (30 dead adults, WAM 511.79, WAM 523.79, FMNH 199041).

Diagnosis

Shell 14.6-21.3 mm (mean 17.96 mm) in diameter, with 4⅞ to 6¼ (mean 5⅛+) normally coiled whorls. Apex and spire strongly and almost evenly elevated, slightly rounded above **(Figs 74b, e, 75b, e)**, height of shell 9.2-13.5 mm (mean 11.35 mm), H/D ratio 0.508-0.815 (mean 0.615). Apical sculpture (**Plate 15a-b**) of fine pustules initially, coalescing into radial, partly anastomosing ridges later, postapical whorls with at most irregular radial growth striae, shell base not noticeably smoother. Shell periphery rounded **(Fig. 75e)** to obtusely angled **(Fig. 74b)**. Body whorl only slightly deflected behind lip, which is only moderately flared laterally, more strongly reflected in umbilical region. No basal lip protrusion or body whorl sulcus. Umbilicus open, regularly and narrowly decoiling, partly covered by reflected lip, umbilical width 2.2-4.5 mm (mean 3.11 mm), D/U ratio 4.16-8.55 (mean 5.86). Based on 364 measured adults.

Genitalia **(Figs 79a, 80a, 81a)** with vas deferens (VD) entering penis sheath (PS) more than half way up sheath, penis retractor muscle (PR) short. Penis (P) of intermediate length, relatively stout, internally **(Figs 79b, 80b, 81b)** variable in details of apical structure, with a short (Sta. WA-427, **Fig. 79b**) to long (Sta. WA-428, **Fig. 80b**) apical plug, followed by a section of longitudinal narrow pilasters. Basal area of penis with two greatly elevated pilasters having a short section of corrugated edges, exact length of the corrugated area varying among populations. Corrugated area **(Fig. 109a)** with large, irregular ridgelets restricted to outer side of pilaster. Based on 7 dissected adults.

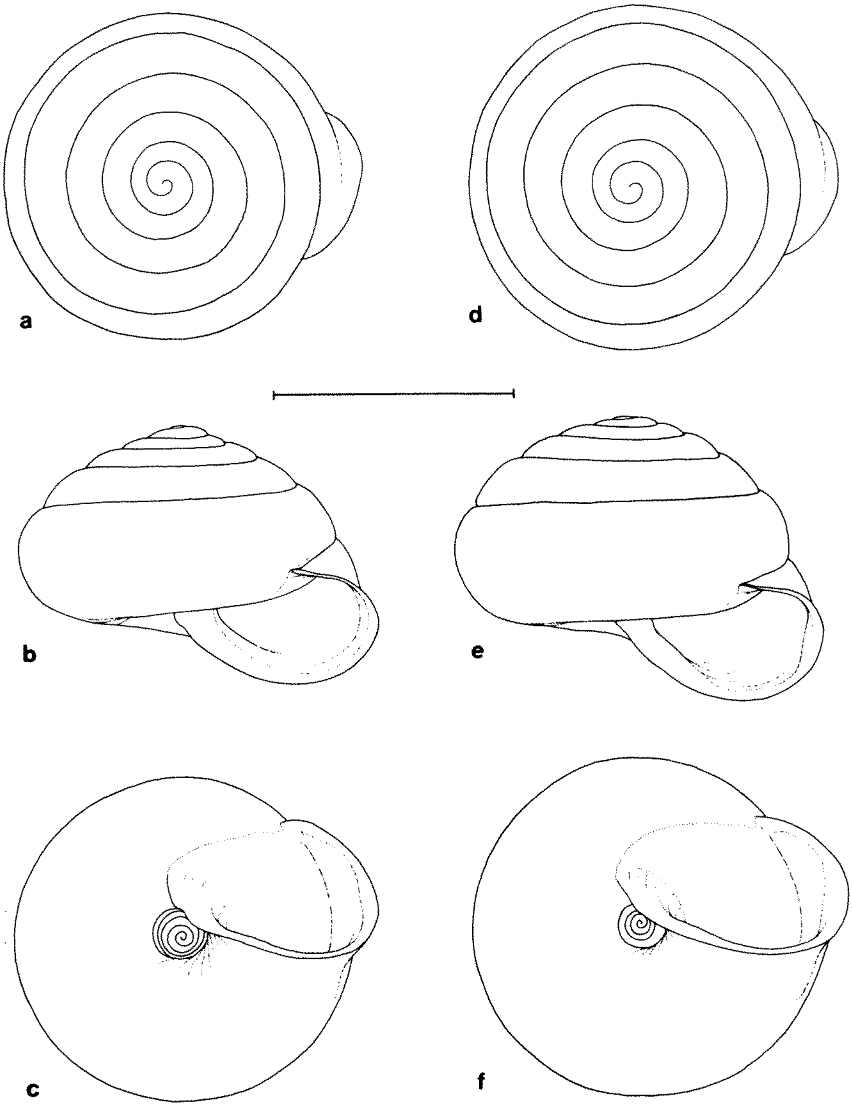


Fig. 76: Shells of *Ningbingia octava*: (a-c) Sta. WA-426, No. 8 Bore, Ningbing Ranges, WAM 565.79, holotype; (d-f) Sta. WA-434, 2nd peak south of No. 8 Bore, Ningbing Ranges, WAM 553.79, paratype. Scale line equals 10 mm.

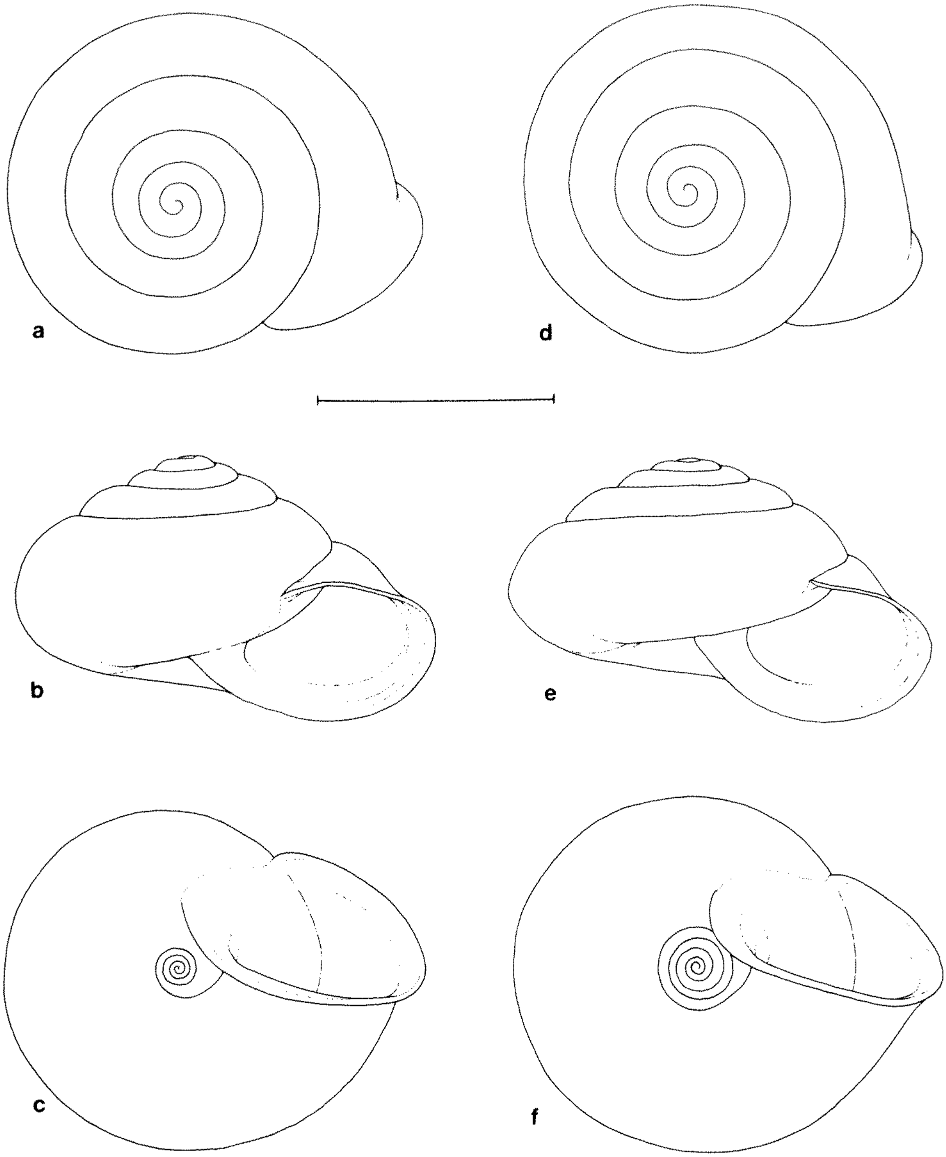


Fig. 77: Shells of *Ningbingia laurina* and *N. australis*: (a-c) *N. laurina*, Sta. WA-434, 2nd peak south of No. 8 Bore, Ningbing Ranges, WAM 551.79, holotype; (d-f) *N. australis*, Sta. WA-231, 3.5 km north of Tanmurra Creek, Ningbing Ranges, WAM 513.79, holotype. Scale line equals 10 mm.

Discussion

Ningbingia bulla has been taken from a cluster of isolated hills less than 2 km north of Knob Peak along the road to Brolga Spring outcamp (**Fig. 110** inset), and from an area just west of Knob Peak itself. This is the northernmost limestone outlier of the Ningbing Ranges, and the name *bulla*, meaning knob, refers to the only nearby landmark. The region between Knob Peak and No. 8 Bore, where *N. octava* is common, has not been sampled, so that the point of transition between the species is unknown.

Stations WA-427 to WA-430 are from portions of the same limestone mass (WA-427, WA-429) or masses separated by only a few hundred yards of grassy alluvial plain. That these are effectively isolated islands, at least occasionally, is evident from two sources. The annual accidental or purposeful burning of the grass covered plain in the mid to late dry season would kill any strayed snails as there are

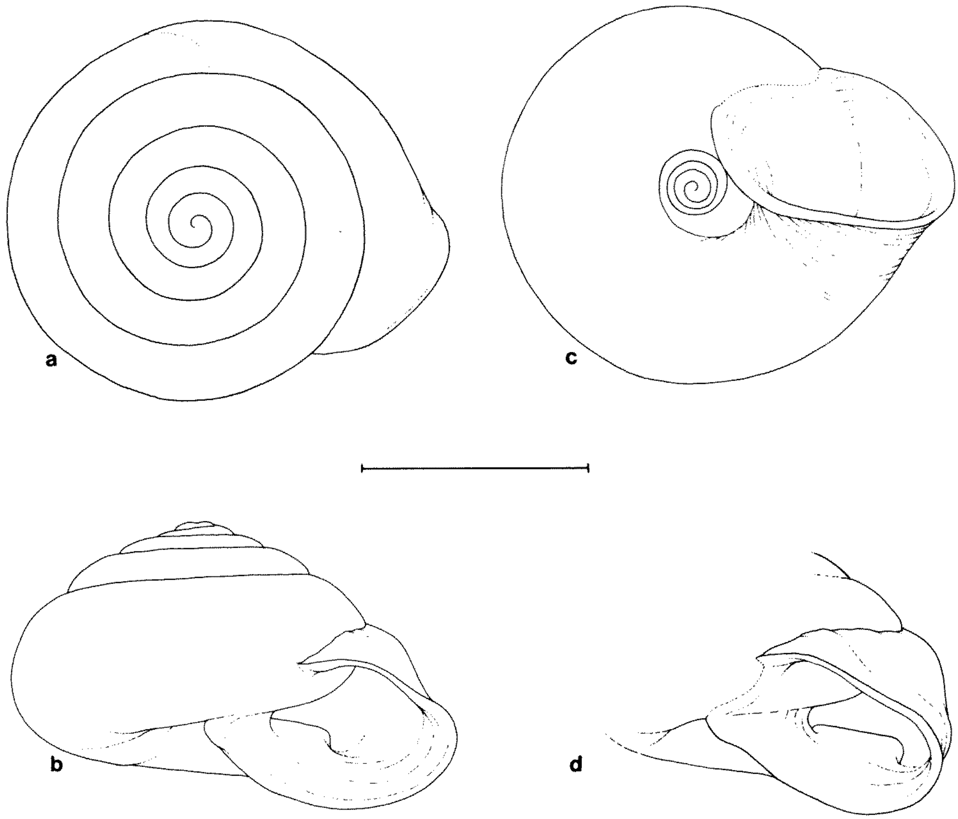


Fig. 78: Shells of *Ningbingia res*: Sta. WA-230, cliffs 7 km north of Tanmurra Creek, Ningbing Ranges, WAM 495.79, holotype, (a) top; (b) side; (c) base; (d) detail of basal lip ridge. Scale line equals 10 mm for a-c.

only rock chips for potential shelter. During the height of the wet season, the dry creek bed normally would be a rushing torrent, and occasionally the entire plain will be flooded to a significant depth. While such floods could and almost certainly do result in accidental transport among colonies, in general the combination of low level inundation and burning over the course of a year would minimize opportunities for genetic interchange and tend to maintain isolation. Thus the existence of minor variation in both shell and anatomy among these populations is not surprising.

Local shell variation in *N. bulla* is summarized in **Table 35**. When the position of the colonies in relation to sun exposure is considered **(Fig. 110** inset), the probable cause of variation is easy to suggest. The colonies at WA-427 and WA-428 have an eastern and northern exposure with little shade, while those at WA-429 and WA-430 have southern and western exposures with a much greater degree of shelter from direct sunlight. Station WA-431 was taken at a tree covered saddle with direct northern exposure, but the shade cover would provide significant protection. The mean diameter of the shells from the more sheltered sites is noticeably larger than from the more exposed situations. The specimens from WA-427 are small because of an earlier cessation of growth (mean whorl count ¼ whorl less), while those from WA-428 are simply smaller in size, with no significant difference in whorl count. The differences in proportions and umbilical size are not significant.

Data on anatomical variation is based on too limited material for statistical analysis, but is suggestive of significant differences among populations. The holotype (Sta. WA-427, **Figs 79a-b)** has the apical pilaster-plug thinner with the pore (not indicated in **Fig. 79b)** subterminal. In material from Sta. WA-428 **(Figs 80a-c)**, where three of seven adults were opened, the apical pilaster-plug was much longer with essentially terminal pore. All of the material had rather deeply retracted within the shell despite use of chloral hydrate as a relaxant, so whether the partially coiled penis inside the sheath is an artifact of contraction or indicates penis elongation is unknown. All three dissected examples agreed in the plug length and coiled nature of the penis inside the sheath. Because of the elasticity of the penis itself, accurate measurements could not be attempted. Of the three dissected from Sta. WA-429, one partly extended individual **(Fig. 81b)** had the penis uncoiled and a moderately thick pilaster-plug, while two contracted individuals had the penis folded within the sheath. The differences in sheath thickness among the three populations were real and not variable. Quite in contrast with the variability in sheath thickness and size of the apical pilaster-plug, the length of the ridged area on the lower penis pilasters **(Figs 79b, 80b, 81b)** was uniform, allowing for the different angles shown in the drawings, and the micro-ridging agreed with **Fig. 109a**. Since this region would function in species recognition, such conservatism is to be expected.

With the limited material now available, resolution of the significance of the outlined conchological and anatomical variations is not possible, but it is evident that the isolated hill structure of the Ningbings provides excellent opportunities for study of local variation.

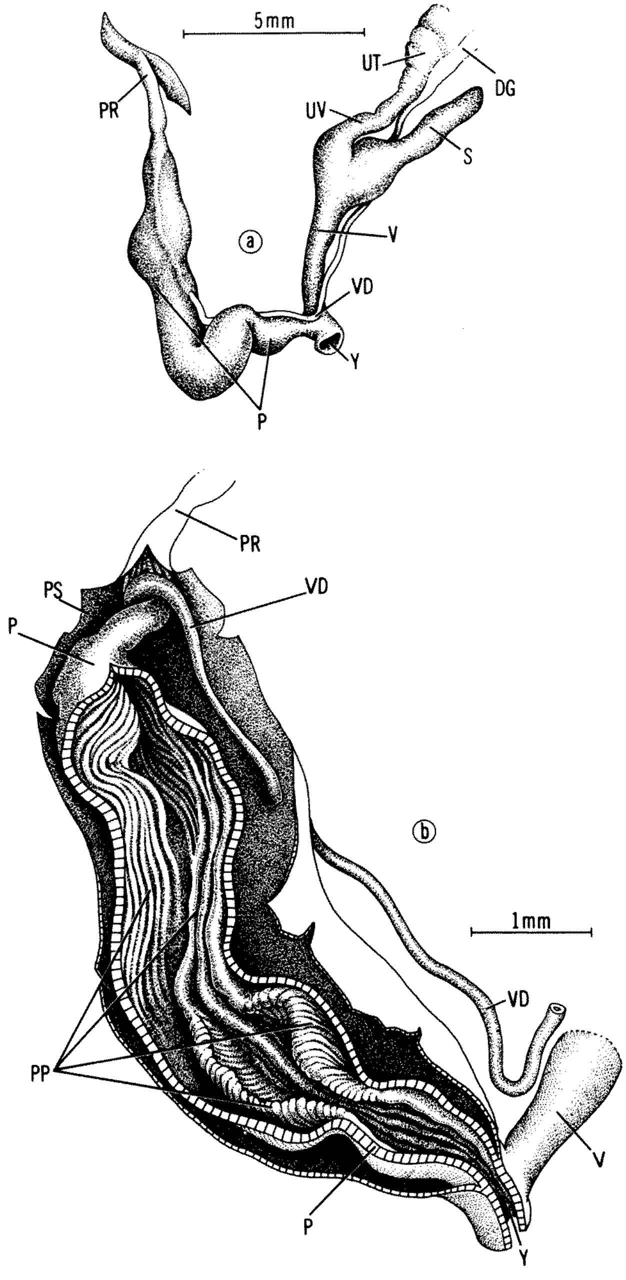


Fig. 79: Genitalia of *Ningbingia bulla*: Sta. WA-427, near Knob Peak, Ningbing Ranges, 17 May 1977, WAM 535.79, holotype, (a) terminal genitalia; (b) interior of penis. Scale lines as marked.

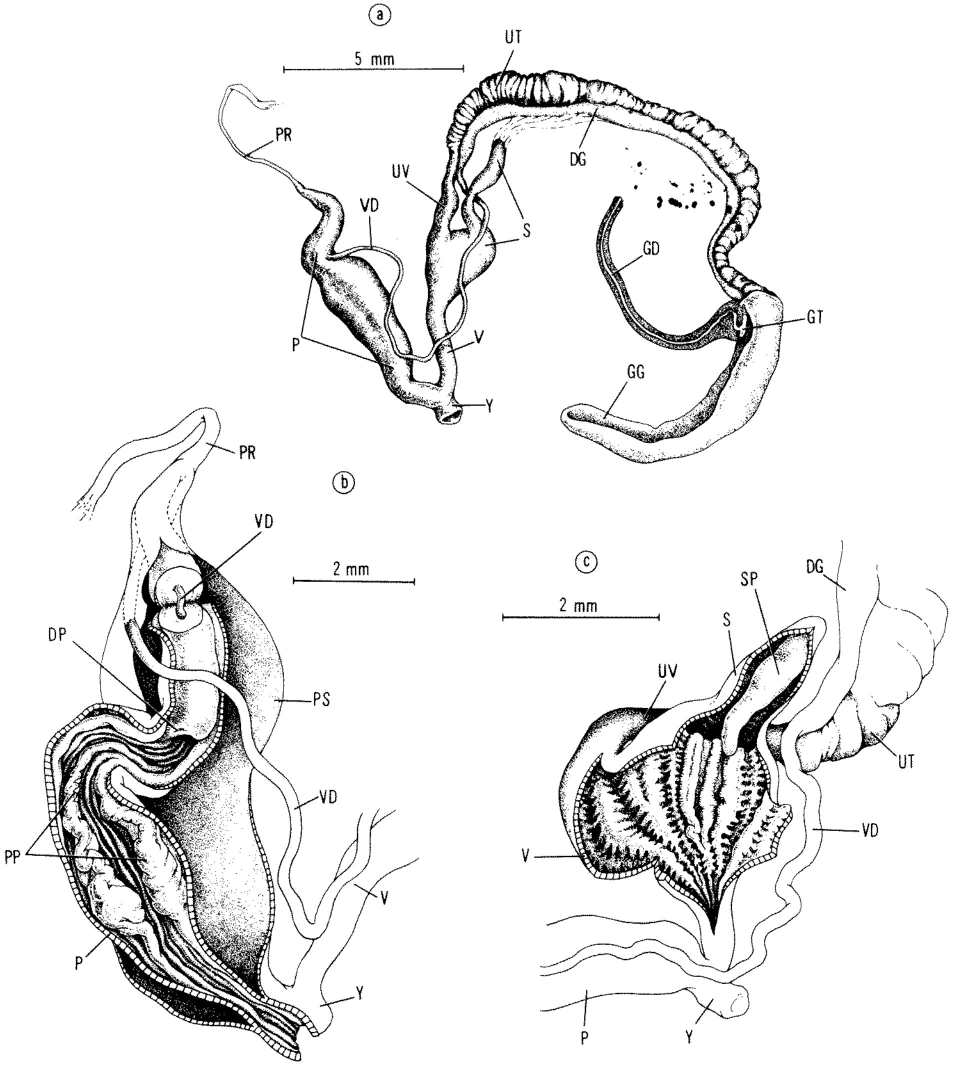


Fig. 80: Genitalia of *Ningbingia bulla*: Sta. WA-428, near Knob Peak, Ningbing Ranges, 17 May 1977, FMNH 199632, paratypes, (a) whole genitalia except for ovotestis, Dissection A; (b) interior of penis, Dissection A; (c) lower female tract interior, Dissection B. Scale lines as marked.

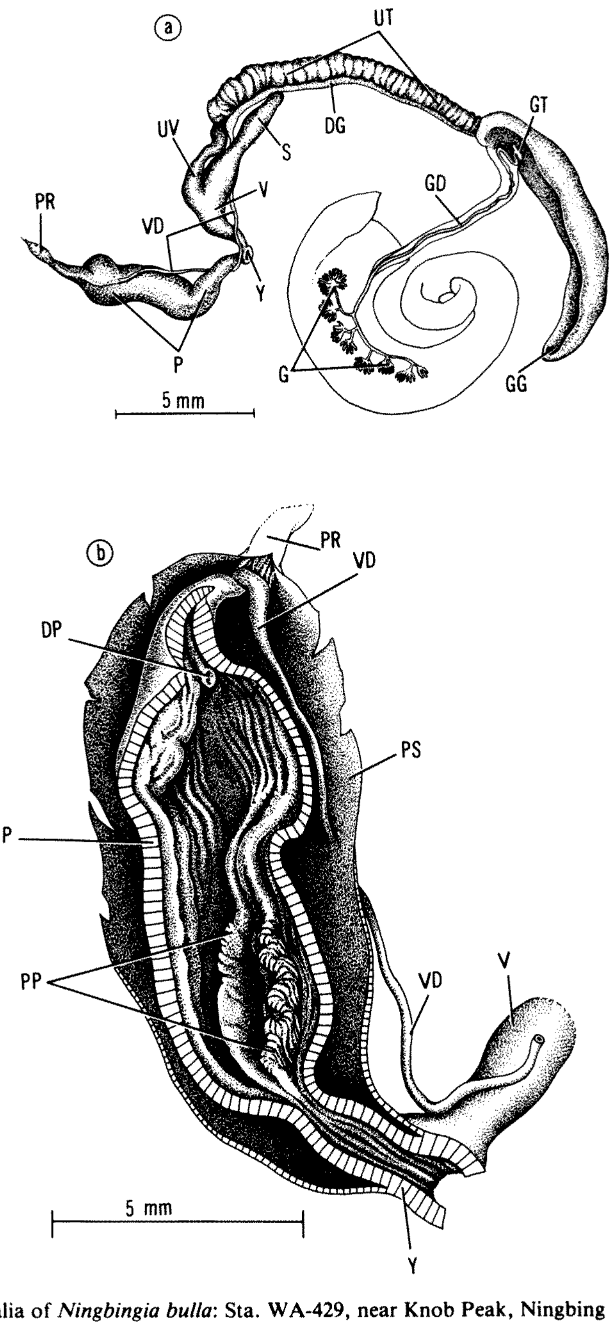


Fig. 81: Genitalia of *Ningbingia bulla*: Sta. WA-429, near Knob Peak, Ningbing Ranges, 17 May 1977, FMNH 199637, paratypes, (a) whole genitalia, Dissection B; (b) interior of penis, Dissection A. Scale lines equal 5 mm.

NINGBINGIA OCTAVA SP. NOV.

(Plate 15c; Figs 76a-f, 82a-c, 83a-b, 109b)

Comparative remarks

Ningbingia octava has an increased whorl count (mean 6 1/8), generally narrow umbilicus, an increased H/D ratio (mean 0.724), tight coiling of the lower spire **(Figs 76a, d)**, and often a domed spire **(Fig. 76e)** compared with the other *Ningbingia*. The presence of a prominent sulcus parallel to the plane of coiling on up to the last quarter of the body whorl and the absence of any basal ridge or protrusion immediately differentiate it from *N. laurina, N. bulla*, and *N. australis. Ningbingia res* **(Figs 78b, d)** has the very prominent, deeply recessed ridge on the basal lip in addition to the very prominent peripheral sulcus. The combination of small size, high H/D ratio, and high whorl count effectively separate *N. octava* from any of the species of *Turgenitubulus* and *Cristilabrum*. Anatomically, the very long penis **(Figs 82b, 83b)** which is twice the length of the sheath, is matched by that of *N. australis* **(Fig. 87b)**, but the restriction of the ridged area in *N. octava* to a very short section of the main pilasters **(Figs 82b, c, 83b)** and slenderness of the penis provide a marked contrast to the situation found in other *Ningbingia*.

Holotype

WAM 565.79, Sta. WA-426, east face of large hill just south of No. 8 Bore at low cave entrance, north end of Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Knob Peak' map sheet 4668—556:448). Collected by Alan Solem 17 May 1977. Height of shell 11.35 mm, diameter 15.15 mm, H/D ratio 0.749, whorls 6¼, umbilical width 1.8 mm, D/U ratio 8.42.

Paratopotypes

WAM 543.79, WAM 577.79, FMNH 199633, FMNH 199028, 70 live and 122 dead adults, 7 live juveniles from the type locality.

Paratypes

Ningbing Ranges, north of Kununurra: Sta. WA-434, 2nd peak south of No. 8 Bore, north-east face in wash channel ('Knob Peak' 4668–562:439) (17 live and 84 dead adults, WAM 499.79, WAM 566.79, WAM 553.79, FMNH 199032, FMNH 199635).

Diagnosis

Shell rather small, 14.1-18.8 mm (mean 15.82 mm) in diameter, with 5 to 6 7/8 (mean 6 1/8) rather tightly coiled whorls. Apex and early spire evenly elevated **(Fig. 76b)** to strongly rounded **(Fig. 76d)**, last whorls descending rather abruptly, height of shell 9.6-13.4 mm (mean 11.44 mm), H/D ratio 0.633-0.844 (mean 0.724). Apical sculpture **(Plate 15c)** typical of genus, postapical whorls with weak irregular radial

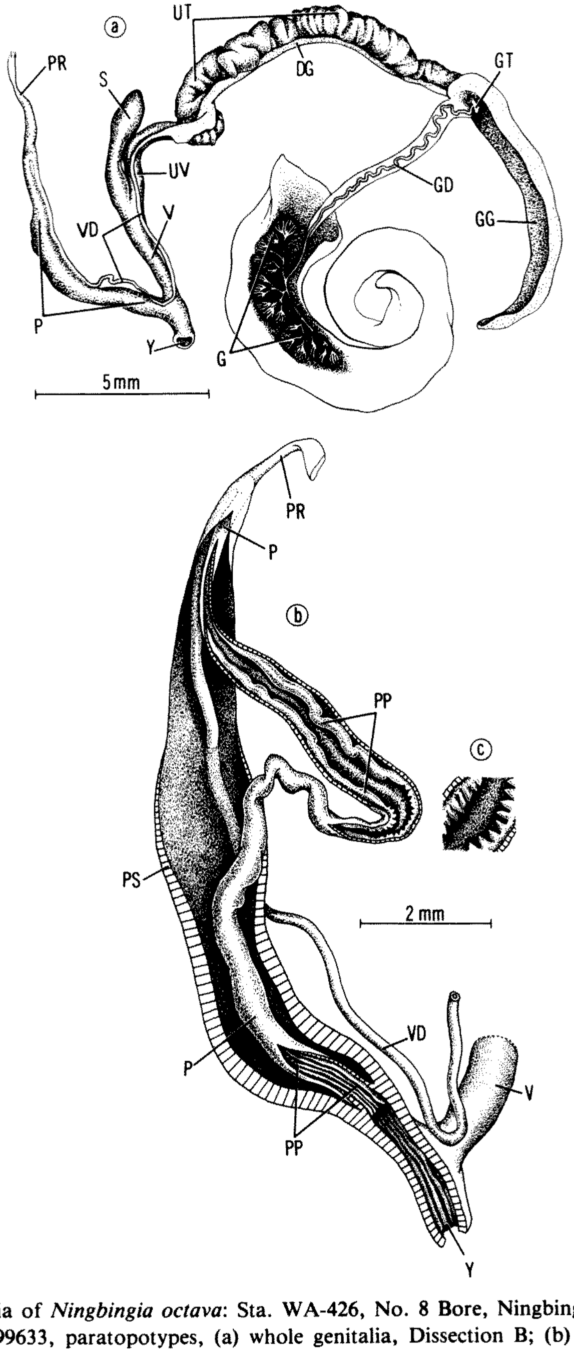


Fig. 82: Genitalia of *Ningbingia octava*: Sta. WA-426, No. 8 Bore, Ningbing Ranges, 17 May 1977, FMNH 199633, paratopotypes, (a) whole genitalia, Dissection B; (b) interior of penis, Dissections D and F composite; (c) detail of ridging on main pilasters. Scale lines as marked.

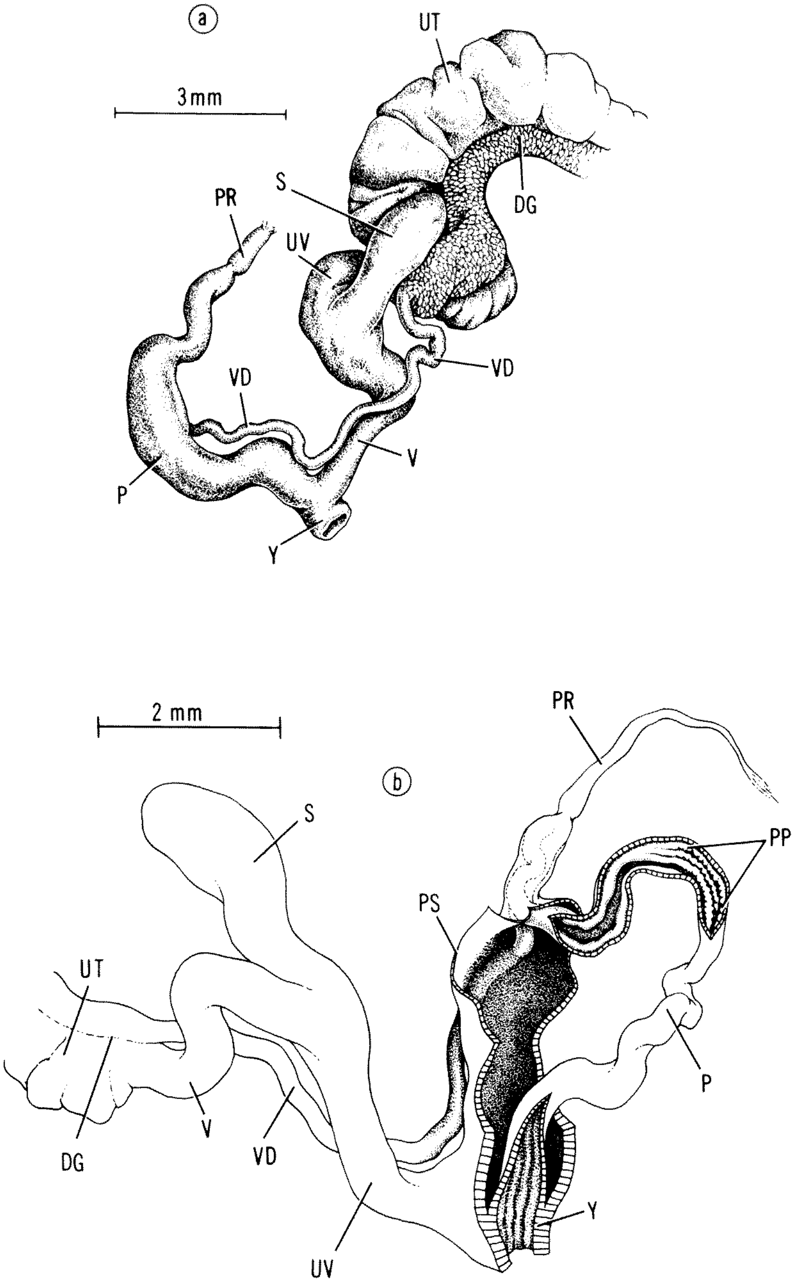


Fig. 83: Genitalia of *Ningbingia octava*: Sta. WA-434, 2nd peak south of No. 8 Bore, Ningbing Ranges, 19 May 1977, FMNH 199635, paratypes, (a) terminal genitalia, Dissection B; (b) interior of penis, Dissection A. Scale lines as marked.

growth striae, shell base with same sculpture. Shell periphery evenly round, except for last eighth to quarter of body whorl which usually has a peripheral sulcus **(Figs 76e-f)**. Body whorl only slightly deflected behind lip, which is moderately reflected to cover part of umbilicus and generally rather sharply but narrowly expanded. Umbilicus narrowly open, regularly decoiling, partly covered by reflected lip, umbilical width 1.0-2.8 mm (mean 1.70 mm), D/U ratio 6.67-16.7 (mean 9.60). Based on 294 measured adults.

