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

IV

TAXA FROM THE KIMBERLEY, *WESTRALTRACHIA* IREDALE, 1933 AND RELATED GENERA

ALAN SOLEM*

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INTRODUCTION

This is the fourth report on the semi-arid zone dominant land snails of Western and central Australia, which belong to the Camaenidae, *sensu lato.* It reviews 29 species level taxa in five genera. Twenty-two species and three genera are new. Most belong to *Westraltrachia* Iredale, 1933, a genus restricted to the south fringes of the Kimberley in limestone hills between Hawkstone Creek, a western tributary of the Meda River, and the Lawford Ranges east of Fitzroy Crossing. Six of the 21 taxa were previously known and 15 are new. Several related genera from the East Kimberley and adjacent portions of the Northern Territory contain eight species. New taxa are *Mouldingia* (one species in the Napier Range, one near Lake Argyle); *Ordtrachia* (four species between Lake Argyle and Nicholson); and *Prototrachia* (one species from east of Timber Creek Police Station, Northern Territory). *Exiligada negriensis* (Iredale, 1933), lives on the southern edges of Lake Argyle and ranges south about to the level of Nicholson.

A total of 12,292 adult specimens were measured: 9,787 belong to *Westraltrachia* and 2,505 to the related genera. Several very large sets were not measured to save time, and thus more than 14,000 specimens were studied.

Part I (Solem, 1979) of this series covered genera with trans-Australian distributions (*Hadra* Albers, 1860; *Xanthomelon* von Martens, 1860; *Damochlora* Iredale, 1938; *Torresitrachia* Iredale, 1939), plus related *Chloritis*-like genera from eastern Australia. Part II (Solem, 1981a) monographed 28 species-level taxa of *Amplirhagada* Iredale, 1933, a genus whose centre of diversity is in the north-west Kimberley, but with species as far south as the King Leopold and Napier Ranges, and as far east as near Wyndham. Part III (Solem, 1981b) described 19 new species-level taxa in four new genera *(Ningbingia, Turgenitubulus, Cristilabrum,* and *Prymnbriareus)* from the Ningbing Ranges north of Kununurra and El Questro Homestead south-west of Wyndham, Western Australia.

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Only a few more genera from the Kimberley remain to be monographed. It is anticipated that Part V will complete this section of the study, and permit biogeographic analysis of the Kimberley land snail fauna. The recent account of Bishop (1981) on the biogeography of Australian land snails merely outlined problems for study and offered little beyond a summary of classic literature.

Major financial sponsorship of this co-operative project between the Western Australian Museum, Perth (hereafter WAM), and Field Museum of Natural History, Chicago (hereafter FMNH), has been provided by National Science Foundation grants DEB 75-20113, DEB 78-21444, and DEB 81-19208 to FMNH for fieldwork and subsequent study of collected materials, and National Science Foundation grant BMS 72-02149 that established a scanning electron microscope laboratory at FMNH. Grateful acknowledgement is made of this support.

Continuing contributions by Mrs. Arthur T. Moulding that permitted extending both field time and sampling into new areas have improved both the depth and breadth of coverage in these reports. These significant contributions are recognised in the dedication of the new genus *Mouldingia*.

Nearly all anatomical and most of the shell line illustrations are by Linnea Lahlum, Illustrator, Division of Invertebrates. Additional illustrations are by Elizabeth A. Liebman and Marjorie M. Connors, formerly illustrators, Division of Invertebrates. Maps (**Figs 159-162, 179**) of collecting localities were drafted by Linnea Lahlum and Elizabeth Lizzio, volunteer Illustrator, Division of Invertebrates. For mounting and labeling the many plates and figures, we are deeply indebted to Dorothy Karall, Associate, Division of Invertebrates. Margaret Baker, Custodian of Collections, Division of Invertebrates, helped with both specimen measuring and data analysis, and later prepared specimens for return shipment to Perth.

Manuscript typing, assistance with proof-reading, and aid with preparation of specimen lists was handled with great efficiency by first Valerie Connor-Jackson and then Patricia Johnson, Secretary, Division of Invertebrates. For field assistance during these surveys, I am indebted to Laurie Price, Field Associate, Division of Invertebrates; Carl C. Christensen, formerly University of Arizona; Fred and Jan Aslin, Mt. Gambier, South Australia; Laurel Keller, peripatetic; and Barbara Duckworth, Australian Museum, Sydney.

Data on the materials collected pre-1920 and studied by Iredale (1939) are presented below under 'Previous studies and nomenclature' of the genus *Westraltrachia*. Activities by the staff of WAM and my grant supported field surveys provided the bulk of studied materials. As is true for so many taxa of Western Australian land molluscs, the field efforts of WAM staff members George W. Kendrick and A.M. Douglas in the mid-1960's produced the first known specimens of several species. These were of infinite help in planning the main field surveys and offering evidence that such efforts would be productive. Barry R. Wilson and Shirley Slack-Smith made highly significant collections in both the Napier and Oscar Ranges during the mid-1970's. To save space in the specimen lists, dates of collecting generally have been omitted, but the following inclusive station numbers identify the month and year of their fieldwork in the Napier (August 1975 Stas. NRI – XXIV; May 1976 – Stas. NRII – 1-31) and Oscar Ranges (early September 1975 – Stas. OR I-IV). Activities of FMNH representatives throughout the range of *Westraltrachia* and related genera (Alan Solem, Laurie Price, Carl C. Christensen, Fred and Jan Aslin, Laurel E. Keller, and Barbara Duckworth) were concentrated in two periods – October 1976 to mid-May 1977 (Stas. WA-189 through WA-402) and May to late June 1980 (Stas. WA-567 through WA-600, WA-707 through WA-717). Collecting dates are provided when necessary to discuss aspects of reproductive seasonality and for illustrated specimens, but for space reasons they are omitted from the lists of specimens and types.

The genera reviewed here form an apparently monophyletic assemblage characterised by complex specialisations primarily in the terminal male genitalia. Variation is at least partly mosaic, in that conchological specialisations do not correlate with anatomical specialisations. The genus with the simplest genitalia, *Mouldingia* **(Figs 164, 165)**, has the most specialised shell **(Figs 163a-f)**, whereas the genera with the most complex genitalia, *Ordtrachia* **(Figs 167, 168, 170, 173)** and *Exiligada* **(Fig 175)**, range the gamut from specialised to very generalised shell features. *Prototrachia*, known from an isolated limestone outcrop in the Northern Territory, has a very generalised shell **(Fig. 176)**, and genitalia **(Figs 176, 177)** that combine generalised and specialised features. The probable directions of character change and reasons for the suggested polarities are reviewed below, and their implications are summarised in the biogeographic discussion of this complex.

LIST OF THE TAXA

SYSTEMATIC REVIEW

The genera reviewed here show a coherent ecological pattern of association with exposed limestone, aestivation as free sealers on the soil surface (most genera) or burrowed into sandy soil *(Exiligada),* and apparent tendency to feed at least opportunistically on seepage face floral blooms. *Mouldingia,* with a disjunct distribution consisting of a few hills near the south-west corner of Lake Argyle and then near McSherry Gap in the Napier Range, combines relatively simple genital structures and highly complex shell features. The most speciose genus, *Westraltrachia* Iredale, 1933, has a unique genital structure: the epiphallus extends into a 'U'-shaped loop, and there is an extension of the penis retractor muscle that reaches the penis head to form a penis muscle. Usually the arms of the epiphallic loop are bound together by muscle fibers. In some species of *Westraltrachia* heavy glandular tissue develops at the base of the loop area. Both *Ordtrachia* and *Exiligada* Iredale, 1939, found near Lake Argyle, have the epiphallic loop and new penis muscle reduced or lost, but the glandular zone remains as a strongly developed area. *Prototrachia,* the easternmost member of this complex, is known from an isolated limestone outcrop in the Northern Territory between Kununurra and Katherine. It has a complex internal penial structure **(Fig. 178),** but lacks any evidence of the special muscle and glandular areas that characterise *Westraltrachia, Ordtrachia,* and *Exiligada.* It is more distantly related, but is included here for geographic, ecologic, and shell structure affinities to the other genera.

The genera are reviewed in geographic order from west to east.

GENUS *WESTRALTRACHIA* IREDALE, 1933

Westraltrachia Iredale, 1933, Records Australian Mus., **19**(1): 55 – type species *Trachia froggatti* Ancey, 1898 by original designation; Iredale, 1938, Australian Zool., **9**(2): 115 – list of species; Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 50-51 – monograph of genus.

Parrhagada Iredale, 1938, Australian Zool., **9**(2): 114 – type species *Thersites (Rhagada) woodwardi* Fulton, 1902 by original designation; Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 63-65 – monograph of genus.

Zygotrachia Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 50 – subgenus of *Westraltrachia* Iredale, 1933, type species *Westraltrachia alterna* Iredale, 1939, by original designation.

Diagnosis

Shell small to medium in size, spire usually moderately to strongly elevated, flattened in *froggatti* **(Figs 122b, e)** and very elevated in *turbinata* **(Fig. 117b).** Umbilicus rarely normally open **(Figs. 128c, 154f),** usually with a simple lateral crack **(Figs. 136c, f),** a callus closure present only in *woodwardi* **(Figs 111c, f, i),** Apical whorls macroscopically smooth, rarely with weak micro-undulations **(Plate 21c)** or pustulations **(Plate 20c, f).** Postapical sculpture normally of irregular radial growth wrinkles **(Plate 24),** becoming nearly smooth in species west of Yammera Gap **(Plates 19a, d, 20a),** never with strong and regular radial ribs. Microsculpture variable, ranging from weak impressed spiral lines in smooth surfaced taxa **(Plate 19c)** to periostracal folds **(Plate 22f),** rarely weak pustulations **(Plate 21f).** Prominent periostracal extensions present in *froggatti* **(Plate 20c-f)** and *ascita* **(Plate 25a, c, d).** Shell base with reduced sculpture. Body whorl slightly to a little deflected behind lip except in most individuals of the carinated *froggatti* **(Figs 122b, e).** Degree of lip expansion variable, greatest in *woodwardi* **(Figs 111a-i)** and *commoda* **(Figs 115a-f),** least in *derbyi* **(Figs 127a-f, 128a-c).** Development of a basal lip nodular ridge occasional in some species, normal in *alterna.* Shell periphery generally rounded, sometimes obtusely angulated **(Figs 155b, e),** subcarinated **(Figs 141b, e),** or rarely with a protruding keel **(Figs 122b, e).** Periphery of juveniles normally angulated to keeled, becoming more rounded on body whorl. Whorls on spire generally more strongly rounded than in *Amplirhagada* **(Plate 51).** Colour pattern geographically variable. Taxa east of Windjana Gorge with irregularly variegated light brown and white pattern on upper shell, stronger toward periphery than near suture, a narrow peripheral white zone, variegated subperipheral area and white basal region. Lip always white. Taxa west of Windjana Gorge show first reduction of colour pattern *(froggatti),* then loss of colour except for faint yellow brown periostracal tone *(inopinata, turbinata),* and finally retention of colour in periostracum of juveniles, but lower spire and body whorl chalk-white *(commoda, woodwardi).* Genitalia with size of both ovotestis (G) and hermaphroditic duct (GD) seasonally variable according to activity state **(Figs 114b, c).** Entrance of hermaphroditic duct onto talon (GT) lateral. Albumen gland (GG) long and finger-shaped with concave lower margin in fully mature adults, much smaller **(Figs 145a, d)** in third wet season adults. Prostate (DG) and uterus (UT) seasonally variable, without unusual features. Spermatheca (S) very short, sac-like, connected to base of prostrate-uterus by tissue strands, without expanded head, equal to **(Figs 114a, b)** or much shorter **(Fig. 116a)** than free oviduct (UV), which will be curved to 'U'-shaped when much longer than spermatheca. Vagina (V) variable in length, both individually and among species, always slender: ranges from very short **(Fig. 112,** *woodwardi),* medium length **(Fig. 118a,** *turbinata),* long **(Figs 137a,** *oscarensis;* **139a,** *cunicula;* **145a,** *tropida),* or very long **(Fig. 147a,** *rotunda).* Terminal male genitalia enclosed in a sheath (PS) that varies from thin for its entire length **(Fig. 116b,** *commoda)* to with very thick walls in section containing penis proper **(Fig. 145b,** *tropida).* Vas deferens (VD) a thin tube throughout its length, entering wall of penis sheath at a position most easily defined in relation to penis or base of epiphallus: rarely above base **(Figs 134b, 135b, c,** *alterna),* often opposite the base **(Figs 113b, 118b, 119b, 140b, 149b, 150b, 152b, 154a, b, 156b, 157b),** sometimes moderately below the base **(Figs 129-132,** *derbyi* and **147b, 148,** *rotunda),* often well below the epiphallus base **(Figs 116c, 123b, 124b, 136b, 139c-e, 142b, 144b, 145b, e).** At apex of penis sheath, vas deferens reflexes and enters epiphallus (E) without special structural change. Penial retractor muscle (PR) originating on base of diaphragm, attaching to vas deferens-epiphallus junction after entering penis sheath. A special penis muscle (PM) extends downward to attach at penis-epiphallus junction, sometimes **(Fig. 157b)** continuing for a significant distance anteriorly, more frequently **(Fig. 113)** only anchoring head of penis. Lateral strands bind main portion of epiphallus into a 'U'-shaped lateral projection. Epiphallus (E) variable in length and diameter, always with its major portion extended laterally in a 'U'-shaped projected tube that varies in length from typically long **(Figs 113a-c),** to rarely shortened **(Figs 129c-e,** some *derbyi),* internally with very narrow, low pilasters. Penis proper (P) a very slender tube of highly variable length, sometimes **(Fig. 153,** *pillarana)* coiled within sheath because of length, but may be much shorter than epiphallus **(Fig. 152b,** *recta).* Interior of upper penis with variable wall sculpture, ranging from the complex and large ridges found in *woodwardi* **(Fig. 113c)** and *rotunda* **(Fig. 148)** to remnants of these or simple pilasters **(Figs 158a-q).** Lower portion of penis chamber with simple pilasters that continue into atrium and also vagina **(Fig. 158).** Most striking differences in terminal male organs involve geographically adjacent or partly sympatric species. Jaw variable, typically ribbed in Oscar Ranges, reduced ribbing in eastern Napier Range, without ribs west of Windjana Gorge. Central and lateral teeth of radula with curved mesocones in eastern zone, becoming highly modified in eastern Napier Range, and achieving a new morphology adapted for algal-fungal film scraping in the central and western Napier Range.

Type species: *Trachia froggatti* Ancey, 1898 by original designation.

Previous studies and nomenclature

James Cox sent material collected about 1883 by W. W. Froggatt to E. A. Smith and C. F. Ancey in Europe. The locality data used in the descriptive papers of Cox (1892), Smith (1894), and Ancey (1898) were much abbreviated and distorted. Etheridge (1889: 200), copied by Iredale (1939: 57-58), summarised Froggatt's collecting stations. This data has been relied on in restricting or correcting type localities. *Westraltrachia derbyi* (Cox, 1892) (+ *derbyana* Smith, 1894 and *orthocheila* Ancey, 1898), *W. oscarensis* (Cox, 1892) (+ *inconvicta* Smith, 1894 and *perca* Iredale, 1939), and *W. froggatti* (Ancey, 1898) definitely came from material collected on Froggatt's trip. Probably the types of *W. woodwardi* (Fulton, 1902) originated in the same collections.

The generic placements of new species in *Trachia* Albers, 1860, *Rhagada* Albers, 1860, or *Hadra* Albers, 1860 represented conservative actions to avoid generic multiplication.

Hedley (1916: 69-70), in his comprehensive check list of Western Australian molluscs, allocated these species between *Rhagada* and *Planispira* Beck, 1837 without any explanatory comments.

Subsequent collections by Herbert Basedow (see Basedow, 1918, for a detailed itinerary), plus the bulk of Froggatt's collections, were used by Iredale (1938, 1939) to describe *Westraltrachia alterna, W. increta, Rhagada oscarensis perca, Parrhagada sedula, P. detecta, P. commoda,* and *P. ferrosa.* One additional species, *Parrhagada koolanensis* Iredale, 1939, from Koolan Island, Yampi Sound, is not related to *Westraltrachia,* but reallocation of this species will be published later. Thus, all of the material available to Iredale (1939) was collected in the early 1880's or 1910's, mostly without any detailed locality data accompanying the specimens.

Iredale was quite confused as to the possible relationships of these species. Initially (Iredale, 1933), he specifically included *Westraltrachia froggatti* (Ancey, 1898) and *Quistrachia monogramma* (Ancey, 1898) together. Subsequently, Iredale (1938) added *W. derbyi* (Cox, 1892) and its synonym, *Trachia orthocheila* Ancey (1898), but separated *Parrhagada woodwardi* (Fulton, 1902) in a new genus of the family Rhagadidae. This was a new family unit that he never described properly. Subsequently, Iredale (1939) placed *Westraltrachia* and a new genus *Quistrachia* in the family Chloritidae; left *Parrhagada* in the Rhagadidae; and transferred one species, *Westraltrachia oscarensis* (Cox, 1892), into the genus *Rhagada.* All of these decisions were made on conchological characters only. Prior to this study, no anatomical or ecological information has been recorded in the literature.

None of Iredale's new generic names were particularly well described even by the laxer standards of the 1930's, but just enough characters were mentioned in Iredale's comments to permit accepting them as having been validly proposed.

The multiple naming of species resulted from the still common practice of forwarding a few specimens for identification and/or description to several overseas experts. Given the delays in ocean mail, lag time in the experts coping with materials from diverse parts of the world, and existence of several land snail authorities, several sendings of specimens was a wise precaution that sometimes led to multiple descriptions. Cox (1892) and Smith (1894) clearly were describing materials of the same two species, *Westraltrachia derbyi* (Cox, 1892) (+ *derbyana* Smith, 1894) and *W. oscarensis* (Cox, 1892) (+ *inconvicta* Smith, 1894). This was pointed out originally by Hedley (1895: 259). The identity of the material used to describe *W. derbyi* and *Trachia orthocheila* Ancey (1898) is less obvious, as the latter taxon was cited as coming from the Oscar Ranges. Ancey (1898: 776) reported that *Amplirhagada burnerensis* (Smith, 1894), *Quistrachia monogramma* (Ancey, 1898), a species of *Rhagada* (listed as *reinga* Pfeiffer, 1846 but probably *R. gatta* Iredale, 1939), and *T. orthocheila* were sent together. He also gave an Oscar Range type locality for *Westraltrachia froggatti* (Ancey, 1898) in the same paper. The ranges of *Amplirhagada burnerensis* (Smith, 1894) and *Quistrachia monogramma* (Ancey, 1898) do not overlap (Solem, unpublished), so that a mixture of lots must have occurred. Furthermore, the range of *W. froggatti* (Ancey, 1898) is in the Napier Range between Yammera Gap and the west bank of Windjana Gorge. *Westraltrachia derbyi* ranges from the east bank of Windjana

Gorge to east of Carpenter Gap. *Quistrachia monogramma* is restricted to the eastern Napier Range and outliers of the Oscar Range, while *Amplirhagada burnerensis* has a range that encompasses those of both *W. froggatti* and *W. derbyi. Rhagada gatta* Iredale, 1939 ranges from McSherry Gap and Cycad Hill east through much of the Oscar Range (Solem, unpublished). Thus, three distinct geographic areas are represented in this material – west of Windjana Gorge, just east of Windjana Gorge, and the eastern Napier and Oscar Ranges. Apparently, all of these specimens originated from W. W. Froggatt's collecting efforts and a mixture of lots and label data occurred prior to study by Ancey (1898). Morphologically, *derbyi* and *derbyana* are based on the dwarf populations found at or near the south-east corner of Windjana Gorge, while the larger (diameter 13-14 mm) *orthocheila* matches more closely materials from a few km east of Windjana Gorge, although a few Windjana Gorge specimens **(Table 55)** reach the size of the *orthocheila* types.

Distribution and basic ecology

Westraltrachia extends from the north-west tip of the Napier Range, near Hawkstone Creek, south-east along the chain of limestone exposures that form the Napiers, continues through the Oscar Ranges and Brooking Gorge past Fitzroy Crossing, Giekie Gorge, Pillara Range, Home Range, Virgin Hills, Emanuel, Laidlaw and through the Lawford Ranges. The southernmost record is from The Pinnacles at Pinnacles Creek. There are no records east of the Lawford Ranges, nor from the many sandstone hills and ridges that lie north of this limestone belt (although sampling for land snails in this region has been minimal). *Westraltrachia* has not been taken in the King Leopold Ranges, nor in areas such as Kongorow Pool of the Barker River and the Van Emmerick Ranges adjacent to the Napier Range. It thus has a very narrow curved strip-like range, about 245 km long. Related genera appear in the limestone exposures around Lake Argyle and south along the Duncan Highway *(Mouldingia, Ordtrachia, Exiligada* Iredale, 1939) and to the east in the Northern Territory *(Prototrachia).* Collecting effort within much of the range of *Westraltrachia* has been fairly intensive. It seems probable that a majority of the species are known. Isolated bits of limestone unmarked on maps, such as yielded *W. porcata* in 1980, and the main ridge of the Oscar Range **(Figs 160-161)** are the most likely places for additional species to be found. This is unlike the situation in the much more widely distributed genus *Amplirhagada* Iredale, 1933 (see Solem, 1981a: 316-319, fig. 73).

Although closely associated with limestone exposures, species of *Westraltrachia* can be found sheltering under spinifex or scattered rocks a fair distance downslope from the actual rock exposures whereas specimens of *Amplirhagada* or *Quistrachia* at the same stations are strictly rock associated. So far as is known, all species of *Westraltrachia* are free sealing, that is, a sheet of mucus (the epiphragm) is secreted across the shell aperture and then thickened internally with layers of calcium. In the eastern part of the range, there is a marked tendency for specimens of *Westraltrachia* to secret multiple epiphragms. Specimens of *W. pillarana* from the Virgin Hills (Sta. WA-587, WA-588) were found to have up to 14 epiphragms spaced over one-eighth whorl. The aestivating snails can be found under rocks, in fissures, crevices, or lodged in the loose debris or rubble under spinifex clumps and other bushes providing shade. There is much greater success in obtaining live individuals from the latter habitat in May and

June than during October and November sampling. This suggests that there is significant dry season mortality among those snails aestivating in the more exposed habitats. Juvenile specimens occasionally have been found sealed to a rock or root surface, but adults invariably are lying free on the surface. This contrasts with the Napier Range species of *Amplirhagada,* where all adult specimens normally are sealed to a surface.

Most species of *Westraltrachia* are completely allopatric, although species transition zones often are very narrow. There are three exceptions. *Westraltrachia turbinata* and *W. froggatti complanata* have 1 km zones east of Yammera Gap on both sides of the Napier Range in which shells of both species have been taken. The extent to which live individuals are actually microsympatric remains to be determined. It probably is significant that they are the extremes in shell shape within the genus **(Figs 117b, 122e).** In the eastern Oscar Ranges and at Giekie Gorge, *W. limbana* and *W. rotunda* have grossly sympatric, but apparently micro-allopatric ranges. *Westraltrachia rotunda* occurs in large numbers on well-shaded talus slopes; *W. limbana* occupies adjacent, more exposed slopes with much thinner vegetation cover. Dead shells of both species, presumably wash-accumulation assemblages, often can be taken microsympatrically. This is probably a secondary phenomenon, resulting from an open upper slope lying above a shaded gulch. Dead specimens were mixed by heavy rains. Possible sympatry between *W. oscarensis* (Ancey, 1892) and *W. cunicula,* and narrow sympatry between *W. tropida* and *W. rotunda* are discussed under those species. Dead examples of both *W. limbana* and *W. recta* have been collected along Llaramalura Creek, Fossil Downs Station.

No other examples of microsympatry for *Westraltrachia* species are known.

In the central part of its range, *Westraltrachia* is either the only camaenid present, or occasionally populations are sympatric with *Rhagada gatta* Iredale, 1939. The latter species prefers sheltering under bushes or spinifex and can burrow down in sandy soil to aestivate, while *Westraltrachia* specimens are always found on the surface. In the western Oscar and Napier Ranges, two camaenid genera that are allopatric to each other, *Amplirhagada* Iredale, 1933, and *Quistrachia* Iredale, 1939, occur sympatrically and in approximately equal abundance with *Westraltrachia.*

In this zone of sympatry, there is simultaneous gradual character convergence and divergence – convergence in respect to shell size, shape, colour, and form; divergence in respect to preferred feeding resource, jaw, and radular structure. Species of *Westraltrachia* and *Amplirhagada* in the western part of the Napiers have converged in shell features to the point that they are difficult to field identify. Their appearance is quite different from the normal patterns found in each genus.

Species in the central Napiers, between Yammera Gap and Windjana Gorge, show less marked similarities and departures from generic norms. *Westraltrachia* species show altered radular structures and partly modified jaws in the area of sympatry with *Quistrachia.* This divergence intensifies in the region just east of Windjana Gorge where *Westraltrachia derbyi* (Cox, 1892) and *Amplirhagada b. burnerensis* (Smith, 1894) are sympatric. From the west bank of Windjana Gorge to the north-west tip of the Napier Range, structural divergence and feeding shift in *Westraltrachia* is both marked and stable. Details of this remarkable set of changes are presented elsewhere (Solem, In press-A).

Patterns of shell variation

A major aspect of this study is the fact that collecting intensity was highly unequal in different segments of the genus range. Whereas the area between Hawkstone Creek and Windjana Gorge was visited on multiple occasions, and the region within a few kilometres each side of Yammera Gap has been subjected to perhaps as intensive collecting for land snails as any area of the world **(Fig. 159),** most of the Oscar Ranges **(Figs 160-161)** has been sampled basically 'on the run' while driving between Napier Downs Homestead and Fitzroy Crossing. The area of the East Kimberley between the Limestone Billy Hills and Lawford Ranges **(Fig. 162)** also has had little attention from collectors.

The above description of the situation is a necessary preamble to the following statements concerning patterns of shell and anatomical variations. For Napier Range taxa, there is an abundance of data; for the Oscar Range and East Kimberley taxa, conclusions have had to be based in part on analogy with situations found in the Napier Range. Taxa described from the Napier Range are based on many population samples, but many Oscar Ranges and East Kimberley taxa are based on single samples. In the Oscar Ranges, exposed limestone is nearly continuous or with gaps of only a few metres. Lack of data is the fault of little collecting effort. In the East Kimberley, limestone exposures usually are widely separated islands rising from snail-free plains and there are thus large geographic gaps between populations. Lack of data for this region is, in part, because snails are physically absent from many places.

Size and shape of shell – The total range in shell diameter for adult specimens of *Westraltrachia* is 10.35 to 24.5 mm, which is essentially equivalent to the total range known in *Amplirhagada* (Solem, 1981a: 151). The range within individual species of *Westraltrachia* and related genera is given in **Tables 43** and **66.** In general, taxa with fewer specimens and from only one or two Stations, show the least variability *(W. subtila, W. porcata, Ordtrachia septentrionalis,* and *Prototrachia sedula).* Those species with rather large ranges and represented by a larger number of different population samples, show the greatest variability *(Westraltrachia woodwardi, W. commoda, W. derbyi, W. ampla, Ordtrachia grandis, O. intermedia,* and *Exiligada negriensis).* The raw data for similar comparisons of shell height, H/D ratio, whorl count, and umbilical features is contained in **Tables 47** and **66.** Discussion of these variables is deferred to an overall discussion of Kimberley land snail variation in a subsequent report.

Within the context of just *Westraltrachia,* it is worthwhile to discuss briefly the geographic patterns of size change, and how these changes are acheived. The genus itself has a rather stable morphotype, with comparatively few radical departures. **Table 44** presents both median and average size parameters for the species. Skewness for large size is indicated for both mean height and mean diameter. Eleven of the 21 species level taxa cluster between 13.9 and 15.24 mm in mean diameter. Four taxa are smaller, six are larger. Reduced diameter in *Westraltrachia turbinata* **(Fig. 117b)** and *W. recta* **(Fig. 151b)** is in part an artifact of spire elevation; in *W. ascita* **(Fig. 155e)** it results from a change in coiling pattern; and in *W. instita* **(Fig. 141b)** a combination of slight reduction in whorl count and tighter coiling seems to be responsible. Increased diameter correlates with increased mean whorl count, and has both geographical and isolation aspects. The two largest species, *Westraltrachia woodwardi* and *W. ampla,* live

Table 43: Adult Size Variability in *Westraltrachia* and Related Genera

Species	Number of Adults	Diameter Range	Species	Number of Adults	Diameter Range
WESTRALTRACHIA			*limbana*	512	47.5%
woodwardi	791	71.9%	*recta*	121	35.3%
commoda	883	69.2%	*pillarana*	368	49.0%
turbinata	930	40.6%	*ascita*	177	48.8%
inopinata	278	64.9%	*ampla*	454	87.6%
f. complanata	843	46.3%	*MOULDINGIA*		
f. froggatti	283	43.4%	*occidentalis*	317	33.3%
derbyi	568	71.2%	*orientalis*	557	47.5%
alterna	370	37.7%	*ORDTRACHIA*		
oscarensis	184	54.5%	*septentrionalis*	74	32.9%
cunicula	272	33.6%	*australis*	530	32.0%
subtila	82	21.2%	*grandis*	289	58.6%
instita	289	31.2%	*intermedia*	468	49.3%
lievreana	377	42.1%	*EXILIGADA*		
tropida	400	59.8%	*negriensis*	201	52.6%
porcata	43	29.7%	*PROTOTRACHIA*		
rotunda	1,562	53.9%	*sedula*	69	27.2%

at the opposite ends of the genus range, respectively, north-west of Barker Gorge in the Napier Range and south-east of Fitzroy Crossing in the Laidlaw and Lawford Ranges. These limestone ranges are more massive than hills between there and the Oscar Ranges, and provide excellent cover for *W. ampla.* In the north-west Napiers, *W. woodwardi* and *Amplirhagada napierana* Solem, 1981 are micro-sympatric and strongly convergent in shell form and size. *Westraltrachia oscarensis,* which flourishes under limestone blocks in the plains between the Napier and Oscar Ranges, and *W. porcata,* found in the drainage of Brooking Creek north of the Oscar Range, both reached large size in isolated areas subject to wet season inundation. These conditions permit longer periods of snail activity, hence a longer 'growing season', and thus greater adult size. The other two large species, *Westraltrachia commoda* and *W. froggatti complanata,* live in the central portion of the Napier Ranges, on either side of Yammera Gap, and are in a zone where shell convergence between *Westraltrachia* and *Amplirhagada* is in progress, with the generally smaller *Westraltrachia* increasing in size through both whorl count and simple enlargement. The major diameter changes are thus explainable as correlating with changes in shell proportions, living in areas that provide better growing conditions, or the byproduct of interactions with sympatric taxa.

Table 44: Mean and Median Shell Parameters in *Westraltrachia*

	Height in mm.	Diameter in mm.	H/D Ratio	Whorls
Mean	9.16	15.16	0.604	5−
Median	8.70	14.63	0.596	5
Range of all specimens	5.0−18.3	10.35−24.5	0.348−0.910	4− to 6

Increased shell height normally is the result of general shell enlargement (*W. woodwardi, W. commoda, W. oscarensis, W. ampla),* or significant spire elevation (*W. turbinata, W. porcata, W. recta).* Actual reduction in spire height seems limited to *Westraltrachia ascita* **(Fig. 155b),** while proportionate reduction in height is correlated with development of a protruding keel in such taxa as *W. instita* **(Fig. 141b)** and both subspecies of *W. froggatti* **(Figs 122b, e).** Most other species have an obtusely angulated to nearly rounded shell periphery, although there is a prominent keel in *W. tropida* **(Fig. 141e),** but that species is average in size. Keel protrusion slightly increases shell diameter, and as a concommitant of shell growth, often the spire whorls are flattened and the relative shell height reduced.

The only really significant change in shape, that shown by *Westraltrachia rotunda* **(Figs 146a-c),** is not reflected in mean measurements. The number of whorls, mean 4⅝+, is the lowest in the genus, but the shell shows average size and proportions. The rate of whorl expansion has increased, resulting in greater cross-sectional areas throughout the growth curve. This change, in turn, is hypothesised as being the feature that permitted *W. rotunda* to retain by far the largest principal penis pilaster **(Fig. 148, PT)** within *Westraltrachia* (see p. 694). The degree of difference in cross-sectional space near the aperture of the body whorl can be seen by comparing the side views of *Westraltrachia rotunda* and *W. limbana* **(Figs 146b, e).**

Changes in whorl count among populations are greater than those found among species, for example 4¾+ to 5½ in *W. commoda* **(Table 49)** and 4⅝+ to 5¼ in *W. derbyi* **(Table 55).** This reflects aspects of life for snails along the south margin of the Kimberley. Total annual rainfall varies from about 500 mm near Halls Creek and Fitzroy Crossing, to a known maximum of almost 750 mm near Napier Downs Homestead in the Napier Range (Solem, In press-A, Table 4). In the south-east Kimberley, there are 50 to 60 days on which 0.2 mm or more of rain is recorded, but only 40 days at Napier Downs. The latter area receives more rain, but in fewer, much heavier showers. The latter soaking rains provide extended periods during which the snails can be active, feed, and grow. A critical, but unmeasured, aspect for Kimberley land snails is the total period of time during which they can be active during a wet season.

Adult shell growth is reached near the end of the snail's second wet season, when the shell lip is reflected and thickened. If the wet season is extended by late rains, the snail may continue additive growth for a fraction of a whorl and reach larger adult size. If the wet season ends early and moisture is not available, the snail may go into aestivation with the shell lip unformed or only partly formed, and only after the start of the third wet season completes shell growth. Male organ sexual maturity occurs near the end of the second wet season and precedes shell lip reflection. Hence the timing of second wet season termination probably is the major factor controlling adult shell size. If the wet season has less rain and less activity days, the shell will be smaller in diameter and with lower whorl count. If the wet season is wetter and activity days increased, the shell will be larger in diameter and with higher whorl count.

Micro-climatic conditions are highly significant. A small, exposed pile of limestone rocks will dry out quicker than a shaded jumble of large boulders a few metres away, and the size of adult snails will reflect this difference. An excellent example of this effect is seen in samples of *Westraltrachia commoda* (Iredale, 1939) from Wombarella Gap in the Napier Range **(Table 49).** Sta. NR II 7 included three samples: a – large rock surrounded by grass, east entrance (mean diameter 19.34 mm, mean whorl count 5¼+); e – fissure of low cliff face, east corner (mean diameter 16.38 mm, mean whorl count 4¾+); and f – isolated rock in east entrance (mean diameter 17.82 mm, mean whorl count 5⅛+). All the above specimens were collected from soil in crevices and year class effects may be involved, but the principle that adult size is heavily influenced by the state of moisture conditions at the end of the second wet season of life is highly significant.

Comparability of samples is important in analysis of variation. In the south Kimberley, land snails are not randomly distributed. Occurrence is extremely patchy, with pockets containing a reservoir of many live specimens separated by many metres of range slope in which very few, if any, live examples can be collected at the end of a good wet season, and no live examples can be taken at the end of a poor wet season. In many spots, live specimens are deep in boulder piles or cliff fissures and are out of reach of collectors during the dry periods, and can be obtained easily only during the few hours immediately following a rain. These facts present difficulties in making even roughly comparable samples.

For the present series of reports, rough comparability is accepted for the following reasons. Experienced semi-arid zone land snail collectors were making initial geographic surveys. Each hillside was approached with the idea, "Where can I find live snails in the minimum time?" We were after accessible reservoir pockets of live specimens, to crop those individuals that had aestivated nearer to the surface of the talus or outer edge of the fissures. On subsequent trips, after preliminary study, we might try to find out exactly where along a section of hillside the transition from species A to species B occurred, and thus sample from other than the 'most favourable' spots. In our efforts to collect live specimens, we would pick up the first 50 to 100 dead adults encountered as we excavated talus, so that we would have minimum sample bias – if the Station was rich enough to yield these numbers.

Subsequent handling of the material also affects meristic data. Positioning of the shell between the calipers for measuring shell height and, to a lesser extent, shell diameter, is a judgmental decision. Different people will place the shell at a slightly different angle. In previous parts of the series, all measurements were made by the author, so that there was uniform bias. The overwhelming numbers of specimens obtained, have necessitated using volunteer help to make and/or record raw measurements. Several examples of 'measurer bias' are reported on in the species accounts below.

All the above qualifications should be kept in mind when reading statements concerning variability of shells.

Umbilical features – Eight of the 21 taxa belonging to *Westraltrachia* have the umbilicus too small to measure, reduced to a lateral crack, or effectively closed. Complete closure, with a smooth callus formed over the unbilical area, is present only in *Westraltrachia woodwardi* (Fulton, 1902) **(Figs 111c, f, i).** A rare individual of another species may have such a smooth closure, but that is unusual.

Only two species, *Westraltrachia ascita* **(Fig. 155f)** and *W. instita* **(Fig. 141b),** have a significant umbilical opening, with the umbilical width averaging 1.4-1.6 mm. Most taxa will have the columellar lip "rolled" and reflected (for example, **Figs 117c, f, 122c, f, 133c, f)** over the umbilicus, partly closing it. In *Westraltrachia derbyi* (Cox, 1892) **(Figs 127c, f, 128c),** this does not occur, but the umbilical opening itself is narrowed. Thus nine species have a mean D/U ratio of 10-14.5, and two more are in the 15.8-18.5 range.

In the remaining taxa, the umbilicus may be narrowly open and measurable, reduced to a lateral crack, or effectively closed. Character state proportions vary among species, and these are summarised in **Table 47.** These range from the mostly open umbilici of *Westraltrachia oscarensis* (Cox, 1892) and *W. ampla;* half open umbilici in *W. tropida* and *W. porcata;* one quarter to one-third open in *W. rotunda* and *W. limbana;* to the 10.5% open in *W. recta.* Of those taxa with strongly elevated spire, *Westraltrachia recta* and *W. porcata* are in the greatly narrowed category, while *W. turbinata* **(Fig. 117c)** retains a normally open umbilicus. In other families of land snails, such as the Endodontidae, there are closer correlations between umbilical size and various shell parameters (Solem, 1976: 19-30), but this does not seem significant within *Westraltrachia.* In the related genera **(Table 66),** the umbilici range from widely open in *Mouldingia* **(Figs 163c, f)** and variable among the species of *Ordtrachia* **(Figs 166c, f 171c, 172c),** to individually variable in *Exiligada negriensis* Iredale, 1939 **(Figs 174c, f).**

Aperture and lip features – Formation of a modest basal lip node is one of the species characters of *Westraltrachia alterna* Iredale, 1939 **(Figs 133b, e),** and both species of *Mouldingia* **(Figs 163b-c, e-f)** have the upper palatal wall extended inwards by the very strong supraperipheral sulcus, giving the effect of a lip node. *Ordtrachia intermedia* **(Figs 172b, c)** has a similar upper palatal extension and the basal lip is generally thickened and elevated, but only occasionally with a delineated node.

Lip expansion is quite variable, both in regard to reflection and actual expansion. *Westraltrachia woodwardi* (Fulton, 1902) **(Figs 111a, d, g)** represents one extreme, with gradual reflection (indicated by the curve behind the lip) and considerable expansion, giving an almost trumpet-shape to the aperture, while its neighbour, *W. commoda* (Iredale, 1939) **(Figs 115a-f),** shows equivalent expansion, but the reflection occurs much more rapidly (indicated by the angle behind the lip). Actual expansion may be relatively minor, with in aperture thickening of the lip giving the appearance of great expansion, as in both subspecies of *Westraltrachia froggatti* (compare top and side views, **Figs 122a-b, d-e).** Minimal lip expansion, combined with sharp reflection, is seen in *W. derbyi* (Cox, 1892) **(Figs 127a-f).** Maximal lip expansion is seen in both *Mouldingia* **(Fig 163a-f)** and *Ordtrachia intermedia* **(Figs 172a-c),** where the lip edge is grossly expanded and rolled over on the palatal and basal margins. Many species, particularly those with narrowed umbilici, have the columellar lip strongly curved and rolled partly over the umbilical opening (i.e., **Figs 117c, f, 133c, f**). In others, the lip extends laterally, giving more of a shield-like covering **(Figs 136c, f, 174c, f)**, and intermediate situations are the most common pattern **(Figs 146c, f)**. The type of columellar lip insertion is most effectively inferred from the illustrations by noticing the degree of curvature at the point of contact between the parietal wall and columellar lip. The sharper the line at the point of contact, and the tighter the curve, the more the lip edge is rolled, rather than extending as a partial shield.

The parietal wall contains only a thin callus, except in *Mouldingia occidentalis* **(Figs 163b-c)**, where there is a continuous raised lip edge. The very last section of the body whorl in this species is free of the penultimate whorl, thus producing a free aperture. *Mouldingia orientalis* **(Figs 163e-f)** has an unusually heavy parietal callus, but no free lip edge. In *Ordtrachia intermedia* **(Figs 172b-c)** the callus also is very thick, and both the columellar lip and upper palatal lip extend partway onto the parietal wall. The central section of the parietal wall has a raised callus in many specimens, but there is no trace of a free lip edge in any specimen seen. These species are the only members of the entire complex with prominent radial ribs on the spire and body whorl. These ribs continue onto the shell base and must be covered by a heavy callus during additive growth.

Body whorl descension is minimal in nearly all taxa, especialy when contrasted with the much greater descension normally found in such genera as *Amplirhagada* Iredale, 1933 (Solem, 1981a: 226, fig. 48) and *Torresitrachia* Iredale, 1939 (Solem, 1979: 56, Plate 7b,e). Generally there is a very slight dip that occurs just before the aperture, involving not even one-sixteenth of a whorl. This is accentuated in *Westraltrachia instita* **(Fig. 141b)**, markedly developed in all *Ordtrachia* **(Figs 166b, e, 171b, 172b)**, then dramatic in *Exiligada negriensis* Iredale, 1939 **(Figs 174b, e)** and both *Mouldingia* **(Figs 163b, e)**. *Prototrachia* **(Fig. 176b)** has the minimal descension typical of *Westraltrachia.*

In part this pattern of minor descension probably correlates with the general tendency in this complex towards a keeled or angulated periphery. Their presence produces physical difficulties in deflecting the shell lip, and such deflection might tend to reduce or even remove one of the advantages found in an angled periphery. This permits the same shell volume with decreased shell height. The latter feature permits entering narrower rock fissures or nooks within talus accumulation. Deflection of the aperture would change the angle at which the shell is carried, and might well make narrow crevice entry more difficult for the snail.

Shell colour – **Table 45** summarises the principal variations in colour pattern on a 'presence or absence' basis. A '+' means present, a '–'means absent. Unusual states are indicated by words. Generally, this complex of genera is characterised by a quite conservative colour pattern. There is a continuous white zone at the shell periphery that continues essentially to the lip. On either side of the white peripheral zone are brownish bands, that occasionally are sharply delineated on their outer margins, but normally fade into the spire colouration. This consists of irregular flammulations of alternating light yellowish-brown to brown. These are extremely variable in tone. A single flame can be light or dark when started, keep the same tone across its width, vary in tone, or fluctuate in tone. Often the spire flammulations invade the supraperipheral brown band, so that it becomes part of the flammulations. Normally

Table 45: Shell Colour Variation in *Westraltrachia*

Taxon	White Peripheral Zone	White Body Whorl	Monochrome Shell Colour	Variegated Colour on Spire	Spiral Bands
WESTRALTRACHIA					
woodwardi	–	+	–	few	–
commoda	–	+	–	"	–
turbinata	–	–	+	–	–
inopinata	–	–	+	–	–
f. complanata	weak	–	–	weak	–
f. froggatti	+	–	–	+	–
derbyi	+	–	–	+	–
alterna	+	–	–	+	–
oscarensis	+	–	–	+	–
cunicula	+	–	–	+	–
subtila	+	–	–	+	–
instita	+	–	–	+	–
lievreana	+	–	–	–	–
tropida	+	–	–	+	–
porcata	+	–	–	+	–
rotunda	–	–	+	–	–
limbana	+	–	–	+	–
recta	large	–	–	+	–
pillarana	+	–	–	+	–
ascita	+	–	–	+	–
ampla	+	–	–	+	–
MOULDINGIA					
occidentalis	–	–	+	–	–
orientalis	–	–	+	–	–
ORDTRACHIA					
septentrionalis	+	–	–	+	–
australis	+	–	–	+	–
grandis	+	–	–	+	–
intermedia	–	–	+	–	–
EXILIGADA					
negriensis	–	some	–	–	+
PROTOTRACHIA					
sedula	+	–	–	+	–

the base of the shell is white, and there may or may not be brown markings in the umbilicus. The reflected shell lip always is white, as well as the parietal callus.

Loss of the peripheral white zone is seen in taxa from the western Napier Ranges that are involved in massive shell convergence with species of *Amplirhagada* Iredale, 1933 (Solem, In press-A); *Westraltrachia rotunda* from the Oscar Ranges; both *Mouldingia* and *Ordtrachia intermedia* that have thick periostracal layers with dark colour and prominent periostracal sculpture; and *Exiligada negriensis* Iredale, 1939, which has totally altered colouration. Juvenile specimens of *W. woodwardi, W. commoda, W. turbinata, W. inopinata,* and *W. rotunda* show traces of this zone, but adults have monochrome body whorls. The peripheral zone is markedly widened only in *W. recta* **(Fig. 151b),** which, when combined with the sharp edges to the brown zones, gives the shell an appearance very close to that of *Rhagada.*

Loss of the peripheral white zone correlates **(Table 45)** with either a totally white body whorl, or monochrome yellow brown to light yellow brown body whorl. Monochrome body whorl normally does correlate with an absence of variegated colouration on the spire, except that both *Westraltrachia woodwardi* and *W. commoda* have traces of spire variegation, and many specimens of *W. lievreana* **(Fig. 143b)** have lost the variegation, but kept the white peripheral zone.

Exiligada negriensis Iredale, 1939 has the most unusual colour pattern. The shell varies from light brown to white in basic tone on the spire and body whorl, although the shell base is always white. Superimposed on this is a pattern of narrow spiral orange to reddish bands, that may be continuous (Iredale, 1939: plate V, fig. 2, form *qualis)* or interrupted (Iredale, 1939: plate V, fig. 4, form *negriensis).* This colour closely mimics that of true *Rhagada* (Iredale, 1939: plate 4, figs 1-17), and suggests why the two genera were associated by Iredale (1939). Both genera can burrow into the ground and are not rock associated, so that there may be selective value to this colour patterning.

The development of a thick and heavily pigmented periostracum, plus micro-projections from the periostracum, seems to have shifted the colouration in *Mouldingia* and *Ordtrachia intermedia.* Worn shells of these taxa show little trace of any shell colour. The other taxa with periostracal projections, *Westraltrachia ascita, W. f. froggatti,* and *W. f. complanata,* retain typical shell colour, although it is reduced in prominence in the latter two species. The periostracal layer is much thinner in the *Westraltrachia* than in the other species.

Shell sculpture – *Westraltrachia* shows considerable reduction in shell sculpture compared with most Kimberley taxa. For example, in *Torresitrachia* Iredale, 1939 (Solem, 1979: Plates 2-4) the surface of post-nuclear whorls varies from nearly smooth to heavily pustulose. *Xanthomelon* von Martens, 1860 (Solem, 1979: Plate 1) has ridges or pustules. *Damochlora* Iredale, 1938 (Solem, 1979: Plate 8a, d-f) has heavy pustulations on the apex, and curved periostracal ridges on the spire and the base (Plate 8b-c). *Amplirhagada* Iredale, 1933 (Solem, 1981a: Plates 12-14) normally has very fine pustulations on the apex, but they are sometimes reduced (Plate 14e) or quite enlarged (Plate 14d).

Westraltrachia normally has the apical whorls macroscopically smooth, at most showing occasional vague radial micro-ridges in the sutures, as for example in *W. woodwardi* (Fulton, 1902) **(Plate 19a),** *W. inopinata* **(Plate 20a),** *W. froggatti* *complanata* **(Plate 20c),** *W. derbyi* (Cox, 1892) **(Plate 21a),** *W. recta* **(Plate 24a),** and *W. ascita* **(Plate 25a-b).** Occasionally somewhat stronger remnants can be detected, as in *W. f. froggatti* (Ancey, 1898) **(Plate 20f).**

Where *Amplirhagada* and *Westraltrachia* are sympatric, juvenile specimens can be identified most readily by inspection of the apical whorls. **Plate 51** shows juveniles of *A. napierana* Solem, 1981 and *W. commoda* (Iredale, 1939) collected at the same station. The fine apical pustulations, less elevated spire, and more gently rounded whorl profile in the *Amplirhagada* **(Plate 51a)** contrast with the smooth surface, greater elevation, and more strongly rounded whorls of the *Westraltrachia* **(Plate 51b).**

Most *Westraltrachia* have very fine and irregular radial sculpture on the post-apical whorls. The situation seen in *W. derbyi* (Cox, 1892) **(Plate 21a),** *W. cunicula* **(Plate 21b),** *W. alterna* Iredale, 1939 **(Plate 21c),** *W. rotunda* **(Plate 23c),** and *W. limbana* **(Plate 23d)** is typical. The few departures from this pattern involve the Oscar Range species *W. subtila* **(Plate 22a),** *W. instita* **(Plate 22d),** *W. lievreana* **(Plate 22e),** *W. tropida* **(Plate 23b)** and *W. porcata* **(Plate 24d).** In all of these, the sculpture is distinctly more varied and usually stronger in appearance, primarily because of coarser growth ridges.

An additional microsculpture in the Oscar Range species **(Plates 22c, f, 23b, e-f)** is for anastomosing radial periostracal folds to be present. This was detected in all Oscar Range taxa except for *Westraltrachia subtila* and *W. rotunda.* An intensified version of these folds is seen in both *W. f. froggatti* (Ancey, 1898) **(Plate 20d)** and *W. ascita* **(Plate 25d).**

Very faint spiral lines, equivalent to those seen in *Amplirhagada percita* (Iredale, 1939) (Solem, 1981a: 160, Plate 14f), are found in fresh specimens of *Westraltrachia woodwardi* (Fulton, 1902) **(Plate 19c),** *W. commoda* (Iredale, 1939), *W. turbinata,* and *W. inopinata* **(Plate 20b).** In even slightly worn individuals, however, this element cannot be detected.

The most striking structural development is the spade-shaped periostracal projections seen in both *Westraltrachia froggatti* (Ancey, 1898) **(Plate 20c-e)** and *W. ascita* **(Plate 25c-d).** They appear to be identical in structure, representing additions to calcareous pustules. The apparent illustrated difference is interpreted as resulting from differential reaction to preservation in alcohol. The very weak pustulations seen in the sutures of *W. oscarensis* (Cox, 1892) **(Plate 21d)** and *W. turbinata* **(Plate 19f)** may be weak remnants of this basic sculpture.

Except for the two species, *Westraltrachia froggatti* (Ancey, 1898) and *W. ascita, Westraltrachia* is characterised by its macroscopically smooth shell surfaces. This contrasts greatly with the situation found in related genera from the East Kimberley. The strong ribbing and highly developed periostracal microsculpture of *Mouldingia* **(Plates 52-53),** strong pustulations found in *Ordtrachia intermedia* **(Plate 56d-f),** remnant pustulations in *O. septentrionalis* **(Plate 54),** *O. australis* **(Plate 55)** and *O. grandis* **(Plate 56a-c),** all are much stronger sculptural elements. *Prototrachia sedula* **(Plate 57a-e)** has a smooth apex, and the spire periostracal projections follow the plane of coiling in long axis rather than the pattern seen in most other taxa. Only the very large *Exiligada negriensis* Iredale, 1939, has equivalent reduction in sculpture to a smooth apex with only weak postapical radial elements **(Plate 57f).**

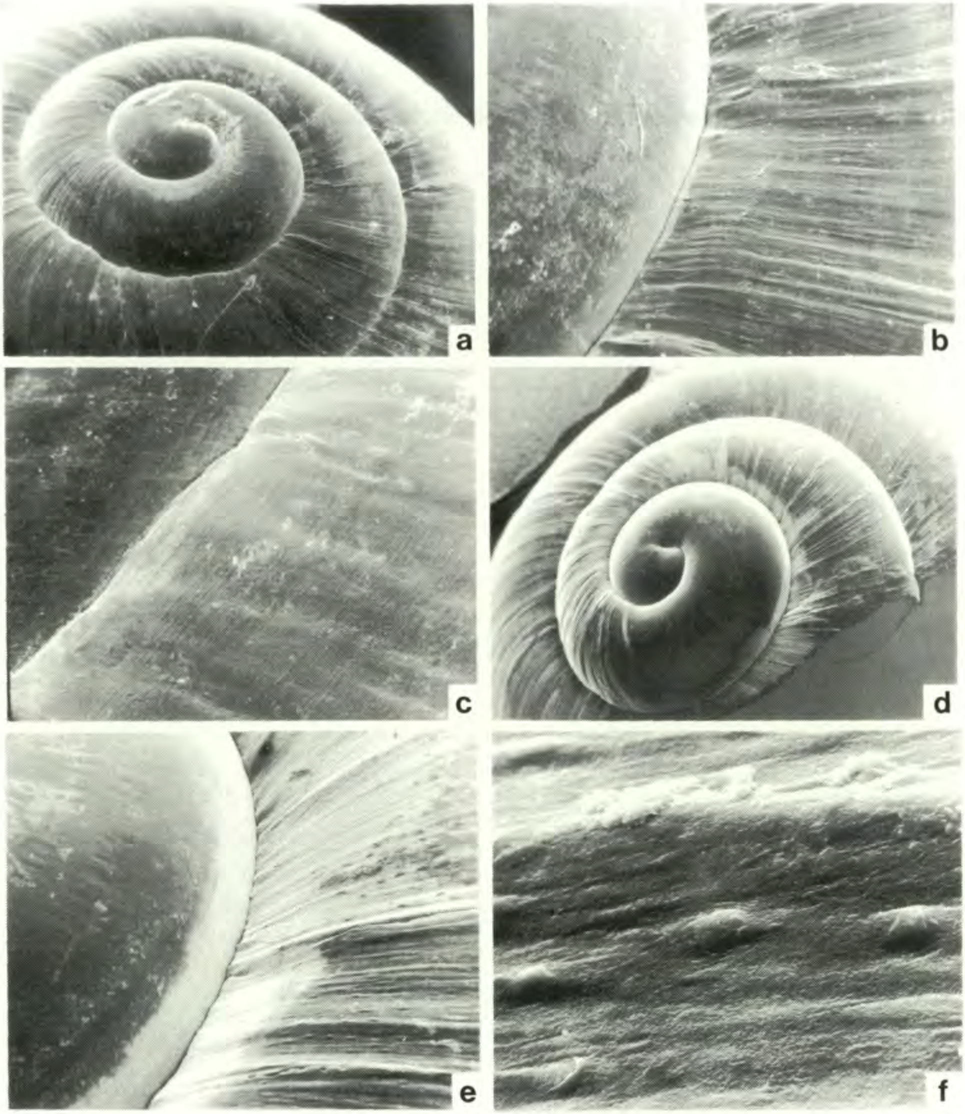


Plate 19: Shell sculpture of *Westraltrachia woodwardi* (Fulton, 1902) and *W. turbinata:* (a-c) *W. woodwardi,* FMNH 200366, Sta. WA-192, 9.1 km west of Barker River, Napier Range, 9 October 1976, juvenile shell, (a) apex and early spire at 13.1X, (b) detail of late apex and early spire at 67X, (c) weak spiral body whorl sculpture at 125X; (d-f) *W. turbinata,* FMNH 199871, Dissection A, Sta. WA-281, 1.3 km west of Yammera Gap, Napier Range, 6 December 1976, (d) apex and early spire at 15.0X, (e)detail of late apex and early spire at 76X,(f) microsculpture on early spire at 700X.

Plate 20: Shell sculpture of *Westraltrachia inopinata* and *W. froggatti* (Ancey, 1898): (a-b) *W. inopinata,* FMNH 200157, Dissection A, Sta. WA-339, 1.1 km south-east of Yammera Gap, Napier Range, 23 December 1976, (a) apex and early spire at 16.0X, (b) detail of early spire at 760X; (c-e) *W. f. complanata,* FMNH 200153, Sta. WA-359, 10.5 km east of Yammera Gap, Napier Range, juvenile shell, 10 January 1977, (c) apex and early spire at 15.8X, (d) mid-spire body whorl sculpture at 35.5X, (e) detail of body whorl sculpture at 365X; (f) *W. f. froggatti* (Ancey, 1898), FMNH 199873, Dissection A, Sta. WA-193, south-west corner of Windjana Gorge, Napier Range, 5 December 1976, apex and early spire at 14.9X.

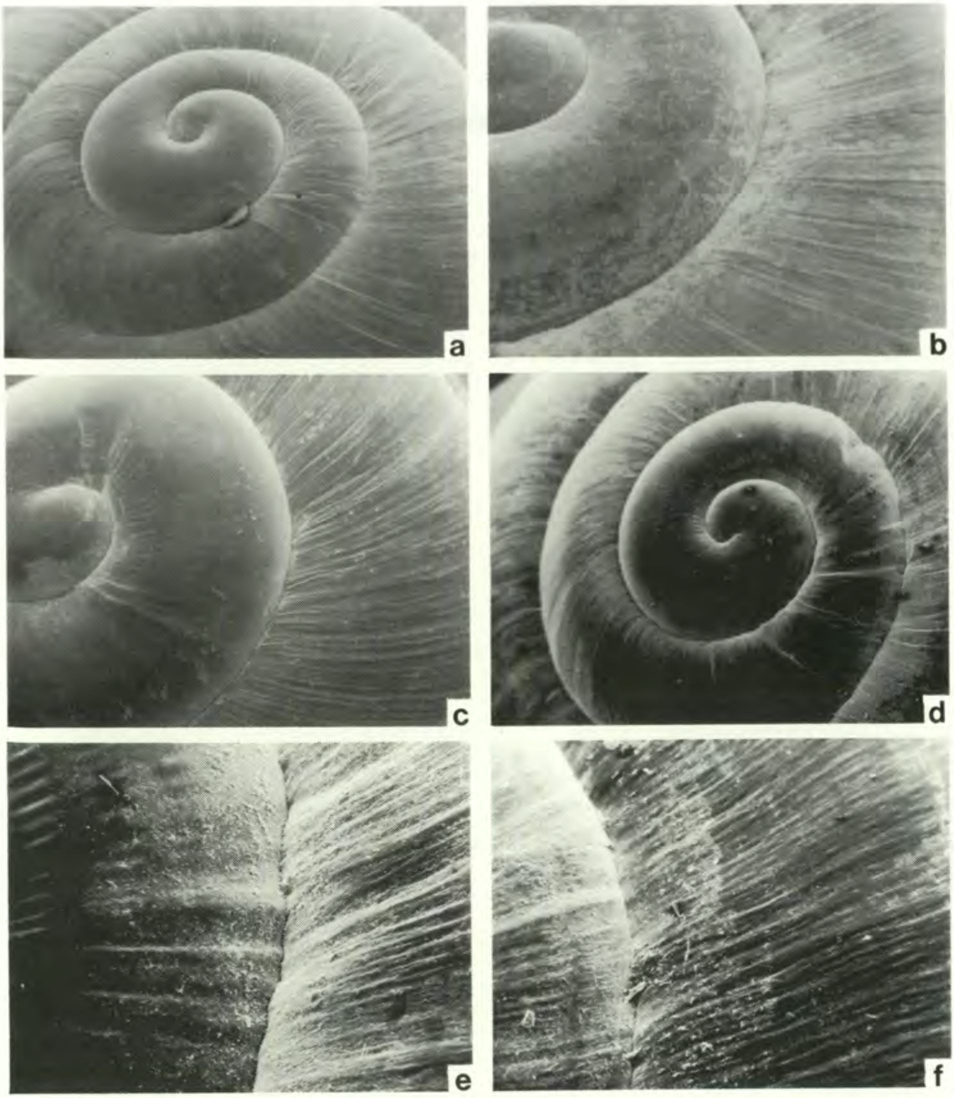


Plate 21: Shell sculpture of eastern Napier Range *Westraltrachia:* (a) *W. derbyi* (Cox, 1892), FMNH 200180, Sta. WA-307, north-east side of Windjana Gorge, Napier Range, 11 December 1976, juvenile, apex and spire at 14.0X; (b) *W. cunicula,* FMNH 200214, Dissection A, Sta. WA-270, east of Tunnel Creek turnoff, north fringes of Napier Range, 2 December 1976, apex and early spire at 35X; (c) *W. alterna,* FMNH 204709, Dissection A, Sta. WA-582, Cycad Hill, south side of Napier Range, 7 May 1980, apex and early spire at 28X; (d-f) *W. oscarensis,* FMNH 200165, Dissection C, Sta. WA-356, plains area between Napier and Oscar Ranges, 1 January 1977, (d) apex and early spire at 15.0X, (e) late apical sculpture at 69X, (f) early body whorl sculpture at 36X.

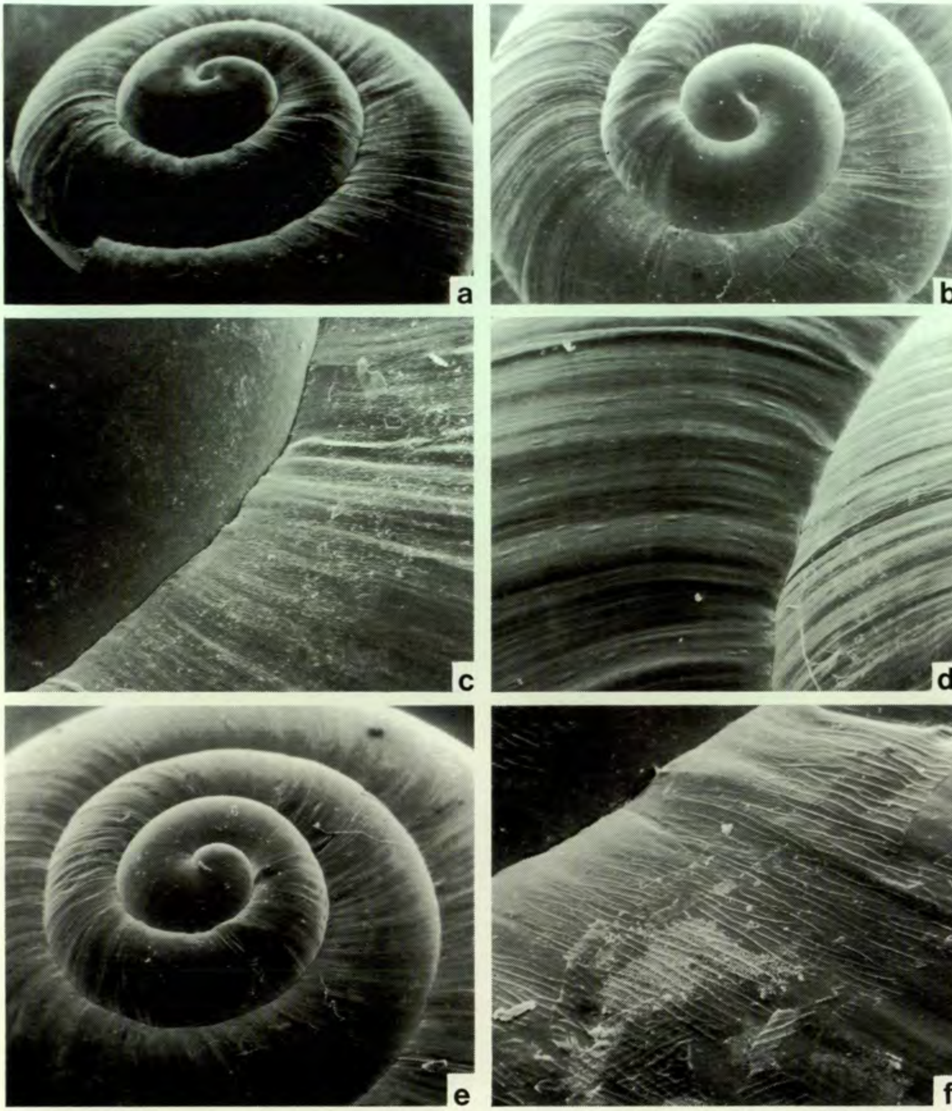


Plate 22: Shell sculpture of western Oscar Ranges *Westraltrachia:* (a) *W. subtila,* FMNH 200216, Dissection A, Sta. WA-265, 6.2 km west of Mt. Wynne Creek, 28 November 1976, apex and spire at 14.6X; (b-d) *W. instita,* FMNH 200224, Sta. WA-264, 0.4 km west of Mt. Wynne Creek, 28 November 1976, juvenile shell, (b) apex and early spire at 15.8X, (c) detail of late apex and early spire at 136X, (d) detail of body whorl sculpture at 37X; (e-f) *W. lievreana,* FMNH 200223, Sta. WA-263, 14.1 km north-west of Linesman Creek, 28 November 1976, juvenile shell, (e) apex and spire at 15.6X, (f) detail of body whorl sculpture at 137X.

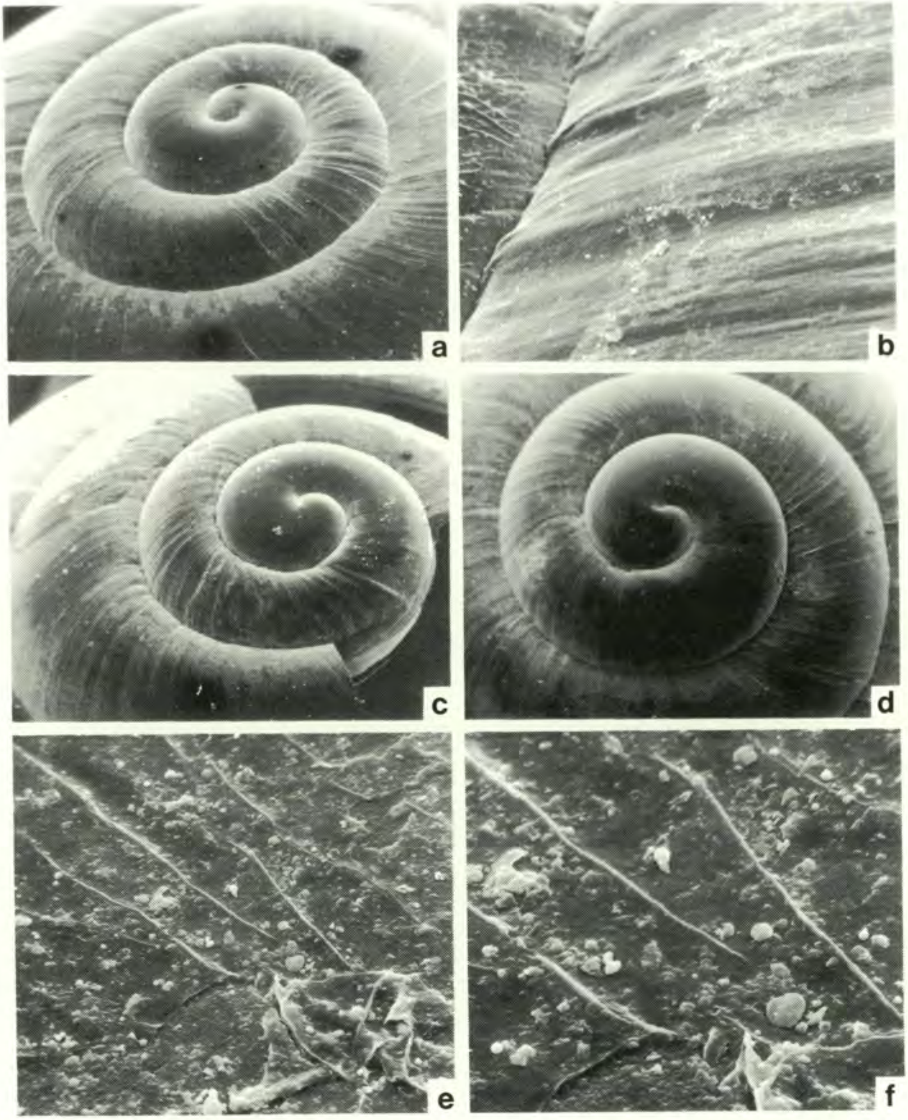


Plate 23: Shell sculpture of eastern Oscar Ranges *Westraltrachia:* (a-b) *W. tropida,* FMNH 200232, Sta. WA-260, north-north-east of Kundra Bore, 27 November 1976, juvenile shell, (a) apex and spire at 15.0X, (b) detail of body whorl sculpture at 135X; (c) *W. rotunda,* FMNH 200208, Dissection A, Sta. WA-258, east side of Brooking Gorge, 26 November 1976, apex and spire at 15.0X; (d-f) *W. limbana,* FMNH 200201, Sta. WA-266, 3.7 km west-south-west of Fossil Downs Homestead, 29 November 1976, adult shell, (d) apex and early spire at 17.0X, (e) detail of body whorl sculpture at 700X, (f) detail of micro-periostracal folds on body whorl at 1,425X.

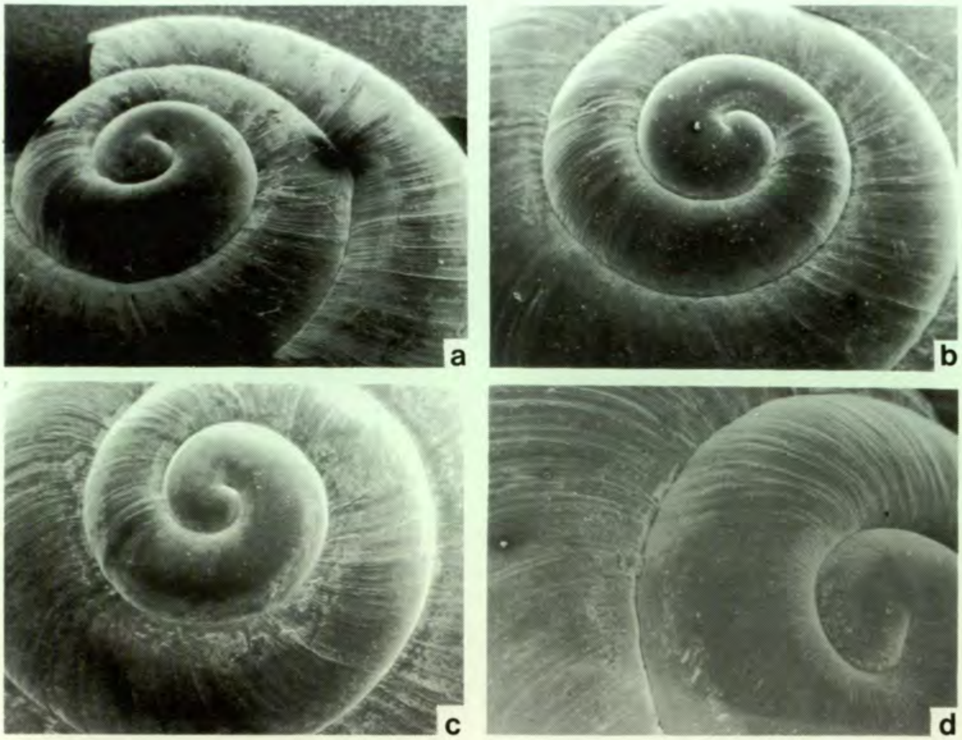


Plate 24: Shell sculpture of *Westraltrachia recta, W. pillarana, W. ampla* and *W. porcata:* (a) *W. recta,* FMNH 200205, Dissection A, Sta. WA-254, Limestone Billy Hills, north-west of Pillara Range, 29 November 1976, apex and spire at 14.4X; (b) *W. pillarana,* FMNH 200229, Dissection A, Sta. WA-253, 0.5 km west of Emanuels Bore, Pillara Range, 24 November 1976, apex and spire at 14.8X; (c) *W. ampla,* FMNH 200276, Sta. WA-366, 4.9 km south of Galeru Gorge, west side of Lawford Range, 10 January 1977, juvenile, apex and early spire at 14.9X; (d) *W. porcata,* FMNH 205311, Dissection A, Sta. WA-711, Brooking Creek at Tunnel Road Crossing, west of Fitzroy Crossing, 19 June 1980, apex and early spire at 27.1X.

Patterns of anatomical variations

Westraltrachia differs markedly from the genera previously revised in this series in that major structural changes have occurred in both the jaw and radula. Hence, considerable effort to establish base-line intrapopulational variability and to document the, at times, rather subtle differences among species was necessary. To my knowledge, this is the first study to demonstrate population and species level differences in such structures as row interlock, cusp angle and curvature, or jaw rib prominence. It has been necessary to document these changes fully. As in previously revised genera, external body features, pallial organ structures and muscle system differences do not

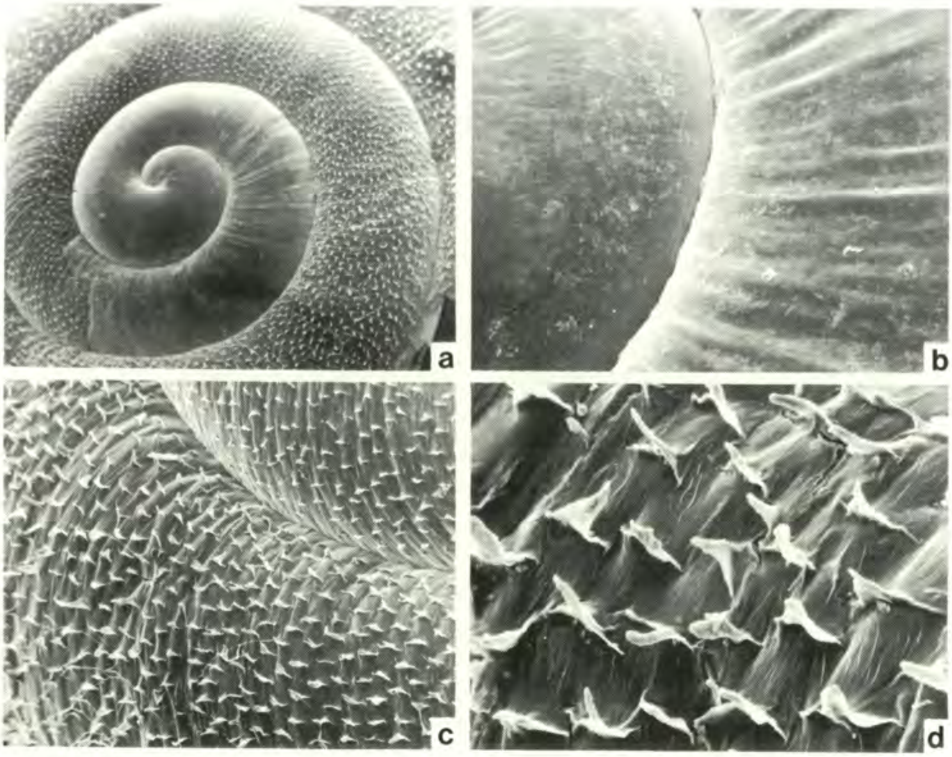


Plate 25: Shell sculpture of *Westraltrachia ascita:* (a-d) FMNH 200182, Sta. WA-370, 3.4 km north of Lloyd Hill summit, west side of Laidlaw Range, 13 February 1977, juvenile shell, (a) apex and spire at 14.1X, (b) detail of apex and early spire at 72X, (c) detail of mid-spire and body whorl sculpture at 35.5X, (d) detail of body whorl sculpture at 135X.

vary significantly at the generic level. Discussion of these organ systems is thus reserved for later contributions.

Jaw – The typical camaenid jaw pattern is well demonstrated by the several genera related to *Westraltrachia* **(Plate 58).** In almost all of the jaw illustrations, it has been oriented so that the upper growth edge of the jaw is in contact with the mounting substrate. The lower edge of the jaw that functions in feeding is shown at the top of each photograph.

Most of the strong contour variation seen on this edge correlates with when the specimen was collected. If the feeding edge is comparatively smooth and/or obviously worn, the snail presumably had been feeding near to the time of collection. When these edges are elongated and extremely variable in height, the specimen was collected after the snail had been aestivating for several months. These elongations are interpreted as incremental growth during aestivation. Such growth during dormancy provides extra length when the snail activates after a rain, permitting intensive feeding and great abrasion immediately. This maximises feeding time when food reserves are at their lowest. Cessation of jaw growth during aestivation would not provide this cushion of jaw edge to be abraded during initial gluttony.

Since the jaw frequently comes into contact with very hard surfaces in the environment, indications of fractures, repaired injuries, and changes in the surface shape are frequently observed. Much of the intrapopulational variation in the number and width of vertical ribs on the jaw can be attributed to the effects of such incidents during the snail's life. As an example of such variation, two jaws of *Ordtrachia septentrionalis* **(Plate 53d-e)** are shown. Many years ago Haniel (1921: 41-42, Figs 11-12) demonstrated even greater jaw rib variability in species of *Amphidromus* Albers, 1850 from Timor. My own recent observations on several species of *Amphidromus* (Solem, 1983) indicate that the jaw in *Amphidromus* is considerably thinner and thus much more easily injured than is the jaws in most Australian camaenids.

Growth in the jaws of camaenids apparently involves primarily addition of incremental horizontal layers. These can be seen clearly in the jaws of *W. commoda* (Iredale, 1939) **(Plate 26c)** and *Ordtrachia grandis* **(Plate 58c)**. The reason for the exceptional strength of the growth lines in the last species is unknown.

Changes in the jaws of *Westraltrachia* species correlate with current or near sympatry with *Amplirhagada burnerensis* (Smith, 1894), *A. napierana* Solem, 1981, *A. percita* (Iredale, 1939), or *Quistrachia monogramma* (Ancey, 1898). Changes in radular structure correlate partly with the jaw changes. Discussion of this is given below.

The following species of *Westraltrachia* have, in examined material, essentially typical camaenid jaw structure – *W. oscarensis* (Cox, 1892) **(Plate 30a)**, *W. tropida* **(Plate 30b)**, *W. subtila* **(Plate 30e)**, *W. porcata* **(Plate 30f)**, *W. limbana* **(Plate 31a-b)**, *W. rotunda* **(Plate 31c-d)**, *W. recta* **(Plate 32a)**, *W. pillarana* **(Plate 32b)**, *W. ampla* **(Plate 31c-d)** and *W. ascita* **(Plate 32e)**. Except for *W. oscarensis* (Cox, 1892), none of these species have been found in sympatry with either *Amplirhagada* or *Quistrachia*. Specimens of both *Q. monogramma* (Ancey, 1898) and *W. oscarensis* (Cox, 1892) have been taken at Stas. WA-277, WA-278, and WA-279, but neither species was found live in abundance. At the Stations where reasonable numbers of living *W. oscarensis* (Cox, 1892) were obtained, WA-276 and WA-356, no *Quistrachia*, live or dead, were found. Both of these Stations are in a flood plain situation with scattered limestone boulders, and not the cliff situation preferred by *Quistrachia*. It is possible that there is interpopulational variation in the jaw of *oscarensis*, but the material needed to check this is not available.

In the Oscar Ranges, the jaws of *Westraltrachia instita* from Sta. WA-264 vary from having prominent **(Plate 30c)** to markedly reduced **(Plate 30d)** ribs, while *W. lievreana* from Sta. WA-263 **(Plate 31e)** has a possibly modified jaw structure. *Westraltrachia instita* occurs sympatrically with *Quistrachia monogramma* (Ancey, 1898).

In the Napier Range to the north, that section lying east of the Lennard River, from the south side of Windjana Gorge to where the Napier Range dwindles to a last few exposed reef edges south-east of Six Mile Bore, there are three species of *Westraltrachia*. *Westraltrachia derbyi* (Cox, 1892) extends from Windjana Gorge to a known limit at Sta. WA-336, 4 km south-east of Carpenter Gap; *W. alterna* Iredale, 1939, from Cycad Hill to a few km south-east of McSherry Gap; and *W. cunicula* from just north-east of the Tunnel to the south-eastern extent of exposed limestone past Six

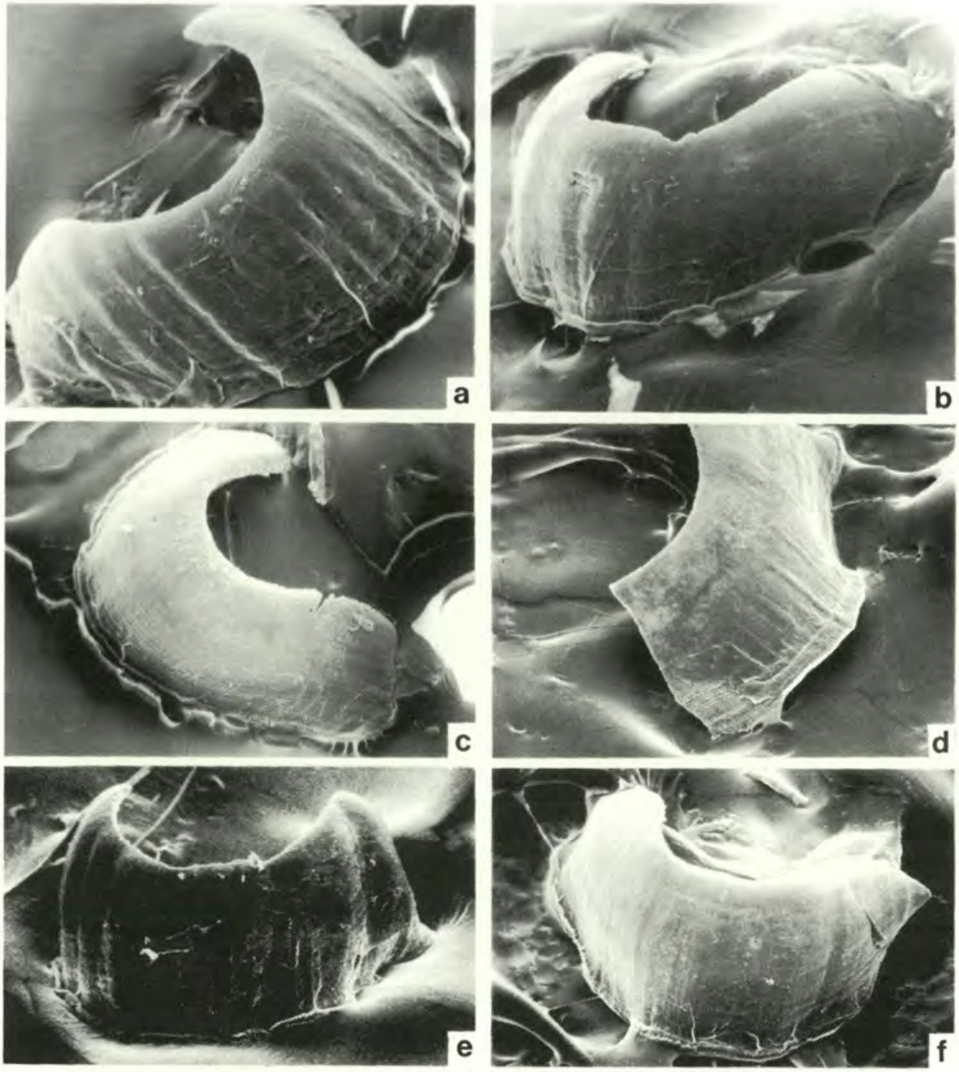


Plate 26: Jaws of western Napier Range *Westraltrachia:* (a-b) *W. woodwardi* (Fulton, 1902), FMNH 200187, Sta. WA-312, 3.2 km west of Barker Gorge, 12 December 1976, (a) Dissection A at 81X, (b) Dissection B at 74X; (c) *W. commoda* (Iredale, 1939), FMNH 200256, Dissection A, Sta. WA-325, 5.9 km north-west of Yammera Gap, 17 February 1977 at 73X; (d) *W. inopinata,* FMNH 200157, Dissection B, Sta. WA-339, 1.1 km south-east of Yammera Gap, 23 December 1976 at 61X; (e) *W. f. complanata,* FMNH 200153, Dissection B, Sta. WA-359, 10.5 km east of Yammera Gap, 10 January 1977 at 90X; (f) *W. f. froggatti* (Ancey, 1898), FMNH 199873, Dissection A, Sta. WA-193, south-west corner of Windjana Gorge, 5 December 1976 at 73X.

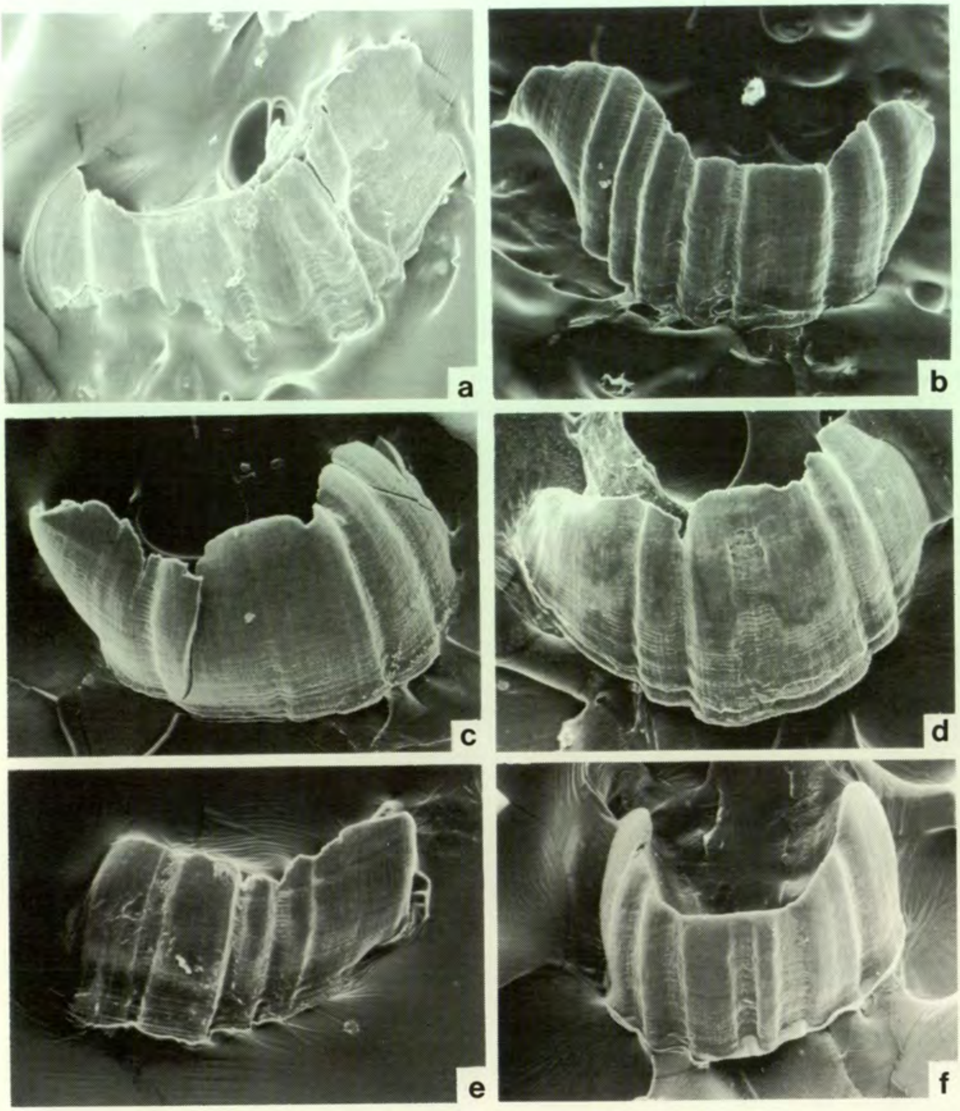


Plate 27: Jaw variation within Sta. WA-194 population of *Westraltrachia derbyi* (Cox, 1892): (a-d) FMNH 200056, Sta. WA-194, south-east corner of Windjana Gorge, Napier Range, 5 December 1976, (a) Dissection A at 82X, (b) Dissection B at 71X, (c) Dissection C at 71X, (d) Dissection D at 72X; (e) FMNH 200054, Sta. WA-194, Dissection A, 4 January 1977 at 72X; (f) FMNH 199853, Sta. WA-194, Dissection A, 21 March 1977 at 70X.

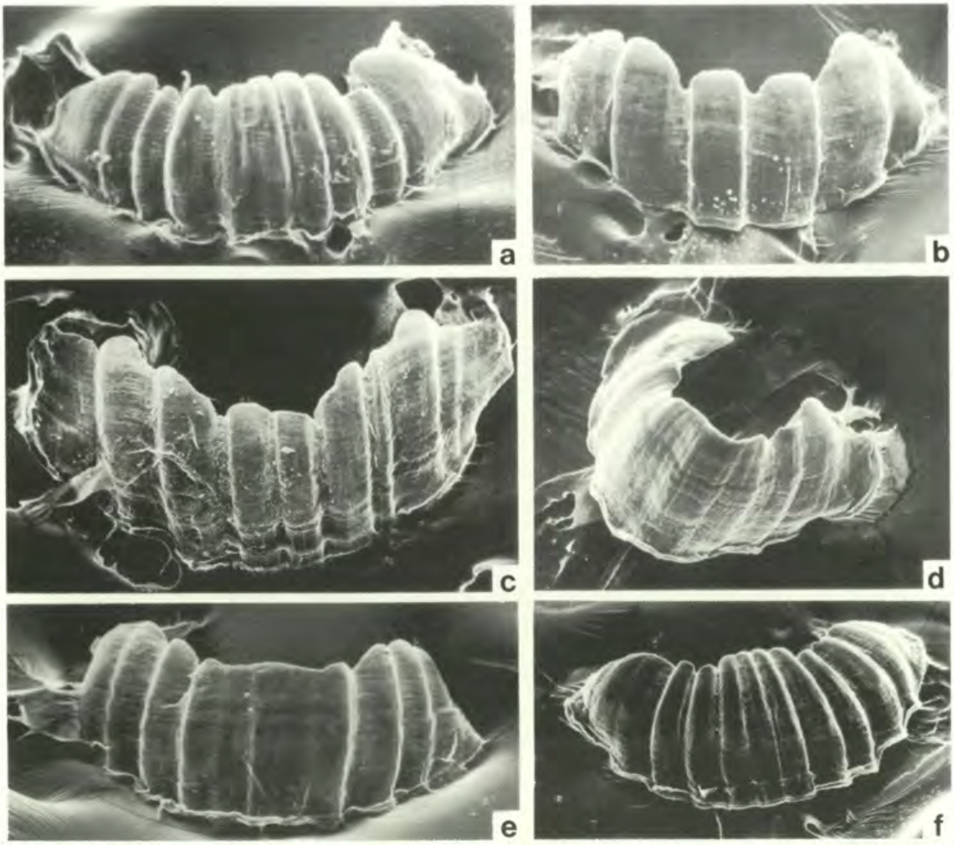


Plate 28: Jaw variation in *Westraltrachia derbyi* (Cox, 1892) from east of Windjana Gorge, Napier Range: (a-b) FMNH 200180, Sta. WA-307, north-east corner, Windjana Gorge, 11 December 1976, (a) Dissection A at 66X, (b) Dissection B at 64X; (c) FMNH 200133, Dissection A, Sta. WA-334, north of Lillimilura Police Station Ruins, 22 December 1976 at 65X; (d-e) FMNH 200147, Sta. WA-335, 3.4 km south-east of Lillimilura Police Station Ruins, 22 December 1976, (d) Dissection A at 65X, (e) Dissection B at 66X; (f) FMNH 200159, Dissection A, Sta. WA-336, 4.3 km south-east of Carpenter Gap, 22 December 1976 at 63X.

Mile Bore. The collecting gap between *W. derbyi* (Cox, 1892) and *W. alterna* Iredale, 1939, consists of rolling hills without obvious limestone exposures and sparse vegetation cover. This area is not accessible for collecting during the wet season, and during the dry season does not appear auspicious for locating snail colonies. The small collecting gap between *W. alterna* Iredale, 1939, and *W. cunicula* is, on the north-east side of the range, a series of precipitous cliffs without talus accumulation at their base. Spot checks in the dry season failed to locate any snails. Living material of *W. cunicula* and *Quistrachia monogramma* (Ancey, 1898) has been taken sympatrically at Sta. WA-270 and WA-274; live *W. cunicula* and dead *Q. monogramma* (Ancey, 1898) at Sta.

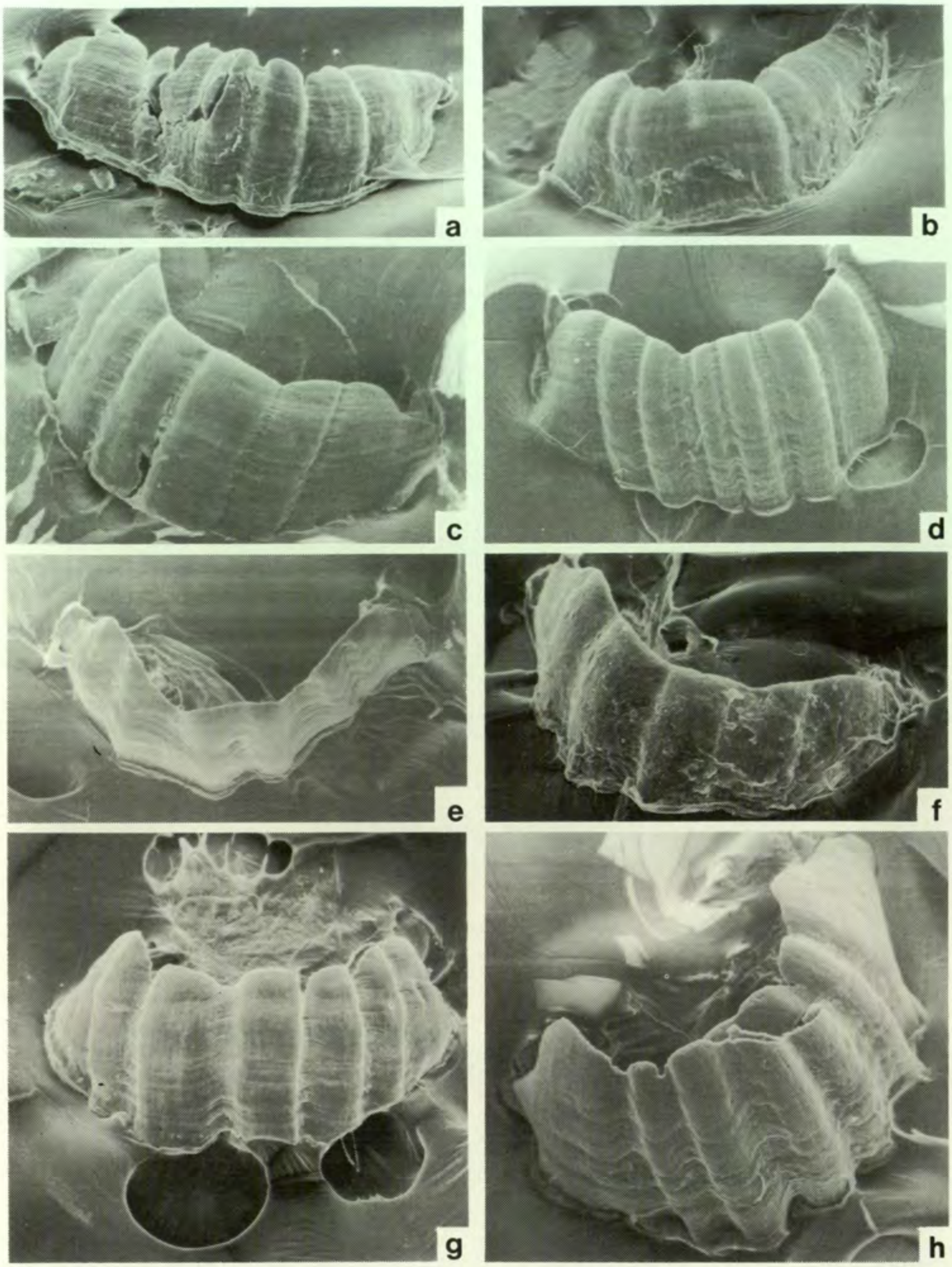


Plate 29: Jaws of *Westraltrachia alterna* Iredale, 1939, and *W. cunicula:* (a-d) *W. alterna* Iredale, 1939, (a-b) FMNH 204709, Sta. WA-582, Cycad Hill, south side of Napier Range, 7 May 1980, (a) Dissection A at 76X, (b) Dissection B at 73X; (c) FMNH 199920, Sta. WA-273, east of McSherry Gap, south side of Napier Range, 3 ▶

▶December 1976, at 82X; (d) FMNH 199930, Sta. WA-275, west of Tunnel Creek turnoff, north side of Napier Range, 3 December 1976, at 76X; (e-h) *W. cunicula*, (e-f) FMNH 199886, Sta. WA-274, Tunnel Creek Gorge entrance, south side of Napier Range, 3 December 1976, (e) Dissection A at 77X, (f) Dissection B at 83X; (g) FMNH 200236, Sta. WA-279, cliffs north of Chestnut Creek, south face of Napier Range, 4 December 1976 at 77X; (h) FMNH 200214, Sta. WA-270, 21.8 km east of Tunnel Creek turnoff, north fringes of Napier Range, 2 December 1976 at 85X.

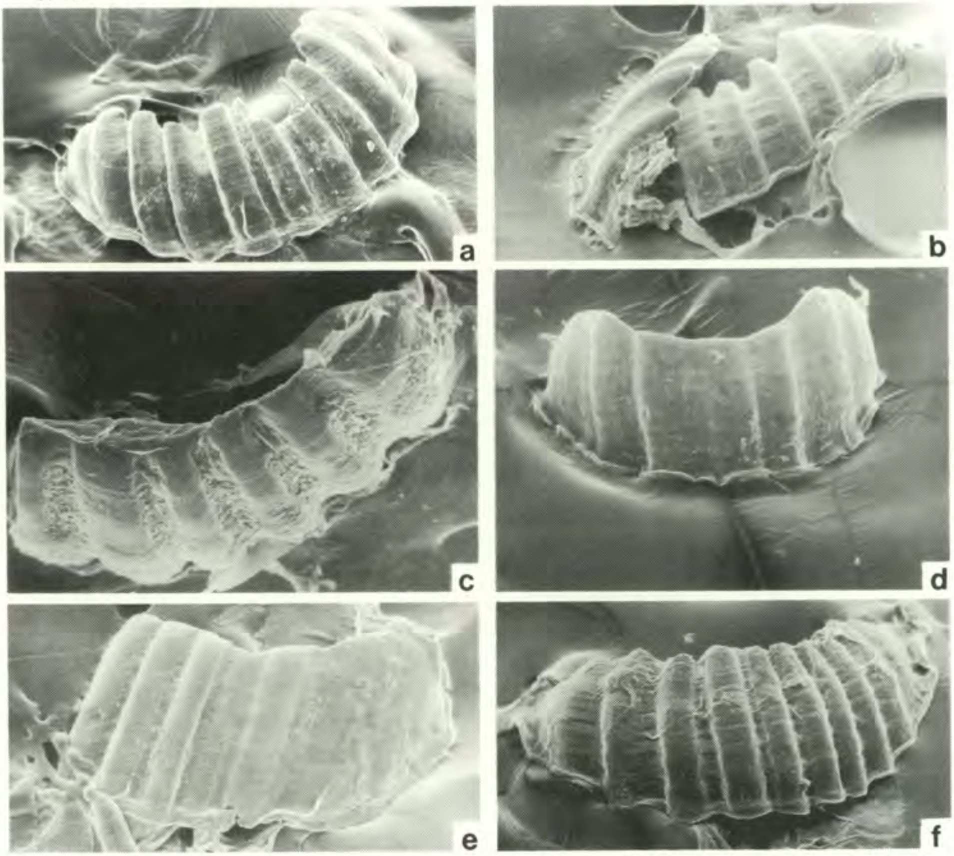


Plate 30: Jaws of *Westraltrachia oscarensis* (Cox, 1892), *W. tropida*, *W. instita*, *W. subtila*, and *W. porcata*: (a) *W. oscarensis* (Cox, 1892), FMNH 200165, Dissection A, Sta. WA-356, south of Chestnut Creek, plains area between Napier and Oscar Ranges, 1 January 1977 at 55X; (b) *W. tropida*, FMNH 205306, Dissection A, Sta. WA-710, gap through Oscar Range at Twelve Mile Bore, 19 June 1980 at 70X; (c-d) *W. instita*, FMNH 200224, Sta. WA-264, 0.4 km west of Mt. Wynne Creek, south side of Oscar Ranges, 28 November 1976, (c) Dissection A at 128X, (d) Dissection B at 64X; (e) *W. subtila*, FMNH 200216, Dissection A, Sta. WA-265, 6.2 km west of Mt. Wynne Creek, Oscar Ranges, 28 November 1976 at 67X; (f) *W. porcata*, FMNH 205311, Dissection A, Sta. WA-711, Brooking Creek on Tunnel Road, west of Fitzroy Crossing, 19 June 1980 at 68X.

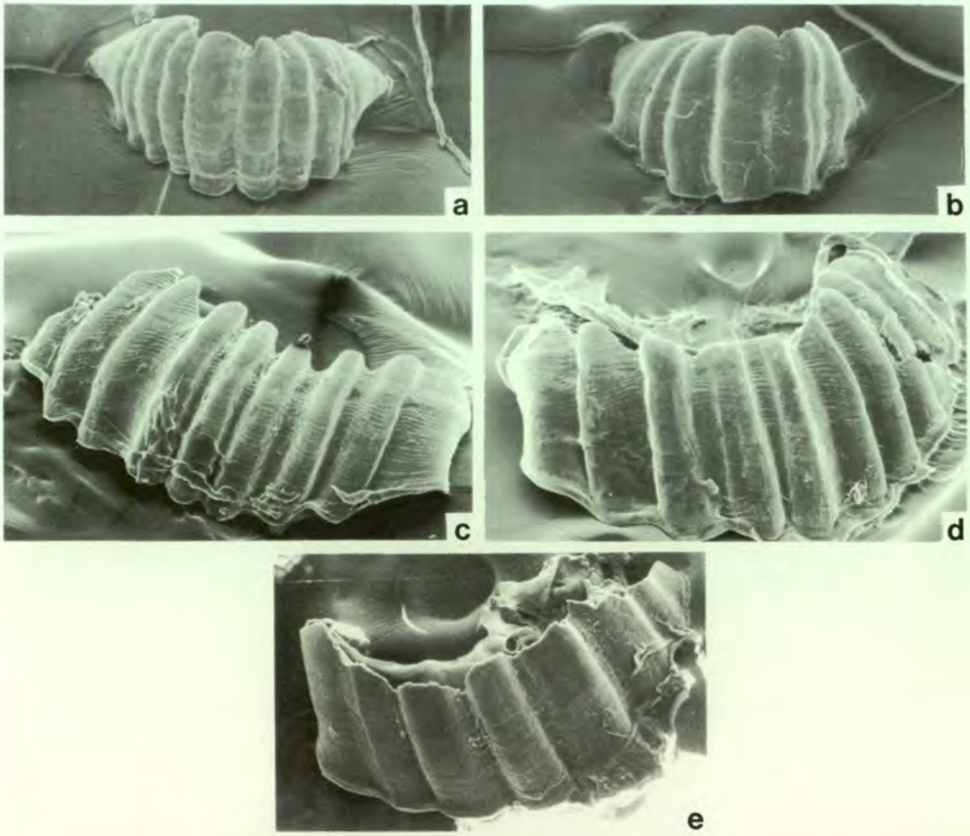


Plate 31: Jaws of *Westraltrachia limbana, W. rotunda,* and *W. lievreana:* (a-b) *W. limbana,* FMNH 200201, Sta. WA-266, 3.7 km west-south-west of Fossil Downs Homestead, 29 November 1976, (a) Dissection A at 61X, (b) Dissection B at 67X; (c-d) *W. rotunda,* FMNH 200208, Sta. WA-258, east side of Brooking Gorge, Oscar Ranges, 26 November 1976, (c) Dissection B at 65X, (d) Dissection A at 70X; (e) *W. lievreana,* FMNH 200223, Dissection A, Sta. WA-263, 14.1 km north-west of Linesman Creek, south side of Oscar Ranges, 28 November 1976, at 60X.

WA-279; live *Q. monogramma* (Ancey, 1898) and dead *W. cunicula* at Sta. WA-272; and dead specimens of both species at Sta. WA-195. Live *W. alterna* Iredale, 1939 and dead *Q. monogramma* (Ancey, 1898) have been taken at Stas. WA-273 and WA-275. At Cycad Hill, Sta. WA-582, *W. alterna* Iredale, 1939 occurs alone. *Amplirhagada burnerensis* (Smith, 1894) and *W. derbyi* (Cox, 1892) are sympatric throughout the known range of the latter species.

The jaw in *Westraltrachia cunicula* has either a few prominent **(Plate 29e, g-h)** or a few reduced vertical ribs **(Plate 29f).** In *W. alterna* Iredale, 1939, the height of the ribs is distinctly reduced **(Plate 29a-d),** even where (Sta. WA-582, **Plate 29a-b)** the species is allopatric to *Quistrachia.*

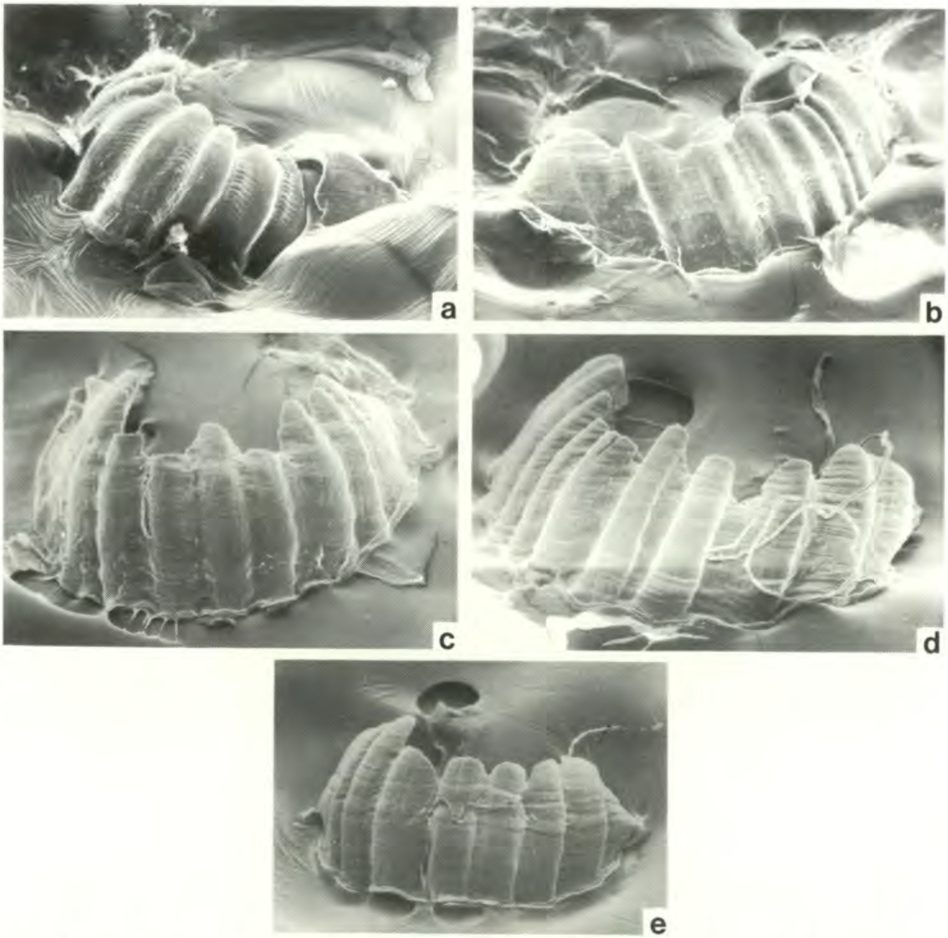


Plate 32: Jaws of *Westraltrachia recta, W. pillarana, W. ampla* and *W. ascita:* (a) *W. recta,* FMNH 200205, Dissection A, Sta. WA-254, Limestone Billy Hills, north-west of Pillara Range, 29 November 1976, at 68X; (b) *W. pillarana,* FMNH 200229, Dissection A, Sta. WA-253, 0.5 km west of Emanuels Bore, Pillara Range, 24 November 1976, at 56X; (c-d) *W. ampla,* WAM 609.79, Cave Spring, Bugle Gap, East Kimberley, 28 May 1966, (c) Dissection B at 66X, (d) Dissection A at 65X; (e) *W. ascita,* FMNH 200182, Sta. WA-370, 3.4 km north of Lloyd Hill summit, west side of Laidlaw Range, 13 February 1977, at 67X.

The situation in *Westraltrachia derbyi* (Cox, 1892) is more complicated. Sta. WA-194, the south-west corner of Windjana Gorge, has been chosen to demonstrate intrapopulational variability **(Plate 27a-f).** Within this one population, the jaw ribs vary from fairly prominent **(Plate 27b),** to a median number that is reduced in prominence **(Plate 27e-f),** to few reduced **(Plate 27a),** and finally only weak traces **(Plate 27c-d).**

At the north-east corner of Windjana Gorge, at Sta. WA-307, the ribs are nearly normal in prominence **(Plate 28a-b).** On the south side of the Napier Range, near Lillimilura Police Station Ruins, Sta. WA-334, the jaws have very prominent ribs **(Plate 28c),** but at Sta. WA-335, the jaw ribs vary from remnant **(Plate 28d)** to very strong **(Plate 28e).** At the known south-east limit of distribution, Sta. WA-336, south-east of Carpenter Gap, the jaw appears normal **(Plate 28f)** for *Westraltrachia.* In general, the south-east populations retain stronger jaw ribbing than is present in the westernmost population at Windjana Gorge (Sta. WA-194).

On the west side of Windjana Gorge, a series of species replace each other in an allopatric sequence to the north-west tip of the Napier Range: *Westraltrachia froggatti* (Ancey, 1898), *W. inopinata, W. turbinata, W. commoda* (Iredale, 1939), and *W. woodwardi* (Fulton, 1902). At most, there are traces of vertical undulations on the jaw **(Plates 26a-b, e, 34d),** although most jaws **(Plate 26c-d, f)** show no traces of the vertical ribbing. These species have been observed feeding on algal-fungal films on seepage slopes (Price and Christensen, personal observation) rather than the normal decayed vegetation food that is characteristic of most camaenids.

In summary, the jaws of *Westraltrachia* species tend toward rib reduction when sympatric with either *Quistrachia* or *Amplirhagada,* with complete loss of ribbing having occurred in the taxa north-west of Windjana Gorge. Observations indicate the latter change correlates with the basic alteration in feeding strategy, but direct feeding observation on the Napier Range taxa occurring south-east of Windjana Gorge is lacking.

Radular structure – Throughout the Camaenidae there is a typical pattern of radular structure, most closely approximated, of these taxa, by *Westraltrachia rotunda* **(Plate 47a-c),** although even this species shows some alterations. Since this is the first extensive SEM survey of radular structure in the Camaenidae, some discussion of the basic features is necessary background before defining the patterns of change observed in *Westraltrachia.*

The central or rachidian tooth normally (Solem, In Press-A, Fig. 6b) is weakly tricuspid, with a broad, bluntly rounded mesocone flanked by two small lateral ectocones that project approximately two-thirds of the way from mesoconal tip to anterior margin. These ectocones are lost in all taxa discussed in this report. Since the radula is organised so that cusps point backward into the mouth, the terminology "anterior" refers to the tooth margin *away from* the cusps, while "posterior" refers to the direction in which the cusps *point.* The anterior margin of the central tooth may be without any flare **(Plate 59a)** or with a noticeable flare **(Plate 60b).** This actually can vary within a population, as for example in specimens of *Ordtrachia septentrionalis* **(Plate 60a-b).** Except in unusual circumstances, the central tooth is noticeably smaller than the adjacent laterals, and is symmetrical. The posterior edge of the basal plate has lateral support ridges on each side **(Plate 59a, c).** These are less elevated than the single support ridge found on the lateral teeth **(Plate 59a, c).** The actual basal plate posterior margin has a broad to narrowly 'U'-shaped indentation **(Plates 42a, 59c).** There is positive inter-row support between central teeth. The rounded anterior margin of one central can rest upon the posterior margin of the next anterior tooth, with its lateral support ridges providing a 'brake' when the former tooth is under cutting stress **(Plate 59a-c).** This pattern is typical not only of the camaenids but most taxa of higher land snails.

Lateral teeth **(Plate 59a-b)** differ from the central tooth in several characters: 1) larger size; 2) size reduction to loss of endocone; 3) distinct enlargement of ectocone; 4) loss of inner support ridge from posterior basal plate margin; 5) increase in both size and complexity of outer support ridge on basal plate posterior margin; 6) development of a slight to strong flared ridge on the anterior margin of the tooth; and 7) frequently a sharper posterior edge to the cusp.

Generally, the early lateral cusps are elevated at about a 45° angle from the basal plate, with the posteriorly projecting mesocone being sharp-tipped to bluntly pointed. The size of the anterior flared ridge is often variable within a population **(Plate 60a-b).** As a general rule, the size of this flare increases for the mid- to outer lateral teeth, reaching a degree of development **(Plate 61a, c-d)** that is a quantum change from that observed in the first lateral.

The function of the lateral teeth is in cutting and tearing loose pieces of food. The relatively sophisticated inter-row support system, involving meshing of the anterior flared ridge with the posterior outer posterior basal support ridge, is perhaps the best means of defining a lateral tooth in the helicoid taxa. The change from early to late laterals frequently involves an increase in accessory cusp size and a slight to moderate lowering of the cusp angle. These changes, easily seen in *Mouldingia* **(Plate 59),** are very difficult to quantify and seem to be relatively variable within populations.

Typical helicoid laterals have the mesoconal cusp of the lateral teeth with a sharp point that is not curved. All taxa reviewed here have at least a slight downward curvature near the tip and slight rounding of the point itself.

The transition from lateral to marginal teeth occurs relatively rapidly. Generally it involves only three or four teeth. The following changes happen: 1) loss of the anterior basal flare; 2) loss of the posterior basal support ridge; 3) shortening of the basal plate itself; 4) marked increase in endocone size; 5) size increase and/or splitting of ectocone; 6) slight to moderate change in mesoconal cusp angle to basal plate; and 7) broadening, rounding, and shortening of the mesocone. Two different angle views of this process are shown in *Mouldingia* **(Plate 59b, d).**

Marginal teeth function to bring the torn pieces of food into the mouth. They have no need for an inter-row support system, and apparently are under little selective pressure for a particular cusp structure, as the variation within a population, such as *Westraltrachia derbyi* (Cox, 1892) **(Plate 40),** is equivalent to that seen among species.

The marginal teeth are not uniform within a row, as demonstrated in *Ordtrachia* **(Plate 61d-f).** The cusp angle to the basal plate starts at about 45° and then gradually lowers until the outermost cusps are almost parallel to the basal plate. There is an increase in prominence of both ectocones and endocones, a marked decrease in size of the mesocone, and a reduction in total size of the individual teeth as the outer margin is approached.

Two part-row views of *Ordtrachia grandis* **(Plate 61e)** and *O. intermedia* **(Plate 62a)** give an indication of both the general patterns and the subtle but continuing nature of changes within both the lateral and marginal fields of an individual radula. It is quite difficult to establish a single tooth limit for lateral or marginal teeth. Frequently the outermost marginals are lost in the process of mounting the radula. Given these uncertainties and difficulties, half row tooth counts provide little useful information in this complex and are not utilised.

The above basic pattern of tooth structure is seemingly ideally suited to reduction of leaves and dead grass fragments by the snails. Departures from this pattern, such as are shown by the species of *Amphidromus* (Solem, 1983), *Westraltrachia*, and taxa from the North West Cape, are indicative of dietary shifts.

All radulae of *Westraltrachia* species are modified at least slightly from the normal pattern. They have lost both the ectocone and endoconal cusps on the central and lateral teeth, except for *W. rotunda* **(Plate 47a-b)**, which retains small ectocones on the laterals. An occasional specimen of *W. oscarensis* (Cox, 1892) **(Plate 41c)** shows an occasional trace of a side cusp on the central and early lateral. But other species lack any trace of the cusp.

Westraltrachia rotunda comes closest to matching the average pattern for the Camaenidae, but the presence of a stronger anterior flare on the early laterals **(Plate 47a-b)** and a clear tendency for curving and slight blunting of the mesocone are noticeable differences. *Westraltrachia pillarana* **(Plate 48c-d)** has the mesoconal cusp elevated at a distinctly higher angle, and also shows a tendency for broadening and rounding of the cusp. Even in the easternmost species, *W. ampla* **(Plate 50)** and *W. ascita* **(Plate 49)**, there are clear patterns of change. The angle of the cusp **(Plate 59b)** is dramatically elevated, the mesocone is clearly elongated and with a more bluntly rounded tip. I have not been able to quantify the obvious degree of tooth narrowing that accompanies the greater elevation and elongation of the cusp, but these changes are evident upon inspecting photographs such as **Plate 50b.** The pattern of higher angling, more rounded tip and curvature continues through *W. recta* **(Plate 48a-b)**, and is accentuated in the Oscar Range taxa **(Plates 44-47)**, where the higher angle is accompanied by markedly curved tips **(Plate 46a-b).** The only exceptions to this are *W. instita* **(Plate 44e)** and *W. subtila* which have broadly rounded tips **(Plate 44c)**, but only comparatively minor changes in tooth angle.

In the area of sympatry with *Quistrachia monogramma* (Ancey, 1898), both *Westraltrachia cunicula* **(Plate 43)** and *W. alterna* Iredale, 1939 **(Plate 42)** show a very high angle followed by strong curvature of the mesocone. *Westraltrachia oscarensis* (Cox, 1892) agrees in the high elevation, but shows less curvature of the tip **(Plate 41a-b).**

Variation in *Westraltrachia derbyi* (Cox, 1892) is substantial both within and among populations. **Plate 38c-f,** taken from a single population at Sta. WA-194, indicates variation from a moderate angle with moderate curvature of the tip to a high angle with strong curve of the tip. Similarly, **Plate 39** demonstrates variation in rounding and angle for populations east of Windjana Gorge.

From the west side of Windjana Gorge to the northern tip of the Napier Range, there is a consistent pattern **(Plate 33-37)** of an elongated cusp held at a very high angle with bluntly rounded tip and strongly curved upper portion of the mesocone. The comparison between these and the normal tooth of *Westraltrachia rotunda* **(Plate 47a-b)** is dramatic, but essentially intermediate situations can be identified in the species discussed above. Field observations of the species living west of Windjana Gorge indicate that these feed upon algal-fungal films in seepage zones, not upon dead angiosperm matter. The ultimate effect of such feeding is shown in **Plate 36e** with worn laterals and centrals demonstrating the extent of tooth wear.

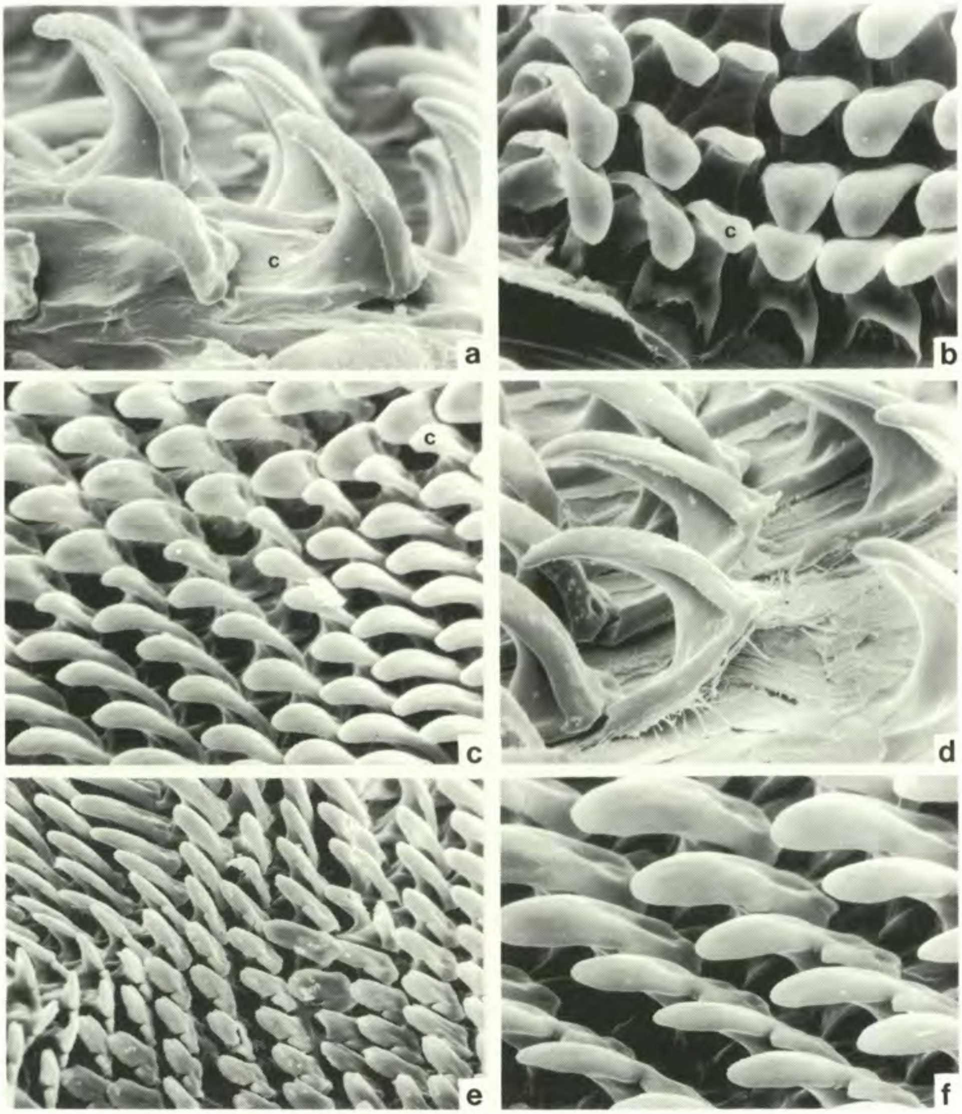


Plate 33: Radular teeth of *Westraltrachia woodwardi* (Fulton, 1902): FMNH 200187, Dissection B, Sta. WA-312, 3.2 km west of Barker Gorge, Napier Range, 12 December 1976, (a) low angle side view of central and first lateral at 690X, (b) high angle front view of central and early laterals at 500X, (c) medium angle side-front view of central and laterals at 335X, (d) low angle side view of middle laterals at 690X, (e) high angle side view of latero-marginal transition at 325X, (f) low angle side view of latero-marginal transition at 700X. Central teeth indicated by a "C".

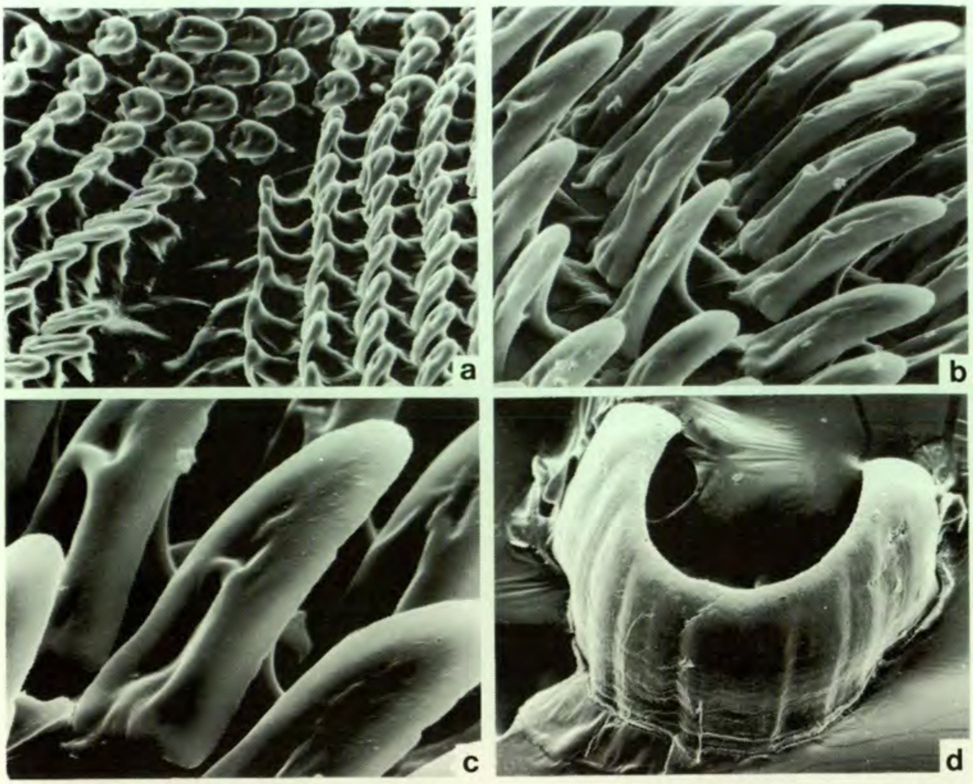


Plate 34: Jaw and radular teeth of *Westraltrachia woodwardi* (Fulton, 1902): (a-c) FMNH 200187, Dissection A, Sta. WA-312, 3.2 km west of Barker Gorge, Napier Range, 12 December 1976, (a) high angle side view of central and laterals at 240X, (b) low angle side view of middle laterals at 690X, (c) low angle side view of laterals at 1,350X; (d) Dissection C, jaw at 68X.

Throughout much of its range, *Westraltrachia* is the only rock-associated camaenid, yet many of the species show an early stage in the structural shift that is fully developed in the zone of sympatry with *Amplirhagada,* and partially developed in zone of sympatry with *Quistrachia.* This is interpreted as an adaptation to use of seepage zone micro-flora in addition to dead leaves in the eastern part of its range, followed by feeding specialisation and character displacement in the zone of sympatry with *Amplirhagada* and *Quistrachia* (Solem, In press-A).

Genitalia – The probable direction of evolution and transformation series of the terminal genitalia in respect to the unique alterations of the penis complex is discussed later in the section on Phylogeny (pp. 694-699). This section concentrates on the minor

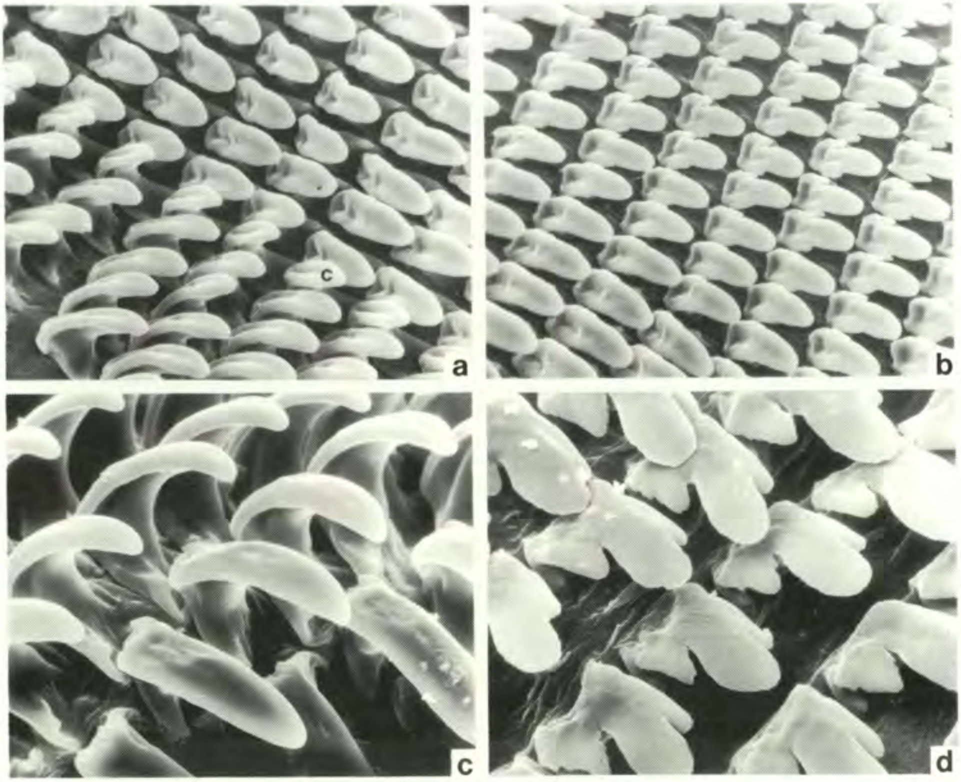


Plate 35: Radular teeth of *Westraltrachia commoda* (Iredale, 1939) and *W. turbinata:* (a-b) *W. commoda* (Iredale, 1939), FMNH 200256, Dissection C, Sta. WA-325, 5.9 km north-west of Yammera Gap, Napier Range, 17 February 1977, (a) medium angle side view of central ("C") and laterals at 320X, (b) high angle top view of latero-marginal transition at 335X; (c-d) *W. turbinata,* FMNH 199871, Dissection C, Sta. WA-281, 1.3 km west of Yammera Gap, Napier Range, 6 December 1976, (c) high angle side view of laterals at 665X, (d) high angle top view of marginals at 975X.

variations among species of *Westraltrachia* and discusses generalities of the reproductive cycle.

Reasonably complete series of collections through the seasons were available for *Westraltrachia woodwardi* (Fulton, 1902), *W. commoda* (Iredale, 1939), *W. turbinata,* and *W. derbyi* (Cox, 1892), thanks to the wet season efforts of Laurie Price and Carl C. Christensen. For the remaining species, mainly late dry season (November or December 1976) or early dry season (May 1977 or 1980) samples were available.

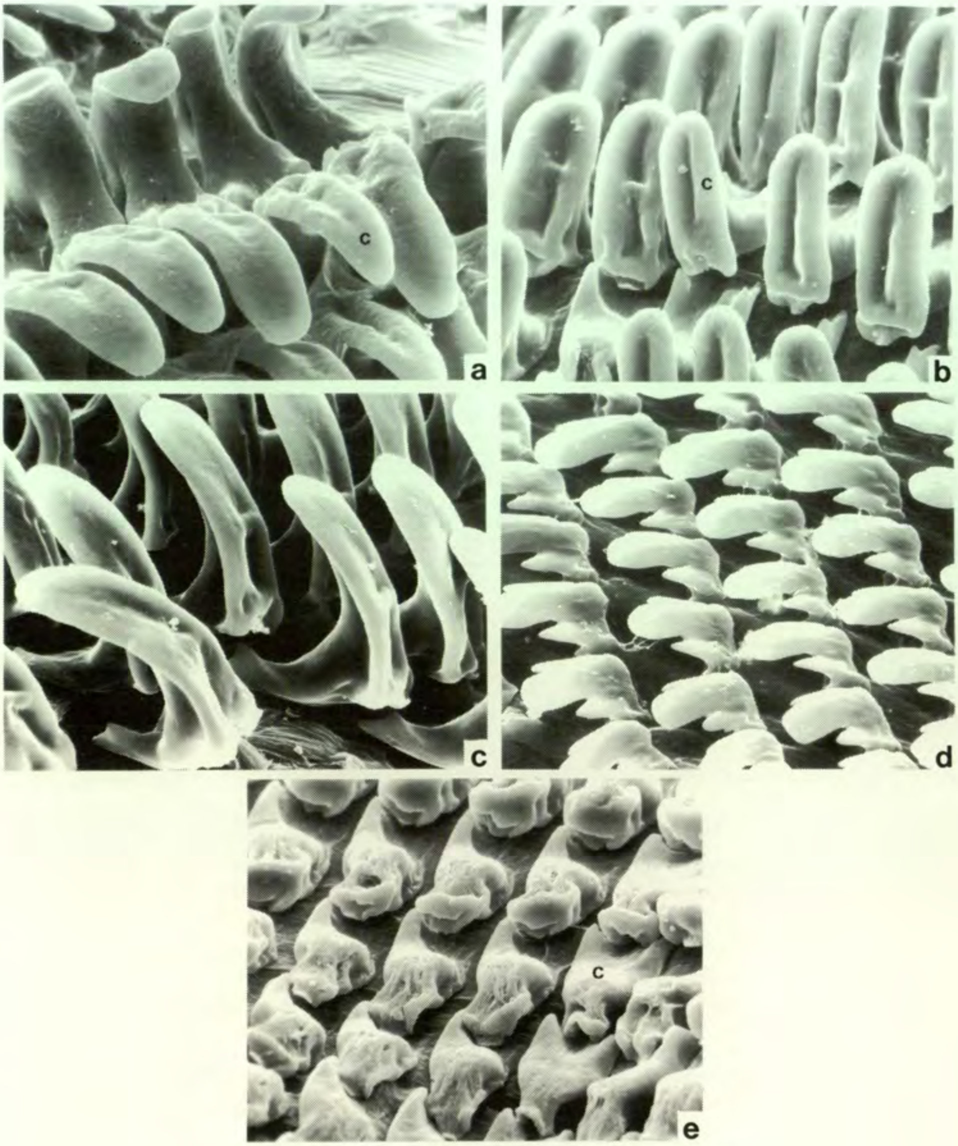


Plate 36: Radular teeth of *Westraltrachia inopinata:* FMNH 200157, Sta. WA-339, 1.1 km south-east of Yammera Gap, Napier Range, 23 December 1976, (a) Dissection B, high angle front view of central and laterals at 550X; (b-e) Dissection A, (b) low angle back view of central and laterals at 565X, (c) low angle side view of laterals at 580X, (d) high angle side view of marginals at 560X, (e) top view of worn central and laterals at 570X. Central teeth indicated by a "C."

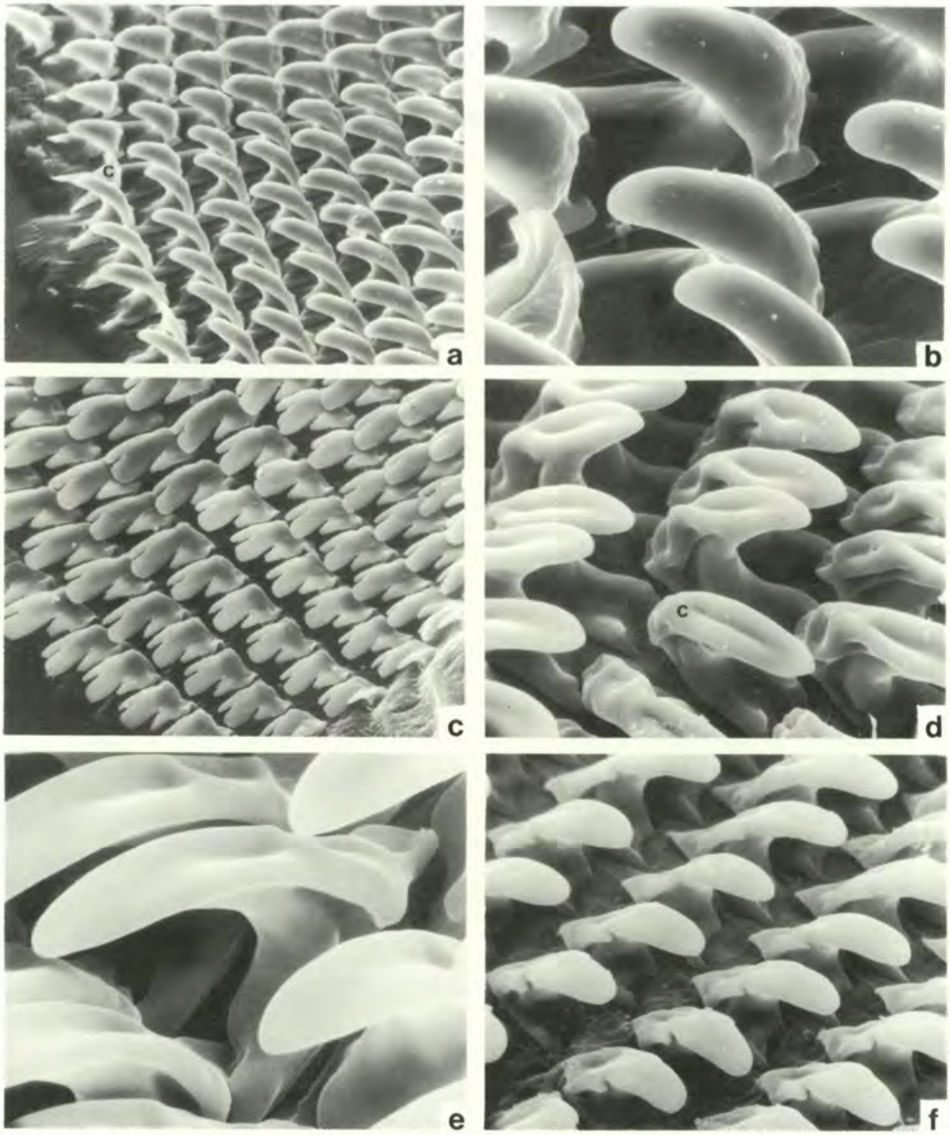


Plate 37: Radular teeth of *Westraltrachia f. complanata* and *W. f. froggatti* (Ancey, 1898): (a-c) *W. f. complanata,* FMNH 200153, Dissection B, Sta. WA-359, 10.5 km east of Yammera Gap, Napier Range, 10 January 1977, (a) high angle side view of central and laterals at 290X, (b) low angle side view of early laterals at 1,185X, (c) high angle top view of marginals at 420X; (d-f) *W. f. froggatti* (Ancey, 1898), FMNH 199873, Dissection A, Sta. WA-193, south-west corner of Windjana Gorge, Napier Range, 5 December 1976, (d) low angle side view of central and laterals at 675X, (e) very low angle side view of laterals at 1,300X, (f) high angle side view of latero-marginal transition at 700X. Central teeth indicated by a "C."

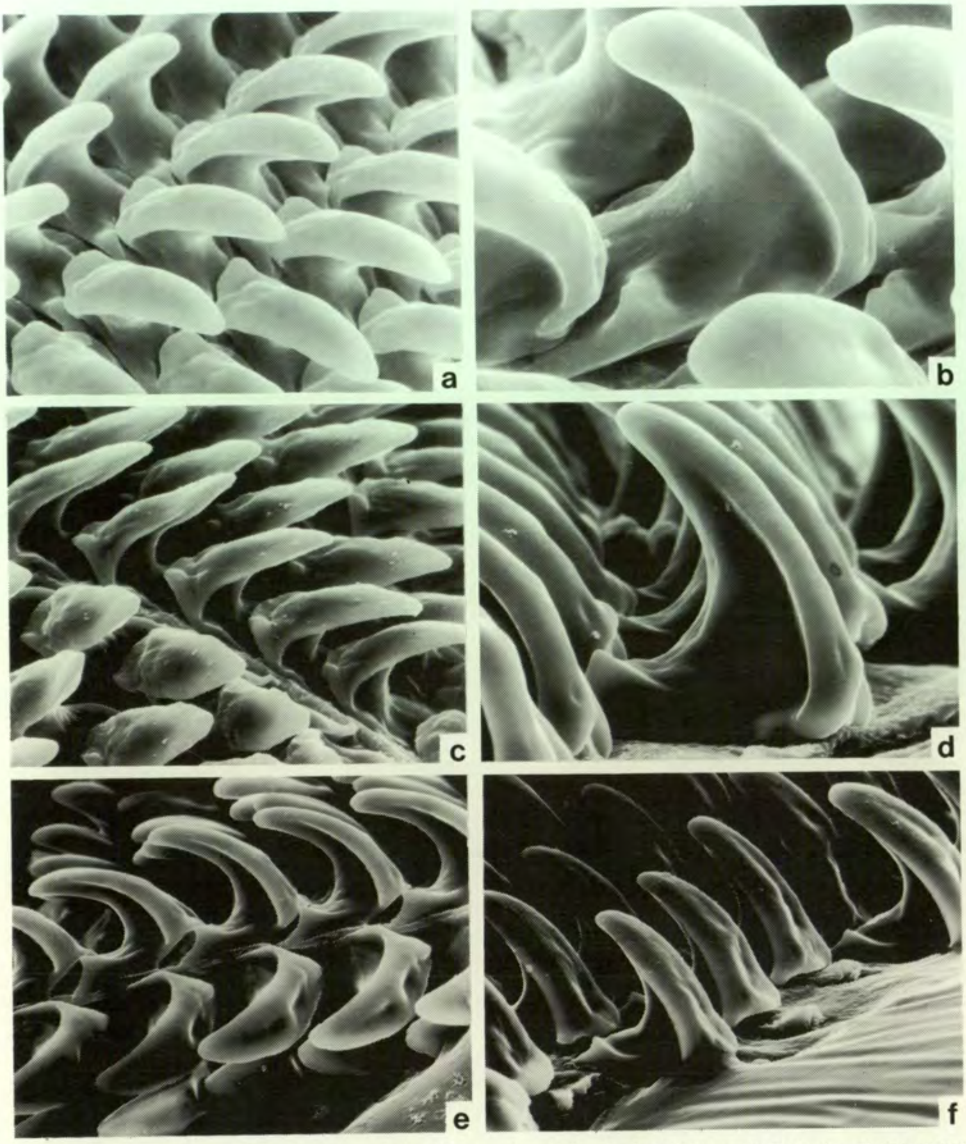


Plate 38: Variation of lateral teeth in *Westraltrachia derbyi* (Cox, 1892): (a-d) FMNH 200056, Sta. WA-194, south-east corner of Windjana Gorge, Napier Range, 5 December 1976, (a) Dissection A, low angle side view at 695X, (b) Dissection A, very low angle view of single early lateral at 1,300X, (c) Dissection C, high angle side view of new, untanned laterals at 660X, Dissection D, very low angle side view of anterior laterals at 1,160X; (e-f) FMNH 200147, Sta. WA-335, 3.4 km south-east of Lillimilura Police Station Ruins, Napier Range, 22 December 1976, (e) Dissection A, low angle side view of anterior laterals at 635X, (f) Dissection B, medium angle side view of laterals at 677X.

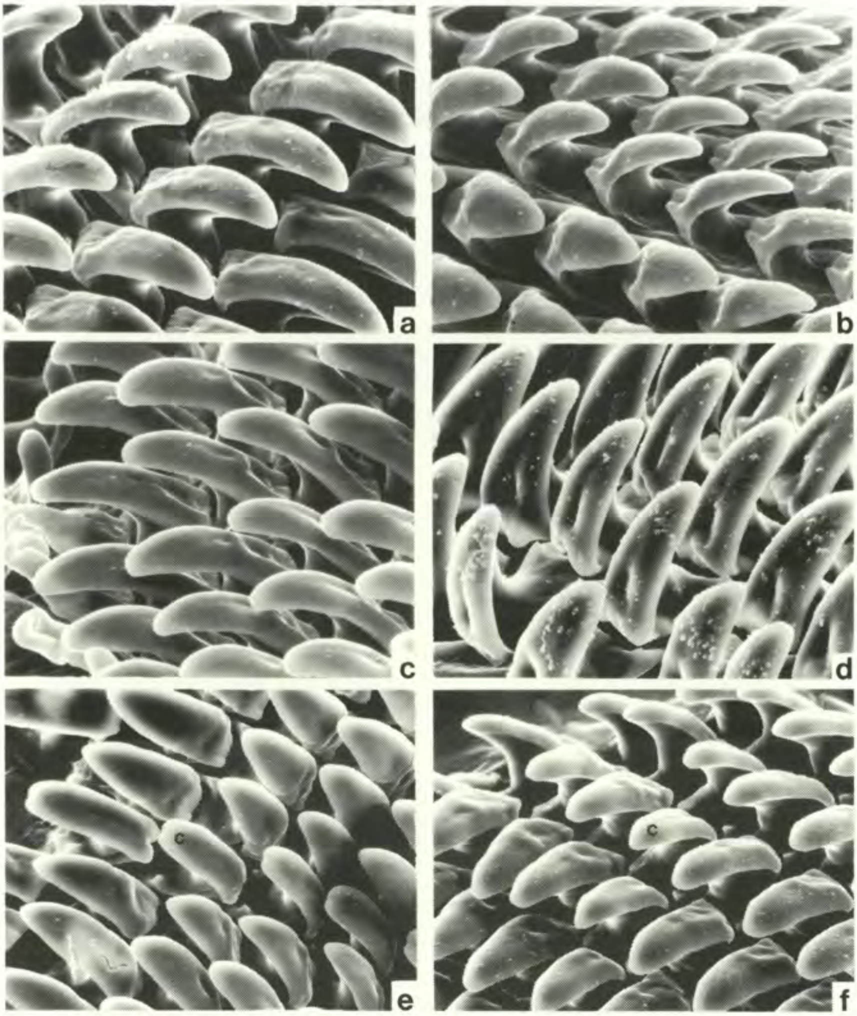


Plate 39: Variation in lateral and central teeth of *Westraltrachia derbyi* (Cox, 1892): (a-b) FMNH 200180, Sta. WA-307, north-east side of Windjana Gorge, Napier Range, 11 December 1976, (a) Dissection A, low angle side view of laterals at 635X, (b) Dissection B, low angle side view of laterals at 625X; (c) FMNH 200159, Dissection A, Sta. WA-336, 4.3 km south-east of Carpenter Gap, Napier Range, 22 December 1976, low angle side view of laterals at 650X; (d) FMNH 200133, Dissection A, Sta. WA-334, just north of Lillimilura Police Station Ruins, Napier Range, 22 December 1976, low angle back view of laterals at 670X; (e) FMNH 200056, Dissection D, Sta. WA-194, south-east corner of Windjana Gorge, Napier Range, 5 December 1976, low angle top view of central and laterals at 460X; (f) FMNH 200054, Dissection A, Sta. WA-194, 4 January 1977, low angle side view of central and laterals at 495X. Central teeth indicated by a "C."