Genitalia **(Figs 82a-c, 83a-b)** with vas deferens (VD) entering sheath less than half way to penial retractor insertion (PR). Penis (P) very slender, approximately twice length of sheath which is thick walled on lower half **(Fig. 82b)** and thin-walled above. Internally **(Figs 82b, c, 83b)** with main pilasters (PP) having only a very short area of corrugated edging **(Fig. 82c)** compared with other *Ningbingia*, no apical plug, ridged pilaster area **(Fig. 109b)** with vertical ridgelets ending in blunt points. Remaining sculpture of penial chamber as in *N. bulla*. Based on 10 dissected adults.

Discussion

Ningbingia octava was collected in quantity at two stations (WA-426, WA-434) in the vicinity of No. 8 Bore. The name *octava* is taken from the most prominent landmark in its territory. Scattered hills to the north of No. 8 Bore and ridge system extending south to Utting Gap remain to be investigated for camaenids. At Sta. WA-434, *N. octava* occurs microsympatrically with *N. laurina*, which is easily separable by its reduced whorl count (mean 5), looser coiling pattern (compare **Figs 76a, d, 77a**), much fatter and shorter penis **(Fig. 84a)** with its extensive area of corrugated pilaster edging **(Fig. 84b)**, which is very different in character **(Fig. 109c)**, and shorter, much thicker vaginal region.

At both stations, live collected individuals were smaller in size than dead specimens from the same station **(Table 36)**. The specimens from Sta. WA-434 had a significantly higher whorl count and increased shell height coupled with a slightly narrower umbilicus. This station was slightly more heavily shaded and since it was located by a wash channel would tend to retain moisture significantly longer than the environment at Sta. WA-426 which was partway up a more open hillside.

Although in the drawing **(Fig. 83a)** of material from Sta. WA-434, the penis looks shorter than in material from Sta. WA-426 **(Fig. 82a)**, this is an artifact of contraction. As seen in **Fig. 83b**, the upper portion of the penis was coiled within the sheath, while in **Fig. 82b** this section is fully stretched out. The latter animal died in a more fully extended position, and thus the apparent different length is artificial.

NINGBINGIA LAURINA SP. NOV.

(Plate 15d; Figs 77a-c, 84a-b, 109c)

Comparative remarks

The rounded periphery, low mean whorl count (5), regularly elevated spire **(Fig. 77b)** and looser coiling pattern **(Fig. 77a)** of *N. laurina* easily distinguish it from *N.*

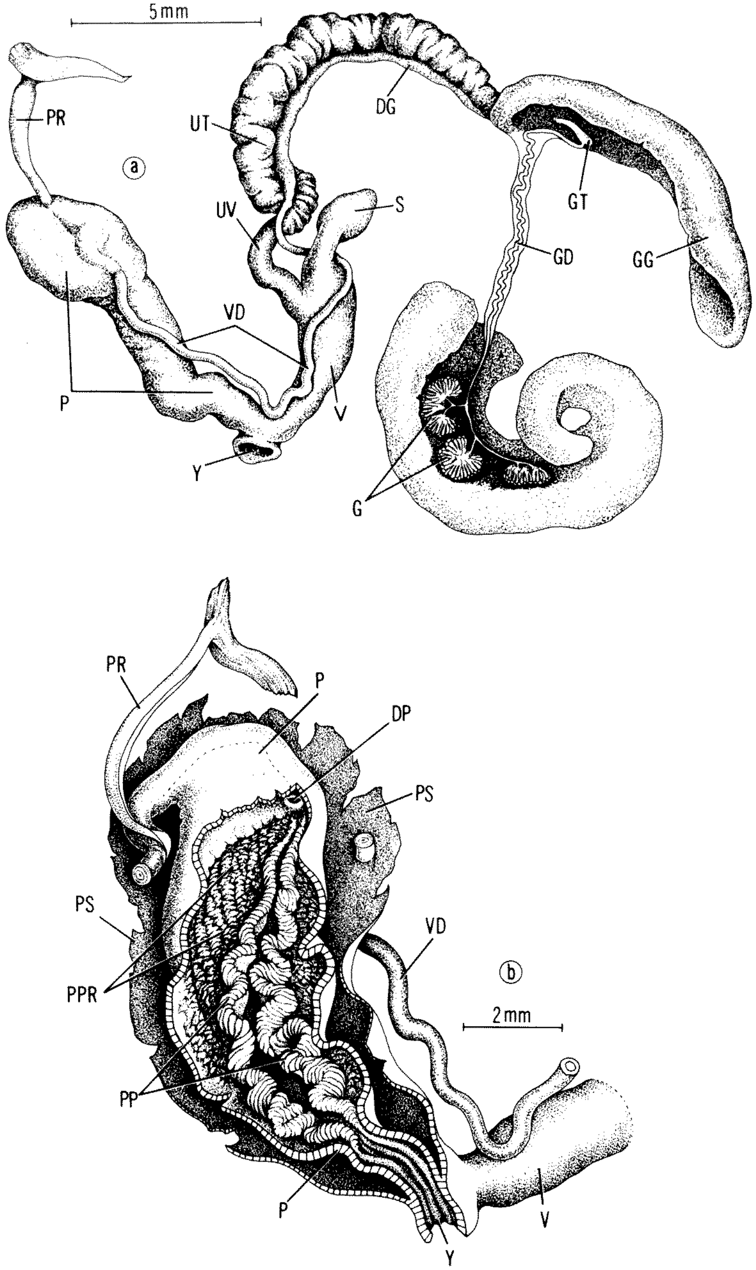


Fig. 84: Genitalia of *Ningbingia laurina*: Sta. WA-434, 2nd peak south of No. 8 Bore, Ningbing Ranges, 19 May 1977, FMNH 200779, paratopotypes, (a) whole genitalia, Dissection A; (b) penis interior, Dissection B. Scale lines as marked.

australis **(Figs 77d-e)**. The tighter coiling, domed spire **(Fig. 76e)** and peripheral sulcus of *N. octava*, the peripheral sulcus and large basal ridge **(Figs 78b, d)** of *N. res*, and the generally angled periphery, wider umbilicus **(Figs 74c, f, 75c, f)**, and lower spire (mean H/D ratio 0.615) of *N. bulla*, enable conchological separation of *N. laurina* from the other *Ningbingia*. Anatomically, the short fat penis **(Fig. 84a)** with its huge apical plug and long area of the main pilasters having corrugated edges **(Fig. 84b)** easily separate *N. laurina* from the sympatric *N. octava* with its very long and slender penis **(Figs 82a-c, 83a-b)** in which the area of corrugations is restricted to a very short portion of the pilasters **(Fig. 82c)**. The structure of the ridging on the corrugated pilaster sections is very distinctive **(Figs 109b-c)**. *Ningbingia bulla* **(Figs 79b, 80b, 81b)** agrees in basic penis shape and often has a large apical plug, but the area of corrugations is much shorter and the nature of the corrugations **(Fig. 109a)** is very different. Both *N. res* **(Figs 85a-b, 86)** and *N. australis* **(Figs 87a-b)** have penes that are longer than their sheath, but agree in having a very long area of corrugated edging to the pilaster, although the nature of the ridgelets is distinctive **(Figs 109d-e)**.

Holotype

WAM 551.79, Sta. WA-434, second peak south of No. 8 Bore, north-east face in wash channel, north part of Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Knob Peak' map sheet 4668−562:439). Collected by Alan Solem and Lucky Laurie 19 May 1977. Height of shell 11.7 mm, diameter 17.6 mm, H/D ratio 0.665, whorls 5 ⅛, umbilical width 2.1 mm, D/U ratio 8.38.

Paratopotypes

WAM 510.79, FMNH 199051, FMNH 200779, 3 live and 16 dead adults from the type locality.

Diagnosis

Shell of average size, 16.5-18.7 mm (mean 17.52 mm) in diameter, with 4¾ to 5 ⅛ (mean 5) regularly coiled whorls. Apex and spire evenly elevated **(Fig. 77b)**, last whorl not descending more rapidly, height of shell 10.8-13.8 mm (mean 11.70 mm), H/D ratio 0.617-0.738 (mean 0.667). Apical sculpture **(Plate 15d)** without unusual features, postapical whorls with irregular, ridge-like growth wrinkles, shell base with same sculpture. Shell periphery evenly rounded, without sulcus **(Fig. 77b)**. Body whorl descending slightly behind lip, which is slightly to moderately reflected to partly cover umbilicus, flared on outer margins, rather thin. Umbilicus narrowly open, last whorl decoiling somewhat more rapidly, umbilical width 1.6-2.8 mm (mean 2.07 mm), D/U ratio 5.96-10.4 (mean 8.64). Based on 19 measured adults.

Genitalia **(Figs 84a-b)** with vas deferens entering penis sheath at upper quarter, reflexing from penis retractor (PR) insertion down through the apical penis plug to open (DP) on one side of the penis. Walls of penis sheath thin, penis walls slightly thicker. Main pilasters with very long area of corrugated ridging that occupies most of the distance from the vas deferens opening to the point of penis sheath attachment, ridgelet sculpture of fine radials that tend to blend into the longitudinal pilasters. Based on 2 dissected adults.

Discussion

Ningbingia laurina is dedicated to Lauries of three countries, boon field companions, only two of whom can read about this. The type collection involved two Lauries—one was quite slow in packing up to break camp and the other was inquisitive. This led to a walk south from the camp at Sta. WA-426. Scratching near a shaded boulder by Lucky Laurie rolled out the first dead specimens. It is thus appropriate to name this species 'of Laurel' after New Zealand, Australian, and American Lauries, field companions in 1976 and 1977.

Ningbingia laurina was microsympatric with *N. octava* at Sta. WA-434. Both species were free sealed in humus and litter under shaded rocks. Only 3 live *N. laurina* and 17 live adult *N. octava* were taken, along with 16 dead *N. laurina* and 84 dead *N. octava.* All adult shells seen were taken, so that the near identity of species proportions, whether live or dead collected, reflects the situation within the particular niche sampled. I could detect no difference in shelter site selection between live examples of the two species, which are recognizable as distinct from three feet away.

Genital differences between *N. octava* **(Figs 82a-c, 83a-b)** and *N. laurina* **(Figs 84a-b)** are dramatic, reflecting their sympatry and the need for effective species recognition. The differences between the sympatric *Turgenitubulus opiranus* **(Fig. 93b)** and *T. depressus* **(Fig. 94b)** from Sta. WA-227 are equivalent in terms of penis length and penis interior structures. The anatomical differences between the sympatric *Cristilabrum simplex* and *C. buryillum* from Sta. WA-235 are unknown as only the former species has been dissected. Their conchological differences are very great **(Figs 97d-f, 98d-f)**, and I have no doubt as to their distinctness.

Whether Utting Gap **(Fig. 110)** marks the dividing line between *N. laurina* and *N. res* remains to be determined, as does the extent of the overlap zone between *N. laurina* and *N. octava*. An extensive hill system occupies both sides of Utting Gap and will be well worth while exploring.

NINGBINGIA RES SP. NOV.

(Plate 15e; Figs 78a-d, 85a-b, 86, 109d)

Comparative remarks

Ningbingia res is the largest species (mean diameter 19.48 mm) of the genus and has a very prominent basal ridge deeply recessed within the aperture of the shell **(Figs 78c-d)**. The sulcus behind the lip on the body whorl is shared with *N. octava*, but is absent from other *Ningbingia* species. In *Turgenitubulus* the basal ridge is

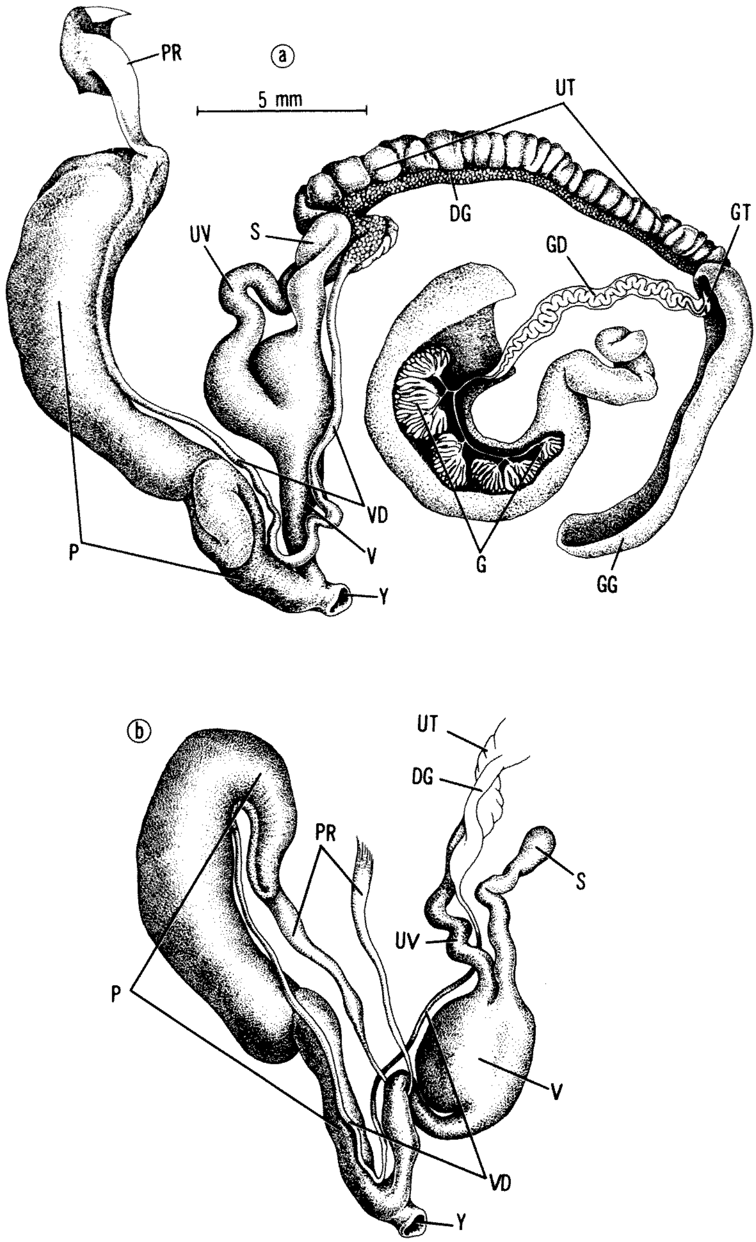


Fig. 85: Genitalia of *Ningbingia res*: Sta. WA-230, 7 km north of Tanmurra Creek, Ningbing Ranges, 12 November 1976, FMNH 199957, paratopotypes, (a) whole genitalia, Dissection B; (b) terminal genitalia with abnormal penial retractor muscle position, Dissection C. Scale line equals 5 mm.

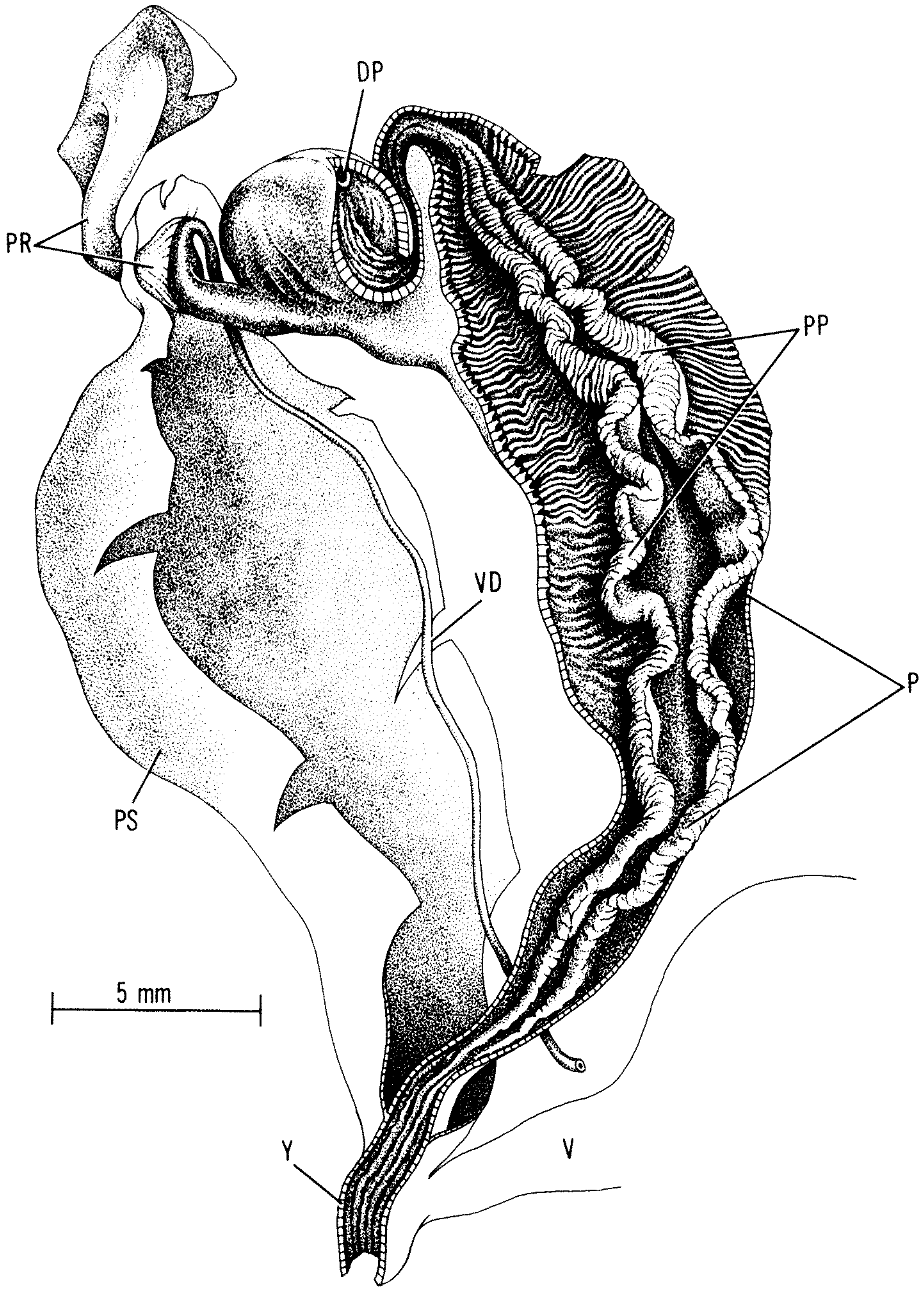


Fig. 86: Penis interior of *Ningbingia res*: Sta. WA-230, 7 km north of Tanmurra Creek, Ningbing Ranges, 12 November 1976, FMNH 199957, paratopotype, Dissection B. Scale line equals 5 mm.

situated on the basal lip **(Figs 88-90)**, not recessed, and in *Cristilabrum*, when present, it is much less recessed and the shell spire has prominent radial ribbing. Anatomically, the greatly enlarged penis **(Figs 85a-b)** and upper vaginal region are immediately recognizable compared with the other *Ningbingia*, while the long corrugated pilasters **(Fig. 86)** with heavy ridgelets on both sides **(Fig. 109d)** and large apical plug are distinctive. The penis of *N. laurina* **(Figs. 84a-b)** is strūcturally a compacted, broadened version. *Ningbingia australis* **(Figs 87a-b)** differs in the much more slender form of the penis, which also lacks the apical plug.

Holotype

WAM 495.79, Sta. WA-230, cliffs 7 km north of Tanmurra Creek, Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667–568:416). Collected by Alan Solem and Carl Christensen 12 November 1976. Height of shell 13.0 mm, diameter 19.7 mm, H/D ratio 0.660, whorls 5 ⅝, umbilical width 3.15 mm, D/U ratio 6.25.

Paratopotypes

WAM 493.79, WAM 554.79, FMNH 199008, FMNH 199957, 18 live and 42 dead adults from the type locality.

Paratypes

Ningbing Ranges, north of Kununurra: Sta. WA-229, cliffs 7 km north of Tanmurra Creek, *ca.* 137 m south of WA-230 ('Carlton' 4667–568: 413) (109 dead adults, 25 live juveniles, WAM 549.79, WAM 544.79, FMNH 199007, FMNH 199952).

Diagnosis

Shell large, 17.8-21.5 mm (mean 19.48 mm) in diameter, with 5 to 5¾ (mean 5 ⅜) normally coiled whorls. Apex and spire almost evenly elevated, slightly rounded above **(Fig. 78b)**, height of shell 10.9-16.6 mm (mean 12.80 mm), H/D ratio 0.567-0.860 (mean 0.657). Apical sculpture **(Plate 15e)** typical, postapical whorls with weak, irregular, radial wrinkles, shell base same in sculpture. Shell periphery evenly rounded to very weakly angled, up to last half of body whorl with a deep peripheral to slightly supraperipheral sulcus **(Fig. 78d)** that continues to the lip. Body whorl descending slightly to moderately at lip, which is thin and moderately flared on outer margin, more strongly reflected to partly cover umbilicus in columellar region. Basal lip with a high, sharply defined, moderately deeply recessed ridge **(Figs 78b, d)**. Umbilicus rather widely open, regularly decoiling until last part of body whorl where lip ridge creates a sulcus, umbilical width 1.9-4.3 mm (mean 3.29 mm), D/U ratio 4.78-12.0 (mean 6.04). Based on 170 measured adults.

Genitalia **(Figs 85a-b, 86)** normally **(Fig. 85a)** with vas deferens (VD) entering penis sheath half way up, reflexing through penial plug from the penial retractor muscle insertion to open (DP) laterally **(Fig. 86)**. Penis very large and long, partly coiled within sheath **(Fig. 85a)**, upper part of vagina (V) swollen. Two main pilasters of penis (PP, **Fig. 86)** very long and with near continuous corrugated ridge area, walls of sheath and penis relatively thin for size. Sculpture of corrugated pilaster area very prominent **(Fig. 109d)**, on both sides of pilaster, blending into spiral ridging on chamber walls, with row of pustules between the two pilasters. Based on 3 dissected adults.

Discussion

While camped overnight at the type locality, discussion wandered as to the desirability of a 'Ningbing Thing'. The natural and inevitable result is *Ningbingia res*, using the latin word *'res'* for thing or object.

Ningbingia res is easily identifiable by its deeply recessed basal ridge **(Figs 78b, d)** and strong peripheral sulcus. The smaller, much more tightly coiled *N. octava*, shares the sulcus **(Fig. 76e)**, but lacks a basal ridge. *N. australis* **(Fig. 77e)** lacks both the ridge and the sulcus. The latter species agrees in the long penis, and long corrugated ridges inside the penis **(Fig. 87b)**, but lacks the penis apical plug and has the penis much more slender.

Sta. WA-229 was on a relatively exposed slope and no live adults were taken in two hours of collecting. The next morning, collecting at a saddle about 150 yards further north (Sta. WA-230) yielded 19 live adults. Variation in this material was moderate **(Table 36)**. Dead adults from Sta. WA-230 were larger than those from Sta. WA-229, but live adults from the former station agreed in size with those from the latter. An extensive ridge system continues north to Utting Gap and south to the area near Tanmurra Creek. A southern outlier of this system (Sta. WA-231) produced *N. australis*, so that the point of transition between species remains unknown.

NINGBINGIA AUSTRALIS SP. NOV.

(Plate 15f; Figs 77d-f, 87a-b, 109e)

Comparative remarks

Ningbingia australis is very similar in shell size and shape to *N. bulla* **(Figs 74-5)**, but has a higher H/D ratio **(Table 35)**. Both *N. res* and *N. octava* have strong peripheral sulci **(Figs 76e, 78b, d)**. *N. laurina* **(Figs 77a-c)** has a rounded periphery, reduced whorl count (mean 5), and a clearly narrower umbilicus. Anatomically, the long penis that is coiled within the sheath of *N. australis* **(Fig. 87b)** is similar in length to that of *N. res* **(Fig. 86)** and *N. octava* **(Figs 82b, 83b)**, but the latter has the corrugated pilaster region confined to a very short segment, and the former has a much fatter, proportionately longer penis **(Figs 85a-b)**. Ridgelet areas on the pilasters are very different in the three species **(Figs 109b, d, e)**. *N. laurina* **(Figs 84a-b)** and *N. bulla* **(Figs 79b, 80b, 81b)** have the penis about equal in length to the sheath. The latter has a relatively slender penis and the corrugated area equalling about one-quarter of the length, while the former has a thicker, short penis with the corrugated pilasters extending almost the entire length of the penis.

Holotype

WAM 513.79, Sta. WA-231, at saddle near start of ridge, 3.5 km north of Tanmurra Creek, Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667–566:388). Collected by Alan Solem and Carl Christensen, 12 November 1976. Height of shell 11.4 mm, diameter 17.8 mm. H/D ratio 0.640, whorls 5 3/8+, umbilical width 3.4 mm, D/U ratio 5.24.

Paratopotypes

WAM 494.79, WAM 570.79, FMNH 199004, FMNH 199954, 16 live and 113 dead adults from the type locality.

Diagnosis

Shell 15.6-19.1 mm (mean 17.96 mm) in diameter, with 4 7/8 to 5 3/4 (mean 5 1/4) normally coiled whorls. Apex and spire strongly and almost evenly elevated **(Fig. 77e)**, at most slightly rounded above, height of shell 9.9-13.6 mm (mean 11.61 mm), H/D ratio 0.558-0.741 (mean 0.647). Apical sculpture typical of genus, postapical sculpture of low, irregular radial ridges, shell base with same sculpture. Shell periphery noticeably angulated **(Fig. 77e)**. Body whorl not to only slightly deflected behind lip, which is moderately flared on periphery, more strongly reflected to cover part of umbilicus. No basal lip ridge or peripheral sulcus. Umbilicus open, regularly decoiling, umbilical width 1.4-4.2 mm (mean 3.07 mm), D/U ratio 4.41-12.9 (mean 5.94). Based on 128 measured adults.

Genitalia **(Figs 87a-b)** with vas deferens (VD) entering sheath near midpoint. Penis (P) very long, folded within sheath, slender, internally **(Fig. 87b)** with two very long pilasters (PP) with corrugated upper edge, no apical plug, tapering apically to penial retractor muscle insertion (PR), walls of both sheath and penis relatively thin. Length of corrugated edging different on the two pilasters, basal section of penis with both pilasters having smooth upper edge. Corrugated area of pilaster with delicate, anastomosing ridgelets **(Fig. 109e)** that continue onto the penis walls as spiral corrugations. Based on 3 dissected adults.

Discussion

Ningbingia australis was collected from the southern outlier of the main ridge system north of Tanmurra Creek. As such it is the southernmost known representative of *Ningbingia*, hence the use of the name *australis* for this species.

Although the shells of *N. australis* and *N. bulla* are almost identical in size and shape **(Table 35)**, the differences in the penial structure are striking **(Figs 81a-b,**

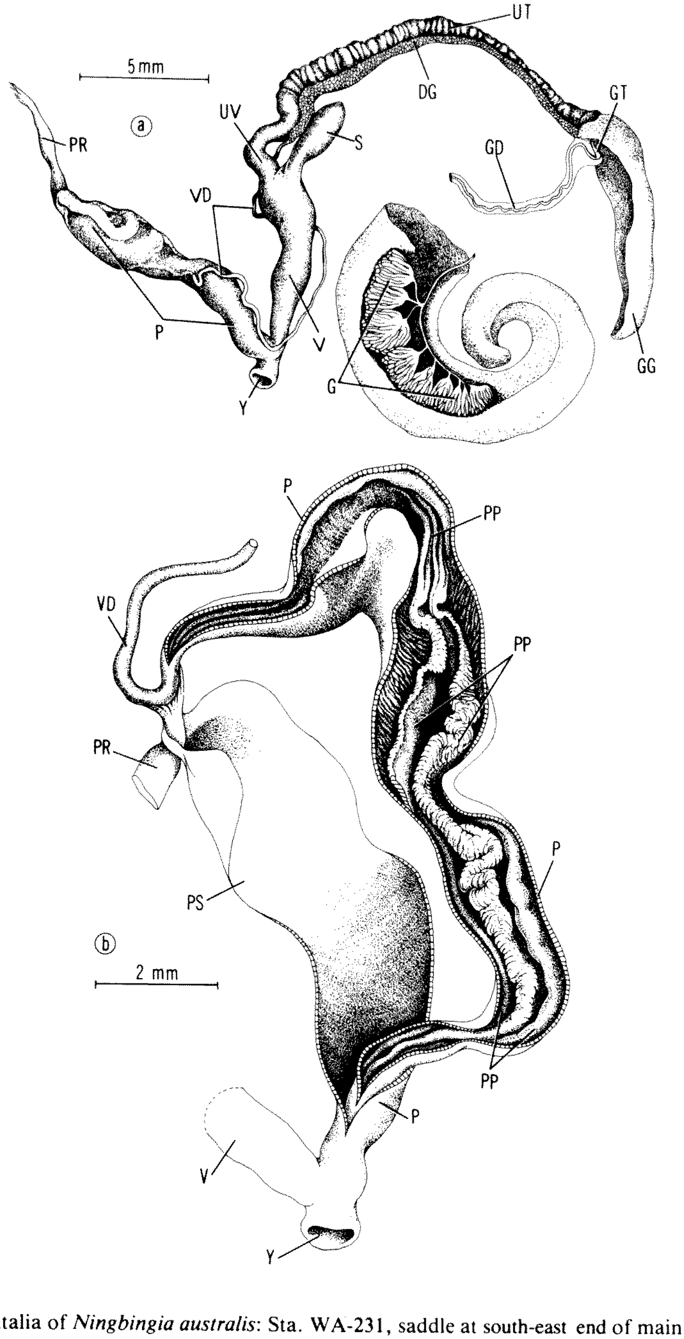


Fig. 87: Genitalia of *Ningbingia australis*: Sta. WA-231, saddle at south-east end of main northern block, Ningbing Ranges, 12 November 1976, FMNH 199954, paratopotypes, (a) whole genitalia, Dissection B; (b) interior of penis, Dissection C. Scale lines as marked.

87a-b) and equivalent to the differences seen between the sympatric *N. octava* and *N. laurina* **(Figs 82a-b, 83a-b, 84a-b)**.

Live collected adults were larger and slightly more elevated **(Table 36)** than dead examples from the same station, exactly the opposite situation observed for material of *N. res* collected on the same day.

GENUS *TURGENITUBULUS* NEW GENUS

Diagnosis

Shell smaller than average in size, spire usually very strongly and evenly elevated, occasionally slightly rounded above. Umbilicus narrowly open, regularly and slowly decoiling, partly covered by reflection of columellar lip. Apical sculpture **(Plate 16)** of radially elongated pustulations, becoming irregular to anastomosing radial riblets on later sections, most prominent in species with heavy postapical sculpture. Spire and body whorl usually with weak to very strong radial ribbing, shell base smooth in all except *T. costus*, where the radial sculpture continues undiminished across the base and into the umbilicus. Body whorl only slightly deflected behind lip, which is sharply and narrowly **(Figs 88a, 89d)** to broadly and gradually flared **(Figs 89a, 90a)**. Basal lip with generally low and broad **(Figs 88b, e, 89b, 90b, e)** ridge, sometimes **(Fig. 89e)** conical, marked on the outside of the shell by a very deep indentation and fairly long depression. Shell periphery generally obtusely angulated, slightly to moderately, more strongly in *T. depressus* **(Fig. 89e)**, with a very weak (*T. costus*) to strong (*T. depressus*) sulcus on the body whorl behind the lip. Parietal callus thin. Colour light yellow horn above periphery, base of shell, expanded lip, and basal ridge white. No colour bands or zones present. Apical genitalia agreeing with *Ningbingia*. Spermatheca (S) very short, with slender shaft. Head of spermatheca lying well below origin of free oviduct (UV), attached by connective tissue to base of uterus (UT). Vagina (V) usually short (long in *T. depressus*, **Fig. 94a**), moderately to strongly swollen, internally vagina and base of spermatheca with same wall sculpture seen in *Ningbingia* **(Fig. 80c)**. Penis complex short, with a sheath normally equal to its length (except *T. depressus*). Vas deferens (VD) unique in being enormously swollen and lengthened immediately after origin, curved upward along the prostate-uterus, then reflexing downward. Narrowing to normal diameter just above, at, or slightly below spermatheca-free oviduct junction. Swollen portion with heavily muscular walls **(Fig. 92b)**, narrow central passage. Vas deferens entering penis sheath just above base **(Fig. 91a)**, ascending to apex of penis sheath, reflexing anteriorly through apical plug of penis after receiving insertion of penial retractor muscle. Penis (P) normally with an apical plug, length and shape differing among species **(Table 37)**, absent in *T. depressus*. Verge (PV) normally conical to finger-shaped with terminal pore, grossly shortened and specialized in *T. opiranus* **(Fig. 93b)**. Chamber walls with longitudinal pilasters, generally one to three enlarged as stimulators, shape differing among species **(Table 37)**.

Type species: *Turgenitubulus christenseni* sp. nov.

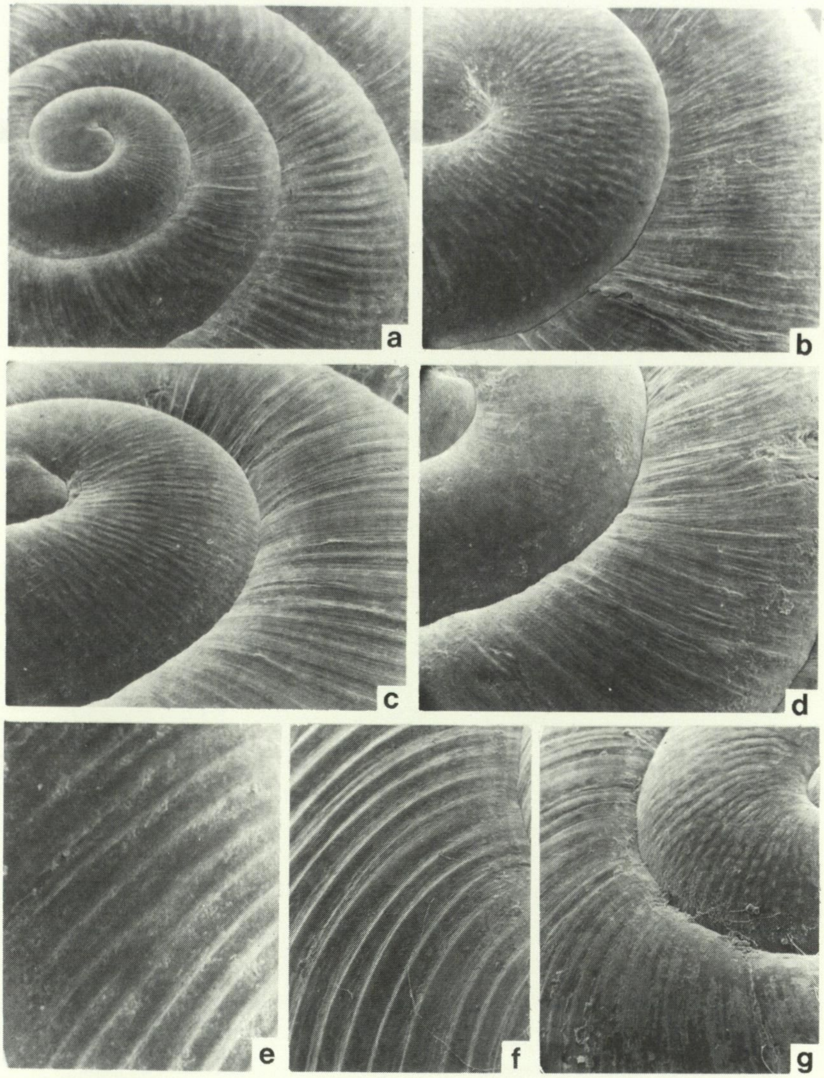


Plate 16: Shell sculpture in *Turgenitubulus*: (a-b) *T. christenseni*, (a) is FMNH 199955, Dissection A, Sta. WA-232, south of Tanmurra Creek, Ningbing Ranges, apex and spire at 14.9X, (b) is FMNH 199636, Sta. WA-228, Dissection A, 1.5 km north of Tanmurra Creek, Ningbing Ranges, apex and early spire at 36.2X; (c) *T. opiranus*, FMNH 200866, Dissection A, Sta. WA-227, 1.5 km north of Tanmurra Bore, Ningbing Ranges, apex and early spire at 38.6X; (d) *T. depressus*, FMNH 199953, Dissection A, Sta. WA-227, 1.5 km north of Tanmurra Bore, portion of apex and early spire at 34.9X; (e) *T. foramenus*, FMNH 199634, Sta. WA-425, opposite Tanmurra Bore, Ningbing Ranges, sculpture on 3rd whorl at 34.3X; (f) *T. costus*, FMNH 199956, Dissection A, Sta. WA-233, 2.5 km south of Tanmurra Bore, Ningbing Ranges, sculpture on 3rd whorl at 37.5X; (g) *T. costus*, FMNH 199956, Dissection A, Sta. WA-233, 2.5 km south of Tanmurra Bore, Ningbing Ranges, apex and early spire at 36.9X.

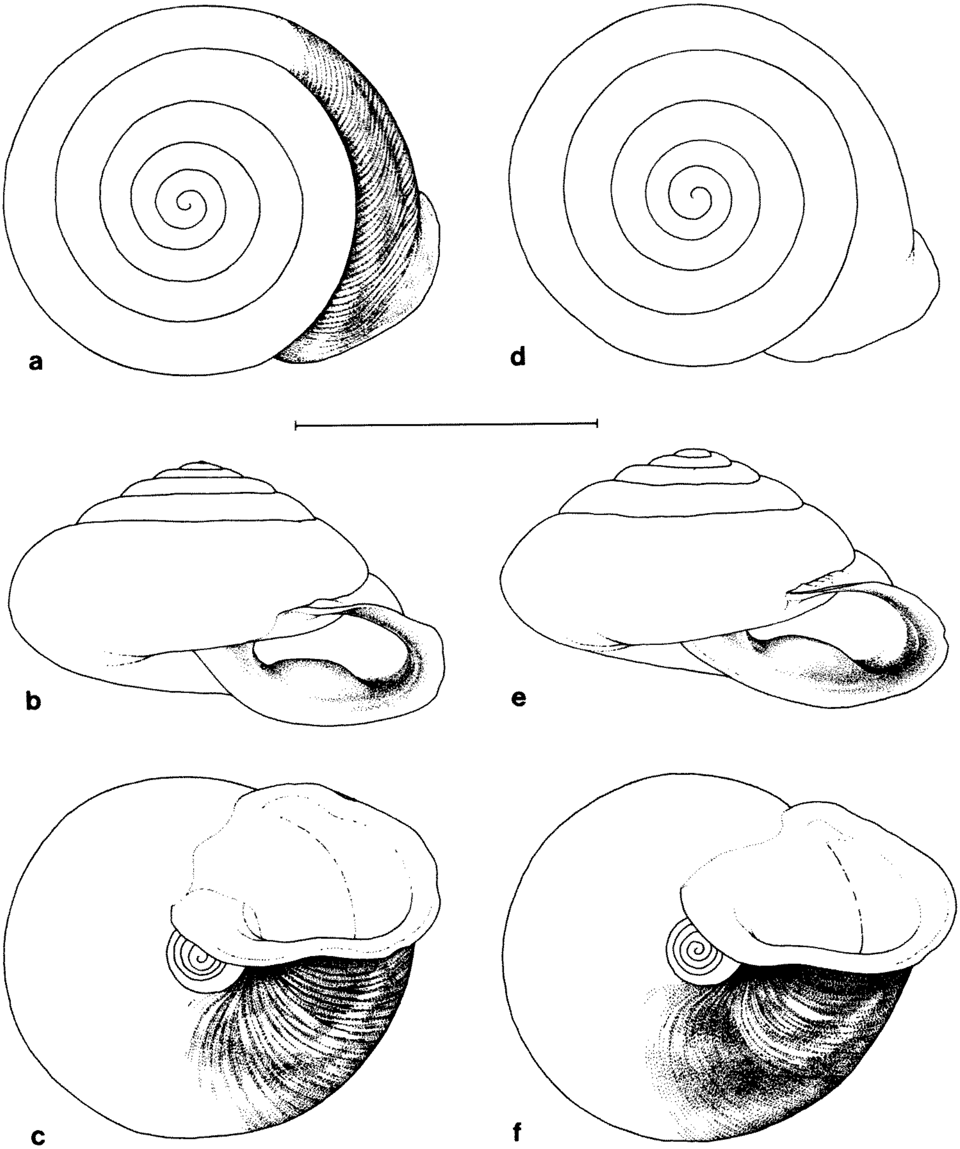


Fig. 88: Shells of *Turgenitubulus christenseni*: (a-c) Sta. WA-228, 1.5 km north of Tanmurra Creek, Ningbing Ranges, WAM 526.79, holotype; (d-f) Sta. WA-232, just south of Tanmurra Creek, Ningbing Ranges, WAM 531.79, paratype. Scale line equals 10 mm.

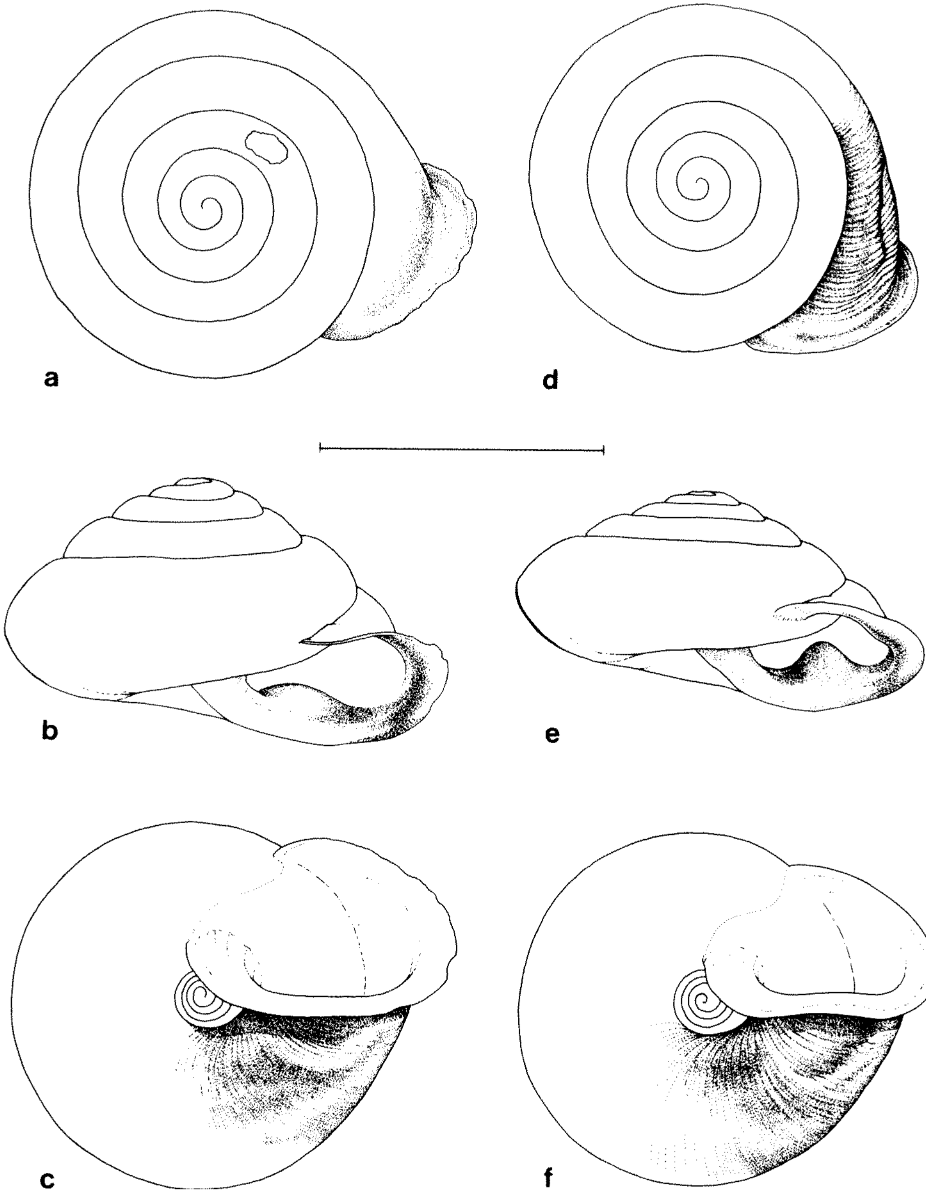


Fig. 89: Shells of *Turgenitubulus opiranus* and *T. depressus*: (a-c) *T. opiranus*, Sta. WA-227, 1.5 km north of Tanmurra Bore, Ningbing Ranges, WAM 496.79, holotype; (d-f) *T. depressus*, Sta. WA-227, 1.5 km north of Tanmurra Bore, Ningbing Ranges, WAM 509.79, holotype. Scale line equals 10 mm.

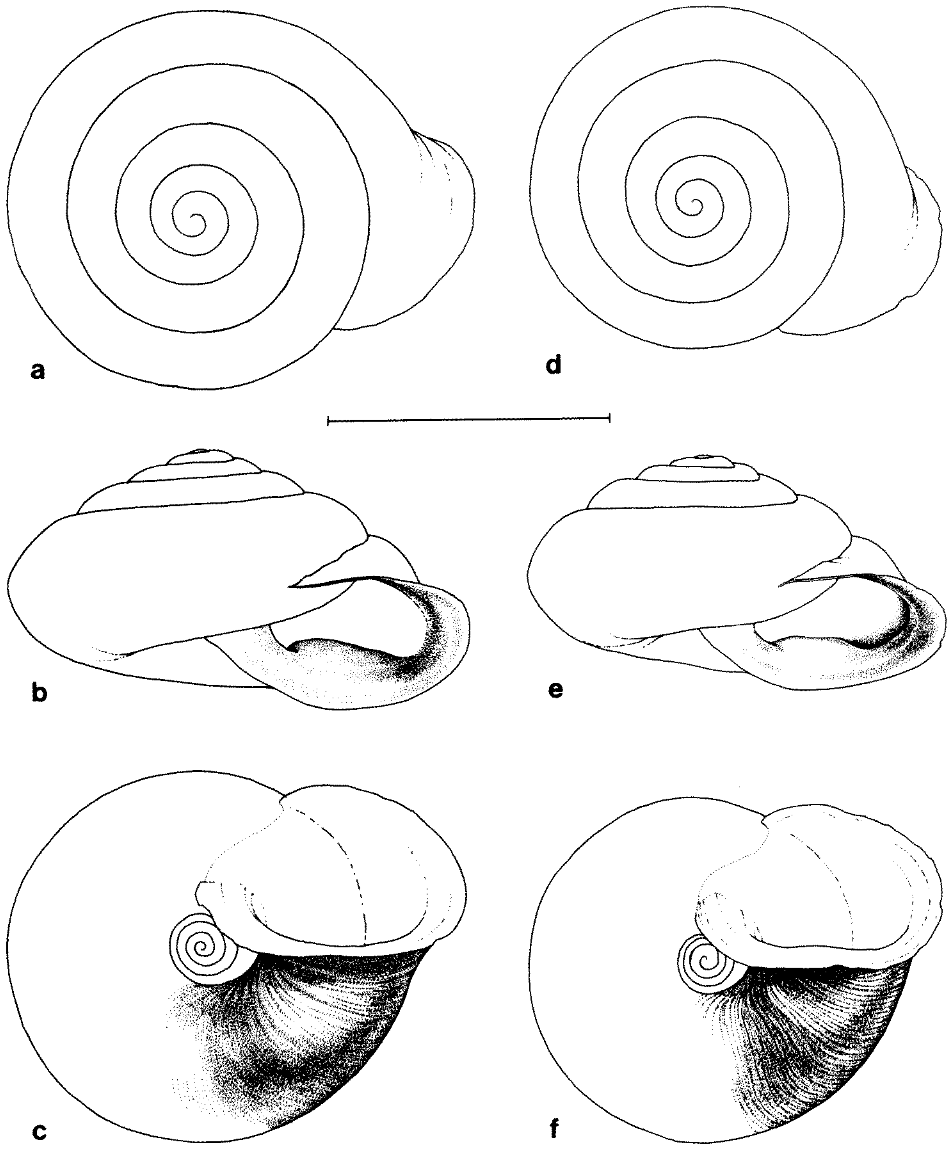


Fig. 90: Shells of *Turgenitubulus foramenus* and *T. costus*: (a-c) *T. foramenus*, Sta. WA-425, Tanmurra Bore, Ningbing Ranges, WAM 517.79, holotype; (d-f) *T. costus*, Sta. WA-233, 2.5 km south of Tanmurra Bore, Ningbing Ranges, WAM 502.79, holotype. Scale line equals 10 mm.

Comparisons

Turgenitubulus differs conchologically from the species of *Ningbingia* in possession of distinct, although sometimes weak, radial ribbing and in always having a prominent basal lip ridge. The only *Ningbingia* species with a basal ridge, *N. res* **(Figs 78c-d),** has it deeply recessed, and no species of *Ningbingia* has distinct radial ribbing on the spire or body whorl. In addition, the species of *Turgenitubulus* are generally smaller and with less ovate shapes (reflected in a lower mean H/D ratio) than those of *Ningbingia* **(Table 35)**. *Cristilabrum* **(Table 39)** generally is much larger in size, with the exception of the relatively dwarfed *C. buryillum*, and generally are more depressed in shape. There is almost complete overlap in shell sculpture between *Cristilabrum* and *Turgenitubulus.* Several *Cristilabrum* species have a basal lip ridge that is quite comparable with the one seen in *Turgenitubulus.* Other species, *C. solitudum* **(Fig. 97b)**, *C. bilarnium* **(Fig. 100b)**, and *C. funium* **(Fig. 100e),** have the basal ridge reduced to a recessed remnant near the columella, while in *C. simplex* **(Fig. 97e)** it is completely absent. While in general there is a slightly different appearance to the shells of *Turgenitubulus* and *Cristilabrum*, it is difficult to quantify any differences and there are no absolute shell features separating them.

Anatomically, *Cristilabrum* differs most obviously in that the vas deferens is of normal size, and most species have a very long penis and vagina. It shares with *Turgenitubulus* a basal insertion of the vas deferens into the penis sheath **(Fig. 101a)**. Except for *C. bilarnium* **(Figs 106a-b),** which is unusual in many features, the penis is considerably longer than the sheath, quite slender, lacks a verge, has small to prominent penial stimulators and simple longitudinal pilasters.

Turgenitubulus is thus an anatomically compact unit, showing major differences from its geographic neighbours, although sharing many shell features with them. While conchologically it is possible to separate *Ningbingia* and *Turgenitubulus*, the shells of *Cristilabrum* cannot be differentiated from those of the latter genus. Within *Turgenitubulus*, there are relatively minor patterns of variation in both shell and anatomy. These are partly summarized in **Table 37**. Except for the continuation of radial sculpture onto the shell base in *T. costus*, differences in sculpture are of degree and could not be quantified. **Plate 16f** shows the very high and sharply defined sculpture of *T. costus* in comparison with the broader, less sharply defined sculpture of *T. foramenus* **(Plate 16e).** The other species have less clearly defined postapical sculpture, and **Plate 16** illustrates the rough correlation between apical sculpture prominence and postapical sculpture strength. The basal lip ridge is broad and prominent in all species except *T. depressus* where it is narrowed into a conial projection **(Fig. 89e)**. There is greater variability in the peripheral sulcus and the degree and type of lip expansion **(Figs 88-90)**, but these are relatively minor variations.

Insufficient data are available to determine if the variations in early apical reflection of the expanded vas deferens have systematic correlation, or if individual

Table 37: Structural Variation in *Turgenitubulus*

Species	Radial Sculpture On Shell Base	Basal Lip Ridge Shape	Peripheral Sulcus	Lip Reflection
T. christenseni	–	broad	medium	sharp, moderate
T. opiranus	–	broad	absent to weak	sharp, wide
T. depressus	–	conical	prominent	sharp, narrow
T. foramenus	–	broad	weak to moderate	gradual, wide
T. costus	+	broad	very weak	sharp, moderate

			PENIS STRUCTURES:			
Species	**Vagina**	**Free Oviduct**	**Verge**	**Circular Collar**	**Enlarged Pilaster**	**Apical Plug**
T. christenseni	short	medium, thin	conical	–	2-3, long	not symmetrical, large
T. opiranus	short	long, thin	finger-shaped	–	2, short	very large
T. depressus	long	short, thin	short, blunt	+	2, long	absent
T. foramenus	medium	short, thick	conical	+	1, short	very large
T. costus	short	long, thin	conical	–	1, huge	medium

variablility exceeds inter-population range. The comparatively minor curvature in *T. opiranus* **(Fig. 93a)** and *T. depressus* **(Fig. 94a)** contrasts with the extreme bending seen in *T. foramenus* **(Fig. 95a)** and *T. costus* **(Fig. 96a)**. This is not a seasonal change, since two extremes in bending came from May and November samples. Particularly in contrast with most *Cristilabrum* species **(Figs 101-105)**, the vaginae in *Turgenitubulus* are extremely short. The significantly elongated vagina in *T. depressus* **(Fig. 94a)** correlates with the greatly lengthened penis **(Fig. 94b)** of that species and is interpreted as part of the species recognition changes resulting from microsympatry with *T. opiranus*.

The very short and chunky penis, generally with large apical plug, although variable among species **(Table 37)**, generally conical verge (altered in *T. opiranus*, **Fig. 93b)**, and the pattern of having one to three stimulatory pilasters that lack any micro-ridgelets, combine to establish this as a monophyletic unit with comparatively minor interspecific adjustments. Two taxa, *T. depressus* **(Fig. 94b)** and *T. foramenus* **(Fig. 95b)**, have an added structure, a circular ridge surrounding the verge.

The only known example of intrageneric sympatry for *Turgenitubulus* involves *T. opiranus* and *T. depressus* from Sta. WA-227. The pattern of changes have been discussed above (p. 326).

Considerable areas within the known range of *Turgenitubulus*, which extends from an isolated hill north of Tanmurra Creek, south to 2.5 km south of Tanmurra Bore, have not been sampled and some unsampled hills exist between the southernmost record at Sta. WA-233 and Sta. WA-234, the northernmost record for *Cristilabrum*. In the limited time available in the Ningbing Ranges, it was not possible to sample the limestone hills in 'The Gorge' of Surprise Creek. Whether *Turgenitubulus* or *Cristilabrum* inhabits this area is unknown.

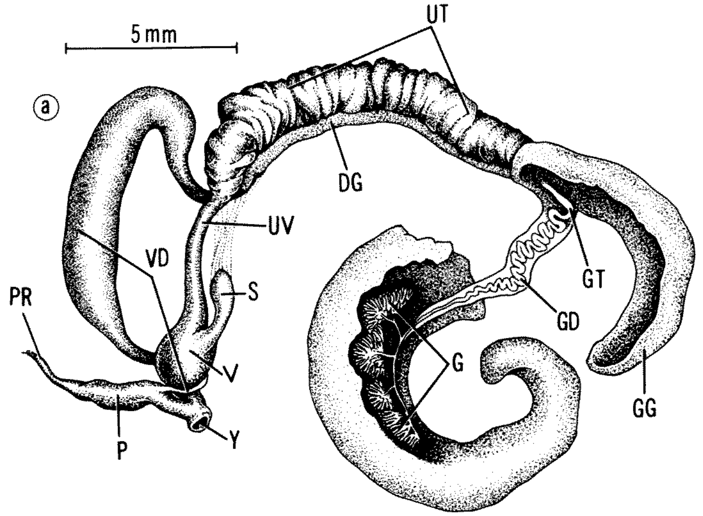
The name *Turgenitubulus*, meaning swollen tube, refers to the gross enlargement of the vas deferens, a situation I have not seen elsewhere in helicoid land snails.

TURGENITUBULUS CHRISTENSENI SP. NOV.

(Plate 16a-b; Figs 88a-f, 91a-b, 92a-b)

Comparative remarks

Turgenitubulus christenseni **(Figs 88a-f)** is distinctly more narrowly umbilicated **(Table 35)** and has a less reflected lip than *T. opiranus* **(Figs 89a-c)**, but otherwise the two species are very similar in size and shape. *T. depressus* **(Fig. 89e)** has a much narrower and sharply defined basal lip ridge, is noticeably less elevated (mean H/D ratio 0.511), and distinctly smaller in size (mean diameter 14.27 mm). *Turgenitubulus foramenus* has the lip more broadly and gradually flared (compare **Figs 88a, d, 90a)** and generally has the basal ridge lower, but there is considerable overlap in this feature. *Turgenitubulus costus* has a slightly reduced whorl count (mean 5 1/8), the same more gradual lip flare **(Fig. 90d)** seen in *T. foramenus*, a much reduced basal ridge **(Fig. 90e)**, and heavy radial sculpture **(Plate 16f)** that continues onto the shell base. Species of *Cristilabrum* with similar basal ridges, *C. grossum* **(Fig. 99b)** and *C. primum* **(Fig. 98b)**, are much more angulated with sculpture as heavy on the shell base as on the spire (compare **Figs 88a, c, f** with **98a, c)**. Anatomically, the conical verge **(Fig. 92b)**, very short penis and vagina **(Fig. 92a)**, and bulbous pilasters inside the penis of *T. christenseni* are diagnostic. *Turgenitubulus costus* **(Figs 96a-b)** is most similar, but differs in the longer vagina (V), less swollen spermathecal-vaginal junction, and in having only one main en-



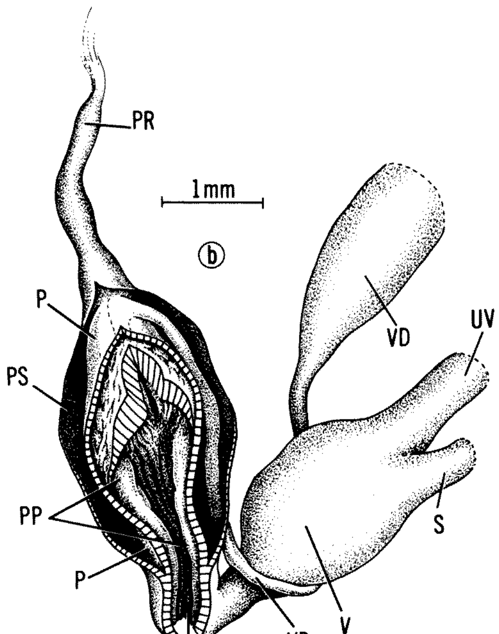


Fig. 91: Genitalia of *Turgenitubulus christenseni*: Sta. WA-228, 1.5 km north of Tanmurra Creek, Ningbing Ranges, 18 May 1977, FMNH 199636, paratopotype, Dissection A, (a) whole genitalia, (b) penis interior. Scale lines as marked.

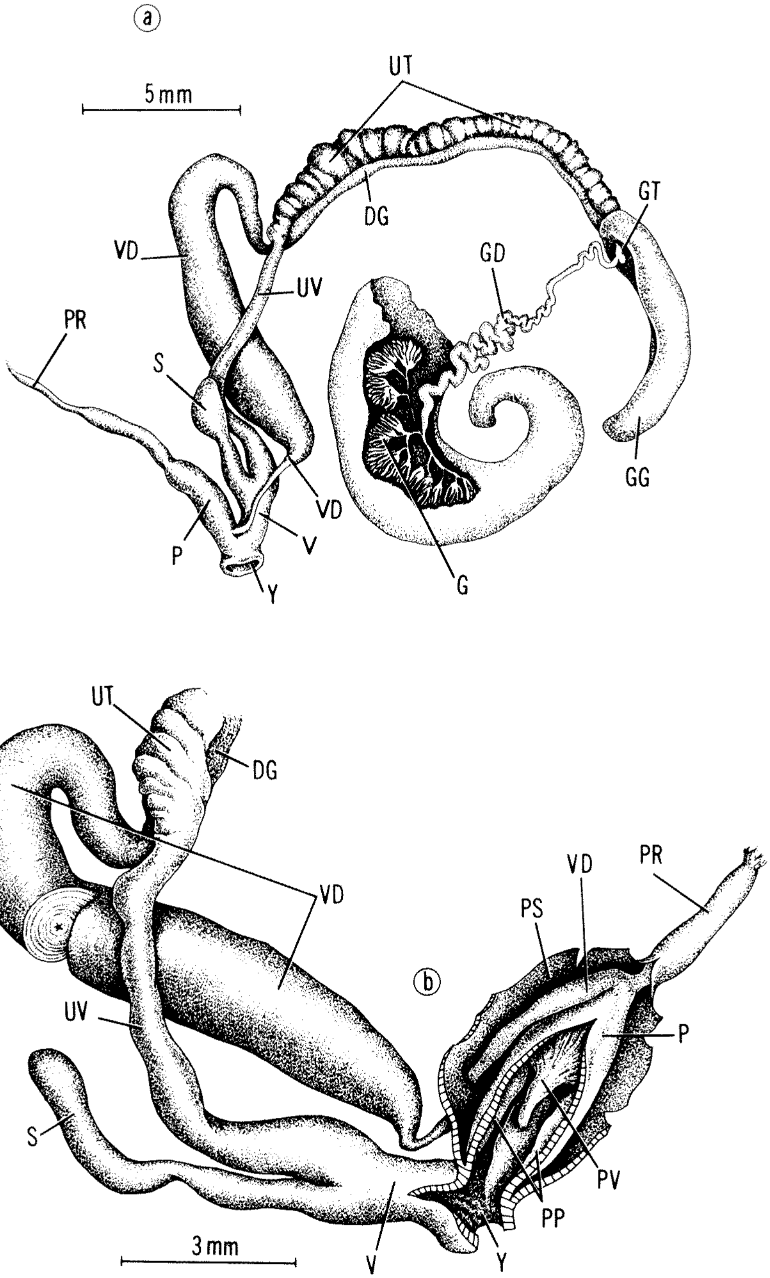


Fig. 92: Genitalia of *Turgenitubulus christenseni*: Sta. WA-232, just south of Tanmurra Creek, Ningbing Ranges, 12 November 1976, FMNH 199955, paratypes, (a) whole genitalia, Dissection B, (b) interior of penis, Dissection C. Scale lines as marked.

larged pilaster inside the penis chamber instead of two or three. *Turgenitubulus opiranus* **(Fig. 93b)** lacks the conical verge of *T. christenseni* **(Fig. 92b)**, while the very elongated penis of *T. depressus* **(Fig. 94b)** immediately separates that species.

Holotype

WAM 526.79, Sta. WA-228, isolated limestone hill 1.5 km north of Tanmurra Creek, Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667–576:367). Collected by Alan Solem and Carl Christensen 11 November 1976. Height of shell 9.9 mm, diameter 16.0 mm, H/D ratio 0.619, whorls 6-, umbilical width 1.5 mm, D/U ratio 10.7.

Paratopotypes

WAM 574.79, WAM 524.79, WAM 533.79, WAM 532.79, FMNH 199019, FMNH 199040, FMNH 199636, 6 live and 69 dead adults from the type locality.

Paratypes

Ningbing Ranges, north of Kununurra: Sta. WA-232, range outlier just south of Tanmurra Creek ('Carlton' 4667–578:348) (8 live, 257 dead adults, 3 live juveniles, WAM 567.79, WAM 531.79, WAM 547.79, FMNH 199011, FMNH 199955).

Diagnosis

Shell of average size, 14.3-18.0 mm (mean 16.13 mm) in diameter, with 4½ to 6 ⅛ (mean 5 ⅜-) normally coiled whorls. Apex and spire strongly and usually evenly elevated **(Figs 88b, e)**, height of shell 8.0-11.4 mm (mean 9.83 mm), H/D ratio 0.493-0.725 (mean 0.591). Apical sculpture **(Plate 16b)** typical, postapical whorls **(Plate 16a)** with rather prominent radial ribs that become more sharply defined on lower spire, but are absent from shell base which shows only vague irregular radial growth lines. Shell periphery obtusely rounded **(Fig. 88b)** to moderately angulated **(Fig. 88e)**, last part of body whorl with a weak to fairly prominent peripheral sulcus **(Fig. 88a)**. Body whorl slightly deflected behind lip, which is sharply and comparatively narrowly reflected on outer margin **(Figs 88b, e)**, and with a high and broad, slightly recessed, basal ridge. Umbilicus regularly and slowly decoiling, partly closed by strong reflection of columellar lip, which sometimes actually curves down into the opening, umbilical width 0.6-2.6 mm (mean 1.64 mm), D/U ratio 5.98-24.6 (mean 10.3). Based on 335 measured adults.