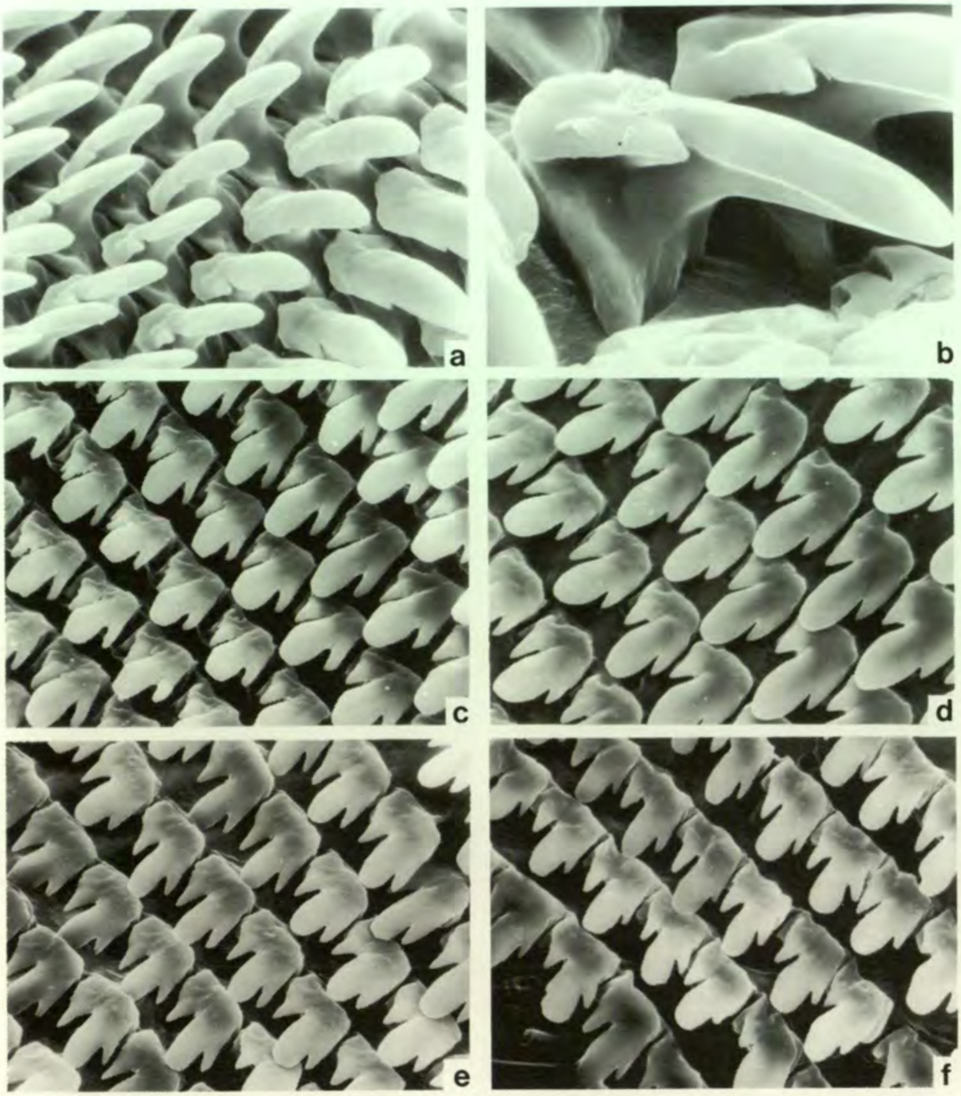


Plate 40: Variation in marginal teeth of *Westraltrachia derbyi* (Cox, 1892): (a-d) FMNH 200056, Sta. WA-194, south-east corner of Windjana Gorge, Napier Range, 5 December 1976, (a) Dissection A, high angle view of latero-marginal transition at 700X, (b) Dissection A, high angle side view of single early marginal at 1,825X, (c) Dissection C, high angle side view of marginals at 610X, (d) Dissection D, low angle top view of marginals at 600X; (e) FMNH 199853, Dissection A, Sta. WA-194, 21 March 1977, high angle top view of marginals at 635X; (f) FMNH 200054, Dissection A, Sta. WA-194, 4 January 1977, high angle top view of marginals at 650X.

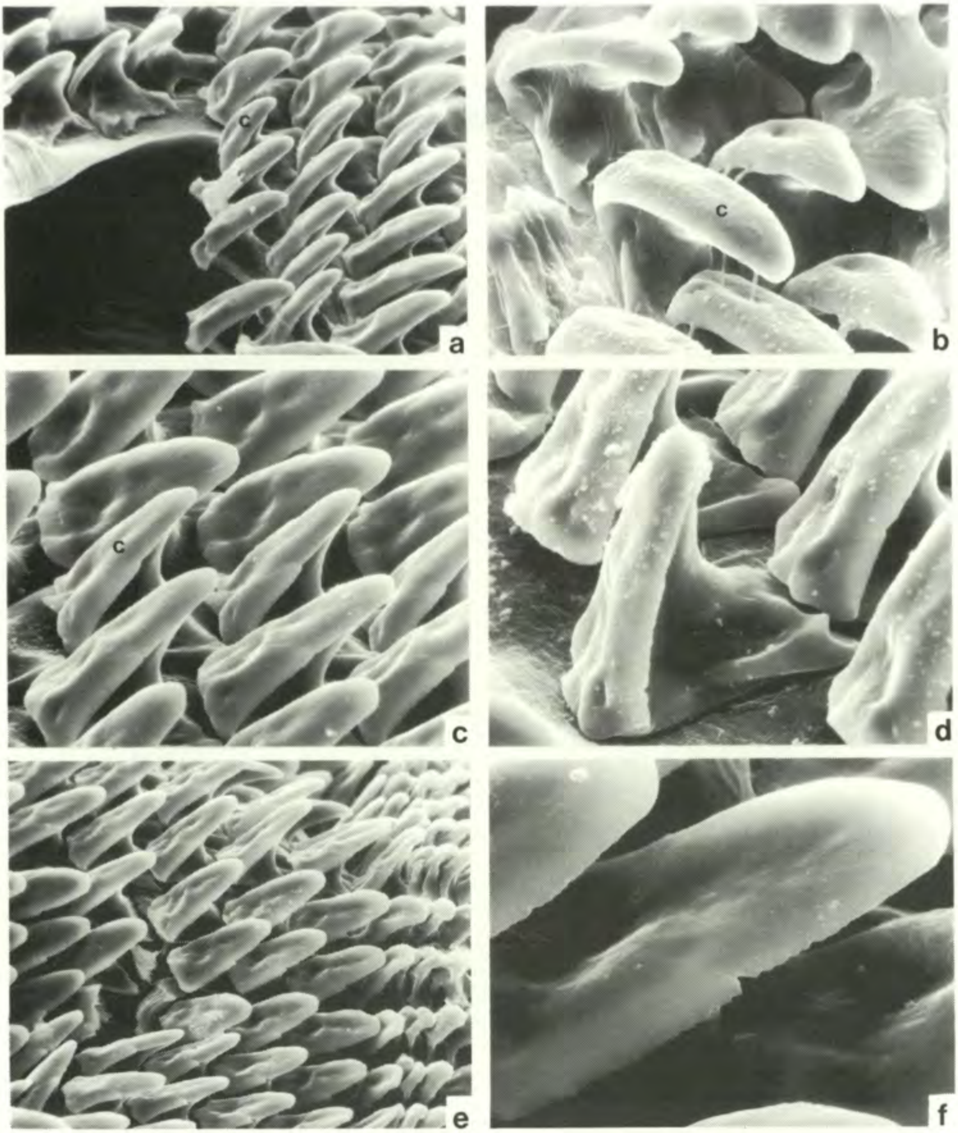


Plate 41: Radular teeth of *Westraltrachia oscarensis* (Cox, 1892): FMNH 200165, Sta. WA-356, plains area between Napier and Oscar Ranges, 1 January 1977, (a-b) Dissection A, (a) mid-angle view of central and laterals at 325X, (b) mid-angle side view of central and laterals at 620X; (c-f) Dissection B, (c) low angle side view of central and laterals at 690X, (d) low angle side view of lateral at 970X, (e) mid-angle side view of latero-marginal transition and deformed rows at 350X, (f) serrated edge of late lateral at 1,675X. Central teeth are indicated by a "C."

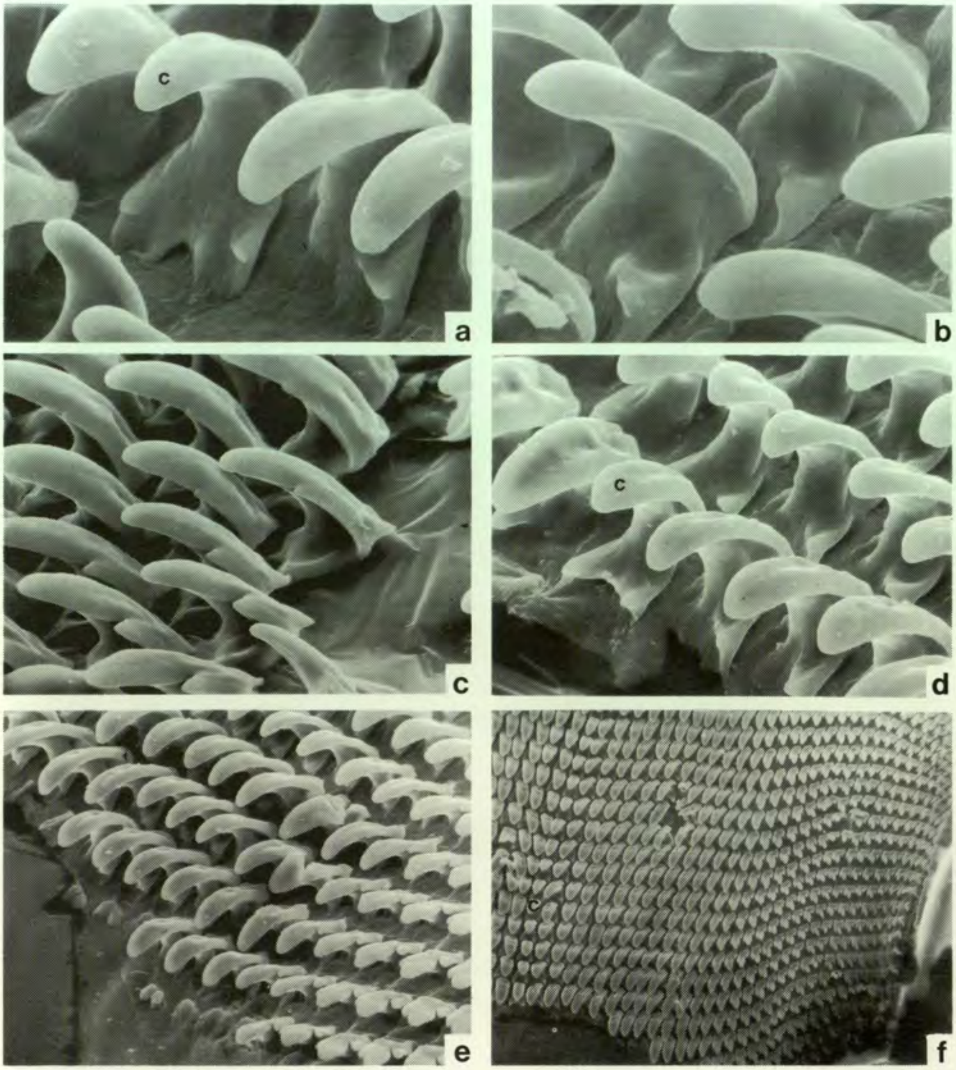


Plate 42: Radular teeth of *Westraltrachia alterna* Iredale, 1939: (a-c) FMNH 204709, Sta. WA-582, Cycad Hill, south side of Napier Range, 7 May 1980, (a) Dissection A, very low angle side view of the central and first lateral teeth at 930X, (b) Dissection B, very low angle side view of laterals at 1,230X, (c) Dissection A, mid-angle side view of latero-marginal transition at 650X; (d-f) FMNH 199930, Sta. WA-275, 5 km west of Tunnel Creek turnoff, Napier Range, 3 December 1976, (d) medium angle front view of central and lateral teeth at 640X, (e) high angle front view of latero-marginal transition at 325X, (f) top view of half row of teeth at 98X. Central teeth indicated by a "C."

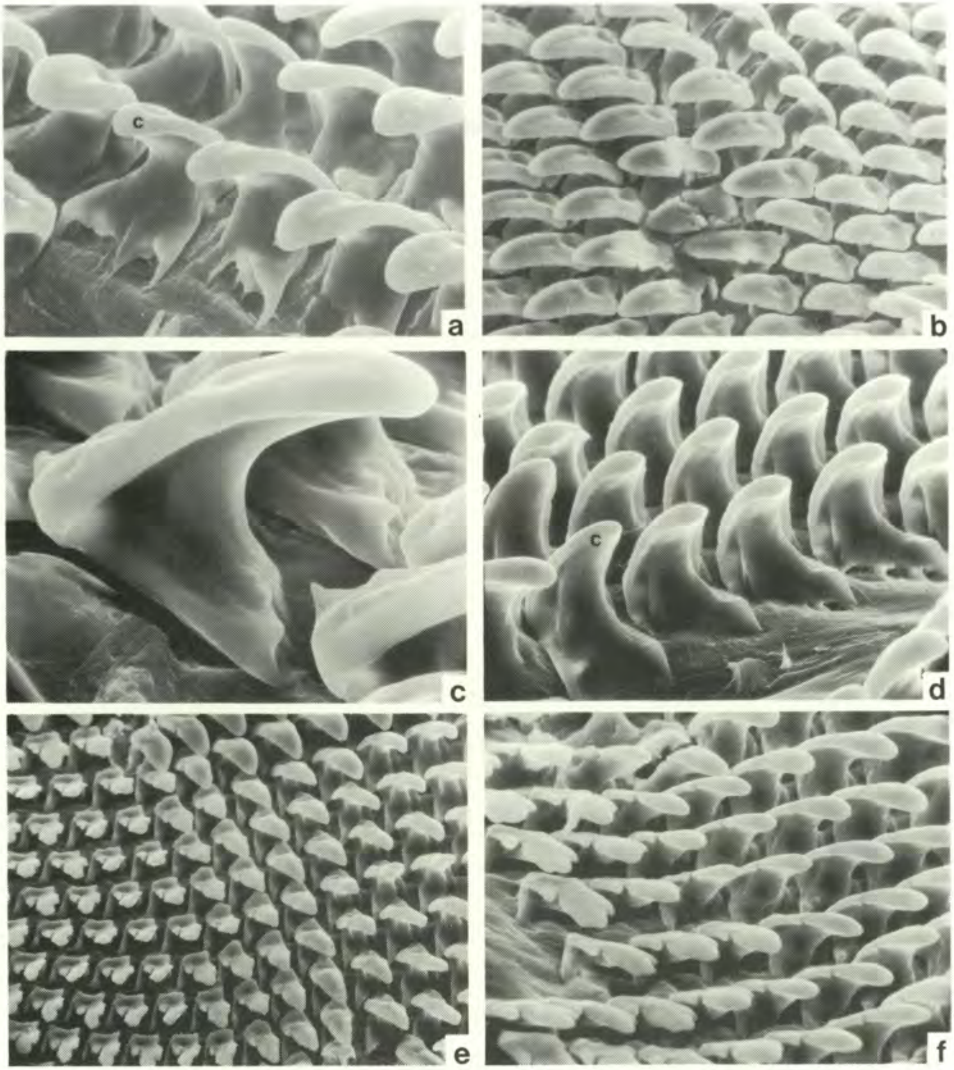


Plate 43: Radular teeth of *Westraltrachia cunicula:* (a-b) FMNH 200236, Sta. WA-279, cliffs north of Chestnut Creek, south face of Napier Range, 4 December 1976, (a) low angle front view of central and early laterals at 635X, (b) mid-angle side view of latero-marginal transition at 330X; (c) FMNH 200214, Sta. WA-270, 21.8 km east of Tunnel Creek turnoff, Napier Range, 2 December 1976, very low angle view of single lateral at 1,200X; (d-f) FMNH 199886, Sta. WA-274, entrance Tunnel Creek Gorge, Napier Range, 3 December 1976, (d) Dissection A, very low angle front view of central and early laterals at 600X, (e) Dissection B, top view of latero-marginal transition at 300X, (f) Dissection A, mid-angle front view of latero-marginal transition at 525X. Central teeth indicated by a "C."

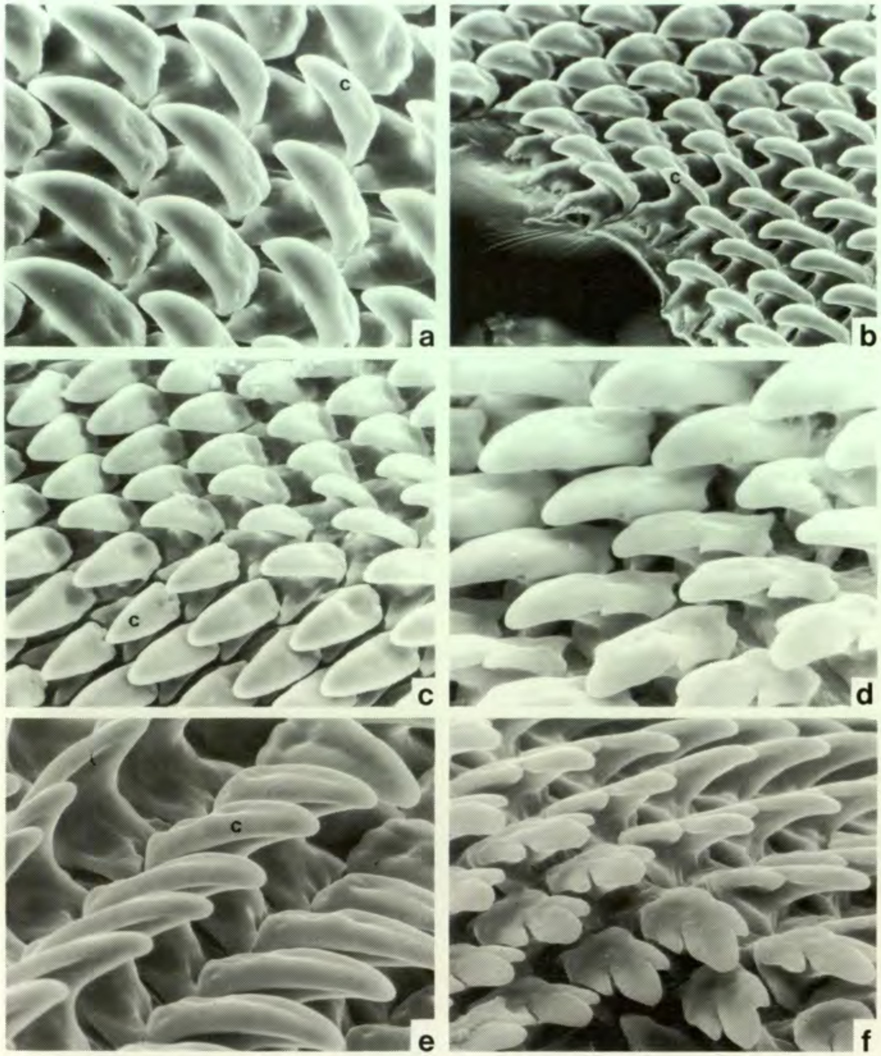


Plate 44: Radular teeth of *Westraltrachia lievreana, W. subtila,* and *W. instita:* (a-b) *W. lievreana,* FMNH 200223, Dissection A, Sta. WA-263, 14.1 km north-west of Linesman Creek, Oscar Ranges, 28 November 1976, (a) mid-angle side view of central and laterals at 590X, (b) high angled side-front view of central and laterals at 320X; (c-d) *W. subtila,* FMNH 200216, Dissection A, Sta. WA-265, 6.2 km west of Mt. Wynne Creek, Oscar Ranges, 28 November 1976, (c) high angle side view of central and laterals at 350X, (d) mid-angle side view of latero-marginal transition at 680X; (e-f) *W. instita,* FMNH 200224, Dissection B, Sta. WA-264, 0.4 km west of Mt. Wynne Creek, Oscar Ranges, 28 November 1976, (e) mid-angle side view of central and laterals at 675X, (f) mid-angle side view of latero-marginal transition at 720X. Central teeth indicated by a "C."

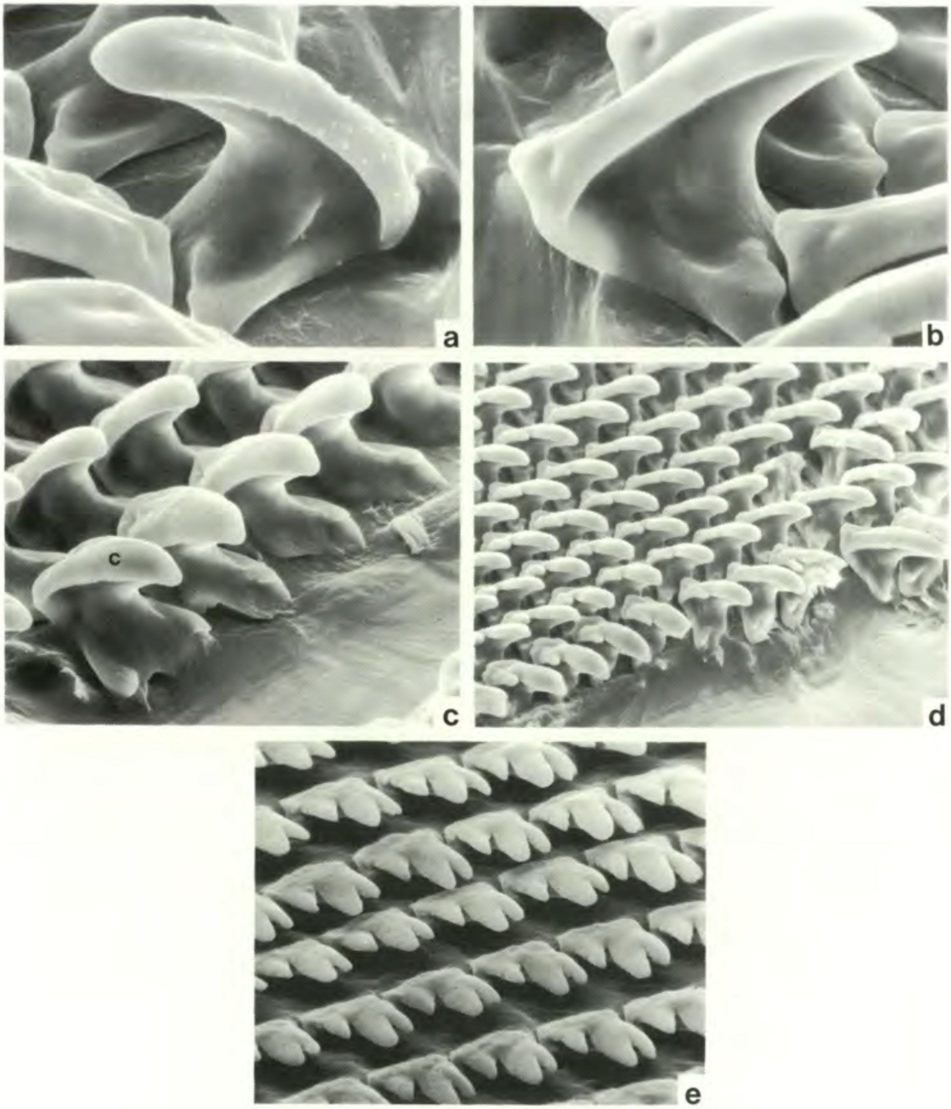


Plate 45: Radular teeth of *Westraltrachia instita* and *W. porcata:* (a) *W. instita,* FMNH 200224, Dissection A, Sta. WA-264, 0.4 km west of Mt. Wynne Creek, Oscar Ranges, 28 November 1976, very low angle side view of single lateral at 1,100X; (b-e) *W. porcata,* FMNH 205311, Dissection A, Sta. WA-711, south of Brooking Creek on Tunnel Road, west of Fitzroy Crossing, 19 June 1980, (b) very low angle side view of single laterals at 1,325X, (c) mid-angle side view of central and early laterals at 635X, (d) high angle side-front view of latero-marginal transition at 335X, (e) mid-angle front view of outer marginals at 650X. Central tooth indicated by a "C."

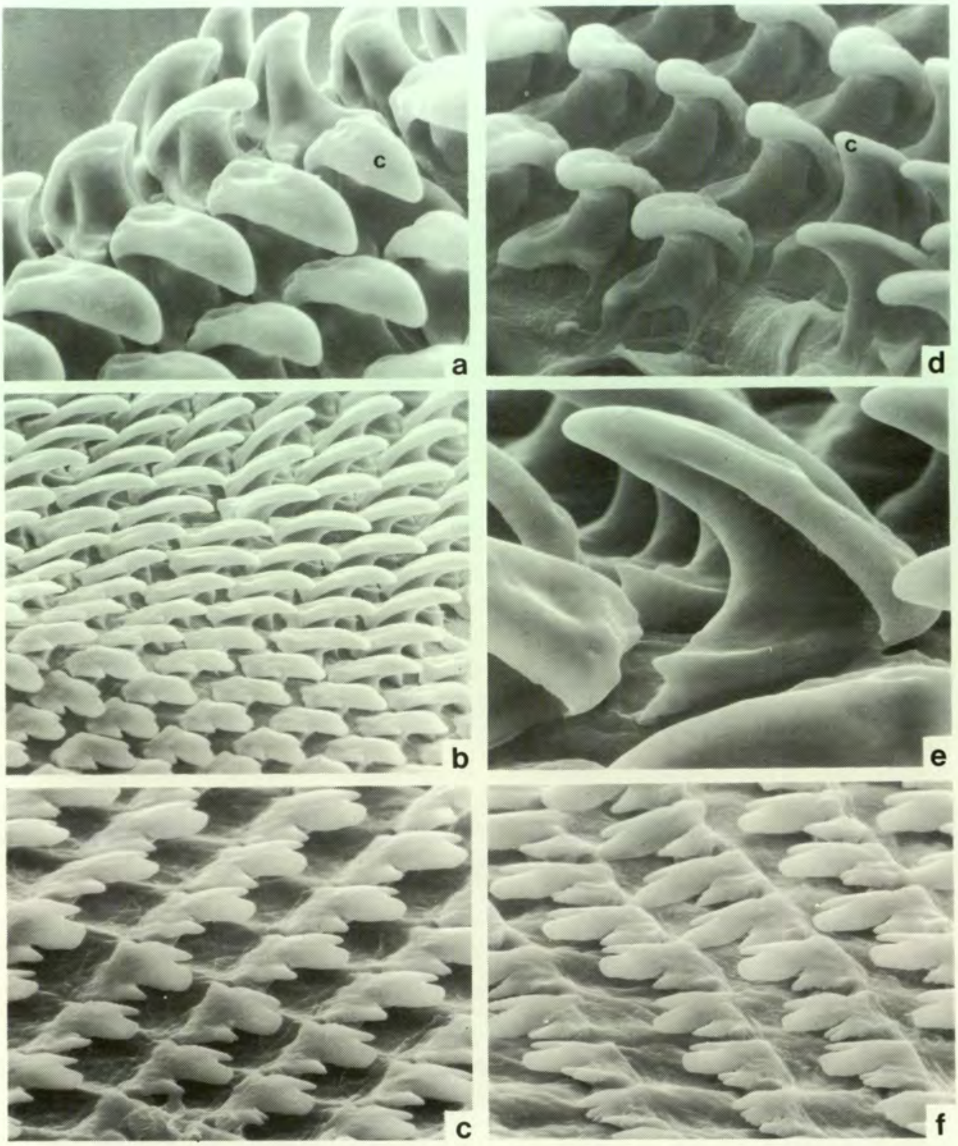


Plate 46: Radular teeth of *Westraltrachia tropida:* (a-f) FMNH 205306, Dissection A, Sta. WA-710, gap through Oscar Ranges at Twelve Mile Bore, 19 June 1980, (a) mid-angle side view of central and laterals at 640X, (b) high angle side view of latero-marginal transition at 330X, (c) low angle side view of marginals at 640X, (d) mid-angle side-front view of central and laterals at 640X, (e) very low angle side view of single laterals at 1,300X, (f) top view of outer marginals at 640X. Central teeth indicated by a "C."

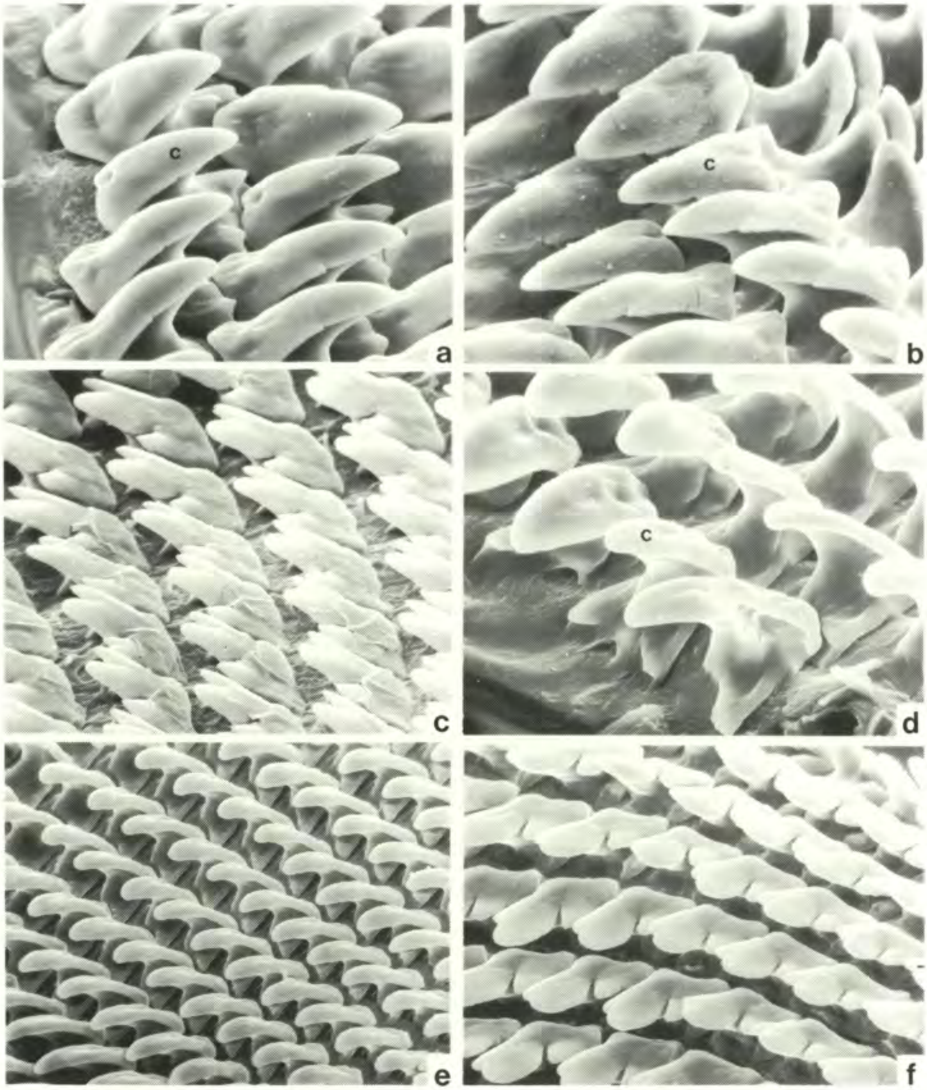


Plate 47: Radular teeth of *Westraltrachia rotunda* and *W. limbana:* (a-c) *W. rotunda*, FMNH 200208, Sta. WA-258, east side of Brooking Gorge, Oscar Ranges, 26 November 1976, (a) Dissection A, mid-angle side view of central and laterals at 710X, (b) Dissection B, high angle side view of central and early laterals at 700X, (c) Dissection B, mid-angle side view of outer marginals at 700X; (d-f) *W. limbana*, FMNH 200201, Sta. WA-266, 3.7 km west-south-west of Fossil Downs Homestead, 29 November 1976, (d) Dissection A, mid-angle front view of central and laterals at 625X, (e) Dissection B, high angle side view of latero-marginal transition at 325X, (f) Dissection B, mid-angle front view of outer marginals at 610X. Central teeth indicated by a "C."

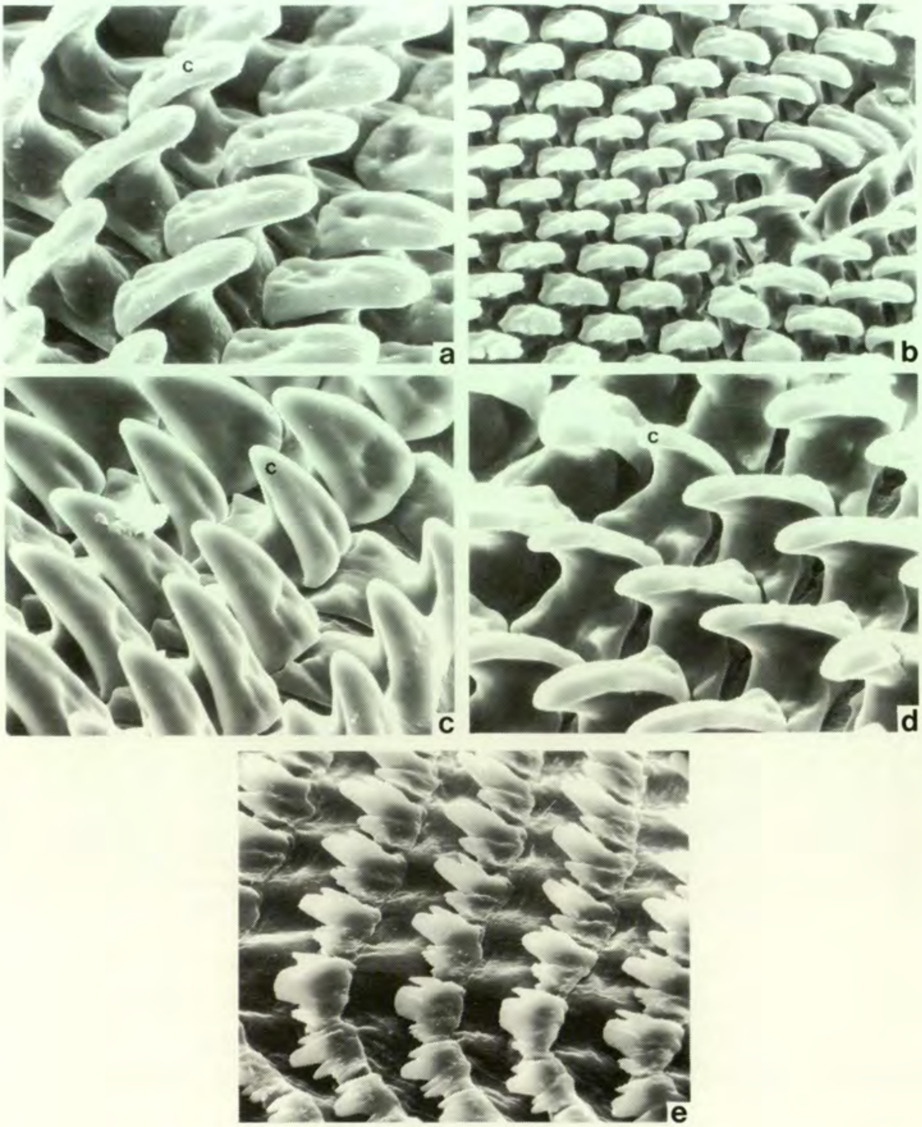


Plate 48: Radular teeth of *Westraltrachia recta* and *W. pillarana:* (a-b) *W. recta,* FMNH 200205, Dissection A, Sta. WA-254, Limestone Billy Hills, north-west of Pillara Range, 29 November 1976, (a) mid-angle side view of worn central and laterals at 655X, (b) mid-angle top view of latero-marginal transition at 340X; (c-e) *W. pillarana,* FMNH 200229, Dissection A, Sta. WA-253, 0.5 km west of Emanuels Bore, Pillara Range, 24 November 1976, (c) high angle back view of central and laterals at 645X, (d) low angle side-front view of centrals and laterals at 675X, (e) high angle top view of outer marginals at 615X. Central teeth indicated by a "C."

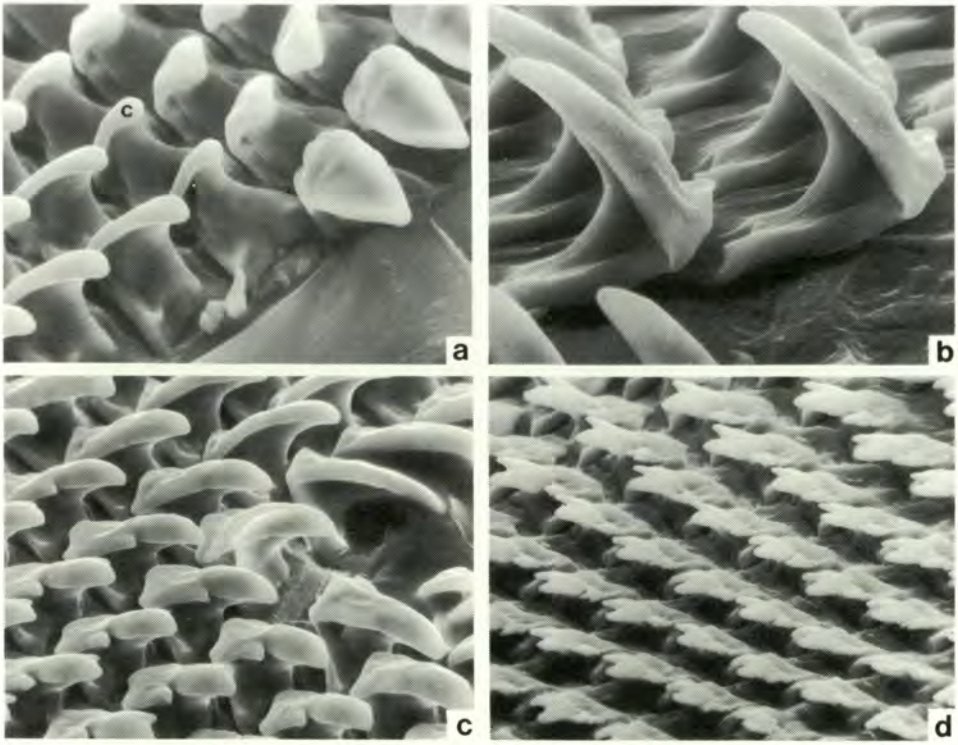


Plate 49: Radular teeth of *Westraltrachia ascita:* (a-d) FMNH 200182, Sta. WA-370, 3.4 km north of Lloyd Hill summit, west side of Laidlaw Range, 13 February 1977, (a) high angle side view of central and early laterals at 660X, (b) very low angle side view of laterals at 1,300X, (c) mid-angle side view of latero-marginal transition at 670X, (d) mid-angle side view of latero-marginal transition at 650X. Central tooth indicated by a "C."

In the following lists, the percentage of live collected adult specimens is based only on material taken by the WAM and FMNH surveys, and ignores type material or specimens collected by non-malacologists. This gives a better idea of actual success rate in finding live individuals. For those species subject to seasonal sampling, with heavy emphasis on revisiting areas to obtain more live adults, the percentage of adult shells that were live collected is respectable:-

W. woodwardi	17.8%
W. commoda	19.8%
W. turbinata	11.9%
W. derbyi	20.7%
W. oscarensis	18.7%

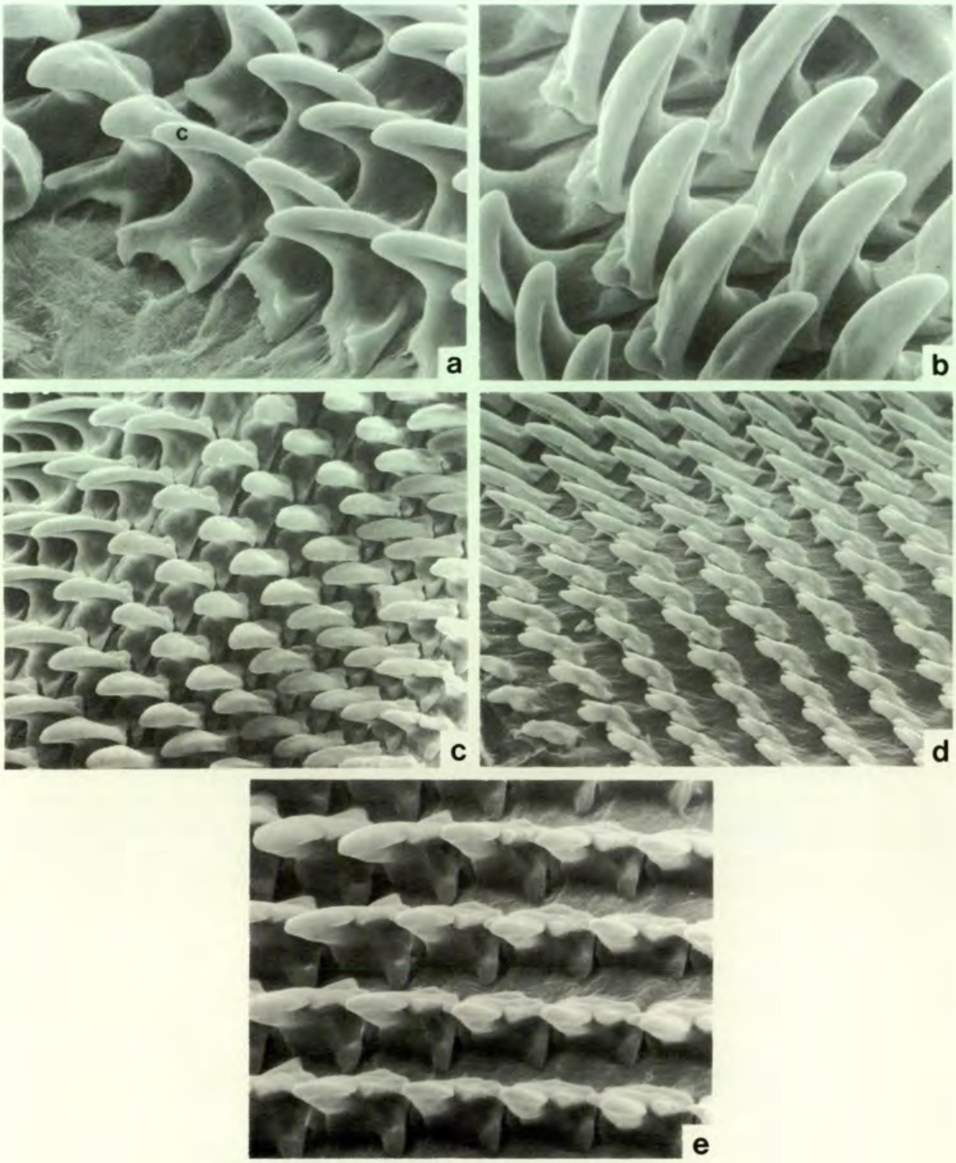


Plate 50: Radular teeth of *Westraltrachia ampla:* (a-e) WAM 609.79, Dissection A, Cave Spring, Bugle Gap, West Kimberley, 28 May 1966, (a) low angle side view of central and early laterals at 600X, (b) mid-angle posterior view of laterals at 660X, (c) mid-angle front view of latero-marginal transition at 300X, (d) high angle side view of latero-marginal transition at 320X, (e) mid-angle front view of early to mid-marginals at 620X. Central tooth indicated by a "C."

Much less wet season collecting was done between Yammera Gap and the west bank of Windjana Gorge because of black mud areas, so that the success rate in this region was reduced:-

W. inopinata	7.9%
W. f. complanata	9.8%
W. f. froggatti	8.2%

Since *Westraltrachia inopinata* was not field recognised as a distinct species, this probably gives an idea of normal collecting success in the central and western Napier Ranges. In the eastern Napiers, Oscar Ranges and most of the East Kimberley, where collecting was dry season 'hit and run' tactics, there is a dramatic difference in success rate:-

W. alterna	3.6%
W. cunicula	3.3%
W. instita	1.4%
W. lievreana	5.8%
W. tropida	2.0%
W. porcata	2.3%
W. rotunda	7.0%
W. limbana	1.0%
W. recta	0.8%
W. ascita	0.6%
W. ampla	0.9%

In this region, there were lucky finds of two species that boosted the success ratio significantly:-

W. subtila	19.5%
W. pillarana	13.3%

Both situations involved finding colonies that had not been battered by fire and the density of specimens was unusually high. Thoughout most of its eastern and central range, *Westraltrachia* is rather rare and difficult to find alive. Reservoir populations will be in boulder piles too massive for hand or pry bar disturbance. In contrast, specimen density is much higher in the Napier Ranges, reflecting the more massive limestone hills and the more favourable moisture conditions.

Material of the related genera proved relatively easy to collect alive:-

Mouldingia occidentalis	49.7%
M. orientalis	24.0%
Ordtrachia septentrionalis	14.9%
O. australis	16.2%
O. grandis	1.6%
O. intermedia	15.8%
Exiligada negriensis	2.3%
Prototrachia sedula	31.9%

One fortunate find of living *Ordtrachia intermedia* at one of several stations increased the success rate for that species, otherwise it would have joined *O. grandis* and *Exiligada* in the rare category.

The above data means that generalisations have been derived by study of the abundant material from the western Napier Range, and that many decisions about East Kimberley taxa have been based on very few or even single dissections, with analogy playing an important role.

In Parts I-III of this series (Solem, 1979, 1981a, 1981b), a pattern of sexual development and time of maturation has been deduced from study of seasonal samples, and specimens at different stages of development. The western Napier Range taxa of *Westraltrachia* are consistent with the pattern found in *Xanthomelon, Torresitrachia, Amplirhagada,* and the Ningbing taxa. This has been partly summarised in Solem (1981a: 164-166), but is further refined here and proposed as the basic reproductive cycle for the Kimberley camaenids in a separate report by Solem and Christensen (In press). Details are presented under particular species, but the following summary of growth and then seasonal variation in adults will help understand individual situations:-

First year – Eggs are laid shortly after first heavy rains in October to December, depending upon locality; young hatch about two weeks later; reach half adult shell size by end of wet season (March to May, depending upon locality); aestivate through next dry season, which ends October to December.

Second year – Become active with rains, feed; near end of second wet season become male mature (ovotestis, penis complex), but are female organs immature, and normally then reach full adult shell size and complete shell growth by reflecting the lip; aestivate through their second dry season.

Third year – Become active as functional males and mate reciprocally, storing the exogenous, but unusable (since they are not mature females), sperm in the spermatheca; become mature females near the end of this wet season; aestivate through their third dry season.

Fourth year on – Become active as both males and females each wet season; aestivate over each dry season.

Many live adults of *Amplirhagada napierana* Solem, 1981 were marked in February 1977. Some of these were found alive in May 1980 and again in January 1981, indicating that they can reach at least seven years in age. A similar longevity is predicted for the other genera of Kimberley camaenids.

Seasonal variation in genital organs of adult *Westraltrachia* is the same as in *Amplirhagada* (Solem, 1981a: 242, fig. 53). The mid-dry season condition is taken as a convenient starting point. The ovotestis **(Fig. 114b, G)** is greatly reduced in size, the hermaphroditic duct **(Fig. 114a, GD)** is very thin and only slightly coiled, both the prostate and uterus are reduced in diameter **(Fig. 114a, DG, UT)**, the spermatheca has the head packed with sperm masses from the previous wet season **(Fig. 112, S)**, and the terminal genital organs and albumen gland **(Fig. 114a, GG)** remain large.

Major changes occur near the normal end of the dry season, that is, the usual statistical date for the first heavy rains. Shortly BEFORE this date, the ovotestis has grossly enlarged and is filled with sperm **(Figs 116a-b, 129b)**, the hermaphroditic duct is grossly thickened and tightly kinked **(Figs 116a, 129a)**, the prostate has thickened **(Fig. 116a)** and the sperm masses within the head of the spermatheca have mostly disappeared. It is quite probable that the stored, exogenous sperm from the previous wet season are partly digested and then used to build endogenous sperm as an energy conserving pattern. The snails are male active by the normal start of the rains.

Mating at the start of the wet season probably triggers start of the female activation process, with energy from newly eaten food providing raw material for the egg nutrients. There seem to be multiple matings, with most sperm stored. About mid-wet season a shutting down process begins, in which the ovotestis, hermaphroditic duct, prostate, and uterus shrink drastically in size. Change in the first two organs frees space in the digestive gland area for storage of digested food to provide reserves for gradual dry season use, and the products of the latter two organs will not be needed until mating at the start of the next wet season. There apparently are no size changes in the albumen gland or terminal genital organs, or such minor changes that I could not recognise these on a gross dissection basis.

Changes in size and proportion of the pallial and apical genital organs are seasonally or age determined, and they are not used in systematic differentiation of species for this reason. The albumen gland is very small in individuals near the end of their second wet season and continues small to sometime in their third wet season. One specimen of all dissected, *Westraltrachia froggatti* **(Fig. 123a),** had a possible indication of wet season size increase in the albumen gland, but dry and wet season collected adults tend to have albumen glands of the same size.

Microsympatry among species of *Westraltrachia* is unusual, so that there are comparatively few gross changes in the genitalia that are directly comparable to the situation found in *Amplirhagada*. Species of that genus show radical differences in armature on the principal penis pilaster (Solem, 1981a: 172-3, figs 36-37), wall sculpture and pilaster size (Solem, 1981a: 260, fig. 58), and the wall sculpture of the lower female tract (Solem, 1981a: 278, fig. 64) when they are microsympatric, which makes identification and characterisation of species simple for the taxonomist.

The grossly sympatric *Westraltrachia rotunda* and *W. limbana* do show rather major differences in the terminal genitalia that are summarised in **Table 46.** These are equivalent, in effect, to the length changes documented for other Kimberley genera **(Table 73,** p. 694), and provide guidelines for interpreting differences between species that replace each other within a single length of exposed limestone.

The patterns of variation within each organ of the terminal genitalia are reviewed below. The patterns are mosaic, most probably the result of species interactions along zones of contact, and correlations among variations are not obvious. Detailed analysis of the latter factor is postponed for a major review of genital variation patterns in all Kimberley species.

Observed variation in the terminal female genitalia consists of relative length changes. No differences were observed in the sculpture on the inner walls. The spermatheca (S) is attached to the lower part of the prostate-uterus (DG, UT) by fibers. In illustrating this section, detachment and decoiling is necessary. Some drawings do not adequately show proportionate lengths because of twisting and folding that occurred in pinning out the genital system. The thickness of the spermatheca depends upon the number of sperm masses stored inside, and this depends upon the date of collection for the specimen. Usually, 14 of 21 species, the spermatheca is distinctly shorter than the free oviduct **(Fig. 116a, UV),** and the spermathecal head is slightly enlarged.

Table 46: Genital Differences between the Sympatric Species *Westraltrachia rotunda* and *W. limbana*

	Species	
	W. rotunda	*W. limbana*
Penis	very long (Fig. 147b)	short (Fig. 150b)
Principal Penis Pilaster	very long (Fig. 148)	short (Fig. 158m)
Vagina	very long (Fig. 147a)	short (Fig. 150a)
Free Oviduct	very long (Fig. 147a)	medium (Fig. 150a)
Epiphallic Loop	typical (Fig. 147b)	compacted (Figs. 149a, 150b)

The free oviduct (UV) normally is strongly curved because its length exceeds that of the spermatheca **(Figs 116a, 145a 147a),** but in about one-third of the species it is subequal in length **(Fig. 112).** Normally the junction between the spermatheca and free oviduct to form the vagina (V) is a true merging of the tubes, although there is a tendency for the free oviduct to enter laterally upon a common channel of the spermatheca and vagina in many genera of camaenids. Since sperm masses are normally deposited into the spermatheca, the latter pattern is functionally advantageous. Vaginal length is highly variable among species. A somewhat subjective division can be made into very short **(Fig. 116a)** or short **(Fig. 112)** with 11 species; medium in length **(Fig. 119a)** with four species; and long **(Fig. 118a)** to very long **(Fig. 137a)** with six species. These do not correlate directly with penis length.

The terminal male genitalia are enclosed in a usually thin-walled sheath (PS). The penial retractor muscle (PR) arises from the base of the diaphragm and merges with the sheath apex without a clear external demarcation. When the penis sheath is opened, the penial retractor muscle is seen to attach immediately to the point of reflexion marking the shift from the vas deferens (VD) to the epiphallus (E). The former has entered the wall of the sheath somewhere below the apex, while both the epiphallus and penis (P) may be kinked or even coiled within the sheath. Thus it is impossible to make an external measurement indicating penis complex length, and internally the tubes are kinked or coiled sufficiently that no accurate length measurements could be taken.

The penis sheath itself can be thin-walled for its entire length **(Fig. 116c),** have the basal portion with slightly thicker wall **(Fig. 113b),** or rarely have the basal portion with much thickened wall **(Figs 134b, 154a-b).**

Entrance of the vas deferens (VD) through the sheath wall can be defined most easily in relation to the epiphallus base-penis head position. In only two taxa, *Westraltrachia alterna* Iredale, 1939 **(Fig. 134b)** and *W. ascita* **(Fig. 156b),** does the vas enter the sheath almost apically. Normally it enters either approximately opposite the base of the epiphallus-penis head **(Figs 113b, 157b),** or near the middle of the penis proper **(Fig. 124b),** with species numbers essentially evenly divided between these states. The variation is mosaic, and has no obvious correlation with other structural variations. After entering the sheath, the vas deferens is free of the wall, extends apically where it reflexes and receives insertion of the penial retractor muscle. This point of reflection is considered the point of transition from a vas deferens into an epiphallus.

The most characteristic feature of the genital system in *Westraltrachia* consists of the epiphallic loop and its added structure, the penis muscle (PM). Extension of the epiphallus into a long loop, that becomes 'U'-shaped, then the two arms are compacted together and bound by fibers, plus the presence of a continuation of the penial retractor muscle extending down to the head of the penis proper, at once identify the genus. The probable origin and direction change for this structural system is discussed below (pp. 694-699), with character states summarised in **Table 74** (p. 695). Western species tend to have very large epiphallic loops, while species from drier eastern parts of the range tend to show various compactions and shortenings of the loop.

The penis muscle (PM) itself differs dramatically in size, but again mosaically. It is comparatively small in four species, *Westraltrachia pillarana* **(Fig. 153c)** from the East Kimberley; *W. f. complanata* **(Fig. 123b)** and *W. f. froggatti* (Ancey, 1892) **(Fig. 124c)** from the central Napier Range; and *W. lievreana* **(Fig. 144b)** from the Oscar Ranges. It is medium in size for *Westraltrachia subtila* **(Fig. 140b)** and *W. instita* **(Fig. 142b)** from the Oscar Ranges, and *W. inopinata* **(Fig. 119b)** from the central Napier Range. It is large **(Fig. 116c)** in five species, massive **(Figs 113, 157b)** in eight species, and massive, but without attachment to the penial retractor muscle in *W. ascita* **(Fig. 156b).**

The penis (P) normally is a very slender tube, becoming thicker only when drastically shortened. Recognition of four length states is useful for discussion purposes, but these are not exclusive groupings and no meristic data is available to quantify the differences. There are three short **(Fig. 134b)**, six long **(Figs 116c, 118b)**, four long with slight kinking or coiling of the penis within the sheath **(Figs 113b-c)**, and eight species with a very long penis that is kinked or coiled **(Fig. 137b)**. Often neighbouring species will have clear differences in penis length, but exceptions do occur.

Within the penis chamber, there are simple longitudinal pilasters and pressure folds, with modified pilasters occurring apically. The reasons for considering, within the context of these genera, the presence of a major foliated pilaster with some hard edges as being primitive, are given below in the discussion of Phylogeny (pp. 694-699). *Westraltrachia rotunda* **(Fig. 148, PT)** and *W. woodwardi* **(Fig. 113)** retain the largest principal penis pilasters. The states in other species are reductions **(Figs 158a-q)**. The taxa living west of Windjana Gorge **(Figs 158a-d)**, and then nearby and east of Fitzroy Crossing **(Figs 158m-q)** have relatively large remnant pilasters, showing varying degrees of shortening, narrowing, and becoming straighter. Two taxa from intermediate areas, *Westraltrachia alterna* **(Fig. 158f)** and *W. lievreana* **(Fig. 158k)**, have the reduction carried further, but the pilaster is recognisable as such. The remaining taxa show reduction to a narrow, at most slightly sinuated ridge **(Figs 158e, g, h)**, a straight ridge **(Fig. 158j)**, or finally reduction to a point that it cannot be distinguished from the simple wall pilasters **(Fig. 158i)**. While reduction is greatest in the central part of the generic range, the geographic extremes both have larger principal penis pilasters.

Discussion of anatomical variation – Genital variation within *Westraltrachia* is relatively minor, except for initial stages in penis muscle and epiphallic loop reduction that indicate how *Ordtrachia* and *Exiligada* could have evolved (see pp. 694-699). The patterns of variation for organs are mosaic, and thus no attempt at indicating directionality is presented at this time. Changes in jaw and radular structure are the most dramatic known within the Camaenidae, but result from a pre-adaptation to an occasionally present food source, floral blooms on the seepage faces, that become accentuated when *Westraltrachia* entered an area in which this resource was common. At the same time it became sympatric with *Quistrachia* and *Amplirhagada*, generalised feeders of approximately equivalent shell size (Solem, In press-A).

Table 47: Range of Variation in *Westraltrachia*

Taxon	Number of Adults Measured	Mean and Range of: Shell Height	Shell Diameter	H/D Ratio
W. woodwardi (Fulton)	791	13.16 (8.4 – 18.3)	19.71 14.25 – 24.5)	0.666 (0.540 – 0.812)
W. commoda (Iredale)	883	11.00 7.8 – 15.3)	17.47 (13.3 – 22.5)	0.628 (0.520 – 0.773)
W. turbinata	930	9.55 (7.3 – 12.7)	13.53 (11.45 – 16.1)	0.706 (0.573 – 0.910)
W. inopinata	278	8.72 (6.55 – 11.1)	14.63 (11.1 – 18.3)	0.596 (0.503 – 0.715)
W. f. complanata	843	7.95 (5.95 – 11.0)	16.41 (13.6 – 19.9)	0.483 (0.394 – 0.703)
W. f. froggatti (Ancey)	283	7.24 (5.0 – 9.7)	14.81 (12.2 – 17.5)	0.503 (0.348 – 0.608)
W. derbyi (Cox)	568	7.72 (5.5 – 11.2)	13.90 (10.4 – 17.8)	0.555 (0.470 – 0.678)
W. alterna Iredale	370	8.32 (6.3 – 11.0)	14.12 (12.2 – 16.8)	0.589 (0.493 – 0.720)
W. oscarensis (Cox)	184	11.55 (7.75 – 14.9)	17.94 (14.3 – 22.1)	0.643 (0.510 – 0.800)
W. cunicula	272	9.12 (7.35 – 11.5)	14.59 (12.5 – 16.7)	0.624 (0.547 – 0.754)
W. subtila	82	8.55 (7.0 – 10.1)	14.86 (13.7 – 16.6)	0.575 (0.531 – 0.654)
W. instita	289	7.09 (5.8 – 8.3)	13.33 (11.7 – 15.35)	0.533 (0.469 – 0.622)
W. lievreana	377	8.21 (6.45 – 10.2)	14.32 (11.75 – 16.7)	0.574 (0.498 – 0.660)
W. tropida	400	8.43 (6.8 – 10.6)	15.00 (12.2 – 19.5)	0.561 (0.467 – 0.695)
W. porcata	43	11.45 (8.05 – 13.9)	16.37 (14.5 – 18.8)	0.699 (0.555 – 0.818)

Table 47: Range of Variation in *Westraltrachia* (continued)

Taxon	Number of Adults Measured	Mean and Range of: Shell Height	Shell Diameter	H/D Ratio
W. rotunda	1,562	9.05 (6.9 – 11.4)	14.15 (11.5 – 17.7)	0.639 (0.527 – 0.757)
W. limbana	512	8.60 (6.25 – 11.75)	15.24 (12.2 – 18.0)	0.564 (0.473 – 0.695)
W. recta	121	9.78 (7.55 – 11.9)	12.70 (10.9 – 14.75)	0.791 (0.669 – 0.869)
W. pillarana	368	8.70 (6.8 – 11.7)	14.48 (12.15 – 18.1)	0.601 (0.502 – 0.767)
W. ascita	177	6.88 (5.65 – 8.8)	12.59 (10.35 – 15.4)	0.544 (0.485 – 0.603)
W. ampla	454	11.26 (7.5 – 14.9)	18.19 (11.3 – 21.2)	0.619 (0.505 – 0.749)

Taxon	Number of Adults Measured	Mean and Range of: Whorls	Umbilical Width	D/U Ratio
W. woodwardi (Fulton)	791	5¼ (4⅜ – 6)	closed	–
W. commoda (Iredale)	883	5⅛ (4½ – 6)	1.38 (0.4 – 2.6)	14.0 (6.18 – 50)
W. turbinata	930	5⅛ – (4⅜ – 5⅞)	1.42 (0.55 – 2.5)	10.0 (5.30 – 25.1)
W. inopinata	278	4¾ – (4⅛ – 5½)	1.51 (0.8 – 2.4)	10.0 (6.00 – 19.4)
W. f. complanata	843	4⅞ + (4 – – 5¾)	1.53 (0.6 – 2.65)	11.3 (6.52 – 27.4)
W. f. froggatti (Ancey)	283	4⅝ + (4 – – 5½ –)	1.34 (0.5 – 2.35)	11.5 (6.15 – 27.3)
W. derbyi (Cox)	568	5 – (4⅛ – – 5⅝)	1.30 (0.5 – 2.25)	11.4 (5.33 – 32)
W. alterna (Iredale)	370	5⅛ (4½ – 5⅝)	1.23 (0.45 – 2.25)	12.2 (6.36 – 29.7)
W. oscarensis (Cox)	184	5⅜ – (4⅝ – 6)	(18.8% closed; 81.2% narrowly open)	
W. cunicula	272	5⅛ (4⅜ – 5⅝)	1.09 (0.5 – 1.8)	14.5 (7.05 – 35)
W. subtila	82	5⅛ – (4¾ – 5½)	0.86 (0.45 – 1.45)	18.5 (9.73 – 32)

Table 47: Range of Variation in *Westraltrachia* (continued)

Taxon	Number of Adults Measured	Mean and Range of: Whorls	Umbilical Width	D/U Ratio
W. instita	289	4¾ – (4¼ + – 5½ –)	1.60 (0.8 – 2.6)	8.73 (5.10 – 16.9)
W. lievreana	377	4¾ + (4¼ – 5⅝ –)	1.21 (0.35 – 2.0)	12.4 (6.87 – 47)
W. tropida	400	5 – (4½ – 5⅝)	(48.5% open; 51.5% cracked)	
W. porcata	43	5⅛ – (4⅞ – 5½ +)	(53.5% open; 37.2% cracked; 9.3% closed)	
W. rotunda	1,562	4⅝ + (4 – 5¼ +)	(23.8% open; 75.3% cracked; 0.9% closed)	
W. limbana	512	5 + (4½ – 5⅞ +)	(34.5% open; 63.0% cracked; 2.5% closed)	
W. recta	121	4⅞ (4¼ – – 5¼ +)	(10.5% open; 69.3% cracked; 21.2% closed)	
W. pillarana	368	5 (4½ – – 5⅝ –)	1.04 (0.3 – 1.8)	15.8 (7.43 – 48)
W. ascita	177	4⅞ + (4⅜ – 5½)	1.40 (0.8 – 2.0)	9.30 (6.11 – 16.9)
W. ampla	454	5⅛ + (4½ + – 5¾ –)	(84.0% open; 16.0% cracked)	

Species accounts

Shell variation is extensive, and many species were recognised as being distinct only after dissection. Preparation of a key including genital, jaw and radular features would provide the best means of species identification, but empty shells could not be keyed out, and few people have the needed skills or time to dissect snails, and most lack access to SEM equipment for routine studies. Thus an artificial key to adult shells has been developed, with geography used as an important factor in moving from couplet to couplet. The key will not work for specimens that are worn to the point that colour has been lost, and samples of 10 or more specimens, for which averaged dimensions are available, will key out more easily and accurately.

It must be emphasised that there probably are additional species in the Oscar Ranges, and possibly from the East Kimberley. Material from new localities may not key out.

KEY TO THE SPECIES OF *WESTRALTRACHIA*

1. Shell with periostracal microprojections **(Plate 25)** when fresh, reduced to pustules when worn 2
   Shell without periostracal projections or dense pustules 4

2. Shell sharply keeled; spire whorls flat; west of Windjana Gorge, Napier Range 3
   Shell at most obtusely angulated; spire whorls strongly rounded; Virgin Hills to Laidlaw Range .... *Westraltrachia ascita* sp. nov.

3. Shell smaller, mean diameter under 15 mm; west bank Windjana Gorge to 5 km west, Napier Range .... *Westraltrachia f. froggatti* (Ancey, 1898)
   Shell larger, mean diameter over 16 mm; Yammera Gap up to 5 km west of Windjana Gorge, Napier Range *Westraltrachia f. complanata* subsp. nov.

4. Body whorl shell colour white when fresh; west of Yammera Gap, Napier Range 5
   Body whorl shell colour yellow-brown to brown, at most a white peripheral zone 6

5. Shell umbilicus closed; west of Barker Gorge, Napier Range .... *Westraltrachia woodwardi* (Fulton, 1902)
   Shell umbilicus a narrow lateral crack; Barker Gorge east almost to Yammera Gap, Napier Range .... *Westraltrachia commoda* (Iredale, 1939)

6. Fresh specimens without white peripheral colour zone; base white, rest of shell almost monochrome to monochrome 7
   Fresh specimens with a white peripheral colour zone; spire variegated; brown zones above and below white periphery; base of shell white 9

7. Within 10 km east or west of Yammera Gap, Napier Range 8
   Oscar Ranges .... *Westraltrachia rotunda* sp. nov.

8. Spire strongly elevated **(Fig. 119b)** .... *Westraltrachia turbinata* sp. nov.
   Spire normally elevated **(Fig. 119e)** .... *Westraltrachia inopinata* sp. nov.

9. Mean shell diameter under 13 mm; spire quite high; Limestone Billy Hills, east of Fitzroy Crossing .... *Westraltrachia recta* sp. nov.
   Mean shell diameter normally well over 13 mm 10

10. Shell periphery of adult acutely angulated 11
    Shell periphery of adult obtusely angulated or rounded 12

11. Umbilicus moderately open **(Fig. 141c)**; near Mount Wynne Creek, Oscar Ranges .... *Westraltrachia instita* sp. nov.
    Umbilicus nearly closed **(Fig. 141e)**; near Twelve Mile Bore, Oscar Ranges .... *Westraltrachia tropida* sp. nov.

12. Shell nearly 18 mm in mean diameter 13
    Shell less than 16.5 mm in mean diameter 14

13. Western Oscar and eastern Napier Ranges; colour lighter; shell surface rougher *Westraltrachia oscarensis* (Cox, 1892)
    Emanuel to Lawford Ranges, east of Fitzroy Crossing; colour nearly typical; shell surface smoother .... *Westraltrachia ampla* sp. nov.

14. Shell strongly elevated **(Fig. 143e)**, mean H/D ratio about 0.700; mean diameter over 16 mm .... *Westraltrachia porcata* sp. nov.
Shell not strongly elevated, mean H/D ratio under 0.625; mean diameter under 15.5 mm 15

15. East Kimberley, Pillara and Home Ranges, Virgin Hills, east of Fitzroy Crossing .... *Westraltrachia pillarana* sp. nov.
Napier or Oscar Ranges, west of Fitzroy Crossing 16

16. Oscar Ranges 17
Napier Ranges 19

17. Shell colour near monochrome above and below white peripheral zone; umbilicus moderately open **(Fig. 143c)**; north-west of Linesman Creek .... *Westraltrachia lievreana* sp. nov.
Shell colour variegated on spire; umbilicus narrowly open or a lateral crack **(Figs 138e, 146e)** 18

18. West of Mount Wynne Creek; umbilicus narrowly open **(Fig. 138e)** .... *Westraltrachia subtila* sp. nov.
Two Mile Bore, Oscar Range to Fitzroy Crossing; umbilicus a lateral crack **(Fig. 146e)** .... *Westraltrachia limbana* sp. nov.

19. Basal lip of shell with a moderate to prominent node **(Figs 133b, e)** .... *Westraltrachia alterna* Iredale, 1939
Basal lip of shell without a prominent node 20

20. Windjana Gorge to 15 km east .... *Westraltrachia derbyi* (Cox, 1892)
Tunnel Creek area, few km west to eastern end of Napiers .... *Westraltrachia cunicula* sp. nov.

The initial reference of these species was to the genus *Trachia* Albers, 1860, now restricted to use for taxa from India, Ceylon, Burma, Malaya, Mergui Islands, and Sumatra. The name *Westraltrachia* was a recognition of conchological similarity and that the included species were found in Western Australia.

The sequence of species is from north-west to south-east.

WESTRALTRACHIA WOODWARDI (FULTON, 1902)

(Plates 19a-c, 26a-b, 33, 34; Figs 111-114)

Thersites (Rhagada) woodwardi Fulton, 1902, Proc. Malac. Soc. London, **5**(1): 33, text fig. – N. W. Australia.

Parrhagada woodwardi (Fulton, 1902), Iredale, 1938, Australian Zool., **9**(2): 114; Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 63-64, pl. IV, fig. 18 – 'On trees off the Limestone Caves,' north end of the Napier Range (H. Basedow).

Parrhagada sedula Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 64, pl. IV, fig. 20 – "in rocks" at Limestone Caves, north end of Napier Range.

Parrhagada detecta Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 64, pl. IV, fig. 22 – Barker River Gorge, Mid Napier Range (Herbert Basedow).

Nomenclature and type localities

The type specimens of *Westraltrachia woodwardi* (Fulton, 1902) are large and white in colour, closely matching material from both Sta. WA-717 near the north-west corner of the Napier Range (**Table 48**) and the specimens taken near Barker Gorge on several occasions. There is no point in restricting the type locality other than to the north end of the Napier Range. This is the same type locality cited for *Amplirhagada percita* (Iredale, 1939) by Solem (1981a: 211, 218) and is based on the supposition that the types of *W. woodwardi* also were collected by Basedow.

The species described by Iredale (1939: 64) are subjective synonyms. The holotype of *Parrhagada sedula* Iredale, 1939, is a dwarf shell (**Figs 111d-f**) collected during Basedow's visit to the north-west corner of the Napier Range. Size and shape variation in other specimens from the same population (AM C.42211, AM C.64910, **Table 48**) is much larger, approaching the material described by Woodward. Samples from near Barnet Cave (Sta. WA-716) taken in 1980 are even smaller in size, representing a dwarf population. The type lot of *Parrhagada detecta* Iredale, 1939 (AM C.42210, AM C.64870) shows standard size and shape variation (**Table 48**) and the holotype (**Figs 111g-i**) compares quite well with the figured paratype of *W. woodwardi* (**Figs 111a-c**). The types of *detecta* undoubtedly were collected on the west side of Barker Gorge, but material from neither Sta. WA-354 nor WA-355 (**Table 48**) match the size and shape range of the types. Thus, a precise Barker Gorge type locality is not designated.