Genitalia **(Figs 91a-b, 92a-b)** with typically enlarged vas deferens (VD) which narrows near head of vagina (V) and enters penis sheath (PS) very near base. Penis (P) very short, with rather thick walls, internally with a slanted apical plug leading to a slender, almost finger-like verge (PV, **Fig. 92b**) with terminal pore. Walls of penis chamber with two **(Fig. 91b)** to three **(Fig. 92b)** prominent longitudinal pilasters, one of which tends to be higher and almost pustulose in mid-section. Apical plug much

Table 38: Local Variation in *Turgenitubulus*

Taxon	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
T. christenseni				
WA-228, FMNH 199636, 18-V-77	7 (L)	9.71 ± 0.299 (9.0-11.3)	16.27 ± 0.135 (15.8-16.75)	0.597 ± 0.020 (0.544-0.706)
WA-228, FMNH 199040, 18-V-77	50 (D)	9.72 ± 0.073 (8.6-11.2)	16.19 ± 0.077 (15.1-17.1)	0.601 ± 0.004 (0.547-0.713)
WA-228, FMNH 199019, 11-XI-76	19 (D)	9.54 ± 0.111 (8.8-10.3)	16.82 ± 0.173 (15.5-18.0)	0.568 ± 0.007 (0.531-0.635)
WA-232, FMNH 199011, 12-XI-76	251 (D)	9.87 ± 0.037 (8.0-11.4)	16.04 ± 0.041 (14.3-17.8)	0.591 ± 0.002 (0.493-0.725)
T. opiranus				
WA-227, FMNH 200864, 11-XI-76	55 (D)	9.29 ± 0.110 (7.0-10.4)	16.29 ± 0.110 (14.0-17.6)	0.572 ± 0.005 (0.476-0.654)
WA-227, FMNH 200865, 11-XI-76	40 (D)	9.08 ± 0.145 (6.4-10.3)	15.9 ± 0.158 (13.3-17.8)	0.571 ± 0.006 (0.478-0.643)
WA-227, FMNH 199044, 16-V-77	15 (D)	10.09 ± 0.128 (9.3-11.05)	16.64 ± 0.118 (15.8-17.35)	0.606 ± 0.008 (0.550-0.656)
T. depressus				
WA-227, FMNH 199953, 11-XI-76	7 (L)	7.56 ± 0.242 (6.7-8.35)	14.16 ± 0.269 (13.4-15.15)	0.534 ± 0.013 (0.488-0.572)
WA-227, FMNH 199012, 11-XI-76	107 (D)	7.27 ± 0.036 (6.5-8.4)	14.21 ± 0.051 (13.2-15.9)	0.512 ± 0.002 (0.459-0.596)
WA-227, 11-XI-76	74 (D)	7.27 ± 0.048 (6.6-8.6)	14.38 ± 0.090 (12.9-16.6)	0.506 ± 0.002 (0.403-0.555)
T. foramenus				
WA-425, FMNH 199033, 16-V-77	221 (D)	9.62 ± 0.052 (8.3-11.5)	16.28 ± 0.042 (14.6-18.4)	0.594 ± 0.002 (0.503-0.688)
T. costus				
WA-233, FMNH 199956, 12-XI-76	19 (L)	8.85 ± 0.089 (8.2-9.4)	14.91 ± 0.096 (14.2-15.7)	0.594 ± 0.005 (0.566-0.626)
WA-233, FMNH 199011, 12-XI-76	58 (D)	8.96 ± 0.079 (8.2-10.5)	15.33 ± 0.085 (14.2-16.5)	0.585 ± 0.004 (0.531-0.659)

Taxon	Number of Adults Measured	Mean, Range and SEM of: Whorls	Umbilical Width	D/U Ratio
T. christenseni				
WA-228, FMNH 199636, 18-V-77	7 (L)	$5\frac{5}{8}$+ ($5\frac{1}{2}$-6)	1.99 ± 0.154 (1.4-2.45)	8.50 ± 0.731 (6.84-11.4)

Table 38: Local Variation in *Turgenitubulus* (continued)

Taxon	Number of Adults Measured	Mean, Range and SEM of: Whorls	Umbilical Width	D/U Ratio
WA-228, FMNH 199040, 18-V-77	50 (D)	5⅝– (5¼-6)	1.73±0.044 (0.9-2.3)	9.70±0.274 (7.1-18.2)
WA-228, FMNH 199019, 11-XI-76	19 (D)	5½ (5¼-5⅝)	1.89±0.070 (1.3-2.4)	9.16±0.398 (7.14-12.9)
WA-232, FMNH 199011, 12-XI-76	251 (D)	5¼ (4½-5⅝)	1.58±0.021 (0.6-2.5)	10.6±0.153 (6.68-24.6)
T. opiranus				
WA-227, FMNH 200864, 11-XI-76	55 (D)	5⅜– (5⅛-5¾)	1.54±0.044 (1.2-2.2)	10.65±0.356 (7.34-12.8)
WA-227, FMNH 200865, 11-XI-76	40 (D)	5¼ (5-5½)	1.56±0.064 (0.9-2.2)	10.61±0.284 (7.02-13.9)
WA-227, FMNH 199044, 16-V-77	14 (D)	5½ – (5¼-5⅝)	1.64±0.072 (1.1-2.3)	10.42±0.437 (7.26-14.4)
T. depressus				
WA-227, FMNH 199953, 11-XI-76	7 (L)	5⅜ (5-5⅝)	1.88±0.141 (1.3-2.4)	7.82±0.671 (5.58-11.2)
WA-227, FMNH 199012, 11-XI-76	107 (D)	5¼ (5-5⅝)	1.79±0.121 (1.1-2.6)	8.13±0.461 (6.10-11.8)
WA-227, 11-XI-76	74 (D)	5¼ + (5-5⅝)	1.95±0.087 (1.2-2.2)	7.64±0.572 (5.11-11.8)
T. foramenus				
WA-425, FMNH 199033, 16-V-77	221 (D)	5⅜ (4⅞-5⅞)	1.78±0.021 (1.0-2.7)	9.42±0.114 (6.10-16.5)
T. costus				
WA-233, FMNH 199956, 12-XI-76	19 (L)	5⅛+ (5-5⅝)	1.81±0.068 (1.2-2.3)	8.46±0.332 (6.54-11.8)
WA-233, FMNH 199011, 12-XI-76	58 (D)	5⅛– (4⅝-5⅜)	1.77±0.040 (1.1-2.4)	8.87±0.201 (6.77-13.0)

thicker on one side **(Fig. 91b)** than the other **(Fig. 92b)**. Vagina (V) very short, tending to be grossly swollen **(Fig. 91a)**. Based on 5 dissected adults.

Discussion

Turgenitubulus christenseni has been taken from isolated hills on both sides of Tanmurra Creek. The specimens from Sta. 228 **(Table 38)** have a slightly higher mean whorl count and a little more open umbilicus than those from Sta. 232. The latter tend to have slightly more prominent radial ribbing (compare **Figs 88c** and **f**). The degree of peripheral angulation shown in **Fig. 88e** occurs more frequently at Sta. 232 than Sta. 228, but sufficient intermediate examples are present that I could not successfully quantify this difference. Since their genital anatomies are essentially identical, the two populations are kept as members of the same species.

Seasonal differences in the genitalia are illustrated in **Figs 91a** and **92a**. The latter were collected in November and represent very late dry season conditions, while the former were taken in early May at the start of the dry season. The larger uterus (UT) and more swollen upper vagina (V) in May **(Fig. 91a)** contrast with the larger ovotestis (G) and hermaphroditic duct (GD) of the November examples. This pattern is consistent with that demonstrated for seasonal variation in *Amplirhagada*, and these variations have no systematic significance.

The penis interiors **(Figs 91b, 92b)** show different aspects and are not directly comparable. In **Fig. 91b**, the apical plug has been slit to show its thickness, and the tapering verge is not shown, but was hidden to the left side. In **Fig. 92b**, the penis has been opened on the side opposite to the apical plug and the verge (PV) is quite prominent.

Turgenitubulus christenseni is dedicated to Carl C. Christensen, companion when the species was collected, and dedicated student of arid region land snails.

TURGENITUBULUS OPIRANUS SP. NOV.

(Plate 16c; Figs 89a-c, 93a-b)

Comparative remarks

Turgenitubulus opiranus has a more broadly flaring lip **(Fig. 89a)** than does *T. christenseni* and is, on average, more widely umbilicated **(Table 35)**. The sculpture on the spire is more closely spaced and less conspicuous **(Plate 16c)** than in *T. christenseni* **(Pl. 16a)**. *Turgenitubulus depressus* **(Figs 89d-f)** is smaller, with a lower spire **(Table 35)**, more angulated periphery **(Fig. 89e)**, and tends to have more prominent spire sculpture. *Turgenitubulus foramenus* **(Plate 16e)** and *T. costus* **(Plate 16f)** both have much more prominent radial sculpture, and show minor differences in size and shape **(Table 35)**. Anatomically, the very large apical plug in the penis **(Fig. 93b)**, verge (PV) with its flaring head, very short pilasters (PP), and short vagina **(Fig. 93a)** of *T. opiranus* are very different from long vagina **(Fig. 94a)**, finger-like verge (PV, **Fig. 94b**), very long penis coiled in the sheath, and large pilaster of the sympatric *T. depressus*. *Turgenitubulus foramenus* has many long pilasters, the same type of verge, but a much shorter free oviduct **(Fig. 95b)**; *T. costus* **(Fig. 96b)** has one large pilaster and a conical verge; while *T. christenseni* **(Figs 91b, 92b)** has a conical verge and two or three large pilasters below the apical plug.

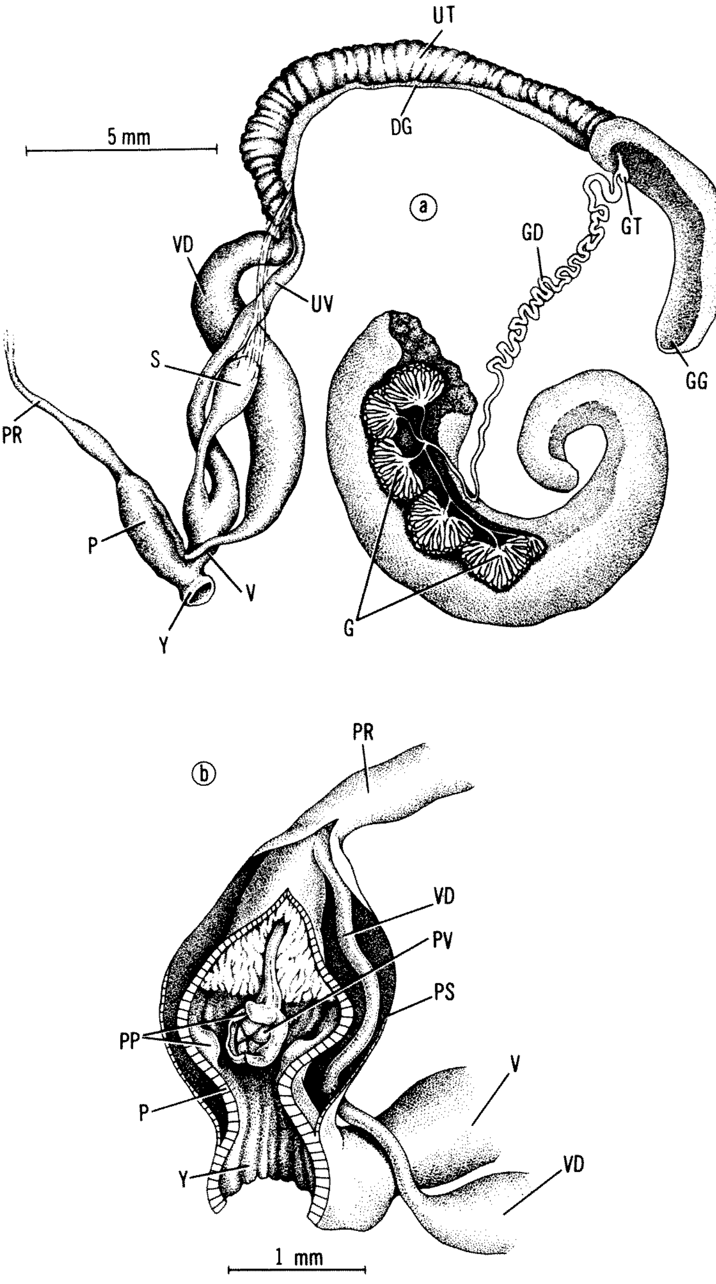


Fig. 93: Genitalia of *Turgenitubulus opiranus*: Sta. WA-227, 1.5 km north of Tanmurra Bore, Ningbing Ranges, 11 November 1976, FMNH 200866, paratopotype, Dissection A, (a) whole genitalia, (b) interior of penis. Scale lines as marked.

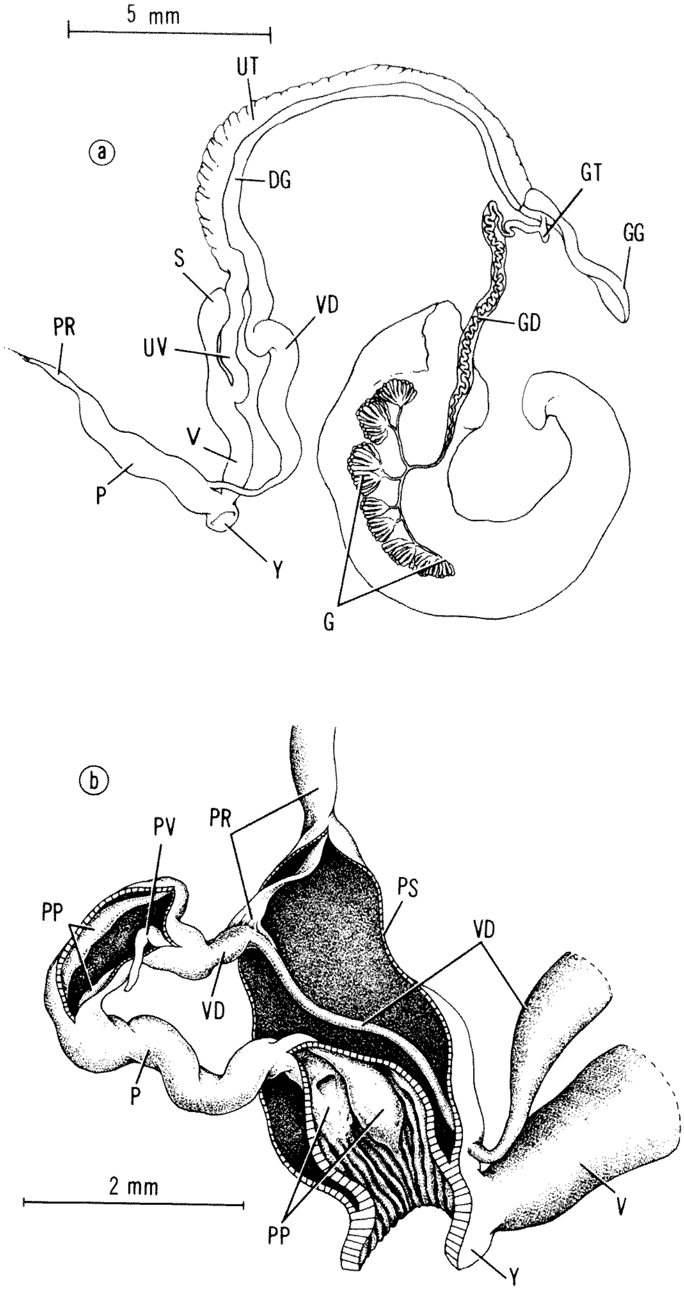


Fig. 94: Genitalia of *Turgenitubulus depressus*: Sta. WA-227, 1.5 km north of Tanmurra Bore, Ningbing Ranges, 11 November 1976, FMNH 199953, paratopotypes, (a) whole genitalia, Dissection C, (b) interior of penis, Dissection B. Scale lines as marked.

Holotype

WAM 496.79, Sta. WA-227, east slope of range, 1.5 km north of Tanmurra Bore, Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667—595:325). Collected by Alan Solem and Carl Christensen 11 November 1976. Height of shell 10.1 mm, diameter 15.8 mm, H/D ratio 0.639, whorls 5½, umbilical width 1.6 mm, D/U ratio 9.88.

Paratopotypes

WAM 501.79, WAM 525.79, WAM 503.79, FMNH 199044, FMNH 200864-6, 1 live and 107 dead adults from the type locality.

Diagnosis

Shell of average size, 13.3-17.8 mm (mean 16.19 mm) in diameter, with 5 to 5¾ (mean 5 ⅜-) normally coiled whorls. Apex and spire strongly and evenly elevated **(Fig. 89b)**, height of shell 6.4-11.1 mm (mean 9.32 mm), H/D ratio 0.476-0.656 (mean 0.576). Apical sculpture **(Plate 16c)** typical, postapical sculpture low and relatively fine, shell base smooth. Periphery normally obtusely angulated **(Fig. 89b)**, rarely rounded, last part of body whorl with an at most weak peripheral sulcus. Body whorl slightly deflected behind lip, which is broadly and sharply expanded **(Fig. 89a)**, partly covering umbilicus, basal lip with a broad, low, rounded ridge **(Fig. 89b)**. Umbilicus slowly and regularly decoiling, partly closed by reflected lip, umbilical width 0.8-2.4 mm (mean 1.68 mm), D/U ratio 7.02-14.4 (mean 10.51). Based on 111 measured adults.

Genitalia **(Figs 93a-b)** with typically enlarged vas deferens (VD) entering base of penis sheath, short vagina which is only moderately swollen, very long free oviduct (UV). Penis very short, rather thick-walled, internally **(Fig. 93b)** with large apical plug, verge (PV) with thin collar and puckered tip, walls with two very small pilasters (PP) lateral to verge tip. Based on 1 dissected adult.

Discussion

Specimens of *T. opiranus* and *T. depressus* collected by Solem and Christensen were bagged separately in the field and then catalogued separately to test for collecting bias. There were no detectable differences **(Table 38)**. The dead adults taken the subsequent May (FMNH 199044) were from a few yards away and thus the differences may reflect microgeographic variation. The two species were not recognized in the field as being distinct, and thus the sample of eight live adults was considered adequate. Unfortunately only one of these is *T. opiranus*, but the differences from *T. depressus* **(Figs 94a-b)** are so dramatic that I had no hesitation in describing both species.

The name *opiranus* is taken from a prominent landmark, Opir Hill, which lies slightly north-north-east of the type locality.

TURGENITUBULUS DEPRESSUS SP. NOV.

(Plate 16d; Figs 89d-f, 94a-b)

Comparative remarks

Turgenitubulus depressus is immediately recognizable by its low spire (mean H/D ratio 0.511), conical and sharply defined basal lip ridge **(Fig. 89e)**, sharply angled periphery, and strong, rather widely spaced radial sculpture. The sympatric *T. opiranus* is much more elevated (mean H/D ratio 0.576), larger (mean diameter 16.19 mm), and has a much more prominent, broader basal lip ridge **(Fig. 89b)**. The large diameters **(Table 35)**, higher spires, and broader, larger lip ridges of *T. christenseni*, *T. foramenus*, and *T. costus* **(Figs 88b, e, 90b, e)** effectively separate shells of these species from *T. depressus*. *Cristilabrum buryillum* **(Figs 98d-f)** is very similar in shape and lip ridge, but averages 2 mm more in diameter at the same whorl count and has much more prominent radial sculpture **(Plate 17d)**. No other Ningbing species can be confused on the basis of shell features. Anatomically, *T. depressus* is immediately separable from the other species by having the penis (P) twice the length of the sheath **(Fig. 94b)** and with an apical finger-shaped verge (PV). The long vagina **(Fig. 94a**, V) is the main external difference. All other *Turgenitubulus* have short vaginae and the penis equal in length to the sheath. Species of *Cristilabrum* mostly agree in having longer vaginae, very different internal pilasters in the very slender penis, and lack the great enlargement of the vas deferens found in all *Turgenitubulus*.

Holotype

WAM 509.79, Sta. WA-227, east slope of range, 1.5 km north of Tanmurra Bore, Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667—595:325). Collected by Alan Solem and Carl Christensen 11 November, 1976. Height of shell 7.7 mm, diameter 14.85 mm, H/D ratio 0.519, whorls 5½, umbilical width 1.55 mm, D/U ratio 9.58.

Paratopotypes

WAM 548.79, WAM 514.79, WAM 522.79, FMNH 199953, FMNH 199012, FMNH 199013, 7 live and 182 dead adults, 2 live juveniles, from the type locality.

Diagnosis

Shell small, 12.9-16.6 mm (mean 14.27 mm) in diameter, with 5 to 5⅝ (mean 5¼) normally coiled whorls. Apex and spire moderately and evenly elevated **(Fig. 89e)**, height of shell 6.5-8.6 mm (mean 7.29 mm), H/D ratio 0.453-0.596 (mean 0.511). Apical sculpture typical **(Plate 16d)**, lower spire and body whorl with relatively prominent, widely spaced radial ribs, absent below periphery. Shell periphery obtusely to nearly acutely angled **(Fig. 89e)**, last part of body whorl normally with a prominent peripheral sulcus **(Fig. 89d)**. Lip thin, sharply and narrowly to moderately expanded **(Fig. 89d)**, strongly reflected to cover part of umbilicus **(Fig. 89f)**. Body whorl very slightly deflected behind lip. Basal lip with a high, narrow ridge **(Fig. 89e)** and deep exterior sulcus **(Fig. 89f)**. Umbilicus regularly and slowly decoiling, partly closed by reflected lip, umbilical width 1.1-2.6 mm (mean 1.86 mm), D/U ratio 5.11-11.8 (mean 7.93). Based on 189 measured adults.

Genitalia **(Figs 94a-b)** with grossly enlarged vas deferens (VD) entering just above base of penis sheath after narrowing. Penis sheath short, penis (P) twice sheath length **(Fig. 94b)**, basally with two pustulose pilasters (PP), longitudinal pilasters and a finger-shaped verge (PV) apically, walls of penis and sheath relatively thin. Vagina **(Fig. 94a)** long for genus, free oviduct (UV) relatively short. Based on 2 dissected individuals.

Discussion

The name *depressus* refers to the noticeably less elevated spire **(Fig. 89e)** in comparison with the other *Turgenitubulus*.

The presence of a greater number of *T. depressus* (167 dead, 7 live adults) than of *T. opiranus* (110 dead, 1 live adult) in the November samples is not the result of field bias. We were attempting to get all observed whole dead shells, plus a reasonable sample of live material, and did not realize that we had two species. In May, 1977, I attempted to revisit this station, but could not locate the exact spot quickly and got only a small sample of *T. opiranus*. All species from Sta. 227 could be assigned to species easily. Conchological confusion would be difficult once the striking differences in size, spire elevation, and basal lip ridge had been described.

The illustrated whole genitalia **(Fig. 94a)** is based on a new adult, hence the small size of the albumen gland (GG), prostate (DG) and uterus (UT). The vas deferens (VD) also is less swollen than is normal. This is exactly equivalent to the new adult genital development seen in *Xanthomelon prudhoensis* (Smith, 1894) (Solem, 1979: Fig. 9b), except that the latter dissection was based on late wet season (March) collection and the ovotestis (G) had not developed, while the newly adult *T. depressus* from very late dry season collecting (November) has the ovotestis **(Fig. 94a)** fully developed for early wet season reproduction. The same situation has been illustrated for *Amplirhagada castra* Solem **(Figs 68a-b)**, and thus seems to be a normal pattern of maturation in Western Australian camaenids.

Despite the recent maturation of this specimen (Dissection C), the penis interior showed no differences in structure from a fully mature adult (Dissection B) that was used to prepare the penis interior illustration **(Fig. 94b)**.

TURGENITUBULUS FORAMENUS SP. NOV.

(Plate 16e; Figs 90a-c, 95a-c)

Comparative remarks

Turgenitubulus foramenus is conchologically generalized except for its strong radial sculpture **(Plate 16e)** and broadly but gradually expanded lip **(Fig. 90b)**. The basal lip ridge **(Fig. 90c)** is high and wide in most examples, although rarely greatly reduced in size, and the umbilicus is somewhat less covered by the reflected lip **(Fig. 90c)**, although the D/U ratio is not significantly different. *Turgenitubulus costus* has even heavier sculpture **(Plate 16f)** that continues onto the shell base, a smaller basal lip ridge **(Fig. 90e)** and is slightly smaller with a reduced whorl count. *Turgenitubulus depressus* has a nearly conical basal lip ridge **(Fig. 89e)**, is smaller and more depressed. *Turgenitubulus opiranus* has weaker radial sculpture **(Plate 16c)**, more sharply expanded lip, and *T. christenseni* has less sharply defined sculpture **(Plate 16a)**. Anatomically, *T. foramenus* has the same type of circular ridge **(Fig. 95b)** seen in *T. opiranus* **(Fig. 93b)**, but it is more massive. While the latter has more than one enlarged pilaster in the lower penis, *T. foramenus* has only one. The conical verge **(Fig. 95c)** is rather similar to that seen in *T. christenseni* **(Fig. 92b)**. The very long vas deferens (VD), relatively short free oviduct (UV) and only slightly swollen vagina (V) are different from other *Turgenitubulus* in details. *Turgenitubulus depressus* is immediately separable by its very long penis **(Fig. 94b)** and long vagina **(Fig. 94a)**.

Holotype

WAM 517.79, Sta. WA-425, small knob and main range opposite Tanmurra Bore, Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667–598:313). Collected by Alan Solem 16 May 1977. Height of shell 9.7 mm, diameter 16.4 mm, H/D ratio 0.591, whorls 5¼+, umbilical width 2.05 mm, D/U ratio 8.00.

Paratopotypes

WAM 542.79, WAM 578.79, FMNH 199634, FMNH 199033, 2 live and 218 dead adults, 3 live juveniles from the type locality.

Diagnosis

Shell of average size, 14.6-18.4 mm (mean 16.28 mm) in diameter, with 4 7/8 to 5 7/8 (mean 5 3/8) normally coiled whorls. Apex and spire strongly and evenly elevated **(Fig. 90b)**, height of shell 8.3-11.5 mm (mean 9.62 mm), H/D ratio 0.503-0.688 (mean 0.593). Apical sculpture typical, spire and body whorl with prominent, rounded, rather widely spaced radial ribs **(Plate 16e)** that are absent from shell base. Periphery obtusely angulated, last part of body whorl with a weak to moderate peripheral sulcus. Body whorl gradually deflected behind lip, which is broadly and slowly reflected **(Fig. 90a)**, only moderately reflexed over part of the umbilicus, basal lip with a high and very broad ridge **(Fig. 90b)**. Umbilicus regularly decoiling, rather narrow, but less closed by reflected lip than is usual, umbilical width 1.0-2.6 mm (mean 1.78 mm), D/U ratio 6.10-16.5 (mean 9.41). Based on 221 measured adults.

Genitalia **(Figs 95a-b)** with very long and grossly swollen vas deferens (VD), short free oviduct (UV) and vagina (V) that is only slightly swollen. Penis short and fat,

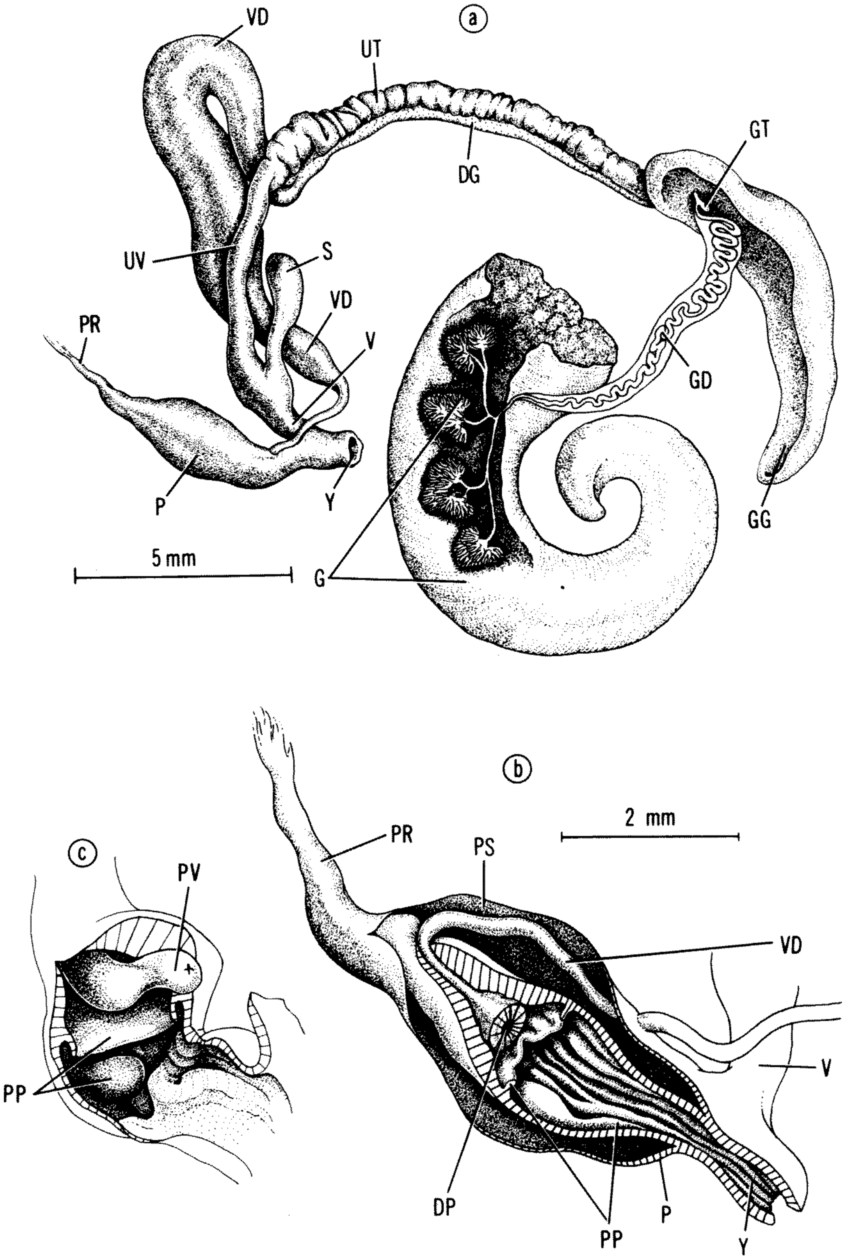


Fig. 95: Genitalia of *Turgenitubulus foramenus*: Sta. WA-425, opposite Tanmurra Bore, Ningbing Ranges, 16 May 1977, FMNH 199634, paratopotypes, (a) whole genitalia, Dissection A, (b) interior of penis, Dissection A, (c) detail of verge and pilasters, drawn from a partly retracted individual, Dissection B, greatly enlarged. Scale lines equal 2 mm.

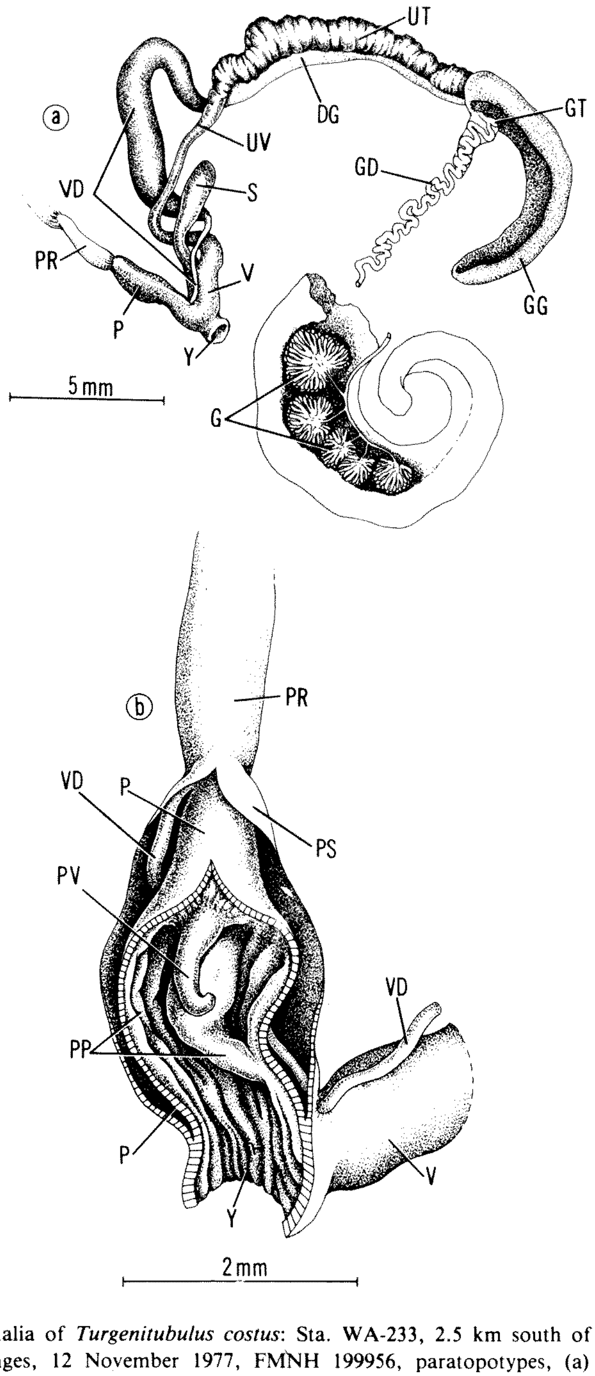


Fig. 96: Genitalia of *Turgenitubulus costus*: Sta. WA-233, 2.5 km south of Tanmurra Bore, Ningbing Ranges, 12 November 1977, FMNH 199956, paratopotypes, (a) whole genitalia, Dissection A, (b) interior of penis, Dissection C. Scale lines as marked.

equal in length to sheath, internally **(Fig. 95b)** with very large apical plug that encloses the descending vas deferens. A long conical verge is cut off in **Fig. 95b**, but shown in **Fig. 95c**, so that the circular collar attached to the penis wall could be shown effectively. Several longitudinal and one pustulose pilasters extend to the atrium (Y). Based on 2 dissected adults.

Discussion

The name *foramenus* refers to the more widely open appearing umbilicus in the shell, which is an artifact caused by a narrower reflection of the lip in this species. Actually the umbilicus is narrower than in some of the other species, but its effective opening (diameter minus lip reflection) is slightly wider.

Conchologically, *T. foramenus* is identical in size and shape to *T. christenseni* and *T. opiranus* **(Table 35)**, but has heavier radial sculpture **(Plate 16)** and the more gradual expansion of the shell lip (compare **Figs 88a, d, 89a, 90a**). The smaller *T. costus* and *T. depressus* also have sharper lip reflection and differences in the basal lip ridge.

Only two live adults were available — one was dissected completely and the penis extracted from the second. The presence of a circular ridge **(Fig. 95b)** around the upper penis chamber, the conical penis **(Fig. 95c)**, and the only one enlarged pilaster are significant differences from neighbouring species. The circular ridge is shared with *T. opiranus*, but the latter **(Fig. 93b)** has a very different verge, while *T. depressus* **(Fig. 94b)** differs radically in its elongated penis, finger-shaped verge, and two elongated pilasters. *Turgenitubulus costus* **(Fig. 96b)** lacks the circular ridge, has a finger-shaped penis, and one enormously enlarged pilaster, thus differing in several aspects.

TURGENITUBULUS COSTUS SP. NOV.

(Plate 16f-g; Figs 90d-f, 96a-b)

Comparative remarks

Turgenitubulus costus **(Figs 90d-f)** has a comparatively small basal lip ridge, very strong and sharply defined radial sculpture above and below the periphery **(Plate 16f)**, and is somewhat smaller in size than congeneric species **(Table 35)**. *Turgenitubulus depressus* is even smaller in size and more depressed, but also differs in its conical basal lip ridge **(Fig. 89e)**. *Turgenitubulus foramenus* has only slightly less prominent sculpture above the periphery **(Plate 16e)**, but differs obviously in its more gradually flared shell lip (compare **Figs 90a, d**), and the absence of radial sculpture from the shell base. Both *T. christenseni* and *T. opiranus* have less prominent sculpture **(Plate 16)** and a very different pattern of flare to the shell lip **(Figs 88a, d, 90a)**. Anatomically, the presence of a conical verge and a single grossly enlarged pilaster **(Fig. 96b)**, and the absence of a circular ridge around the upper penis chamber serve to distinguish *T. costus* from other *Turgenitubulus* species. The neighbouring *T. foramenus* **(Figs 95b, c)** has a circular ridge and one moderately enlarged pilaster, plus a larger apical plug; *T. depressus* **(Fig. 94b)** has the greatly elongated penis and longer vagina; *T. opiranus* **(Fig. 93b)** has a small circular ridge and a grossly altered verge; and *T. christenseni* **(Figs 91b, 92b)** has several enlarged pilasters and a very large apical plug.

Holotype

WAM 502.79, Sta. WA-233, eastern outlier, 2.5 km south of Tanmurra Bore, Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667—613:287). Collected by Alan Solem and Carl Christensen 12 November 1976. Height of holotype 8.7 mm, diameter 15.1 mm, H/D ratio 0.576, whorls 5¼, umbilical width 1.9 mm, D/U ratio 7.95.

Paratopotypes

WAM 573.79, WAM 506.79, FMNH 199001, FMNH 199956, 19 live, 57 dead adults, 1 live juvenile from the type locality.

Diagnosis

Shell of slightly less then average size, 14.2-16.5 mm (mean 15.22 mm) in diameter, with 4⅝ to 5⅝ (mean 5⅛) normally coiled whorls. Apex and spire strongly and almost evenly elevated, height of shell 8.2-10.5 mm (mean 8.93 mm), H/D ratio 0.531-0.659 (mean 0.587). Apical sculpture typical **(Plate 16g)**, postapical **(Plate 16f)** of high, sharply defined radial ribs that continue onto shell base with only slight decrease in prominence. Periphery **(Fig. 90e)** very obtusely angulated, last part of body whorl with a weak peripheral sulcus. Body whorl slightly deflected behind lip, which is narrowly and rather sharply reflected **(Fig. 90d)**, partly covering umbilicus, basal lip with a broad low ridge **(Fig. 90e)**. Umbilicus regularly and slowly decoiling, umbilical width 1.1-2.4 mm (mean 1.78 mm), D/U ratio 6.54-13.0 (mean 8.77). Based on 77 measured adults.

Genitalia **(Figs 96a-b)** with typically enlarged vas deferens (VD) which narrows well above head of vagina (V) and enters penis sheath at base. Walls of sheath (PS) and penis (P) rather thin **(Fig. 96b)**. Penis short, rather slender, internally **(Fig. 96b)** with large apical plug, slender conical verge (PV), one grossly enlarged pilaster (PP) and several weak longitudinal pilasters. Vagina **(Fig. 96a**, V) of nearly uniform diameter, fairly short, free oviduct (UV) very long and slender. Based on 3 dissected and 2 partly opened adults.

Discussion

The most obvious shell difference of *Turgenitubulus costus* is having the strong radial sculpture **(Plate 16f)** continue onto the shell base and into the umbilicus. All other *Turgenitubulus* and all *Ningbingia* have the shell base smooth even if there is strong radial sculpture above the periphery. *Cristilabrum primum* **(Figs 98a, c)** is the other Ningbing Ranges species in which the sculpture is carried over onto the base in undiminished splendour, though it differs from *T. costus* in its much larger size, sharply angulated periphery **(Fig. 98b)**, and small, recessed basal lip ridge. The sculptural difference led to the name *costus* for this species.

In other respects, the shell of *T. costus* is a smaller version of *T. foramenus*, with the small basal ridge and heavier sculpture providing distinguishing characters.

All dissected individuals showed the unusually long and slender free oviduct **(Fig. 96a**, UV). In the other *Turgenitubulus* **(Figs 91-95)**, the free oviduct is noticeably shorter and usually thicker. The expanded vas deferens in the other species narrows to a normal size at or below the junction of the spermatheca and free oviduct. Only in *T. costus* does this narrowing occur significantly above the free oviduct-spermathecal junction. The rather short apical plug and single enlarged pilaster of *T. costus* also are identifying features.

GENUS *CRISTILABRUM* NEW GENUS

Diagnosis

Shell medium to large in size, spire normally strongly and evenly elevated, rarely (*C. funium*) slightly elevated or rounded above. Umbilicus narrowly open, slightly to moderately narrowed by reflection of columellar lip, usually regularly decoiling. Apical sculpture (**Plates 17, 18**) of radially elongated pustulations, becoming coalesced partly into radial riblets by end of apex, postapical sculpture varying from vague growth wrinkles (*C. simplex*) to very prominent radial ribs, which are absent from the shell base in all taxa but *C. primum* and some *C. bilarnium*. Body whorl slightly or not deflected behind lip, except *C. grossum*. Lip narrowly (*C. funium*) to very broadly (most species) expanded and sharply reflected, curved over in *C. buryillum*. Basal lip without (*C. simplex*), a remnant (*C. solitudum*, most *C. bilarnium*, *C. funium*), broad and high (*C. primum*, *C. grossum*), or high conical (*C. buryillum*, *C. bubulum*) basal ridge, a second lip thickening in *C. bubulum* **(Fig. 99e)**. Shell periphery normally obtusely **(Fig. 97e)** to strongly **(Fig. 98b)** angulated, peripheral sulcus prominent in some (*C. primum*, *C. grossum*, *C. bubulum*), absent in most. Parietal callus thin. Colour light yellow horn above periphery, shell base and reflected lip white. No colour bands or zones present. Apical genitalia as in *Ningbingia* and *Turgenitubulus*. Free oviduct (UV) short to long, normally kinked. Spermatheca (S) short, shape of head variable, appressed to base of prostate-uterus (except *C. bilarnium*). Vagina (V) normally very long (except *C. bilarnium*, *C. solitudum*), slender, with same internal sculpture as *Ningbingia* **(Fig. 80c)**. Penis complex long (except *C. bilarnium*), equal in length to terminal female tract. Vas deferens (VD) normal in diameter, entering penis sheath (PS) at base (except mid-way in *C. bilarnium*), reflexing down from insertion of penial retractor muscle through a short apical plug to open into penis chamber. A pair of microscopic (*C. bilarnium*) to prominent (*C. grossum*) penial stimulators (PD) flanking opening of vas deferens. Penis equal in length (*C. bilarnium*), slightly longer (*C. solitudum*), to more than twice length (*C. simplex*, *C. grossum*) of sheath, whose walls differ in thickness from uniform (*C. simplex*) to extremely thick on lower portion (*C. primum*, *C. grossum*). Interior of penis with variable sized plug, two small to large stimulators, walls with large (*C. solitudum*) to very fine (*C. simplex*) longitudinal pilasters, basal enlargement of pilasters only in *C. bilarnium*. No verge or vergic papilla present.

Type species: *Cristilabrum primum* sp. nov.

Comparisons

Cristilabrum differs conchologically from *Ningbingia* in the possession of moderately distinct to very prominent radial ribbing on the spire and body whorl (except *C. simplex*, which apparently has the ribbing secondarily reduced), and in having a trace to high and conical basal lip ridge (except, again, in *C. simplex*). The only *Ningbingia* with a basal lip ridge, *N. res* **(Figs 78c-d)**, has it deeply recessed within the aperture. Species of *Turgenitubulus* generally are smaller in size than species of *Cristilabrum*, but there is essentially complete overlap in sculptural and apertural features. Conchologically, I could not quantify differences between these two genera.

Anatomically, *Cristilabrum* is characterized by its normally very long vagina, basal entrance of a normal sized vas deferens into the penis sheath, presence of two minute to prominent penial stimulators by the opening of the vas deferens into the penis chamber, which is lined with simple longitudinal pilasters. As discussed under that species, *C. bilarnium* is aberrant in structure, but temporarily is best included as a species of *Cristilabrum*. *Turgenitubulus* differs most obviously by its very small penis with an apical verge, enormously swollen vas deferens, and removal of the spermathecal head from the prostate-uterus base. *Ningbingia* differs most obviously in having two raised pilasters in the penis with corrugated edges bearing complicated hardened ridgelets **(Fig. 109)**, lack of penial stimulators and short vaginae. *Prymnbriareus* has penial pilasters equivalent to those found in *Ningbingia*, a single long penial stimulator **(Fig. 108b**, PD), mid-sheath entrance of the normal sized vas deferens and a relatively long vagina.

Nearly all the species of *Cristilabrum* known to date have been taken from relatively small and isolated limestone hills. Very limited numbers of live individuals were obtained, probably as a result of small populations. Thus, only for *C. primum* was it possible to dissect an adequate number of adult individuals and thus establish a meaningful range of intrapopulation variation in genital structure. So little variation was found in this species, that I am confident that observed differences among the other species are real. The basic pattern for the genus is conservative, but differences in penis length, penial stimulator size, vaginal length, and spermathecal shape among populations are large and obvious. They correlate with changes in shell features that are greater than those found among the species of *Turgenitubulus* or *Ningbingia*. Despite the limited anatomical material, we are studying well differentiated taxa.

Table 40 summarizes the more obvious patterns of shell and genital variation. It will serve in place of a key for identification, since unquestionably collections from the many unsampled areas will produce additional taxa. The many scattered limestone areas along tributaries of Surprise and Station Creek to the north-west of

Table 39: Range of Variation in *Cristilabrum* and *Prymnbriareus*

Taxon	Number of Adults Measured	Mean and Range of: Shell Height	Shell Diameter	H/D Ratio
C. solitudum	117	10.77 (9.1-12.7)	18.01 (16.2-21.0)	0.599 (0.538-0.718)
C. simplex	94	10.60 (9.5-13.0)	18.58 (17.05-20.7)	0.570 (0.510-0.678)
C. buryillum	7	8.05 (7.6-8.5)	16.28 (15.8-16.9)	0.495 (0.468-0.539)
C. primum	570	9.01 (7.8-10.65)	17.07 (14.1-20.0)	0.528 (0.455-0.678)
C. grossum	247	11.29 (9.0-13.4)	20.95 (18.8-22.9)	0.539 (0.455-0.618)
C. bubulum	183	8.94 (7.6-11.2)	17.41 (15.1-19.2)	0.513 (0.444-0.600)
C. bilarnium	91	11.41 (10.0-13.0)	20.29 (18.2-23.2)	0.563 (0.507-0.663)
C. funium	1	12.25	24.9	0.492
P. nimberlinus	15	9.92 (8.6-11.1)	17.23 (15.8-18.5)	0.572 (0.520-0.630)

Taxon	Number of Adults Measured	Mean and Range of: Whorls	Umbilical Width	D/U Ratio
C. solitudum	117	5½ (5⅛-6)	2.39 (1.6-3.5)	7.35 (5.09-11.3)
C. simplex	94	5⅜ (5-5¾)	2.95 (2.2-3.8)	6.38 (4.99-8.59)
C. buryillum	7	5¼ (5-5⅝)	1.78 (1.1-2.3)	9.67 (7.28-14.0)
C. primum	570	4⅞− (4⅜-5½)	2.44 (1.6-3.6)	7.09 (5.29-10.5)
C. grossum	247	5⅜− (4⅞-6)	2.52 (1.0-3.6)	8.65 (5.85-20.4)
C. bubulum	183	5⅜− (4⅞-6)	1.79 (0.7-2.9)	9.81 (5.67-24.5)
C. bilarnium	91	5¾ (5⅛-6⅜)	2.23 (1.4-3.2)	9.42 (6.69-14.3)
C. funium	1	5⅝+	2.8	8.89
P. nimberlinus	15	4⅞ (4⅝-5⅜)	2.11 (1.8-2.6)	8.27 (7.02-9.42)

Ningbing Bore, areas directly west of Sta. WA-226 and in the upper reaches of Four Mile Creek, can all be investigated profitably. Local variation in size and shape is summarized in **Table 41**. The same pattern of variations found in *Ningbingia* and *Turgenitubulus* are repeated here, in that dead and live adult specimens from the same talus will differ slightly in size, but not predictably in directions. Populations from different parts of the same hill (*C. primum*, WA-226, WA-432) or adjacent hills (*C. bubulum*, Sta. WA-237, WA-433), also differ noticeably in adult size. In some cases these differences can be most simply explained by an earlier cessation of growth, resulting in a slightly decreased mean whorl count, but in other situations there is minor differentiation at the same whorl count. The same observation applies in considering the average adult size of each species (**Table 39**). *C. primum*, with a mean whorl count of 4⅞ –, has small size produced by whorl decrease; *C. buryillum* is small, despite a normal whorl count; while *C. grossum* is significantly enlarged while retaining an average whorl count.

Apical shell sculpture is typical, with the postapical sculpture highly variable (**Plates 17-18**). Fresh shells show a faint (**Plate 17e-f**) periostracal sculpture that I interpret as

Table 40: Structural Variation in *Cristilabrum*

Species	SHELL: Peripheral Sulcus	Basal Lip Ridge	Radial Sculpture on Spire	Radial Sculpture on Shell Base	Lip Flare
C. solitudum	–	remnant	reduced	–	sharp, broad
C. simplex	–	–	absent	–	sharp, medium
C. buryillum	–	large, conical	strong	–	sharp, broad
C. primum	+	large, broad	strong	+	sharp, broad
C. grossum	+	very large, broad	strong	–	sharp, broad
C. bubulum	+	conical, high, second	strong	–	sharp, broad
C. bilarnium	–	remnant, usually	strong	+ or – –	sharp, very narrow
C. funium	–	remnant	strong	–	sharp, narrow

Table 40: Structural Variation in *Cristilabrum* (continued)

Species	GENITAL STRUCTURES: Vagina/ Penis Length	Free Oviduct	Penis Apical Plug	Penis/ Penis Sheath	Penial Stimulator	Vas Enters Base of Sheath	Penis Sheath Wall Thickness
C. solitudum	much shorter	long	very short	1.1	minute	+	tapering
C. simplex	subequal	long	very short	2+	minute	+	all thin
C. buryillum	?	?	?	?	?	?	?
C. primum	equal	medium	medium	1.5	medium	+	base very thick, top thin
C. grossum	⅔	short	short, thick	2+	large	+	base very thick, top thin
C. bubulum	shorter	medium	short	1.5–	fairly large	+	all medium
C. bilarnium	much shorter	long	large	1.0	minute	–	slight tapering
C. funium	?	?	?	?	?	?	?

the result of surface shrinkage. Most individuals have this very thin periostracal layer eroded.

The name *Cristilabrum*, meaning crested-lip, refers to the striking development of a basal lip ridge in many of the species of this genus.

CRISTILABRUM SOLITUDUM SP. NOV.

(Plate 17a; Figs 97a-c, 101a-b)

Comparative remarks

Cristilabrum solitudum has the highest mean H/D ratio (0.599) in the genus, greatly reduced radial sculpture (**Plate 17a**) on the spire and body whorl, a relatively widely open umbilicus (**Fig. 97c**), and the basal lip ridge (**Fig. 97b**) reduced to a small remnant that has shifted near to the columellar wall. It lacks any trace of a peripheral sulcus. Most *Cristilabrum* have prominent basal lip ridges (**Figs 98b, e, 99b, e**) and strong radial sculpture on the spire and body whorls (**Plates 17, 18**). The species without basal lip ridges or a reduced basal lip ridge are easily separated. The very large shells (mean diameters 20.3, 24.9 mm) of *C. bilarnium* and *C. funium* are

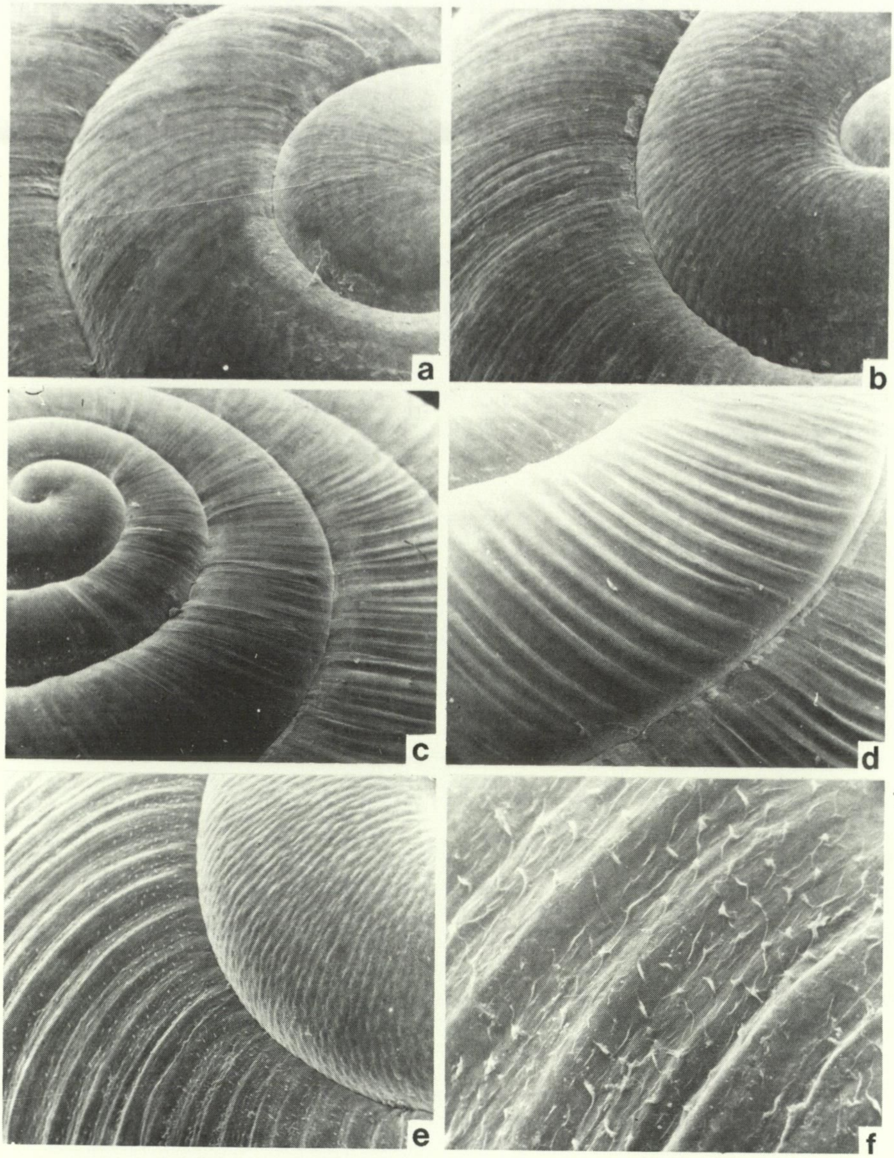


Plate 17: Shell sculpture in *Cristilabrum*: (a) *C. solitudum*, FMNH 199642, Dissection A, Sta. WA-234, 7.35 km south of Tanmurra Bore, Ningbing Ranges, apex and early spire at 36.9X; (b) *C. simplex*, FMNH 199961, Dissection A, Sta. WA-235, 1.7 km south of Ningbing Bore, Ningbing Ranges, apex and early spire at 36.8X; (c-d) *C. buryillum*, WAM 534.79, Holotype, Sta. WA-235, 1.7 km south of Ningbing Bore, Ningbing Ranges, (c) apex and spire at 16.7X; (d) sculpture on 3rd and 4th whorls at 16.9X; (e-f) *C. primum*, FMNH 199962, Sta. WA-226, 4.3 km south of Ningbing Bore, Ningbing Ranges, (e) apex and early spire at 39.8X, (f) details of microsculpture on 1st postapical whorl at 15.5X.

Table 41: Local Variation in *Cristilabrum*

Taxon	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
C. solitudum				
WA-234, FMNH 199642, 18-V-77	7 (L)	10.76 ± 0.154 (10.3-11.4)	17.53 ± 0.296 (16.2-18.4)	0.614 ± 0.007 (0.579-0.633)
WA-234, FMNH 199045, 18-V-77	69 (D)	10.98 ± 0.073 (9.3-12.7)	18.07 ± 0.099 (16.3-19.6)	0.608 ± 0.004 (0.544-0.718)
WA-234, FMNH 199006, 12-XI-76	41 (D)	10.42 ± 0.095 (9.1-11.6)	17.97 ± 0.123 (16.6-21.0)	0.582 ± 0.004 (0.538-0.648)
C. simplex				
WA-235, FMNH 199014, 12-XI-76	93 (D)	10.59 ± 0.070 (9.5-13.0)	18.57 ± 0.083 (17.1-20.7)	0.571 ± 0.003 (0.510-0.678)
C. buryillum				
WA-235, FMNH 200868, 12-XI-76	7 (D)	8.05 ± 0.131 (7.6-8.5)	16.28 ± 0.156 (15.8-16.9)	0.495 ± 0.009 (0.468-0.539)
C. primum				
WA-226, FMNH 199962, 11-XI-76	39 (L)	9.20 ± 0.094 (8.3-10.2)	16.97 ± 0.091 (16.1-18.1)	0.543 ± 0.005 (0.459-0.605)
WA-226, FMNH 199005, 11-XI-76	351 (D)	9.11 ± 0.030 (8.0-10.6)	17.21 ± 0.045 (15.1-20.0)	0.530 ± 0.002 (0.455-0.678)
WA-432, FMNH 199641, 18-V-77	24 (L)	8.54 ± 0.093 (7.8-9.5)	16.24 ± 0.107 (15.4-17.0)	0.526 ± 0.006 (0.488-0.613)
WA-432, FMNH 199034, 18-V-77	147 (D)	8.80 ± 0.038 (7.8-9.9)	16.94 ± 0.066 (15.3-19.9)	0.520 ± 0.002 (0.456-0.578)
C. grossum				
WA-236, FMNH 199638, 18-V-77	10 (L)	11.60 ± 0.178 (10.7-12.7)	21.29 ± 0.188 (20.7-22.5)	0.545 ± 0.008 (0.514-0.576)
WA-236, FMNH 199020, 18-V-77	199 (D)	11.32 ± 0.047 (9.4-13.4)	20.98 ± 0.059 (18.8-22.9)	0.540 ± 0.002 (0.455-0.618)
WA-236, FMNH 199010, 12-XI-76	38 (D)	11.01 ± 0.135 (9.0-12.8)	20.67 ± 0.142 (19.1-22.2)	0.532 ± 0.006 (0.467-0.588)
C. bubulum				
WA-237, FMNH 199009, 12-XI-76	107 (D)	8.61 ± 0.053 (7.6-9.9)	17.06 ± 0.079 (15.1-19.0)	0.505 ± 0.003 (0.455-0.582)
WA-237, FMNH 199039, 18-V-77	25 (D)	9.34 ± 0.152 (7.9-11.2)	17.53 ± 0.114 (16.5-18.9)	0.533 ± 0.008 (0.444-0.593)
WA-433, FMNH 199031, 18-V-77	50 (D)	9.43 ± 0.080 (8.3-10.8)	18.09 ± 0.085 (16.6-19.1)	0.521 ± 0.004 (0.462-0.600)
C. bilarnium				
Bilarni Cave, WAM 424-77	3 (D)	11.78 ± 0.460 (11.3-12.7)	20.70 ± 0.361 (20.0-21.2)	0.560 ± 0.020 (0.545-0.599)
WA-435, FMNH 199035, 19-V-77	85 (D)	11.41 ± 0.076 (10.2-13.0)	20.30 ± 0.122 (18.2-23.2)	0.564 ± 0.003 (0.507-0.663)

Table 41: Local Variation in *Cristilabrum* (continued)

Taxon	Number of Adults Measured	Mean, Range and SEM of: Whorls	Umbilical Width	D/U Ratio
C. solitudum				
WA-234, FMNH 199642, 18-V-77	7 (L)	5⅝+ (5¼-5⅞)	2.46 ± 0.117 (2.0-2.8)	7.20 ± 0.309 (6.07-8.18)
WA-234, FMNH 199045, 18-V-77	69 (D)	5½ (5⅛-5⅞)	2.36 ± 0.045 (1.6-3.1)	7.84 ± 0.149 (6.02-11.3)
WA-234, FMNH 199006, 12-XI-76	41 (D)	5½ – (5⅛-6)	2.77 ± 0.060 (2.1-3.5)	6.54 ± 0.142 (5.09-8.50)
C. simplex				
WA-235, FMNH 199014, 12-XI-76	93 (D)	5⅜ (5-5¾)	2.94 ± 0.040 (2.2-3.8)	6.39 ± 0.080 (4.99-8.59)
C. buryillum				
WA-235, FMNH 200868, 12-XI-76	7 (D)	5¼ (5-5⅝)	1.78 ± 0.166 (1.1-2.3)	9.67 ± 0.340 (7.28-14.0)
C. primum				
WA-226, FMNH 199962, 11-XI-76	39 (L)	5 – (4¾-5⅛)	2.63 ± 0.057 (1.95-4.0)	6.54 ± 0.121 (4.53-8.56)
WA-226, FMNH 199005, 11-XI-76	351 (D)	4¾ (4½-5¼)	2.42 ± 0.016 (1.6-3.4)	7.21 ± 0.044 (5.30-10.5)
WA-432, FMNH 199641, 18-V-77	24 (L)	4⅞ (4⅝-5⅛)	2.45 ± 0.061 (1.9-3.1)	6.73 ± 0.155 (5.29-8.16)
WA-432, FMNH 199034, 18-V-77	147 (D)	5 – (4⅜-5⅞)	2.43 ± 0.020 (1.7-3.2)	7.02 ± 0.052 (5.84-9.83)
C. grossum				
WA-236, FMNH 199638, 18-V-77	10 (L)	5½ – (5⅛-5¾)	2.76 ± 0.117 (2.3-3.5)	7.85 ± 0.322 (6.23-9.22)
WA-236, FMNH 199020, 18-V-77	199 (D)	5⅜ – (4⅞-6)	2.47 ± 0.032 (1.0-3.6)	8.87 ± 0.130 (5.93-20.4)
WA-236, FMNH 199010, 12-XI-76	38 (D)	5¼ (4⅞-5½)	2.75 ± 0.067 (2.0-3.6)	7.67 ± 0.191 (5.85-9.95)
C. bubulum				
WA-237, FMNH 199009, 12-XI-76	107 (D)	5¼ (4⅞-5⅞)	1.74 ± 0.039 (0.7-2.9)	9.68 ± 0.463 (5.67-24.5)
WA-237, FMNH 199039, 18-V-77	25 (D)	5½ – (5¼-5¾)	1.62 ± 0.065 (1.1-2.5)	11.25 ± 0.426 (7.35-15.0)
WA-433, FMNH 199031, 18-V-77	50 (D)	5½ – (5⅛-6)	2.01 ± 0.056 (1.1-2.8)	9.38 ± 0.287 (6.36-16.2)
C. bilarnium				
Bilarni Cave, WAM 424.77	3 (D)	5½ + (5¼-5¾)	2.65 ± 0.076 (2.5-2.75)	7.83 ± 0.315 (7.27-8.36)
WA-435, FMNH 199035, 19-V-77	85 (D)	5¾ (5⅛-6⅜)	2.22 ± 0.048 (1.4-3.2)	9.47 ± 0.175 (6.69-14.3)

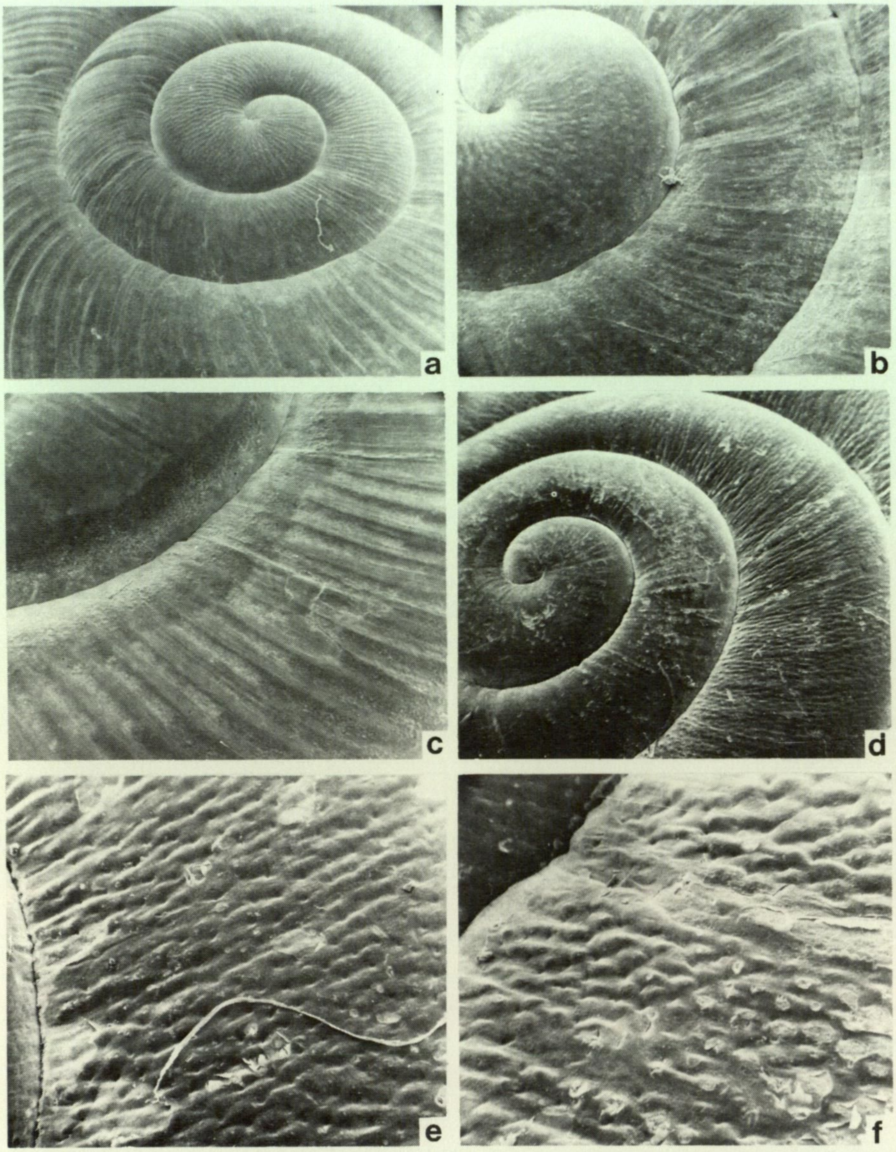


Plate 18: Shell sculpture in *Cristilabrum* and *Prymnbriareus*: (a) *C. grossum*, FMNH 199638, Dissection B, Sta. WA-236, 1.8 km north of Four Mile Creek, Ningbing Ranges, apex and spire at 15.6X; (b) *C. bubulum*, FMNH 199640, Dissection A, Sta. WA-237, 0.9 km north of Four Mile Creek, Ningbing Ranges, apex and spire at 36.2X; (c) *C. bilarnium*, FMNH 199631, Dissection A, Sta. WA-435, isolated limestone hills, NW of Kununurra, apex and spire at 39.6X; (d-f) *P. nimberlinus*, Sta. WA-225, Nimberline area, El Questro Homestead, south-west of Wyndham, (d) FMNH 199003, apex and spire at 16.6X; (e) FMNH 199003, sculpture on 4th whorl at 40.8X; (f) FMNH 199725, Dissection B, sculpture on body whorl at 48.5X.

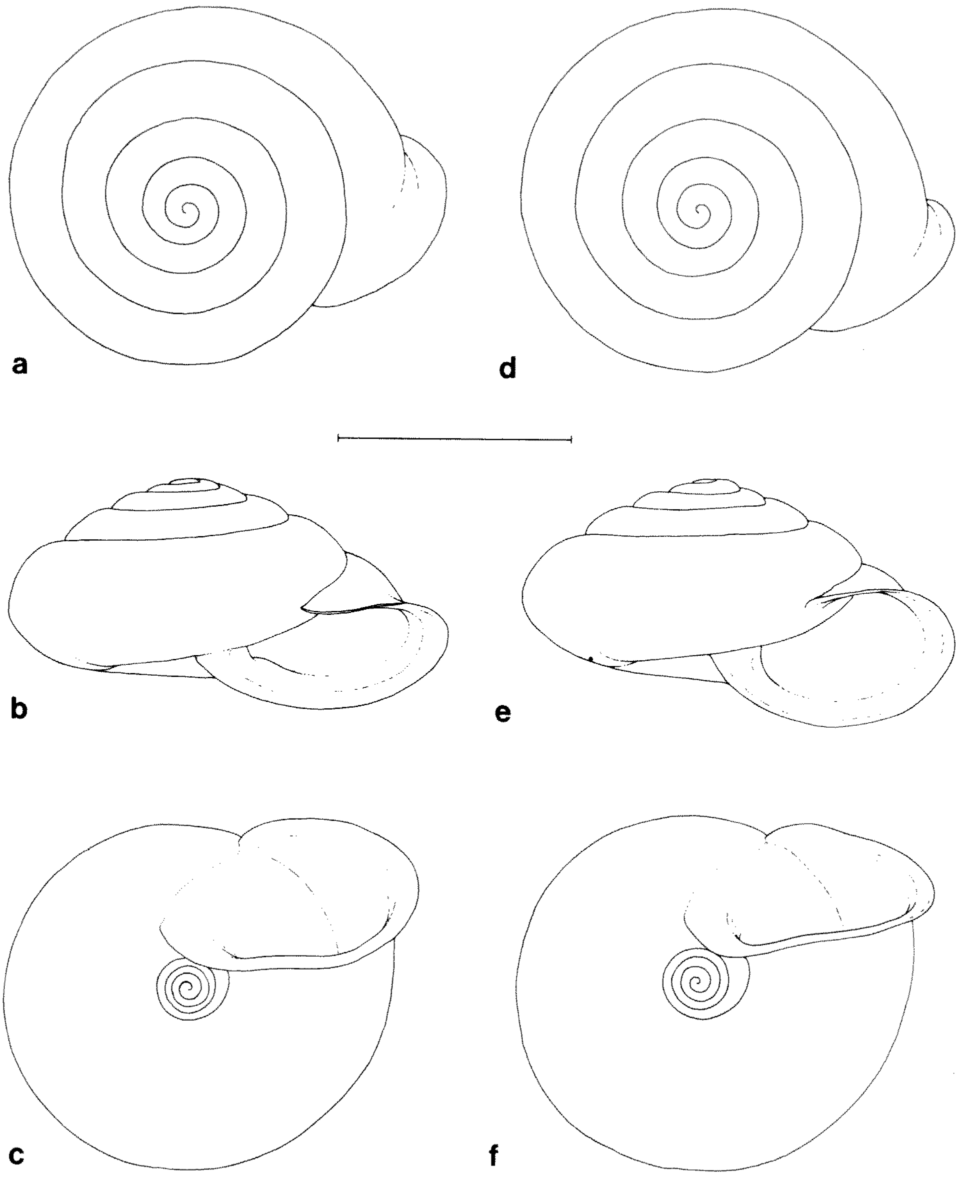


Fig. 97: Shells of *Cristilabrum solitudum* and *C. simplex*: (a-c) *C. solitudum*, Sta. WA-234, 7.35 km south of Tanmurra Bore, Ningbing Ranges, WAM 537.79, holotype; (d-f) *C. simplex*, Sta. WA-235, 1.7 km south of Ningbing Bore, Ningbing Ranges, WAM 529.79, holotype. Scale line equals 10 mm.