Comparative remarks

Westraltrachia woodwardi (Fulton, 1902) is recognisable by its closed umbilicus with a smooth covering callus (**Figs 111c, f, i**), white colour with only rarely a faint brownish cast on spire and penultimate whorl, strongly expanded lip (**Figs 111a, d, g**), large diameter (mean 19.71 mm), high whorl count (mean 5-1/4), relatively high spire (mean H/D ratio 0.666), and range west of the Barker River. *Westraltrachia commoda* (Iredale, 1939), which ranges from the east bank of the Barker River to near Yammera Gap, has the umbilicus narrowly open (**Figs 115c, f**), and generally is smaller (mean diameter 17.47 mm), and lower (mean H/D ratio 0.628), although showing considerable overlap in dimensions. Other large *Westraltrachia,* such as *W. oscarensis* (Cox, 1892) from the Oscar Ranges and *W. ampla,* from the Laidlaw, Lawford and Emanuel Ranges, have strong colour patterns, are less elevated, have the umbilicus open or cracked, and show much less lip expansion. *Amplirhagada percita* (Iredale, 1939) and *A. napierana* Solem, 1981, are sympatric with *W. woodwardi* at different places throughout its range. Both species of *Amplirhagada* tend to seal themselves to a rock, log or another shell, while *W. woodwardi,* except for juveniles, secretes a mucus sheet across the aperture and lies free on the ground surface under the sheltering rocks or logs to which *Amplirhagada* may be sealed. Adult specimens of the two genera are relatively easily distinguished. The smoothly sealed umbilicus and strongly expanded lip of *W. woodwardi* (**Figs 111a, c-d, f-g, i**) contrast with the light brown colour, open umbilicus, and much less strongly reflected lip of *A. percita* (Solem, 1981a: 219, **Figs 47a, c, e, g**). *Amplirhagada napierana* is much more similar to *W. woodwardi,* sharing white colour and a closed umbilicus, but has the lip less reflected (Solem, 1981a: 226, **Figs 48a-b**) and the periphery in the adult always rounded. Juvenile and subadult specimens of both *Amplirhagada* are most easily separated by the presence of radial apical sculpture and more flatly rounded spire whorls, compared with the smooth

Table 48: Local Variation in *Westraltrachia woodwardi* (Fulton, 1902)

Locality	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
NRII-6, N corner, WAM 301.80, WAM 303.80	9D	11.76 ± 0.246 (10.35 – 12.4)	18.36 ± 0.228 (17.4 – 19.4)	0.640 ± 0.009 (0.595 – 0.674)	5⅛ + (5 – – 5⅜ +)
WA-717, 2.1 km S of N end, FMNH 205352-3	7 (2L, 5D)	13.99 ± 0.546 (11.7 – 15.9)	20.14 ± 0.474 (18.1 – 21.7)	0.693 ± 0.013 (0.646 – 0.743)	5⅜ (5 – – 5⅝)
NR-VII, WAM 892.76, WAM 959.76	6D	11.32 ± 0.538 (9.7 – 12.95)	17.51 ± 0.415 (16.0 – 18.8)	0.645 ± 0.019 (0.567 – 0.689)	5 (4¾ – 5¼)
WA-300, FMNH 199251, 6-XII-1976	19D	12.02 ± 0.185 (10.7 – 13.3)	18.92 ± 0.210 (17.3 – 20.4)	0.635 ± 0.008 (0.569 – 0.688)	5¼ (5 – – 5½ +)
WA-300, FMNH 199212, 30-XII-1976	25D	12.12 ± 0.151 (10.6 – 13.7)	18.84 ± 0.171 (17.1 – 21.1)	0.643 ± 0.006 (0.590 – 0.714)	5¼ + (5 – – 5½ +)
NR-VIII, Barnett Cave, WAM 963.76	3D	10.08 (8.8 – 11.0)	16.65 (15.85 – 17.5)	0.605 (0.555 – 0.663)	4¾ – (4⅜ – 4⅞)
WA-716, near Barnett Cave, FMNH 205345-6	28 (IL, 27D)	9.48 ± 0.115 (8.40 – 10.5)	16.09 ± 0.153 (14.25 – 17.6)	0.589 ± 0.005 (0.540 – 0.640)	4⅝ + (4⅜ – 5)
limestone caves, AM C.64910, AM C.42211	11D	14.45 ± 0.260 (13.0 – 15.45)	21.29 ± 0.245 (20.0 – 22.55)	0.679 ± 0.012 (0.606 – 0.757)	5½ (5¼ – 5¾)
NR-IX, nr. Barnett Cave, WAM 893.76, WAM 896.76	10D	10.76 ± 0.331 (9.5 – 12.7)	17.22 ± 0.466 (15.0 – 20.05)	0.624 ± 0.006 (0.598 – 0.665)	4⅞ – (4⅜ – – 5¼)
NR-IXb, S of Barnett, WAM 894.76	5	14.33 ± 0.273 (13.6 – 15.1)	21.45 ± 0.477 (20.4 – 23.1)	0.669 ± 0.009 (0.639 – 0.693)	5⅝ – (5⅜ – – 5¾)
NR-V, WAM 890.76 and NR-VI, WAM 891.76	9D	11.31 ± 0.297 (10.15 – 13.3)	17.58 ± 0.308 (15.9 – 19.0)	0.644 ± 0.014 (0.600 – 0.739)	5 (4¾ + – 5⅛)
WA-715, FMNH 205343	15L	13.76 ± 0.213 (12.3 – 15.35)	20.76 ± 0.187 (18.9 – 22.1)	0.663 ± 0.008 (0.618 – 0.734)	5¼ (5 – – 5⅝)
NR-IV, WAM 965.76	13D	10.84 ± 0.114 (10.05 – 11.4)	17.90 ± 0.209 (16.4 – 19.0)	0.606 ± 0.006 (0.563 – 0.646)	4⅞ (4⅝ – 5 +)
NRII-15, Wagon Pass, WAM 1205.76	55D	14.07 ± 0.123 (12.4 – 16.6)	20.80 ± 0.135 (18.9 – 22.8)	0.677 ± 0.005 (0.593 – 0.763)	5⅜ + (5 – 5⅞)
NRII-16, Wagon Pass, WAM 1206.76	17D	14.33 ± 0.226 (12.7 – 16.35)	21.19 ± 0.269 (19.5 – 24.1)	0.676 ± 0.007 (0.629 – 0.731)	5½ (5¼ – 5⅞ –)
NRII-17, Wagon Pass, WAM 1204.76	30D	14.62 ± 0.235 (12.8 – 18.3)	21.34 ± 0.219 (19.0 – 24.5)	0.685 ± 0.009 (0.615 – 0.802)	5⅜ – (5⅛ – 5¾ +)
WA-714, Wagon Pass, FMNH 205325	8L	14.60 ± 0.278 (13.45 – 15.4)	20.56 ± 0.234 (19.6 – 21.4)	0.704 ± 0.009 (0.677 – 0.742)	5⅜ – (5⅛ – 5⅝)

Table 48: Local Variation in *Westraltrachia woodwardi* (Fulton, 1902) (continued)

Locality	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio	Whorls
NRII-18, 5 km SE Wagon Pass, WAM 1207.76	14D	15.40 ± 0.268 (13.9 – 17.5)	21.60 ± 0.260 (20.4 – 23.3)	0.713 ± 0.012 (0.650 – 0.782)	5½ – (5¼ – – 5¾)
WA-322, FMNH 199331	40D	12.89 ± 0.185 (10.7 – 16.0)	19.88 ± 0.172 (17.4 – 22.7)	0.648 ± 0.006 (0.581 – 0.729)	5¼ (4¾ + – 5⅞ –)
WA-321, FMNH 200139	4L	11.85 ± 0.380 (11.1 – 12.6)	17.45 ± 0.491 (16.6 – 18.3)	0.681 ± 0.027 (0.617 – 0.747)	5 + (5 – – 5⅛ +)
WA-321, FMNH 199311	21D	11.79 ± 0.214 (10.0 – 13.2)	17.97 ± 0.193 16.2 – 19.2)	0.655 ± 0.008 (0.592 – 0.759)	5⅛ – (4¾ – – 5¼ +)
Old Napier Downs Cave, WAM 305.80	6D	12.48 ± 0.424 (11.5 – 14.45)	17.61 ± 0.387 (15.8 – 18.4)	0.709 ± 0.023 (0.658 – 0.812)	5⅛ + (4⅞ – – 5⅜)
NRII-5a, 9 km W of Barker Gorge, WAM 1208.76	19D	15.95 ± 0.235 (13.8 – 17.8)	22.08 ± 0.484 (19.7 – 24.45)	0.723 ± 0.007 (0.671 – 0.773)	5⅜ + (5 – 5¾)
WA-192, Chedda Cliffs, FMNH 199863	8L	12.90 ± 0.411 (11.3 – 15.1)	19.26 ± 0.386 (17.7 – 20.9)	0.669 ± 0.014 (0.611 – 0.729)	5¼ – (5 + – 5½ –)
WA-192, Chedda Cliffs, FMNH 199417	102D	12.21 ± 0.102 (9.65 – 14.6)	18.42 ± 0.088 (16.5 – 21.4)	0.662 ± 0.004 (0.555 – 0.741)	5⅛ + (4⅝ + – 5⅜ +)
WA-324, 7.1 km W of Barker Gorge, FMNH 200770	5L	13.06 ± 0.269 (12.5 – 13.9)	19.68 ± 0.344 (18.7 – 20.6)	0.664 ± 0.016 (0.616 – 0.713)	5¼ – (5⅛ – – 5⅜ –)
WA-324, FMNH 199086	17D	13.74 ± 0.170 (12.3 – 14.8)	20.24 ± 0.290 (18.3 – 22.4)	0.679 ± 0.006 (0.643 – 0.733)	5¼ + (5⅛ – – 5¾ +)
WA-320, 4.7 km W of Barker Gorge, FMNH 200046	14L	14.01 ± 0.254 (12.5 – 15.8)	20.67 ± 0.250 (18.8 – 21.9)	0.677 ± 0.008 (0.626 – 0.742)	5⅜ – (5⅛ + – 5½ –)
WA-320, FMNH 199343	35D	13.43 ± 0.148 (11.8 – 15.6)	20.83 ± 0.166 (19.0 – 23.2)	0.644 ± 0.006 (0.578 – 0.771)	5¼ (4⅞ + – 5½ –)
WA-312, 3.2 km W of Barker Gorge, FMNH 200187	30L	12.96 ± 0.177 (11.0 – 15.1)	19.16 ± 0.238 (16.2 – 21.9)	0.677 ± 0.006 (0.612 – 0.776)	5¼ + (5 – – 5¾ –)
WA-312, FMNH 199339	38D	13.13 ± 0.167 (11.0 – 14.6)	19.59 ± 0.208 (16.5 – 22.0)	0.670 ± 0.005 (0.579 – 0.716)	5⅜ – (5 – – 5⅝ +)
WA-355, Barker Gorge, FMNH 199107	39D	14.36 ± 0.144 (12.9 – 16.4)	21.19 ± 0.190 (18.6 – 23.7)	0.678 ± 0.004 (0.617 – 0.726)	5⅜ + (5⅛ + – 6 –)
WA-354, Barker Gorge, FMNH 200297	9L	14.39 ± 0.391 (12.6 – 15.8)	21.42 ± 0.215 (20.5 – 22.7)	0.671 ± 0.014 (0.615 – 0.730)	5⅜ + (5¼ + – 5⅝ –)
WA-354, FMNH 199109	40D	14.35 ± 0.149 (12.0 – 16.5)	21.45 ± 0.176 (18.1 – 23.4)	0.670 ± 0.006 (0.593 – 0.772)	5⅜ + (5 – – 5¾ +)
Barker Gorge, Types of *detecta*, AM C.42210, AM C.64870	22D	13.75 ± 0.242 (11.3 – 15.6)	19.70 ± 0.205 (18.1 – 21.9)	0.697 ± 0.009 (0.624 – 0.776)	5⅜ – (5 + – 5⅝)

apical whorl surface and much more strongly rounded whorls of *Westraltrachia* (**Plate 51**). Juvenile specimens of *W. woodwardi* also have the periphery of the shell strongly angulated, while it is usually, at most, weakly angulated in *Amplirhagada* of comparable size. Anatomically, *W. woodwardi* shows the following differences from *W. commoda*. The vagina (V) of the former is longer (compare **Figs 112, 114a, c** with **Fig. 116a**), the spermatheca (S) is nearly equal in length to the free oviduct (UV) instead of being distinctly shorter (compare **Figs 112, 114a, c** with **Fig. 116a**), the penis muscle (PM) is far more massive (**Figs 113a-c** with **Fig. 116c**), and the main pilaster (PT) within the penis proper is much larger in *W. woodwardi* (**Fig. 113c**) than in *W. commoda* (**Fig. 158a**).

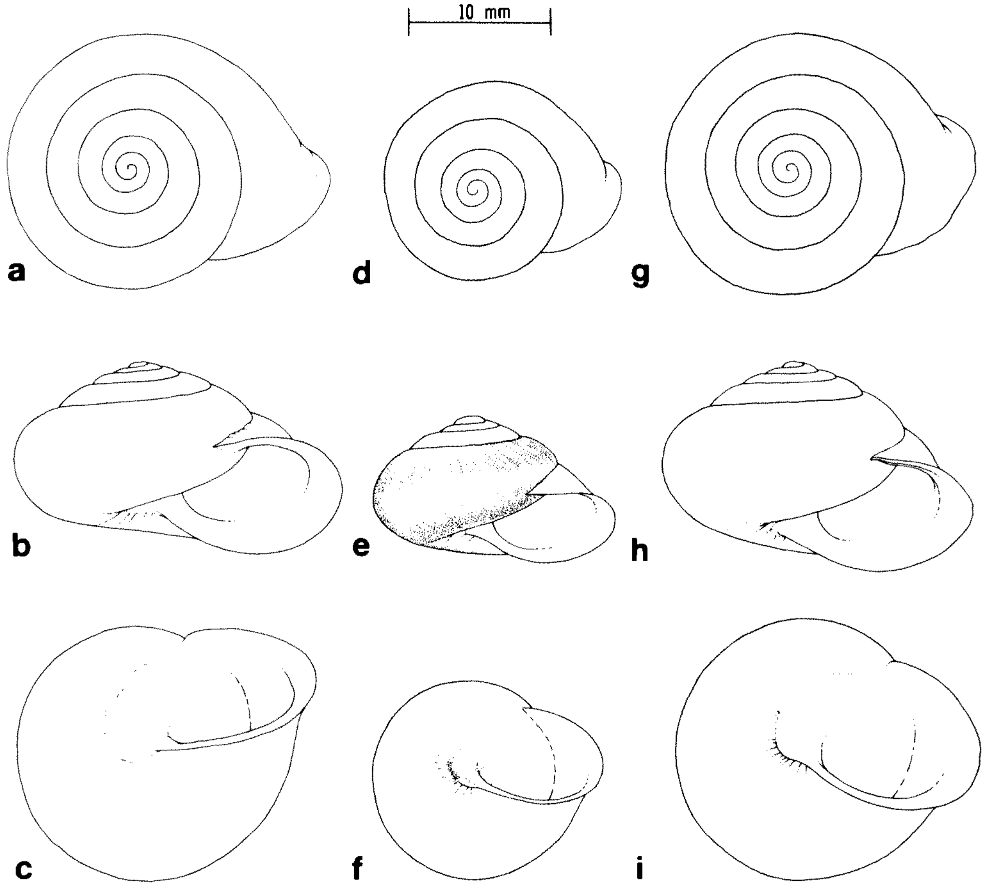


Fig. 111: Shells of *Westraltrachia woodwardi* (Fulton, 1902): (a-c) paratype of *W. woodwardi*, FMNH 41630; (d-f) holotype of *Parrhagada sedula* Iredale, 1939, AM C.64869; (g-i) holotype of *Parraghada detecta* Iredale, 1939, AM C.64870. Scale line equals 10 mm. Drawings by Elizabeth Leibman.

Holotype of *Thersites woodwardi* Fulton, 1902

BM(NH) 1902.5.28.19, N. W. Australia. Type locality here restricted to north end of Napier Range, opposite Hawkstone Creek (1:100,000 'Lennard' map sheet 3863, between grid references 653:096 and 680:153). Height of shell 14.8 mm, diameter 21.3 mm, H/D ratio 0.695, whorls 5½ – , umbilicus closed.

Paratypes of *Thersites woodwardi* Fulton, 1902

WAM 221.80, WAM 222.80, AM C.64971, FMNH 41630, 4 dead adults from the type lot.

Holotype of *Parrhagada sedula* Iredale, 1939

AM C.64869, "in rocks at Limestone Caves;" north end of Napier Range. Collected by H. Basedow. Height of shell 11.1 mm, diameter 16.9 mm, H/D ratio 0.669, whorls 5 + , umbilicus closed.

Holotype of *Parrhagada detecta* Iredale, 1939

AM C.64870, Barker River Gorge, Mid Napier Range. Type locality here restricted to cliffs along east side of Barker Gorge. Collected by H. Basedow. Height of shell 15.25 mm, diameter 21.7 mm, H/D ratio 0.703, whorls 5⅝, umbilicus closed.

Paratopotypes of *Parrhagada detecta* Iredale, 1939

AM C.42210, WAM 65.40, FMNH 198995, 26 dead adults from the type locality.

Measured adults

Napier Range, geographic sequence north-west to south-east: NR II – 6, near north corner Napier Range at junction with Van Emmerick Range (9 dead adults, WAM 301.80, WAM 303.80); Sta. WA-717, 2.1 km south of Hawkstone Creek Crossing, 1 km in from track, north end Napier Range ('Lennard' 3863 – 674:147) (2 live, 6 dead adults, WAM 75.80, FMNH 205352-3); NR VII, north side of gully, north of Barnet Cave ('Lennard' 3863 – *ca.* 674:119) (6 dead adults, WAM 892.76, WAM 959.76); Sta. WA-300, cliffs at north-west end, west of Van Emmerick (= Patterson) Range, 18.3 km from Red Bull Bore ('Lennard' 3863 – 660:110) (1 live, 44 dead adults, WAM 802.79, WAM 803.79, FMNH 199212, FMNH 199251, FMNH 199943); NR VIII, north side of embayment, north entrance to Barnet Cave ('Lennard' 3863 – 653:098) (3 dead adults, WAM 963.76); Sta. WA-716, north-west section of Napier Range, near Barnet Cave ('Lennard' 3863 – *ca.* 652:098) (1 live, 27 dead adults, WAM 74.80, FMNH 205345-6); on trees off limestone caves, north end Napier Range (11 dead adults, AM C.64910); NR IXb just south of NR IX near Barnet Cave (15 dead adults, WAM 893.76, WAM 894.76, WAM 896.76); NR VI, north-west of Sta. NR V, north-west of Stumpy's Well ('Lennard' 3863 – 695:082) (9 dead adults, WAM 891.76); Sta. WA-715, 7.6 km north of Original Napier Downs Homestead, north Napier Range ('Lennard' 3863 – *ca.* 707:064) (15 live adults, WAM 73.80, FMNH 205343); NR V, bluff north-west of Stumpy's Well ('Lennard' 3863 – 708:057) (5 dead adults, WAM 890.76); 5 km north of original Napier Downs Homestead (1 dead adult, WAM 307.80); NR IV, *ca.* 4.5 km north of Original Napier Downs Homestead ruins ('Lennard' 3863 – *ca.* 702:045) (13 dead adults, WAM 965.76); NR II, north-east corner of Wagon Pass ('Lennard' 3863 – *ca.* 723:005) (2 dead adults, WAM 889.76); Station Creek, near

Original Napier Downs Homestead (3 dead adults, WAM 898.76); NR II-15, *ca.* 4 km north-east of east end Wagon Pass (55 dead adults, WAM 1205.76); NR II-16, *ca.* 2 km east of east entrance to Wagon Pass, north side (1:250,000 'Lennard River' SE 51-8 – 244:838) (17 dead adults, WAM 1206.76); NR II-17, north-east corner of Wagon Pass, limestone cliff facing south-east ('Lennard River' SE 51-8 – 242:8375) (30 dead adults, WAM 1204.76); Sta. WA-714, 2.1 km into south side Wagon Pass, north Napier Range, east of Derby ('Lennard' 3863 – 730:001) (8 live, 3 dead adults, WAM 72.80, FMNH 205316, FMNH 205325); NR II-18, *ca.*3 km south-east of east entrance to Wagon Pass ('Lennard River' SE 51-8 – 245:836) (14 dead adults, WAM 1207.76); Sta. WA-322, 0.6 km east of road along south side Napier Range, 3.0 km south-east Original Napier Downs Homestead ('Lennard' 3863 – 719:985) (3 live, 40 dead adults, WAM 807.79, FMNH 199331, FMNH 200144); Sta. WA-321, 12.7 km west of Barker Gorge, south side Napier Range ('Lennard' 3863 – 719:955) (4 live, 24 dead adults, WAM 804.79, FMNH 199311, FMNH 200139, FMNH 200502-3); near Old Napier Downs Cave (6 dead adults, WAM 305.80); NR II-5a, dry waterfall, *ca.* 9 km north-west of Barker Gorge ('Lennard River' SE 51-8 – 242:831) (19 dead adults, WAM 1208.76); Sta. WA-192, near Chedda Cliffs, 9.1 km from Barker River Gorge bank, south-west side Napier Range, just west of large cave ('Lennard' 3863 – 757:945) (22 live, 102 dead adults, WAM 67.80, WAM 808.79, FMNH 199417, FMNH 199863); Sta. WA-324, 7.1 km west of Barker Gorge, south side Napier Range ('Lennard' 3863 – 765:935) (5 live, 18 dead adults, WAM 809.79, WAM 810.79, FMNH 199086, FMNH 200770, FMNH 201506); Sta. WA-320, 4.7 km west of Barker Gorge, south side Napier Range ('Lennard' 3863 – 788:921) (14 live, 35 dead adults, WAM 811.79, WAM 812.79, FMNH 199343, FMNH 200046); Sta. WA-312, crevices in rock walls, under rocks, 3.2 km west of Barker Gorge, south side Napier Range ('Lennard' 3863 – 808:914) (44 live, 38 dead adults, WAM 70.80, WAM 813.79, WAM 814.79, FMNH 199339, FMNH 200673, FMNH 200187, FMNH 200194); Sta. WA-355, cliff base north of Barker Gorge, 1.4 km west of Barker River, north side Napier Range ('Lennard' 3863 – 829:928) (7 live, 39 dead adults, WAM 4.80, WAM 5.80, FMNH 199107, FMNH 200291); Sta. WA-354, north-west side Barker Gorge, 0.7 km south Barker River ford, north side Napier Range ('Lennard' 3863 – 832:913) (9 live, 40 dead adults, WAM 6.80, FMNH 199109, FMNH 200297); Barker Gorge. "Kaularre" (22 dead adults, AM C.42210, AM C.64870).

Distribution limits in Napier Range

Westraltrachia woodwardi has an uninterrupted distribution from the west bank of Barker Gorge north-west to the end of limestone outcrops near Hawkstone Creek and the Van Emmerick Range, about 32.5 km along the curve of the Napier Range.

Diagnosis

Shell very large, 14.25-24.5 mm (mean 19.71 mm) in diameter, with 4⅞ to 6 (mean 5¼) normally coiled whorls. Apex and spire strongly and almost evenly elevated, height of shell 8.4-18.3 mm (mean 13.16 mm), H/D ratio 0.540-0.812 (mean 0.666). Apical whorls with at most vague micro-ridges in the sutures **(Plate 19a).** Postnuclear whorls macroscopically smooth, occasional irregular radial growth wrinkles visible, microsculpture of faint spiral lines **(Plate 19b-c).** Shell periphery rounded **(Figs 111b, e, h)** except for smaller adults that will have a noticeable obtuse angulation on first part of

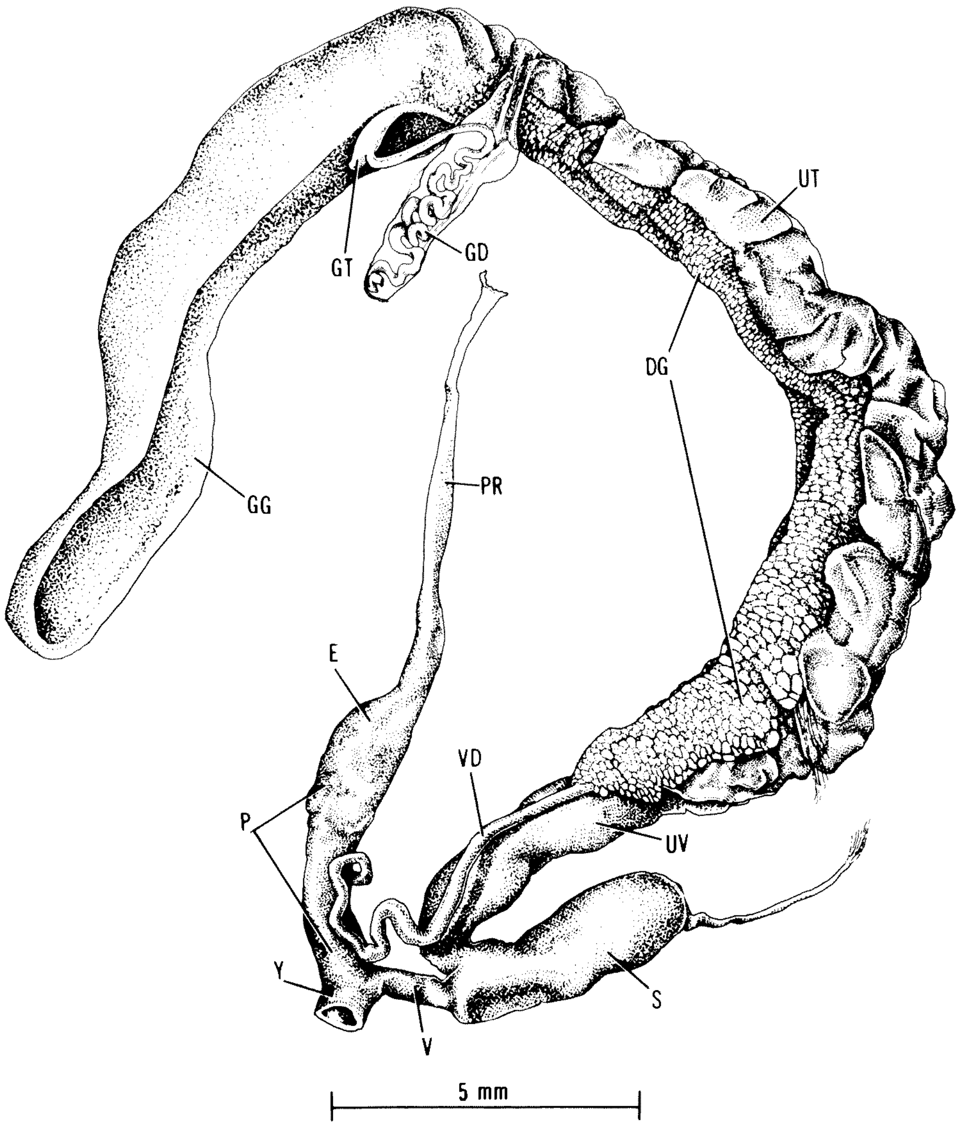


Fig. 112: Whole genitalia of *Westraltrachia woodwardi* (Fulton, 1902): Sta. WA-312, 3.2 km west of Barker Gorge, Napier Range, 12 December 1976, FMNH 200187. Scale line equals 5 mm. Drawing by Linnea Lahlum.

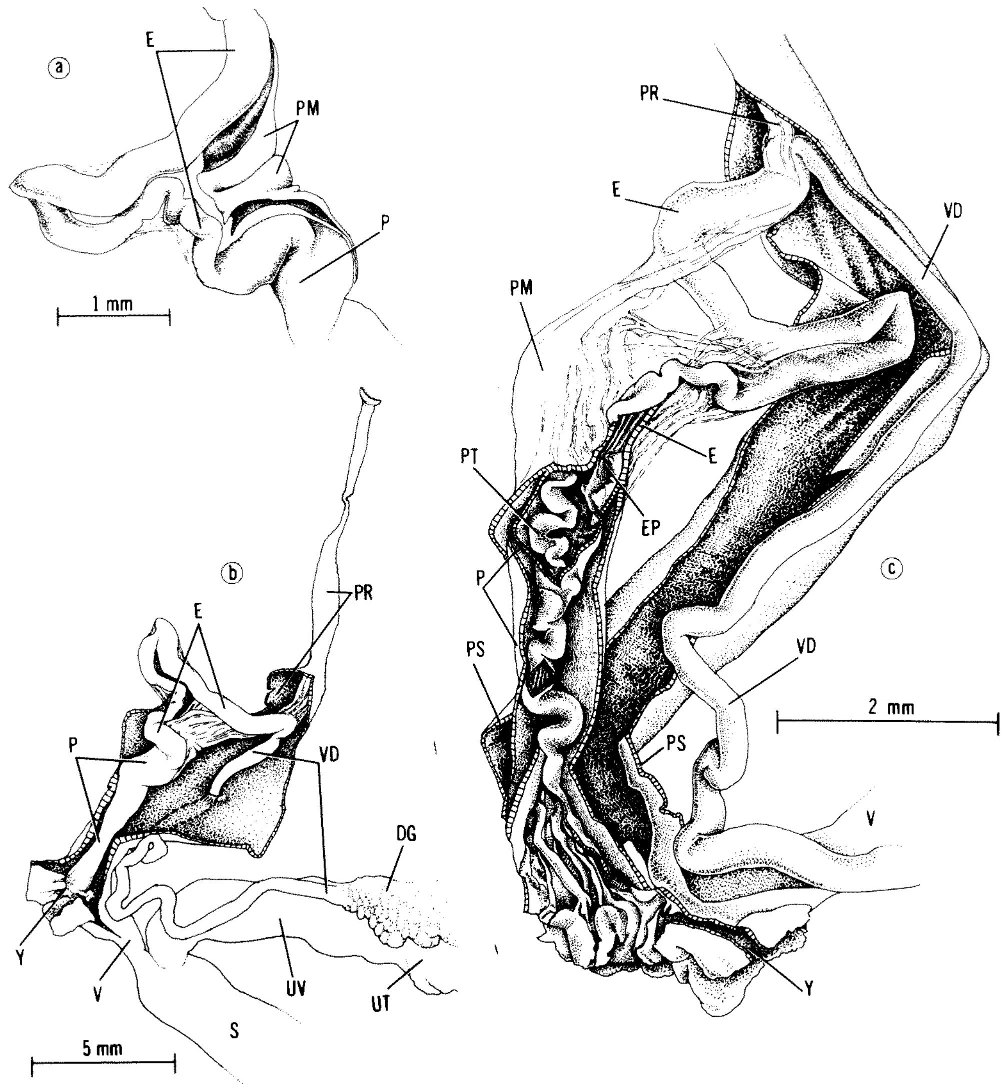


Fig. 113: Genitalia of *Westraltrachia woodwardi* (Fulton, 1902): Sta. WA-312, 3.2 km west of Barker Gorge, Napier Range, 12 December 1976, FMNH 200187, (a) detail of penis muscle attachments (PM), Dissection A, (b) interior of penis sheath, Dissection A, (c) interior of penis, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

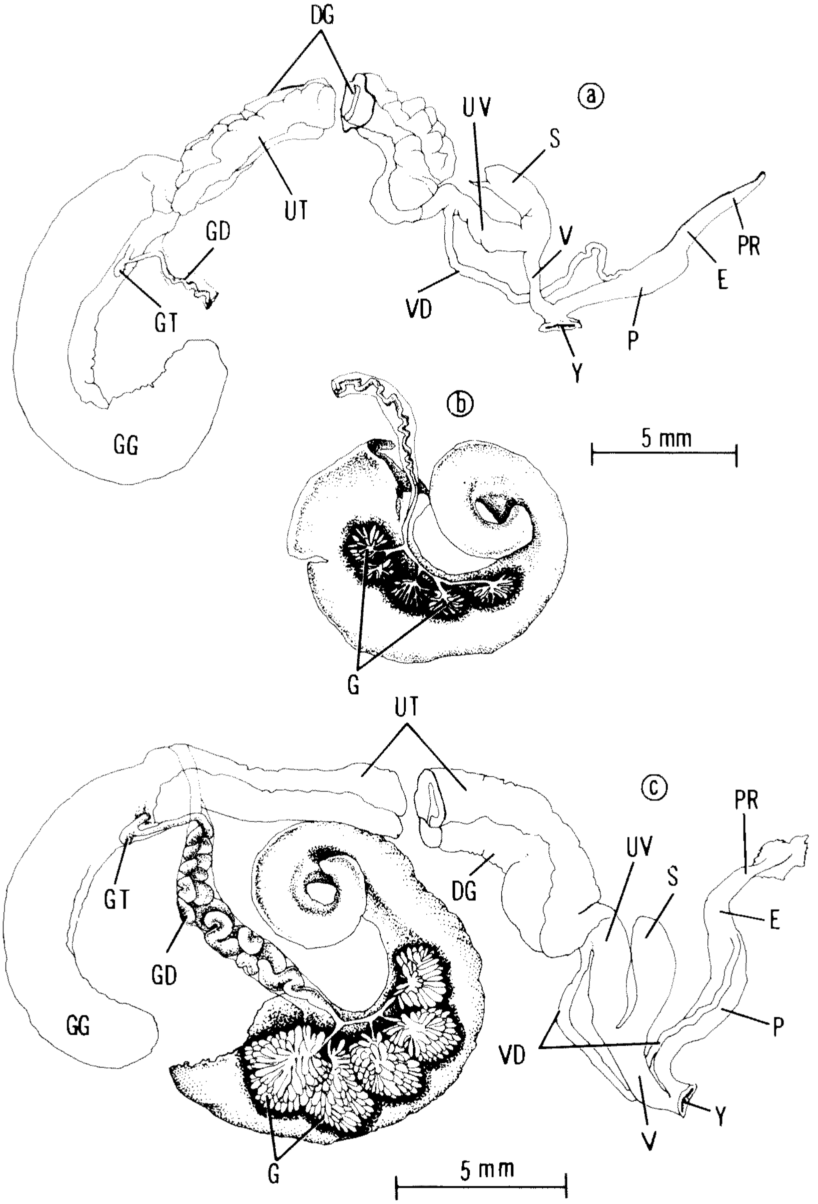


Fig. 114: Genitalia of *Westraltrachia woodwardi* (Fulton, 1902): (a-b) Sta. WA-192, near Chedda Cliffs, 9.1 km west of Barker River Gorge, south side Napier Range, 9 October 1976, FMNH 199863, Dissection A, (a) genitalia in inactive phase, (b) ovotestis in inactive phase; (c) specimen collected on same date, but kept aestivating in a sealed box on a laboratory shelf until 25 February 1977, hyper-male active phase. Scale lines equal 5 mm. Drawings by Linnea Lahlum.

body whorl. Lip strongly expanded and reflected **(Figs 111a-b, d-e, g-h)**, body whorl weakly **(Figs 111b, h)** to moderately **(Fig. 111e)** descending behind lip. Umbilicus completely closed by reflection of basal lip and secretion of a smooth callus, very rarely (Stations WA-354, WA-355) a few individuals with a slight lateral crack. Colour usually white over entire shell, sometimes a weak beige to light brown variegated tone visible on mid-to upper spire, some small sized shells in the Barnet Cave to Wagon Gap area (Stations WA-714, WA-715) of sympatry with *Amplirhagada percita* (Iredale, 1939) with light tan variegated colour pattern persisting well onto body whorl, a white peripheral band visible on early part of body whorl. Juveniles often with brownish colour and white peripheral band, periphery strongly angulated to carinated. Based on 791 measured adults.

Genitalia **(Figs 112-114)** with massive penial muscle **(Figs 113a-c, PM)** and large epiphallic loop. Principal penis pilaster **(Fig. 113c, PT)** sinuated and with prominent hardened edges **(Fig. 180c)**, lower portion of penis with weak longitudinal folds and straight ridges. Penis relatively short **(Fig. 113b)**, but not kinked within sheath, relatively large in diameter. Wall of penis sheath thin for entire length **(Fig. 113c, PS)**. Vas deferens **(VD, Fig. 113b)** entering penis sheath opposite base of epiphallus. Vagina **(Figs 112, 114a, V)** normally narrow, relatively long, becoming enlarged in diameter during early stages of mating cycle **(Fig. 114b)**. Spermatheca (S) only slightly shorter than free oviduct **(UV, Fig. 112)**.

Jaw **(Plate 26a-b, 34d)** macroscopically smooth, sometimes with vague vertical undulations, never with distinct vertical ribs, fine horizontal growth striae present. Radular teeth highly modified. Central and laterals unicuspid, mesocone with rounded tip, curved shape and highly elevated. Marginal teeth typical **(Plates 33a-f, 34a-c)**.

Discussion

In size and shape, *Westraltrachia woodwardi* (Fulton, 1902) is the most variable species in the genus, with a 9.9 mm range in shell height and 10.25 mm range in shell diameter **(Table 47)**. The populations that have smaller adult shells simply stopped growing at an earlier whorl count, since those with a mean whorl count of 5⅜ or more were over 20 mm in mean diameter **(Table 48)**. In part there is a geographic basis to the variation, with samples from the high cliffs and thin talus from Barnet Cave north being mostly smaller in size and those from the Wagon Pass area and Barker Gorge, where boulder jumbles and talus piles are more plentiful, averaging larger.

The resemblance to *Amplirhagada napierana* Solem, 1981, alluded to in the Comparative remarks and Diagnosis, is extraordinary. In colour, size, and shape the two species are very close, although the lip expansion, apical sculpture, and spire whorl contour differences **(Plate 51)** enable separation under the microscope. They are the end products of a massive, but gradual, convergence in shell size, shape, and colour (Solem, In press-A). Juveniles are more easily identified from the sharp keel or peripheral angulation found in *Westraltrachia woodwardi,* and the generally slightly darker tone to the juvenile shell. Where *A. percita* (Iredale, 1939) replaces *A. napierana* from Barnet Cave to near Wagon Pass, many *W. woodwardi* retain a darker shell tone, thus approaching more closely the very light-brown tone typical of most *A. percita.*

The two *Amplirhagada* have a different aestivation strategy, sealing to rocks, logs or shells, while *Westraltrachia woodwardi* is a free-sealer lying on the soil surface under rocks or logs, but they are found in the same rock piles in the north-west Napier Range. Annual burning is so intensive in this area that we saw essentially no shelter sites of spinifex clumps or snail-inhabitable rock piles that were away from the main range or a few interior valley pockets. While in other parts of the range of *Westraltrachia,* species such as *W. alterna* on Cycad Hill (Sta. WA-582) can be found in debris under spinifex at a significant distance from the limestone exposures, this habitat has been removed by man within the range of *W. woodwardi.*

Specimens from Station WA-192 collected 9 October 1976 were exposed to the same aestivation experiment as specimens of *Amplirhagada b. burnerensis* (Smith, 1894) (Solem, 1981a: 165, 247). Materials of both species were shipped live to Perth in a closed box containing tied cloth bags. The box was left unopened on a laboratory shelf until late February 1977. Material preserved on the date of collection **(Figs 114a-b)** and those killed and dissected on 25 February 1977 **(Fig. 114c)** show changes identical to those reported for the *Amplirhagada.* Gross enlargement of the ovotestis (G), hermaphroditic duct (GD), and prostate (DG); partial enlargement of the free oviduct (UV) and thickening of the vagina (V); but no detectable change in the albumen gland (GG), talon (GT), organs of the penis complex, or uterus (UT) were found in specimens that had extended aestivation; all these changes indicate that the male system is active and the female system had not been activated. Since late February collected field material had both systems starting to shut down in preparation for the long dry season, this 'super male' development under prolonged aestivation is highly significant.

WESTRALTRACHIA COMMODA (IREDALE, 1939)

(Plates 26c, 35a-b, 51b; Figs 115-116, 158a)

Parrhagada commoda Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 64, pl. IV, fig. 10 – Barker River Gorge, Napier Range (Herbert Basedow).

Parrhagada ferrosa Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 65, pl. IV, fig. 21 – Barker River Gorge, Napier Range (Herbert Basedow).

Nomenclature and type localities

Both of Iredale's species were collected by Herbert Basedow in the Barker River Gorge. The holotype of *Westraltrachia commoda* (Iredale, 1939) is almost the largest example seen of this species **(Figs 115a-c),** while the holotype of *Parrhagada ferrosa* Iredale, 1939 **(Figs 115d-f)** is one of the smallest examples known **(Table 49).** From direct encrustation and wear on the shell surfaces, probably two slightly different localities were involved. The small, red dirt covered shells excavated from a crevice in talus buried under red dust; the larger white shells loose on open ground or newly dead in larger crevices. Other than to state that the east bank of Barker Gorge was the site of collection, no more detailed type locality restriction is possible. Combined measurements of paratypes are presented in **Table 49,** and show only a slight increment in the standard error of the means, suggesting that they may have come from the same populations, allowing for 'trading bias' in distribution of paratypes. The name *commoda* has page priority and thus is used for this species.

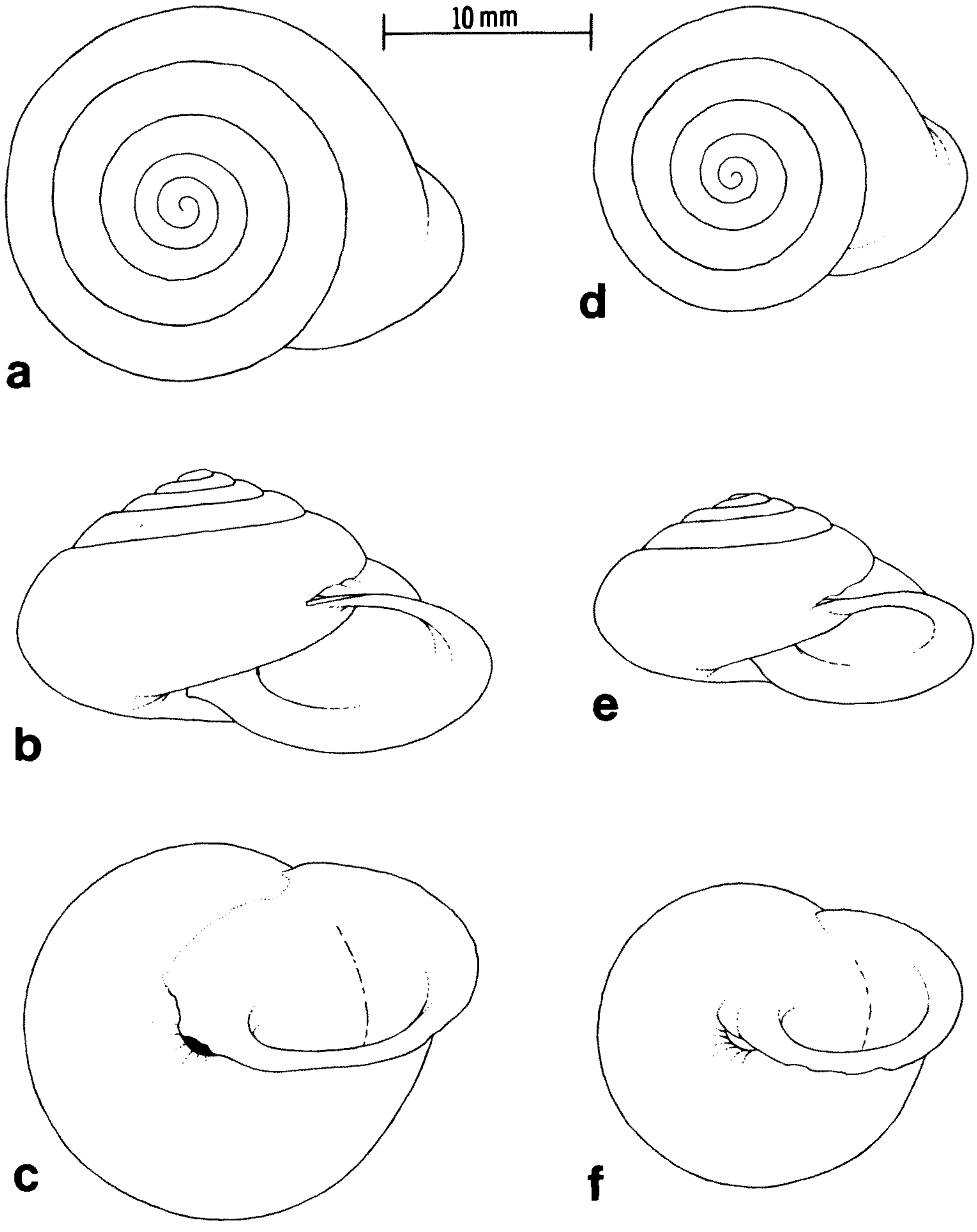


Fig. 115: Shells of *Westraltrachia commoda* (Iredale, 1939): (a-c) holotype of *Parrhagada commoda* Iredale, 1939, AM C.64871; (d-f) holotype of *Parrhagada ferrosa* Iredale, 1939, AM C. 64872. Scale line equals 10 mm. Drawings by Elizabeth Liebman.

Comparative remarks

Westraltrachia commoda (Iredale, 1939) is a slightly smaller, generally lower-spired version of *W. woodwardi* (Fulton, 1902) that has a narrowly open umbilicus **(Table 47).** Most shells are white in colour, but some have a faint yellow-brown tone on the spire. *Westraltrachia turbinata,* the next species to the east, is a distinctly smaller, much more elevated shell **(Table 47)** with a proportionately more open umbilicus **(Figs 117a-c).** *Westraltrachia inopinata* from just east of Yammera Gap, is very similar in shape to *W. commoda,* but is smaller **(Table 47),** has a less expanded lip, and the umbilicus is proportionately more open **(Figs 117d-f).** All of these species share the absence of significant radial shell sculpture, a white to faint yellow-brown shell colour, rather expanded lip, and thus differ from the more heavily coloured and sculptured taxa to the east. The partly sympatric *Amplirhagada percita* (Iredale, 1939) and *A. napierana* Solem, 1981, differ, respectively, in their brown shell colour, radial apical sculpture, and flatter whorls **(Plate 51)** and closed umbilicus, more rounded shape, and radial apical sculpture. Anatomically, the short and thick vagina (V), the free oviduct (UV) distinctly longer than the spermatheca (S), and proportionately longer penis (P) **(Figs 116a, c)** of *W. commoda* separate it from *W. woodwardi* (Fulton, 1902) **(Figs 112-113).** *Westraltrachia turbinata* **(Figs 118a-b)** has a longer vagina (V), sub-equal free oviduct (UV) and spermatheca (S), slenderer and proportionately much shorter penis (P). *Westraltrachia inopinata* **(Figs 119a-b)** has the free oviduct (UV) distinctly elongated, the vagina (V) of medium length, and the penis shortened.

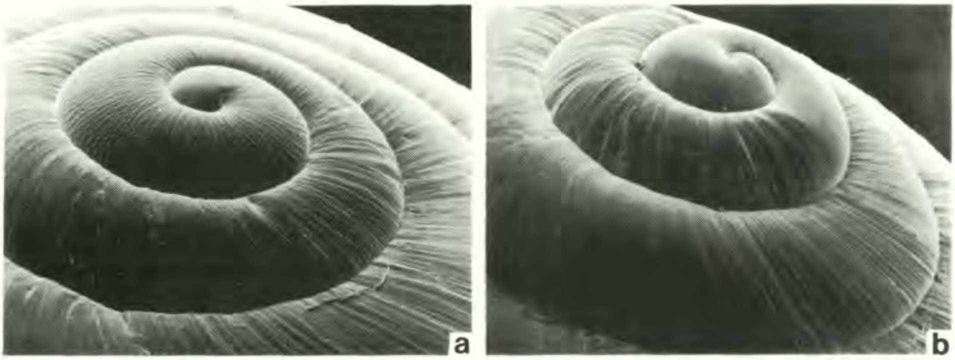


Plate 51: Apical sculpture and whorl profile in *Amplirhagada napierana* Solem, 1981 and *Westraltrachia commoda* (Iredale, 1939): (a) *Amplirhagada napierana,* FMNH 199858, Sta. WA-325, 5.9 km north-west of Yammera Gap, Napier Range, apex and early spire at 33.6X; (b) *Westraltrachia commoda* (Iredale, 1939), FMNH 199857, Sta. WA-325, apex and early spire at 28.0X.

Holotype of *Parrhagada commoda* Iredale, 1939

AM C.64871, Barker River Gorge, Napier Range. Collected by Herbert Basedow. Height of shell 14.55 mm, diameter 22.4 mm, H/D ratio 0.650, whorls 5¾ +, umbilicus with a narrow lateral opening.

Paratypes of *Parrhagada commoda* Iredale, 1939

AM C.64912, WAM 66.40, FMNH 198997, 15 dead adults from the type locality.

Holotype of *Parrhagada ferrosa* Iredale, 1939

AM C.64872, Barker River Gorge, Napier Range. Collected by Herbert Basedow. Height of shell 11.0 mm, diameter 18.1 mm, H/D ratio 0.608, whorls 5¼, umbilical width 0.7 mm, D/U ratio 25.9.

Paratypes of *Parrhagada ferrosa* Iredale, 1939

AM C.64913, WAM 67.40, FMNH 198996, 10 dead adults from the type locality.

Measured adults

Napier Range, geographic sequence north-west to south-east: NR II-12, south corner, east side Barker Gorge ('Lennard River' SE 51-8 – 252:827) (67 dead adults, WAM 1209.76); Narlaala Mine, north side range, 2½ mi south-east Barker Gorge (24 dead adults, 7 September 1972, WAM 309.80); Sta. WA-330, 0.2 km south-east of Barker Gorge, south-west side ('Lennard' 3863 – 833:904) (2 live, 41 dead adults, WAM 8.80, FMNH 199262, FMNH 199948); Sta. WA-190, south-east side of Barker Gorge, north side ('Lennard' 3863 – 841:914) (13 live, 75 dead adults, WAM 9.80-14.80, FMNH 199413, FMNH 199435, FMNH 199716, FMNH 199877, FMNH 200067); Sta. WA-357, cliffs and caves 0.2 km south of Wombarella Creek, north side ('Lennard' 3863 – 841:914) (47 live, 7 dead adults, WAM 15.80-20.80, FMNH 199791-3, FMNH 200314, FMNH 200316-8, FMNH 200320, FMNH 200324); Sta. WA-331, 1.6 km south-east of Barker Gorge, south-west side ('Lennard' 3863 – 844:893) (7 live, 38 dead adults, WAM 21.80, WAM 22.80, FMNH 199089, FMNH 199865); Sta. WA-191, 3.4 km east of Wombarella Creek Crossing, north side ('Lennard' 3863 – 861:890) (5 live adults, WAM 23.80, FMNH 199441); NR II-11, 2 km north-west of Wombarella Gap, south-west side ('Lennard River' SE 51-8 – 254:8245) (29 dead adults, WAM 1210.76); Sta. WA-326, 1.5 km north-west of Wombarella Gap, south side ('Lennard' 3863 – 862:878) (21 dead adults, WAM 24.80, FMNH 199074); Sta. WA-332, north-west side of Wombarella Gap, south-west side ('Lennard' 3863 – 872:872) (6 live, 17 dead adults, WAM 25.80, WAM 26.80, FMNH 199095, FMNH 199922, FMNH 200168); Sta. WA-333, south-east side of Wombarella Gap, south-west side ('Lennard' 3863 – 874:870) (11 live adults, WAM 29.80, FMNH 199091); NR II-7f, isolated rock in east entrance to Wombarella Gap ('Lennard River' SE 51-8 – 256:825), (12 dead adults, WAM 1218.76); NR II-7a, large rock surrounded by grass, east entrance Wombarella Gap (19 dead adults, WAM 1217.76); NR II-7e, fissure of low cliff face, east corner Wombarella Gap (22 dead adults, WAM 1211.76); Sta. WA-376, north-west side, south-east of Wombarella Gap ('Lennard' 3863 – 878:871) (8 live, 23 dead adults, WAM 27.80, WAM 28.80, FMNH 199304, FMNH 200149); Sta. WA-327, 1.6 km south-east of Wombarella Gap, south side ('Lennard' 3863 – 885:863) (2 live, 35 dead adults, WAM 30.80, FMNH 199074, FMNH 199912); Sta. WA-325, 0.6 km south-west of road along north-east side, 5.9 km north-west of Yammera Gap ('Lennard' 3863 – 891:862) (60 live, 37 dead adults, WAM 31.80-36.80, FMNH 199263, FMNH 199857, FMNH 199859, FMNH 200212, FMNH 200103, FMNH 200108, FMNH 200242, FMNH 200244, FMNH 200249, FMNH 200250, FMNH 200253-6); Sta. WA-377, 5.5 km west of Yammera Gap, north side ('Lennard' 3863 – 893:857) (7 live adults, WAM 37.80, FMNH 199854); NR II-9b, 3 km south-east of Wombarella Gap, south face ('Lennard River' SE 51-8 – 258:822) (12 dead adults, WAM 1215.76); Sta. WA-311, 5.3 km north-west of Yammera Gap, north-east side ('Lennard 3863 – 902:855) (2 live, 36 dead adults, WAM 38.80, FMNH 199345, FMNH 200142); Sta. WA-328, 4.0 km south-east of Wombarella Gap, south side ('Lennard' 3863 – 904:847) (1 live, 45 dead adults, WAM 39.80, FMNH 199274, FMNH 200351); Sta. WA-401, 3.4 km north-west of Yammera Gap, north side ('Lennard' 3863 – 913:843) (39 dead adults, WAM 40.80, FMNH 199371); NR 11-8, *ca.* 2 km north-west of Napier Downs Homestead, north side (9 dead adults, WAM 1219.76); WA-578, 3.15 km west of Yammera Gap, east edge of small valley, north side (30 dead adults, WAM 76.80, FMNH 104698); Sta. WA-577, 3.05 km west of Yammera Gap, heavily vegetated, north side (48 dead adults, WAM 77.80, FMNH 204696); Sta. WA-579, 2.95 km west of Yammera Gap, east side of moderate valley, north side (32 dead adults, WAM 78.80, FMNH 204700).

Distribution limits in Napier Range

Westraltrachia commoda (Iredale, 1939) has a continuous distribution of 11 km from the east bank of Barker Gorge to a point 2.95 km west of Yammera Gap on the north side of the Napier Range and somewhere between 4.0 km south-east of Wombarella Gap (Sta. WA-401) and 6.9 km south-east of Wombarella Gap (Sta. WA-329) on the south side of the range. On both sides it is abruptly replaced by *W. turbinata*, which continues east across Yammera Gap.

Diagnosis

Shell large, 13.3-22.5 mm (mean 17.47 mm) in diameter, with 4½ to 6 (mean 5⅛) normally coiled whorls. Apex and spire strongly and evenly elevated **(Figs 115b, e)**, height of shell 7.8-15.3 mm (mean 11.00 mm), H/D ratio 0.520-0.773 (mean 0.628). Apical whorls rarely with even faint traces of micro-ribbing in the sutures **(Plate 51b)**. Postnuclear whorls macroscopically smooth, fresh specimens with very faint radial growth striae, never with prominent sculpture. Shell periphery of adults rounded **(Figs 115b, e)**, angulated to sharply keeled in juveniles, smallest adults with angulation present on first part of body whorl. Lip strongly expanded and reflected **(Figs 115a-f)**, body whorl at most slightly descending behind lip. Umbilicus narrowly open, rarely reduced to a crack at western range limit, moderately open in populations at east end of range, umbilical width 0.4-2.6 mm (mean 1.38 mm), D/U ratio 6.18-50 (mean 14.0). Colour white, at least on lower spire and body whorl, juveniles and upper spire of adults frequently with a light brown tone or variegated pattern of brown and white. Based on 883 measured adults.

Genitalia **(Figs 116a-c)** with large penial muscle (PM) and loop of epiphallus. Principal pilaster **(Fig. 158a)** slightly smaller than in *Westraltrachia woodwardi*. Penis (P) of medium length **(Fig. 116c)**, not folded within sheath, slender on lower portion. Walls of penis sheath very thin for entire length **(Fig. 116c, PS)**. Vas deferens **(Fig. 116c, VD)** entering penis sheath opposite base of epiphallus. Vagina **(Fig. 116a, V)** very short, large in diameter, spermatheca (S) distinctly shorter than free oviduct (UV), which is normally looped **(Fig. 116a)**.

Jaw **(Plate 26c)** macroscopically smooth, without trace of vertical ribbing, often showing strong horizontal incremental growth ridglets. Radular teeth highly modified. Centrals and laterals unicuspid, mesoconal tip bluntly rounded, cusp markedly elevated, upper part curved backward **(Plate 35a)**, latero-marginal transition **(Plate 35b)** typical, marginal teeth typical and variable.

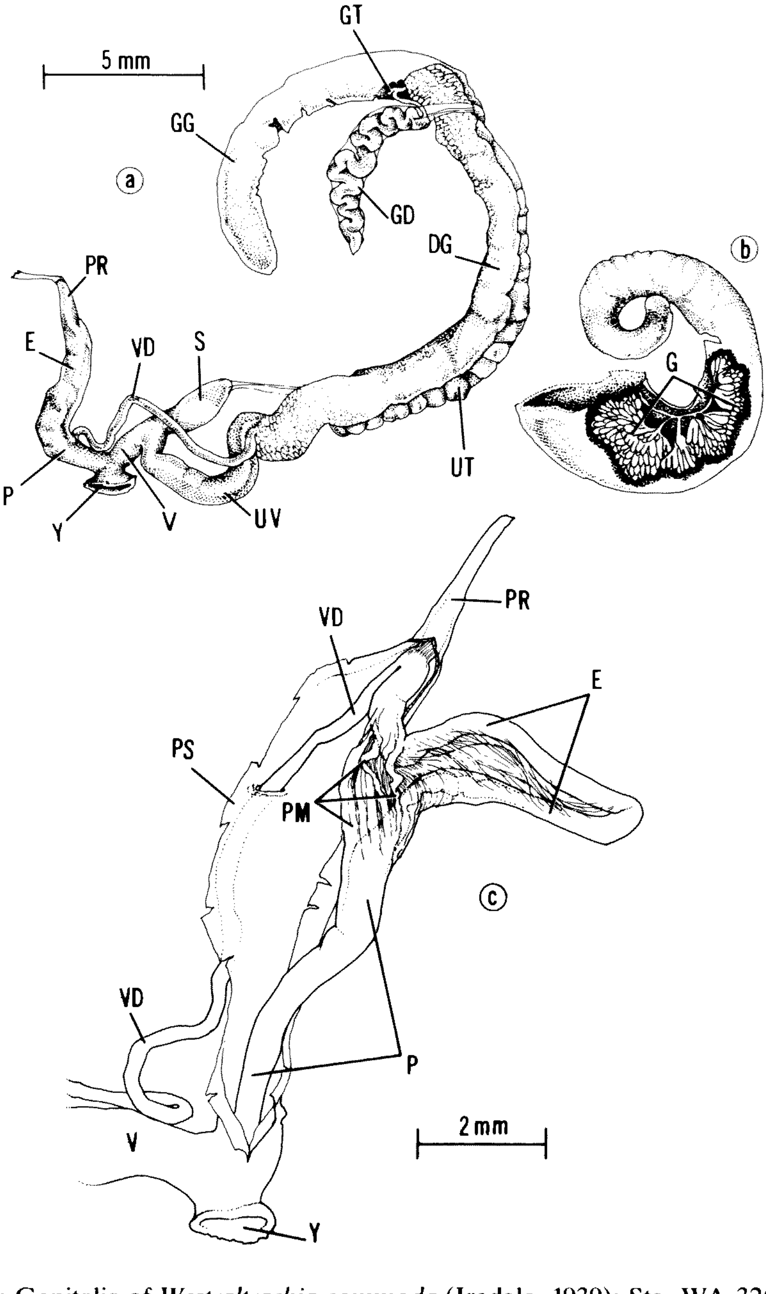


Fig. 116: Genitalia of *Westraltrachia commoda* (Iredale, 1939): Sta. WA-325, 5.9 km north-west of Yammera Gap, Napier Range, 18 December 1976, FMNH 200103, (a) whole genitalia, Dissection B, (b) ovotestis, Dissection B, (c) interior of penis sheath, Dissection A. Scale lines as marked. Drawings by Linnea Lahlum.

Discussion

The shell of *Westraltrachia commoda* (Iredale, 1939) shows significant variation at both ends of its range. At its western limit, there is some evidence of possible introgression with *W. woodwardi*, in that a few individuals of *W. commoda* have the umbilicus reduced to a lateral crack. At and near Barker Gorge, 3 of 67 adults at NR II-12, 4 of 24 adults from Narlaala Mine, 2 of 41 adults from Sta. WA-190 (FMNH 199435) show this condition, while at NR II-11, 2 km north-west of Wombarella Gap, 8 of 29 adults have the narrowed umbilicus. Throughout the range there is moderate variation in umbilical width and D/U ratios **(Table 49).**

At the eastern range extremity, just before the shift to *Westraltrachia turbinata*, *W. commoda* shows a reduction in shell size, widening of the umbilicus, and finally ends with a very high spired population (**Table 50,** Sta. WA-579) that may be intermediate between the two species. The eastern area of transition, from 2.7-2.95 km west of Yammera Gap, is an area of low rolling hillocks with little exposed talus. After the short and quite dry wet season of 1979-1980, 20 inches instead of the normal 40 inches of rain at Napier Downs Station, it was impossible in May 1980 to find live material or even whole dead shells in most of the Yammera Gap to Wombarella Gap area. It is quite probable that this is a fringe area for *Westraltrachia*. There would thus be relatively frequent extinctions of colonies, subsequent gradual recolonisation, establishment of scattered modest size populations over a series of good or normal years, then decline and extinction recurring under stress. The unsampled 0.25 km of range face would represent a frequent snail-free barrier zone between species on the north side of the range that even in better years would not shelter large numbers of live snails. Collecting access to the south side transition zone was not possible in 1980 for both lack of time and vehicle track disappearance between 1977 and 1980. Thus, the exact point of species shift on the south side of the range remains to be determined.

Between Barker Gorge and Sta. WA-332 on the west side of Wombarella Gap, the size of *Westraltrachia commoda* is large, most populations averaging more than 19 mm in diameter **(Table 49).** In Wombarella Gap itself, there is considerable variation tending toward noticeable size reduction, with material from a fissure on a low cliff face (NR II-7e) averaging almost 3 mm less in diameter than specimens from a nearby large rock isolated by grass from the main range (NR II-7a). As is usual, the difference in diameter reflects earlier cessation of shell growth, the mean whorl count of the former, $4\frac{3}{4}+$, being much less than that of the latter, $5\frac{1}{4}+$. It is also noteworthy that the populations with reduced whorl count tend to have more widely open umbilici **(Table 49).** The varied exposures to direct insolation, marked variation in talus accumulation, and partial island effects around Wombarella Gap would provide significant differences in terms of moisture retention time, and thus length of activity for the snails. The size variation here is interpreted as being ecophenotypic.

To the east of Wombarella Gap **(Fig. 159),** shell diameter stays in the general Wombarella Gap low size range, with mean diameters of 16.77-17.34 mm, mean whorl counts of $4\frac{7}{8}+$ to $5\frac{1}{8}$, and moderately open umbilici (mean D/U ratios 10.8-14.2), except for some larger shells from 3 km south-east of Wombarella Gap on the south side of the range (NR II-9b) that are 19.04 mm in mean diameter with $5\frac{1}{4}+$ whorls, and have a narrow umbilicus (mean D/U ratio 17.4). Materials from Stas. WA-311 and WA-328 are consistent with this pattern, although with increased H/D ratio (means 0.644-0.662).

Table 49: Local Variation in *Westraltrachia commoda* (Iredale, 1939)

Locality	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
Types of *W. commoda* and *W. ferrosa* combined	19D	12.80 ± 0.367 (10.1 – 15.5)	19.68 ± 0.360 (17.15 – 21.9)	0.647 ± 0.011 (0.577 – 0.750)
NRII-12, WAM 1209.76	67D	11.96 ± 0.126 (10.0 – 15.0)	18.63 ± 0.136 (16.5 – 21.45)	0.642 ± 0.004 (0.583 – 0.730)
Narlarla Mine, WAM 309.80	24D	13.06 ± 0.231 (10.9 – 15.05)	19.90 ± 0.236 (17.2 – 21.65)	0.656 ± 0.008 (0.589 – 0.737)
WA-330, FMNH 199262	41D	11.10 ± 0.176 (8.52 – 12.9)	18.34 ± 0.183 (15.7 – 20.4)	0.605 ± 0.007 (0.523 – 0.700)
WA-190, FMNH 199877, 8-X-1976	6L	11.77 ± 0.659 (10.2 – 14.8)	19.57 ± 0.761 (17.0 – 22.5)	0.600 ± 0.016 (0.548 – 0.658)
WA-190, FMNH 199435, 8-X-1976	41D	12.19 ± 0.198 (9.4 – 14.6)	19.51 ± 0.195 (17.0 – 22.0)	0.624 ± 0.006 (0.528 – 0.702)
WA-190, FMNH 199413, 9-X-1976	34D	12.62 ± 0.175 (11.0 – 14.5)	19.68 ± 0.192 (17.4 – 21.6)	0.641 ± 0.005 (0.591 – 0.735)
WA-357, FMNH 200320	7L	11.83 ± 0.198 (11.2 – 12.5)	19.19 ± 0.278 (18.1 – 20.0)	0.617 ± 0.008 (0.584 – 0.641)
WA-331, FMNH 199865	7L	11.03 ± 0.422 (9.5 – 12.3)	17.81 ± 0.347 (16.6 – 19.2)	0.618 ± 0.017 (0.572 – 0.684)
WA-331, FMNH 199089	38D	10.59 ± 0.210 (8.15 – 13.6)	18.18 ± 0.206 (14.8 – 21.6)	0.581 ± 0.006 (0.525 – 0.680)
WA-191, FMNH 199441	5D	11.72 ± 0.698 (10.2 – 14.3)	17.76 ± 0.516 (16.8 – 19.7)	0.658 ± 0.019 (0.607 – 0.726)
NRII-11, WAM 1210.76	29D	12.31 ± 0.175 (10.5 – 14.15)	19.13 ± 0.176 (17.4 – 21.15)	0.643 ± 0.006 (0.556 – 0.703)
WA-326, FMNH 199074	21D	11.13 ± 0.190 (9.5 – 12.9)	18.73 ± 0.210 (17.3 – 20.3)	0.594 ± 0.009 (0.525 – 0.688)
WA-322, FMNH 200168	5L	10.68 ± 0.403 (9.5 – 11.7)	17.12 ± 0.416 (15.8 – 18.4)	0.624 ± 0.017 (0.592 – 0.680)
WA-322, FMNH 199095	17D	9.73 ± 0.456 (8.15 – 12.2)	16.15 ± 0.478 (14.4 – 19.0)	0.601 ± 0.007 (0.551 – 0.659)
WA-333, FMNH 199091	11D	10.14 ± 0.299 (9.25 – 12.4)	17.01 ± 0.354 (15.8 – 20.0)	0.596 ± 0.009 (0.547 – 0.671)
NRII-7f, WAM 1218.76	12D	11.20 ± 0.331 (9.65 – 13.6)	17.82 ± 0.307 (16.1 – 19.15)	0.628 ± 0.012 (0.558 – 0.710)
NRII-7a, WAM 1217.76	19D	12.45 ± 0.274 (10.4 – 14.75)	19.34 ± 0.327 (16.85 – 21.9)	0.643 ± 0.008 (0.586 – 0.702)

Table 49: Local Variation in *Westraltrachia commoda* (Iredale, 1939) (continued)

Locality	Number of Adults Measured	Mean, Range and SEM of: Shell Height	Shell Diameter	H/D Ratio
NRII-7e, WAM 1211.76	22D	9.61 ± 0.173 (8.35 – 11.6)	16.38 ± 0.174 (15.1 – 17.7)	0.587 ± 0.008 (0.520 – 0.655)
WA-376, FMNH 200149	8L	10.29 ± 0.378 (8.3 – 12.0)	17.45 ± 0.448 (15.5 – 20.0)	0.589 ± 0.011 (0.535 – 0.634)
WA-376, FMNH 199304	23D	10.45 ± 0.234 (8.85 – 12.5)	17.22 ± 0.279 (15.4 – 20.5)	0.606 ± 0.007 (0.548 – 0.658)
WA-327, FMNH 199074	35D	10.20 ± 0.187 (7.78 – 12.5)	16.93 ± 0.180 (14.5 – 19.4)	0.602 ± 0.007 (0.536 – 0.683)
WA-325, FMNH 199263	37D	10.58 ± 0.166 (9.05 – 13.1)	17.03 ± 0.179 (15.4 – 20.1)	0.621 ± 0.006 (0.562 – 0.699)
WA-325, FMNH 200256, 7-II-1977	11L	10.75 ± 0.252 (9.5 – 12.0)	17.23 ± 0.228 (16.4 – 18.9)	0.624 ± 0.012 (0.563 – 0.690)
WA-325, FMNH 199857, 1-III-1977	10L	10.77 ± 0.211 (9.45 – 11.6)	17.34 ± 0.296 (15.9 – 18.9)	0.621 ± 0.007 (0.590 – 0.657)
WA-377, FMNH 199854	7L	10.22 ± 0.158 (9.6 – 10.8)	16.77 ± 0.268 (16.0 – 18.0)	0.610 ± 0.012 (0.561 – 0.650)
NRII-9b, WAM 1215.76	12D	13.08 ± 0.429 (11.0 – 16.0)	19.04 ± 0.437 (16.95 – 22.4)	0.686 ± 0.126 (0.641 – 0.792)

Locality	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
Types of *W. commoda* and *W. ferrosa* combined	19D	5½ – (5 – 5⅞)	1.07 ± 0.101 (0.55 – 2.3)	20.6 ± 1.489 (7.94 – 32)
NRII-12, WMA 1209.76	67D	5¼ + (4¾ + – 5¾)	1.16 ± 0.042 (0.65 – 2.15)	17.3 ± 0.631 (8.35 – 28.6)
Narlarla Mine, WAM 309.80	24D	5½ (5⅛ + – 5⅞)	1.10 ± 0.48 (0.8 – 1.5)	18.8 ± 0.891 (12.3 – 25.8)
WA-330, FMNH 199262	41D	5¼ + (4⅞ – – 5⅝ +)	1.36 ± 0.060 (0.7 – 2.4)	14.6 ± 0.729 (8.17 – 27.7)
WA-190, FMNH 199877, 8-X-1976	6L	5⅜ – (5⅛ + – 5⅞ –)	0.93 ± 0.123 (0.5 – 1.3)	23.7 ± 4.560 (15.1 –
WA-190, FMNH 199435, 8-X-1976	41D	5⅜ – (5 – – 6 –)	1.20 ± 0.061 (0.4 – 2.0)	18.3 ± 1.258 (10.6 – 50)
WA-190, FMNH 199413, 9-X-1976	34D	5⅜ – (4⅞ – – 5⅞ –)	1.22 ± 0.071 (0.6 – 2.55)	17.9 ± 1.140 (8.39 – 35)

Table 49: Local Variation in *Westraltrachia commoda* (Iredale, 1939) (continued)

Locality	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
WA-357, FMNH 200320	7L	5⅜ − (5⅛ + − 5½ −)	1.16 ± 0.144 (0.8 − 1.9)	18.0 ± 1.984 (9.53 − 25.0)
WA-331, FMNH 199865	7L	5⅛ + (4⅞ + − 5¾ −)	1.39 ± 0.180 (0.75 − 2.1)	14.49 ± 0.252 (7.91 − 25.6)
WA-331, FMNH 199089	38D	5¼ − (4½ − − 5⅝ +)	1.44 ± 0.057 (0.75 − 2.30)	13.46 ± 0.615 (7.05 − 25.5)
WA-191, FMNH 199441	5D	5¼ − (5 − − 5⅝ −)	1.23 ± 0.183 (0.8 − 1.65)	16.2 ± 3.03 (10.2 − 24.6)
NRII-11, WAM 1210.76	29D	5⅜ − (4⅞ − 5¾)	1.00 ± 0.052 (0.7 − 1.	19.9 ± 1.09 (12.9 − 28.0)
WA-326, FMNH 199074	21D	5⅛ − (5 − − 5½ −)	1.78 ± 0.102 (1.05 − 2.6)	11.2 ± 0.655 (7.08 − 17.7)
WA-332, FMNH 200168	5L	5⅛ + (4¾ + − 5½ −)	1.31 ± 0.126 (1.0 − 1.55)	13.7 ± 1.68 (10.3 − 18.4)
WA-332, FMNH 199095	17D	4⅞ + (4½ − − 5⅜ −)	1.58 ± 0.089 (0.6 − 2.15)	11.2 ± 1.27 (7.67 − 30)
WA-333, FMNH 199091	11D	5⅛ − (4¾ + − 5¾ +)	1.68 ± 0.130 (1.05 − 2.3)	10.9 ± 1.04 (6.97 − 16.5)
NRII-7f, WAM 1218.76	12D	5⅛ + (4⅞ − 5⅝ −)	1.45 ± 0.106 (0.8 − 2.05)	13.2 ± 1.14 (8.44 − 22.1)
NRII-7a, WAM 1217.76	19D	5¼ + (5 − 5⅞ −)	1.31 ± 0.059 (0.8 − 1.7)	15.5 ± 0.928 (10.9 − 26.3)
NRII-7e, WAM 1211.76	22D	4¾ + (4½ − 5¼)	1.60 ± 0.078 (1.1 − 2.4)	10.7 ± 0.557 (7.33 − 16.1)
WA-376, FMNH 200149	8L	5⅛ − (5 − − 5¼ −)	1.72 ± 0.123 (1.3 − 2.25)	10.6 ± 0.887 (7.21 − 14.3)
WA-376, FMNH 199304	23D	5 (4⅝ − − 5⅜ +)	1.59 ± 0.067 (1.1 − 2.3)	11.2 ± 0.485 (7.04 − 15.2)
WA-327, FMNH 199074	35D	5 (4½ − − 5¾ −)	1.69 ± 0.071 (0.85 − 2.6)	10.8 ± 0.617 (6.46 − 22.8)
WA-325, FMNH 199263	37D	5⅛ − (4¾ − − 5⅝ +)	1.37 ± 0.037 (0.9 − 1.8)	12.8 ± 0.400 (9.38 − 18.5)
WA-325, FMNH 200256, 7-II-1977	11L	5 + (4⅞ + − 5¼ +)	1.49 ± 0.096 (0.8 − 2.0)	12.1 ± 0.976 (8.7 − 21.0)
WA-325, FMNH 199857, 1-III-1977	10L	5⅛ (5 − − 5¼ +)	1.31 ± 0.113 (0.8 − 2.0)	14.2 ± 1.27 (7.95 − 21.6)
WA-377, FMNH 199854	7L	4⅞ + (4¾ − − 5¼ +)	1.46 ± 0.112 (1.0 − 1.9)	12.0 ± 1.08 (8.42 − 16.6)
NRII-9b, WAM 1215.76	12D	5¼ + (5 + − 5⅞)	1.14 ± 0.069 (0.7 − 1.5)	17.4 ± 1.15 (12.1 − 27.1)

The dramatic change occurs between 2.95 and 3.4 km west of Yammera Gap, where the populations from Stas. WA-401, WA-577, WA-578, and WA-579 have reduced mean diameters of 14.17-15.86 mm, whorl counts of 4⅞+ to 5⅛–, increased umbilical widths (mean 1.53-1.67 mm), and more open D/U ratios (mean 9.06-9.93). From west to east, they show a progression in mean H/D ratios of 0.619, 0.638, 0.652 to 0.690. These populations, known only from dead specimens at present, come close to the size and shape of *Westraltrachia turbinata* **(Tables 50 and 51)**. Further study is needed to determine whether this is a narrow hybrid zone, a step cline, or a mixed population of both species. Particularly the very high spired population from Sta. WA-579 gives the visual impression of containing specimens referable to each species. In the absence of live-collected material, however, the problem cannot be resolved. The increased umbilical width and D/U ratio of these populations correlates with the reduction in whorl count, and is matched by the dwarfed populations in the Wombarella Gap area. Thus, I do not interpret this as an indication of introgression from *W. turbinata*.