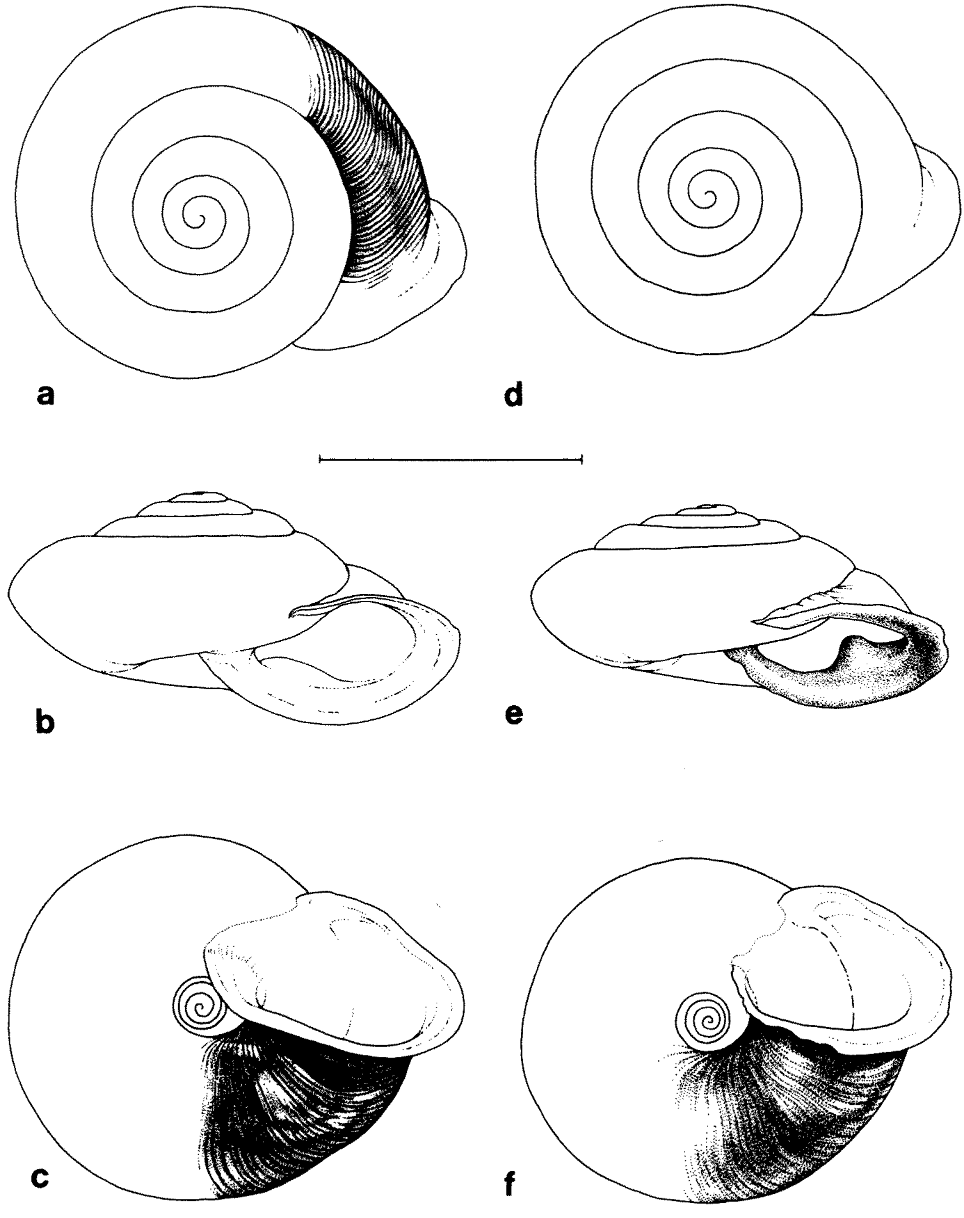


Fig. 98: Shells of *Cristilabrum primum* and *C. buryillum*: (a-c) *C. primum*, Sta. WA-226, 4.3 km south of Ningbing Bore, Ningbing Ranges, WAM 505.79, holotype; (d-f) *C. buryillum*, Sta. WA-235, 1.7 km south of Ningbing Bore, Ningbing Ranges, WAM 534.79, holotype. Scale line equals 10 mm.

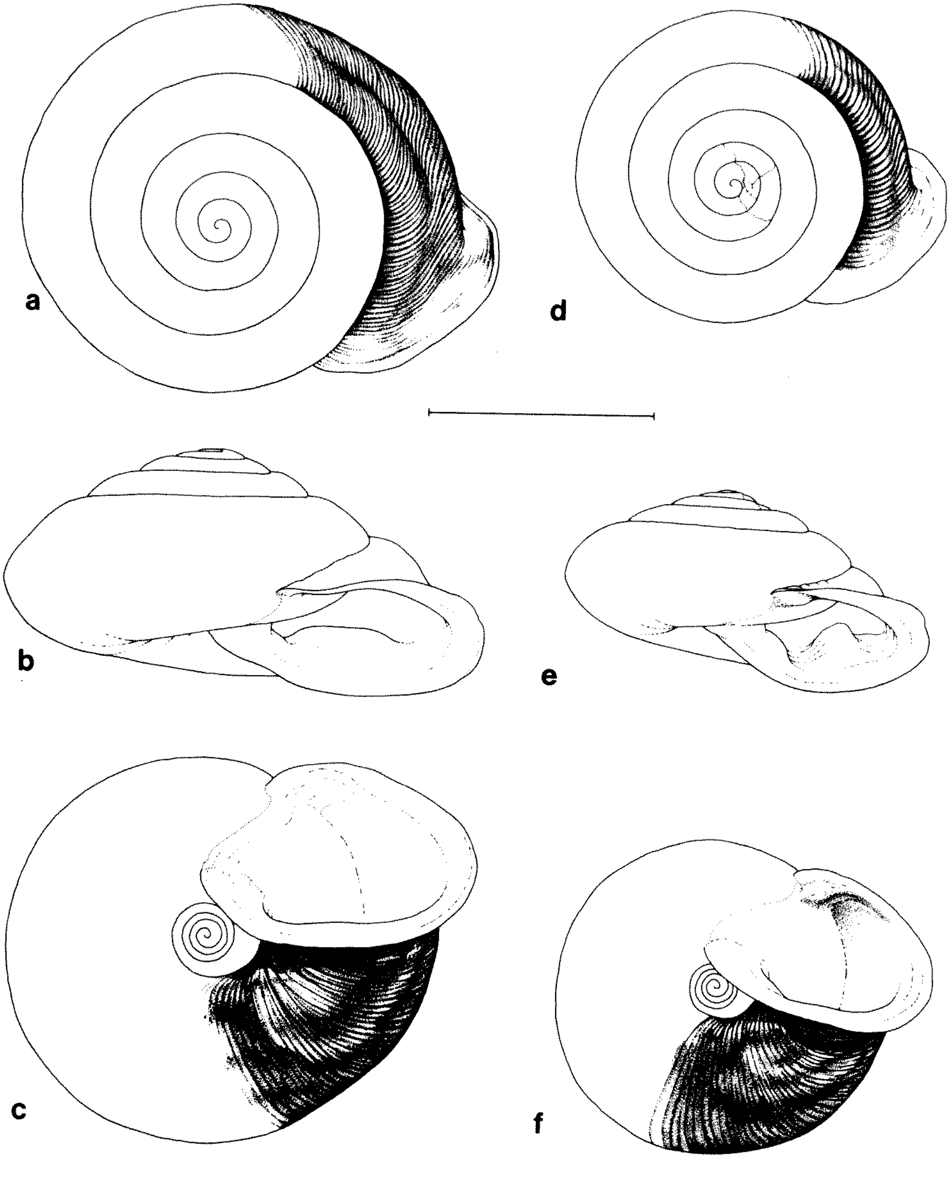


Fig. 99: Shells of *Cristilabrum grossum* and *C. bubulum*: (a-c) *C. grossum*, Sta. WA-236, 1.8 km north of Four Mile Creek, Ningbing Ranges, WAM 530.79, holotype; (d-f) *C. bubulum*, Sta. WA-237, 0.9 km north of Four Mile Creek, Ningbing Ranges, WAM 492.79, holotype. Scale line equals 10 mm.

much less strongly elevated, have a more narrowly expanded lip **(Figs 100b, e)**, very heavy radial sculpture above the periphery (**Plate 18c**), and a slightly flattened shell base **(Figs 100b, e)**. The most similar species, *C. simplex*, has no trace of a basal lip ridge **(Fig. 97e)**, a slightly angulated periphery **(Fig. 97e)**, and is slightly larger in size **(Table 39)**. Anatomically, the relatively short penis **(Fig. 101b)**, which is perhaps one-quarter longer than the penis sheath, enlargement of the pilasters in the apical region, reduction of the penial stimulators in size (not shown in **Fig. 101b**), and having the vagina significantly shorter than the penis sheath **(Fig. 101a)** are the main differentiating characters. *C. simplex* **(Fig. 102b)** and *C. grossum* **(Fig. 104b)** have the penes twice the sheath length; *C. primum* **(Fig. 103b)** and *C. bubulum* **(Fig. 105b)** have the penis about 1.5 times the sheath length and long vaginae; while *C. bilarnium* **(Figs 106a, b)** is grossly altered in both penis length and structure.

Holotype

WAM 537.79, Sta. WA-234, 1.0 km north of big creek bed, 7.35 km south of Tanmurra Bore, Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667–618:257). Collected by Alan Solem 18 May 1977. Height of shell 10.55 mm, diameter 18.6 mm, H/D ratio 0.567, whorls 5½, umbilical width 2.65 mm, D/U ratio 7.02.

Paratopotypes

WAM 518.79, WAM 512.79, WAM 576.79, FMNH 199006, FMNH 199045, FMNH 199642, 7 live and 110 dead adults from the type locality.

Diagnosis

Shell of average size, 16.2-21.0 mm (mean 18.01 mm) in diameter, with 5 ⅛ to 6 (mean 5½) normally coiled whorls. Apex and spire strongly and evenly elevated **(Fig. 97b)**, height of shell 9.1-12.7 mm (mean 10.77 mm), H/D ratio 0.538-0.718 (mean 0.599). Apical sculpture (**Plate 17a**) typical, postapical whorls with low and irregular radial growth wrinkles, shell base nearly smooth. Shell periphery bluntly and obtusely angulated **(Fig. 97b)**, no peripheral sulcus. Body whorl gently and slightly deflected behind lip, which is broadly and sharply reflected on outer margin **(Figs 97a-c)**, partly covering umbilicus, basal lip margin usually with remnant of a ridge shifted over to near the columellar margin, occasionally obscured by the thickening of the lip. Umbilicus slowly and regularly decoiling, partly covered by lip reflection, umbilical width 1.6-3.5 mm (mean 2.39 mm), D/U ratio 5.09-11.3 (mean 7.35). Based on 118 measured adults.

Genitalia **(Figs 101a-b)** without unusual apical features. Vagina (V) rather short, free oviduct (UV) long and coiled, spermatheca (S) long for genus with enlarged head. Vas deferens (VD) typical, entering sheath at base, ascending to penial retractor muscle (PR) insertion and then reflexing slightly before opening (DP) into penis chamber. Two minute penial stimulators lie to one side of vas opening (not

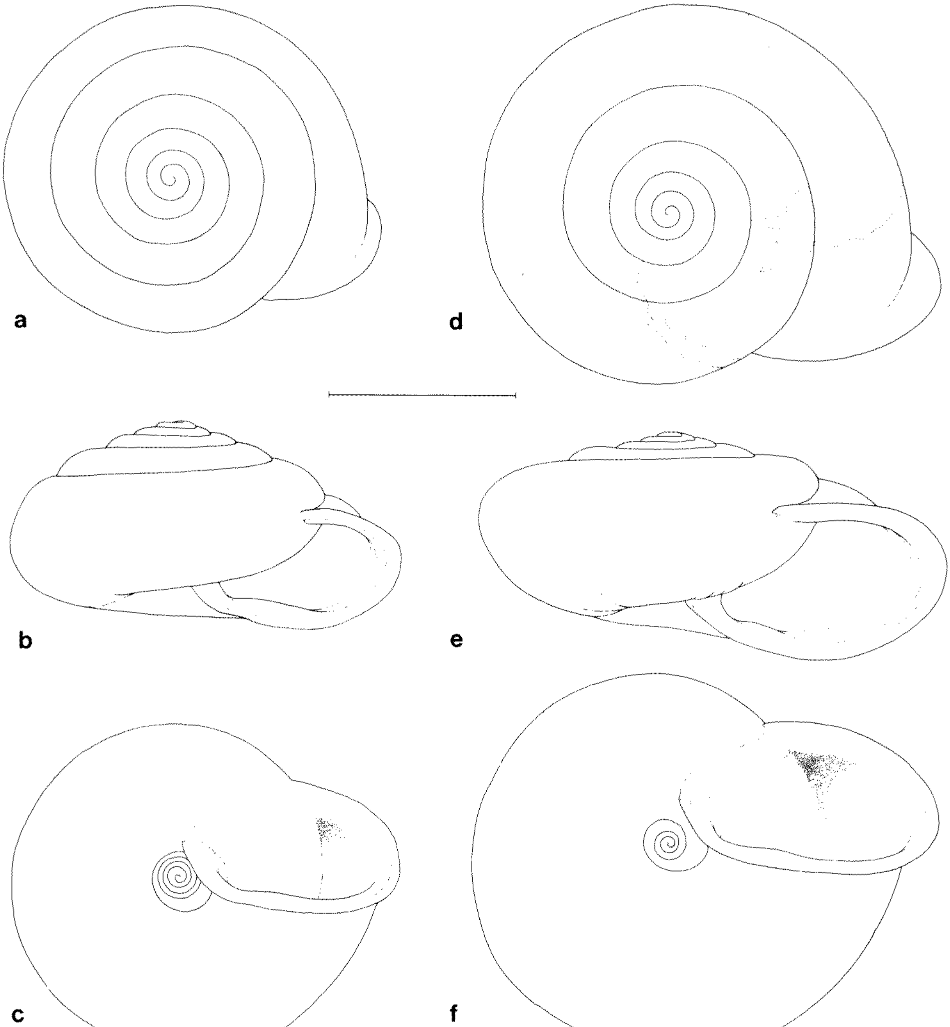


Fig. 100: Shells of *Cristilabrum bilarnium* and *C. funium*: (a-c) *C. bilarnium*, Sta. WA-435, south-east of Jeremiah Hills, north of Kununurra, WAM 527.79, holotype; (d-f) *C. funium*, *ca.* 40 km north-east of Roper River Settlement, Northern Territory, WAM 423.77, holotype. Scale line equals 10 mm.

shown in **Fig. 101b**). Penis sheath (PS) with basal walls slightly thicker than above mid-point. Penis only slightly longer than sheath, slightly kinked apically, internally **(Fig. 101b)** with very large pilasters that become more expanded and complicated apically. One pilaster hollow, with a near central opening. Based on 2 dissected adults.

Discussion

Cristilabrum solitudum is known from an isolated hill (Sta. WA-234) located 7.35 km south of Tanmurra Bore and a considerable track distance north of Surprise Creek, The Gorge, and Station Creek. This is about 3.0 km directly south of Sta. WA-233, the southernmost record for *Turgenitubulus costus*, and about 11 km by air north of Sta. WA-235, the next recorded occurrence of *Cristilabrum*. Hence the name *solitudum* was considered appropriate for this species. I would anticipate that taxa will be found in The Gorge and other limestone areas between Stas WA-234 and WA-235, but no collections are available at this time.

Only dead examples were taken in November 1976 (FMNH 199006). In May 1977 this station was revisited to obtain living examples. Dead specimens from the two visits differ marginally in shell height and umbilical width, probably reflecting the choice of slightly different areas of the east face of the hill for sampling on the two visits **(Table 41)**. The few live specimens were noticeably smaller.

Considerable difficulty was encountered in working out the details of the upper penis chamber, and the illustration **(Fig. 101b)** does not include the minute penial stimulators (hidden by the curve of the outer penis wall) as they were missed in the initial study. The hollow pilaster was seen in both adults examined. Since the remaining live collected adults were partly retracted, and partial retraction typically causes extensive folding and distortion in this region, it was decided to leave this structural problem unresolved until better relaxed specimens were available.

The heavy penis chamber pilaster development, relatively short penis, quite short vagina, and enlarged spermatheca are sufficient to permit species identification. They represent unusual situations for *Cristilabrum*.

CRISTILABRUM SIMPLEX SP. NOV.

(Plate 17b; Figs 97d-f, 102a-b)

Comparative remarks

Cristilabrum simplex is distinguishable from presently known congeners in totally lacking any trace of a basal lip ridge **(Fig. 97e)**, and having only very weak traces of radial ribbing on the spire (**Plate 17b**). The umbilicus (**Fig. 97f**) is widely open for the genus (mean D/U ratio 6.38). Only *C. solitudum* could be confused on the basis of reduced sculpture (**Plate 17a**), but that species has a distinct basal lip ridge trace (**Fig.**

97b) and differs slightly in size and shape **(Table 39)**. *C. bilarnium* and *C. funium* **(Figs 100b, e)** have a slight basal ridge on the lip, which is more narrowly expanded, heavy radial sculpture on the spire, and are much larger in size. Anatomically, the vagina of *C. simplex* (V) is very long **(Fig. 102a)** and the spermatheca (S) is rather short, with a slender, tapering head. The penis is more than twice the length of the sheath **(Fig. 102b,** PS), and internally the pilasters are quite slender, with two partly enlarged. The penial stimulators are short, and in the form of a fringed ridge to one side of the vas opening (DP). All other *Cristilabrum* species, except *C. grossum*, differ in having the penis much less than twice the length of the penis sheath, larger penial stimulators, and different shaped spermathecae. *C. grossum* **(Fig. 104b)** has the penis almost as long, but very large penial stimulators and much thicker walls to the lower part of the penis sheath. *C. solitudum* appears very similar in penis interior structures, but has the very short penis **(Fig. 101b)** and great pilaster enlargement.

Holotype

WAM 529.79, Sta. WA-235, isolated peak 1.7 km south of Ningbing Bore, Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667—649:129). Collected by Alan Solem and Carl Christensen 12 November 1976. Height of shell 11.1 mm, diameter 18.8 mm, H/D ratio 0.590, whorls 5½ −, umbilical width 2.95 mm, D/U ratio 6.37.

Paratopotypes

WAM 508.79, FMNH 199014, FMNH 199961, 1 live and 92 dead adults, 3 live juveniles from the type locality.

Diagnosis

Shell of average size, 17.05-20.7 mm (mean 18.58 mm) in diameter, with 5 to 5¾ (mean 5⅜) normally coiled whorls. Apex and spire strongly and evenly elevated **(Fig. 97e)**, height of shell 9.5-13.0 mm (mean 10.60 mm), H/D ratio 0.510-0.678 (mean 0.570). Apical sculpture **(Plate 17b)** typical, postapical whorls with very low and irregular remnants of radial ribs, occasionally more prominent on body whorl, always absent from shell base. Shell periphery obtusely angulated **(Fig. 97e)**, no peripheral sulcus. Body whorl very slightly deflected behind lip, which is sharply and moderately reflected on outer margin **(Figs 97d, e)**, slightly reflected to cover umbilicus. Basal lip without trace of ridge. Umbilicus with last whorl decoiling slightly more rapidly, partly covered by reflected lip, umbilical width 2.2-3.8 mm (mean 2.95 mm), D/U ratio 4.99-8.59 (mean 6.38). Based on 94 measured adults.

Genitalia **(Figs 102a-b)** without unusual apical features. Free oviduct (UV) very long and tightly coiled, spermatheca (S) slender, tapered above, head next to prostate-uterus margin, base not expanded. Vagina (V) very long, slender. Vas deferens (VD) slender for entire length, entering penis sheath (PS) at base, extending significantly longer than sheath and coiled, reflexing after penial retractor muscle

(PR) insertion through a short plug to enter penis. Penis pore (DP) flanked by two minute stimulators and a short area of very fine longitudinal pilasters. Penis (P) more than twice length of penis sheath, complexly coiled inside, lower sections **(Fig. 102b)** with many very fine longitudinal pilasters and two that are moderately enlarged, actual numbers greater than shown because of scale problems. Based on 1 dissected adult.

Discussion

Cristilabrum simplex derives its name from the reduction in radial ribbing and loss of the basal lip ridge, slenderization and elongation of the penis complex, and simple pilaster structure in comparison with the other *Cristilabrum.*

Sta. WA-235 is the first peak south of Ningbing Bore near the track and is rather isolated from the next series of hills to the south. Only one adult, a juvenile 14.9 mm in diameter with 4 7/8 whorls, and two juveniles 7.0 and 7.3 mm with 3 3/8 whorls each were obtained alive. The latter probably were hatched in the 1975-1976 wet season, and the larger juveniles in the 1974-1975 wet season on the basis of data from *Amplirhagada* and *Xanthomelon* species (see Solem, 1979). The enlarged ovotestis (G) and kinked hermaphroditic duct (GD) are typical of male active, start of wet season conditions.

The extreme length of the penis **(Fig. 102b)** is interpreted as probably indicating a species recognition difference from the sympatric *C. buryillum*, and is comparable to the type of differences seen between sympatric *Ningbingia* (*N. octava*, **Figs 82b, c, 83b**, and *N. laurina*, **Fig. 84b)** and *Turgenitubulus* (*T. opiranus*, **Fig. 93b**, and *T. depressus*, **Fig. 94b)**. The differences in shell sculpture **(Plate 17b-d)**, shape, basal lip (compare **Figs 97e** and **98e)**, and size **(Table 39)** between *C. simplex* and *C. buryillum* are dramatic. Species level differentiation is accepted despite the lack of anatomical material for *C. buryillum.*

Only 7 specimens of *C. buryillum* were taken compared with 94 of *C. simplex.* This represents a more disproportionate representation than in the examples of sympatry in *Ningbingia*, where 101 *N. octava* were with 20 *N. laurina*, or in *Turgenitubulus*, where 96 *T. opiranus* and 188 *T. depressus* were collected at one time.

C. simplex is the most similar to *Ningbingia* in shell structure of any *Cristilabrum*. The minor differences in shell proportions are insufficient to enable separation, but the remnants of radial sculpture on the body whorl in *C. simplex*, wider umbilicus and slightly narrower lip expansion of *N. bulla* are noticeable differences.

CRISTILABRUM BURYILLUM SP. NOV.

(Plate 17c-d; Figs 98d-f)

Diagnosis

Cristilabrum buryillum is small in size (mean diameter 16.28 mm), depressed in shape (mean H/D ratio 0.495), and has a high conical lip ridge **(Fig. 98e)** that in some individuals is transversely slanted as a 'U'-shaped ridge. A minority of the specimens have a slight swelling on the columellar lip, but not as developed as in *C. bubulum* **(Fig. 99e)**. The latter species is larger (mean diameter 17.41 mm), with stronger basal ridges and relatively heavy sculpture. *Cristilabrum primum* has the radial ribbing continuing onto the base and a lower, broader lip ridge **(Fig. 98b)**, as does the very large (mean diameter 20.95 mm) *C. grossum* **(Fig. 99b)**. The remaining *Cristilabrum* species **(Figs 97b, 100b, e)** have only a trace of a basal ridge, or, in the case of the sympatric *C. simplex* **(Fig. 97e)**, totally lack the basal lip ridge. *Turgenitubulus depressus* also has a high conical basal lip ridge **(Fig. 89e)**, but is more than 2 mm smaller (mean diameter 14.27 mm), more narrowly umbilicated, and has a much less expanded lip (compare **Figs 89d, 98d**). Anatomy unknown.

Holotype

WAM 534.79, Sta. WA-235, isolated peak 1.7 km south of Ningbing Bore, Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667—649:129). Collected by Alan Solem and Carl C. Christensen 12 November 1976. Height of shell 8.3 mm, diameter 16.45 mm, H/D ratio 0.505, whorls 5¼, umbilical width *ca.* 2.2 mm, estimated D/U ratio 7.48.

Paratopotypes

WAM 516.79, FMNH 200868, 6 dead adults from the type locality.

Description

Shell rather small, 15.8-16.9 mm (mean 16.28 mm) in diameter, with 5 to 5⅝ (mean 5¼) normally coiled whorls. Apex and spire strongly and almost evenly elevated, slightly rounded above in some examples, height of shell 7.6-8.5 mm (mean 8.05 mm), H/D ratio 0.468-0.539 (mean 0.495). Apical sculpture **(Plate 17c)** typical, upper spire with low, vague radial swellings, increasing to rather prominent radial ribs by 3rd whorl **(Plate 17d)**, shell base without clear radial sculpture. Shell periphery strongly angled, bluntly rounded **(Fig. 98e)**, no peripheral sulcus. Body whorl very slightly deflected behind lip, which is broadly and sharply expanded **(Figs 98d, e)**, partly reflexing to cover umbilicus. Outer portion of basal lip with a high, conical to 'U'-shaped ridge, some specimens with a rather prominent thickening near the columellar margin, about equivalent in position to the basal lip ridge remnant of *C. solitudum* **(Fig. 97b)**. Umbilicus slowly and regularly decoiling, partly covered by reflected lip, umbilical width 1.1-2.3 mm (mean 1.78 mm), D/U ratio 7.28-14.0 (mean 9.67). Based on 7 measured adults.

Anatomy unknown.

Discussion

Cristilabrum buryillum takes its name from Buryill Point near the type locality. Despite the lack of anatomical material, the shell aperture, size and shape are so different from the sympatric *C. simplex* **(Figs 97d-f, 98d-f)**, that I have no hesitation in naming it as a distinct species.

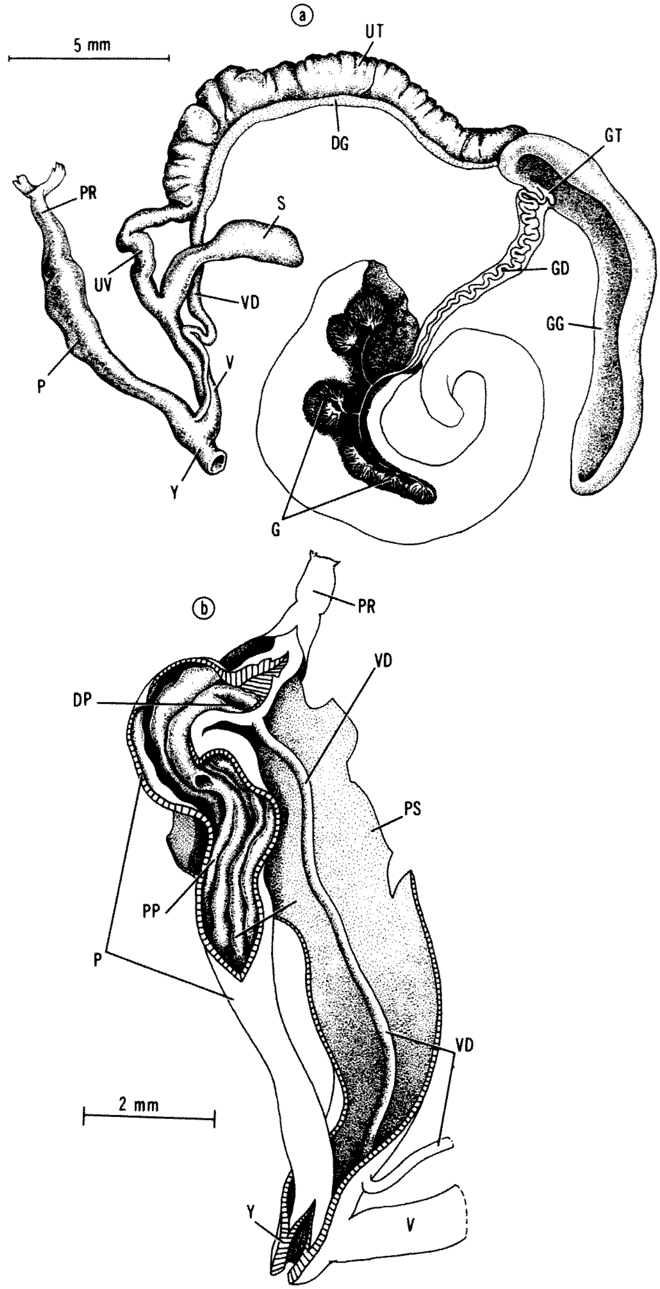


Fig. 101: Genitalia of *Cristilabrum solitudum*: Sta. WA-234, 7.35 km south of Tanmurra Bore, Ningbing Ranges, 18 May 1977, FMNH 199642, paratopotypes, (a) whole genitalia, Dissection B, (b) interior of penis, Dissection A. Scale lines as marked.

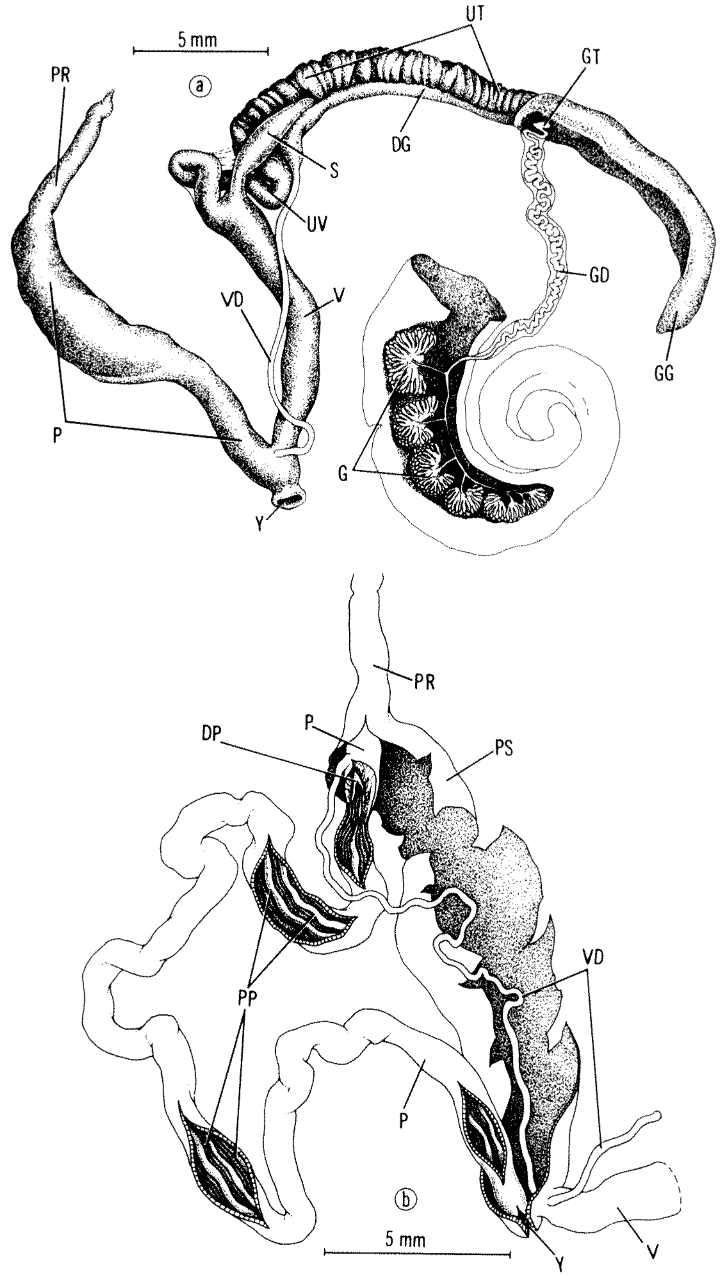


Fig. 102: Genitalia of *Cristilabrum simplex*: Sta. WA-235, 1.7 km south of Ningbing Bore, Ningbing Ranges, 12 November 1976, FMNH 199961, paratopotype, Dissection A, (a) whole genitalia, (b) interior of penis. Scale lines equal 5 mm.

CRISTILABRUM PRIMUM SP. NOV.

(Plate 17e-f; Figs 98a-c, 103a-b)

Comparative remarks

Cristilabrum primum is most readily identified by the very strong radial ribbing **(Plate 17e)** continuing undiminished across the shell base and into the umbilicus. Of the known Ningbing taxa, only *Turgenitubulus costus* **(Figs 90d-f)** and some specimens of *C. bilarnium* have this feature. The former differs in the much less sharply angulated periphery, higher spire (compare **Figs 90e** and **98b**), and smaller size (mean diameter 15.22 mm). Other *Cristilabrum* species are separable by lip and sculpture features. *Cristilabrum simplex* **(Fig. 97e)** totally lacks any basal ridge, and in *C. solitudum* **(Fig. 97b)**, *C. bilarnium* **(Fig. 100b)** and *C. funium* **(Fig. 100e)** it is reduced to a small remnant compared with that of *C. primum* **(Fig. 98b)**. *Cristilabrum buryillum* **(Fig. 98e)** has a high conical or 'U'-shaped basal lip ridge, *C. bubulum* **(Fig. 99e)** and *C. grossum* **(Fig. 99b)** have large ridges, but are much less sharply angulated and the shell base has irregular growth lines rather than prominent radial ribs. Anatomically, the vagina (V) exceeding the length of the penis sheath **(Fig. 103a**, P), short spermatheca (S) with a short ovate to elongate head, relatively prominent penial stimulators **(Fig. 103b**, PD), and the penis being about 1.5 times the length of the sheath **(Fig. 103b)** enable separation from the other species of *Cristilabrum*. Both *C. simplex* **(Fig. 102b)** and *C. grossum* **(Fig. 104b)** have the penis greatly elongated and shorter vaginae. *Cristilabrum solitudum* **(Fig. 101b)** and *C. bubulum* **(Fig. 103b)** have much shorter penes and vaginae, while *C. bilarnium* **(Fig. 106b)** is grossly altered in penis structure.

Holotype

WAM 505.79, Sta. WA-226, limestone hill 4.3 km south of Ningbing Bore, south end of Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667–658:108). Collected by Alan Solem and Carl C. Christensen 11 November 1976. Height of shell 9.45 mm, diameter 17.4 mm, H/D ratio 0.543, whorls 5 ⅛+, umbilical width 1.9 mm, D/U ratio 9.16.

Paratopotypes

WAM 572.79, WAM 546.79, FMNH 199005, FMNH 199015, FMNH 199962, 39 live and 351 dead adults from the type locality.

Paratypes

Ningbing Ranges, north of Kununurra: Sta. WA-432, at gate ca. 200 yds south of Sta. WA-226, cave mouth, 4.3 km south of Ningbing Bore ('Carlton' map sheet 4667—659:105) (24 live and 147 dead adults, 9 live juveniles, WAM 563.79, WAM 552.79, WAM 515.79, FMNH 199034, FMNH 199641, FMNH 200352).

Diagnosis

Shell slightly smaller than average, 14.1-20.0 mm (mean 17.07 mm) in diameter, with a slightly reduced whorl count of 4⅜ to 5½ (mean 4⅞−) normally coiled whorls. Apex and spire moderately and evenly elevated **(Fig. 98b)**, height of shell 7.8-10.65 mm (mean 9.01 mm), H/D ratio 0.455-0.678 (mean 0.528). Apical sculpture **(Plate 17e)** typical, postapical whorls with very prominent radial ribbing that continues across shell base to umbilicus without size change. Shell periphery sharply angulated **(Fig. 98b)**, generally a weak to strong sulcus behind lip on periphery. Body whorl very slightly deflected behind lip, which is broadly and sharply reflected **(Figs 98a, b)** on outer margin, partly reflected to cover umbilicus, basal lip margin with a strong ridge located relatively near to columellar margin, occasionally slightly recessed. Umbilicus slowly decoiling, last whorl a little more rapidly, partly covered by lip reflection, umbilical width 1.6-3.6 mm (mean 2.44 mm), D/U ratio 5.29-10.5 (mean 7.09). Based on 570 measured adults.

Genitalia **(Figs 103a-b)** with apical features typical, prostate (DG) and uterus (UT) shorter than usual in *Cristilabrum*. Vagina (V) very long, exceeding length of penis sheath **(Fig. 103a)**, free oviduct (UV) with a 'U'-coil, relatively short, spermatheca (S) with short stalk and elongately ovate head lying at prostate-uterus base. Vas deferens (VD) typical, entering penis sheath at base, not coiled within sheath **(Fig. 103b)**, reflexing to enter penis chamber through a short plug. Two prominent penial stimulators **(Fig. 103b**, PD**)** flank the vas opening, and a series of short high pilasters lie opposite the stimulators. Lower part of penis chamber with longitudinal pilasters of intermediate size compared with other *Cristilabrum*. Based on 5 dissected and 6 checked adults.

Discussion

Cristilabrum primum was the first species collected in the Ningbing Ranges, hence its specific name.

Both collecting stations for this species were on the east facing slope of a large rock mass right by the track and at a fence gate or *ca* 185 m north of it. Sta. WA-226 was taken from rock pockets about 7.5 m above the level of the plain, and Sta. WA-432 was taken near the open mouth of a very shallow cave. At both stations the live adults were distinctly smaller than the dead adults, and specimens from WA-432 were slightly smaller than the equivalent shells from Sta. WA-226 **(Table 41)**. Notes and photographs indicate that there was heavier tree cover at Sta. WA-226.

The elongated vagina is not necessarily correlated with the evident shortening of the prostate and uterus **(Fig. 103a)** when compared with the remaining species of *Cristilabrum*. It more probably relates to the reduction in mean whorl count (⅜ to ½). Most specimens were preserved in retracted or semi-retracted condition, so that no attempt at measurements of organ lengths could be attempted.

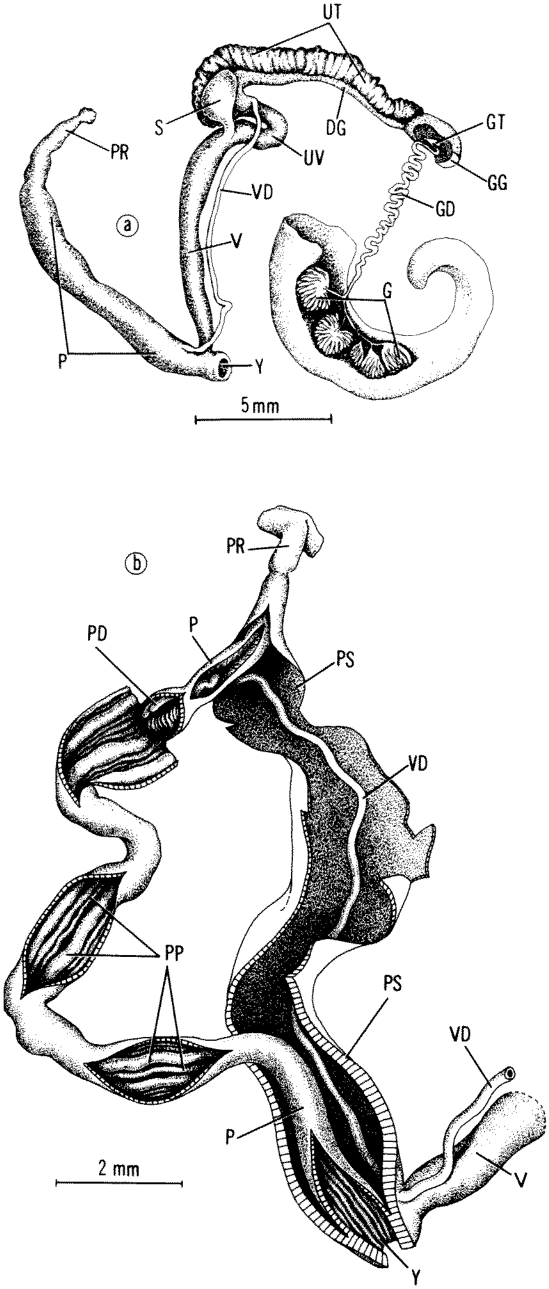


Fig. 103: Genitalia of *Cristilabrum primum*: Sta. WA-226, 4.3 km south of Ningbing Bore, Ningbing Ranges, 11 November 1976, FMNH 199962, paratopotype, Dissection A, (a) whole genitalia, (b) interior of penis. Scale lines as marked.

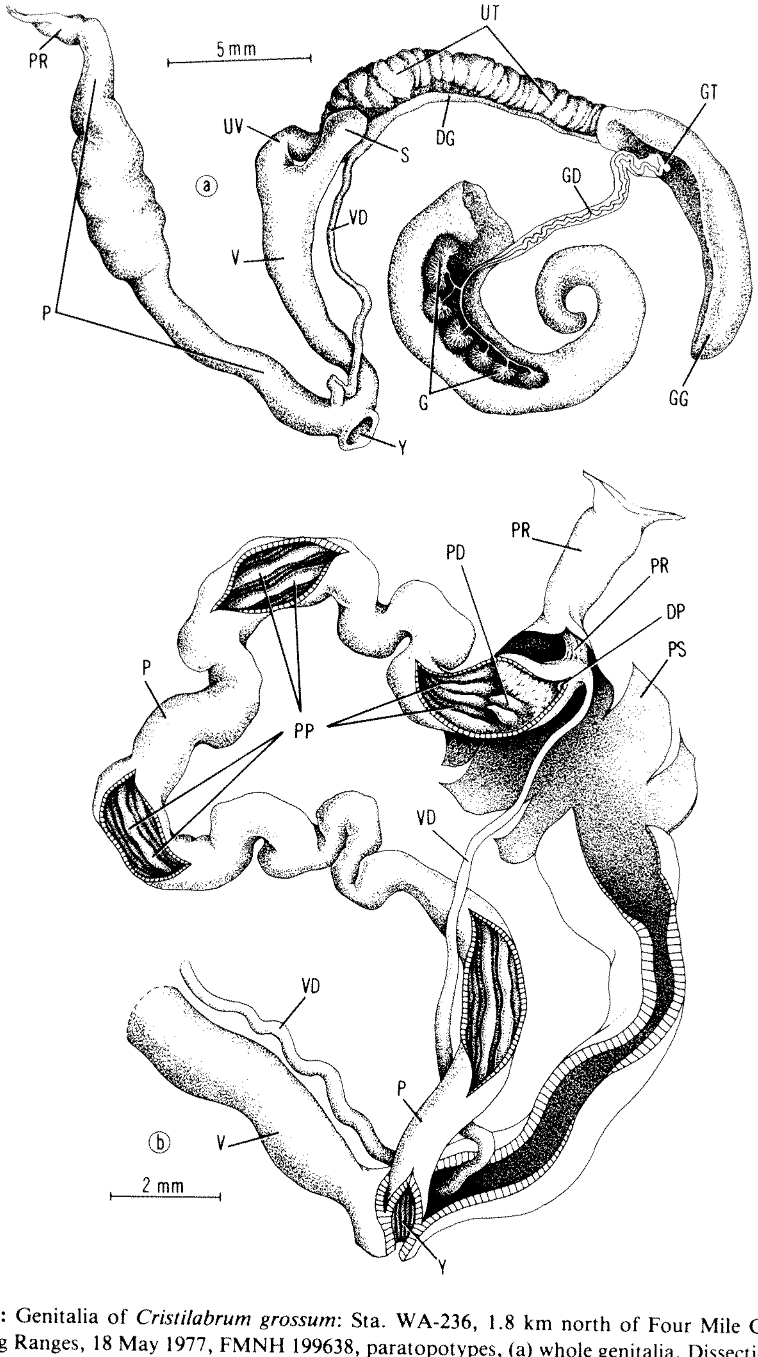


Fig. 104: Genitalia of *Cristilabrum grossum*: Sta. WA-236, 1.8 km north of Four Mile Creek, Ningbing Ranges, 18 May 1977, FMNH 199638, paratopotypes, (a) whole genitalia, Dissection A, (b) interior of penis, Dissection B. Scale lines as marked.

The very strong radial ribbing on the shell base, sharp angulation of the periphery, and broad, low basal ridge make *C. primum* one of the most distinctive Ningbing species in shell features.

Seasonal differences in genitalia were standard. The November examples have a swollen ovotestis, enlarged and strongly kinked hermaphroditic duct **(Fig. 103a)**, and partly enlarged prostate gland, while in the May specimens, the ovotestis was very small, the hermaphroditic duct narrow and partly unkinked, and both prostate and uterus very small. The illustrated specimen **(Fig. 103a)** is a new adult (indicated by the very small albumen gland) that reached shell maturity in the previous wet season. While capable of being male active, it probably would become female active only late in the coming wet season, or not until the following year.

Spermathecal shape was somewhat variable, in part correlated with the degree of packed material inside the head — elongated and narrower when this was reduced, nearly ovate when filled.

CRISTILABRUM GROSSUM SP. NOV.

(Plate 18a; Figs 99a-c, 104a-b)

Comparative remarks

Cristilabrum grossum is significantly larger (mean diameter 20.95 mm), with a very broad basal ridge **(Fig. 99b)**, extremely prominent and long peripheral sulcus **(Fig. 99a)**, heavy and rather widely spaced radial ribbing above the shell periphery **(Fig. 99a; Plate 18a)**, and a very broad and deep basal sinus **(Fig. 99c)**. The conical basal ridges of *C. bubulum* **(Fig. 99e)**, and *C. buryillum* **(Fig. 98e)** easily separate them; *C. primum* differs in its smaller size (mean diameter 17.07 mm), reduced whorl count (mean 4⅞−, and in having the radial sculpture continue undiminished across the shell base. The other *Cristilabrum* have the basal lip ridge absent **(Fig. 97e)** or reduced to a remnant **(Figs 97b, 100b, e)**. None of the *Turgenitubulus* or *Ningbingia* species can be confused. Anatomically, the penis that is twice the length of the sheath **(Fig. 104b)**, large penial stimulators (PD), and relatively short vagina (V) are diagnostic. Only *C. simplex* **(Fig. 102b)** exceeds it in penis length, and its very small penial stimulators and very thin penis contrast with the structures in *C. grossum*. The other *Cristilabrum* that have been dissected have much shorter penes **(Figs 101b, 103b, 105b, 106b)** and differ in details of vaginal length and penial stimulator size.

Holotype

WAM 530.79, Sta. WA-236, east slope of hill, 2.1 km south of gate at WA-432, 1.8 km by track north of Four Mile Creek, south end of Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667−653:093). Collected by Alan Solem 18 May 1977. Height of shell 11.1 mm, diameter 21.3 mm, H/D ratio 0.521, whorls 5½ +, umbilical width 3.05 mm, D/U ratio 6.98.

Paratopotypes

WAM 541.79, WAM 504.79, WAM 562.79, FMNH 199010, FMNH 199020, FMNH 199638, FMNH 199960, 10 live and 236 dead adults, 1 live juvenile from the type locality.

Diagnosis

Shell very large, 18.8-22.9 mm (mean 20.95 mm) in diameter, with 4 ⅞ to 6 (mean 5⅜ −) normally coiled whorls. Apex and spire strongly and almost evenly elevated, some specimens rounded above **(Fig. 99b)**, height of shell 9.0-13.4 mm (mean 11.29 mm), H/D ratio 0.455-0.618 (mean 0.539). Apical sculpture **(Plate 18a)** typical, but very prominent, spire and body whorl above periphery with prominent, low, broad, rather widely spaced radial ribs, base of shell with prominent growth lines but no ribbing. Shell periphery bluntly angulated **(Fig. 99b)**, periphery with a very strong sulcus extending up to one-quarter whorl behind lip **(Fig. 99a)**. Body whorl moderately to very strongly and sharply deflected behind lip **(Fig. 99b)**, which is broadly and sharply reflected, partly covering umbilicus **(Fig. 99c)**, basal lip with a very broad, high ridge **(Fig. 99b)**, marked outside by a very deep and long sinus **(Fig. 99c)**. Umbilicus with last whorl decoiling more rapidly, partly covered by reflection of lip, umbilical width 1.0-3.6 mm (mean 2.52 mm), D/U ratio 5.85-20.4 (mean 8.65). Based on 247 measured adults.

Genitalia **(Figs 104a-b)** with typical apical structures and normal length for the prostate-uterus. Vagina (V) long, about two-thirds length of very long penis, spermatheca (S) very short, with only slight enlargement of head. Vas deferens (VD) typical, entering penis sheath (PS) at base **(Fig. 104b)**, not coiled within sheath, reflexing apically through a short plug to enter penis chamber, opening flanked by two prominent stimulators (PD). Penis sheath with walls of lower two-thirds very thick, walls of upper third extremely thin. Penis (P) more than twice length of sheath, internally with a few prominent longitudinal pilasters **(Fig. 104b)**, when retracted, complexly coiled and kinked in the upper third of the penis sheath **(Fig. 104a)**. Based on 2 dissected adults.

Discussion

Cristilabrum grossum was collected in quantity from the same small hill in both November and May, but live material was obtained only in May. The live specimens were not significantly larger than the dead examples, and both collections of the latter were very close in size and shape **(Table 41)**. The name *grossum* refers to the large size, heavy sculpture, and broad basal lip ridge.

C. primum **(Fig. 103b)** shares the very thick lower walls of the penis sheath with *C. grossum* **(Fig. 104b)**, but the latter is unique in the degree of coiling and folding of the penis within the upper third of the sheath. Taxa with equally long penes, such as *Ningbingia octava* **(Figs 82b, 83b)**, *N. australis* **(Fig. 87b)**, and *C. simplex* **(Fig. 102b)**, have simple folding or several long folds, but the tight coiling of *C. grossum* finds its nearest equivalent in *Xanthomelon obliquirugosa* (Smith, 1894) (Solem, 1979: Figs 11a, c), which also has thickened lower penis sheath walls. The length of the vagina (**Fig. 104a**, V) also is slightly reduced in proportion, but otherwise the genitalia shows little difference from the typical *Cristilabrum*.

The very prominent peripheral sulcus (**Fig. 99a**), broad and low basal lip ridge (**Fig. 99b**), and extensive basal sinus (**Fig. 99c**), all are more prominent than in other *Cristilabrum* species and add to its gross appearance.

CRISTILABRUM BUBULUM SP. NOV.

(Plate 18b; Figs 99d-f, 105a-b)

Comparative remarks

Cristilabrum bubulum has the most constricted appearing aperture of any Ningbing species, caused by the very high and conical, slightly recessed basal lip ridge (**Fig. 99e**) and by the presence of a secondary thickening of the columellar lip, which, in effect, is a second lip ridge. In other respects, the shell is rather generalized, a little smaller than average (mean diameter 17.41 mm), with a weak to moderate peripheral sulcus (**Fig. 99d**), strong radial sculpture on the lower spire and body whorl, and slight flattening of the whorl sides. The geographically nearest species, *C. grossum* (**Figs 99a-c**), is much larger (mean diameter 20.95 mm), has a single very broad basal lip ridge, and a much more prominent peripheral sulcus. *C. buryillum* is even smaller (mean diameter 16.28 mm), with a single conical basal lip ridge (**Fig. 98e**). *C. primum* differs most obviously in having only a single basal lip ridge (**Fig. 98b**) and the radial sculpture continuing onto the shell base without size reduction. The other *Cristilabrum* species have only a remnant basal lip ridge or no ridge at all. Anatomically, the gradual diminution in penis sheath wall thickness (**Fig. 105b**), shorter penis (P), small penial stimulators, and slightly longer free oviduct (UV) and spermatheca (**Fig. 105a**, S) are the main characters separating *C. bubulum* from the neighbouring *C. grossum*. *C. solitudum* (**Figs 101a-b**) has a much shorter vagina (V) and penis (P), much larger pilasters, a much thinner walled sheath, and much longer free oviduct and spermatheca. *Cristilabrum simplex* (**Figs 102a-b**) and *C. primum* (**Figs 103a-b**) have much longer vaginae and clear differences in penial length. *Cristilabrum bilarnium* (**Figs 106a-b**) with its mid-sheath entrance of the vas deferens, very short vagina, shortened penis, and changed penis interior, is immediately separable in structure.

Holotype

WAM 492.79, Sta. WA-237, horizontally bedded limestone hill 0.9 km north of Four Mile Creek, south end of Ningbing Ranges, north of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667–645:094). Collected by Alan Solem and Carl C. Christensen 12 November, 1976. Height of shell 8.85 mm, diameter 16.75 mm, H/D ratio 0.536, whorls 5½, umbilical width 1.75 mm, D/U ratio 9.43.

Paratopotypes

WAM 507.79, WAM 536.79, FMNH 199009, FMNH 199039, FMNH 199640, 2 live and 131 dead adults from the type locality.

Paratypes

Ningbing Ranges, north of Kununurra: Sta. WA-433, hill just to north of Sta. WA-237, 0.9 km north of Four Mile Creek, south end of Ningbing Ranges ('Carlton' map sheet 4667–646:095) (50 dead adults, WAM 528.79, FMNH 199031).

Diagnosis

Shell less than average size, 15.1-19.2 mm (mean 17.41 mm) in diameter, with 4 ⅞ to 6 (mean 5⅜–) normally coiled whorls. Apex and spire moderately and evenly elevated, whorls slightly flattened, height of shell 7.6-11.2 mm (mean 8.94 mm), H/D ratio 0.444-0.600 (mean 0.513). Apical sculpture **(Plate 18b)** typical, postapical sculpture rather weak on early spire, becoming as prominent as in *C. grossum* **(Plate 18a)** on body whorl, shell base with only weak growth wrinkles. Shell periphery bluntly rounded **(Fig. 99e)**, peripheral sulcus weak to moderate **(Fig. 99d)**. Body whorl gently and slightly deflected behind lip, which is gradually and broadly reflected on outer margin, sometimes actually recurved **(Fig. 99d)**, partly covering umbilicus. Basal lip with a high, conical, slightly recessed ridge, plus a significant thickening of the columellar lip that is equivalent to the basal ridge remnant of *C. solitudum* **(Fig. 97b)**. Sinus behind lip very prominent **(Fig. 99f)**, lip often significantly thickened, including a marked ridging at the parietal-palatal margin **(Fig. 99f)**. Umbilicus with last whorl decoiling more rapidly, umbilical width 0.7-2.9 mm (mean 1.79 mm), D/U ratio 6.69-14.3 (mean 9.42). Based on 183 measured adults.

Genitalia **(Figs 105a-b)** with typical apical features. Vagina (V) distinctly shorter than penis (P), free oviduct (UV) and spermatheca (S) rather short. Vas deferens (VD) typical, entering base of penis sheath (PS), not coiled in sheath **(Fig. 105b)**, ascending to penis retractor muscle (PR) insertion, then reflexing through a short apical plug before opening lateral to two penial stimulators (PD). Penis sheath with walls thicker below, gradually tapering apically **(Fig. 105b)**. Penis about one-third to one-half longer than sheath, coiled apically, internally **(Fig. 105b)** with large longitudinal pilasters. Based on 1 dissected adult.

Discussion

Cristilabrum bubulum was taken first at an isolated limestone hill right by the track with very distinctive, nearly horizontal bedding planes (Sta. WA-237). In May, considerable effort was required to located 2 live adults, as the area of accessible talus was very small. On both occasions, cattle of highly inquisitive personality had to be dispersed before collecting was possible — hence the specific name *bubulum*,

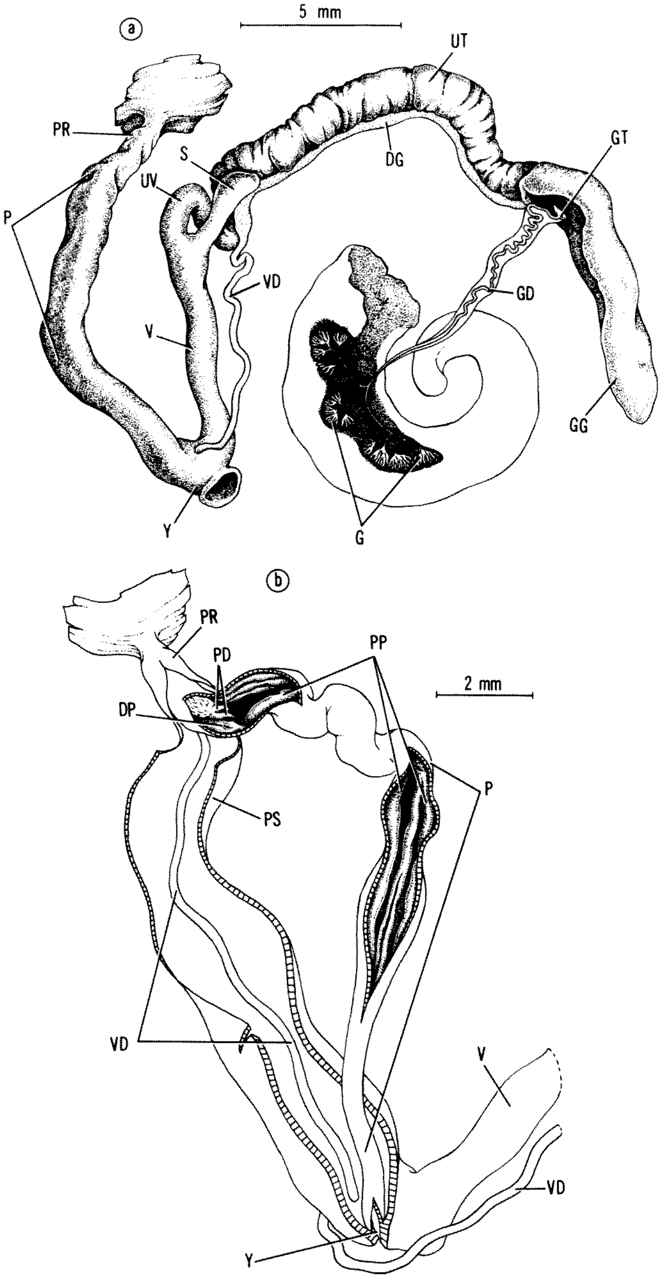


Fig. 105: Genitalia of *Cristilabrum bubulum*: Sta. WA-237, 0.9 km north of Four Mile Creek, Ningbing Ranges, 18 May 1977, FMNH 199640, paratopotype, Dissection A, (a) whole genitalia, (b) interior of penis. Scale lines as marked.

'of cattle'. The May and November collections were made from slightly different facies of the hill, and are slightly different in size **(Table 41)**. The difference is the result of the lower whorl count in the November collections (FMNH 199009).

Another isolated hill located directly north of Sta. WA-237 was sampled in May as Sta. WA-433. Only dead shells, which averaged a little larger in size **(Table 41)**, were obtained, again despite the attention of cattle.

In having the highly constricted aperture with two basal lip ridges, *C. bubulum* stands out conchologically from the other Ningbing genera. Only *Ningbingia res* **(Figs 78c-d)**, whose basal lip ridge is deeply recessed, approaches the degree of apertural narrowing seen in *C. bubulum.*

The dissected adult was reasonably well expanded, but the second specimen had contracted into the shell. Because of the difficulty in finding even two examples, it was decided to keep the second specimen available for more critical study. The differences in penial sheath thickness, penis length, vaginal length, and penial stimulator size between *C. grossum* **(Figs 104a-b)** and *C. bubulum* **(Figs 105a-b)** are substantial within the context of the genus and sufficient to delineate the species for comparison with other populations.

CRISTILABRUM BILARNIUM SP. NOV.

(Plate 18c; Figs 100a-c, 106a-b)

Comparative remarks

Cristilabrum bilarnium is relatively large (mean diameter 20.29 mm), with an increased whorl count (mean 5¾), an elevated spire and rounded periphery **(Fig. 100b)**, the basal lip ridge usually reduced to a remnant, heavy sculpture that in some specimens extends across the shell base, and has the lip much less expanded **(Figs 100a-b)** than usual. *Cristilabrum solitudum* **(Figs 97a-c)** and *C. simplex* **(Figs 97d-f)** have clearly angulated peripheries, much more broadly expanded lips to the shell, and greatly reduced postapical sculpture, although agreeing in the lip ridge reduction. The most similar shell is that of the very large *C. funium* **(Figs 100d-f)**, which has the same sculpture, whorl contour, and lip features, but is easily separable by its much flatter spire and hence reduced H/D ratio of 0.492, and much greater size (diameter 24.9 mm). Other *Cristilabrum* species have much more prominent basal lip ridges and thus are immediately separable. No *Turgenitubulus* or *Ningbingia* species approach the shell features of *C. bilarnium.* Anatomically, *C. bilarnium* is highly distinctive **(Figs 106a-b)**. The mid-penis sheath entry of the vas deferens (VD), greatly shortened penis (P) and vagina (V), and short spermatheca (S) slightly removed from the prostate-uterus, immediately distinguish *C. bilarnium* from any of the other *Cristilabrum* species, with their long penes and vaginae with basal entry of the vas deferens into the penis sheath **(Figs 101-105)**. Internally **(Fig. 106b)**, *C. bilarnium* has the basal section of the penis expanded and with two enlarged pilasters. Slightly below midpoint it narrows drastically and has nearly smooth walls up to the level of the vas deferens entrance, which is flanked by two minute penial stimulators. The base of the penis has the features of *Turgenitubulus*, and the mid-penis sheath entry of the vas deferens agrees with *Ningbingia*. The normal size of the vas deferens which enters through an apical plug, and the presence of the penial stimulators influence classification in *Cristilabrum*, despite its aberrant features.

Holotype

WAM 527.79, Sta. WA-435, isolated chain of limestone ridges south-east of Limestone Mill, north-west of Kununurra, Western Australia (1:100,000 'Carlton' map sheet 4667—733:908). Collected by Alan Solem and Laurel E. Keller 19 May 1977. Height of shell 11.85 mm, diameter 20.6 mm, H/D ratio 0.575, whorls 6+, umbilical width 2.5 mm, D/U ratio 8.24.

Paratopotypes

WAM 539.79, WAM 540.79, WAM 557.79, FMNH 199035, FMNH 199631, 3 live and 84 dead adults, 3 live juveniles from the type locality.

Paratypes

North-west of Kununurra: 'Bilarni Cave,' 44.5 km north of Kununurra on the Ningbing Road (3 dead adults, 13 dead juveniles, Michael Archer, 17-21 May 1975, WAM 424.77); top of hill *ca* 25 km north of Kimberley Research Station (1 broken adult, D. Beech, 3 October 1962, WAM 426.77).

Diagnosis

Shell relatively large, 18.2-23.2 mm (mean 20.29 mm) in diameter, with 5 1/8 to 6 3/8 (mean 5¾) normally coiled whorls. Apex and spire strongly and almost evenly elevated, sometimes slightly rounded above **(Fig. 100b)**, height of shell 10.0-13.0 mm (mean 11.4 mm), H/D ratio 0.507-0.663 (mean 0.563). Apical sculpture typical, postapical whorls **(Plate 18c)** with low, prominent radial ribs, usually stopping at shell base, but in about one-third of the individuals continuing across the shell base. Shell periphery at most slightly angulated **(Fig. 100b)**, usually rounded, no trace of a peripheral sulcus. Body whorl not to very slightly deflected behind lip, which is sharply reflected but very narrowly expanded **(Figs 100a-b)**, slightly reflected to partly cover umbilicus. Basal lip without (one-third), with a small remnant **(Fig. 100b**, one-third), or with (one-third) a modest elevated ridge slightly smaller than in *C. primum* **(Fig. 98b)**, but more centrally located on basal lip. Umbilicus slowly and regularly decoiling, umbilical width 1.4-3.2 mm (mean 2.23 mm), D/U ratio 6.69-14.3 (mean 9.42). Based on 91 measured adults.

Genitalia of smooth based form with remnant lip ridge **(Figs 106a-b)** having typical apical structures, prostate (DG) and uterus (UT) long. Free oviduct (UV) and spermatheca (S) short, head of spermatheca slightly removed from base of prostate-

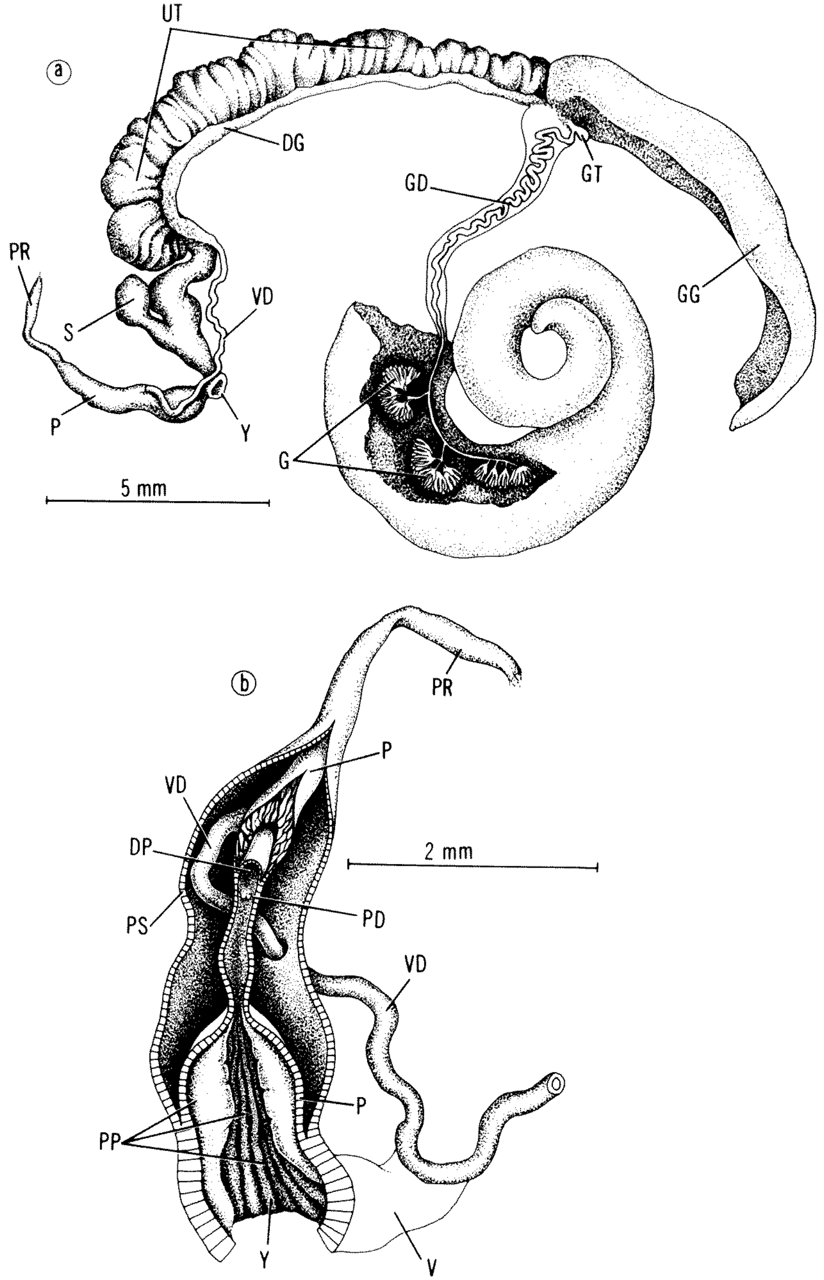


Fig. 106: Genitalia of *Cristilabrum bilarnium*: Sta. WA-435, south-east of Jeremiah Hills, north of Kununurra, 19 May 1977, FMNH 199631, paratopotype, Dissection A, (a) whole genitalia, (b) interior of penis. Scale lines as marked.

uterus. Vagina (V) very short, tapering. Vas deferens (VD) of normal diameter, entering penis sheath slightly below midpoint, reflexing below insertion of penial retractor muscle through an apical plug to open into the penis chamber flanked by two minute penial stimulators (PD). Penis and penis sheath very short, equal in length, walls of sheath tapering in thickness. Penis (**Fig. 106b**, P) very narrow apically with only two stimulators as visible wall sculpture, lower third of penis chamber grossly expanded in comparison, with two large and a number of slender longitudinal pilasters. Based on 2 dissected adults.