Anatomical variation in *Westraltrachia commoda* was insignificant. I found no geographic variation, and dissection of specimens from the periodic samples taken at Sta. WA-325 confirmed the mid-wet to early dry season pattern of changes outlined for *Amplirhagada b. burnerensis* (Smith, 1894) (Solem, 1981a; 240-248, Figs 52-53) and expanded above (p. 482). The genital system is male active at the normal start of the wet season, regardless of whether the season is 'on time' or 'late'; mating triggers activation of the female system; multiple matings result in filling and enlarging the spermatheca; in mid-wet season the system begins to shut down, with extreme shrinkage of the ovotestis, hermaphroditic duct, and prostate-uterus, but no major change in the albumen gland; and no change in the penis complex.

WESTRALTRACHIA TURBINATA SP. NOV.

(Plates 19d-f, 35c-d; Figs 117a-c, 118, 120, 121, 158b)

Comparative remarks

Westraltrachia turbinata is a very small (mean diameter 13.53 mm), quite high spired (mean H/D ratio 0.706) species with a light yellow-brown tone to the shell when alive or newly dead, and the umbilicus is moderately open (mean D/U ratio 10.0) **(Figs 117a-c)**. The shell lip is less broadly expanded than in *W. commoda* (Iredale, 1939) **(Figs 115a-f)**, which also is larger, less elevated, with a narrower umbilicus (mean D/U ratio 14.0), and generally whiter in colour. *Westraltrachia inopinata*, from just east of Yammera Gap on the south side of the Napier Range, is somewhat larger (mean diameter 14.63 mm), distinctly less elevated (mean H/D ratio 0.596), with reduced mean whorl count (4¾-), and has a more expanded lip **(Figs 117d-f)**. *Westraltrachia woodwardi* (Fulton, 1902), the other unicoloured species, ranges north-west from Barker Gorge, is white in colour, has a closed umbilicus, and is much larger in size (mean diameter 19.71 mm). Anatomically, *W. turbinata* **(Figs 118a-b)** differs most obviously from *W. commoda* (Iredale, 1939) **(Figs 116a-c)** by its much longer vagina (V), long and slender penis (P), subequal lengths of the spermatheca (S) and free oviduct (UV), and reduced size of the penial muscle (PM). *Westraltrachia inopinata*

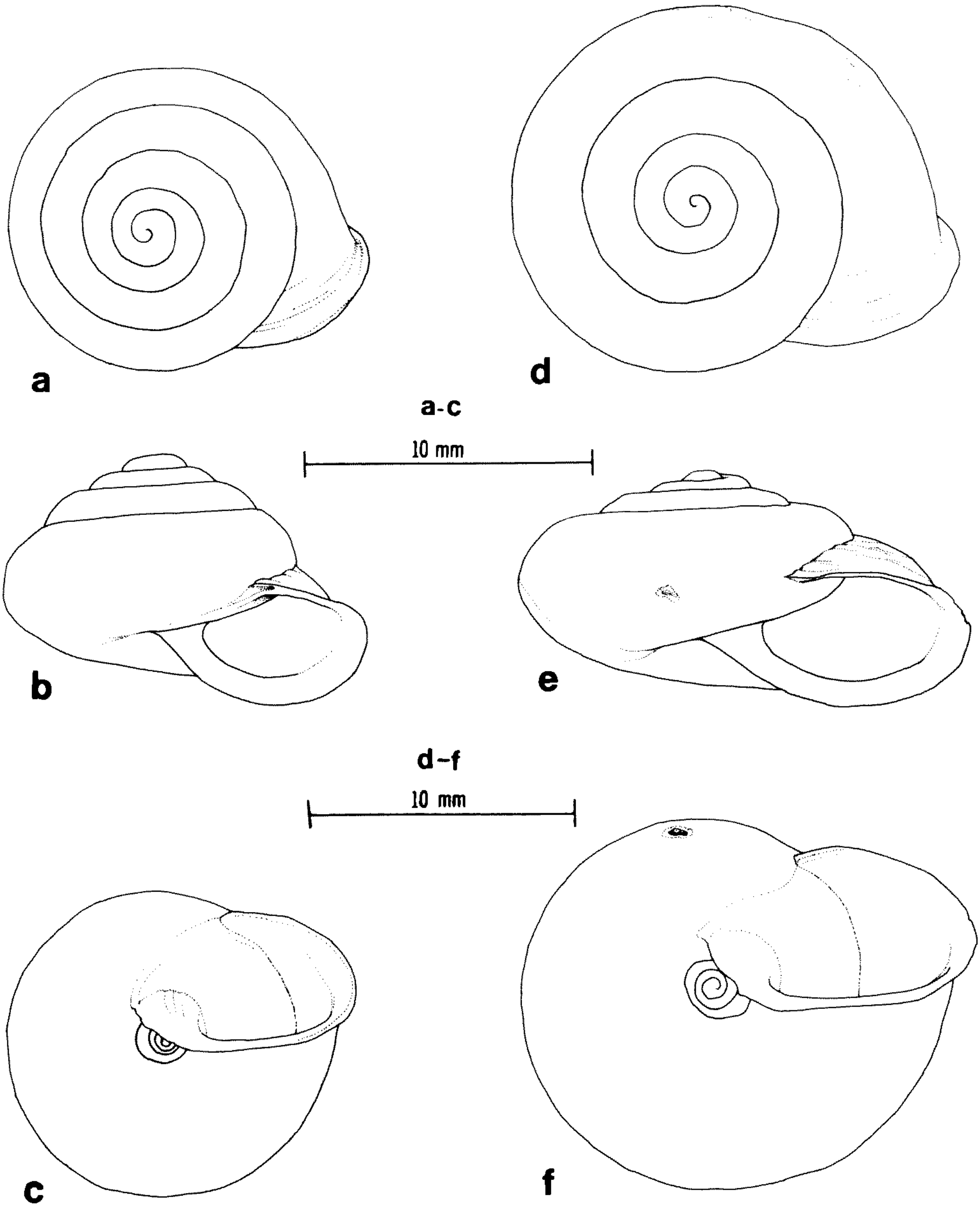


Fig. 117: Shells of *Westraltrachia turbinata* and *W. inopinata:* (a-c) holotype of *W. turbinata*, Sta. WA-281, 1.3 km west of Yammera Gap, north side Napier Range, WAM 805.79; (d-f) holotype of *W. inopinata*, Sta. WA-339, 1.1 km east of Yammera Gap, south side Napier Range, WAM 733.79. Scale lines equal 10 mm. Drawings by Linnea Lahlum.

(**Figs 119a-b**) has a shorter, thicker penis (P), much shorter vagina (V), the free oviduct (UV) much longer than the spermatheca (S), and much larger penial muscle (PM). *Westraltrachia froggatti complanata* (**Figs 123a-b**) is immediately separable by its very long and thin penis (P) that is folded within the penis sheath (PS), entrance of the vas deferens (VD) through the penis sheath midway up the penis rather than opposite the epiphallic base, and its very short vagina (V).

Holotype

WAM 805.79, Sta. WA-281, slope above stockmen's hut, Napier Downs Station homestead, 1.3 km west of Yammera Gap, north side of Napier Range, Western Australia (1:100,000 'Lennard' map sheet 3863, grid reference 928:827). Collected by A. Solem, L. Price and C. Christensen 6 December 1976. Height of shell 9.3 mm, diameter 12.4 mm, H/D ratio 0.750, whorls 5+, umbilical width 1.1 mm, D/U ratio 11.3.

Paratopotypes

WAM 69.80, WAM 744.79, WAM 745.79, FMNH 199869, FMNH 199871, FMNH 200269, FMNH 200271, FMNH 200347-8, 41 live, 12 dead adults, 18 live, 2 dead juveniles from the type locality.

Paratypes

Napier Range, geographic sequence north-west to south-east: Sta. WA-200, north slope, 2.7 km west of Yammera Gap ('Lennard' 3863 – 917:840) (34 dead adults, WAM 734.79-735.79, FMNH 199383, FMNH 199400); Sta. WA-358, 2.6 km west of Yammera Gap, north side ('Lennard' 3863 – 918:828) (20 live adults, 1 live juvenile, WAM 736.79-738.79, FMNH 200163, FMNH 200278-9); Sta. WA-381, 2.4 km west of Yammera Gap, north side ('Lennard' 3863 – 918:826) (46 dead adults, WAM 757.79, FMNH 199143); Sta. WA-380, 2.3 km west of Yammera Gap, north side ('Lennard' 3863 – 920:825) (1 live, 38 dead adults, WAM 758.79, FMNH 199145, FMNH 199837); Sta. WA-382, 2.1 km west of Yammera Gap, north side ('Lennard' 3863 – 921:835) (51 dead adults, WAM 739.79, FMNH 199346); Sta. WA-329, 6.9 km south-east of Wombarella Gap, south side ('Lennard' 3863 – 921:828) (39 dead adults, WAM 740.79, FMNH 199271); Sta. WA-573, 2.08 km west of Yammera Gap, north side (3 dead adults, WAM 79.80, FMNH 204687); Sta. WA-575, 1.93 km west of Yammera Gap, north side (10 dead adults, WAM 80.80, FMNH 204692); Sta. WA-574, 1.83 km west of Yammera Gap, north side (2 dead adults, WAM 81.80, FMNH 204693); Sta. WA-580, 1.65 km west of Yammera Gap, north side (8 dead adults, WAM 82.80, FMNH 204702); Sta. WA-306, 1.6 km north-west of Yammera Gap, north side ('Lennard' 3863 – 922:831) (2 live, 37 dead adults, WAM 759.79, FMNH 199169, FMNH 200097); Sta. WA-571, west slope, valley 1.58 km west of Yammera Gap, north side (9 dead adults, WAM 83.80, FMNH 204682); Sta. WA-572, west entrance, valley 1.58 km west of Yammera Gap, north side (8 dead adults, WAM 84.80, FMNH 204686); Sta. WA-570, north-east corner, valley 1.58 km west of Yammera Gap, north side (9 dead adults, WAM 85.80, FMNH 204681); Sta. WA-569, east slope of valley 1.58 km west of Yammera Gap, north side (1 live adult, FMNH 204678); Sta. WA-360, 1.5 km west of Yammera Gap, north side ('Lennard' 3863 – 923:831) (10 dead adults, 1 live juvenile, WAM 741.79, FMNH 199149, FMNH 200299); Sta. WA-402, 1.5 km west Yammera Gap, north side ('Lennard' 3863 – 925:830) (28 dead adults, WAM 742.79, FMNH

199358); Sta. WA-199, 1.2 km west of Yammera Gap, north side ('Lennard' 3863 – 928:826) (32 dead adults, 4 dead juveniles, WAM 743.79, FMNH 199402); Sta. WA-400, 0.5 km west of Yammera Gap, north side ('Lennard' 3863 – 932:822) (29 dead adults, WAM 746.79, FMNH 199301); Sta. WA-301, Yammera Gap, south-west side ('Lennard' 3863 – 933:819) (7 live, 86 dead adults, WAM 760.79-761.79, FMNH 199183, FMNH 200295); NR II-20, north-west side Yammera Gap (16 dead adults, WAM 1221.76); NR II-19, south-east side Yammera Gap (45 dead adults, WAM 1225.76); Sta. WA-303, 1.0 km east of Yammera Gap, north side ('Lennard' 3863 – 944:818) (55 dead adults, WAM 747.79, FMNH 199180); Sta. WA-568, 1.3 km east of Yammera Gap, north side (23 dead adults, WAM 86.80-87.80, FMNH 204676-7); NR II-31, 2 km south-east of Yammera Gap, north side (28 dead adults, WAM 302.80); Sta. WA-196, 2 km east of Yammera Gap, north side ('Lennard' 3863 – 954:815) (25 dead adults, WAM 748.79, WAM 762.79, FMNH 199189, FMNH 199421); Sta. WA-351, 2.1 km east of Yammera Gap, north side ('Lennard' 3863 – 955:815) (36 live, 40 dead adults, 31 live juveniles, WAM 749.79-752.79, WAM 763.79, FMNH 199133, FMNH 200112, FMNH 200114, FMNH 200238, FMNH 200258); Sta. WA-348, canyon mouth 2.4 km east of Yammera Gap, south side ('Lennard' 3863 – 955:807) (1 dead adult, FMNH 199122); Sta. WA-347, canyon 2.9 km east of Yammera Gap, south side ('Lennard' 3863 – 956:806) (32 dead adults, 1 dead juvenile, WAM 753.79, FMNH 199106); Sta. WA-341, 3.1 km east of Yammera Gap, south side ('Lennard' 3863 – 959:806) (3 live, 40 dead adults, 6 live juveniles, WAM 754.79-755.79, FMNH 199137, FMNH 200136); Sta. WA-344, north-east side of low cliff, south-east side of canyon, 3.2 km east of Yammera Gap, south side ('Lennard' 3863 – 960:807) (24 dead adults, WAM 756.79, FMNH 199080.

Distribution limits in Napier Range

Westraltrachia turbinata extends at least 2.7 km east of Yammera Gap on the north side of the Range (Sta. WA-200) and to somewhere between Stas. WA-328 (*W. commoda* present) and WA-329 (*W. turbinata* present) on the south side of the Range **(Fig. 159).** It crosses Yammera Gap, is replaced at the south-east corner and for 2 km on the south side of the Range by *W. inopinata.* On the north side of the Range and between Stas. WA-303 and WA-351, and on the south side of the Range between Stas. WA-348 and WA-346, *W. turbinata* overlaps with the very distinctive *W. froggatti complanata.* Available records consist mainly of dead shells, so that the exact relationship of viable populations in this overlap zone remains to be determined. Its total linear range is about 5.5 km.

Diagnosis

Shell very small, 11.45-16.1 mm (mean 13.53 mm) in diameter, with 4⅜ to 5⅞ (mean 5⅛-) tightly coiled whorls. Apex and spire normally quite strongly and almost evenly elevated **(Fig. 117b),** height of shell 7.3-12.7 mm (mean 9.55 mm), H/D ratio 0.573-0.910 (mean 0.706). Apical whorls **(Plates 19d, f)** smooth, rarely with faint micro-radial wrinkling in the suture. Postnuclear whorls macroscopically smooth, faint spiral lines visible on fresh shells, occasionally weak radial growth striae developed. Shell periphery rounded, lip sharply, but moderately expanded **(Figs 117a-c),** body whorl normally only slightly descending behind lip. Umbilicus slightly to moderately open, reflected lip partially closing it **(Fig. 117c),** umbilical width 0.55-2.5 mm (mean 1.42 mm), D/U ratio 5.30-25.1 (mean 10.0). Colour light yellow-brown on apex and spire, becoming lighter

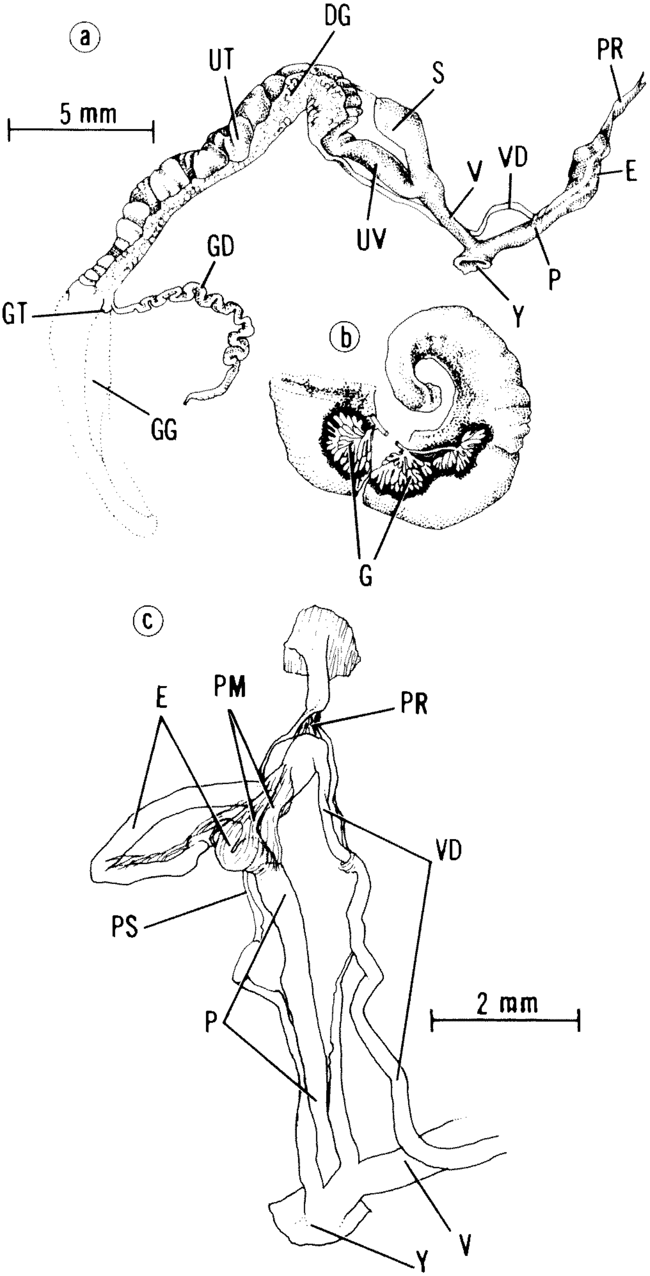


Fig. 118: Genitalia of *Westraltrachia turbinata:* Sta. WA-281, 1.3 km west of Yammera Gap, Napier Range, 6 December 1976, FMNH 199871, (a) whole genitalia, Dissection C, (b) ovotestis, Dissection C, (c) interior of penis sheath, Dissection A. Scale lines as marked. Drawings by Linnea Lahlum.

to white on body whorl, dead shells mostly bleached white. Based on 930 measured adults.

Genitalia (**Figs 118a-b**) with relatively small penial muscle (PM), epiphallic loop large. Principal pilaster (**Fig. 158b**) typical, medium in size. Penis relatively long, slender, not folded within sheath (**Fig. 118b**). Vas deferens (VD, **Fig. 118b**) entering penis sheath opposite base of epiphallus. Vagina (V, **Fig. 118a**) long, thin, spermatheca (S) and free oviduct (UV) subequal in length.

Jaw without vertical ribs, horizontal growth striae visible particularly in aestivating individuals. Radular teeth (**Plate 35c-d**) same as in *Westraltrachia woodwardi* (Fulton, 1902).

Discussion

Westraltrachia turbinata typically is immediately recognisable by the combination of conical shape, hence the name *turbinata*, yellow-brown spire, and small size. The transition to *W. commoda* (Iredale, 1939) on the west occurs abruptly, and the pattern of variation has been discussed above under that species. On the east side of Yammera Gap, the situation becomes more complicated. On the south-east side of the Gap, *W. inopinata* is found high up on the cliff face (Sta. NR II-19a) and continues on the south side of the range to Sta. WA-349, 2.0 km east of Yammera Gap. It is then replaced by additional populations of *W. turbinata* until the zone of transition to *W. froggatti complanata* occurs. On the north side of the range, *W. turbinata* extends from Yammera Gap to the zone of transition with *W. f. complanata* discussed below under *W. froggatti*.

Variability among populations of both *Westraltrachia turbinata* and *W. inopinata* is fairly extensive. **Figs 120** and **121** chart out mean and ranges of shell diameter and H/D ratio for each population. As an indication of geographic position, the east-west grid numbers from the 1:100,000 'Lennard' map sheet 3863 provide the distance scale. The slightly larger size and proportionately lower spire of *W. turbinata* at the western limits of its range, near to the point of transition to *W. commoda*, is obvious. On the exposed west-facing slope of Yammera Gap, the populations of *W. inopinata* are dwarfed, but have the depressed spire typical of that species. At the eastern range limit of *W. inopinata*, differences between the two species are more obvious. Throughout most of its range, *W. turbinata* shows only minor size and shape variation (**Tables 50** and **51**).

Field observations suggest that *Westraltrachia turbinata* may exploit a somewhat different shelter niche than *W. commoda* (Iredale, 1939) and *W. woodwardi* (Fulton, 1902). Both of the latter species are found commonly in shallow talus, under 0.3-1 m in diameter boulders, and occasionally under bush debris on sheltered slopes. At Sta. WA-281, 1.3 km west of Yammera Gap, four hours were spent in October 1976 in an unsuccessful hunt for live material of *W. turbinata*. An one hour hunt on 5 December 1976 was equally unsuccessful. Mid-afternoon on 6 December saw a 15 minute drenching thunder storm, followed by collecting 59 live adults and juveniles in less than 20 minutes. The snails emerged from deep fissures in the cliff itself, and during subsequent emergences were observed to browse on algal seepage films on fissure sides shaded from direct insolation. Mating individuals were observed and collected on 6 December within five minutes after cessation of rain. Dissection of two mating pairs indicated that copulation was mutual and reciprocal. This was the first shower since April 1976, and thus the snails had not been activated during the prior eight months.

Table 50: Shell Variation in *Westraltrachia commoda* (Iredale, 1939) and *W. turbinata* Replacement Zone

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
W. commoda				
WA-311, 5.3 km W of Yammera, FMNH 199345	36D	11.59 ± 0.177 (10.0 – 13.9)	17.96 ± 0.190 (16.0 – 21.2)	0.644 ± 0.005 (0.575 – 0.698)
WA-328, 4.0 km E of Wombarella Gap, S side, FMNH 199274	45D	10.97 ± 0.112 (9.1 – 12.8)	16.56 ± 0.120 (14.85 – 18.45)	0.662 ± 0.005 (0.568 – 0.744)
WA-401, 3.4 km W of Yammera, FMNH 199371	39D	9.83 ± 0.129 (8.4 – 12.0)	15.86 ± 0.146 (14.4 – 18.2)	0.619 ± 0.005 (0.562 – 0.693)
WA-578, 3.15 km W of Yammera, FMNH 204698	30D	9.42 ± 0.113 (8.4 – 10.7)	14.17 ± 0.137 (13.4 – 16.9)	0.638 ± 0.005 (0.589 – 0.699)
WA-577, 3.05 km W of Yammera, FMNH 204696	48D	9.66 ± 0.119 (8.25 – 11.7)	14.82 ± 0.124 (13.55 – 16.95)	0.652 ± 0.005 (0.596 – 0.757)
WA-579, 2.95 km W of Yammera, FMNH 204700	32D	10.27 ± 0.147 (8.0 – 11.9)	14.88 ± 0.125 (13.3 – 16.5)	0.690 ± 0.007 (0.602 – 0.773)
W. turbinata				
WA-200, 2.7 km W of Yammera, FMNH 199400	27D	9.30 ± 0.132 (8.1 – 10.9)	13.99 ± 0.136 (12.9 – 15.7)	0.664 ± 0.006 (0.593 – 0.726)
WA-358, 2.6 km W of Yammera, FMNH 200279	6L	9.26 ± 0.203 (8.75 – 9.8)	13.83 ± 0.188 (13.1 – 14.3)	0.670 ± 0.019 (0.615 – 0.725)
WA-381, 2.4 km W of Yammera, FMNH 199143	46D	9.60 ± 0.088 (8.4 – 11.0)	14.05 ± 0.093 (12.8 – 16.0)	0.683 ± 0.005 (0.628 – 0.782)
WA-380, 2.3 km W of Yammera, FMNH 199145	38D	8.90 ± 0.108 (7.65 – 10.4)	13.65 ± 0.094 (12.7 – 14.9)	0.652 ± 0.007 (0.575 – 0.759)
WA-329, S side, 6.9 km SE of Wombarella, FMNH 199271	39D	8.68 ± 0.113 (7.3 – 10.35)	13.03 ± 0.109 (11.5 – 14.5)	0.666 ± 0.007 (0.573 – 0.801)
WA-382, 2.1 km W of Yammera, FMNH 199346	51D	9.07 ± 0.091 (7.8 – 10.7)	13.29 ± 0.080 (12.1 – 14.8)	0.682 ± 0.006 (0.603 – 0.811)
WA-573, 2.08 km W of Yammera, FMNH 204687	3D	9.83 (9.4 – 10.2)	13.72 (13.5 – 13.9)	0.717 (0.684 – 0.756)
WA-575 1.93 km W of Yammera, FMNH 204692	10D	9.56 ± 0.331 (7.9 – 11.3)	13.50 ± 0.182 (12.9 – 14.9)	0.706 ± 0.021 (0.612 – 0.812)
WA-580, 1.65 km W of Yammera, FMNH 204702	8D	9.96 ± 0.150 (9.2 – 10.5)	13.76 ± 0.150 (13.3 – 14.6)	0.725 ± 0.015 (0.652 – 0.780)
WA-306, 1.6 km W of Yammera, FMNH 199169	37D	9.61 ± 0.116 (8.3 – 11.7)	13.55 ± 0.104 (12.4 – 15.0)	0.710 ± 0.008 (0.634 – 0.806)

Table 50: Shell Variation in *Westraltrachia commoda* (Iredale, 1939) and *W. turbinata* Replacement Zone (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
W. commoda				
WA-311, 5.3 km W of Yammera, FMNH 199345	36D	5¼ (4⅞+ – 5⅞+)	1.22 ± 0.051 (0.8 – 2.0)	15.4 ± 0.659 (8.70 – 23.5)
WA-328, 4.0 km E of Wombarella Gap, S side, FMNH 199274	45D	5⅛+ (4⅞+ – 5⅞+)	1.22 ± 0.051 (0.6 – 2.25)	14.7 ± 0.685 (7.51 – 28.7)
WA-401, 3.4 km W of Yammera, FMNH 199371	30D	5 (4½+ – 5¼–)	1.64 ± 0.037 (1.2 – 2.1)	9.82 ± 0.215 (7.74 – 13.3)
WA-578, 3.15 km W of Yammera, FMNH 204698	30D	4⅞+ (4¾– – 5¼–)	1.53 ± 0.047 (1.2 – 1.95)	9.90 ± 0.279 (7.62 – 12.6)
WA-577, 3.05 km W of Yammera, FMNH 204696	48D	5– (4⅝– – 5¼+)	1.53 ± 0.036 (1.0 – 2.1)	9.93 ± 0.246 (7.47 – 15.5)
WA-579, 2.95 km W of Yammera, FMNH 204700	32D	5⅛– (4¾– – 5⅝)	1.67 ± 0.037 (1.3 – 2.1)	9.06 ± 0.227 (6.95 – 11.9)
W. turbinata				
WA-200, 2.7 km W of Yammera, FMNH 199400	27D	4¾+ (4½ – 5⅛)	1.75 ± 0.050 (1.3 – 2.4)	8.16 ± 0.237 (5.88 – 10.5)
WA-358, 2.6 km W of Yammera, FMNH 200279	6L	5+ (4⅞+ – 5¼–)	1.46 ± 0.272 (1.2 – 1.7)	9.58 ± 0.487 (8.41 – 11.8)
WA-381, 2.4 km W of Yammera, FMNH 199143	46D	5 (4⅝– – 5½+)	1.54 ± 0.042 (0.9 – 2.3)	9.46 ± 0.274 (6.09 – 14.9)
WA-380, 2.3 km W of Yammera, FMNH 199145	38D	5– (4½+ – 5¾–)	1.71 ± 0.045 (1.1 – 2.15)	8.23 ± 0.269 (6.14 – 13.5)
WA-329, S side, 6.9 km SE of Wombarella, FMNH 199271	39D	4⅞ (4½– – 5¼)	1.61 ± 0.052 (0.9 – 2.2)	8.47 ± 0.312 (5.64 – 13.7)
WA-382, 2.1 km W of Yammera, FMNH 199346	51D	4⅞+ (4½ – 5⅜)	1.64 ± 0.042 (0.9 – 2.5)	8.41 ± 0.246 (5.30 – 14.6)
WA-573, 2.08 km W of Yammera, FMNH 204687	3D	5	1.48 (1.3 – 1.7)	9.37 (8.09 – 10.7)
WA-575, 1.93 km W of Yammera, FMNH 204692	10D	5⅛– (4¾+ – 5⅜–)	1.34 ± 0.089 (0.9 – 1.9)	10.6 ± 0.835 (6.79 – 15.1)
WA-580, 1.65 km W of Yammera, FMNH 204702	8D	5⅛– (5 – 5¼+)	1.12 ± 0.114 (0.6 – 1.5)	13.6 ± 1.850 (9.4 – 25.1)
WA-306, 1.6 km W of Yammera, FMNH 199169	37D	5⅛ (4⅝+ – 5½+)	1.42 ± 0.046 (1.0 – 2.25)	9.83 ± 0.296 (6.53 – 13.5)

Table 51: Local Variation in Typical *Westraltrachia turbinata*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
W of Yammera Gap				
WA-571, 1.58 km W of Yammera, FMNH 204682	9D	10.21 ± 0.213 (9.3 – 11.25)	13.40 ± 0.133 (12.65 – 13.9)	0.761 ± 0.010 (0.716 – 0.812)
WA-572, 1.58 km W of Yammera, FMNH 204686	8D	9.42 ± 0.305 (8.45 – 10.95)	12.73 ± 0.272 (11.75 – 13.85)	0.739 ± 0.010 (0.715 – 0.791)
WA-570, 1.58 km W of Yammera, FMNH 204681	9D	10.12 ± 0.212 (9.65 – 11.65)	13.09 ± 0.178 (12.35 – 14.1)	0.773 ± 0.021 (0.699 – 0.910)
WA-402, 1.5 km W of Yammera, FMNH 199358	28D	9.92 ± 0.116 (8.5 – 11.5)	13.28 ± 0.114 (11.55 – 14.5)	0.747 ± 0.008 (0.664 – 0.818)
WA-360, 1.5 km W of Yammera, FMNH 199149	10D	9.85 ± 0.195 (8.9 – 10.8)	13.25 ± 0.137 (12.55 – 14.0)	0.744 ± 0.015 (0.674 – 0.797)
WA-568, 1.3 km W of Yammera, FMNH 204676	15D	10.10 ± 0.204 (8.9 – 12.2)	13.32 ± 0.232 (12.6 – 14.7)	0.759 ± 0.014 (0.636 – 0.831)
WA-281, 1.3 km W of Yammera, FMNH 200269	7D	9.60 ± 0.039 (9.5 – 9.75)	13.16 ± 0.097 (12.9 – 13.65)	0.730 ± 0.008 (0.696 – 0.756)
WA-281, FMNH 199871	31D	9.09 ± 0.104 (7.8 – 10.35)	12.30 ± 0.140 (11.45 – 13.6)	0.732 ± 0.008 (0.677 – 0.808)
WA-199, 1.2 km W of Yammera, FMNH 199402	32D	10.21 ± 0.130 (9.15 – 12.0)	13.23 ± 0.101 (12.3 – 14.4)	0.773 ± 0.009 (0.677 – 0.896)
WA-400, 0.5 km W of Yammera, FMNH 199301	29D	9.58 ± 0.133 (8.5 – 11.15)	12.73 ± 0.086 (11.85 – 13.5)	0.752 ± 0.010 (0.678 – 0.878)
WA-301, NW side of Yammera, FMNH 200295	7L	10.58 ± 0.400 (9.0 – 11.7)	13.76 ± 0.523 (13.8 – 14.7)	0.734 ± 0.021 (0.647 – 0.796)
WA-301, FMNH 199183	86D	9.34 ± 0.085 (7.60 – 11.5)	13.53 ± 0.073 (12.2 – 15.6)	0.690 ± 0.004 (0.590 – 0.801)
E of Yammera Gap				
NR II-19, SE side of Yammera, WAM 1225.76	45D	9.71 ± 0.110 (8.2 – 11.1)	13.91 ± 0.096 (12.7 – 16.0)	0.698 ± 0.006 (0.608 – 0.767)
WA-303, 1.0 km W of Yammera, FMNH 199180	55D	9.53 ± 0.113 (7.9 – 12.3)	13.23 ± 0.096 (11.8 – 14.75)	0.721 ± 0.007 (0.617 – 0.837)
WA-196, 2.0 km W of Yammera, FMNH 199189	22D	9.91 ± 0.171 (9.0 – 11.6)	13.94 ± 0.165 (12.3 – 15.2)	0.711 ± 0.007 (0.658 – 0.773)
WA-351, 2.1 km W of Yammera, FMNH 200112	9D	10.41 ± 0.222 (9.8 – 11.6)	14.31 ± 0.121 (13.9 – 14.95)	0.727 ± 0.013 (0.690 – 0.795)
WA-351, FMNH 200114	15L	9.75 ± 0.150 (9.1 – 10.9)	13.64 ± 0.147 (12.8 – 14.6)	0.714 ± 0.006 (0.673 – 0.749)
WA-351, FMNH 199133	41D	9.61 ± 0.102 (8.5 – 10.9)	14.08 ± 0.113 (13.0 – 15.5)	0.683 ± 0.005 (0.623 – 0.745)

Table 51: Local Variation in Typical *Westraltrachia turbinata* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
NR II – 31, 2 km S of Yammera, WAM 302.80	28D	9.90 ± 0.127 (8.8 – 11.1)	13.98 ± 0.150 (12.3 – 15.9)	0.709 ± 0.008 (0.629 – 0.809)
WA-347, 2.9 km W of Yammera, FMNH 199106	32D	10.21 ± 0.147 (8.5 – 12.7)	13.83 ± 0.152 (12.3 – 15.95)	0.739 ± 0.009 (0.644 – 0.883)
WA-341, 3.1 km W of Yammera, FMNH 199137	40D	9.28 ± 0.096 (7.95 – 10.5)	13.57 ± 0.105 (12.3 – 15.3)	0.684 ± 0.005 (0.620 – 0.750)
WA-344, 3.2 km W of Yammera, FMNH 199080	24D	9.71 ± 0.147 (8.1 – 11.1)	14.31 ± 0.115 (13.5 – 15.4)	0.678 ± 0.007 (0.600 – 0.739)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
W of Yammera Gap				
WA-571, 1.58 km W of Yammera, FMNH 204682	9D	5¼ + (5 + – 5⅝ +)	1.19 ± 0.051 (0.95 – 1.45)	11.4 ± 0.481 (9.17 – 13.3)
WA-572, 1.58 km W of Yammera, FMNH 204686	8D	5 + (4⅝ – 5⅜)	1.25 ± 0.089 (0.9 – 1.7)	10.5 ± 0.753 (8.03 – 13.9)
WA-570, 1.58 km W of Yammera, FMNH 204681	9D	5⅛ + (4⅞ + – 5½)	1.17 ± 0.065 (0.9 – 1.4)	11.5 ± 0.567 (9.64 – 14.3)
WA-402, 1.5 km W of Yammera, FMNH 199358	28D	5¼ – (4⅞ – – 5⅝ –)	1.33 ± 0.030 (1.0 – 1.6)	10.2 ± 0.244 (8.25 – 12.7)
WA-360, 1.5 km W of Yammera, FMNH 199149	10D	5⅛ (4¾ + – 5⅜)	1.33 ± 0.082 (1.0 – 1.7)	10.3 ± 0.582 (7.77 – 12.6)
WA-568, 1.3 km W of Yammera, FMNH 204676	15D	5¼ (4⅞ – 5⅞)	1.26 ± 0.086 (0.7 – 2.0)	11.3 ± 0.777 (7.0 – 18.3)
WA-281, 1.3 km W of Yammera, FMNH 200269	7D	5⅛ (5 – – 5¼)	1.49 ± 0.092 (1.2 – 1.9)	9.04 ± 0.521 (7.18 – 11.1)
WA-281, FMNH 199871	31D	5 (4¾ – – 5⅜)	1.30 ± 0.048 (0.75 – 1.85)	10.0 ± 0.397 (6.74 – 16.1)
WA-199, 1.2 km W of Yammera, FMNH 199402	32D	5¼ – (4¾ – – 5¾)	1.23 ± 0.052 (0.65 – 1.90)	11.4 ± 0.488 (6.89 – 19.9)
WA-400, 0.5 km W of Yammera, FMNH 199301	29D	5⅛ (4⅝ – 5⅜ +)	1.25 ± 0.043 (0.85 – 1.7)	10.5 ± 0.369 (7.63 – 14.9)
WA-301, NW side of Yammera, FMNH 200295	7L	5⅛ + (5 + – 5⅜ +)	1.30 ± 0.095 (1.0 – 1.7)	11.3 ± 0.815 (8.53 – 14.5)
WA-301, FMNH 199183	86D	5⅛ (4⅝ – – 5½ –)	1.51 ± 0.032 (0.75 – 2.3)	9.39 ± 0.236 (6.25 – 17.6)
E of Yammera Gap	45D	5 + (4⅝ + – 5¼ +)	1.31 ± 0.044 (0.6 – 2.1)	11.2 ± 0.389 (6.81 – 21.8)

Table 51: Local Variation in Typical *Westraltrachia turbinata* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
NR II-19, SE side of Yammera, WAM 1225.76				
WA-303, 1.0 km W of Yammera, FMNH 199180	55D	5+ (4½ – 5½)	1.31 ± 0.041 (0.7 – 2.1)	10.6 ± 0.341 (6.45 – 18.8)
WA-196, 2.0 km W of Yammera, FMNH 199189	22D	5¼ – (4⅞ + – 5½ +)	1.42 ± 0.061 (0.9 – 2.1)	10.2 ± 0.476 (6.64 – 14.8)
WA-351, 2.1 km W of Yammera, FMNH 200112	9D	5¼ (4⅞ + – 5½)	1.24 ± 0.072 (0.9 – 1.55)	11.9 ± 0.776 (9.16 – 16.2)
WA-351, FMNH 200114	15L	5⅛ + (5 – – 5⅝)	1.31 ± 0.076 (0.85 – 1.95)	10.9 ± 0.572 (7.05 – 15.2)
WA-351, FMNH 199133	41D	5 + (4⅜ + – 5½ –)	1.33 ± 0.039 (0.8 – 1.86)	11.1 ± 0.451 (6.99 – 17.0)
NR II – 31, 2 km W of Yammera, WAM 302.80	28D	5⅛ (4¾ – 5⅝ –)	1.28 ± 0.048 (0.9 – 1.9)	11.3 ± 0.426 (8.0 – 15.1)
WA-347, 2.9 km W of Yammera, FMNH 199106	32D	5¼ – (4⅞ – – 5½ +)	1.24 ± 0.045 (0.8 – 1.7)	11.6 ± 0.418 (7.65 – 16.2)
WA-341, 3.1 km W of Yammera, FMNH 199137	40D	5 + (4½ + – 5¼ +)	1.49 ± 0.038 (0.9 – 2.05)	9.39 ± 0.290 (6.88 – 15.9)
WA-344, 3.2 km W of Yammera, FMNH 199080	24D	5⅛ (4¾ – – 5¾ –)	1.63 ± 0.067 (1.1 – 2.4)	9.14 ± 0.370 (6.17 – 13.1)

WESTRALTRACHIA INOPINATA SP. NOV.

(Plates 20a-b, 26d, 36; Figs 117d-f, 119-121, 158c)

Comparative remarks

Westraltrachia inopinata is a medium-sized species with moderately elevated spire, an open umbilicus, strongly curved spire whorls, and very pale yellow-brown colour on the spire. It is larger and much less elevated than the neighbouring *W. turbinata* **(Table 47),** smaller and with fewer, more loosely coiled, more strongly rounded whorls than *W. commoda* (Iredale, 1939) (compare **Figs 115** and **117).** The keeled periphery and dense surface sculpture distinguish *W. froggatti* (Ancey, 1898). The lack of radial sculpture other than irregular growth striae, and broadly expanded lip combine with the plain shell colour to distinguish *W. inopinata* from any of the other eastern species. Anatomically **(Figs 119a-b),** the relatively massive penis muscle (PM), long free oviduct (UV), relatively short and thick penis (P), and shorter, thicker vagina (V) separate *W. inopinata* from *W. turbinata* **(Figs 118a-b),** while *W. commoda* (Iredale, 1939) has a much shorter and thicker vagina (V), longer penis (P), and noticeably longer free oviduct (UV, **Figs 116a-c).**

Holotype

WAM 733.79, Sta. WA-339, 1.1 km east of Yammera Gap, south side of Napier Range, Western Australia (1:100,000 'Lennard' map sheet 3863, grid reference 942:812). Collected by L. Price and C. Christensen 23 December 1976. Height of shell 8.8 mm, diameter 15.9 mm, H/D ratio 0.533, whorls 4⅝, umbilical width 1.6 mm, D/U ratio 9.94.

Paratopotypes

WAM 68.80, WAM 730.79, FMNH 199097, FMNH 200157, 8 live, 45 dead adults from the type locality.

Paratypes

Napier Range, geographic sequence north-west to south-east: Sta. WA-302, east side of Yammera Gap, centre of gap ('Lennard' 3863 – 937:819) (32 dead adults, WAM 725.79, FMNH 199186); NR II-19a, south-east side Yammera Gap, high on cliff (40 dead adults, WAM 1224.76); NR II-19b, around south-east corner Yammera Gap (25 dead adults, WAM 1223.76); Sta. WA-305, 0.5 km east of Yammera Gap, south side ('Lennard' 3863 – 938:815) (13 live, 70 dead adults, 10 live, 2 dead juveniles, WAM 726.79-729.79, FMNH 199194, FMNH 199247, FMNH 200262, FMNH 200265); Sta. WA-340, 1.9 km east of Yammera Gap, south side ('Lennard' 3863 – 948:808) (33 dead adults, WAM 731.79, FMNH 199082); Sta. WA-349, 2.0 km east of Yammera Gap, south side ('Lennard' 3863 – 950:808) (1 live, 19 dead adults, WAM 732.79, FMNH 199131, FMNH 200137).

Distribution limits in Napier Range

Westraltrachia inopinata ranges from the centre of the east side of Yammera Gap for 2 km along the south face of the Range to Sta. WA-349 **(Fig. 159).**

Diagnosis

Shell of medium size, diameter 11.1-18.3 mm (mean 14.63 mm), with 4⅛ to 5½ (mean 5⅛ –) rather loosely coiled whorls **(Fig. 117d).** Apex and spire moderately and evenly elevated **(Fig. 117e),** whorls of spire strongly rounded, spire of shell rounded, height of shell 6.55-11.1 mm (mean 8.72 mm), H/D ratio 0.503-0.715 (mean 0.596). Apical whorls **(Plate 20a-b)** smooth, occasionally micro-ridges visible in suture. Postnuclear whorls with fine spiral lines visible in very fresh shells, otherwise only occasional weak radial growth striae. Shell periphery rounded or weakly obtusely angulated **(Fig. 117e).** Lip markedly expanded and reflected **(Figs 117d-f),** body whorl normally descending moderately just behind lip. Umbilicus open, only partially closed by basal lip reflection **(Fig. 117f),** umbilical width 0.8-2.4 mm (mean 1.51 mm), D/U ratio 6.00-19.4 (mean 10.0). Colour on spire yellow-brown to light yellow-brown, becoming lighter in tone to white on body whorl, juveniles darker. Based on 278 measured adults.

Genitalia **(Figs 119a-b)** with large penis muscle (PM) extending down along penis (P), epiphallic loop large. Principal pilaster (PT, **Fig. 158c)** typical, short. Penis (P) relatively short, thick, not folded. Penis sheath (PS) slightly thicker near base. Vas deferens (VD) entering penis sheath opposite base of epiphallus (E, **Fig. 119b).** Vagina (V) medium in length and diameter, spermatheca (S) much shorter than free oviduct (UV), which normally is slightly looped.

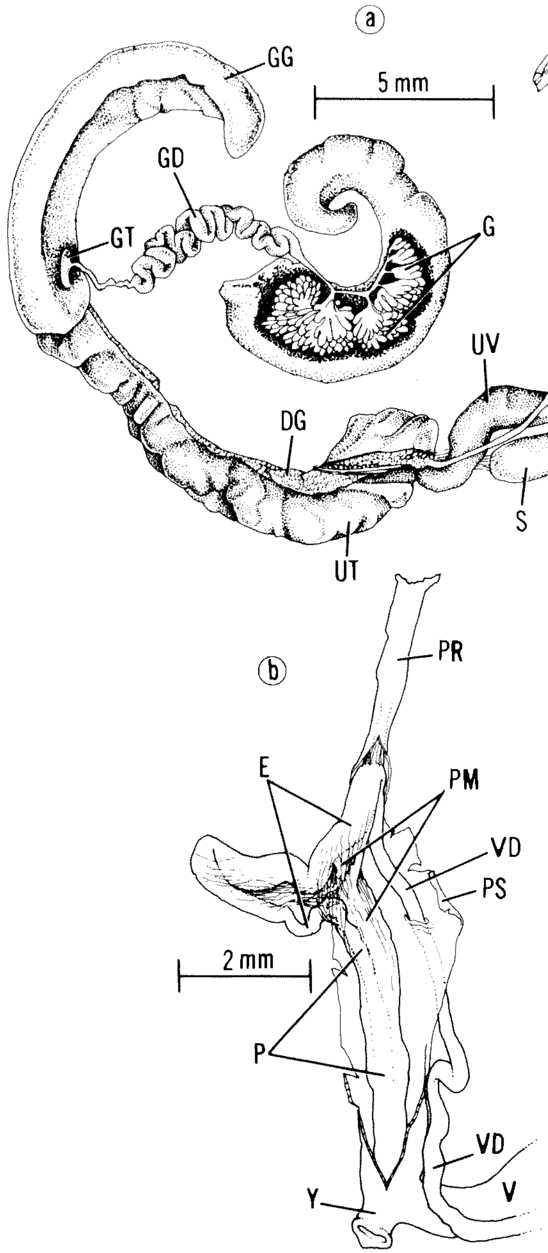


Fig. 119: Genitalia of *Westraltrachia inopinata:* Sta. WA-339, 1.1 km east of Yammera Gap, Napier Range, 23 December 1976, FMNH 200157, (a) whole genitalia, Dissection A, (b) interior of penis sheath, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

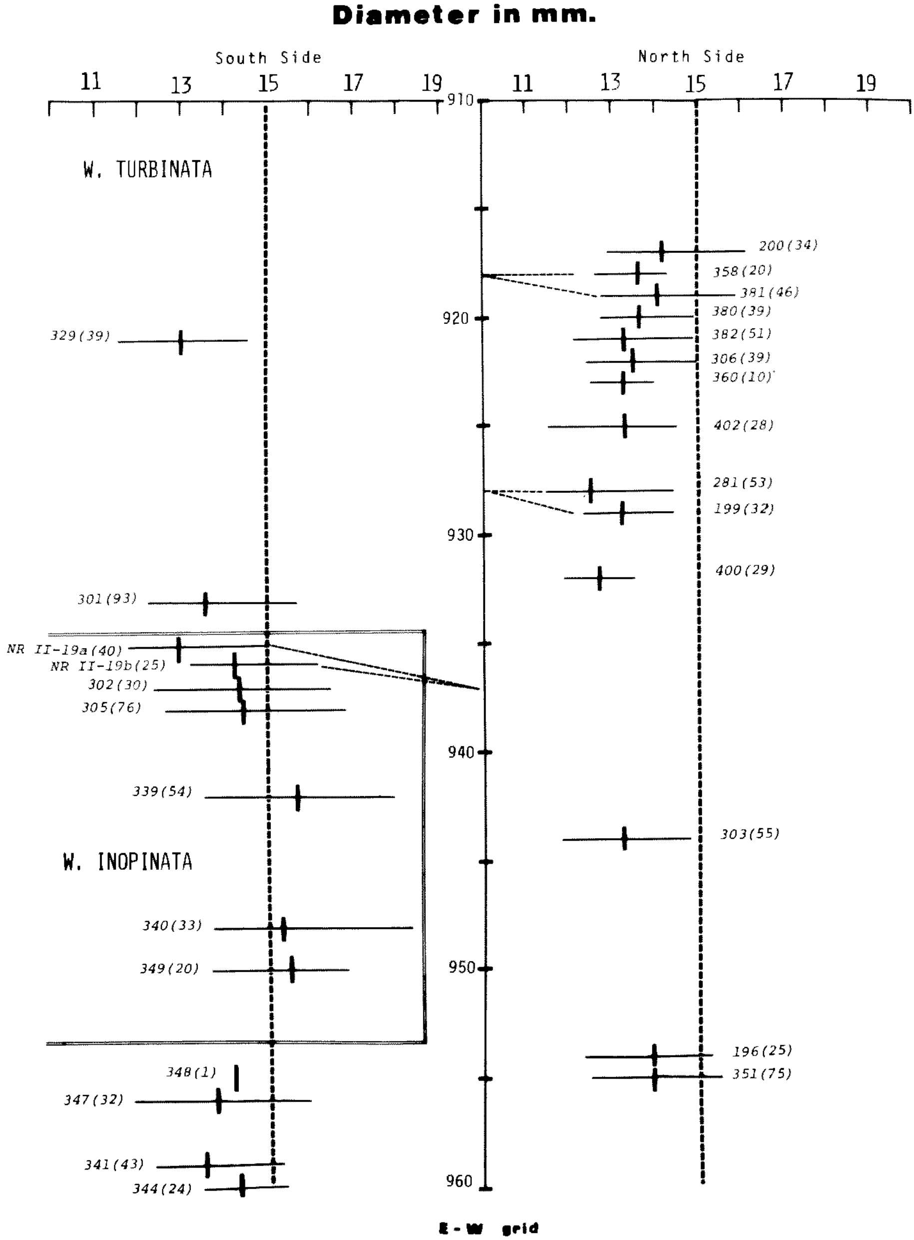


Fig. 120: Geographic variation in shell diameter in *Westraltrachia turbinata* and *W. inopinata.* Center line E-W grid coordinates from 1:100,000 "'Lennard" 3863 map sheet. Station numbers as listed in text, number of specimens measured in "()", plotted as to south and north side of range localities. Mean and range indicated for each station. Drafted by Dorothy Karall.

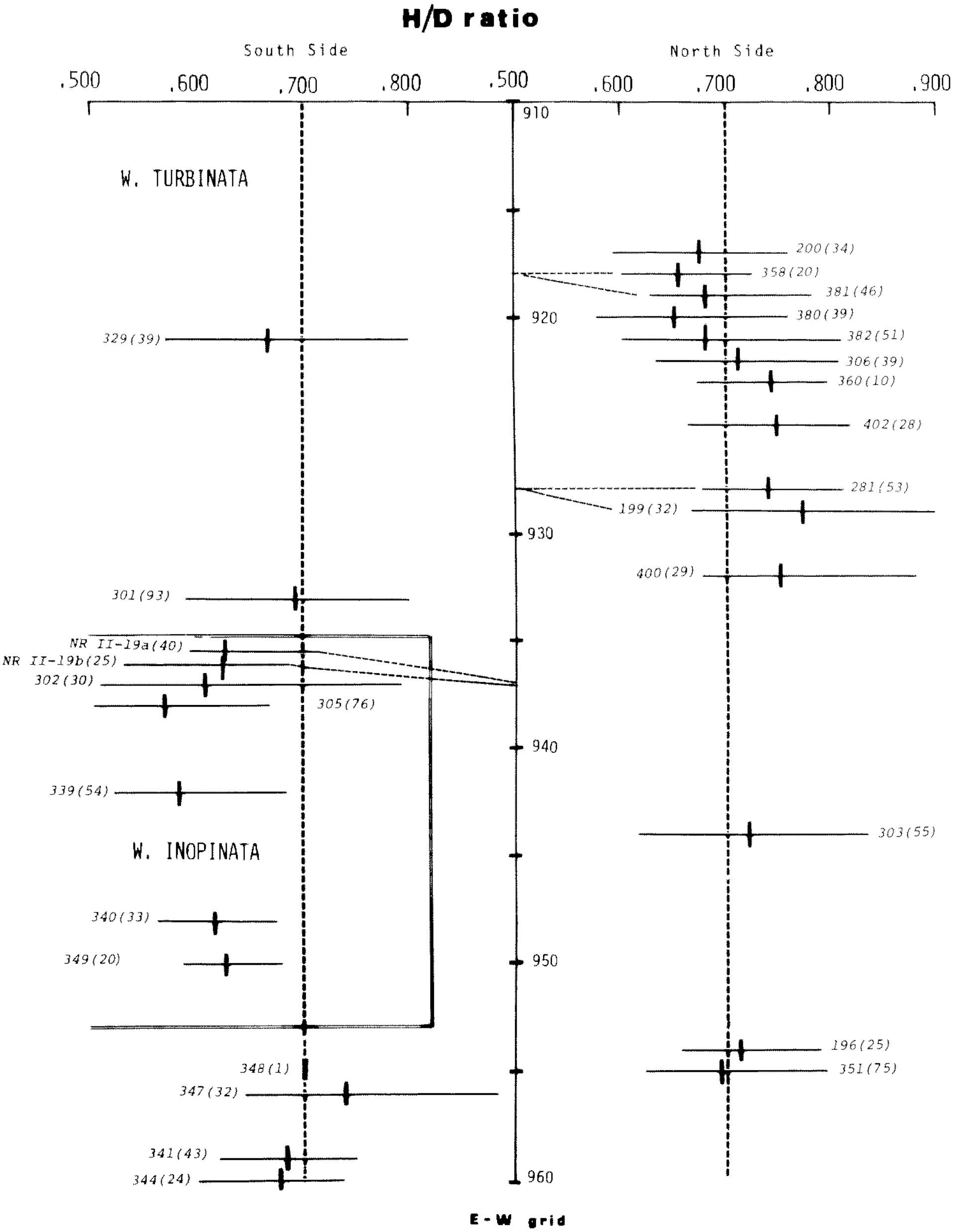


Fig. 121: Geographic variation in shell H/D ratio for *Westraltrachia turbinata* and *W. inopinata*. Center line E-W grid coordinates from 1:100,000 "'Lennard" 3863 map sheet. Station numbers as listed in text, number of specimens measured in "()", plotted as to south and north side of range localities. Mean and range indicated for each station. Drafted by Dorothy Karall.

Jaw (**Plate 26d**) macroscopically smooth, horizontal growth striae often prominent. Radular teeth highly modified (**Plate 36**) to pattern seen in *Westraltrachia woodwardi* (Fulton, 1902).

Discussion

Westraltrachia inopinata looks like a darker coloured, slightly smaller form of *W. commoda* (Iredale, 1939) in general appearance. Comparison of shells demonstrate that the whorls of *W. inopinata* are much more strongly rounded on the spire, increase in width more rapidly, the umbilicus is more open, and the lip less expanded. These are difficult features to quantify, and, except for the umbilical changes, are not quantified here (**Tables 47, 52**). In colour, whorl contour, lip expansion, and umbilical form, *W. inopinata* is much more like *W. turbinata*, and I interpret the similarities to *W. commoda* as convergent shape and size results. The only species of camaenid sympatric with *W. inopinata* is *Amplirhagada b. burnerensis* (Smith, 1894), which ranges east from Yammera Gap to well east of Windjana Gorge. It has a similar spire

Table 52: Local Variation in *Westraltrachia inopinata*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
NR II-19a, SE side Yammera Gap, WAM 1224.76	40D	8.28 ± 0.107 (7.2—10.0)	12.87 ± 0.150 (11.1—14.7)	0.644 ± 0.006 (0.581—0.715)
NR II-19b, around SE corner Yammera Gap, WAM 1223.76	25D	8.49 ± 0.155 (7.3—9.65)	14.63 ± 0.160 (13.4—16.15)	0.581 ± 0.008 (0.503—0.673)
WA-302, SE side Yammera Gap, centre of gap, FMNH 199186	30D	8.44 ± 0.167 (6.95—10.8)	14.24 ± 0.163 (12.3—16.2)	0.595 ± 0.007 (0.507—0.684)
WA-305, 0.5 km E of Yammera, S side FMNH 199247	63D	8.20 ± 0.124 (6.55 – 10.3)	14.32 ± 0.135 (12.3 – 16.8)	0.569 ± 0.005 (0.503 – 0.667)
WA-305, FMNH 200062, FMNH 200265	8L	8.61 ± 0.242 (7.75 – 9.90)	15.42 ± 0.307 (14.2 – 16.45)	0.559 ± 0.011 (0.526 – 0.611)
WA-339, 1.1 km SE of Yammera Gap, S side, FMNH 199097	46D	9.20 ± 0.125 (7.2 – 10.6)	15.73 ± 0.138 (13.5 – 17.9)	0.584 ± 0.005 (0.522 – 0.684)
WA-339, FMNH 200157	8L	8.83 ± 0.251 (8.3 – 10.3)	15.21 ± 0.232 (14.3 – 16.35)	0.580 ± 0.009 (0.546 – 0.630)
WA-340, 1.9 km SE of Yammera Gap, S side, FMNH 199082	33D	9.44 ± 0.124 (8.0 – 11.1)	15.32 ± 0.177 (13.7 – 18.3)	0.617 ± 0.005 (0.563 – 0.673)
WA-349, 2.0 km SE Yammera Gap, S side, FMNH 199131	19D	9.72 ± 0.122 (8.75 – 10.5)	15.52 ± 0.179 (13.7 – 16.8)	0.626 ± 0.005 (0.586 – 0.679)

Table 51: Local Variation in Typical *Westraltrachia turbinata* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
NR II-19a, SE side Yammera Gap, WAM 1224.76	40D	4 ¾ – (4 ⅛ – 5 +)	1.36 ± 0.035 (1.0 – 2.05)	9.66 ± 0.224 (6.1 – 12.6)
NR II-19b, around SE corner Yammera Gap, WAM 1223.76	25D	4 ¾ – (4 ¼ – 5 ¼ –)	1.41 ± 0.051 (1.0 – 2.0)	10.7 ± 0.366 (7.33 – 13.9)
WA-302, SE side Yammera Gap, centre of gap, FMNH 199186	30D	4 ¾ + (4 ¼ – 5 ⅛ +)	1.59 ± 0.058 (1.2 – 2.1)	9.36 ± 0.358 (6.52 – 13.5)
WA-305, 0.5 km E of Yammera, S side, FMNH 199247	63D	4 ⅝ (4 ⅛ + – 5 ¼ +)	1.63 ± 0.037 (1.1 – 2.4)	9.10 ± 0.245 (6.00 – 13.9)
WA-305, FMNH 200062, FMNH 200265	8L	4 ⅞ (4 ½ – 5 ¼)	1.78 ± 0.125 (1.3 – 2.2)	9.00 ± 0.694 (6.77 – 12.6)
WA-339, 1.1 km SE of Yammera Gap, S side, FMNH 199097	46D	4 ⅝ + (4 ¼ + – 5 ⅛ –)	1.61 ± 0.038 (1.05 – 2.15)	10.0 ± 0.264 (7.46 – 14.3)
WA-339, FMNH 200157	8L	4 ¾ – (4 ⅜ + – 5 +)	1.63 ± 0.125 (1.35 – 2.4)	9.64 ± 0.621 (6.33 – 11.7)
WA-340, 1.9 km SE of Yammera Gap, S side, FMNH 199082	33D	4 ¾ + (4 ⅜ + – 5 ⅛ +)	1.41 ± 0.046 (0.9 – 1.85)	11.3 ± 0.429 (7.62 – 17.6)
WA-349, 2.0 km SE Yammera Gap, S side, FMNH 199131	19D	5 – (4 ¾ – 5 ½)	1.30 ± 0.079 (0.8 – 2.1)	12.7 ± 0.745 (7.21 – 19.4)

colour, but is immediately recognisable by its closed umbilicus, almost complete absence of lip expansion, bright red colour behind the aperture and on part of the body whorl, evenly rounded shell periphery, much larger size (mean diameters 18.44-19.44 mm) and higher whorl count (means 5⅝+ to 5⅞) in populations from this area (Solem, 1981a: 244, figs. 48c-d).

At the time of collection this was not recognised as being a distinct species and thus no special notes were made on the occurrence of the few live specimens obtained. The name *inopinata,* from the Latin word for unexpected, celebrates this fact.

WESTRALTRACHIA FROGGATTI (ANCEY, 1898)

Comparative remarks

This is perhaps the most readily recognised species of *Westraltrachia.* The combination of keeled, acutely angled periphery **(Figs 122b, e),** and postnuclear sculpture of triangular protrusions **(Plates 20c-f)** is unique. *Westraltrachia ascita,* which ranges, from the Virgin Hills to the fringes of the Laidlaw Range, east of Fitzroy Crossing, has the same postnuclear sculpture (**Plate 25**), but a shell shape very similar to that of *Semotrachia,* with brown colour, rounded periphery, and only slightly elevated spire. Some of the Oscar Range species have an angled periphery, but none of these show any traces of the distinctive postnuclear sculpture. Anatomical changes are equally gross.

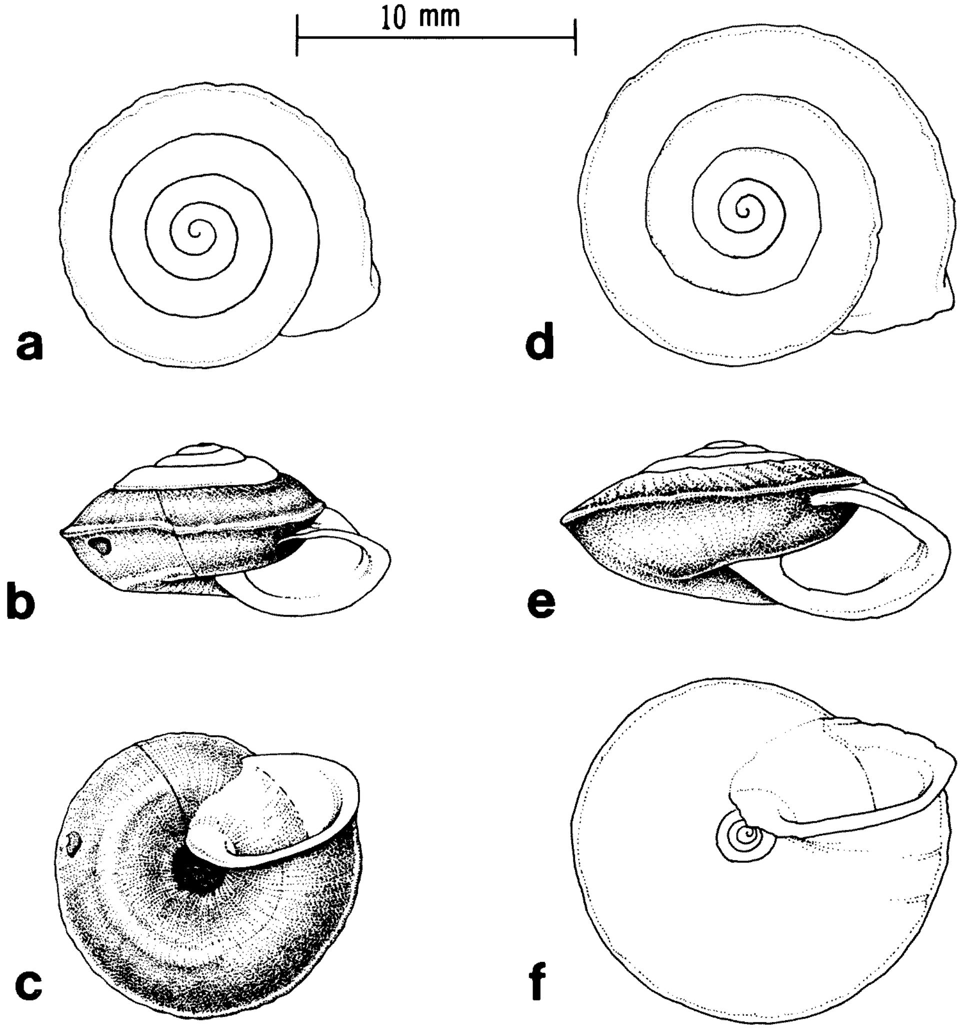


Fig. 122: Shells of *Westraltrachia froggatti* (Ancey, 1898): (a-c) holotype of *Trachia froggatti* Ancey, 1898, AM C.64884; (d-f) holotype of *Westraltrachia froggatti complanata,* Sta. WA-350, 2.4 km east of Yammera Gap, north side Napier Range, WAM 806.79. Scale line equals 10 mm. Drawings of (a-c) by Elizabeth Liebman, (d-f) by Linnea Lahlum.

The vas deferens enters the penis sheath midway along the penis **(Figs 123b, 124c)** and the elongated penis is folded within the sheath, a situation that contrasts markedly with structures in the Western Napier Range *Westraltrachia.*

Westraltrachia froggatti (Ancey, 1898) ranges from 1 km east of Yammera Gap to the west bank of Windjana Gorge, except for the small area on the south side of the Napier Range occupied by *W. inopinata,* 2.0 km from Yammera Gap at Sta. WA-349, with the first record for *W. froggatti* occurring at 2.4 km east (Sta. WA-249). No collecting has been done in the intermediate 400 metres of cliff face. Variation in *W. froggatti* is comparatively minor over much of its range, but shortly before Windjana Gorge, somewhere between Stas. WA-193 and WA-337 on the south side, and WA-310 (8.5 km north-west of Windjana Gorge) and NR II-23 (Biltyara Spring embayment, *ca.* 5 km north-west of Windjana Gorge), there is a sharp reduction in whorl count and diameter **(Figs 125, 126)** that is recognised by subspecific designations. The populations nearer to Windjana Gorge are *W. f. froggatti* (Ancey, 1898) and those ranging east almost to Yammera Gap are here named *W. f. complanata.*

Table 53: Local Variation in Selected Populations of *Westraltrachia froggatti* (Ancey, 1898)

Taxon	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
W. f. complanata				
WA-303,dead, FMNH 199177	20	8.92 ± 0.139 (8.0 – 10.5)	17.00 ± 0.206 (15.3 – 18.9)	0.526 ± 0.008 (0.480 – 0.607)
WA-348, dead, FMNH 199124	33	9.24 ± 0.103 (7.3 – 10.4)	17.81 ± 0.184 (15.0 – 19.7)	0.520 ± 0.006 (0.454 – 0.591)
WA-344, dead, FMNH 199079	23	8.16 ± 0.103 (7.4 – 9.0)	16.71 ± 0.202 (14.5 – 18.2)	0.489 ± 0.005 (0.448 – 0.548)
WA-350, dead, FMNH 199126	37	7.75 ± 0.091 (6.7 – 9.4)	16.03 ± 0.138 (14.1 – 17.8)	0.484 ± 0.005 (0.432 – 0.555)
WA-197, dead, FMNH 199390	120	7.84 ± 0.050 (6.5 – 9.45)	16.40 ± 0.077 (14.3 – 18.3)	0.478 ± 0.002 (0.402 – 0.568)
WA-310, dead, FMNH 199336	52	8.26 ± 0.084 (7.0 – 10.0)	16.18 ± 0.119 (14.3 – 18.2)	0.511 ± 0.004 (0.448 – 0.599)
W. f. froggatti				
WA-193A, dead, FMNH 199430	105	7.29 ± 0.055 (6.0 – 8.6)	13.98 ± 0.076 (12.2 – 16.0)	0.521 ± 0.003 (0.430 – 0.589)
WA-309, dead, FMNH 199173	25	7.50 ± 0.127 (6.4 – 8.9)	14.98 ± 0.165 (13.7 – 16.8)	0.501 ± 0.007 (0.438 – 0.584)
WA-308, dead, FMNH 199175	36	6.23 ± 0.108 (5.0 – 7.8)	14.98 ± 0.193 (12.2 – 16.9)	0.416 ± 0.005 (0.348 – 0.478)

Table 53: Local Variation in Selected Populations of *Westraltrachia froggatti* (Ancey, 1898) (continued)

Taxon	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
W.f. complanata				
WA-303, dead, FMNH 199177	20	5 + (4¾ – 5⅜)	1.37 ± 0.082 (0.7 – 2.1)	13.4 ± 0.92 (8.24 – 25.1)
WA-348, dead, FMNH 199124	33	5⅛ + (4¾ – 5½)	1.80 ± 0.067 (1.0 – 2.45)	10.4 ± 0.44 (7.48 – 17.9)
WA-344, dead, FMNH 199079	23	4⅞ (4¼ – 5¼)	1.51 ± 0.058 (1.1 – 2.19)	11.5 ± 0.45 (7.40 – 15.7)
WA-350, dead, FMNH199126	37	4⅞ (4½ – 5⅜)	1.35 ± 0.059 (0.6 – 2.25)	12.8 ± 0.68 (7.23 – 27.4)
WA-197, dead, FMNH 199390	120	4⅞ + (4½ – 5⅜)	1.47 ± 0.026 (0.85 – 2.2)	11.61 ± 0.21 (7.45 – 19.3)
WA-310, dead, FMNH 199336	52	5 – (4 – 5½)	1.39 ± 0.035 (0.9 – 2.1)	11.97 ± 0.30 (8.14 – 20.2)
W. f. froggatti				
WA-193A, dead, FMNH 199430	105	4½ + (4⅛ – 5½)	1.21 ± 0.025 (0.65 – 1.95)	12.13 ± 0.28 (7.31 – 22.9)
WA-309, dead, FMNH 199173	25	4¾ + (4 – 5⅜)	1.34 ± 0.066 (0.7 – 2.1)	11.85 ± 0.62 (6.95 – 20.3)
WA-308, dead, FMNH 199175	36	4⅝ – (4¼ – 5)	1.69 ± 0.048 (1.05 – 2.3)	9.10 ± 0.27 (6.94 – 13.8)

Further fieldwork is needed to determine the exact western limits of live snails, and the exact nature of overlap and replacement between *Westraltrachia froggatti* and *W. turbinata.* On the north side of the Range, we collected:

Station	*W. turbinata*		*W. f. complanata*	
	Live	Dead	Live	Dead
WA-303	–	55	–	20
WA-196	–	25	–	6
WA-351	67	40	–	3
WA-304	–	–	1	46

On the south side of the Range we collected:

Station	*W. turbinata*		*W. f. complanata*	
	Live	Dead	Live	Dead
WA-348	–	1	4	33
WA-347	–	33	–	22
WA-341	9	40	–	–
WA-344	–	24	–	23
WA-345	–	–	–	22
WA-346	–	–	12	18

The boundary between *W. inopinata* (1 live, 19 dead adults at Sta. WA-349) and *W. f. complanata* (1 live, 33 dead adults, 3 live juveniles at Sta. WA-348) is somewhere in the unsampled 0.4 km of cliff face between the two stations.