Discussion

The few specimens collected at 'Bilarni Cave' by Michael Archer in 1975 were the first indication that this area of the Kimberley had significantly different snails. They led directly to my field work in this region that disclosed the remarkable Ningbing Ranges radiation. Hence, selection of the name *bilarnium* for this species is appropriate. I am indebted to Mr A.L. Chapman, Division of Tropical Crops and Pastures, Kimberley Research Station, Kununurra, for assistance in providing the grid reference for the type locality, and for correcting my own imperfect kilometre readings on the confusing tracks in this area.

What I am calling *C. bilarnium* presents a number of currently insoluble problems in terms of both species limits and appropriate classification. In keeping this as a single species and placing it within *Cristilabrum*, I am being conservative.

There are two shell morphs present. In the less common one (Form A), the radial sculpture continues undiminished onto the shell base, there is never any trace of a ridge on the basal lip, and the shell aperture is more open and rounded. In the second (typical) form, there is no radial sculpture present below the periphery, the basal lip has a weak to moderate ridge (only rarely absent), and the aperture is slightly compressed. The holotype and all live collected adults belong to the second morph. These morphs differ slightly in size and proportions, although the lumped measurements (**Table 41**) do not show any noticeable increase in dispersion tendencies. For space reasons, the data on the separated morphs have been included in **Table 42** rather than in **Table 41**. Form A is noticeably larger, has a significantly lower whorl count, and a more open umbilicus. The overlap between measurements is quite extensive, except for whorl count, and the increase in standard deviation for the lumped data as opposed to the isolated morphs is less than 30% for all parameters, and thus within the range of variation among monomorphic sets of other Ningbing Ranges taxa.

Besides the above structural differences, there is a difference in the average condition of the dead shells. No specimens of Form A were 'freshly dead', while about half of the typical morph were in this condition. Only a few specimens of each morph were picked up in the open and represent 'washed down and bleached' individuals, presumably dead at least two dry seasons — died in the first, washed into open during the next wet season, and became eroded and bleached sub-

Table 42: Local Variation in *Prymnbriareus nimberlinus* and Forms of *Cristilabrum bilarnium*

Taxon	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
P. nimberlinus				
WA-225, FMNH 199725, 9-XI-76	3 (L)	10.77 ± 0.209 (10.4-11.0)	17.57 ± 0.142 (17.4-17.9)	0.613 ± 0.010 (0.595-0.630)
WA-225, FMNH 199003, 9-XI-76	12 (D)	9.71 ± 0.251 (8.6-11.1)	17.15 ± 0.265 (15.8-18.5)	0.562 ± 0.009 (0.520-0.616)
C. bilarnium				
Typical, WA-435	55 (D)	10.84 ± 0.080 (9.65-12.3)	19.52 ± 0.119 (17.2-21.6)	0.556 ± 0.004 (0.470-0.634)
Form A, WA-435	30 (D)	12.06 ± 0.091 (11.0-13.0)	21.43 ± 0.118 (18.75-22.85)	0.563 ± 0.003 (0.528 ± 0.591)

Taxon	Number of Adults Measured	Mean, Range and SEM of: Whorls	Umbilical Width	D/U Ratio
P. nimberlinus				
WA-225, FMNH 199725, 9-XI-76	3 (L)	5⅛+ (5-5⅜)	2.07 ± 0.145 (1.8-2.3)	8.60 ± 0.690 (7.59-9.92)
WA-225, FMNH 199003, 9-XI-76	12 (D)	4¾ + (4⅝-5⅛)	2.12 ± 0.070 (1.8-2.6)	8.18 ± 0.248 (7.02-9.42)
C. bilarnium				
Typical, WA-435	55 (D)	5⅞ (5½-6¼)	2.11 ± 0.041 (1.55-3.0)	9.43 ± 0.167 (6.75-12.21)
Form A, WA-435	30 (D)	5½ + (5⅜-5⅞)	2.93 ± 0.044 (2.55-3.35)	7.35 ± 0.115 (6.24-8.79)

sequently. Nearly all specimens of Form A had a crust of dirt cemented to the shell, indicating burial in dirt for a sufficient time so that debris could solidify on the surface. Only about ten of the typical morph showed this feature. Thus the two morphs may have a different time span in the area, although both were 'scratched out' from the same talus areas.

Without additional fieldwork and careful checking of the exact depositional occurrences of these morphs, I prefer to leave them lumped as one species, although their shell features are sufficiently distinctive to suggest possible species level differentiation. Form A could be a genetic variant recently displaced, since some of the typical shells have almost no trace of the basal ridge. This is another of the many intriguing features in Ningbing area taxa that need investigation.

The anatomy of *C. bilarnium* (typical form) is aberrant. Inclusion of this species in *Cristilabrum* is based on a reluctance to describe another genus at this time, rather than any certainty that it is strictly monophyletic with *Cristilabrum*. The presence of two very minute penial stimulators **(Fig. 106b**, PD), a definite apical plug, absence of any verge, normal size of the vas deferens' descending arm, and very short spermatheca agree with *Cristilabrum* and contrast with the same structures in *Turgenitubulus*. The very small size of the penis **(Fig. 106a)** and presence of two enlarged pilasters in the lower part of the penis agree with *Turgenitubulus*, and are very different from the normal pattern of *Cristilabrum*. The mid-penis sheath entrance of the vas deferens **(Figs 106a, b)** in *C. bilarnium* agrees with *Ningbingia*, and contrasts with both *Turgenitubulus* and *Cristilabrum*, which have basal entrance of the vas deferens.

The only known locality for *C. bilarnium*, Sta. WA-435 **(Fig. 110)**, is 20.1 km in a straight line from the nearest known colony of a *Cristilabrum*, *C. grossum* at Sta. WA-236, and 15.3 km from the Point Spring locality of *Torresitrachia weaberana* Solem, 1979, in the Weaber Ranges (Sta. WA-238). Much of the area in-between is not inhabitable by snails. The sandstone hills flanking Redbank Creek south of Eight Mile Bore and north of Waggon Bottle Tree Bore were camped among on 12 November 1976. No snails or signs of snails could be located in early evening searching. I do not know if the Jeremiah Hills are limestone or not, but Sta. WA-435 seems quite isolated from other snail colonies.

In view of its geographic isolation, structural peculiarities, and presence of two shell 'morphs', the decision to classify this as one species in *Cristilabrum* is a temporary expedient. The strong shell similarities with *C. funium* from the Roper River, Northern Territory (see below), make me suspect that this may be an independent development from the same stock that produced the Ningbing radiation, but much more data is required.

CRISTILABRUM FUNIUM SP. NOV.

(Figs 100d-f)

Comparative remarks

Cristilabrum funium is by far the largest species known of the Ningbing radiation (diameter 24.9 mm), is relatively depressed in shape (H/D ratio 0.492), has a basal lip ridge remnant **(Fig. 100e)**, narrowly expanded lip **(Fig. 100d)**, and prominent radial sculpture that stops at the periphery. *Cristilabrum bilarnium* **(Figs 100a-c)** is most similar in shell features, but is more elevated, smaller in size, and frequently has the basal lip ridge more strongly developed. The other species with reduced basal lip ridge, *C. solitudum* **(Fig. 97b)** and *C. simplex* **(Fig. 97e)** have greatly reduced radial sculpture, more broadly expanded lips, and more elevated spires. None of the *Turgenitubulus* and *Ningbingia* are conchologically similar to *C. funium*. Anatomy unknown.

Holotype

WAM 423.77, about 40 km north-east of Roper River Settlement on way to Numbulwar (Rose River) Mission, Roper River, Arnhem Land, Gulf of Carpentaria, Northern Territory. Located about 14° 30′ S, 135° 10′ E. Collected by E. Brandl in September 1968.

Diagnosis

Shell very large, diameter 24.9 mm, with 5 ⅝ + rather loosely coiled whorls. Apex and spire slightly and evenly elevated, last whorl not descending more rapidly, height of shell 12.25 mm, H/D ratio 0.492. Apex eroded, postapical whorls with narrow, crowded, sharply defined, prominent radial ribs that stop at the shell periphery, shell base smooth. Periphery rounded, whorls slightly flattened laterally below periphery **(Fig. 100e)**, no trace of a peripheral sulcus. Body whorl very slightly deflected behind lip, which is sharply and only moderately expanded **(Fig. 100d)**, very slightly reflected to cover a small portion of the umbilicus. Basal lip with a very weak ridge located near columellar margin **(Fig. 100e)**, a very slight basal sinus on outside of shell. Umbilicus regularly decoiling, slightly narrowed by reflexion of columellar lip, umbilical width 2.8 mm, D/U ratio 8.89. Based on holotype.

Anatomy unknown.

Discussion

Description of this geographically remote, worn and injured shell as a new species, *C. funium*, is done with reluctance. Its close similarities to the shell of *C. bilarnium* warrant temporary association of these species, and its description does call attention to an area that is still malacologically unknown at the present time. The name *funium* is a slightly whimsical reference to the Roper River area.

Several parts of the shell show repaired breaks (indicated by dotted lines in **Fig. 100d**), one of which may have resulted in lowering the H/D ratio. Otherwise it seems unchanged by the injuries.

GENUS *PRYMNBRIAREUS* NEW GENUS

Diagnosis

Shell smaller than average in size, spire strongly and evenly elevated, last whorl not descending. Umbilicus narrow, slowly and regularly decoiling, only slightly covered by reflection of columellar lip. Apical sculpture eroded in all examples, so details unknown. Postapical sculpture **(Plate 18d-f)** of irregular pustulations that sometimes anastomose, when slightly worn giving impression of pitting at optical magnifications, sculpture continuing across shell base into umbilicus. Body whorl not descending behind lip, which is narrow and sharply reflected **(Figs 107a-c)**. Shell periphery rounded. Parietal callus very thin. Colour brownish yellow horn, base much lighter in tone, almost white. Apical genitalia agreeing with *Ningbingia.* Spermatheca (S) and free oviduct (UV) short, vagina **(Fig. 108a,** V) very long, swollen apically as is base of spermatheca. Penis (P) longer than vagina, walls of sheath very thin **(Fig. 108b)**. Vas deferens normal, entering sheath about midpoint, reflexing from insertion of penial retractor muscle (PR), opening through a simple pore flanked by a single long penial stimulator **(Fig. 108b,** PD). Penis slightly longer than sheath, apically with longitudinal pilasters, lower two-thirds with three high stimulatory pilasters, whose upper edges have hardened ridgelets **(Fig. 109f)**.

Type species: *Prymnbriareus nimberlinus* sp. nov.

Comparisons

Inclusion of *Prymnbriareus* in this report is based upon its strong similarity to *Ningbingia* in basic genital features. The use of stimulatory pilasters with hardened microridgelets, thin sheath with mid-entry of the vas deferens, absence of a verge, short spermatheca — all are characters shared by the two genera. The presence of a penial stimulator, different number of stimulatory pilasters, long vagina, very different postapical shell sculpture **(Plate 18d-f),** narrow lip, and simpler shell shape of

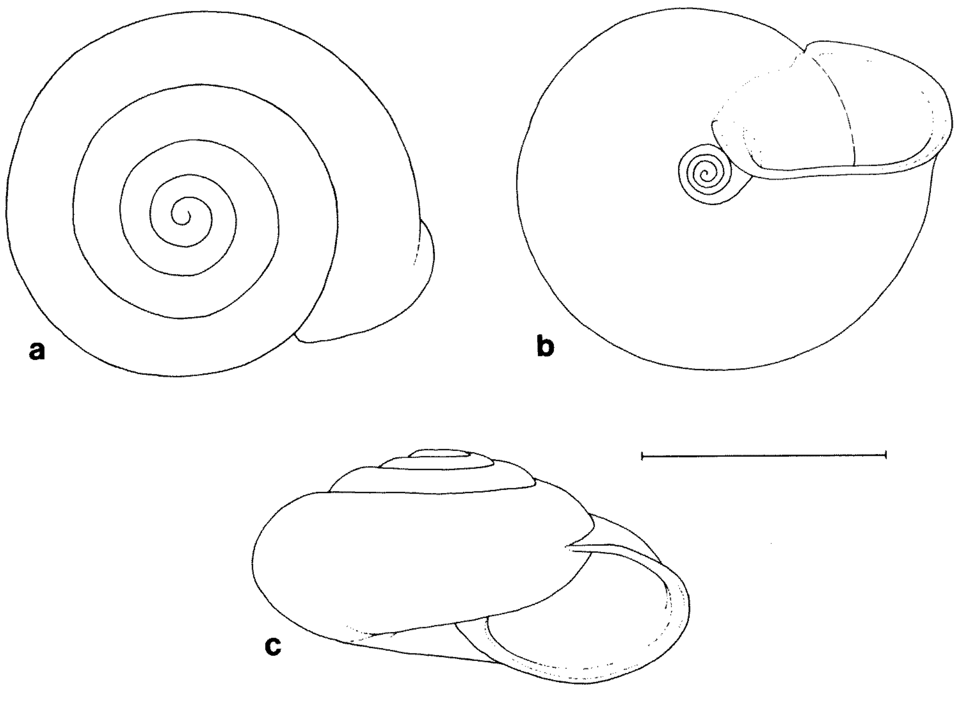


Fig. 107: Shell of *Prymnbriareus nimberlinus*: Sta. WA-225, Nimberline area, El Questro Station, south-west of Wyndham, WAM 519.79, holotype. Scale line equals 10 mm.

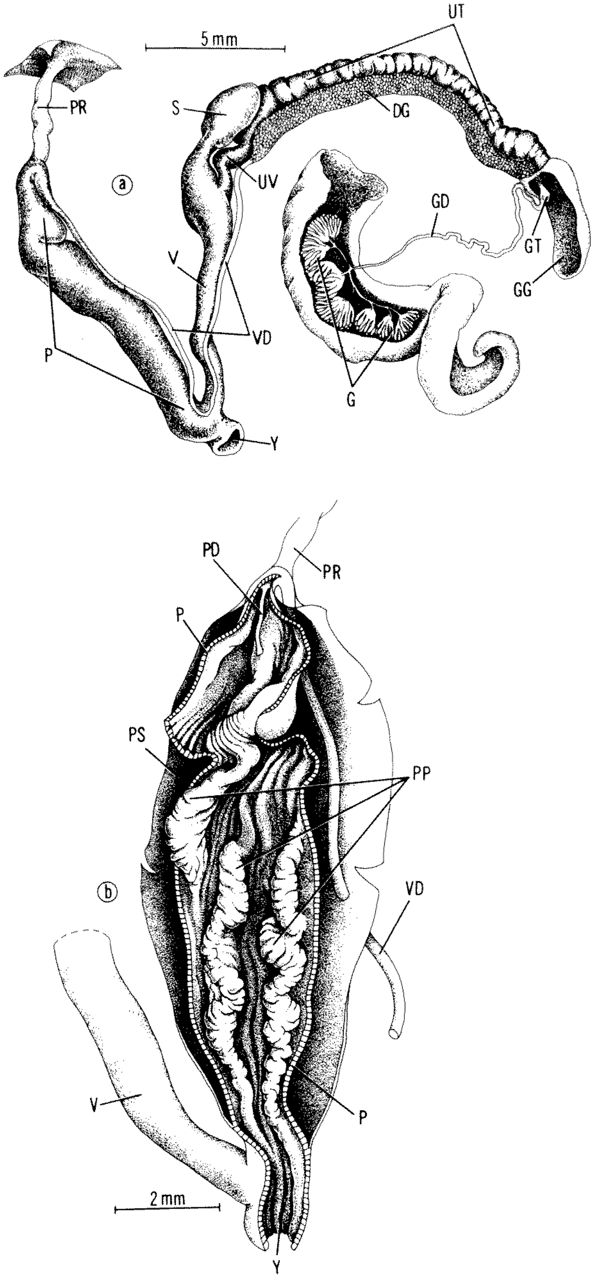


Fig. 108: Genitalia of *Prymnbriareus nimberlinus*: Sta. WA-225, Nimberline area, El Questro Station, south-west of Wyndham, 9 November 1976, FMNH 199725, Dissection A, paratopotype (a) whole genitalia, (b) interior of penis. Scale lines as marked.

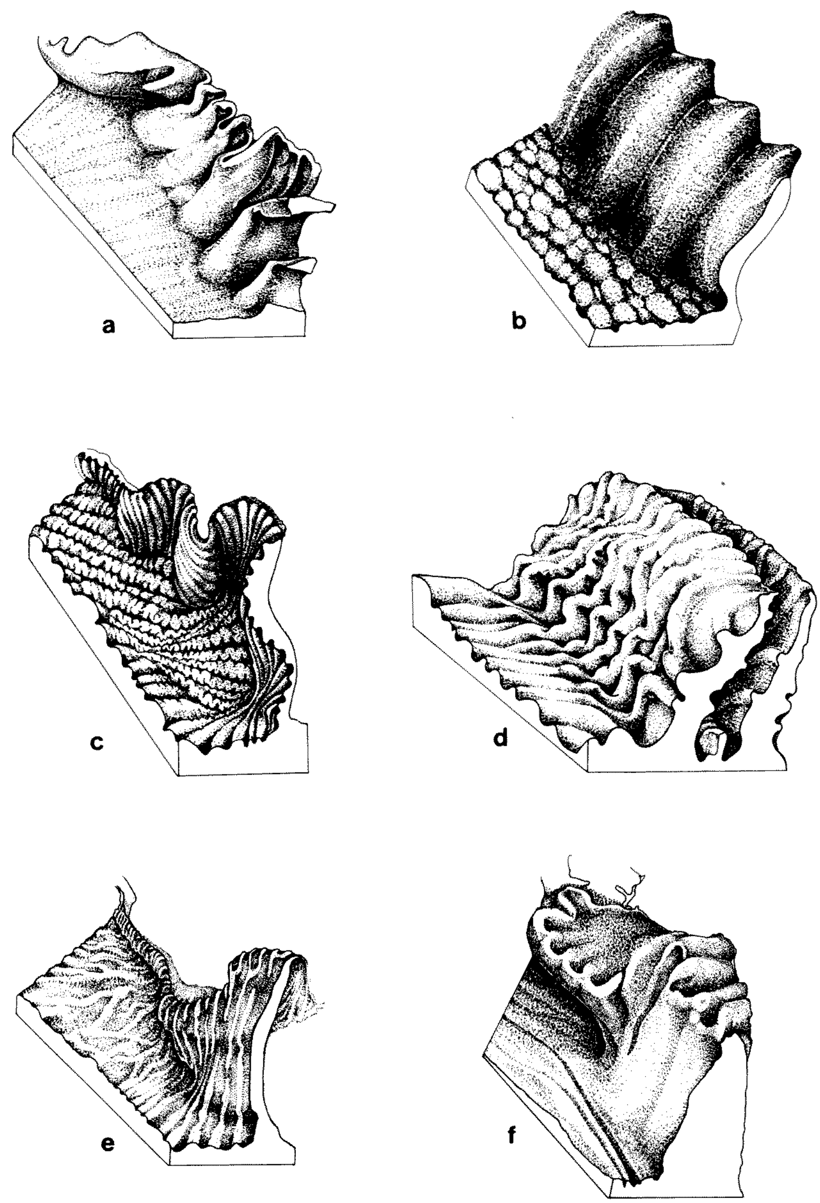


Fig. 109: Corrugated pilaster armature in *Ningbingia* and *Prymnbriareus*: (a) *N. bulla*, Sta. WA-429, FMNH 199637, Dissection A; (b) *N. octava*, Sta. WA-434, FMNH 199635, Dissection A; (c) *N. laurina*, Sta. WA-434, FMNH 200779, Dissection B; (d) *N. res*, Sta. WA-230, FMNH 199957, Dissection B; (e) *N. australis*, Sta. WA-231, FMNH 199954, Dissection C; (f) *Prymnbriareus nimberlinus*, Sta. WA-225, FMNH 199725, Dissection B. Not drawn to same scale, all greatly enlarged. Drawn by Marjorie M. Connors.

Prymnbriareus easily differentiates it from *Ningbingia*. Both *Turgenitubulus* and *Cristilabrum* present gross differences in genitalia that have been outlined in the comparisons of the latter genus.

At present only the single species of *Prymnbriareus* is known. In the same general region, *Amplirhagada questroana* has been collected near the junction of the Pentecost and Chamberlain Rivers, but this is the only other camaenid currently known from the Wyndham area. Quite possibly other isolated patches of wet forest may yield additional species, although such obvious possibilities as 'The Grotto' just south of Wyndham proved to be 'snail free'.

The name *Prymnbriareus* comes from the Greek *prymn* for end-most or undermost, and *briar* for strong, robust or hardy, referring to its occurrence on the fringes of snail inhabitable areas in a minute pocket of talus under some ancient figs.

PRYMNBRIAREUS NIMBERLINUS SP. NOV.

(Plate 18d-f; Figs 107a-c, 108a-b, 109f)

Comparative remarks

Prymnbriareus nimberlinus is most readily recognized by its postapical sculpture **(Plate 18d-f)** of anastomosing pustules, narrow lip, and lack of any apertural ridges. Species of *Torresitrachia* (Solem, 1979) have much more complex postapical sculpture, while the species of *Ningbingia, Turgenitubulus,* and *Cristilabrum* have postapical sculpture **(Plates 15-18)** of radial growth striae to prominent ribs, but never anything approaching the sculptural type of *Prymnbriareus*. The deciduous periostracal ridges of *Damochlora* (Solem, 1979: Plate 8b-c), or the minute rows of setae in *Parglogenia* (Solem, 1979: Plate 11b) might look similar at very low optical magnifications, but they cannot be confused at higher magnifications. Anatomically, the short spermatheca **(Fig. 108a)**, long vagina (V), mid-sheath entrance of the normal sized vas deferens (VD), and gross appearance of the large penial pilasters **(Fig. 108b)** suggest affinity with *Ningbingia* **(Figs 79-87)**, but the presence of a long penial stimulator (PD), three raised pilasters that have a unique ridgelet system **(Fig. 109f)**, and restriction of longitudinal penial low pilasters to the upper part of the penis, are significant differences from *Ningbingia*. *Cristilabrum* **(Figs 101-106)** differs in having two small penial stimulators, usually no raised pilasters, a much longer penis, and no microridging on the pilasters.

Holotype

WAM 519.79, Sta. WA-225, gulch in Nimberline area, 7.3 km from El Questro Homestead toward main road, south-west of Wyndham, Western Australia (1:100,000 'Erskine' map sheet 4566−957:309). Collected by Alan Solem and Carl C. Christensen 9 November 1976. Height of shell 10.3 mm, diameter 18.0 mm, H/D ratio 0.572, whorls 5, umbilical width 2.2 mm, D/U ratio 8.18.

Paratopotypes

WAM 538.79, WAM 558.79, FMNH 199003, FMNH 199725, 3 live and 11 dead adults, 3 live and 11 dead juveniles from the type locality.

Diagnosis

Shell of average size, 15.8-18.5 mm (mean 17.23 mm) in diameter, with 4 5/8 to 5 3/8 (mean 4 7/8) normally coiled whorls. Apex and spire moderately and evenly elevated **(Fig. 107c)**, last whorl not descending more rapidly, height of shell 8.6-11.1 mm (mean 9.92 mm), H/D ratio 0.520-0.630 (mean 0.572). Apical sculpture **(Plate 18d)** typical, with radially oriented pustules that tend to coalesce on lower part. Postapical sculpture **(Plate 18e-f)** pustulate, sometimes anastomosing into radially oriented patterns, usually somewhat irregular. Sculpture continuing across shell base into umbilicus. Shell periphery rounded, sometimes with slight lateral flattening above and below. Body whorl not descending behind lip, which is sharply but very narrowly reflexed and expanded, only slightly covering umbilicus. Aperture rounded, inclined about 30° from shell axis. Umbilicus open, regularly decoiling, umbilical width 1.8-2.6 mm (mean 2.11 mm), D/U ratio 7.02-9.42 (mean 8.27). Based on 15 measured adults.

Genitalia **(Figs 108a-b, 109f)** without unusual apical features. Free oviduct (UV) short, only slightly kinked, spermathecal base and upper vagina (V) swollen, head of spermatheca elongated. Vagina (V) about three-quarters length of penis, internally with same sculpture seen in *Ningbingia* **(Figs 80c)**. Vas deferens (VD) typical, entering at about midpoint of penis sheath, reflexing apically to enter penis through a simple pore flanked by a long penial stimulator **(Fig. 108b**, PD). Penis sheath (PS) only slightly shorter than penis, very thin-walled. Penis chamber **(Fig. 108b)** with thin, tapering walls, upper portion with low longitudinal pilasters, most of lower three-quarters occupied with three very high pilasters with corrugated edges and microridging **(Fig. 109f)** that is very different from those found in *Ningbingia* **(Figs 109a-e)**. Lower walls of opened penes without longitudinal pilasters. Based on 2 dissected adults.

Discussion

Prymnbriareus nimberlinus is named after the Nimberline area of El Questro Station, where the only specimens were taken in two hours of hunting on the north side of a steep gully among large rocks in the shade of figs. The previous evening 33 mm of rain had hit El Questro Station and the site of collecting was very damp. The live specimens had not resealed and both dissected adults had typical sperm packets **(Fig. 52e)** two-thirds or all the way up the vagina, indicating mating activity the previous night. All specimens were found in the upper part of a raceway within a very limited area. This was one of the few shaded, tree-covered sites known to 'Digger' and Anne Flohr, long time residents at El Questro, whose help and suggestions are gratefully acknowledged.

The lack of longitudinal pilasters in the lower part of the penis chamber could be the result of turgor of the main pilasters during mating, but without further material, this idea cannot be tested. The pattern of the hardened ridgelets on the raised pilasters (**Fig. 109f**) is very different from those observed in *Ningbingia*, although obviously similar in origin and function. The penial stimulator is highly unusual, and, combined with the very unusual shell sculpture, are the main reasons for separating *Prymnbriareus* from *Ningbingia.*

DISTRIBUTION

It is somewhat remarkable in the 1980s for a descriptive paper organized on a geographic basis to deal only with new taxa. Iredale (1939) had no material available from this part of Western Australia, and nothing described from the Northern Territory previously can be related to these taxa from the Ningbing Ranges.

Because of its highly dissected topography an extensive development of micro-geographic differentiation of the molluscan fauna could be expected, but the evolution into generic units was not anticipated. At the present time, in our limited knowledge of distribution within the Ningbing Ranges, patterns of distribution are strictly linear on a north to south basis. *Ningbingia* is replaced by *Turgenitubulus* and *Turgenitubulus* in turn by *Cristilabrum.* The evidence that speciation, rather than clinal or micro-geographic subspecific variation, has occurred is provided by the existence of several sympatric species pairs (**Fig. 110**). At Sta. WA-434, *Ningbingia octava* and *N. laurina* share the same rocks; at Sta. WA-227, *Turgenitubulus opiranus* and *T. depressus* are found together; at Sta. WA-235, *Cristilabrum simplex* and *C. buryillum* occur together; and at Sta. WA-435, *Cristilabrum bilarnium* (typical form) occurs with a possibly distinct type (Form A). The patterns of anatomical differences under conditions of sympatry were discussed earlier.

At the species level, distances of less than 1 km are sufficient for different species within a genus to occur. For example, the shift between *Turgenitubulus depressus* at Sta. WA-227 (**Fig. 110**) and *T. foramenus* at Sta. WA-425 or between *Cristilabrum grossum* at Sta. WA-236 and *C. bubulum* at Stas WA-237 and WA-433 occur in distances of about 1 km. As is obvious from **Fig. 110**, currently there are many areas of unsampled limestone hills encompassing far greater distances than 1 km. Hence one can anticipate that the number of taxa eventually to be recovered from the Ningbing Ranges will significantly exceed the number described here.

For this reason, I have not attempted constructing formal keys to the species, but in **Tables 34, 37,** and **40** have attempted to summarize the obvious variable shell and anatomical features for each of the known taxa. Using these tables as a checklist for characters, plus reference to the tables giving range of variation and local variation will permit association of new samples with known taxa or determination that they may represent new taxa.

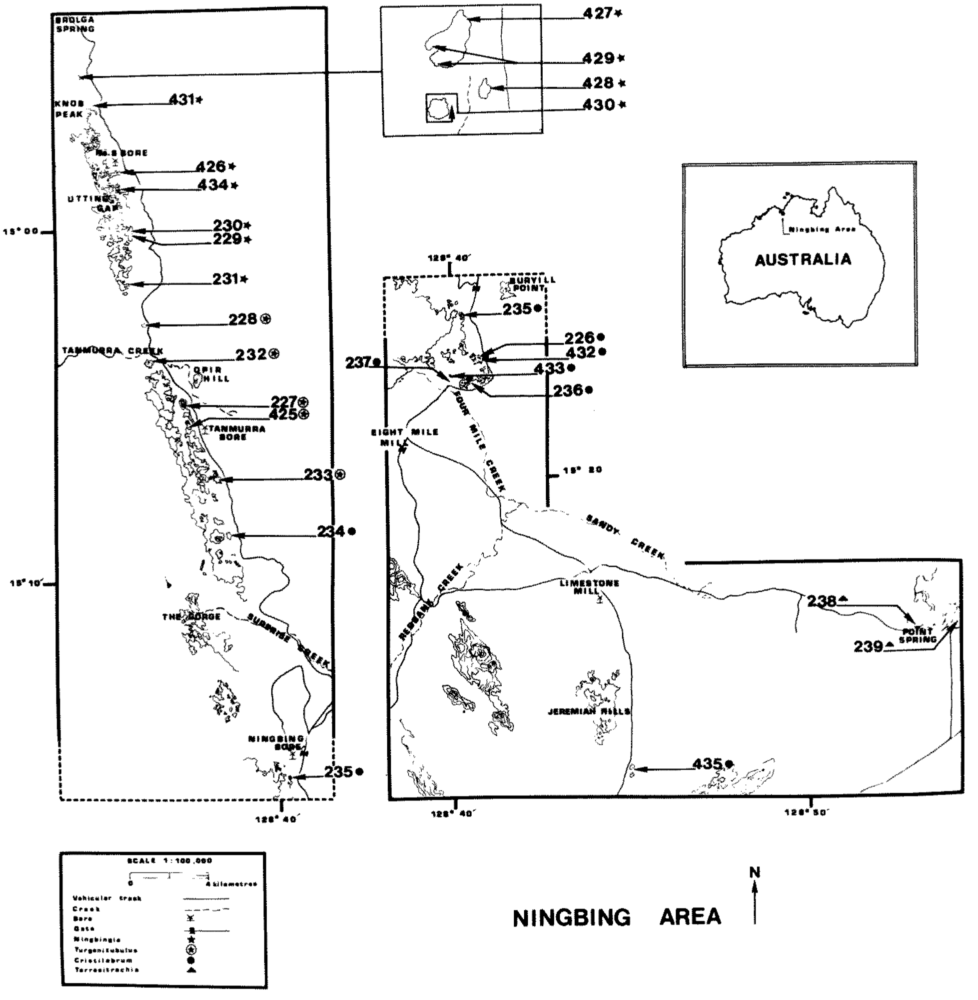


Fig. 110: Collecting stations in the Ningbing Ranges and adjacent areas north of Kununurra. Drafted by Elizabeth Lizzio.

The Ningbing Ranges present an extremely favourable situation for study of speciation events in camaenid land snails. The limited identified nodes of sympatry provide a starting place for studying micro-changes in species recognition characters, assuming that one can identify lateral areas of allopatry for each of the taxa. For almost all of the species, careful collecting in areas between the localities mentioned above can be expected to produce equivalent data.

At the present time, the points of transition between genera do not coincide with logical geographic boundaries. Both *Turgenitubulus* and *Ningbingia* occur north of Tanmurra Creek, with no obvious barrier between Stations WA-228 (northernmost *Turgenitubulus*) and WA-231 (southernmost *Ningbingia*). Similarly, Surprise and Station Creek do not separate *Turgenitubulus* from *Cristilabrum*, as *C. solitudum* (Sta. WA-234) is about 3 km south of *Turgenitubulus costus* (Sta. WA-233). Identification of more precise limits between genera will be extremely important. Particularly in regard to the differences between *Ningbingia* and *Turgenitubulus*, I can conceive of their differences arising as a by-product of species recognition changes under sympatry.

In addition to the sampling for additional taxa and study of current sympatry, attempts to obtain good samples of long dead specimens may provide data on micro-changes in distribution.

As indicated by the outlying sample of *Cristilabrum bilarnium* (**Fig. 110**, WA-435), description of *C. funium* from the Roper River in Arnhem Land, and the occurrence of *Prymnbriareus* south-west of Wyndham, all suggest that exploration of limestone areas in adjacent sections of the Northern Territory could be expected to yield not only new taxa, but probably material whose anatomy would yield significant data on the probable phylogeny of the Ningbing taxa.

This radiation is not only one of the most, if not the most, spectacular among the Australian camaenid land snails, but offers magnificent opportunities for the study of speciation and species interaction. Unlike the situation in *Amplirhagada* on the Mitchell Plateau, where specializations in aestivation strategy and restriction to vegetation types has occurred, the Ningbing radiation, so far as is known, exhibits uniformity in aestivation tactic (free sealing), and has no apparent shifts in aestivation site preference (loose in litter among rocks).

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