It is interesting that in part of the area of overlap, specimens of *Westraltrachia f. complanata* (Stas. WA-347 and WA-348) are slightly enlarged **(Tables 51-53)** in both diameter and whorl count **(Figs. 125, 126).** This could be an example of character displacement in shell size, but detailed observations on the micro-distribution of the two taxa are needed to see if potential space competition exists between the similar sized, but very differently shaped *W. turbinata* and *W. f. complanata.*

The two subspecies are discussed in geographic order, west to east.

WESTRALTRACHIA FROGGATTI COMPLANATA SUBSP. NOV.

(Plates 20c-e, 26c, 37a-c; Figs 122d-f, 123, 125, 126, 158d)

Comparative remarks

Westraltrachia froggatti complanata differs from the nominate race in averaging 1.6 mm more in diameter, and ¼ whorl more **(Table 47).** The combination of acutely angled, keeled periphery **(Fig. 122e),** very low H/D ratio (mean 0.483), and postnuclear sculpture of crowded projections **(Plate 20d-e)** easily separate *W. froggatti complanata* from other species of *Westraltrachia.* In the Napier Range, only *Mouldingia occidentalis* from near McSherry Gap could be confused, but that species has very prominent radial ribs, sulci above and below a rounded periphery, and a much more open umbilicus **(Figs 163a-c).** Anatomically, the long folded penis (P) and entry of the vas deferens (VD) through the penis sheath occurring far below the epiphallic base **(Figs 123b, 124c)** are sufficient to separate *W. f. complanata* from any of the western Napier Range species, while *W. derbyi* (Cox, 1892) on the east side of Windjana Gorge has the penis shortened, epiphallic loop reduced, a slightly higher entrance of the vas deferens **(Figs 129c-e),** and the principal pilaster in the penis is a long, partly corrugated ridge **(Fig. 158e).**

Holotype

WAM 806.79, Sta. WA-350, 2.4 km south-east of Yammera Gap, north side of Napier Range, Western Australia (1:100,000 'Lennard' map sheet 3863, grid reference 960:814). Collected by L. Price and C. Christensen 28 December 1976. Height of shell 7.95 mm, diameter 16.7 mm, H/D ratio 0.476, whorls 5, umbilical width 1.6 mm, D/U ratio 10.4.

Paratopotypes

WAM 772.79, WAM 774.79, FMNH 199126, FMNH 200170, 10 live, 37 dead adults, 9 live juveniles from the type locality.

Paratypes

Napier Range, geographic sequence north-west to south-east: Sta. WA-303, 1.0 km east of Yammera Gap, north side ('Lennard' 3863 – 944:818) (1 live, 20 dead adults, WAM 764.79, FMNH 199177, FMNH 200096); Sta. WA-196, 2 km east of Yammera

Gap, north side ('Lennard' 3863 – 954:815) (4 dead adults, 2 dead juveniles, WAM 765.79, WAM 766.79, FMNH 198989, FMNH 199190, FMNH 199420); Sta. WA-348, canyon mouth 2.4 km east of Yammera Gap, south side ('Lennard' 3863 – 955:807) (1 live, 33 dead adults, 3 live juveniles, WAM 767.79, FMNH 199124, FMNH 200160); Sta. WA-351, 2.1 km east of Yammera Gap, north side ('Lennard' 3863 – 955:815) (3 dead adults, WAM 766.79, FMNH 199134, FMNH 200113); Sta. WA-347, canyon 2.9 km east of Yammera Gap, south side ('Lennard' 3863 – 956:806) (22 dead adults, WAM 769.79, FMNH 199105); Sta. WA-344, north-east side of low cliff, south-east side canyon, 3.2 km east of Yammera Gap, south side ('Lennard' 3863 – 960:807) (23 dead adults, 2 dead juveniles, WAM 770.79, FMNH 199079); Sta. WA-345, hill just north-east of WA-344, 3.2 km east Yammera Gap, south side ('Lennard' 3863 – 960:807) (22 dead adults, 2 dead juveniles, WAM 771.79, FMNH 199128); Sta. WA-346, north-east slope canyon *ca.* 0.2 km from WA-344, 3.4 km east Yammera Gap, south side ('Lennard' 3863 – 962:808) (5 live, 18 dead adults, 7 live juveniles, WAM 773.79, WAM 775.79, FMNH 199136, FMNH 200132); Sta. WA-343, 3.6 km east Yammera Gap, south side ('Lennard' 3863 – 964:807) (30 dead adults, 5 dead juveniles, WAM 776.79, FMNH 199113); Sta. WA-304, 3.2 km east of Yammera Gap, north side ('Lennard' 3863 – 969:815) (46 dead adults, 1 live juvenile, WAM 777.79, FMNH 199249, FMNH 200106); Sta. WA-342, 4.8 km east of Yammera Gap, south side ('Lennard' 3863 – 973:807) (1 live, 42 dead adults, 1 live juvenile, WAM 778.79, FMNH 199099, FMNH 200117, FMNH 200743); Sta. WA-338, 4.3 km east of Yammera Gap, south side ('Lennard' 3863 – 977:808) (5 live, 35 dead adults, 2 live, 2 dead juveniles, WAM 779.79-780.79, FMNH 199276, FMNH 200154); Sta. WA-198, 4.25 km east of Yammera Gap, north side ('Lennard' 3863 – 978:811) (38 dead adults, 5 dead juveniles, WAM 781.79, FMNH 199447); NR II-30, *ca.* 5 km south-east of Yammera Gap, north side (66 dead adults, WAM 1226.76); NR II-21, *ca.* 5.3 km south-east of Yammera Gap, north side (48 dead adults, WAM 1227.76); Sta. WA-197, 5.8 km east of Yammera Gap, north side ('Lennard' 3863 – 991:807); (2 live, 120 dead adults, 2 live, 16 dead juveniles, WAM 782.79, FMNH 199390, FMNH 200009, FMNH 200714); Sta. WA-337, cliff base 6.4 km east of Yammera Gap, south side ('Lennard' 3863 – 991:786) (32 dead adults, 1 dead juvenile, WAM 783.79, FMNH 199269); Sta. WA-352, 6.0 km east of Yammera Gap, north side ('Lennard' 3863 – 994:805) (9 live, 46 dead adults, 3 live, 3 dead juveniles, WAM 784.79, WAM 785.79, FMNH 199140, FMNH 200262); NR II-25, *ca.* 11 km north-west of Windjana Gorge, north side (46 dead adults, WAM 1228.76); Sta. WA-353, 10.0 km east of Yammera Gap, north side ('Lennard' 3863 – 031:787) (5 live, 43 dead adults, 3 live juveniles, WAM 786.79-787.79, FMNH 199138, FMNH 200300); Sta. WA-359, 10.5 km east of Yammera Gap, north side ('Lennard' 3863 – 033:782) (44 live, 50 dead adults, 38 live juveniles, WAM 788.79-791.79, FMNH 199116, FMNH 199822, FMNH 200153, FMNH 200281-4); Sta. WA-310, 8.5 km north-west of Windjana Gorge, north side ('Lennard' 3863 – 050:778) (52 dead adults, 2 dead juveniles, WAM 792.79, FMNH 199337).

Distribution limits in Napier Range

Westraltrachia froggatti complanata has a total range of about 11-12 km. It extends west to within 1 (north side) or 2.4 (south side) km of Yammera Gap, where it is replaced by *W. turbinata* and *W. inopinata,* respectively, with some overlap between *turbinata* and *f. complanata*. The eastern limit lies a few kilometres west of Windjana Gorge, where *W. f. complanata* is replaced by *W. f. froggatti* (Ancey, 1898). The area between WA-310 and NR II-24 is still to be sampled.

Diagnosis

Shell large, 13.6-19.9 mm (mean 16.41 mm) in diameter, with 4 to 5¾ (mean 4⅞+) rather loosely coiled whorls. Apex and spire moderately elevated, usually with nearly straight sides to the spire, sometimes rounded above, height of shell 5.95-11.0 mm (mean 7.95 mm), H/D ratio 0.394-0.703 (mean 0.483). Apical whorls occasionally with vague micro-radial ridges in the sutures **(Plate 20c)**, postnuclear sculpture **(Plate 20d-e)** of dense, triangular protrusions that give a weakly pebbled appearance when viewed without magnification. Sculpture present on shell base as well as upper surface. Upper surface normally with a series of rather prominent irregular growth ridges **(Plate 20d)**. Shell periphery acutely angled with a distinct protruded keel **(Fig. 122e)**. Lip strongly expanded and reflected **(Figs 122d-f)**, body whorl rarely deflecting slightly behind lip. Umbilicus narrow, partly closed by reflexion of lip, regularly decoiling, umbilical width 0.6-2.65 mm (mean 1.53 mm), D/U ratio 6.52-27.4 (mean 11.3). Colour yellow-brown to light brown, keel white, lighter on mid-whorl areas and shell base, darker zones above and below keel, lip white. Occasional radial lighter zones paralleling growth striae give an illusion of variegation. Based on 843 measured adults.

Genitalia **(Figs 123a-b)** with relatively small penial muscle (PM) and large epiphallic loop. Principal pilaster **(Fig. 158d)** short, typical in structure. Penis (P) long, folded within sheath, slender basally, slightly wider above. Walls of penis sheath (PS) noticeably thicker at base **(Fig. 123b)**. Vas deferens (VD) entering penis sheath slightly above mid-point of penis. Vagina (V, **Fig. 123a**) short, thick, free oviduct (UV) slightly longer than spermatheca (S).

Jaw usually smooth, occasionally with weak vertical ribs **(Plate 26e)**, horizontal growth striae sometimes prominent. Radular teeth highly modified. Centrals and laterals unicuspid, mesoconal tip rounded, shaft markedly elevated, then curved backward at tip **(Plate 37a-b)**, marginals typical **(Plate 37c)**.

Discussion

Variation in diameter **(Fig. 125)** and whorl count **(Fig. 126)** is minimal except at the eastern limits of distribution, where *Westraltrachia froggatti complanata* becomes larger. Otherwise the populations appear uniform in size and shape **(Table 53)**.

Live specimens were obtained readily only during the wetter parts of the wet season. Once the seepage areas on which they browse began to dry out, no more live specimens could be found. While dead shells were fairly common in talus, most of the live individuals were found crawling during wet weather or resting on drip surfaces in the tops of small caves. We presume that they retreat into deep fissures and thus agree in habitat, although certainly not in shape and size, with *Westraltrachia turbinata* from further west. A comparative study on activity and shelter site preference in the zone of overlap mentioned above would be well worth the effort, and this area is accessible by foot in the wet season.

The specimen used for illustration of the whole genitalia **(Fig. 123a)** is unusual in the great size of the albumen gland (GG). It was collected 10 January 1977, well into the wet season and at a time just before appearance of crawling young of several species. It is

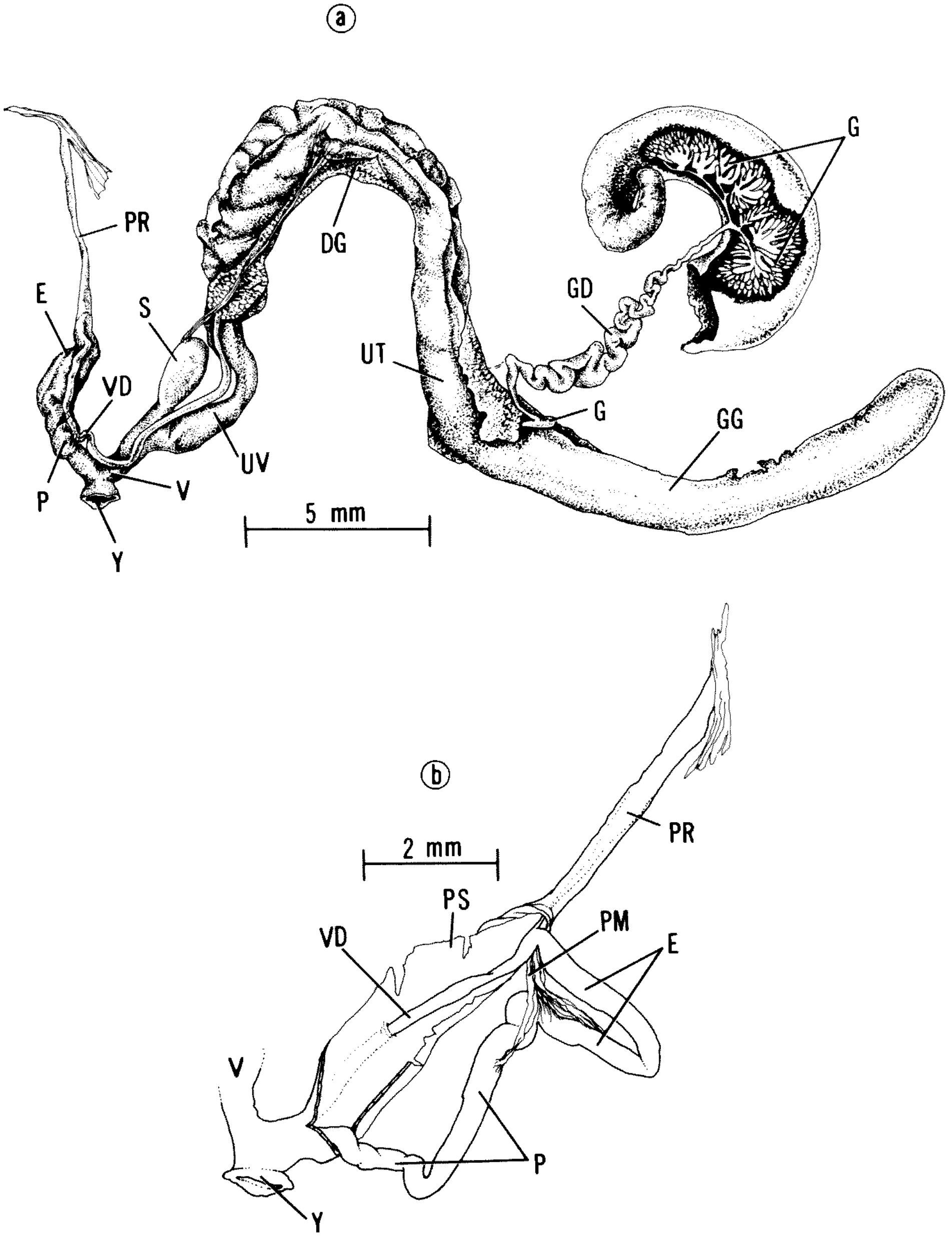


Fig. 123: Genitalia of *Westraltrachia froggatti complanata:* Sta. WA-359, 10.5 km east of Yammera Gap, Napier Range, 10 January 1977, FMNH 200153, (a) whole genitalia, Dissection A, (b) interior of penis sheath, Dissection C. Scale lines as marked. Drawings by Linnea Lahlum.

the only indication seen that albumen gland size may increase during female-active time in the reproductive cycle. Other specimens from the same set that were dissected showed a more normal-sized albumen gland. The contrast with the figured example of *Westraltrachia froggatti froggatti* (Ancey, 1898) **(Fig. 124a)** is misleading. That example, collected 5 December 1976, is a specimen that reached adult shell size near the end of the previous wet season. The small size of its albumen gland (GG) is typical of a third wet season adult and indicates a specimen that will be male, but not female, functional in the forthcoming wet season.

The name *complanata* refers to the flattened appearance of the shell in comparison with other species of *Westraltrachia*, and its contrast with the very high spired *W. turbinata*.

WESTRALTRACHIA FROGGATTI FROGGATTI (ANCEY, 1898)

(Plates 20f, 26f, 37d-f; Figs 122a-c, 124-126)

Trachia froggatti Ancey, 1898, Proc. Linn. Soc. N. S. W., **22**(4): 774, pl. 36, fig. 2 – Oscar Range, N. W. Australia (W. W. Froggatt).

Westraltrachia froggatti (Ancey), Iredale, 1933, Rec. Aust. Mus., **19**(1): 55; Iredale, 1938, Australian Zool., **9**(2): 115; Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 50, pl. III, fig. 10.

Comparative remarks

Westraltrachia froggatti froggatti (Ancey, 1898) differs from *W. froggatti complanata* in averaging 1.6 mm less in diameter and with ¼ whorl less **(Table 47).** The keeled, acutely angulated periphery **(Fig. 122b),** low mean H/D ratio (0.503), and postnuclear sculpture of micro-projections **(Plate 20f)** separate both races from other species of *Westraltrachia.* Anatomically, the long, folded penis (P, **Fig. 124c)** with mid-penis entrance of the vas deferens (VD) through the penis sheath (PS), and large epiphallic loop separate *W. f. froggatti* from any of the western Napier Range species. Differences from *W. derbyi* (Cox, 1892) are discussed above under *W. f. complanata.*

Holotype

AM C.64884, Oscar Range, N. W. Australia. Here restricted to south-west corner of Windjana Gorge, west side of Lennard River, Napier Range, Western Australia (1:100,000 'Lennard' map sheet 3863, grid reference 063:743). Collected by W. W. Froggatt in the 1880's. Height of shell 8.1 mm, diameter 14.75 mm, H/D ratio 0.549, whorls 4⅞, umbilical width 1.4 mm, D/U ratio 10.5.

Measured adults

Napier Range, geographical sequence west to east: One-half mile west of Windjana Gorge entrance, south side (8 dead adults, WAM 1232.76, A. M. Douglas and G. Kendrick 5 July 1966); Sta. WA-193, south-west corner Windjana Gorge ('Lennard' 3863 – 063:743) (6 live adults, WAM 793.79, FMNH 199652, FMNH 199873); Sta. WA-193a, south-west corner Windjana Gorge, single fissure ('Lennard' 3863 – 063:743) (4 live, 105 dead adults, WAM 131.79, WAM 794.79, FMNH 199430, FMNH 200026);

NR 10, Windjana Gorge (68 dead adults, WAM 725.76); Sta. WA-193b, south-west corner Windjana Gorge, second large fissure from gorge ('Lennard' 3863 – 063:743) (5 live, 21 dead adults, WAM 1347.78, WAM 796.79-797.79, FMNH 200038-9, FMNH 200042, FMNH 200044); Sta. WA-713, 4th cleft from floodline, south-west corner Windjana Gorge (4 live adults, WAM 196.80, FMNH 205322); NR II-23, Billyara Spring embayment, *ca.* 5 km north-west Windjana Gorge entrance, north side (10 dead adults, WAM 300.80); NR II-24, *ca.* 4.5 km north-west north entrance to Windjana Gorge, north side (20 dead adults, WAM 1229.76); NR II-22 *ca.* 4 km north-west Windjana Gorge entrance, north side (35 dead adults, WAM 1230.76, WAM 1231.76); rubble piles in Windjana Gorge (49 dead adults, WAM 134.68, A. M. Douglas and G. Kendrick 2 July 1966); Sta. WA-309, 3.1 km north-west Windjana Gorge, north-east side ('Lennard' 3863 – 073:758) (3 live, 25 dead adults, WAM 798.79-799.79, FMNH 199173, FMNH 200094); Sta. WA-308, north-west side Windjana Gorge at entrance, north-east side ('Lennard' 3863 – 093:740) (1 live, 36 dead adults, WAM 800.79-801.79, FMNH 199175, FMNH 200099).

Distribution limits in Napier Range

Westraltrachia froggatti froggatti (Ancey, 1898) ranges from the west bank of Windjana Gorge to about 5 or 6 km west, where it is replaced by *W. froggatti complanata.* The boundary lies in the unsampled country between WA-310 and NR II-24 **(Figs 159-160).**

Diagnosis

Shell average in size, 12.2-17.5 mm (mean 14.81 mm) in diameter, with 4 – to 5½ – (mean 4⅝ +) almost normally coiled whorls. Apex and spire moderately to strongly and almost evenly elevated, height of shell 5.0-9.7 mm (mean 7.24 mm), H/D ratio 0.348-0.608 (mean 0.503). Apical whorls smooth **(Plate 20f),** postnuclear whorls with micro-projections as in *Westraltrachia froggatti complanata* **(Plate 20d-e).** Upper surface of shell with relatively prominent irregular growth striae. Shell periphery acutely angulated **(Fig. 122b)** with strongly protruded keel. Lip strongly expanded and reflected **(Figs 122a-c),** body whorl often slightly deflected behind lip. Umbilicus narrow, partly covered by reflection of lip, umbilical width 0.5-2.35 mm (mean 1.34 mm), D/U ratio 6.15-27.3 (mean 11.5). Colour yellow-brown to light brown, lighter radial areas of growth giving a variegated character to colour. Keel and lip white, shell base lighter in tone. Based on 283 measured adults.

Genitalia **(Figs 124a-c)** with relatively small penial muscle (PM), large epiphallic loop. Principal pilaster of penis as in *Westraltrachia froggatti complanata* **(Fig. 158d).** Penis (P) long, folded in sheath, slightly larger in diameter apically. Walls of penis sheath (PS) thicker basally. Vas deferens (VD, **Fig. 124c)** entering penis sheath about mid-point on penis (P). Vagina (V) short, thick, free oviduct (UV) longer than spermatheca (S).

Jaw **(Plate 26f)** without vertical ribs, horizontal growth striae often evident. Radular teeth **(Plate 37d-f)** highly modified, central and laterals unicuspid with bluntly rounded mesoconal tip, upper part of strongly elevated shaft of laterals curved backward noticeably.

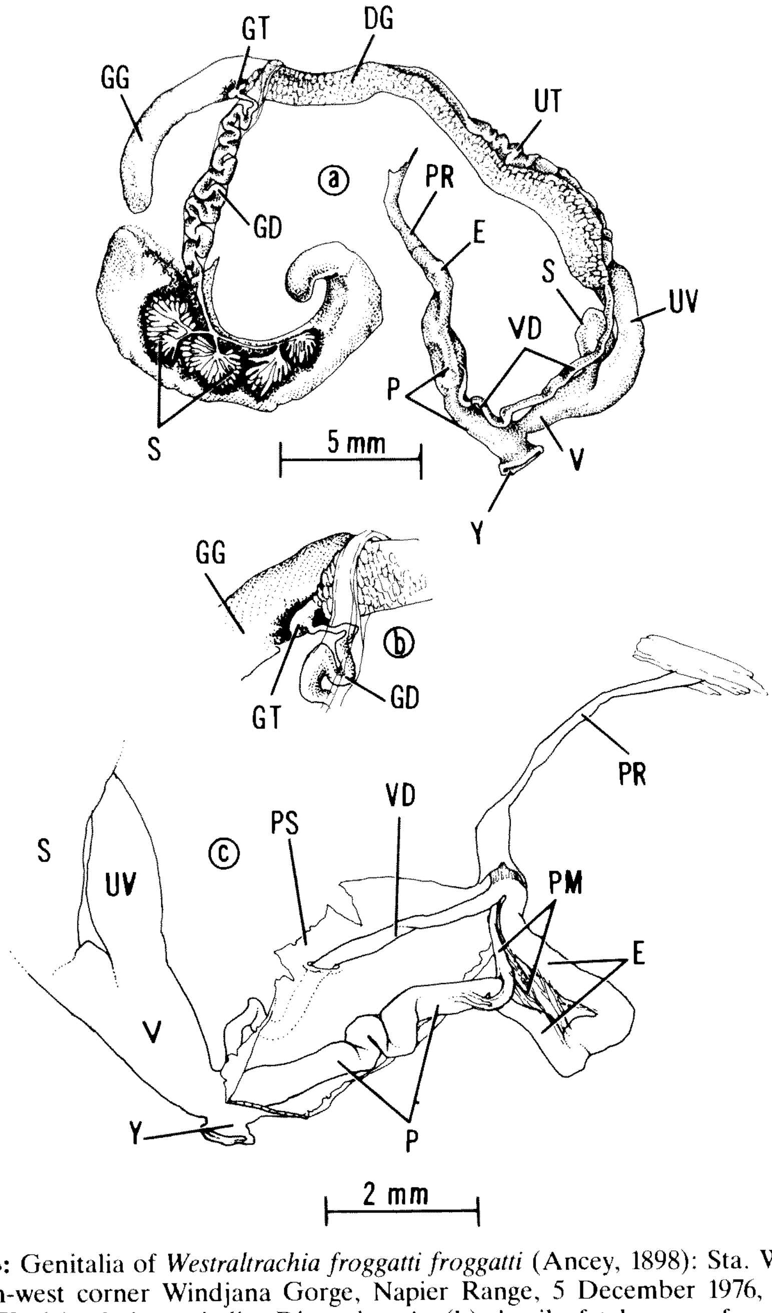


Fig. 124: Genitalia of *Westraltrachia froggatti froggatti* (Ancey, 1898): Sta. WA-193, south-west corner Windjana Gorge, Napier Range, 5 December 1976, FMNH 199873, (a) whole genitalia, Dissection A, (b) detail of talon-carrefour region, Dissection A, (c) interior of penis sheath, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

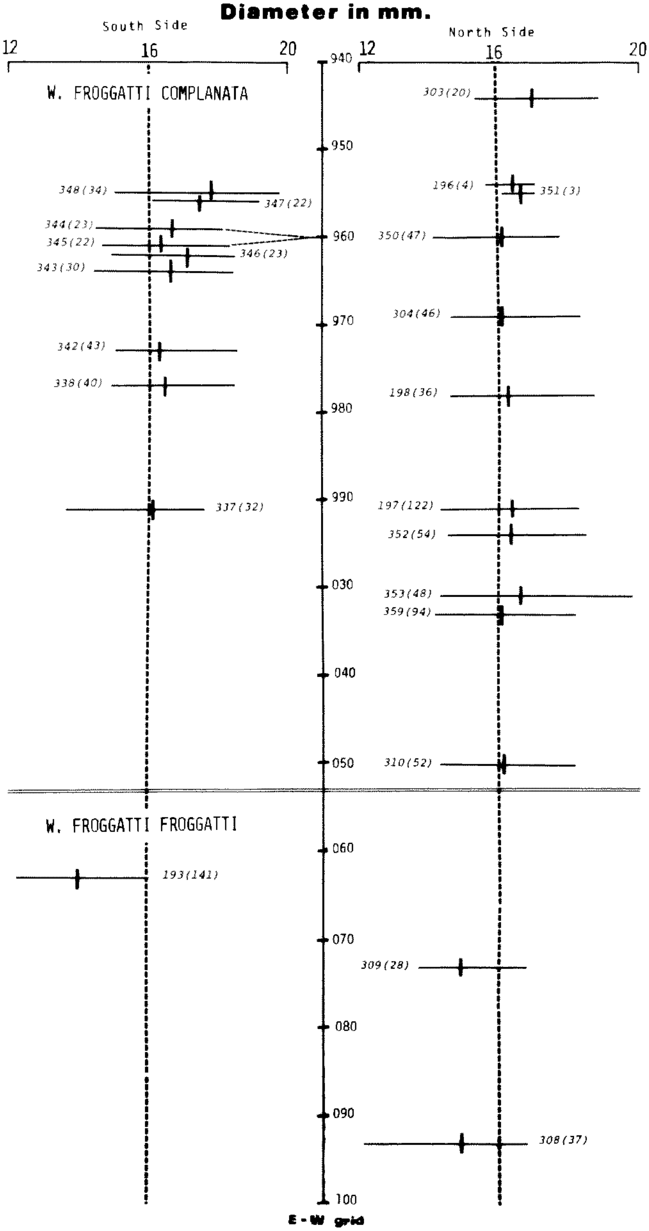


Fig. 125: Geographic variation in shell diameter for *Westraltrachia froggatti froggatti* (Ancey, 1898) and *W. f. complanata.* Center line E-W grid coordinates from 1:100,000 "'Lennard" 3863 map sheet. Station numbers as listed in text, number of specimens measured in "()", plotted as to south and north side of range localities. Mean and range indicated for each station. Drafted by Dorothy Karall.

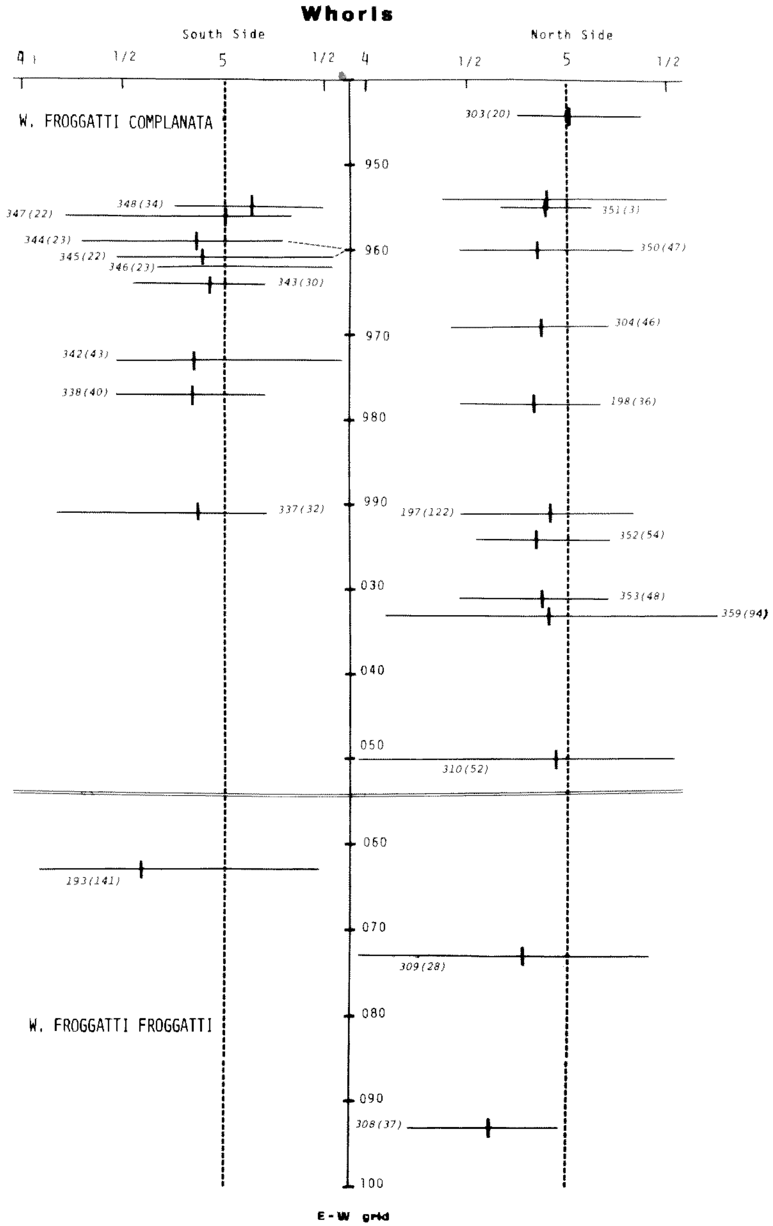


Fig. 126: Geographic variation in shell whorl count for *Westraltrachia froggatti froggatti* (Ancey, 1898) and *W. f. complanata*. Center line E-W grid coordinates from 1:100,000 "'Lennard" 3863 map sheet. Station numbers as listed in text, number of specimens measured in "()", plotted as to south and north side of range localities. Mean and range indicated for each station. Drafted by Dorothy Karall.

Discussion

Despite the striking change in shape, sculpture and keeling, *Westraltrachia froggatti* appears to be more closely related to the western Napier Range taxa than to those across Windjana Gorge to the east. The principal pilaster in the penis **(Fig. 158d)**, smooth jaw, and highly modified radular teeth are shared with the western taxa. Of the eastern species, only *W. ascita* has the distinctive sculpture found in *W. froggatti*. The low entrance of the vas deferens through the penis sheath and long folded penis are shared with several eastern species.

The range of *Westraltrachia froggatti froggatti* is not accessible during the wet season, as from the east the flooding Lennard River is impassible, and station tracks from Napier Downs to the west become black mud bogs. Thus, comparatively few samples of the nominate race were available for study. Size and shape variation was minor **(Table 53, Figs 125, 126)**, with specimens from Sta. WA-308 having a lower spire, wider umbilicus, and slightly reduced whorl count. The type falls within the range of the Windjana Gorge south-east corner materials, and the type locality is thus restricted to that area.

WESTRALTRACHIA DERBYI (COX, 1892)

(Plates 21a, 27, 28, 38-40; Figs 127-132, 158e)

Helix (Hadra) derbyi Cox, 1892, Proc. Linn. Soc. N. S. W., (2) **6**(3): 566, pl. xx, figs 4-5 – The Derby District, Barrier Ranges, Western Australia (Froggatt); Pilsbry, 1893, Man. Conch., (2) **8:** 280, pl. 58, figs 20-21.

Helix (Trachia) derbyana, E.A. Smith, 1894, Proc. Malac. Soc. London, **1:** 92-93, pl. VII, fig. 19 – Burner Range, Derby District, N. W. Australia.

Trachia orthocheila Ancey, 1898, Proc. Linn. Soc. N. S. W., **22**(4): 774-5, pl. 36, fig. 4 – Oscar Range, 100 miles inland, Derby, King's Sound, N. W. Australia (W. W. Froggatt).

Westraltrachia derbyi (Cox), Iredale, 1938, Australian Zool., **9**(2): 115; Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 50, pl. III, fig. 6.

Westraltrachia orthocheila (Ancey), Iredale, 1938, Australian Zool., **9**(2): 115; Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 51, pl. III, fig. 8.

Nomenclature and type localities

Specimens from Froggatt's original collection were rather widely dispersed, and the species was described three times. The holotypes of *Helix derbyi* Cox, 1892, and *H. derbyana* Smith, 1894 **(Figs 127a-f)** are nearly identical in size and shape, while the lectotype of *Trachia orthocheila* Ancey, 1898 is 3 mm larger in diameter and more openly umbilicated **(Figs 128a-c)**. The latter was described from the 'Oscar Range', a probable error in labeling. The first two specimens are among the smallest adult examples seen. In form and sculpture they exactly match material from the south-east corner of Windjana Gorge, and in size match material from the "walls of Windjana Gorge". The types of *orthocheila* match the size and shape of south-east Windjana

Table 54: Geographic Variation in *Westraltrachia derbyi* (Cox, 1892)

Locality	Number of Adults Measured	Mean and Range of: Shell Height	Shell Diameter	H/D Ratio
Types of *derbyi* and *orthocheila*	12	6.54 (5.6 – 7.8)	12.61 (10.35 – 14.1)	0.522 (0.475 – 0.594)
SE corner, Windjana Gorge	206	6.84 (5.50 – 9.25)	12.75 (10.4 – 14.7)	0.538 (0.471 – 0.661)
Lillimilura Police Station Ruins	52	6.76 (5.8 – 8.4)	12.83 (10.6 – 14.75)	0.527 (0.472 – 0.597)
NE corner, Windjana Gorge	41	7.71 (6.75 – 9.75)	14.15 (12.6 – 15.9)	0.550 (0.493 – 0.668)
3.4 km S, Lillimilura Police Station	37	7.27 (6.25 – 8.7)	13.57 (12.15 – 15.6)	0.533 (0.470 – 0.600)
Carpenter Gap	122	8.79 (7.5 – 10.5)	15.23 (13.45 – 17.8)	0.578 (0.505 – 0.677)
4.3 km S, Carpenter Gap	40	8.88 (7.85 – 10.4)	15.38 (13.8 – 16.6)	0.578 (0.520 – 0.665)
15 km SE, Windjana Gorge	57	9.24 (7.5 – 11.2)	15.41 (13.8 – 17.35)	0.599 (0.528 – 0.678)

Locality	Number of Adults Measured	Mean and Range of: Whorls	Umbilical Width	D/U Ratio
Types of *derbyi* and *orthocheila*	12	4⅝ + (4¼ – 5 +)	1.62 (1.35 – 2.25	8.03 (5.91 – 10.0)
SE corner, Windjana Gorge	206	4¾ + (4⅛ – 5¼)	1.37 (0.75 – 2.15)	9.71 (5.33 – 16.3)
Lillimilura Police Station Ruins	52	4¾ + (4⅜ – 5⅛)	1.51 (0.95 – 1.9)	8.76 (6.08 – 13.3)
NE corner, Windjana Gorge	41	5⅛ (4¾ – 5⅝)	1.46 (0.85 – 1.85)	9.95 (7.33 – 16.8)
3.4 km S, Lillimilura Police Station	37	5 – (4⅝ – 5⅜ –)	1.22 (0.8 – 1.95)	11.9 (6.82 – 18.4)
Carpenter Gap	122	5⅛ + (4¾ – 5⅝ –)	1.15 (0.5 – 2.0)	14.2 (7.39 – 29.8)
4.3 km S, Carpenter Gap	40	5⅛ (4⅞ – 5⅜)	1.16 (0.5 – 1.6)	14.1 (8.9 – 32)
15 km SE, Windjana Gorge	57	5⅛ + (4¾ – 5⅝ –)	1.16 (0.8 – 1.7)	14.0 (8.72 – 21.3)

Gorge modern collections, although showing a relatively wide umbilicus, and differ significantly from any of the Oscar Range taxa. Thus, the type locality of all three species is here restricted to the south-east corner of Windjana Gorge, which was one of Froggatt's collecting localities in the Napier Range.

Comparative remarks

Westraltrachia derbyi (Cox, 1892) is a geographically variable, small to medium sized species **(Table 54)**, with moderately open to narrowly open umbilicus. Eastern populations are larger in diameter and narrower of umbilicus. It ranges from the east bank of Windjana Gorge to a few km east of Carpenter Gap. The rather tight coiling of the whorls, narrow reflexion of the lip **(Figs 127-128)**, variegated colour pattern of brown and white with white peripheral spiral band, lighter basal colour, and irregular growth wrinkles on the postnuclear whorls **(Plate 21a)** easily separate it from any species west of Windjana Gorge. *Westraltrachia alterna* Iredale, 1939, the next species east, is identical in size and shape to some of the *W. derbyi* populations, but generally has the shell lip more reflected over the umbilicus, a brighter colour pattern, more expanded lip, has a greater tendency toward subangulation of the periphery, and there is a subnodose projection on the basal lip **(Figs 133b, e)**. *Westraltrachia cunicula* is a much more elevated shell **(Figs 138b-c)**, with narrower umbilicus **(Table 47)**, and less marked colour patterning. Anatomically, the generally reduced epiphallic loop **(Figs 129c-e, 130b-c, 131b-d, 132b-c)**, medium to long penis (P), rather high entrance of the vas deferens through the penis sheath, and change of the principal pilaster (PT) into a long corrugated ridge **(Fig. 158e)** easily separate *W. derbyi* from any of the species west of Windjana Gorge with their typical principal pilasters **(Figs 158a-d)**. *Westraltrachia alterna* Iredale, 1939, has a shorter penis **(Figs 134-135)** with massive penis muscle, larger epiphallic loop, often very thick sheath walls, and a small, but typical, principal pilaster **(Fig. 158f)**. *Westraltrachia cunicula* **(Fig. 139)** has a very long slender penis (P) and vagina (V) with the principal pilaster altered into a long straight ridge **(Fig. 158g)**. The highly variable jaw **(Plates 27-8)** and radular structure **(Plates 38-40)** of *W. derbyi* prevent any simple comparisons with other species, and are discussed below.

Holotype of *Helix derbyi* Cox, 1892

AM C.64883, Barrier (=Napier) Ranges, Derby District, Western Australia. Collected by W. W. Froggatt. Height of shell 6.15 mm, diameter 10.35 mm, H/D ratio 0.594, whorls 4⅝, umbilical width 1.7 mm, D/U ratio 6.09.

Paratypes of *Helix derbyi* Cox, 1892

AM C.64883, WAM 52.40, 3 dead adults from the type locality.

Holotype of *Helix derbyana* Smith, 1894

BMNH 1888.11.28.70, Burner (=Napier) Range, Northwest Australia. Height of shell 5.7 mm, diameter 10.5 mm, H/D ratio 0.543, whorls 4¾, umbilical width 1.45 mm, D/U ratio 7.24.

Lectotype and Paratypes of *Trachia orthocheila* Ancey, 1898

AM C.64887, WAM 53.40, 7 dead adults, height of shell 6.45 mm, diameter 13.3 mm, H/D ratio 0.485, whorls 4⅝, umbilical width 2.25 mm, D/U ratio 5.91.

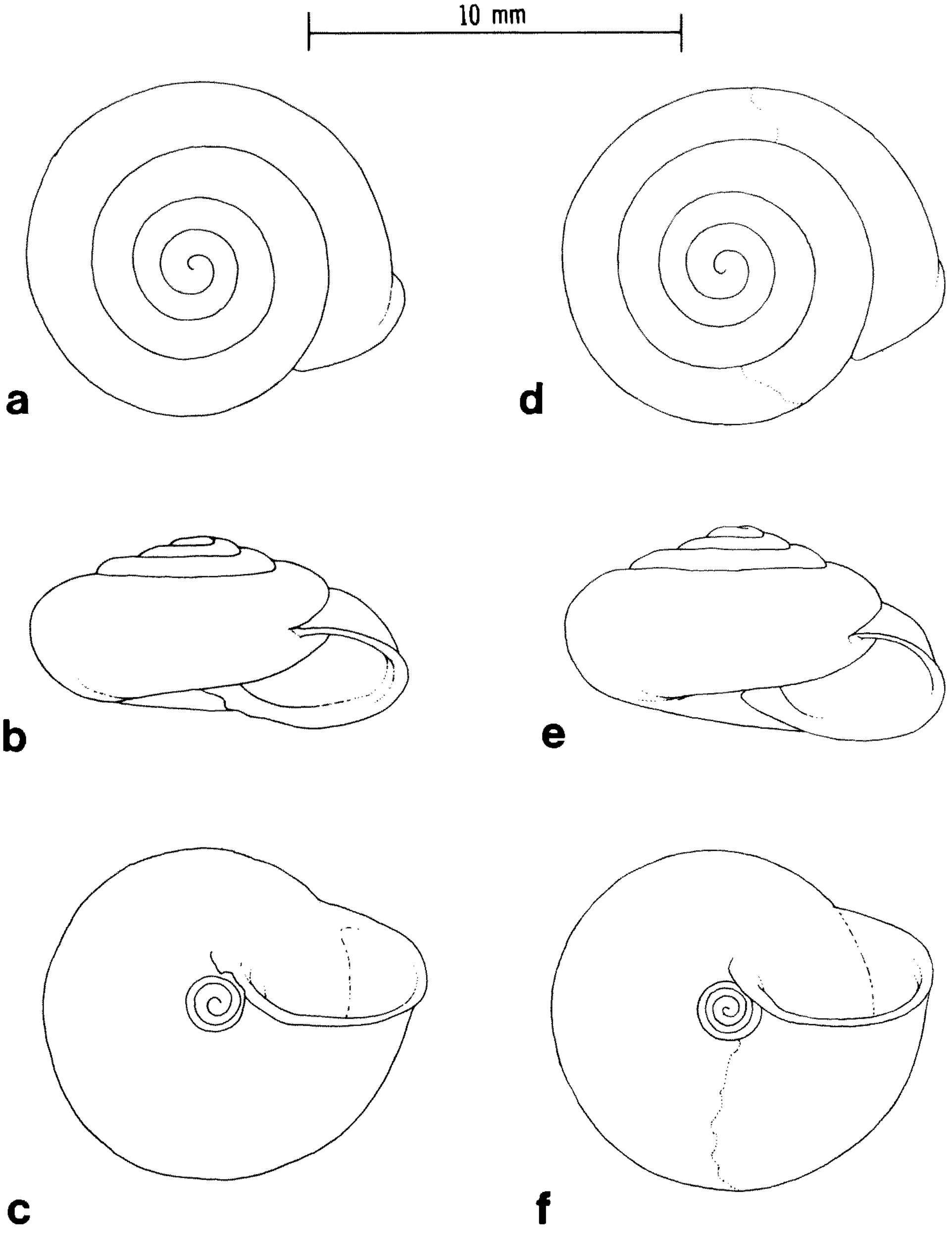


Fig. 127: Shells of *Westraltrachia derbyi* (Cox, 1892): (a-c) holotype of *Helix (Hadra) derbyi* Cox, 1892, AM C.64883; (d-f) holotype of *Helix (Trachia) derbyana* E.A. Smith, 1894, BMNH 1888.11.28.70. Scale line equals 10 mm. Drawings by Elizabeth Liebman.

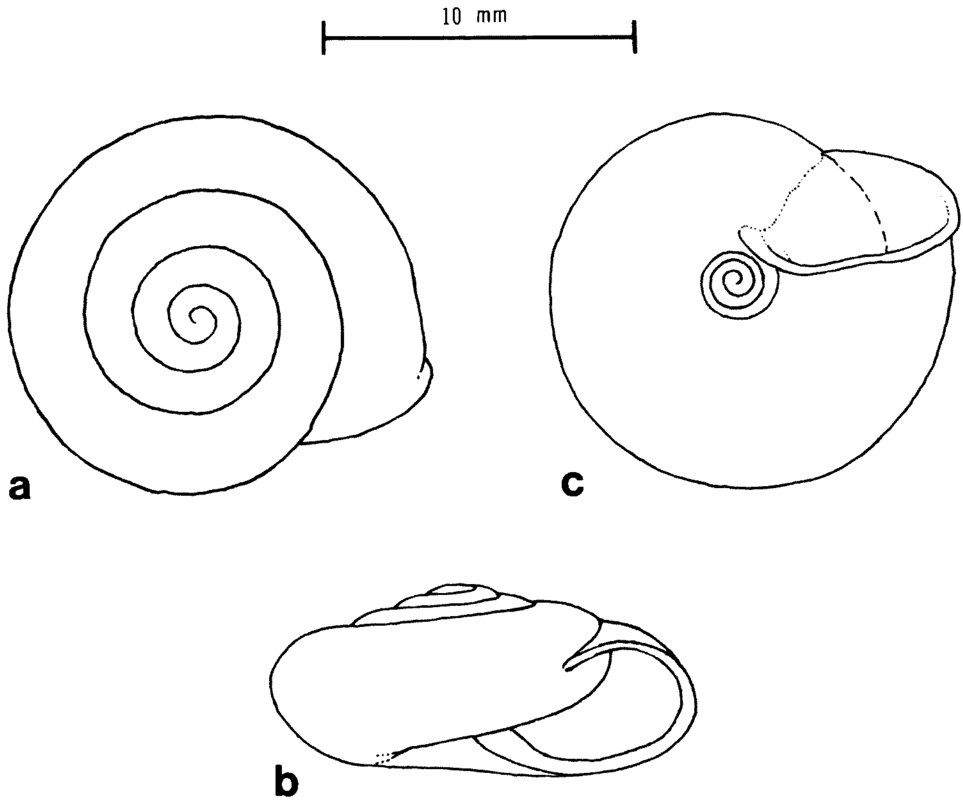


Fig. 128: Shell of *Westraltrachia derbyi* (Cox, 1892): Paratype of *Trachia orthocheila* Ancey, 1898. Oscar Range, 100 miles inland from Derby (probably error for Windjana Gorge, Napier Range), AM C.64887. Scale line equals 10 mm. Drawings by Elizabeth Liebman.

Measured adults

Napier Range: along walls, east side of Windjana Gorge (1:250,000 'Lennard River' map sheet SE 51-8, grid reference 2770:8095) (50 dead adults, NMV, ex. F. W. Aslin 2375, collected by A. C. Beauglehole, 20 July 1974); Sta. WA-194 ('Lennard' 3863 – 065:737) and Sta. WA-581 (= WA-194), south-east corner Windjana Gorge (79 live, 77 dead adults, WAM 185.80-195.80, WAM 202.80, WAM 482.80, WAM 485.80, FMNH 199197, FMNH 199200, FMNH 199723, FMNH 199853, FMNH 200017-8, FMNH 200054, FMNH 200056, FMNH 200059, FMNH 200302, FMNH 200304-6, FMNH 200308, FMNH 200310, FMNH 200370, FMNH 204704-6); Sta. WA-334, cliff base just north of Lillimilura Police Station ruins, 3 km south-east Windjana Gorge, south side ('Lennard' 3863 – 088:725) (14 live, 38 dead adults, WAM 183.80, WAM 483.80, FMNH 199094, FMNH 200133); Sta. WA-307, south-east side Windjana

Gorge at entrance, north-east side of Napier Range ('Lennard' 3863 – 097:737) (13 live, 28 dead adults, WAM 181.80, WAM 484.80, FMNH 199208, FMNH 200180); Sta. WA-335, cliffs and caves 0.5 km north-east of road, 3.4 km south-east of Lillimilura Police Station ruins, south-west side Napier Range ('Lennard' 3863 – 123:708) (5 live, 32 dead adults, WAM 201.80, WAM 486.80, FMNH 199265, FMNH 200147); NR II-32, north-east corner Carpenter Gap, Napier Range (1 live, 10 dead adults, WAM 1237.76); NR II-33, south-east corner of Carpenter Gap ('Lennard River' SE 51-8 – 285:806) (83 dead adults, WAM 1233.76, WAM 1235.76); Sta. WA-280, 11.4 km east of Windjana Gorge turnoff, south side Napier Range ('Richenda' 3963 – 142:674) (27 dead adults, WAM 182.80, FMNH 199230); Sta. WA-336, cliffs north-east of road, 4.3 km south-east of Carpenter Gap, south-west side Napier Range ('Richenda' 3963 – 149:663) (3 live, 37 dead adults, WAM 184.80, WAM 203.80, FMNH 199278, FMNH 200159); NR XVIII, 15 km south-east Windjana Gorge ('Richenda' 3963 – *ca.* 168:641) (57 dead adults, WAM 731.76, WAM 935.76).

Distribution limits in Napier Range

Westraltrachia derbyi (Cox, 1892) ranges from the east side of Windjana Gorge along the Napier Range south-east to above 14 km south-south-east of the Gorge (Sta. NR XVIII), several km past Carpenter Gap. There is then a 6.7 km distributional gap in the range of low rolling hills, rather barren of vegetation and without exposed reefs or rock talus until Cycad Hill, north-north-west of McSherry Gap, the westernmost known locality for *W. alterna* Iredale, 1939. Track access is poor in the intervening area and no sampling has been done near Mt. Behn.

Diagnosis

Shell smaller than average to average, 10.4-17.8 mm (mean 13.90 mm) in diameter, with 4⅛ – to 5⅝ (mean 5 –) normally coiled whorls. Apex and spire normally moderately and evenly elevated, sometimes strongly elevated, not rounded above **(Figs 127b, e, 128b)**, height of shell 5.5-11.2 mm (mean 7.72 mm), H/D ratio 0.470-0.678 (mean 0.555). Apical whorls macroscopically smooth, micro-radial wrinkles present in suture **(Plate 21a)**. Postnuclear whorls with irregular radial growth wrinkles, much more prominent than in western Napier Range taxa. Periphery of body whorl rounded **(Figs 127b, e, 128b)** to obtusely angulated in some populations. Lip moderately expanded and reflected **(Figs 127, 128)**, body whorl descending slightly behind lip. Umbilicus moderately **(Figs 127c, f, 128c)** to narrowly open, umbilical width 0.5-2.25 mm (mean 1.30 mm), D/U ratio 5.33-32 (mean 11.4). Colour with light to medium brown variegations above on spire, a white peripheral zone, brownish spiral bands above and below peripheral zone, base of shell lighter to white, sometimes brownish tones in umbilicus, lip white. Based on 568 measured adults.

Genitalia **(Figs 129-132)** variable geographically, but consistently with the principal penis pilaster (PT, **Fig. 158e)**, a long ridge corrugated at base. Penial muscle (PM) large to small, epiphallic loop large in eastern populations **(Figs 131-132)**, smaller in Windjana Gorge **(Figs 129c-e, 130b-c)**. Penis (P) of medium length generally, rarely folded within sheath, walls of sheath somewhat thicker basally. Vas deferens (VD) entering sheath from near termination of penis muscle **(Figs 129c-e)**, at base of epiphallus **(Fig. 131b)**, or just below attachment of penial retractor muscle (PR, **Fig. 132c)**. Vagina (V) short to medium in length, spermatheca (S) in most populations much shorter than free oviduct (UV), which normally is distinctly curved.

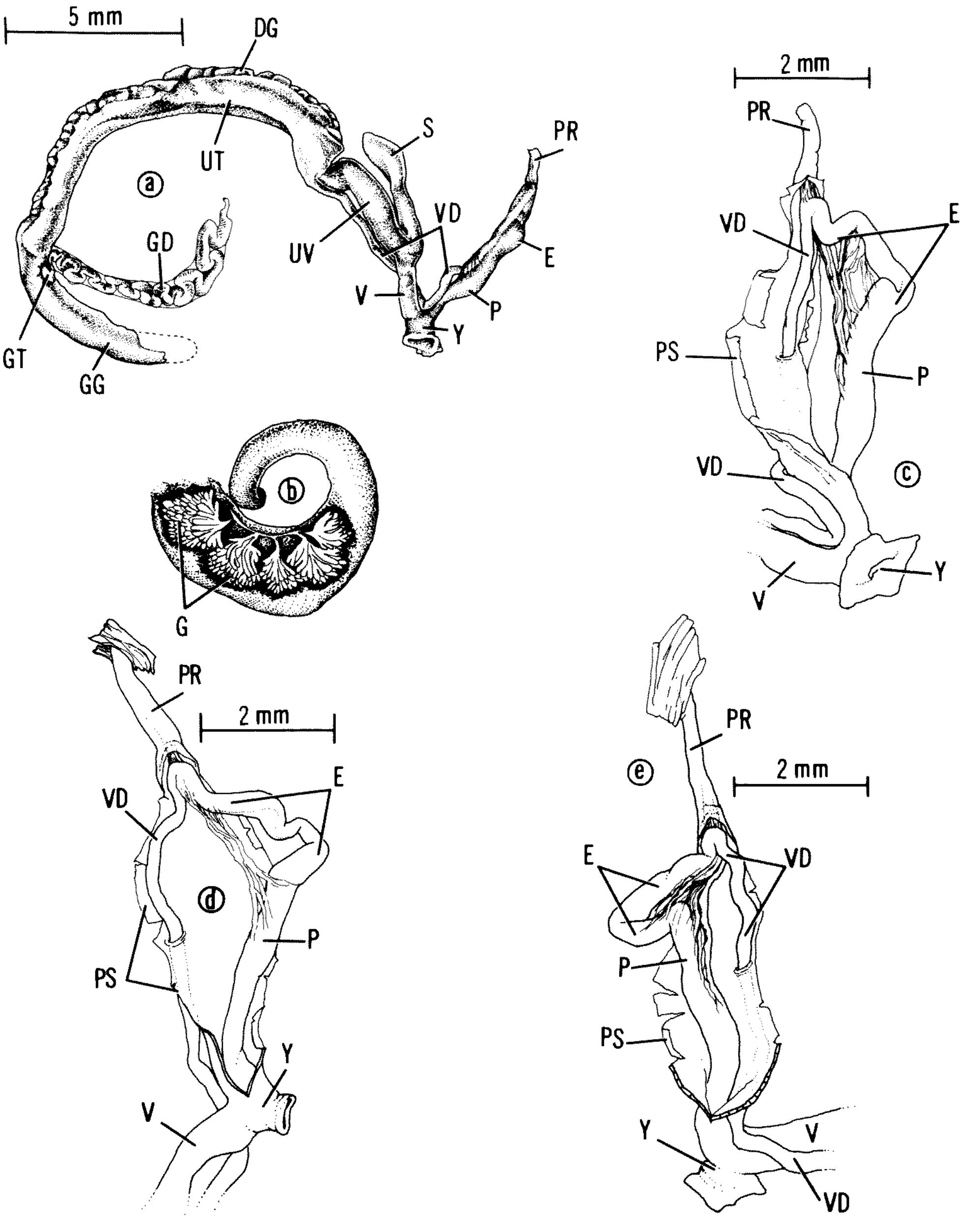


Fig. 129: Genital variation in *Westraltrachia derbyi* (Cox, 1892): Sta. WA-194, southeast corner Windjana Gorge, Napier Range, 5 December 1976, FMNH 200056, (a) whole genitalia, Dissection A, (b) ovotestis, Dissection A, (c) interior of penis sheath, Dissection A, (d) interior of penis sheath, Dissection C, (e) interior of penis sheath, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

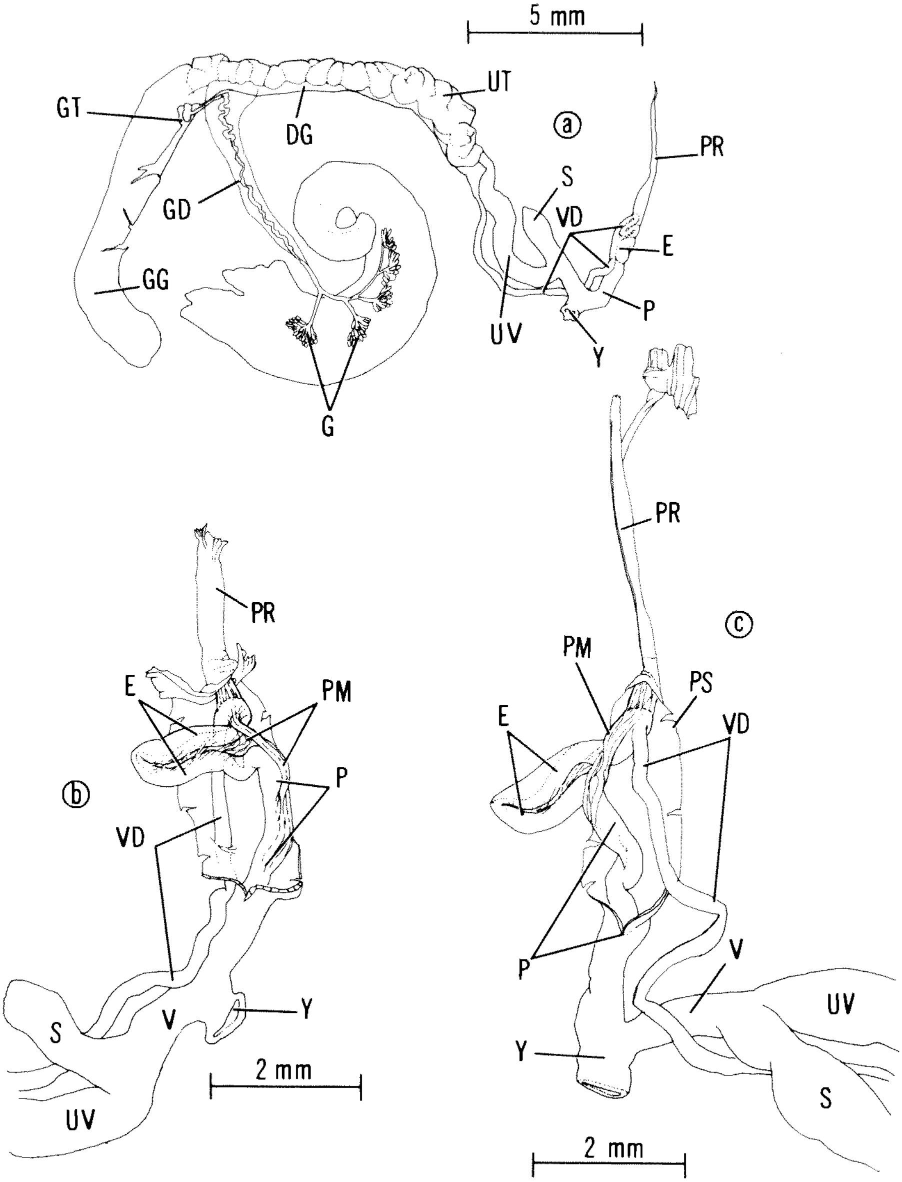


Fig. 130: Genital variation in *Westraltrachia derbyi* (Cox, 1892): Sta. WA-194, southeast corner of entrance to Windjana Gorge, Napier Range, (a) whole genitalia, 21 March 1977, FMNH 199853, Dissection A, (b) interior of penis sheath, 5 December 1976, FMNH 200056, Dissection D, (c) interior of penis sheath, 4 January 1977, FMNH 200054, Dissection A. Scale lines as marked. Drawings by Linnea Lahlum.

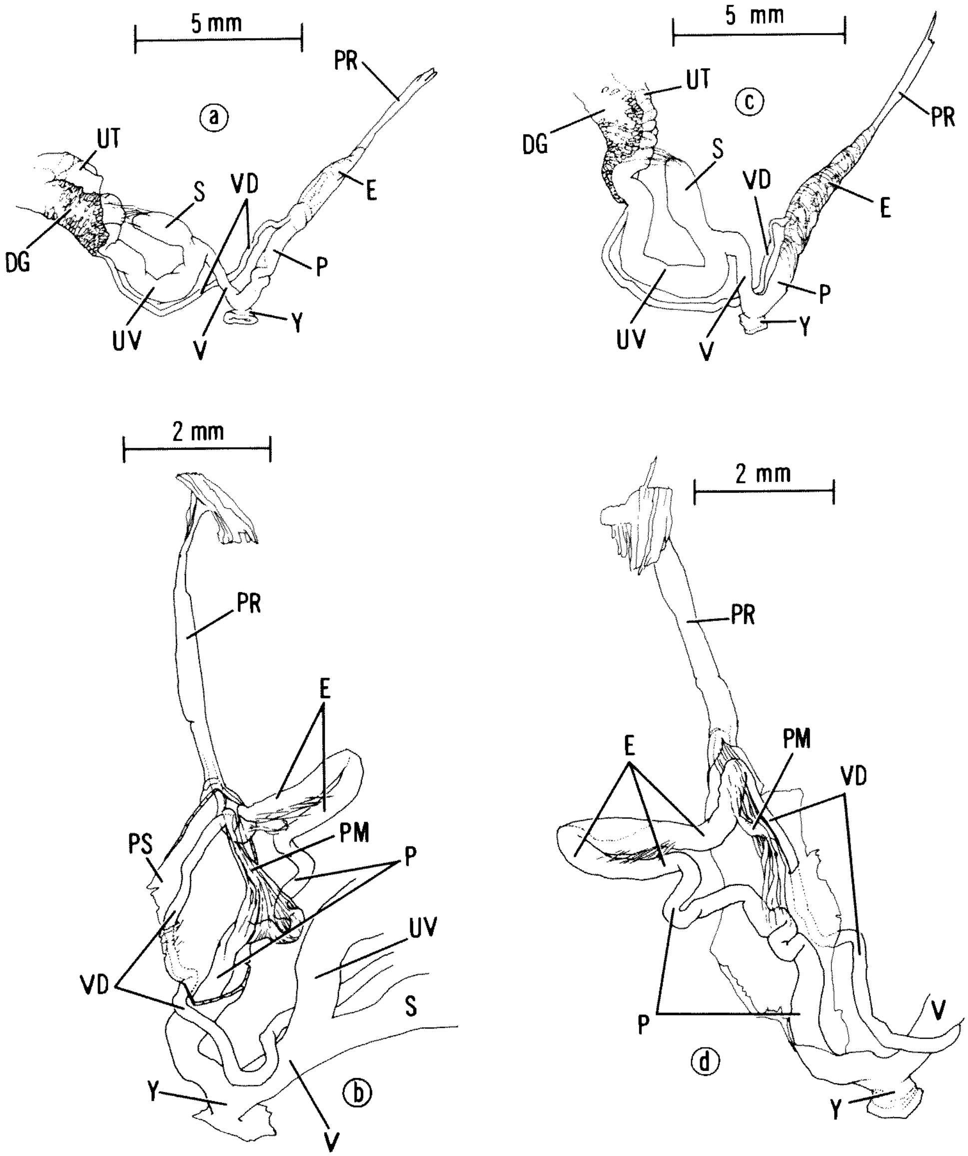


Fig. 131: Genital variation in *Westraltrachia derbyi* (Cox, 1892): (a-b) Sta. WA-335, 3.4 km south-east of Lillimilura Police Station ruins, Napier Range, 22 December 1976, FMNH 200147, a is terminal genitalia, Dissection A, b is interior of penis sheath, Dissection B; (c-d) Sta. WA-307, north-east corner of Windjana Gorge, Napier Range, 11 December 1976, FMNH 200150, c is terminal genitalia, Dissection A, d is interior of penis sheath, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

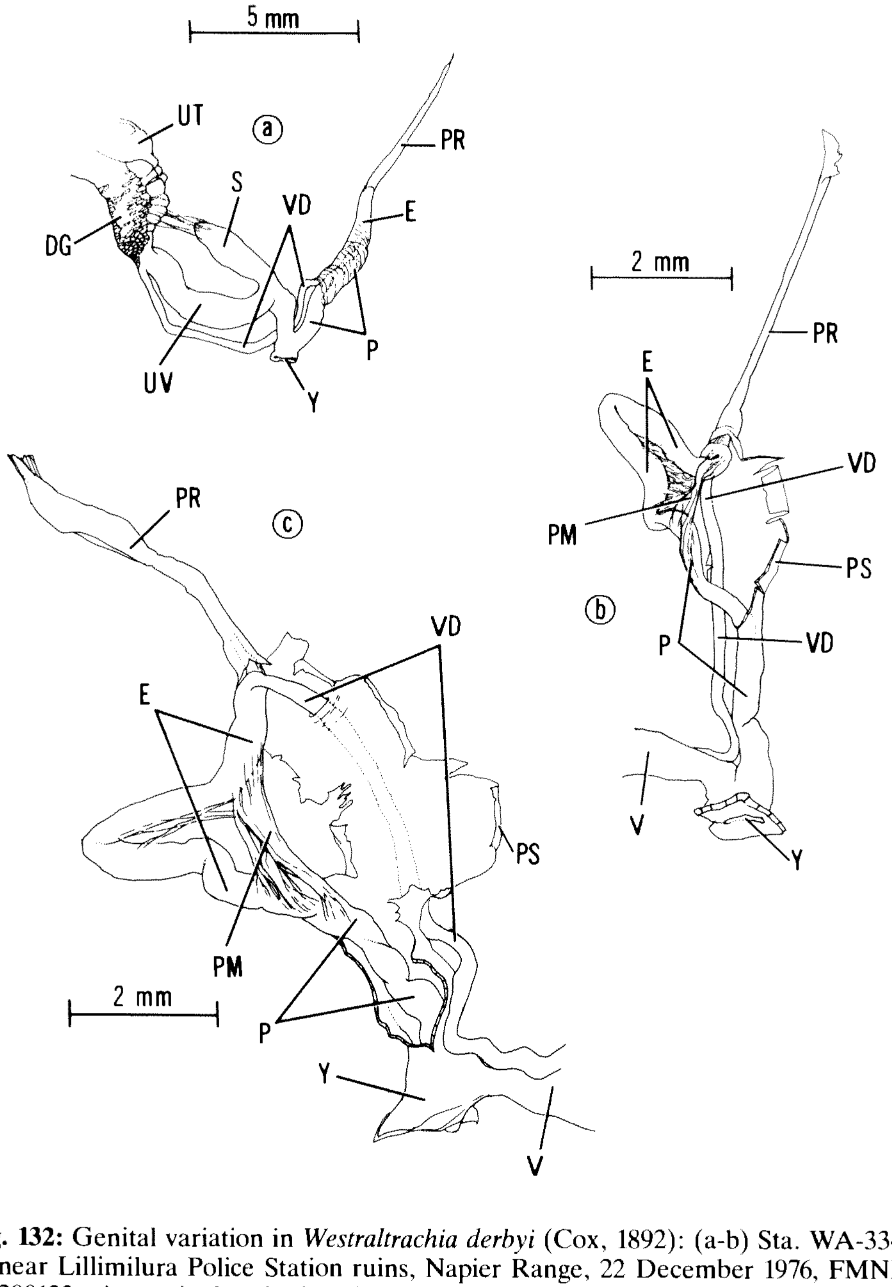


Fig. 132: Genital variation in *Westraltrachia derbyi* (Cox, 1892): (a-b) Sta. WA-334, near Lillimilura Police Station ruins, Napier Range, 22 December 1976, FMNH 200133, a is terminal genitalia, Dissection A, b is interior of penis sheath, Dissection B; (c) Sta. WA-336, 4.3 km south-east of Carpenter Gap, Napier Range, 22 December 1976, FMNH 200159, interior of penis sheath, Dissection A. Scale lines as marked. Drawings by Linnea Lahlum.

Jaw highly variable in ribbing (**Plates 27-28**), ranging from typical camaenid with strong vertical ribs to remnant ribbing in some individuals from the south-east corner of Windjana Gorge. Radular teeth (**Plates 38-40**) highly variable in terms of lateral mesocone elevation and tip curvature, most populations with considerable individual variation that is discussed below. Marginal teeth (**Plate 40**) individually variable from specimen to specimen in all populations.

Discussion

Westraltrachia derbyi (Cox, 1892) shows what probably is the greatest amount of variation among populations yet known for a Kimberley species. The major populations are mostly isolated by stretches of uninhabitable country, and normally consist of small areas with great snail abundance. It is probable that genetic interchange between populations is a rare event, and the opportunity for local differentiation has been great. More refined analyses and breeding experiments may demonstrate that more than one species is lumped here, but present data is not sufficient to discriminate different species.

Size and shape variation of the shell is summarised in **Tables 54** and **55.** The existence of allochronic variation at Windjana Gorge (Stas. WA-194 and WA-581) is demonstrated in **Table 55.** The 1976 and 1980 samples were taken from crevices in the same large boulder pile and thus exactly the same population was resampled, with clear size differences. Geographic summations (**Table 54**) show that the Windjana and Lillimilura Police Station ruins populations are small (because of reduced whorl count) and rather widely umbilicated, while those from Carpenter Gap and south-east are distinctly larger in diameter (increased whorl count) and narrowed umbilical opening. They also tend more toward having an angulated periphery. The smallest known specimens are probably washed down examples from along the east walls of Windjana Gorge (**Table 55**).

The decision to keep these populations as a single species is based upon their sharing a unique structure – the very elongated and corrugated main pilaster in the penis (**Fig. 158e**). Otherwise, there is much more variation in the genitalia than was observed in other species of *Westraltrachia*.

Seasonal variation at Sta. WA-194 is typical and has not been illustrated in full. The 1976-1977 wet season was late, with the first showers at Windjana Gorge occurring no earlier than 1 December 1976. Material collected in October was in late dry season condition equivalent to the situation in *Amplirhagada b. burnerensis* (Smith, 1894) (Solem, 1981a: 242, Fig. 53), with small ovotestis, hermaphroditic duct, and prostate. On 5 December (**Figs 129a-b**), the ovotestis (G) is male functional and grossly enlarged, thė hermaphroditic duct (GD) and prostate (DG) are full-sized, the uterus (UT) is still very small. An unusual feature of the dissected *Westraltrachia derbyi* from 5 December was the state of the digestive gland. It was almost completely empty of granular matter, reduced to a nearly empty sac around the swollen ovotestis. The change is much more dramatic than in *A.b. burnerensis* collected the same day. Quite possibly this relates to the smaller size of the *Westraltrachia* (mean diameter 12.92 mm) compared with the *Amplirhagada* (mean diameter 18.79 mm) from the same station. The delayed start of the 1976-1977 wet season would cause both species to use up major portions of their food reserves, but quite possibly the smaller species would need proportionately greater use. Through January samples, uterine size fluctuated greatly, suggesting the possibility of several egg clutches being deposited. Starting in February there was the beginning of deactivation, with dry season proportions attained by 21 May 1977 **(Fig. 130a).** The reduced uterus (UT), prostate (DG), hermaphroditic duct (GD), and grossly shrunken ovotestis (G) of this example contrast with the unchanged albumen gland (GG).

Table 55: Local Variation in *Westraltrachia derbyi* (Cox, 1892)

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
WA-194, SE Windjana Gorge, FMNH 200017, 10.X.1976	37(D)	6.88 ± 0.089 (6.1 – 7.9)	12.67 ± 0.129 (11.3 – 14.6)	0.543 ± 0.005 (0.471 – 0.661)
WA-194, FMNH 199197, 4.I.1977	19(L)	6.91 ± 0.086 (6.3 – 7.7)	12.63 ± 0.125 (11.7 – 13.45)	0.547 ± 0.005 (0.504 – 0.588)
WA-581, FMNH 204705, 7.V.1980	13(L)	7.00 ± 0.164 (6.1 – 8.0)	13.1 ± 0.198 (12.1 – 14.7)	0.543 ± 0.008 (0.471 – 0.586)
WA-581, FMNH 204704, 7.V.1980	11(D)	7.44 ± 0.223 (6.8 – 9.25)	13.61 ± 0.134 (13.1 – 14.7)	0.629 ± 0.011 (0.502 – 0.583)
Walls of Windjana Gorge, NMV	50(D)	6.54 ± 0.062 (5.5 – 7.25)	12.20 ± 0.103 (10.4 – 13.35)	0.536 ± 0.003 (0.492 – 0.582)
WA-334, Lillimilura, FMNH 200133	14(L)	6.74 ± 0.130 (5.8 – 7.5)	13.01 ± 0.173 (12.3 – 14.35)	0.518 ± 0.007 (0.472 – 0.559)
WA-334, FMNH 199094	38(D)	6.76 ± 0.091 (5.85 – 8.4)	12.77 ± 0.144 (10.6 – 14.75)	0.530 ± 0.004 (0.478 – 0.597)
WA-307, NE Windjana Gorge, FMNH 200180	13(L)	7.72 ± 0.176 (6.8 – 9.1)	14.1 ± 0.244 (12.6 – 15.65)	0.547 ± 0.008 (0.506 – 0.607)
WA-307, FMNH 199208	28(D)	7.71 ± 0.116 (6.75 – 9.75)	14.16 ± 0.157 (12.7 – 15.9)	0.551 ± 0.010 (0.493 – 0.668)
WA-335, SE Lillimilura, FMNH 200147	5(L)	6.53 ± 0.070 (6.25 – 6.6)	13.07 ± 0.146 (12.6 – 13.3)	0.500 ± 0.009 (0.470 – 0.524)
WA-335, FMNH 199265	32(D)	7.34 ± 0.099 (6.25 – 8.7)	13.65 ± 0.145 (12.15 – 15.6)	0.538 ± 0.005 (0.486 – 0.600)
NR-II, Carpenter Gap, WAM 1235.76	50(D)	8.87 ± 0.089 (7.5 – 10.5)	15.67 ± 0.119 (13.9 – 17.8)	0.566 ± 0.004 (0.521 – 0.639)
WA-280, SE of Carpenter Gap, FMNH 199230	27(D)	8.68 ± 0.092 (7.9 – 9.55)	14.67 ± 0.154 (13.5 – 16.8)	0.592 ± 0.006 (0.529 – 0.677)
WA-336, SE of Carpenter Gap, FMNH 199278	37(D)	8.88 ± 0.101 (7.85 – 10.4)	15.38 ± 0.111 (13.8 – 16.6)	0.577 ± 0.005 (0.520 – 0.665)
NR-XVIII, 15 km SE Windjana, WAM 731.76	55(D)	9.17 ± 0.099 (7.5 – 10.8)	15.36 ± 0.107 (13.8 – 17.35)	0.597 ± 0.004 (0.528 – 0.678)

Table 55: Local Variation in *Westraltrachia derbyi* (Cox, 1892) (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
WA-194, SE Windjana Gorge, FMNH 200017, 10.X.1976	37(D)	4¾+ (4⅜–5¼–)	1.30±0.41 (0.75–1.85)	10.2±0.364 (6.85–15.9)
WA-194, FMNH 199197, 4.I.1977	19(L)	4¾– (4⅛– –5)	1.26±0.051 (0.9–1.8)	10.4±0.465 (7.22–14.7)
WA-581, FMNH 204705, 7.V.1980	13(L)	4⅞– (4¾– –5+)	1.52±0.086 (1.0–2.0)	8.96±0.576 (6.47–13.8)
WA-581, FMNH 204704, 7.V.1980	11(D)	4⅞+ (4¾– –5¼)	1.34±0.084 (0.9–1.9)	10.6±0.759 (7.13–16.3)
Walls of Windjana Gorge, NMV	50(D)	4⅝+ (4¼+ –5)	1.44±0.041 (1.0–2.1)	8.83±0.256 (5.33–12.3)
WA-334, Lillimilura, FMNH 200133	14(L)	4⅞ (4⅝–5⅛–)	1.63±0.061 (1.3–1.9)	8.16±0.372 (6.65–11.0)
WA-334, FMNH 199094	38(D)	4¾ (4⅜–5⅛)	1.47±0.044 (0.95–1.9)	8.99±0.282 (6.08–13.3)
WA-307, NE Windjana Gorge, FMNH 200180	13(L)	5+ (4¾–5⅜)	1.43±0.058 (1.0–1.85)	10.1±0.527 (7.35–15.0)
WA-307, FMNH 199208	28(D)	5⅛+ (5–5⅝)	1.48±0.046 (0.85–1.85)	9.89±0.395 (7.33–16.8)
WA-335, SE Lillimilura, FMNH 200147	5(L)	4⅞ (4¾–5+)	1.37±0.108 (1.15–1.70)	9.76±0.706 (7.82–11.1)
WA-335, FMNH 199265	32(D)	5– (4⅝–5⅜–)	1.19±0.053 (0.8–1.95)	12.2±0.564 (6.82–18.4)
NR-II, Carpenter Gap, WAM 1235.76	50(D)	5¼– (4¾–5⅝–)	1.25±0.041 (0.8–2.0)	13.2±0.437 (7.39–20.6)
WA-280, SE of Carpenter Gap, FMNH 199230	27(D)	5⅛– (4⅞–5⅜)	1.10±0.059 (0.5–1.7)	15.8±0.811 (8.35–29.8)
WA-336, SE of Carpenter Gap, FMNH 199278	37(D)	5⅛ (4⅞–5⅜)	1.16±0.040 (0.5–1.6)	14.1±0.672 (8.9–32)
NR-XVIII, 15 km SE Windjana, WAM 731.76	55(D)	5⅛+ (4¾–5⅝–)	1.17±0.036 (0.8–1.7)	13.9±0.442 (8.72–21.3)

Four specimens from 5 December 1976 are illustrated with the penis sheath open **(Figs 129c-e, 130b)**, plus one specimen collected 4 January 1977 **(Fig. 130c)**. They agree in having the penis muscle (PM) descend along the penis for a distance, the vas deferens (VD) enters the sheath (PS) near the lower margin of the penis muscle, except for the 4 January example the penis (P) is short and uncoiled, and the epiphallic loop is reduced in size. The slight twist in the penis of the 4 January example (**Fig. 130c**) may be a partial artifact of contraction within the shell rather than indicate a morphologic difference. These examples indicate the normal pattern of within population consistency.

The northern and eastern populations of *Westraltrachia derbyi* show distinct differences (**Figs 131-132**). At the north-east corner of Windjana Gorge (Sta. WA-307), a population isolated from Sta. WA-194 at the south-east corner by the sheer cliffs and water-gouged base of Windjana Gorge (a snail-free zone), the penis is elongated and coiled (**Fig. 131d**) and the epiphallic loop enlarged. Entrance of the vas deferens (VD) into the penis sheath (PS) and structure of the penis muscle (PM) is the same. At Stas. WA-335 (**Fig. 131b**) and WA-334 (**Fig. 132b**), the penis is intermediate in length, but otherwise structures agree well with those found at Sta. WA-307. South-east of Carpenter Gap (Sta. WA-336), the penis is shorter and the entrance of the vas deferens is now almost at the top of the penis sheath (**Fig. 132c**). All agree in having the altered main pilaster (**Fig. 158e**).

Other structures show little variation, with the short vagina (V), free oviduct (UV) noticeably longer than the spermatheca (S), and simple talon (GT) the same in all individuals examined.

Plates 27 and **28** illustrate the great variability in jaw structure found among specimens of *Westraltrachia derbyi* (Cox, 1892). Six specimens from Sta. WA-194, four collected on the same day (**Plate 27a-d**) just at the start of the wet season, and two (**Plate 27e-f**) during the main part of the wet season, indicate the range of variation. They include almost typical-looking camaenid jaws (**Plate 27b, f**), some having the central portion of the jaw smooth with vertical ribbing preserved laterally (**Plate 27c-d**), plus intermediate conditions (**Plate 27a, e**), with lateral smooth zones and central vertical ribbing. The specimens collected on 5 December 1976 show mixed indication of feeding activity, in that there is a nearly smooth exposed edge in two of them (**Plate 27a-b**), suggesting recent feeding, and a strongly serrated exposed edge indicative of growth (probably during aestivation) in two others (**Plate 27c-d**). Although the dry season ended on 6 December at Napier Downs, scattered showers to the east were recorded earlier that month and some of the Windjana populations could have been activated before 5 December 1976. The specimen collected on 21 March (**Plate 27f**) has a smooth edge indicative of feeding. It was not possible to provide an accurate estimate of vertical rib relief, so that the reader must form their own impression of jaw-rib prominence in the material shown on **Plate 28.** Specimens from Sta. WA-307 (**Plate 28a-b**) from the north-east corner of Windjana Gorge, have very strong vertical ribs. The two specimens differ dramatically, but typically, in rib numbers. The specimen from Sta. WA-334, north-west of Lillimilura Police Station ruins, has quite strong ribbing. Two specimens from 3.4 km south-east of Lillimilura Police Station ruins (Sta. WA-335, **Plate 28d-e**) show central area rib reduction, but differ in prominence of lateral ribs. The south-eastern-most available specimen (**Plate 28f**), from Sta. WA-336, 4.3 km south-east of Carpenter Gap, has very strong central and lateral ribs, with the outer margins of the jaw nearly smooth.

Given the extensive intra- and inter-populational variation in rib number and rib prominence on the jaws of *Westraltrachia derbyi*, it is obvious that neither rib number nor differences in rib prominence can be used to identify populations. It is, in some specimens of other camaenid species examined, possible to detect a repaired injury to a jaw, that is followed by altered rib prominence during subsequent growth. In none of the individuals of *W. derbyi* with reduced ribbing in the central area did I find such a repaired injury. Nevertheless, it is quite possible that at least some of these conditions were produced by injuries during the previous wet season, evidence for which was eroded during subsequent feeding activities.

Plates 38-40 survey variation in radular tooth structure. All specimens of *Westraltrachia derbyi* agree in having unicuspid central and lateral teeth with marked elevation of the mesocone. The extent to which the mesocone curves backward and the effective angle of the elevated cusp varies dramatically **(Plate 38).** Four individuals collected 5 December 1976 from Windjana Gorge (Sta. WA-194) are shown in **Plate 38a-d.** There is marked difference in the development of an anterior flare (compare **Plate 38a, d-e),** basic cusp angle of elevation **(Plate 38a-b, d-f),** and degree to which the upper edge of the cusp is curved backward **(Plate 38d-e).** The teeth portrayed in **Plate 38c** are from the generative area of the radula, were incompletely tanned, and thus warped during air drying of the radula onto the stub. Time did not permit extensive study of lateral tooth variation within individual radulae, but my impression is that there is a strong internal consistency as to the elevation and curvature within the same series of rows in the same radula, except for obvious injuries. There may be a difference from side to side of the radula, but difficulties in establishing exactly comparable angles of view and time for such study prevented pursuing this. Two specimens from the north-east corner of Windjana Gorge, Sta. WA-307, show equivalent differences in anterior flare, cusp elevation and backward curvature **(Plate 39a-b).** One of the sharpest cusp elevations was shown by a specimen from Sta. WA-334 **(Plate 39d).** Other figures on **Plate 39** show variation in cusp tip width and curvatures, plus lateral tooth width.

The transition from lateral to marginal teeth in *Westraltrachia derbyi* is typical, involving reduction and loss of anterior flare, reappearance of side cusps, loss of basal plate support ridges, change in cusp elevation to about a 45° angle, and loss of backward curvature **(Plate 40a-f).** A single early marginal tooth is shown in **Plate 40b.** Typical mid-marginal to late marginal teeth are tri-cuspid but highly variable in individual cusp size and total tooth width **(Plate 40c-f).** Apparently there is little or no pressure for a particular configuration of marginal tooth cusping in *Westraltrachia.*

The above outline of individual and populational variation in the jaw and radular teeth of *Westraltrachia derbyi* indicates that caution must be used in assigning taxonomic importance to minor changes in these structures, and single specimen observations have little utility unless changes are relatively gross in nature.

WESTRALTRACHIA ALTERNA IREDALE, 1939

(Plates 21c, 29a-d, 42: Figs 133-135, 158f)

Westraltrachia alterna Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 51, pl. III, fig. 17 – Barrier (= Napier) Range, Western Australia.

Westraltrachia increta Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 51, pl. III, fig. 16 – Barrier (= Napier) Range, Western Australia.

Nomenclature and type localities

The type specimens of both *Westraltrachia alterna* and *W. increta* have the rather flattened shape, narrow umbilicus, and protruded basal lip node found in material from McSherry Gap, and the type locality is restricted to this area, despite the large diameter of the holotype of *W. alterna* (16.8 mm). Iredale (1939: 51) followed his typical pattern of selecting a very large specimen as type of one species *(alterna)* and a smaller example from the same set as type of a second species *(increta)*. The differences between the two specimens are well within normal range of intrapopulational variation.

Comparative remarks

Westraltrachia alterna is very similar in size and shape to *W. derbyi* **(Table 47)**, differing most obviously in generally having a distinct node on the basal lip **(Figs 133b, e)** that is lacking in *W. derbyi* **(Figs 127b, e)**, the lip more widely reflected and often more nearly covering the umbilicus (see **Figs 127c, f, 133c, f)**, although the easternmost populations of *W. derbyi* **(Table 55**, Stations NR-II, WA-280, WA-336, NR-XVIII) tend to have a nearly closed umbilicus. *W. cunicula* **(Figs 138a-c)** from 2.4 km west of Tunnel Cave turnoff to the easternmost rock exposures of the Napier Range, is generally higher, with a more open umbilicus, and lacks the lip node. Anatomically, the presence of a small, typical primary pilaster in the upper penis **(Fig. 158f)**, near apical entrance of the vas deferens through the penis sheath **(Figs 134b, 135b)**, relatively short penis that is at most slightly coiled, and massive penial muscle with medium to large epiphallic loop, combine to separate *W. alterna* from its neighbours. *W. derbyi* has a unique single corrugated pilaster in the upper penis **(Fig. 158e)**, mid-penis entry of the vas deferens **(Figs 129c-e, 130b-c, 131b-c)**, a longer penis, and smaller penis muscle. *W. cunicula* has a single slender pilaster in the upper penis **(Fig. 158g)**, and a long penis that is coiled and kinked within the penis sheath.

Holotype of *Westraltrachia alterna* Iredale, 1939

AM C.64888, "on the Barrier Range," here restricted to the vicinity of McSherry Gap, Napier Range, South Kimberley, Western Australia. Collected by W.W. Froggatt. Height of shell 8.8 mm, diameter 16.8 mm, H/D ratio 0.524, whorls 5⅜, umbilical width 1.3 mm, D/U ratio 12.9.

Holotype of *Westraltrachia increta* Iredale, 1939

AM C.64888, "on the Barrier Range," here restricted to the vicinity of McSherry Gap, Napier Range, South Kimberley, Western Australia. Collected by W.W. Froggatt. Height of shell 8.7 mm, diameter 15.2 mm, H/D ratio 0.572, whorls 5⅜ –, umbilical width 0.9 mm, D/U ratio 16.9.

Paratopotypes of *Westraltrachia alterna* Iredale, 1939

AM C.1359, 4 dead adults from the type locality.

Paratopotypes of *Westraltrachia increta* Iredale, 1939

WAM 53.40, 2 dead adults from the type locality.

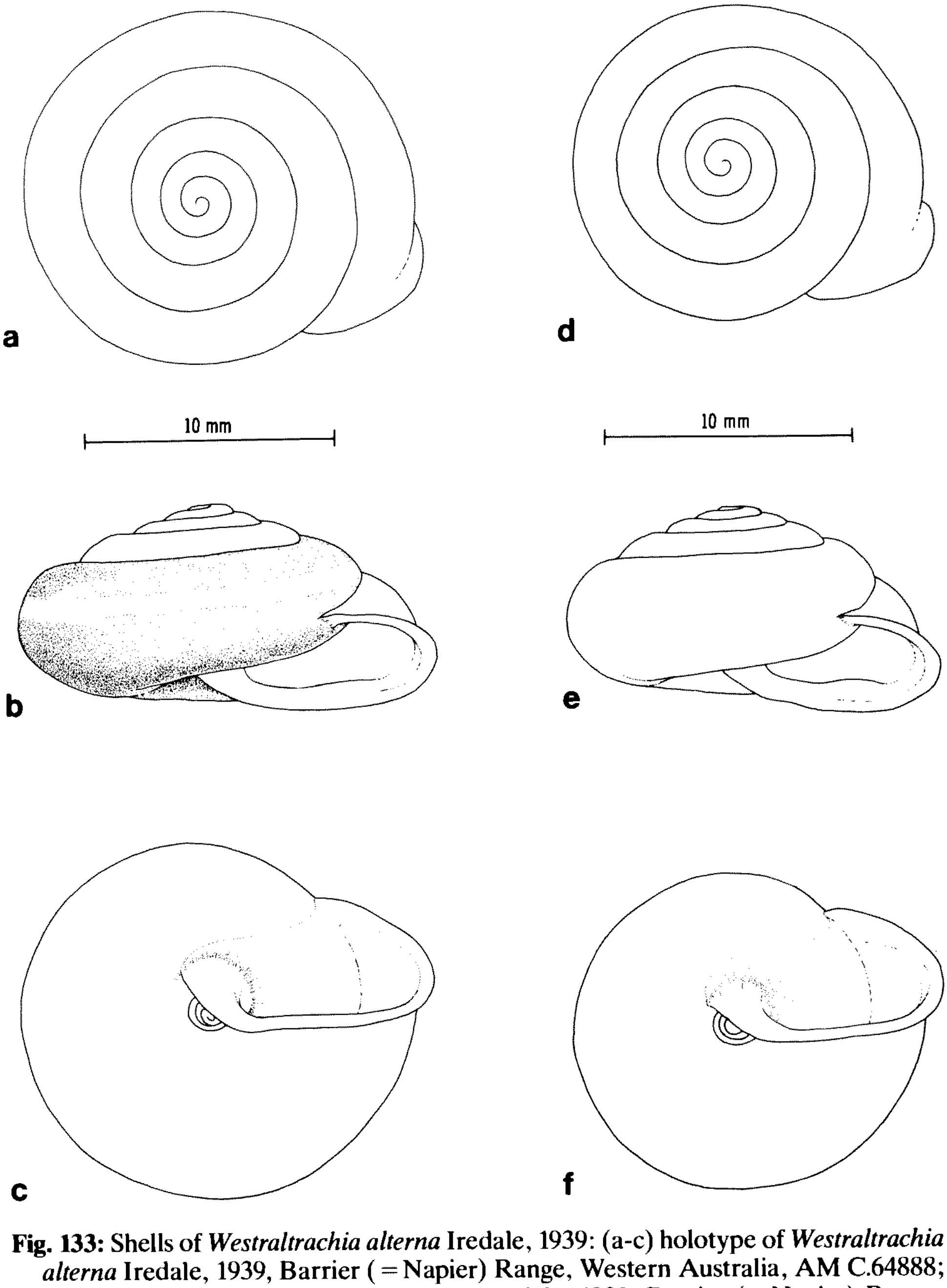


Fig. 133: Shells of *Westraltrachia alterna* Iredale, 1939: (a-c) holotype of *Westraltrachia alterna* Iredale, 1939, Barrier (= Napier) Range, Western Australia, AM C.64888; (d-f) holotype of *Westraltrachia increta* Iredale, 1939, Barrier (= Napier) Range, Western Australia, AM C.64886. Scale lines equal 10 mm. Drawings by Elizabeth Leibman.

Measured adults

Napier Range, South Kimberley: Sta. WA-582, west slope of Cycad Hill, north-north-east of McSherry Gap in talus and under spinifex ('Leopold Downs' 3962 – 221:603) (7 live, 75 dead adults, WAM 141.80-142.80, FMNH 204709-10); NR II-35, inside west corner of McSherry Gap (5 dead adults, WAM 1238.760); NR II-34, north corner of McSherry Gap (51 dead adults, WAM 1236.76); NR XXIII and NR XXIV, just south-east of McSherry Gap (1 live, 8 dead adults, WAM 739.76, WAM 740.76, WAM 937.76); Sta. WA-712, 100 m east of McSherry Gap, south side (3 live, 30 dead adults, WAM 147.80-148.80, FMNH 205319-20); Sta. WA-273, 0.8 km east of McSherry Gap, south side of range ('Leopold Downs' 3962 – 232:563) (1 live, 48 dead adults, WAM 144.80-146.80, FMNH 199201, FMNH 199472, FMNH 199920); NR XIX, 2.2 km south-east of McSherry Gap, north side of range (51 dead adults, WAM 730.76, WAM 742.76, WAM 934.76); Sta. WA-275, 5 km west of Tunnel Creek turnoff, north side of range ('Leopold Downs' 3962 – 244:554) (1 live, 85 dead adults, WAM 143.80, FMNH 199223, FMNH 199930).

Distribution limits in Napier Range

The known range of *W. alterna* covers 5.5 km, from the south slope of Cycad Hill (Sta. WA-582) to Sta. WA-275, about 5 km west of The Tunnel **(Fig. 160).** It is quite probable that scattered small colonies will be found for about 1.5 km further east, giving a total range of perhaps 7.0 km.

Diagnosis

Shell smaller than average, 12.2-16.8 mm (mean 14.12 mm) in diameter, with 4½ to 5⅝ (mean 5⅛) normally coiled whorls. Apex and spire moderately to strongly elevated **(Figs 133b, e),** sometimes rounded above, height of shell 6.3-11.0 mm (mean 8.32 mm), H/D ratio 0.493-0.720 (mean 0.589). Apical whorls with faint traces of microribbing in the sutures **(Plate 21c),** postnuclear whorls with faint microriblets and some irregular growth lines, former absent from shell base. Shell periphery obtusely and weakly angulated to rounded in adults **(Figs 133b, e),** more sharply angulated in juveniles. Lip moderately expanded and reflected, basal zone with a weak to prominent elevated node. Body whorl only slightly descending behind lip, columellar lip normally strongly reflected over and narrowing umbilicus, which is rarely reduced to a lateral crack. Umbilical width 0.45-2.25 mm (mean 1.23 mm), D/U ratio 6.36-29.7 (mean 12.2). Colour white on periphery and shell base, variegated light brown and white on spire, brownish just below periphery, and with some brownish patches visible in umbilicus. Degree of colour darkness and variegations individually variable. Based on 370 measured adults.

Genitalia **(Figs 134-135)** with large penis muscle (PM) and reduced epiphallic loop. Principal pilaster **(Fig. 158f)** small, typical in form, without hard edges. Penis (P) fairly short, not kinked unless animal retracted **(Fig. 135c),** penis sheath (PS) with lower walls only slightly thicker. Vas deferens **(Figs 134b, 135b,** VD) entering sheath near apex, well above epiphallic loop. Vagina **(Figs 134a, 135a,** V) of medium length, slender. Spermatheca **(Figs. 134a, 135a,** S) attached by fibers to base of prostate-uterus, distinctly shorter than free oviduct (UV), which is normally sinuated or looped. Based on six dissected adults.

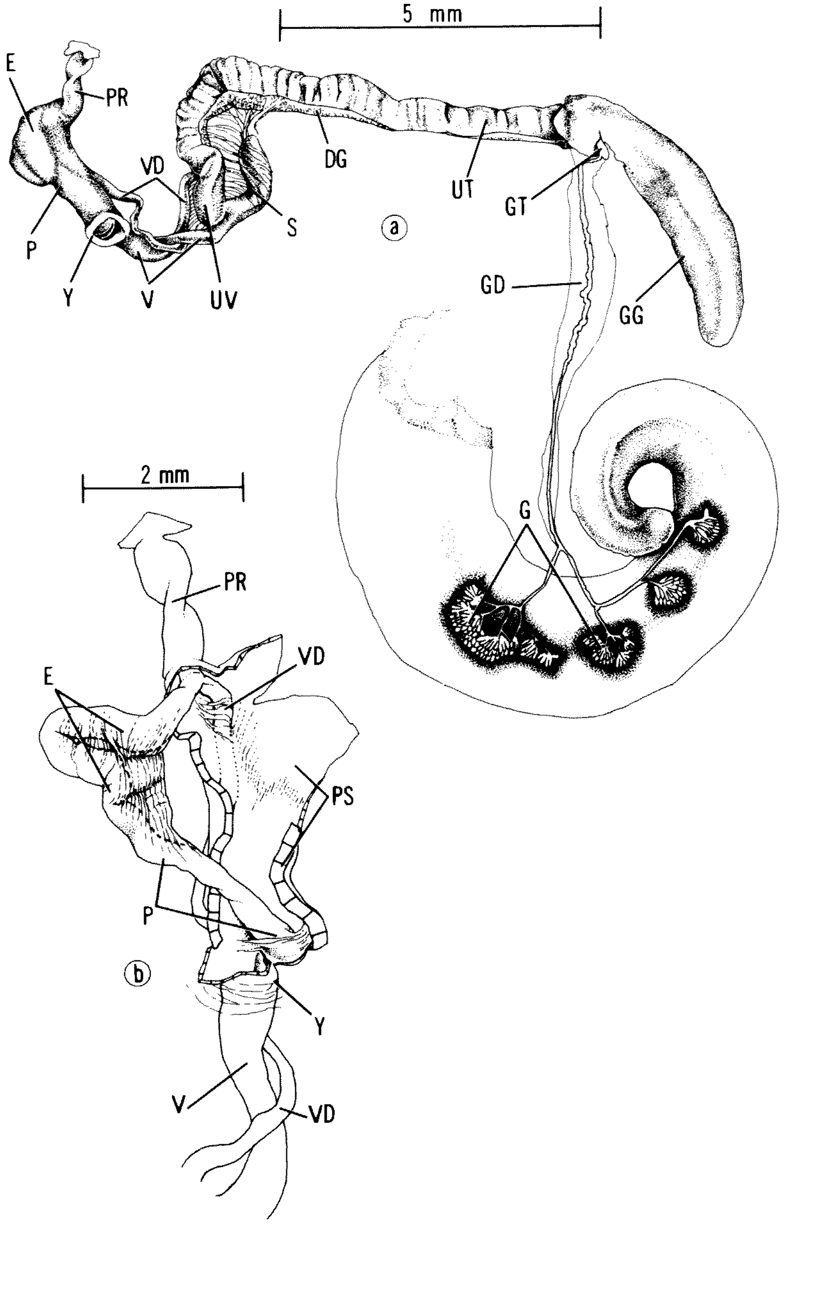


Fig. 134: Genitalia of *Westraltrachia alterna:* Sta. WA-582, Cycad Hill, Napier Range, 7 May 1980, FMNH 204709, Dissection B, (a) whole genitalia, (b) interior of penis sheath. Scale lines as marked. Drawings by Linnea Lahlum.

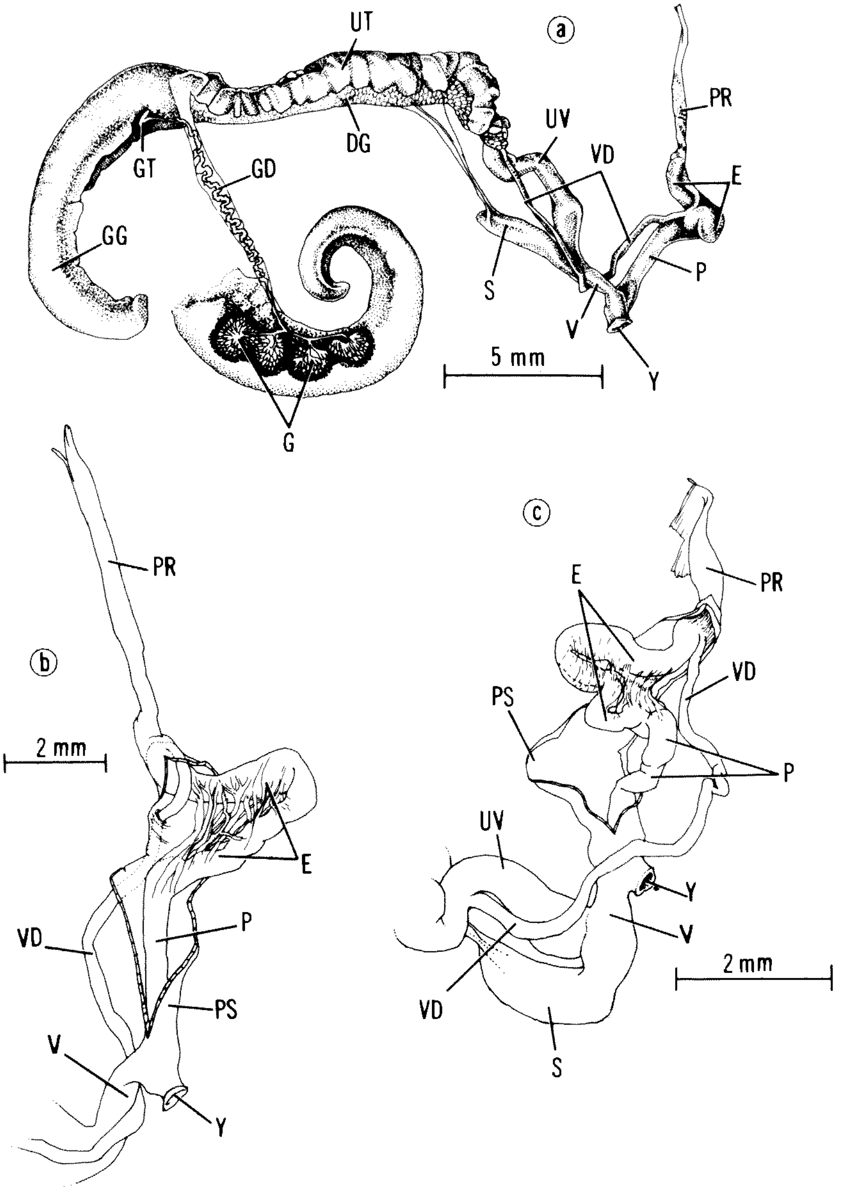


Fig. 135: Genital variation in *Westraltrachia alterna:* (a-b) Sta. WA-275, 5 km west of Tunnel Creek, Napier Range, 3 December 1976, FMNH 199930, Dissection A, (a) whole genitalia, (b) interior of penis sheath; (c) interior of penis sheath, Sta. WA-273, 0.8 km east of McSherry Gap, Napier Range, 3 December 1976, FMNH 199920. Scale lines as marked. Drawings by Linnea Lahlum.

Jaw (**Plate 29a-d**) with vertical ribs variable in number and reduced in prominence. Radula (**Plate 42**) with central and laterals highly modified, unicuspid, strongly elevated mesocone with curved, blunt tip, marginals typical in structure.

Discussion

Westraltrachia alterna was not recognised as a distinct species in this review until it had been dissected. The basal lip node does separate typical specimens, but in at least 20% of the examined adults it is reduced to the point that differences from *W. derbyi* and *W. cunicula* are obscured. Retention of a typical penis pilaster in *W. alterna,* compared with the elongated single pilasters in the other two species, near apical entrance of the vas deferens into the penis sheath, and relatively short penis, are the main features characterising it as a distinct species.

Size and shape variation among the larger samples of *W. alterna* (**Table 56**) are minimal, compared with the great variability found in *W. derbyi* (**Tables 54** and **55).**

From its easternmost locality through McSherry Gap, *Westraltrachia alterna* is sympatric with *Quistrachia monogramma* (Ancey, 1898). The comparatively great alteration of the central and lateral teeth of the radula (**Plate 42**) and noticable reduction in prominence of the jaw ribs (**Plate 29a-d**) are interpreted as character displacement (Solem, In press-A). West of McSherry Gap, at Cycad Hill, *W. alterna* is the only camaenid present, but the jaw and radula do not differ from those specimens taken in sympatry. Since colonisation of *Westraltrachia* is hypothesised as having occurred from the east, presumably populations would have passed through the zone of sympatry with *Quistrachia* prior to reaching Cycad Hill. Thus retention of the previously altered pattern would be the probable explanation for this situation.

Table 56: Local Variation in *Westraltrachia alterna* Iredale, 1939 and *W. cunicula*

Locality	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
W. alterna				
WA-582, Cycad Hill, FMNH 204709	7L	8.18 ± 0.222 (7.5 – 9.25)	14.74 ± 0.279 (14.0 – 15.8)	0.555 ± 0.016 (0.493 – 0.600)
WA-582, FMNH 204710	75D	7.98 ± 0.074 (6.3 – 9.4)	14.16 ± 0.089 (12.2 – 15.5)	0.563 ± 0.004 (0.498 – 0.648)
NRII-35, W corner, McSherry Gap, WAM 1238.76	5D	7.67 ± 0.293 (6.9 – 8.6)	14.24 ± 0.453 (13.1 – 15.7)	0.539 ± 0.011 (0.500 – 0.559)
NRII-34, N corner, McSherry Gap, WAM 1236.76	51D	7.84 ± 0.102 (6.6 – 9.6)	13.96 ± 0.129 (12.3 – 15.9)	0.562 ± 0.005 (0.500 – 0.681)
WA-712, 100 m E of McSherry Gap, S side, FMNH 205319	3L	8.25 ± 0.362 (7.65 – 8.9)	14.40 ± 0.643 (13.4 – 15.6)	0.574 ± 0.021 (0.539 – 0.612)
WA-712, FMNH 205320	30D	8.38 ± 0.106 (7.05 – 9.9)	14.27 ± 0.125 (13.1 – 16.0)	0.587 ± 0.005 (0.517 – 0.641)

Table 56: Local Variation in *Westraltrachia alterna* Iredale, 1939 and *W. cunicula* (continued)

Locality	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
NRXXIV, just SE, McSherry Gap, WAM 740.76	7D	8.38 ± 0.352 (7.4 – 10.3)	14.23 ± 0.371 (12.95 – 16.05)	0.588 ± 0.012 (0.547 – 0.642)
WA-273, 0.8 km E of McSherry Gap, FMNH 199201	15D	8.43 ± 0.168 (7.7 – 9.65)	13.90 ± 0.139 (13.1 – 14.7)	0.606 ± 0.012 (0.556 – 0.715)
WA-273, FMNH 199472	33D	8.22 ± 0.091 (7.05 – 9.3)	13.82 ± 0.097 (12.6 – 15.15)	0.595 ± 0.006 (0.540 – 0.660)
NRXIX, 2.2 km SE McSherry Gap, NE side, WAM 730.76	37D	8.73 ± 0.095 (7.05 – 9.8)	14.20 ± 0.101 (13.0 – 15.65)	0.615 ± 0.006 (0.522 – 0.684)
NRXIX, WAM 742.76	13D	9.05 ± 0.259 (8.1 – 11.0)	14.56 ± 0.153 (13.6 – 15.7)	0.621 ± 0.014 (0.557 – 0.702)
WA-275, 5 km W of Tunnel Creek, FMNH 199223	85D	8.63 ± 0.058 (7.4 – 9.9)	14.03 ± 0.065 (12.6 – 15.3)	0.615 ± 0.004 (0.538 – 0.720)
W. cunicula				
WA-583, 2.4 km W of Tunnel Creek, FMNH 204704	12D	9.05 ± 0.234 (8.3 – 10.75)	14.26 ± 0.306 (12.5 – 16.4)	0.635 ± 0.009 (0.593 – 0.696)
NRXXI, S entrance Tunnel Cave, WAM 743.76	7D	8.59 ± 0.209 (8.0 – 9.6)	14.36 ± 0.194 (13.55 – 14.9)	0.598 ± 0.011 (0.562 – 0.644)
NRXXII, SW side Tunnel Creek Yard, WAM 744.76	9D	8.79 ± 0.146 (8.4 – 9.85)	14.00 ± 0.337 (12.5 – 15.5)	0.630 ± 0.013 (0.558 – 0.680)
WA-274, S entrance Tunnel Creek Cave, FMNH 199886	5L	8.39 ± 0.287 (7.35 – 9.05)	14.08 ± 0.404 (12.75 – 15.15)	0.596 ± 0.013 (0.575 – 0.642)
WA-274, FMNH 199241	20D	8.40 ± 0.117 (7.45 – 9.3)	13.95 ± 0.137 (12.9 – 14.9)	0.602 ± 0.006 (0.568 – 0.676)
WA-195, N side Tunnel Creek Cave, FMNH 200082	8D	8.68 ± 0.253 (8.0 – 10.25)	14.04 ± 0.220) (13.35 – 15.1)	0.618 ± 0.010 (0.586 – 0.679)
WA-272, 1.7 km E of Tunnel Creek Cave, N side, FMNH 199450	61D	8.76 ± 0.091 (7.4 – 10.6)	14.22 ± 0.084 (12.65 – 15.65)	0.616 ± 0.005 (0.550 – 0.744)
WA-279, N of Chestnut Creek, FMNH 199233	81D	9.34 ± 0.078 (7.9 – 11.4)	14.99 ± 0.074 (13.8 – 16.6)	0.623 ± 0.004 (0.547 – 0.736)
WA-270, 21.8 km E of TunnelCreek, FMNH 199257	53D	9.78 ± 0.105 (8.45 – 11.5)	15.02 ± 0.087 (13.8 – 16.7)	0.651 ± 0.006 (0.569 – 0.754)

Table 56: Local Variation in *Westraltrachia alterna* Iredale, 1939 and *W. cunicula* (continued)

Locality	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
W. alterna				
WA-582, Cycad Hill, FMNH 204709	7L	5⅛+ (5+ – 5¼)	1.14 ± 0.129 (0.6 – 1.6)	14.3 ± 1.993 (9.0 – 23.5)
WA-582, FMNH 204710	75D	5⅛ (4¾– – 5½+)	1.16 ± 0.027 (0.5 – 1.7)	12.8 ± 0.368 (8.32 – 28.1)
NRII-35, W corner McSherry Gap, WAM 1238.76	5D	5⅛– (4⅞– – 5¼+)	1.35 ± 0.130 (1.0 – 1.65)	10.9 ± 0.988 (8.85 – 14.3)
NRII-34, N corner, McSherry Gap, WAM 1236.76	51D	5 (4½ – 5⅝)	1.13 ± 0.039 (0.6 – 1.9)	13.2 ± 0.513 (7.03 – 23.5)
WA-712, 100 m E of McSherry Gap, S side, FMNH 205319	3L	5+ (4⅞+ – 5¼–)	1.67 ± 0.203 (1.3 – 2.0)	8.86 ± 0.938 (7.1 – 10.3)
WA-712, FMNH 205320	30D	5⅛– (4⅝ – 5⅜+)	1.33 ± 0.041 (1.0 – 1.9)	11.1 ± 0.340 (7.18 – 14.3)
NRXXIV, just SE McSherry Gap, WAM 740.76	7D	5⅛ (5– – 5½)	1.49 ± 0.054 (1.3 – 1.7)	9.61 ± 0.441 (8.18 – 11.5)
WA-273, 0.8 km E of McSherry Gap, FMNH 199201	15D	5¼– (5– – 5⅜)	1.32 ± 0.074 (0.9 – 1.8)	11.0 ± 0.621 (7.56 – 15.5)
WA-273, FMNH 199472	33D	5⅛– (4¾ – 5½)	1.27 ± 0.049 (0.55 – 1.8)	11.5 ± 0.541 (7.5 – 23.1)
NRXIX, 2.2 km SE McSherry Gap, NE side, WAM 730.76	37D	5⅛+ (4¾ – 5⅝–)	1.28 ± 0.056 (0.55 – 1.95)	12.0 ± 0.585 (6.92 – 26.4)
NRXIX, WAM 742.76	13D	5¼+ (5+ – 5⅝)	1.44 ± 0.064 (1.0 – 1.85)	10.4 ± 0.499 (7.76 – 13.6)
WA-275, 5 km W of Tunnel Creek, FMNH 199223	85D	5⅛ (4⅞ – 5½)	1.20 ± 0.033 (0.45 – 2.25)	12.5 ± 0.372 (6.36 – 29.7)
W. cunicula				
WA-583, 2.4 km W of Tunnel Creek, FMNH 204704	12D	5¼– (5 – 5⅝)	1.09 ± 0.088 (0.55 – 1.75)	14.1 ± 1.295 (9.26 – 25.3)
NRXXI, S entrance Tunnel Cave, WAM 743.76	7D	5+ (4¾ – 5¼+)	1.11 ± 0.118 (0.6 – 1.65)	13.9 ± 1.706 (8.97 – 23.5)
NRXXII, SW side Tunnel Creek Yard, WAM 744.76	9D	5⅛ (5– – 5⅜+)	0.91 ± 0.073 (0.7 – 1.3)	15.9 ± 0.926 (11.9 – 19.0)
WA-274, S entrance Tunnel Creek Cave, FMNH 199886	5L	5⅛ (4⅞+ – 5⅜)	0.92 ± 0.146 (0.6 – 1.4)	16.6 ± 2.236 (10.4 – 23.0)
WA-274, FMHH 199241	20D	5 (4⅝ – 5⅜–)	1.18 ± 0.057 (0.8 – 1.7)	12.4 ± 0.587 (8.53 – 16.5)

Table 56: Local Variation in *Westraltrachia alterna* Iredale, 1939 and *W. cunicula* (continued)

Locality	Number of Adults Measured	Whorls	Mean, SEM and Range of: Umbilical Width	D/U Ratio
WA-195, N side Tunnel Creek Cave, FMMH 200082	8D	5+ (4⅝+ – 5¼)	1.38 ± 0.129 (0.7 – 1.8)	11.1 ± 1.471 (7.42 – 20.6)
WA-272, 1.7 km E of Tunnel Creek Cave, N side, FMNH 199450	61D	5⅛– (4⅜ – 5⅝)	1.17 ± 0.044 (0.6 – 2.0)	13.1 ± 0.515 (7.05 – 24.0)
WA-279, N of Chestnut Creek, FMNH 199233	81D	5⅛+ (4¾ – 5½)	1.10 ± 0.026 (0.6 – 1.75)	14.3 ± 0.380 (9.00 – 27.3)
WA-270, 21.8 km E of Tunnel Creek, FMNH 199257	53D	5⅛+ (4¾ – 5½)	0.92 ± 0.039 (0.5 – 1.55)	17.8 ± 0.835 (9.48 – 31)

WESTRALTRACHIA OSCARENSIS (COX, 1892)

(Plates 21d-f, 30a, 41; Figs 136, 137, 158h)

Helix (Hadra) oscarensis Cox, 1892, Proc. Linn. Soc. N. S. W., (2) **6** (3): 565-6, pl. xx, figs 6-7 – The Oscar Ranges, 20 miles from the Barrier Ranges, Western Australia (Froggatt); Pilsbry, 1893, Man. Conch., (2) **8:** 279-280, pl. 58, figs. 25-26.

Helix (Rhagada) inconvicta E.A. Smith, 1894, Proc. Malac. Soc. London, **1:** 90, pl. VII, fig. 10 – Oscar Ranges, 120 miles south-east of King Sound, N. W. Australia.

Rhagada oscarensis (Cox), Iredale, 1938, Australian Zool., **9** (2): 113; Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 62-63, pl. IV, fig. 15.

Rhagada oscarensis perca Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 63, pl. IV, fig. 16 – Oscar Ranges, "crawling about on the ground", Western Australia.

Nomenclature and type localities

Helix oscarensis Cox, 1892 and *H. inconvicta* Smith, 1894 were based upon material from the same set of specimens, as was pointed out by Hedley (1895: 259). Unfortunately, the exact locality where they were taken "under stones" was not specified, and none of the modern collections are an exact match in shell form with the types. Thus no formal type locality designation is presented. The types of *Rhagada oscarensis perca* Iredale, 1939 were "crawling about on the ground" and agree fairly well with some of the Oscar Plateau fringe samples, but type locality designation is postponed until after more thorough sampling of this region.

Comparative remarks

Westraltrachia oscarensis (Cox, 1892) averages more than 3 mm more in diameter and a quarter whorl more in mean whorl count than species from the middle part of the generic range (**Table 47**). The west Napier *Westraltrachia woodwardi* (Fulton, 1902) and the east Napier *W. ampla* are much more similar in size, but the closed umbilicus and white colour of the former, and the angulated periphery and lower spire of the latter provide easy identification. The relatively high, rounded spire (**Figs 136b, e**), lighter colour, almost closed umbilicus, relatively thin lip, and rather prominent growth striae (**Plate 21f**) also serve to characterise *W. oscarensis*. *Westraltrachia alterna* Iredale, 1939 is much flatter in shape (**Figs 133b, e**), normally has a basal lip node, is much more strongly coloured, averages 3.7 mm less in mean diameter (**Table 47**), and has less radial sculpture. *Westraltrachia cunicula,* which may be sympatric with *W. oscarensis* at Station WA-279, is smaller (**Table 47**), more depressed, with a more open umbilicus, rounded periphery, and much darker colouration. Anatomically, the large epiphallic loop (**Fig. 137b**, E), long, slender, kinked penis (P) with slender single pilaster (**Fig. 158g**), long vagina (V), and mid-penis entry of the vas deferens (VD) into the penis sheath combine to separate it from *W. alterna,* while *W. cunicula* has the epiphallic loop reduced (**Figs 139c-e**), a much longer penis, and very distinctive penis pilaster (**Fig. 158g**).

Lectotype of *Helix oscarensis* Cox, 1892

AM C.106524, Oscar Ranges, 20 miles from the Barrier (= Napier) Ranges, Western Australia. Collected by W. W. Froggatt. Height of shell 14.0 mm, diameter 19.8 mm, H/D ratio 0.707, whorls 6+, umbilical width 0.95 mm, D/U ratio 20.8.

Paralectotypes of *Helix oscarensis* Cox, 1892

AM C.64909, 6 dead adults from the type locality.

Lectotype of *Helix inconvicta* Smith, 1894

BM(NH) 88.11.28.64, Oscar Ranges, 20 miles from the Burner (= Napier) Ranges, Western Australia. Collected by W. W. Froggatt. Height of shell 12.75 mm, diameter 20.15 mm, H/D ratio 0.633, whorls 5¾−, umbilicus a narrow crack.

Holotype of *Rhagada oscarensis perca* Iredale, 1939

AM C.64882, crawling on the ground, Oscar Ranges, Western Australia. Height of shell 10.45 mm, diameter 17.2 mm, H/D ratio 0.608, whorls 5⅛, umbilical width 1.05 mm, D/U ratio 16.4.

Paratypes of *Rhagada oscarensis perca* Iredale, 1939

AM C.79035, 20 dead adults from the type locality.

Measured adults

Edge of Oscar Plateau and Fairfield Valley to edge of Napier Range, geographic sequence west to east: OR VI and OR VII, north of Palm Spring, Le Lievre's Ridge ('Ellendale' 3862 – *ca.* 095:425) (19 dead adults, WAM 901.76-903.76); Sta. WA-277, Elimberrie Spring ('Leopold Downs' 3962 – 169:458) (5 dead adults, WAM 63.80, FMNH 200197); Sta. WA-278, cliffs 0.5 km east of Elimberrie Spring ('Leopold Downs' 3962 – 172:455) (1 live, 39 dead adults, WAM 65.80-66.80, FMNH 199237, FMNH 200218); Sta. WA-276, 3.6 km north-west of Wine Spring, plains area between Oscar and Napier Ranges, Fairfield Valley ('Leopold Downs' 3962 – 241:442) (13 live, 23 dead adults, WAM 1345.78, WAM 59.80, WAM 61.80-62.80, WAM 64.80, FMNH

199205, FMNH 199239, FMNH 200100, FMNH 200190, FMNH 200346); Sta. WA-356, 1.3 km north-east of yard, north of Wine Spring, 0.3 km south of Chestnut Creek, plains area between Napier and Oscar Ranges ('Leopold Downs' 3962 – 284:437) (14 live, 12 dead adults, WAM 57.80, WAM 60.80, FMNH 199102, FMNH 200165); Sta. WA-279, cliffs north of Chestnut Creek, east of Wine Spring Road, south face of Napier Range ('Leopold Downs' 3962 – 322:447) (1 dead adult, FMNH 198988); Sta. WA-271, cliffs 11.3 km east of Tunnel Creek turnoff, north side of Napier Range ('Leopold Downs' 3962 – 342:449) (1 live, 19 dead adults, WAM 58.80, FMNH 199454, FMNH 200199).

Distribution limits in Oscar and Napier Ranges

The westernmost locality for *Westraltrachia oscarensis* is just north of Palm Spring on Ninety Two Mile Creek, the south-west fringe of the Oscar Plateau. Quite probably it ranges along the scattered limestone that continues about 8 km north-west, but this area has not been sampled for land snails. It then ranges along the Oscar Plateau south of Chestnut Creek at least as far as Wine Spring, lives in Fairfield Valley under scattered limestone blocks, and has crossed successfully to the fringes of the Napier Range at Sta. WA-271, 11.3 km east of The Tunnel, and possibly at Sta. WA-279 on the south face of the Napier Range **(Fig. 160).** Thus a total of up to 28.5 km of limestone ridges may be inhabited by this species.

Diagnosis

Shell very large, 14.3-22.1 mm (mean 17.94 mm) in diameter, with 4⅝ to 6 (mean 5⅜ –) rather tightly coiled whorls. Apex and spire strongly elevated, usually slightly rounded above **(Figs 136b, e),** body whorl descending very slightly before aperture, height of shell 7.75-14.9 mm (mean 11.55 mm), H/D ratio 0.510-0.800 (mean 0.643). Apical whorls **(Plate 21d-f)** normally worn smooth, at most with micro-riblet remnants in the sutures, postapical sculpture of irregular growth striae and micro-riblets. Shell periphery of larger adults rounded **(Fig. 136b)** to obtusely angulated, almost right-angled in smaller adults **(Fig. 136e).** Lip narrowly to moderately expanded **(Figs 136a-f),** without basal node, columellar portion strongly reflected. Umbilicus rarely open, effectively closed in 18.8% of measured adults, a lateral crack to slightly open in 81.2%. Colour variable within and among populations. At most with purplish-brown markings on both sides of white peripheral band, more often light brownish and yellow-white variegations on spire, with base lighter. Often colour reduced to almost white on spire and much of body whorl. Based on 184 measured adults.

Genitalia **(Figs 137a-c)** with very large penis muscle (PM) and epiphallic loop, with arms of loop tightly bound together. Principal pilaster of penis **(Fig. 158h)** narrow, retaining some indication of sinuation, but clearly modified. Penis (P) long and slender, tightly kinked within penis sheath (PS), which has comparatively thin walls for entire length **(Fig. 137b).** Vas deferens **(Fig. 137b,** VD) with mid-penis entry into penis sheath. Vagina (V) very long, slender, free oviduct (UV) sinuated, noticeably longer than spermatheca (S), which is attached to base of prostate-uterus by fibers.

Jaw **(Plate 30a)** at least in plains area with prominent vertical ribs. Radular teeth **(Plate 41)** greatly modified. Central and laterals sharply elevated, ectocones greatly reduced to absent, mesocone quite blunt tipped, but only slightly curved posteriorly, sides of laterals sometimes weakly serrated **(Plate 41f).** Transition to marginals typical **(Plate 41e).**

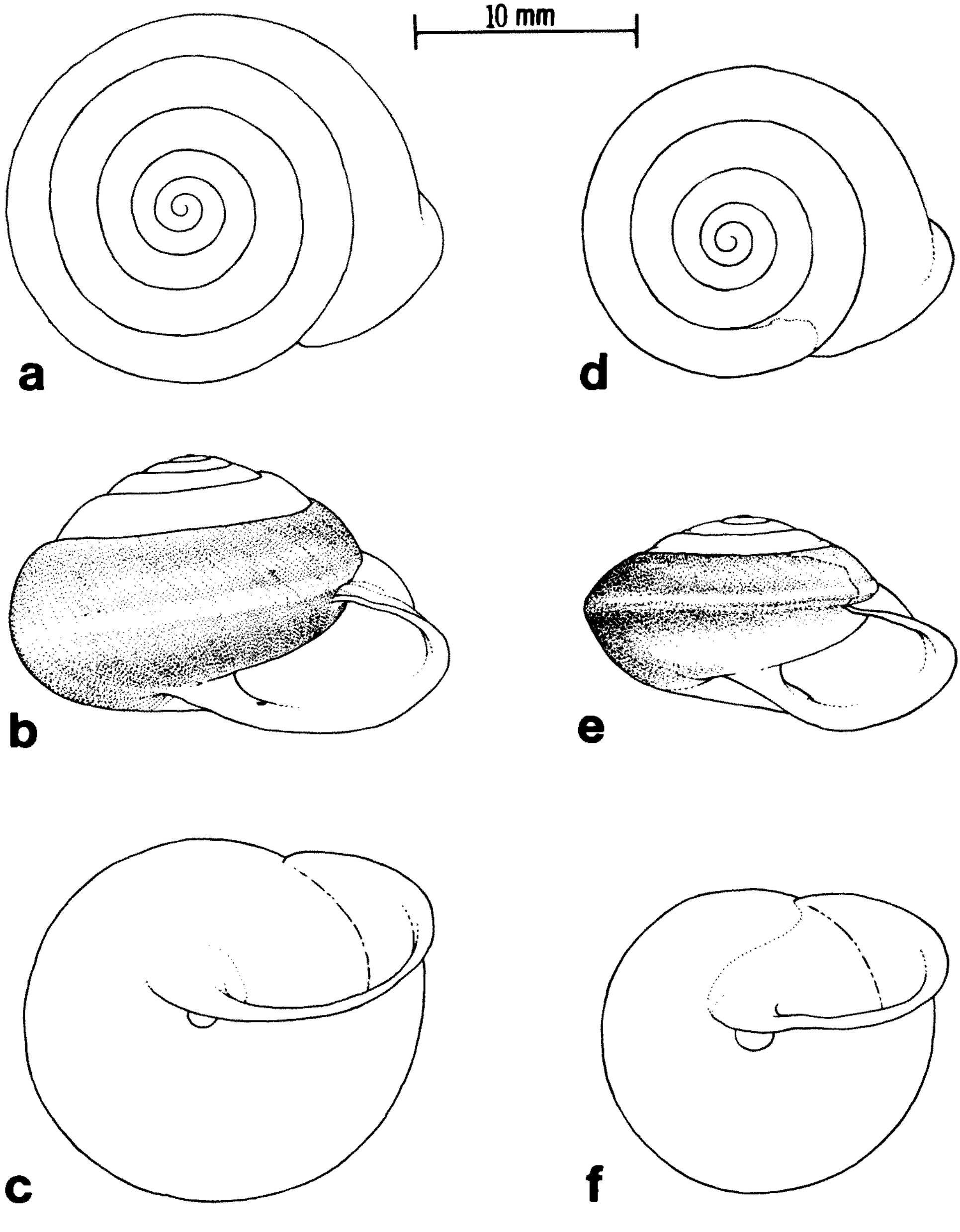


Fig. 136: Shells of *Westraltrachia oscarensis* (Cox, 1892): (a-c) lectotype of *Helix oscarensis* Cox, 1892, AM C.106524; (d-f) holotype of *Rhagada oscarensis perca* Iredale, 1939, AM C.64882. Scale line equals 10 mm. Drawings by Elizabeth Liebman.

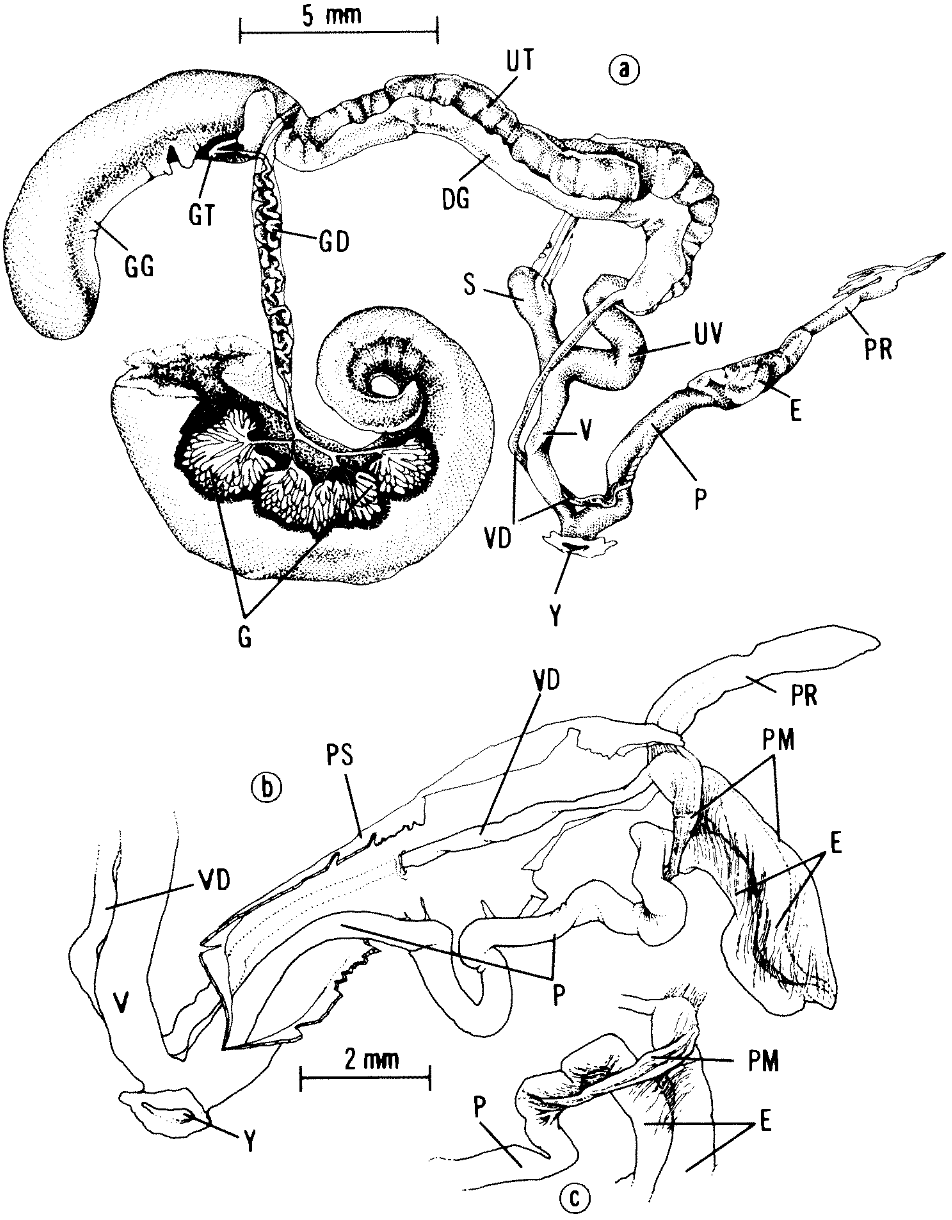


Fig. 137: Genitalia of *Westraltrachia oscarensis* (Cox, 1892): Sta. WA-356, Wine Spring, between Napier and Oscar Ranges, 1 January 1977, FMNH 200165, (a) whole genitalia, Dissection C, (b) interior of penis sheath, Dissection B, (c) detail of penial muscle (PM) attachment, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

Discussion

Westraltrachia oscarensis (Cox, 1892) occupies a limited area on the edge of the Oscar Plateau **(Fig. 160)** between Palm Spring east to the area of the Napier Range between 'The Tunnel' and 6 Mile Bore (Sta. WA-271), a total of 28.5 km. Whether it extends east to 6 Mile Bore or nearer to 'The Tunnel' in the Napiers is unknown. This region is isolated during the wet season by black mud plains and sampling, of necessity, has been limited to dry season visits when traveling between Napier Downs and Fitzroy Crossing. Thus the intensity of collecting has been less, and comparatively little live material was available for study. Unlike *Quistrachia monogramma* (Ancey, 1898), which has an overlapping range, but is restricted to the hill areas, *W. oscarensis* is more common in the open areas of Fairfield Valley (drainages of Tunnel Creek and Chestnut Creek), than on the hillsides.

The few sets with precise locality data show comparatively minor variation in size and shape **(Table 58).** The 'plains' populations (Stas. WA-276, WA-356) average a trifle larger than those from the Oscar Plateau edge (Stas. WA-277, WA-278, Palm Spring). The size difference in diameter is mainly accounted for by a slight change in mean whorl count.

Table 57: Allochronic Variation in *Westraltrachia oscarensis* (Cox, 1892)

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
WA-276, FMNH 200190, 4.XII.1976	10L	12.39±0.194 (11.2–13.2)	18.88±0.241 (17.6–20.0)	0.657±0.010 (0.605–0.706)
WA-276, FMNH 199329, 4.XII.1976	17D	12.14±0.248 (10.6–13.6)	18.27±0.241 (15.8–20.4)	0.664±0.009 (0.598–0.731)
WA-356, FMNH 200165, 1.I.1977	14L	11.89±0.150 (10.8–12.6)	18.06±0.145 (17.3–18.9)	0.659±0.008 (0.590–0.697)
WA-356, FMNH 199102, 1.I.1977	12D	11.67±0.215 (10.8–13.2)	17.88±0.330 (16.5–20.2)	0.656±0.013 (0.599–0.718)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
WA-276, FMNH 200190, 4.XII.1976	10L	5⅜– (5⅛+ – 5¾+)	1.35±0.109 (1.0–2.0)	14.6±1.04 (10.0–19.7)
WA-276, FMNH 199239, 4.XII.1976	17D	5¼+ (4⅞– – 5⅝+)	1.12±0.066 (0.6–1.5)	17.5±1.27 (12.2–31)
WA-356, FMNH 200165, 1.I.1977	14L	5⅜– (4⅞+ – 5½+)	1.20±0.112 (0.65–1.95)	16.7±1.62 (9.49–29.1)
WA-356, FMNH 199102, 1.I.1977	12D	5¼+ (5– – 5⅝)	0.66±0.073 (0.4–1.2)	31.2±2.72 (14.5–43)

Table 58: Geographic Variation in *Westraltrachia oscarensis* (Cox, 1892)

Locality	Number of Adults Measured	Mean and Range of: Shell Height	Shell Diameter	H/D Ratio
Near Palm Spring	19	11.48 (9.6 – 13.25)	17.36 (14.7 – 19.2)	0.661 (0.602 – 0.746)
WA-277	5	9.83 (7.75 – 11.1)	16.74 (15.2 – 18.1)	0.586 (0.510 – 0.656)
WA-278	40	10.26 (8.25 – 13.0)	17.56 (15.6 – 19.4)	0.583 (0.517 – 0.714)
WA-276	36	12.26 (10.6 – 13.6)	18.56 (15.8 – 20.4)	0.661 (0.598 – 0.731)
WA-356	26	11.79 (10.8 – 13.2)	17.98 (16.5 – 20.2)	0.658 (0.590 – 0.718)
WA-271	20	13.10 (11.2 – 14.8)	18.24 (17.0 – 20.2)	0.719 (0.656 – 0.800)
Types of *perca*	20	10.01 (8.45 – 11.3)	16.28 (14.3 – 18.0)	0.615 (0.556 – 0.714)
Types of *oscarensis*	12	13.28 (12.0 – 14.35)	19.92 (19.0 – 22.1)	0.667 (0.602 – 0.707)

Locality	Number of Adults Measured	Mean and Range of: Whorls	Umbilical States
Near Palm Spring	19	5⅜ + (5 – 6)	7 cracked, 12 open
WA-277	5	5¼ – (5 – – 5½ +)	5 open
WA-278	40	5¼ – (4⅝ – – 5⅞ +)	1 cracked, 39 open
WA-276	36	5⅜ – (4⅞ – 5¾ +)	2 cracked, 34 open
WA-356	26	5⅜ – (4⅞ + – 5⅝)	2 cracked, 24 open
WA-271	20	5⅜ (5 – – 5⅝ +)	18 cracked, 2 open
Types of *perca*	20	5¼ (5 – 5⅝)	20 open
Types of *oscarensis*	12	5¾ – (5⅜ – 6 +)	4 cracked, 8 open

The only collection of *Westraltrachia oscarensis* known from the north slopes of the Napiers was taken at Sta. WA-271. These specimens are significantly more elevated and have a reduced umbilical opening **(Table 58).** They come closest to matching the type specimens in size and shape, but are a little smaller and proportionately higher. Eventual designation of a type locality from this section of the Napier Range may be desirable, but this action is withheld pending a better match between types and extant population. In contrast, Iredale's form *perca* compares well with material from Elimberrie Spring (Sta. WA-277), which could well be the type locality. Again, formal type locality restriction is withheld.

The 'plains population' show some indication of allochronic variation **(Table 57),** with live adults being slightly larger than dead adults collected the same day. These habitats are much less sheltered from drying out than are the hill side aestivation niches, so that year class effects would be expected.

The exact geographic relationship between *Westraltrachia oscarensis* and *W. cunicula* remains to be determined. One dead example of the former and four live plus 93 dead of the latter were taken on the barren, south-facing slopes of the Napier Range north of Chestnut Creek (WA-279). This lies between the main range of *W. oscarensis* and its isolated occurrence at Station WA-271 on the north slope of the Napier Range, where one live and 19 dead examples were collected. Other positive localities for *Westraltrachia cunicula* lie both east and west of this locality (see below). Who is replacing whom cannot be predicted on presently available data.

In retaining strong vertical ribs on the jaw **(Plate 21d-f)** and showing partly modified central and lateral teeth on the radula **(Plate 41),** *Westraltrachia oscarensis* is less modified that either *W. alterna* **(Plates 29a-d, 42)** to the west or *W. cunicula* **(Plates 29e-h, 43)** to the east. The observations on *W. oscarensis* were based on 'plains populations' where it is the only camaenid present, whereas these populations of the other taxa were sympatric with *Quistrachia monogramma.* Not enough live collected material was available to permit SEM radular study of *oscarensis* specimens from populations sympatric with *Quistrachia,* and solution of this question is left to others.

Both Smith (1894) and Iredale (1939) were misled by the shell form and colour, and classified this species with *Rhagada* Albers, 1860, a very different genus in anatomy. *Exiligada* Iredale, 1939, shown below to be derived from a *Westraltrachia* ancestor, also was misclassified for similar reasons.

WESTRALTRACHIA CUNICULA SP. NOV.

(Plates 21b, 29e-h, 43; Figs 138a-c, 139, 158g)

Comparative remarks

Westraltrachia cunicula is slightly larger **(Table 47)** and distinctly more umbilicated **(Fig. 138c)** than *W. alterna* **(Figs 133b, e),** while its rounded periphery and smaller size immediately separate it from *W. oscarensis* (Cox, 1892) **(Figs 136a-f).** *W. subtila* **(Figs 138d-f)** from further east in the Oscar Ranges, is very similar in size and shape, but has a narrower umbilicus, more angulated periphery, and greater descension of the body whorl **(Table 47).** Anatomically, *W. cunicula* has a very long, coiled or kinked, slender penis (**Figs 139a-c,** P), reduced epiphallic loop (E), short spermatheca (S), somewhat shortened vagina (V), and very simple, elongated penis pilaster (**Fig. 158g**). These features easily separate it from *W. alterna* with its short vagina (V), short penis (P), massive penis muscle (**Figs 134-135**), and typical pilaster (**Fig. 158f**), and *W. subtila* (**Figs 140a-b**) with its very short penis (P) and vagina (V), plus near apical entrance of the vas deferens (VD) into the penis sheath.

Holotype

WAM 132.80, Sta. WA-274, east side of Tunnel Creek Gorge entrance on south side of Napier Range, South Kimberley, Western Australia (1:100,000 'Leopold Downs' map sheet 3962, grid reference 270:510). Collected by Alan Solem, Laurie Price and Carl Christensen 3 December 1976. Height of shell 8.45 mm, diameter 14.75 mm, H/D ratio 0.573, whorls 5, umbilical width 1.4 mm, D/U ratio 10.5.

Paratopotypes

WAM 133.80, WAM 134.80, FMNH 199241, FMNH 199886, 5 live, 19 dead adults, 3 live juveniles from the type locality.

Paratypes

Napier Range: Sta. WA-583, 2.4 km west of Tunnel Creek turnoff, north side ('Leopold Downs' 3962 – 256:533) (12 dead adults, 3 dead juveniles, WAM 140.80, FMNH 204714); NR XXI, near south entrance to Tunnel Creek Cave (1 live, 7 dead adults, WAM 738.76, WAM 743.76); NR XX, near north end of Tunnel Creek Cave (6 dead adults, WAM 741.76, WAM 936.76); doline in Tunnel Cave (3 dead adults, WAM 4670.68 collected by George Kendrick and A.M. Douglas 2 July 1966); NR XXII, south-west side Tunnel Creek Yard (9 dead adults, WAM 744.76); Sta. WA-195, near north entrance to Tunnel Creek Cave ('Leopold Downs' 3962 – 275:518) (8 dead adults, 1 dead juvenile, WAM 138.80, FMNH 200082); Sta. WA-272, 1.7 km east of Tunnel Creek turnoff, north side of range ('Leopold Downs' 3962 – 287:508) (61 dead adults, 1 dead juvenile, WAM 137.80, FMNH 199450); NR XXVI, *ca.* 7 km south-east of Tunnel Creek Cave, north side of range (3 dead adults, WAM 737.76); Sta. WA-279, cliffs north of Chestnut Creek, east of Wine Spring track, south face of range ('Leopold Downs' 3962 – 322:447) (2 live, 81 dead adults, 2 live, 12 dead juveniles, WAM 135.80-136.80, FMNH 199233, FMNH 200236); Sta. WA-270, 21.8 km east of Tunnel Creek turnoff, north side of range ('Leopold Downs' 3962 – *ca.* 441:416) (1 live, 53 dead adults, 3 live, 4 dead juveniles, WAM 139.80, FMNH 199257, FMNH 200214.

Distribution limits in Napier Range

Known localities extend from Sta. WA-583, 2.4 km west of The Tunnel, to WA-270, 21.8 km east of The Tunnel road turnoff, near the easternmost rock reef exposures, an air distance of approximately 22.5 km along the Napier Range. A collecting gap of about 2.4 km exists between Sta. WA-275, the easternmost known locality for *Westraltrachia alterna* Iredale, 1939, and WA-583, the westernmost known locality for *W. cunicula* (**Fig. 160**). On the basis of topography, I would guess that the species change would occur about 0.9 km west of WA-583, where a natural gap occurs in the raised limestone, thus giving a perhaps 23.4 km linear range for *W. cunicula.*

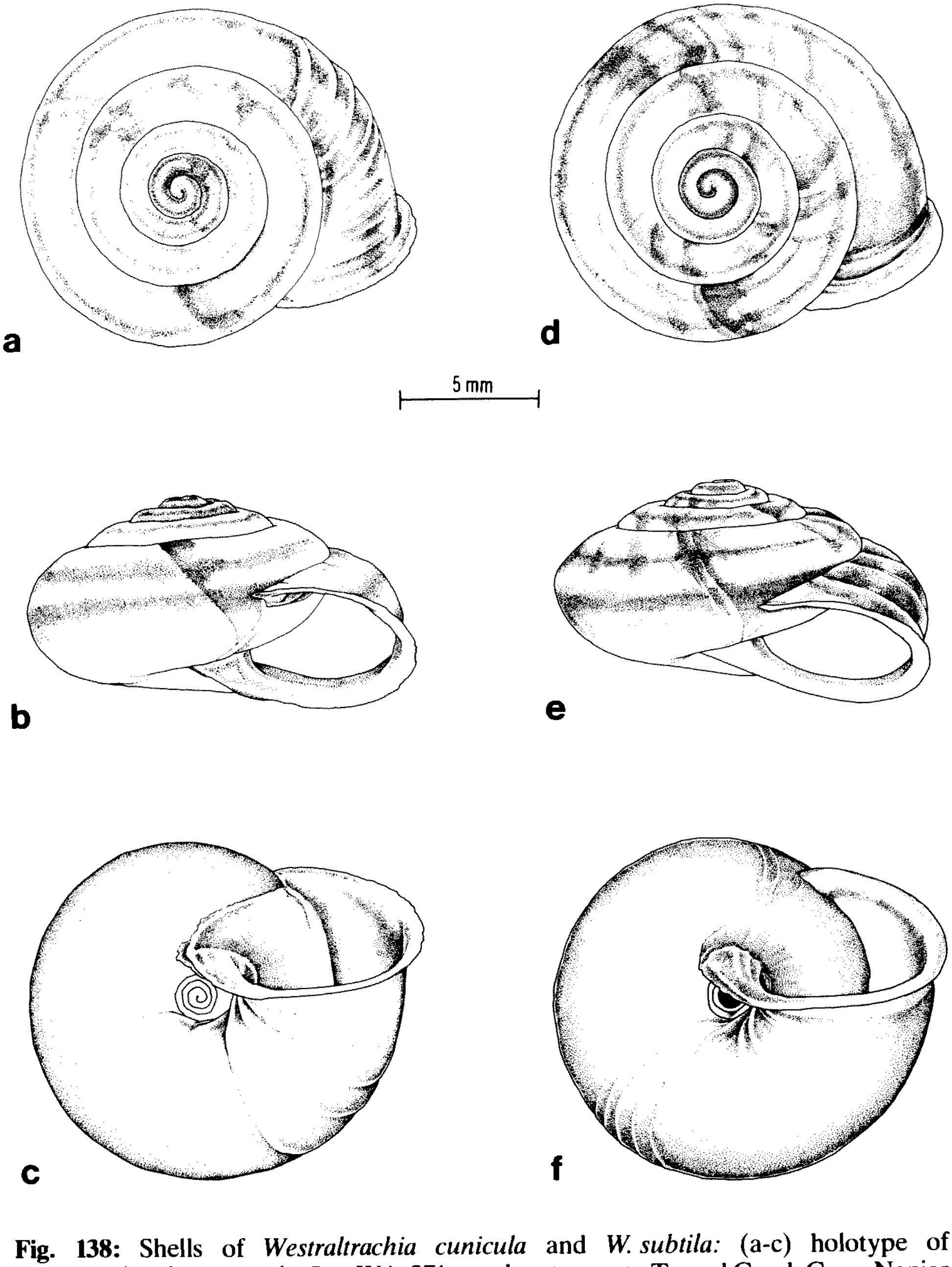


Fig. 138: Shells of *Westraltrachia cunicula* and *W. subtila:* (a-c) holotype of *Westraltrachia cunicula,* Sta. WA-274, south entrance to Tunnel Creek Cave, Napier Range, WAM 132.80; (d-f) holotype of *Westraltrachia subtila,* Sta. WA-265, 6.2 km west of Mt. Wynne Creek, Oscar Ranges, WAM 120.80. Scale line equals 5 mm. Drawings by Linnea Lahlum.

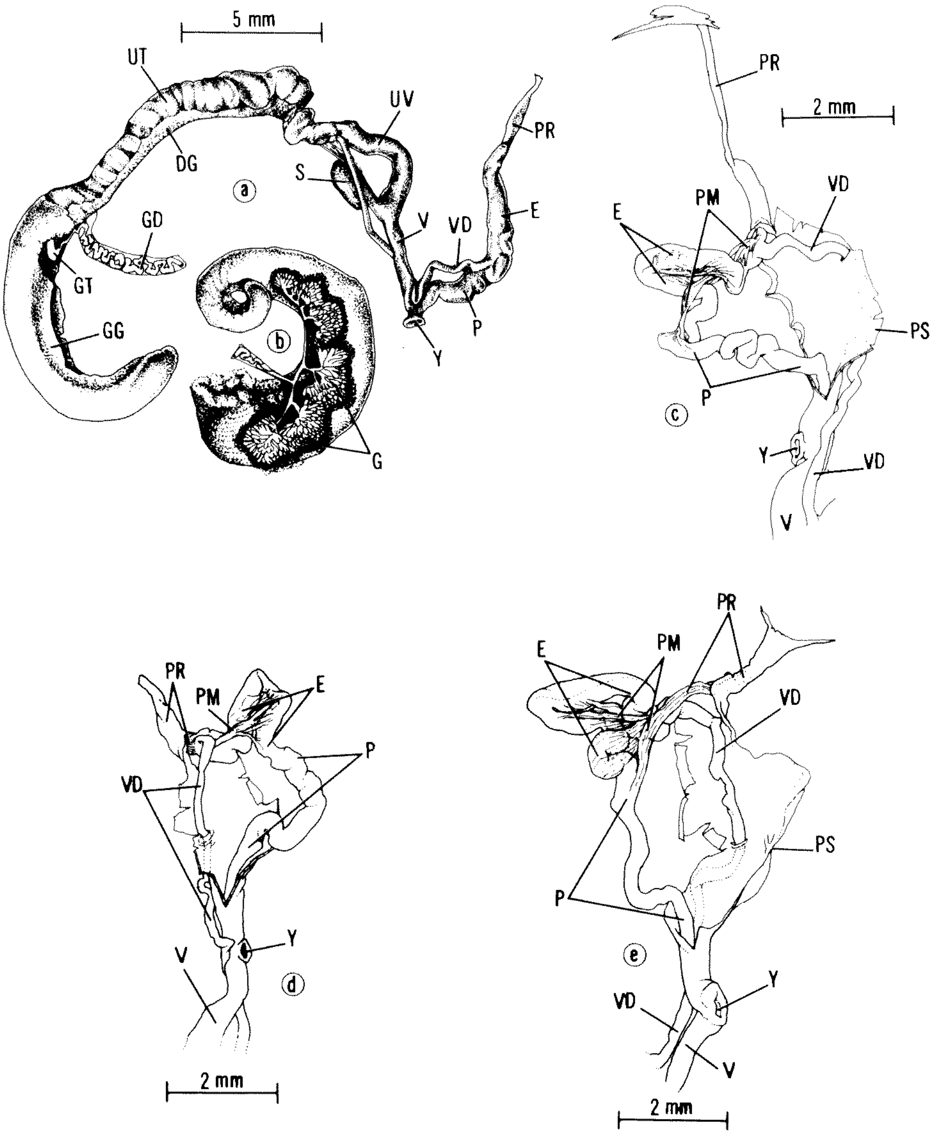


Fig. 139: Genitalia of *Westraltrachia cunicula:* (a-c) Sta. WA-274, south entrance to Tunnel Creek Cave, Napier Range, 3 December 1976, FMNH 199886, a is whole genitalia, Dissection A, b is ovotestis, Dissection A, c is interior of penis sheath, Dissection B; (d) interior of penis sheath, Sta. WA-270, 21.8 km east of turnoff to Tunnel Creek Cave, Napier Range, 2 December 1976, FMNH 200214, Dissection A; (e) interior of penis sheath, Sta. WA-279, cliffs north of Chestnut Creek, Napier Range, 4 December 1976, FMNH 200236, Dissection A. Scale lines as marked. Drawings by Linnea Lahlum.

Diagnosis

Shell of median size, 12.5-16.7 mm (mean 14.59 mm) in diameter, with 4⅜ to 5⅝ (mean 5⅛) normally coiled whorls. Apex and spire moderately to strongly elevated, usually only slightly rounded above, last whorl descending only very slightly before aperture, height of shell 7.35-11.5 mm (mean 9.12 mm), H/D ratio 0.547-0.754 (mean 0.624). Apical whorls **(Plate 21b)** macroscopically smooth, postapical sculpture of weak radial riblets and occasional radial growth lines. Shell periphery of larger adults rounded **(Fig. 138b)**, smaller adults with obtusely angled periphery. Lip rather strongly expanded and reflected, partly covering umbilicus, which is moderately open, umbilical width 0.5-1.8 mm (mean 1.09 mm), D/U ratio 7.05-35 (mean 14.5). Shell colour typical, darker brownish markings on either side of white peripheral zone, base of shell white, spire with light yellow and brown variegations. Based on 272 measured adults.

Genitalia **(Figs 139a-e)** with well developed penial muscle (PM) and reduced epiphallic loop (E). Principal pilaster **(Fig. 158g)** very long and slender, slightly sinuated. Penis (P) very long and slender, kinked within thin-walled penis sheath **(Figs 139c-e,** PS). Vas deferens (VD) entering at mid-penis level. Vagina **(Fig. 139a)** relatively long, spermatheca (S) quite short, free oviduct (UV) much longer and sinuated.

Jaw **(Plate 29e-h)** with moderately prominent, but clearly reduced, vertical ribs. Radula **(Plate 43)** with typical marginal teeth and latero-marginal transition **(Plate 43b, e, f)**. Central and lateral teeth **(Plate 43a-d)** without side cusps, mesocone sharply elevated, with blunt, curved tip, basal plate interrow locking system modified and anterior flare greatly reduced.

Discussion

Only nine of the 272 available adult specimens of *Westraltrachia cunicula* were collected alive, and five of these were from the type population. This reflects both the late dry season timing of the collections, and the relatively unvegetated slopes in this area of the Napier Range. This region is not 'good snail country'. The various populations from both sides of The Tunnel **(Table 56)** show very minor variation, but the samples from Sta. WA-279 and WA-270 are distinctly larger in diameter, although with an unchanged whorl count.

Material from three different populations have been dissected and illustrated **(Figs 139c-e)**. The entrance of the vas deferens (VD) into the penis sheath (PS) appears higher in the specimen from WA-274 **(Fig. 139c)**, but this example was retracted into the shell, with resultant curving of the penis. The drawing angle incorrectly suggests that the entrance occurs higher up the sheath.

Quistrachia monogramma (Ancey, 1898) has been taken at every Station from which material of *Westraltrachia cunicula* has been collected. Hence the reduced ribbing on the jaw **(Plate 29e-h)** and great modification of the central and lateral teeth on the radula **(Plate 43)** are interpreted as resulting from character displacement.

The name *cunicula,* from the Latin 'cuniculus', refers to the most famous geographic feature within its range, the passage of Tunnel Creek through a cave, familiarly known as the Tunnel, that penetrates the Napier Range.

WESTRALTRACHIA SUBTILA SP. NOV.

(Plates 22a, 30e, 44c-d; Figs 138d-f, 140, 158i)

Comparative remarks

Westraltrachia subtila has a more angulated periphery, slightly lower spire, slightly greater body whorl descent, and a narrower umbilicus **(Figs 138e, f)** than does its nearest neighbour, *W. cunicula* **(Figs 138b, c)** from the Napier Range. *Westraltrachia oscarensis* (Cox, 1892) from both the Oscar and Napier area, is much larger, more elevated, and with the umbilicus closed or nearly closed **(Figs 136b-c, e-f).** *Westraltrachia instita* **(Figs 141a-c)** is much more sharply angulated, openly umbilicated, with a rough surface texture, and noticable descent of the body whorl. Anatomically, *W. subtila* **(Figs 140a-b)** has a short vagina (V), reduced penis muscle (PM), rather small epiphallic loop, shorter penis (P) with multiple, thin apical pilasters **(Fig. 158i),** and penis head entrance of the vas deferens (VD) into the penis sheath (PS), which has a moderately thicker basal wall. These conditions contrast with the longer vagina, massive penis muscle, smaller epiphallic loop, long, kinked penis with single long apical pilaster **(Fig. 158g),** and mid-penis entry of the vas deferens into a thinner walled penis sheath found in *W. cunicula. Westraltrachia alterna* has the typical penis pilaster **(Fig. 158f)** and a much shorter penis **(Fig. 135b),** while *W. oscarensis* has a single main penis pilaster **(Fig. 158h)** and much longer penis with massive penis muscle **(Fig. 137b).** *Westraltrachia instita* **(Figs 142a-b)** has a very long, thin penis, mid-penis entry of the vas deferens into the sheath, reduced epiphallic loop, and slightly longer vagina.

Holotype

WAM 120.80, Sta. WA-265, 6.2 km west of Mount Wynne Creek, south side of Oscar Ranges, north-west of Fitzroy Crossing, South Kimberley, Western Australia (1:100,000 'Leopold Downs' map sheet 3962 – grid reference *ca.* 195:352). Collected by Alan Solem, Laurie Price and Carl Christensen 28 November 1976. Height of shell 8.6 mm, diameter 14.7 mm, H/D ratio 0.585, whorls 5⅛ –, umbilical width 0.95 mm, D/U ratio 15.5.

Paratopotypes

WAM 121.80, WAM 122.80, FMNH 199458, FMNH 200216, 16 live and 65 dead adults, 4 live, 3 dead juveniles from the type locality.

Distribution limits in Oscar Ranges

Only the single collection from a short distance west of Ninety Seven Mile Creek is known. It is approximately 10 km north or north-west through probably snail-free plains to the nearest colonies of *Westraltrachia oscarensis* (Cox, 1892) at Sta. WA-276 and WA-278, and 6.3 km south-east along the Oscar Range to the type locality of *W. instita* near Mount Wynne Creek **(Fig. 160).** The intervening area has not been sampled for land snails. It is about 11 km west-north-west along the edge of the Oscar Plateau to the Palm Spring record of *W. oscarensis,* with the intervening zone forming another unsampled area. There is thus a maximum potential range of 17.3 km for *W. subtila,* although the actual range undoubtedly will be less than this.

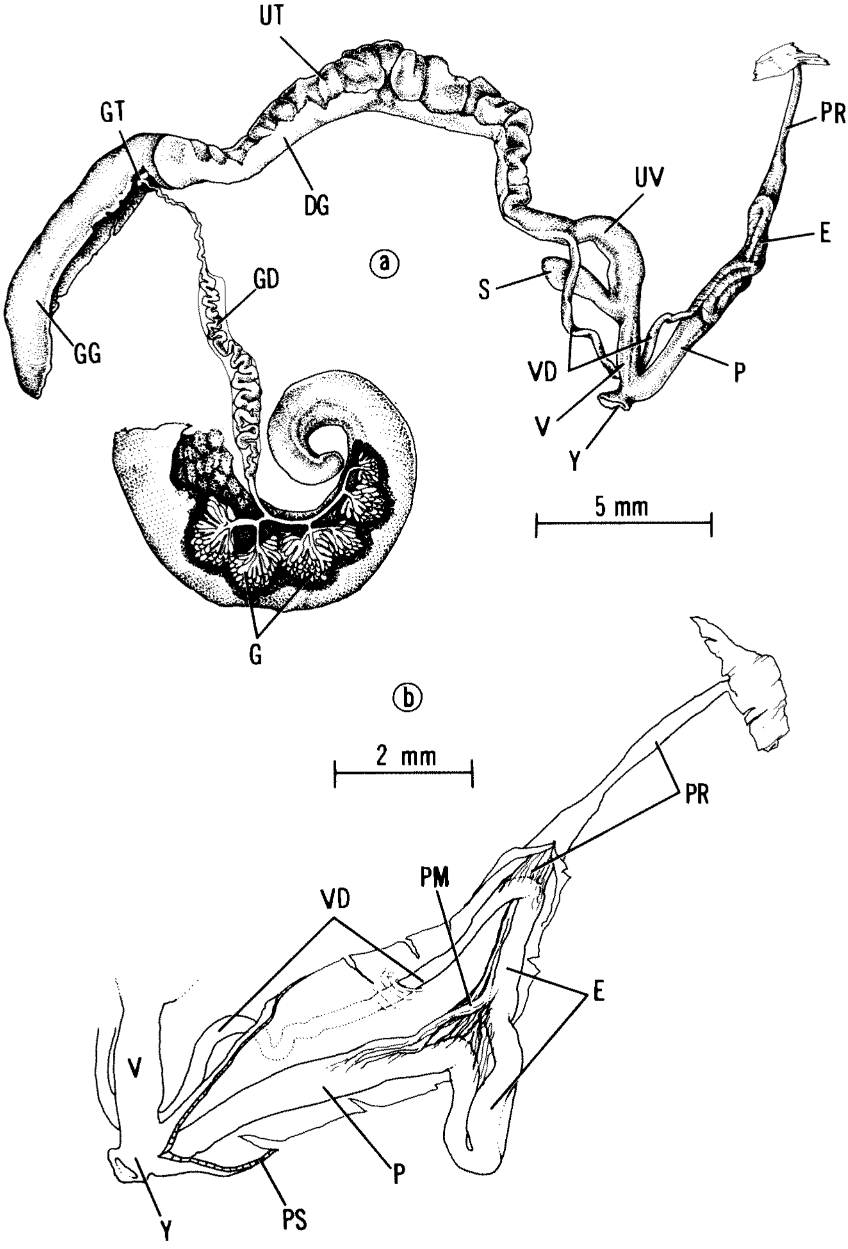


Fig. 140: Genitalia of *Westraltrachia subtila:* Sta. WA-265, west of Mt. Wynne Creek, Oscar Ranges, 28 November 1976, FMNH 200216, Dissection A, (a) whole genitalia, (b) interior of penis sheath. Scale lines as marked. Drawings by Linnea Lahlum.

Diagnosis

Shell of average size, 13.7-16.6 mm (mean 14.86 mm) in diameter, with 4¾ to 5½ (mean 5⅛ –) normally coiled whorls. Apex and spire moderately and evenly elevated, at most slightly rounded above **(Fig. 138e),** body whorl descending slightly before aperture, height of shell 7.0-10.1 mm (mean 8.55 mm), H/D ratio 0.531-0.654 (mean 0.575). Apical whorls **(Plate 22a)** smooth, postapical sculpture of relatively prominent radial growth lines and fine micro-riblets. Shell periphery **(Fig. 138e)** obtusely angulated in adults, sharply angulated in juveniles. Lip strongly expanded and reflected over much of umbilicus **(Fig. 138f),** which is narrowly open, umbilical width 0.45-1.45 mm (mean 0.86 mm), D/U ratio 9.73-32 (mean 18.5). Colour typical, darker brownish zones above and below white peripheral zone, shell base white, spire variegated with white and brown. Based on 82 measured adults.

Genitalia **(Figs 140a-b)** with large penis muscle (PM) and medium sized epiphallic loop (E). Principal pilaster of penis **(Fig. 158i)** reduced or fragmented, wall with several simple longitudinal ridges. Penis (P) short, not kinked, relatively thick. Penis sheath wall slightly thicker along base. Vas deferens (VD) entering sheath opposite penis apex. Vagina (V) short, spermatheca (S) short, free oviduct (UV) significantly longer and curved.

Jaw **(Plate 30e)** with prominent vertical ribs. Radula **(Plate 44c-d)** with typical marginal and latero-marginal teeth. Central and laterals without side cusps. Mesocone sharply elevated, with blunt, curved tip, but a strong trace of the anterior flare present and the laterals much less narrowed than in taxa found to the west of Windjana Gorge **(Plates 33-37).** The laterals of *Westraltrachia derbyi* (Cox, 1892) **(Plates 38-39),** *W. alterna* Iredale, 1939 **(Plate 42),** and *W. oscarensis* (Cox, 1892) **(Plate 41)** also are strongly narrowed, but those of *W. cunicula* **(Plate 43)** are nearer in width to those of *W. subtila.*

Discussion

Since the conchological similarity of *Westraltrachia subtila* to such taxa as *W. alterna* Iredale, 1939, *W. cunicula,* and *W. derbyi* (Cox, 1892) is so great, choice of the Latin word for subtle seemed appropriate. Differences among these taxa are summarised in the Comparative remarks above.

Only the one population was sampled, so that geographic variation is unknown. Live adults were 0.55 mm smaller than dead specimens taken at the same time **(Table 59).** Similar situations were found in the species to the east, *W. lievreana* and *W. tropida* **(Table 59),** suggesting existence of small sized year classes during the period of collecting.

No specimens of *Quistrachia monogramma* (Ancey, 1898) were taken at the type locality, although that species occurs in abundance at both the next station west (Palm Spring) and east (WA-264, where Mount Wynne Creek passes through the Oscar Range, **Fig. 160).** The greater reduction in the anterior flare and narrower lateral radular teeth **(Plate 44e-f)** of *Westraltrachia instita* from WA-264, compared with those of *W. subtila* **(Plate 44c-d),** and reduced jaw ribs of *W. instita* **(Plate 30c-d),** are interpreted as evidence for character displacement by *W. instita* as a result of sympatry with *Quistrachia.*

In 1976, mining tracks permitted access to this section of the Oscar Range, but by 1980 these tracks had been washed out. In retrospect, more intensive collecting should have been attempted in 1976. Many questions remain to be resolved about the species living in this region. The ranges of *Westraltrachia subtila, W. instita. W. lievreana,* and *W. tropida* are inadequately known, and the exact conditions of micro-sympatry between *Quistrachia* and *Westraltrachia* need to be determined. The width of the collecting gaps are sufficient that discovery of additional species in this zone is quite possible.

Table 59: Local Variation in Oscar Range *Westraltrachia*

Taxon	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
W. subtila				
WA-265, W of Mt. Wynne Creek, FMNH 200216	16L	8.15 ± 0.092 (7.6 – 8.9)	14.42 ± 0.113 (13.9 – 15.6)	0.565 ± 0.005 (0.531 – 0.596)
WA-265, FMNH 199458	66D	8.64 ± 0.068 (7.0 – 10.1)	14.97 ± 0.084 (13.7 – 16.6)	0.578 ± 0.004 (0.551 – 0.654)
W. instita				
WA-264, Mt. Wynne Creek, FMNH 200224	4L	7.35 ± 0.270 (6.9 – 8.05)	13.79 ± 0.153 (13.4 – 14.1)	0.534 ± 0.024 (0.493 – 0.588)
WA-264, FMNH 199500	154D	6.97 ± 0.033 (5.8 – 8.0)	13.27 ± 0.049 (11.7 – 15.3)	0.525 ± 0.002 (0.471 – 0.610)
ORIII, N of Stumpy's Spring, WAM 747.76	55D	7.06 ± 0.053 (6.3 – 8.2)	13.20 ± 0.094 (11.75 – 15.0)	0.535 ± 0.004 (0.469 – 0.610)
ORIV, SE of Stumpy's Spring, WAM 749.76	46L	7.32 ± 0.066 (6.5 – 8.05)	13.45 ± 0.092 (12.0 – 15.1)	0.544 ± 0.004 (0.479 – 0.622)
ORIV, WAM 748.76	27D	7.50 ± 0.103 (6.2 – 8.3)	13.62 ± 0.144 (12.05 – 15.35)	0.551 ± 0.006 (0.482 – 0.609)
W. lievreana				
WA-263, NW Linesman Creek, FMNH 200223	22L	7.92 ± 0.109 (7.1 – 8.9)	13.67 ± 0.119 (12.75 – 14.5)	0.580 ± 0.007 (0.523 – 0.646)
WA-263, FMNH 199481	355D	8.23 ± 0.602 (6.45 – 10.2)	14.36 ± 0.429 (11.75 – 16.7)	0.574 ± 0.002 (0.498 – 0.660)
W. tropida				
ORII, 12 Mile Bore Gap, WAM 746.76	58D	7.99 ± 0.084 (6.8 – 9.9)	13.64 ± 0.113 (12.2 – 16.3)	0.586 ± 0.004 (0.522 – 0.648)
WA-262, 12 Mile Bore Gap, FMNH 199480	150D	8.29 ± 0.059 (6.8 – 10.6)	14.53 ± 0.073 (12.25 – 16.8)	0.570 ± 0.003 (0.505 – 0.695)
WA-710, 12 Mile Bore Gap, FMNH 205306	6L	8.25 ± 0.162 (7.45 – 8.5)	13.96 ± 0.208 (13.4 – 14.9)	0.591 ± 0.010 (0.556 – 0.618)

Table 59: Local Variation in Oscar Range *Westraltrachia* (continued)

Taxon	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
WA-710, FMNH 205307	49D	8.05 ± 0.084 (7.25 – 9.5)	14.16 ± 0.124 (12.7 – 16.3)	0.568 ± 0.005 (0.500 – 0.644)
WA-260, Kundra Bore, FMNH 199478	131D	8.95 ± 0.057 (7.7 – 10.35)	16.74 ± 0.070 (14.95 – 19.5)	0.535 ± 0.003 (0.467 – 0.607)
W. porcata WA-711, Brooking Creek, FMNH 205310	43D	11.45 ± 0.151 (8.05 – 13.9)	16.37 ± 0.138 (14.5 – 18.8)	0.699 ± 0.007 (0.555 – 0.818)

Taxon	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
W. subtila				
WA-265, W of Mt. Wynne Creek, FMNH 200216	16L	5⅛ – (4¾ – 5⅜)	0.88 ± 0.062 (0.55 – 1.5)	17.5 ± 1.083 (9.73 – 26.4)
WA-265, FMNH 199458	66D	5⅛ – (4¾ – 5½)	0.85 ± 0.029 (0.45 – 1.3)	18.7 ± 0.067 (11.0 – 32)
W. instita				
WA-264, Mt. Wynne Creek, FMNH 200224	4L	4¾ (4⅝ – 4⅞)	1.56 ± 0.128 (1.3 – 1.85)	8.98 ± 0.642 (7.54 – 10.3)
WA-264, FMNH 199500	154D	4¾ – (4¼ + – 5½ –)	1.60 ± 0.026 (0.8 – 2.6)	8.61 ± 0.141 (5.10 – 15.4)
ORIII, N of Stumpy's Spring, WAM 747.76	55D	4¾ – (4⅜ + – 5⅛)	1.63 ± 0.044 (0.95 – 2.6)	8.42 ± 0.230 (5.58 – 13.9)
ORIV, SE of Stumpy's Spring, WAM 749.76	46L	4⅞ – (4½ – – 5 +)	1.54 ± 0.048 (0.8 – 2.25)	9.12 ± 0.310 (6.24 – 16.9)
ORIV, WAM 748.76	27D	4¾ + (4½ – 5⅛)	1.47 ± 0.054 (1.0 – 1.95)	9.56 ± 0.366 (6.79 – 13.5)
W. lievreana				
WA-263, NW Linesman Creek, FMNH 200223	22L	4¾ (4⅜ – 5 –)	1.14 ± 0.052 (0.6 – 1.65)	12.6 ± 0.627 (8.18 – 21.3)
WA-263, FMNH 199481	355D	4¾ + (4½ – 5⅝ –)	1.21 ± 0.013 (0.35 – 2.0)	12.4 ± 0.171 (6.87 – 47)

Table 59: Local Variation in Oscar Range *Westraltrachia* (continued)

Taxon	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
W. tropida				
ORII, 12 Mile Bore Gap, WAM 746.76	58D	4⅞ – (4½ – 5¼)	(41.4% open; 58.6% cracked)	
WA-262, 12 Mile Bore Gap, FMNH 199480	150D	4⅞ + (4½ + – 5⅜)	(47.3% open; 52.7% cracked)	
WA-710, 12 Mile Bore Gap, FMNH 205306	6L	4⅞ + (4¾ – 5 +)	(50.0% open; 50.0% cracked)	
WA-710, FMNH 205307	49D	4⅞ (4⅝ – – 5¼)	(83.7% open; 16.3% cracked)	
WA-260, Kundra Bore, FMNH 199478	131D	5⅛ (4¾ – 5⅝)	(38.2% open; 35.1% cracked; 26.7% closed)	
W. porcata				
WA-711, Brooking Creek, FMNH 205310	43D	5⅛ – (4⅞ – 5½ +)	(53.5% open; 37.2% cracked; 9.3% closed)	

WESTRALTRACHIA INSTITA SP. NOV.

(Plates 22b-d, 30c-d, 44e-f, 45a; Figs 141a-c, 142, 158j)

Comparative remarks

Westraltrachia instita **(Figs 141a-c)** is immediately recognisable by its strongly angulated periphery, open umbilicus, relatively low spire, rough shell surface, small size, and normal colour pattern. Its nearest neighbours, *W. subtila* to the west **(Fig. 160,** Sta. WA-265) and *W. lievreana* to the east **(Fig. 143b,** Sta. WA-263) both have rounded or nearly rounded peripheries **(Figs 138e, 143b),** much narrower umbilical openings **(Figs 138f, 143c),** smoother surfaced shells, average 1-1.5 mm larger in diameter, are more elevated, and have normal *(subtila)* or more nearly monochrome *(lievreana)* colouration. *Westraltrachia tropida,* found further east near Twelve Mile Bore (Sta. WA-262), is larger **(Table 59),** much more sharply angulated at the periphery and has a nearly closed umbilicus **(Figs 141b, c).** Anatomically, *W. instita* **(Figs 142a, b)** has a well developed penial muscle (PM) with normal sized epiphallic loop (E), relatively short vagina (V), long and slender penis (P), one large apical penis pilaster **(Fig. 158j),** entrance of the vas deferens (VD) occurring above mid-point of penis, typical spermatheca (S), and only slightly longer free oviduct (UV). *Westraltrachia subtila* **(Figs 140a-b)** has a much shorter penis, penis apex entrance of the vas deferens through the penis sheath, and no single large apical penis pilaster **(Fig. 158i).** *Westraltrachia* *lievreana* **(Figs 144a-b)** has a huge epiphallic loop, short penis, mid-penis entry of the vas deferens through the sheath, much shorter vagina and penis, and a large, sinuated main penis pilaster **(Fig. 158k)**. The reduced ribbing on the jaw **(Plate 30c-d)** and relatively modified central and lateral radular teeth **(Plates 44e-f, 45a)** contrast with neighbouring species.

Holotype

WAM 114.80, Sta. WA-264, 0.4 km west of Mount Wynne Creek, south side of Oscar Ranges, north-west of Fitzroy Crossing, South Kimberley, Western Australia (1:100,000 'Leopold Downs' map sheet 3962, grid reference 243:312). Collected by Alan Solem, Laurie Price, and Carl Christensen 28 November 1976. Height of shell 6.9 mm, diameter 13.3 mm, H/D ratio 0.519, whorls 4⅝, umbilical width 1.55 mm, D/U ratio 8.58.

Paratopotypes

WAM 115.80, WAM 116.80, FMNH 199500, FMNH 200224, 4 live, 153 dead adults, 6 live, 5 dead juveniles from the type locality.

Paratypes

Oscar Ranges: OR III, just north of Stumpy's Spring (1 live, 57 dead adults, WAM 747.76, WAM 859.76, WAM 931.76); OR IV, south-east of Stumpy's Spring under outcrops of limestone rocks on plains (46 live, 27 dead adults, WAM 748.76-749.76).

Distribution limits in Oscar Ranges

The only known localities are around Mount Wynne Creek to 0.4 km west (Sta. WA-264), on the south margin of the Oscar Range **(Fig. 161)**. It is about 6.3 km north-west to Sta. WA-265, the type locality of *Westraltrachia subtila,* and 3.3 km south-east to Sta. WA-263, the type locality of *W. lievreana.* This gives a maximum range of only 9.6 km for *W. instita,* although the actual range undoubtedly will be less, once these zones are sampled for land snails.

Diagnosis

Shell small, 11.7-15.35 mm (mean 13.33 mm) in diameter, with 4¼+ to 5½− (mean 4¾−) normally coiled whorls. Apex and spire moderately and evenly elevated, not rounded above, body whorl descending noticeably just before aperture, height of shell 5.8-8.3 mm (mean 7.09 mm), H/D ratio 0.469-0.622 (mean 0.533). Apical whorls **(Plate 22b-d)** without sculpture except for growth lines, postapical whorls with quite prominent growth lines, micro-riblets, and minute periostracal folds visible in unworn, live collected examples. Shell periphery **(Fig. 141b)** obtusely angulated, slightly protruded into a keel. Lip strongly expanded **(Figs 141a-c)**, columellar edge rolled. Umbilicus **(Fig. 141c)** open, only partly covered by reflected lip, umbilical width 0.8-2.6 mm (mean 1.60 mm), D/U ratio 5.10-16.9 (mean 8.73). Colour typical, base white, shell periphery with white zone, brownish markings above and below zone, spire with brown and white variegations. Based on 289 measured adults.

Genitalia **(Figs 142a-b)** with large penis muscle (PM), normal epiphallic loop (E). Principal penis pilaster **(Fig. 158j)** long and slender, distinctly higher than other pilasters present. Penis (P) long, slender, at most slightly kinked, vas deferens (VD)

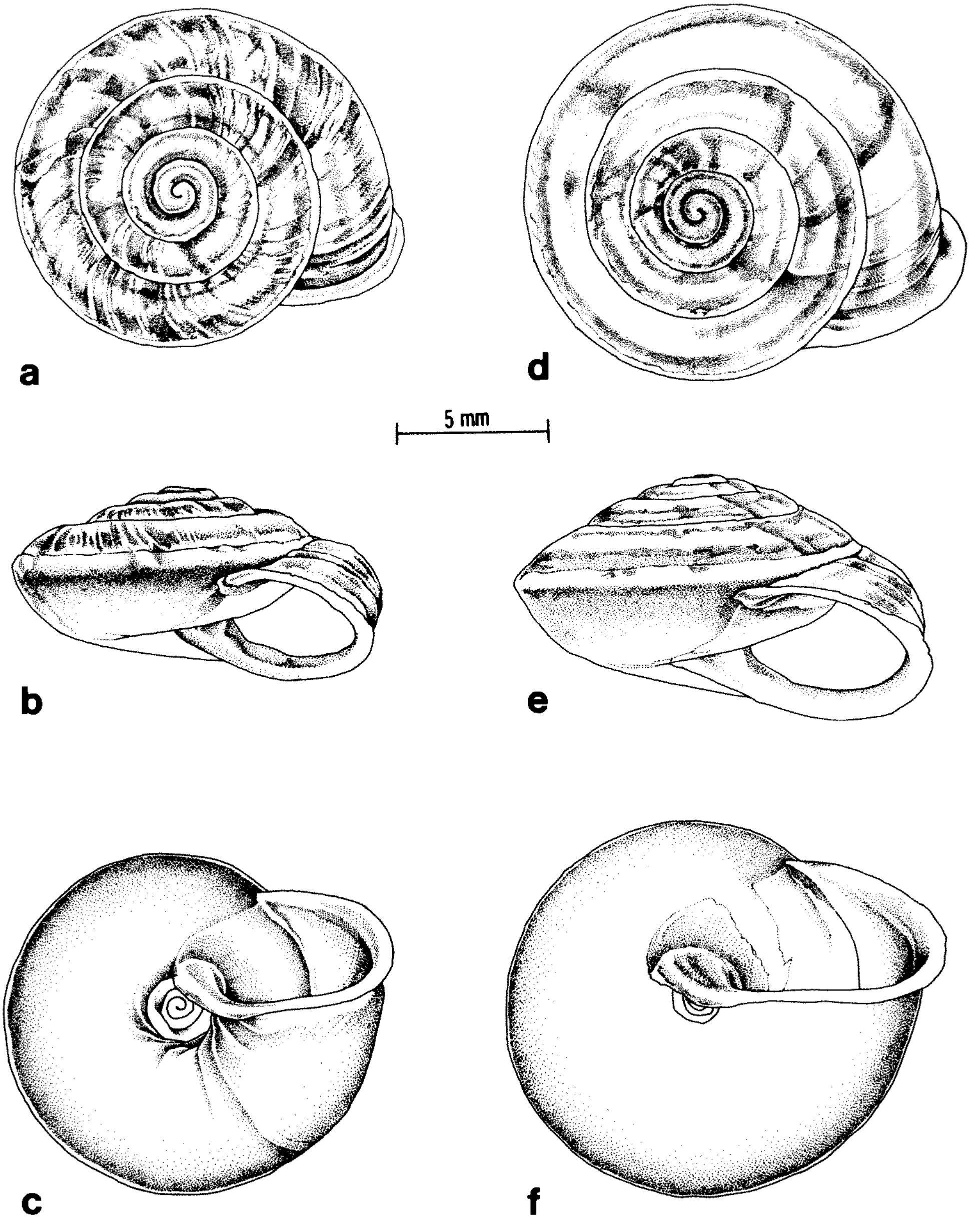


Fig. 141: Shells of *Westraltrachia instita* and *W. tropida:* (a-c) holotype of *Westraltrachia instita,* Sta. WA-264, Mt. Wynne Creek, Oscar Ranges, WAM 114.80; (d-f) holotype of *Westraltrachia tropida,* Sta. WA-710, pass near Twelve Mile Bore, Oscar Ranges, WAM 123.80. Scale line equals 5 mm. Drawings by Linnea Lahlum.

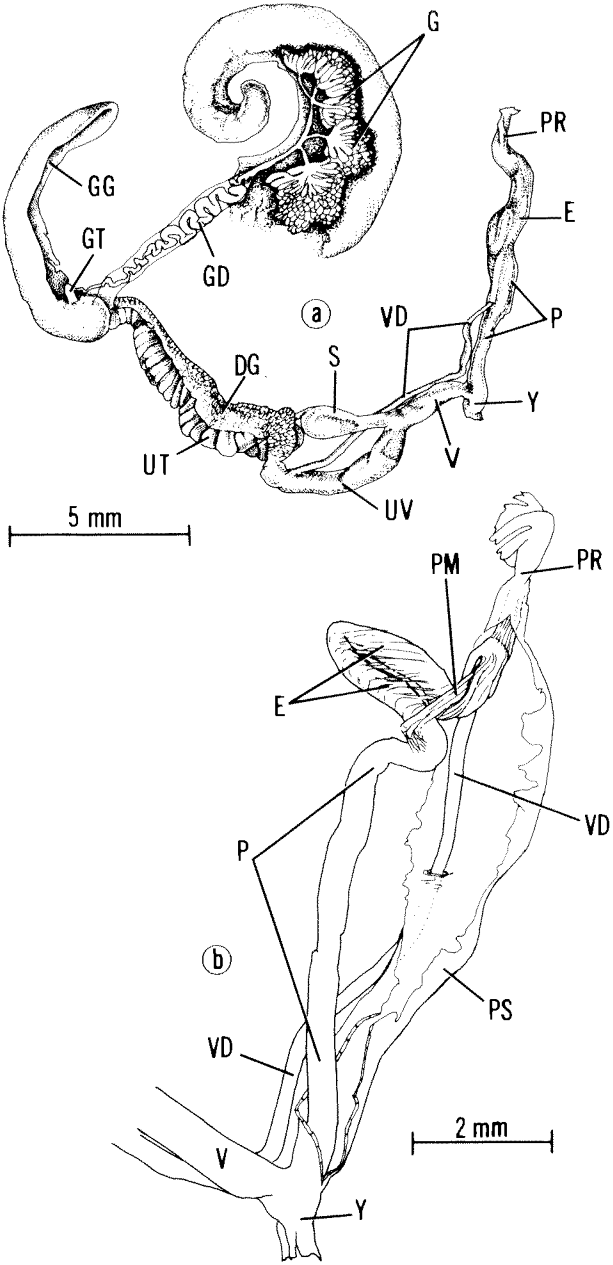


Fig. 142: Genitalia of *Westraltrachia instita;* Sta. WA-264, near Mt. Wynne Creek, Oscar Ranges, 28 November 1976, FMNH 200224, (a) whole genitalia, Dissection A, (b) interior of penis sheath, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

entering thin walled penis sheath (PS) above middle of penis. Vagina (V) relatively short, as is spermatheca (S) which attaches to base of prostate-uterus. Free oviduct (UV) longer, curved.

Jaw **(Plate 30c-d)** with reduced vertical ribs. Teeth of radula **(Plates 44e-f, 45a)** with marginals typical. Central and lateral teeth without side cusps, somewhat narrowed, mesoconal shaft strongly elevated, mesoconal tip bluntly rounded, curved.

Discussion

The name *instita* is taken from the Latin for border or ridge, and refers both to the peripheral keel on the shell and the sharp ridge-like limestone exposures from which the species was collected.

The exact geographic relationship of the two known localities is uncertain, as the WAM staff were working with the 'Lennard River' 1:250,000 map sheet, and thus could not fix their position accurately. Certainly the samples show quite minor variation **(Table 59).** The difference between live and dead collected material is less than was found in *Westraltrachia subtila, W. lievreana,* and *W. tropida* **(Table 59),** probably reflecting the greater shade and thus reduced water loss potential at this Station compared with the other localities.

The rough surface occurs on most examples, and is of unknown origin. This could reflect greater periodicity of growth. Certainly the late dry season experience of finding four live and 153 dead adults at WA-264, a talus situation, suggests a low population level. The mid-dry season collecting by WAM staff (early September 1975) produced many more live individuals, but these were taken in the vicinity of a water hole and thus came from a more favourable situation. Unfortunately, these specimens had been fixed and preserved in formalin. Degenerative tissue changes had proceeded to the point that they could not be used for this study, and thus anatomical knowledge is based on only two dissections.

WESTRALTRACHIA LIEVREANA SP. NOV.

(Plates 22e-f, 31e, 44a-b; Figs 143a-c, 144, 158k)

Comparative remarks

Westraltrachia lievreana **(Figs 143a-c)** has a narrowly open umbilicus, rounded or at most slightly angulated periphery, strongly reflected lip, a colour pattern approaching yellow-brown except for the white peripheral zone, and is average in size. *Westraltrachia porcata* from the upper reaches of Brooking Creek (WA-711) is more than 2 mm larger in diameter **(Table 47),** much more elevated, retains a typically variegated colour pattern, and with a narrow or closed umbilicus **(Figs 143d-f).** Both *W. instita* to the west (WA-264, **Fig. 160)** and *W. tropida* to the east (WA-262) **(Figs 141a-f)** have strongly angulated peripheries, variegated colouration, different umbilici, and are less elevated. Anatomically, *W. lievreana* **(Figs 144a-b)** has a relatively small penis muscle (PM) despite a massive epiphallic loop (E), a very short vagina (V), rather short penis (P), and the vas deferens (VD) passes through the penis sheath (PS) a little above mid-point of the penis. The basal section of the penis sheath is slightly thickened. The spermatheca (S) is very short, with the free oviduct (UV) much longer and curved. *Westraltrachia tropida* **(Figs 145a-c)** and *W. porcata* **(Figs 145d-e)** both have very long, kinked, slender penes, reduced epiphallic loops, and much longer vaginae. *Westraltrachia instita* **(Figs 142a-b)** also has a reduced epiphallic loop, longer penis, and longer vagina, while *W. subtila* **(Figs 140a-b)** has a shorter penis, much smaller epiphallic loop, longer vagina, and different entrance of the vas deferens into the penis sheath.

Holotype

WAM 117.80, Sta. WA-263, 14.1 bush track km north-west of Linesman Creek, south side of Oscar Ranges, north-west of Fitzroy Crossing, South Kimberley, Western Australia (1:100,000 'Leopold Downs' map sheet 3962, grid reference 269:287). Collected by Alan Solem, Laurie Price, and Carl Christensen 28 November 1976. Height of shell 8.35 mm, diameter 14.4 mm, H/D ratio 0.580, whorls 4¾+, umbilical width 1.25 mm, D/U ratio 11.5.

Paratopotypes

WAM 118.80, WAM 119.80, FMNH 199481, FMNH 200223, 22 live, 354 dead adults, 12 live juveniles from the type locality.

Distribution limits in Oscar Ranges

The only known colony (WA-263, **Fig. 160**) is about 3.3 air km south-east of Mount Wynne Creek, the type locality of *Westraltrachia instita*, and approximately 18 km northwest of the two Twelve Mile Bore localities for *W. tropida*. The maximum potential range is thus 21.3 km, a figure that undoubtedly will be greatly reduced by further collecting in this section of the Oscar Ranges.

Diagnosis

Shell of average size, 11.75-16.7 mm (mean 14.32 mm) in diameter, with 4¼ to 5⅝− (mean 4¾+) rather loosely coiled whorls. Apex and spire slightly to moderately elevated, sometimes rounded above, body whorl descending very slightly just before aperture, height of shell 6.45-10.2 mm (mean 8.21 mm), H/D ratio 0.498-0.660 (mean 0.574). Apical whorls **(Plate 22e-f)** smooth, except for growth lines, postapical sculpture of fine micro-riblets, microscopic periostracal folds, and irregular growth lines. Shell periphery **(Fig. 143b)** rounded or at most slightly angulated in adults, strongly angulated in juveniles. Lip strongly expanded and partly reflexed over umbilicus **(Fig. 143c)**. The umbilicus thus is narrowly to moderately open, umbilical width 0.35-2.0 mm (mean 1.21 mm), H/D ratio 6.87-47 (mean 12.4). Colour yellow-brown with narrow white peripheral zone, base of shell white, spire almost monotone with only occasional faint trace of lighter colour at irregular intervals. Based on 377 measured adults.

Genitalia **(Figs 144a-b)** with massive epiphallic loop (E) whose arms are lightly bound by fibers, penis muscle (PM) rather small. Principal penis pilaster **(Fig. 158k)** sinuated, without hard edges, clearly reduced from primitive condition. Penis (P) rather short, not kinked or coiled. Vas deferens (VD) entering slightly above mid-point of penis. Penis sheath (PS) with only very basal portion showing thickened wall. Vagina (V) and spermatheca (S) very short, free oviduct (UV) distinctly longer and curved.

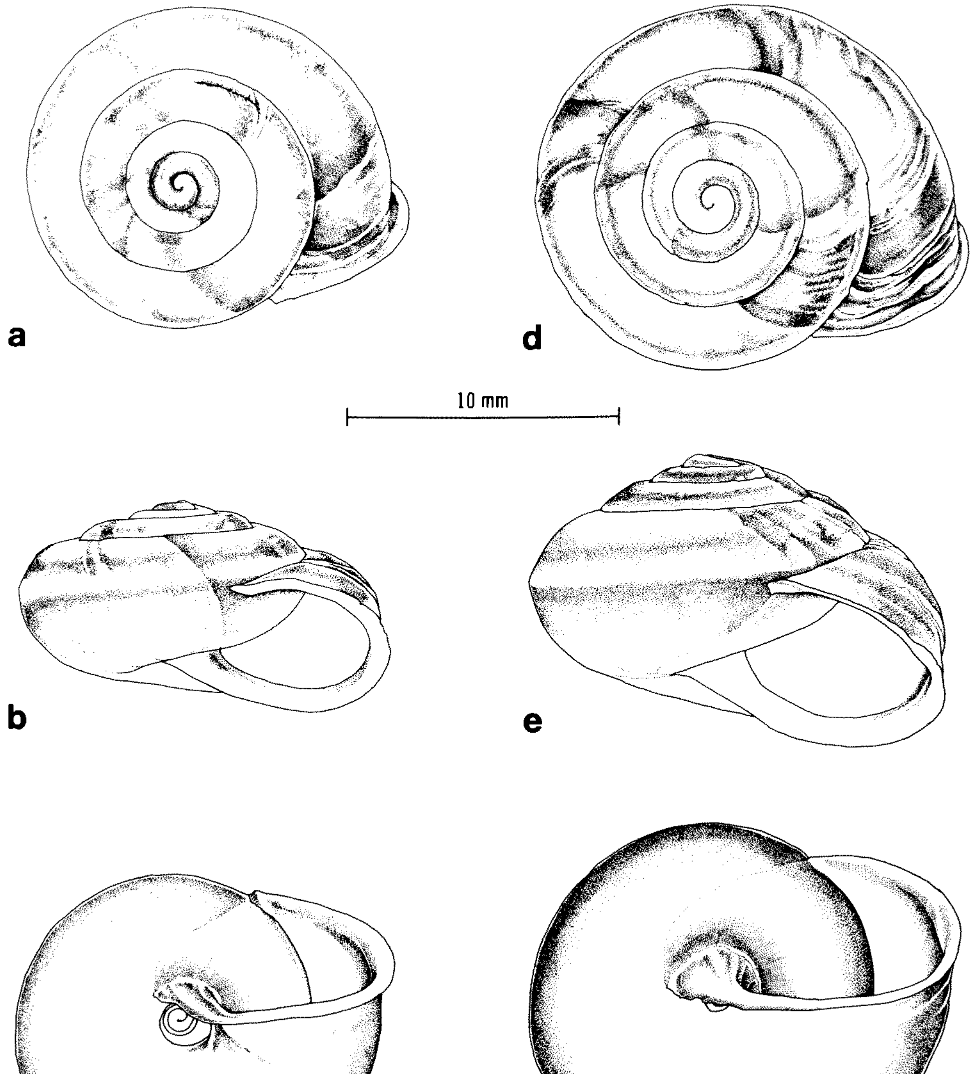


Fig. 143: Shells of *Westraltrachia lievreana* and *W. porcata:* (a-c) holotype of *Westraltrachia lievreana,* Sta. WA-263, north-west of Linesman Creek, Oscar Ranges, WAM 117.80; (d-f) holotype of *Westraltrachia porcata,* Sta. WA-711, 2.0 km south of Brooking Creek on Tunnel Road, north of Oscar Ranges, WAM 129.80. Scale line equals 10 mm. Drawings by Linnea Lahlum.

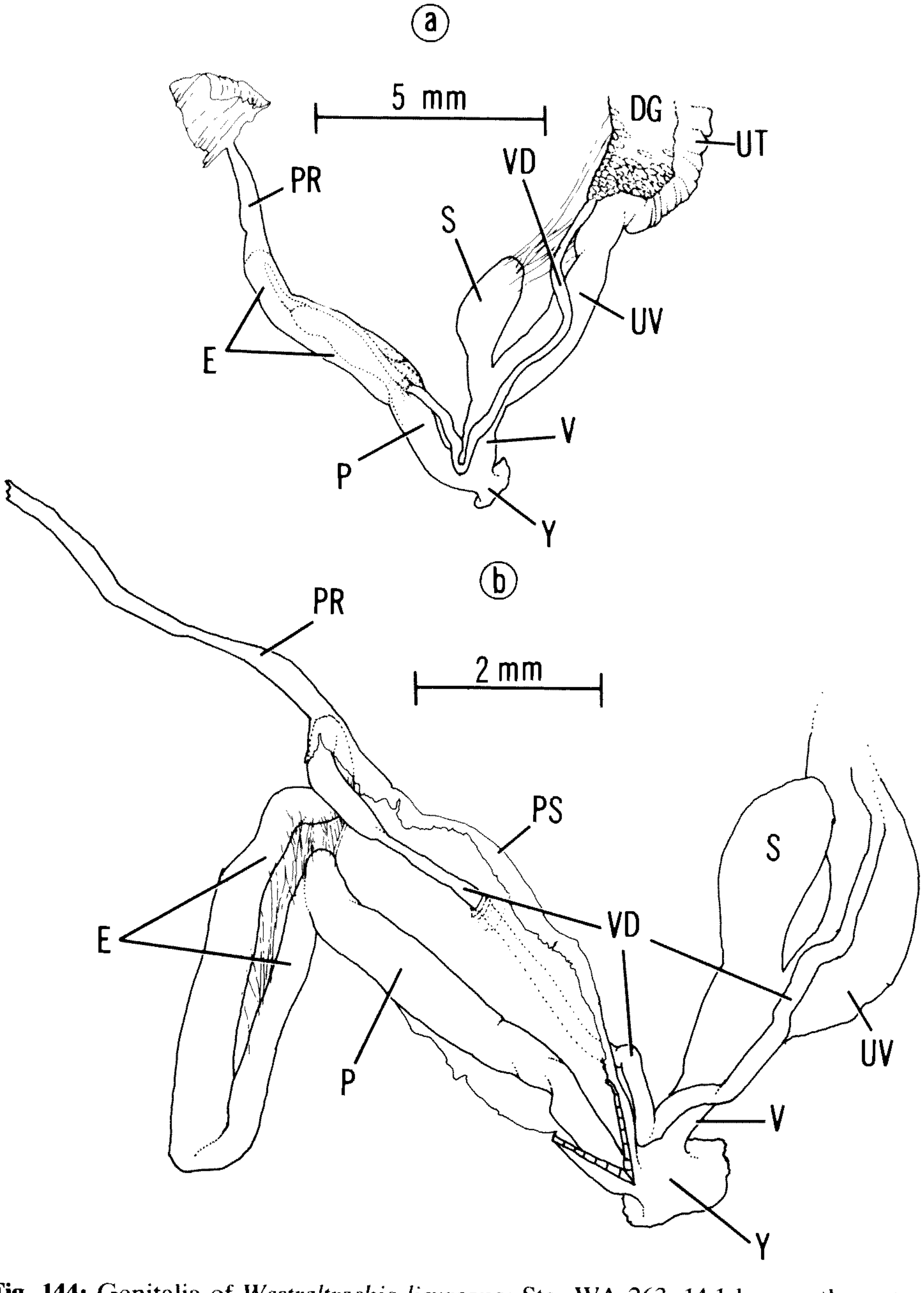


Fig. 144: Genitalia of *Westraltrachia lievreana;* Sta. WA-263, 14.1 km north-west of Linesman Creek, Oscar Ranges, 28 November 1976, FMNH 200223, (a) terminal genitalia, Dissection A, (b) interior of penis sheath, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

Jaw (**Plate 31e**) with relatively prominent vertical ribs that are variable in number. Marginal teeth of radula typical. Lateral teeth occasionally with minute trace of ectocone (**Plate 44a**), both central and lateral with strongly elevated cusp shaft and noticeably curved mesoconal tip, anterior flare reduced, but teeth not significantly narrowed and tip of mesocone less bluntly rounded than in western taxa such as *Westraltrachia instita* (**Plate 44e**).

Discussion

The name *lievreana* is taken from the prominent Le Lievre Ridge of the Oscar Ranges, as this species was collected from a southern outlier of that ridge. At Sta. WA-263 a projecting small cliff came near to the track, and a brief collecting stop yielded many specimens. The southward projecting exposure is more important than any mileage, as track distances undoubtedly will be different in the future.

The 22 live adults averaged 0.7 mm less in diameter than the many dead specimens taken at the same time (**Table 59**). This phenomenon also existed in material of the other species collected along this section of the Oscar Ranges (see above).

Why *Westraltrachia lievreana* should have an altered colour pattern of almost monochrome brown, except for the white peripheral zone and base, is unknown. Equally distinctive compared with other *Westraltrachia* from the Oscar Ranges is its rounded shell periphery.

Access to the limestone areas between WA-263 and Twelve Mile Bore to the south-east is made difficult by the meanderings and washes of Linesman, Mount Hardman, and Camarotochia Creeks as they exit from the Oscar Ranges. In 1980 neither the old telegraph line track nor the mining tracks used in 1976 could be followed easily. Combined with the poor previous wet season in the Napier Range, which caused collecting difficulties (see *Westraltrachia commoda* Discussion above), and the limited number of live *Westraltrachia* obtained in 1976 from Sta. WA-263, WA-264, and WA-265 (42 of 617 adults, only 6.8%), it was decided to put our main collecting effort that year into north-east Kimberley and Northern Territory localities.

The very large epiphallic loop (**Fig. 144b**, E) was present in all dissected individuals, and is the most unusual feature of the genital anatomy of *Westraltrachia lievreana*. The retention of prominent vertical ribs on the jaw (**Plate 31e**) and relatively minor modification of the central and lateral radular teeth (**Plate 44a-b**) is interpreted as the result of *W. lievreana* being the only camaenid present at WA-263, whereas its western neighbour, *W. instita*, which shows much greater jaw and radular alterations, is sympatric with *Quistrachia monogramma* (Ancey, 1898) at WA-264.

WESTRALTRACHIA TROPIDA SP. NOV.

(Plates 23a-b, 30b, 46; Figs 141d-f, 145a-c)

Comparative remarks

Westraltrachia tropida (**Figs 141d-f**) has a right angled, slightly protruded periphery, barely open umbilicus or only a lateral crack, strongly reflected lip, and is larger than most of its near neighbours (**Table 47**). The variegated colour pattern is typical, with quite dark tones on the shell. *Westraltrachia instita* (**Figs 141a-c**) is noticeably smaller and more depressed, with an open umbilicus, while *W. lievreana*, the nearest known species to the west (WA-263), has a rounded periphery (**Fig. 143b**), nearly monochrome colouration, and a more open umbilicus. *Westraltrachia limbana* (**Figs 146d-f**) is most similar in size and proportions, but has only a faint peripheral angulation and generally reduced colour pattern. Anatomically, *W. tropida* (**Figs 145a-c**) has a large penis muscle (PM), a reduced epiphallic loop (E), and there is no principal penis pilaster. The vagina (V) is normal in length, but the spermatheca (S) is short and the free oviduct (UV) significantly longer. The penis is slender, very long, tightly kinked within the relatively thick-walled penis sheath (PS). Entrance of the vas deferens (VD) into the sheath is above the penis mid-point. *Westraltrachia porcata* (**Figs 145d-e**) has a much longer penis with higher entrance of the vas deferens into the penis sheath, a very long vagina, and much longer free oviduct (UV). *Westraltrachia lievreana* (**Figs 144a-b**) has a short penis, massive epiphallic loop, and a large principal penis pilaster (**Fig. 158k**), while *W. limbana* (**Figs 149-150**) has a much more massive penis muscle, and very large principal penis pilaster (**Fig. 158m**).

Holotype

WAM 123.80, Sta. WA-710, gap through Oscar Ranges at 12 Mile Bore, north-west of Fitzroy Crossing, South Kimberley, Western Australia (1:100,000 map sheet 'Leopold Downs' 3962, grid reference 418:177). Collected by Alan Solem, Laurie Price, and Barbara Duckworth 19 June 1980. Height of shell 8.5 mm, diameter 14.0 mm, H/D ratio 0.567, whorls $4\frac{1}{8}$, umbilicus with a lateral crack.

Paratopotypes

WAM 124.80, WAM 131.80, FMNH 205306-7, 6 live, 48 dead adults, 1 live, 8 dead juveniles from the type locality.

Paratypes

Gap through Oscar Ranges at 12 Mile Bore: Sta. WA-262, south-east of quarry, east side of road ('Leopold Downs' 3962 – 419:177) (150 dead adults, 8 live juveniles, WAM 126.80-127.80, FMNH 199480, FMNH 200595); OR II, in bower bird's bower, south-west side of pass ('Leopold Downs' 3962 – 417:179) (2 live, 62 dead adults, WAM 746.76, WAM 930.76, WAM 1009.76); Sta. WA-260, north-north-east of Kundra Bore, south side of Oscar Ranges, north-east of Fitzroy Crossing ('Leopold Downs' 3962 – 511:112) (131 dead adults, 4 live, 7 dead juveniles, WAM 125.80, WAM 128.80, FMNH 199478, FMNH 200232).

Distribution limits in Oscar Ranges

Westraltrachia tropida ranges from the road gap just north of Twelve Mile Bore (WA-262, WA-710, OR II) south-east for at least 11.3 km (**Fig. 161**) to north-north-west of Kundra Bore (WA-260). There is then a collecting gap of about 8 km south-east to WA-259, where *W. limbana* and *W. rotunda* have been collected. North-west from Twelve Mile Bore, there is about 18 km of unsampled limestone to the type locality of *W. lievreana*. Thus the potential total range is about 37 km, although the known range is 11.3 km. The actual range will be somewhere in between these two figures.

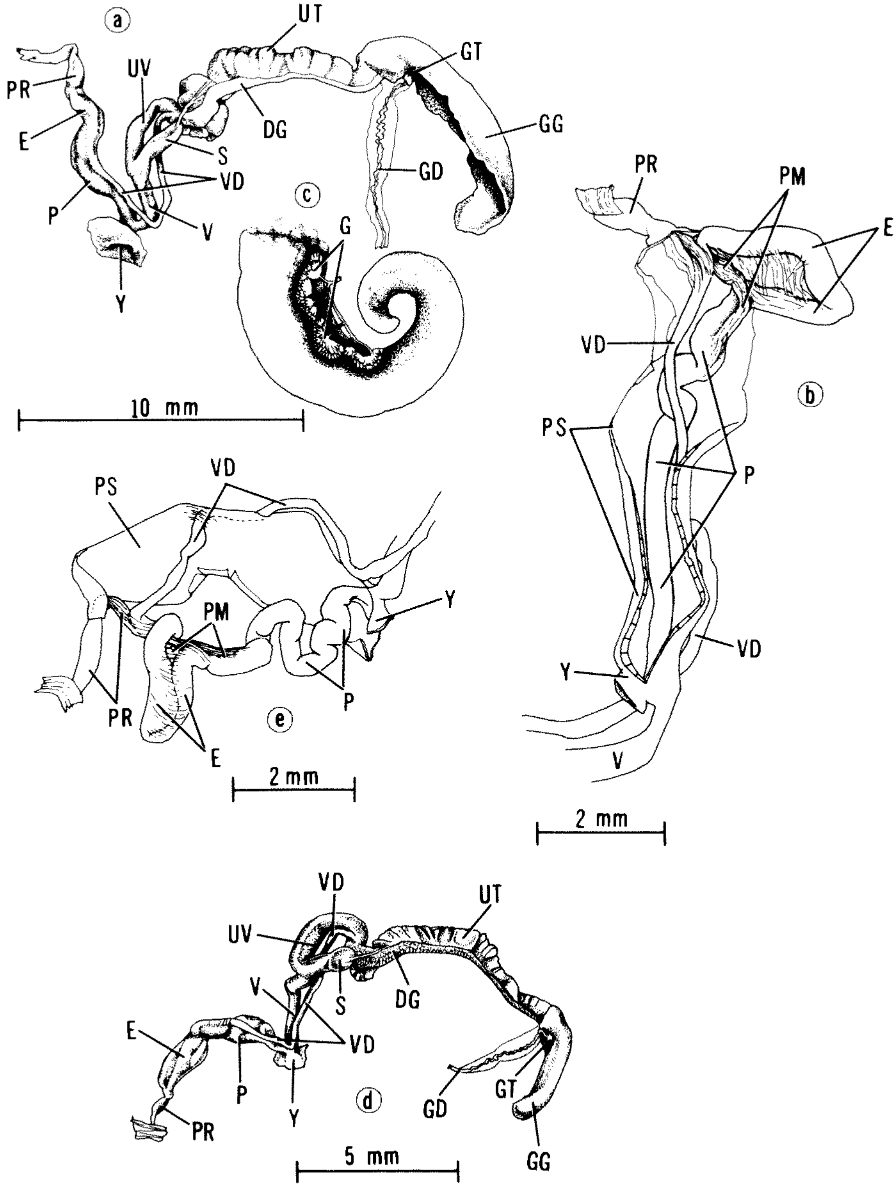


Fig. 145: Genitalia of *Westraltrachia tropida* and *W. porcata:* (a-c) *W. tropida,* Sta. WA-710, Oscar Range gap at 12 Mile Bore, north-west of Fitzroy Crossing, 19 June 1980, FMNH 205306, Dissection A, (a) whole genitalia, (b) interior of penis sheath, (c) ovotestis; (d-e) *W. porcata,* Sta. WA-711, 2.0 km south of Brooking Creek, Tunnel Road, west of Fitzroy Crossing, 19 June 1980, FMNH 205311, (d) whole genitalia, (e) interior of penis sheath. Scale lines as marked. Drawings by Linnea Lahlum.

Diagnosis

Shell slightly larger than average, 12.2-19.5 mm (mean 15.00 mm) in diameter, with 4½ to 5⅝ (mean 5 –) normally coiled whorls. Apex and spire moderately to strongly elevated, rarely rounded above, body whorl descending slightly just before aperture, height of shell 6.8-10.6 mm (mean 8.43 mm), H/D ratio 0.467-0.695 (mean 0.561). Apical whorls **(Plate 23a-b)** without micro-sculpture, postapical whorls with rather prominent growth striae. Shell periphery **(Fig. 141e)** right angled, slightly protruded into a keel, rarely obtusely angled. Lip strongly expanded and reflected over most of umbilicus, columellar edge rolled. Umbilicus slightly open (48.5%) or only a lateral crack (51.5%). Colour typical, with white peripheral zone and shell base, brown solid markings above and below peripheral zone, spire strongly variegated with brown and yellowish areas. Based on 400 measured adults.

Genitalia **(Figs 145a-c)** with large penis muscle (PM) and epiphallic loop (E). Principal penis pilaster reduced to same size as other wall pilasters, equalling the condition in *Westraltrachia subtila* **(Fig. 158i).** Penis (P) long, slender, kinked within penis sheath (PS), which has a rather thick wall on basal half. Vas deferens (VD) entering penis sheath about mid-point of penis. Vagina (V) fairly long, spermatheca (S) short, free oviduct (UV) much longer and curved.

Jaw **(Plate 30b)** with relatively prominent vertical ribs. Radula with typical marginal teeth **(Plate 46c, f),** tricuspid, cusp angle almost parallel to basal membrane. Central and lateral teeth **(Plate 46a-b, d-e)** without ectocones, basal interlock system large, anterior flare greatly reduced. Mesoconal shaft elevated to above 60°, tip blunted, degree of tip curvature rather variable.

Discussion

Westraltrachia tropida is sympatric with *W. rotunda* at Sta. WA-260. Many dead and a few live juveniles of both species were collected. At the time of collection in 1976, the ecological distinction between *W. rotunda* and *W. limbana* was unknown, and future collections will have to determine if there is any difference between *tropida* and *rotunda*. Somewhere between WA-260 and WA-259, near Two Mile Bore, *W. tropida* is replaced by *W. limbana*. Although these two species are very similar in size and proportions **(Table 47),** the sharp peripheral keel of the former contrasts with the obsoletely angled periphery of the latter, and the very large main penis pilaster of *limbana* **(Fig. 158m)** contrasts with the lost pilaster of *tropida*. There is no doubt that they are distinct species.

Local variation among populations is substantial **(Table 59),** but without additional field work, no reasons for this can be proposed. The long stretch of limestone between the record of *Westraltrachia lievreana* at WA-263, south-east of Mount Wynne Creek, and *W. limbana* at WA-259, near Two Mile Bore **(Figs 160, 161),** needs investigation, both faunistic and ecological. While the jaw and radula of these species do not show any evidence of character displacement, the possibility of micro-allopatry needs to be investigated, and the actual range limits of the taxa determined.

The name *tropida* is from the Latin for keel, referring to the nearly carinated periphery of this species.

WESTRALTRACHIA PORCATA SP. NOV.

(Plates 24d, 30f, 45b-e; Figs 143d-f, 145d-e, 158l)

Comparative remarks

Westraltrachia porcata **(Figs 143d-f)** has a very high spired, almost globose shell, with weakly angulated periphery, typical colour pattern, and closed or nearly closed umbilicus. It is one of the largest species **(Table 47)** in the East Kimberley. *Westraltrachia lievreana* from near Mount Wynne Creek (WA-263) **(Figs 143a-c)** is smaller and more depressed, with an open umbilicus **(Table 47)**, and nearly monochrome colouration. *Westraltrachia rotunda* **(Figs 146a-c)** also has monochrome colouration and very weak peripheral angulation, but is distinctly smaller in size, more depressed, and averages about ½ whorl less. *Westraltrachia tropida* **(Figs 141d-f**, WA-262, WA-710, WA-260) and *W. limbana* **(Figs 146d-f**, WA-259 near Two Mile Bore east to WA-266, Fossil Downs Station) are smaller, more depressed, and with more strongly angulated peripheries. Anatomically, *Westraltrachia porcata* **(Figs 145d-e)** has a massive penis muscle (PM) and large epiphallic loop (E). The principal penis pilaster **(Fig. 158l)** is reduced to the same size as other wall pilasters. Vagina (V) very long, penis (P) very long, slender, kinked within very thin-walled penis sheath (PS). Vas deferens (VD) entering penis sheath below head of penis. Spermatheca (S) normal in size, free oviduct (UV) much longer and curved. *Westraltrachia tropida* **(Figs 145a-c)** has a shorter vagina and penis, while *W. lievreana* **(Figs 144a-b)** differs in having a massive epiphallic loop and both penis and vagina comparatively short. *Westraltrachia rotunda* **(Figs 147a-b, 148)** and *W. limbana* **(Figs 149a-b, 150a-b)** are very similar in genital morphology, ignoring the variation in length of terminal female genitalia, but differ radically in having very large principal penis pilasters **(Figs 148, 158m).**

Holotype

WAM 129.80, Sta. WA-711, limestone ledges 2.0 km south of Brooking Creek on Tunnel Road, north-west of Fitzroy Crossing, South Kimberley, Western Australia (1:100,000 'Leopold Downs' map sheet 3962, grid reference 479:238). Collected by Alan Solem, Laurie Price, and Barbara Duckworth 19 June 1980. Height of shell 11.25 mm, diameter 16.25 mm, H/D ratio 0.692, whorls 4⅞, umbilicus with a lateral crack.

Paratopotypes

WAM 130.80, FMNH 204310-1, 42 dead adults, 1 live, 13 dead juveniles from the type locality.

Distribution limits in Oscar Ranges

A rock exposure less than 100 metres in diameter, located in the upper drainage of Brooking Creek north of the Oscar Ranges. It is quite probable that other isolated colonies exist, as the surrounding area has not been surveyed for land snails.

Diagnosis

Shell larger than average, 14.5-18.8 mm (mean 16.37 mm) in diameter, with 4⅞ to 5½+ (mean 5⅛−) normally coiled whorls. Apex and spire strongly elevated, rounded above, body whorl barely descending before aperture **(Fig. 143e)**, height of shell 8.05-13.9 mm (mean 11.45 mm), H/D ratio 0.555-0.818 (mean 0.699). Apical whorls

(Plate 24d) with traces of micro-riblets in the sutures, postapical whorls with fine radial riblets and irregular growth lines. Shell periphery **(Fig. 143e)** weakly angulated and slightly protruded. Lip moderately expanded, columellar section rolled to cover most or all of umbilicus, which varies from narrowly open (53.5%), to with a lateral crack (37.2%), to closed (9.3%). Colour typical, but lighter in tone than most East Kimberley taxa. Based on 43 measured adults.

Genitalia **(Figs 145d-e)** with large penis muscle (PM) and large, tightly bound epiphallic loop (E). Principal penis pilaster **(Fig. 158l)** reduced to same size as other wall pilasters. Penis (P) very long, tightly kinked within thin-walled penis sheath. Vas deferens (VD) entering sheath above mid-point of penis. Vagina (V) very long, free oviduct (UV) quite long and strongly curved, spermatheca (S) of normal length, bound with fibers to base of prostate-uterus.

Jaw **(Plate 30f)** typical, with very prominent vertical ribs. Radula with typical marginal teeth **(Plate 45e)** and latero-marginal transition **(Plate 45d)**. Central and lateral teeth **(Plate 45b-e)** without ectocones, anterior basal flare shortened, row interlock system large. Mesoconal shaft slightly elevated above normal angle, cusp bluntly rounded and slightly curved **(Plate 45b-c)**.

Discussion

Westraltrachia porcata was taken from a small reef exposure located about 2 km south of the main channel of Brooking Creek on the road from Fitzroy Crossing to The Tunnel. The exposure is less than 100 metres in diameter. About five person hours of searching on 19 June 1980 yielded only one live subadult, on which the anatomical description is based, and 43 dead adults. Since the previous wet season was abnormally dry, the "subadult" in all probability was an end of second wet season new adult who had not reflected and completed the shell lip because of shortened activity periods in the previous months. In the features of its anatomy **(Figs 145d-e)**, it is quite comparable to 'male adult, female juvenile' specimens with fully reflected lip collected from late in their second wet season to the beginning of their third wet season. I am confident that it accurately portrays essential features of the genital system.

It is quite probable that other such islands of limestone exist in the drainage of Brooking Creek north of the Oscar Ranges, but vehicle tracks do not exist and determination of their existence and their land snail fauna is left to others.

The combination of globose shape **(Fig. 143e)**, normal colour pattern, nearly closed umbilicus, and relatively large size immediately identify this species. Its name, *porcata*, is taken from the Latin 'porca', a ridge between two furrows, and refers to the type locality, a small exposure of limestone elevated between two branches of Brooking Creek.

WESTRALTRACHIA ROTUNDA SP. NOV.

(Plates 23c, 31c-d, 47a-c; Figs 146a-c, 147, 148)

Comparative remarks

Westraltrachia rotunda **(Figs 146a-c)** is immediately recognisable, when unworn, by its monochrome, yellow-brown colour, absence of a white peripheral zone, rather flat whorls on the spire, obtusely rounded periphery, low whorl count (**Table 47**), and near average size. At most localities, *Westraltrachia limbana* (**Figs 146d-f**) is present nearby or upslope, and unworn specimens can be recognised by their variegated colour pattern, white peripheral zone, distinctly angulated periphery, larger diameter, and lower H/D ratio (**Table 47**). The only other nearly monochrome coloured species in the East Kimberley, *W. lievreana* (**Figs 143a-c**), retains the white peripheral zone, and has much more rounded whorls. The unicoloured species from west of Windjana Gorge have white body whorls, *W. woodwardi* (Fulton, 1902), *W. commoda* (Iredale, 1939); very light periostracal tones with an open umbilicus and flatter spire – *W. inopinata* (**Figs 117e-f**); or a very high spire and reduced diameter – *W. turbinata* (**Fig. 117b**). Anatomically, *W. rotunda* (**Figs 147, 148**) has a massive penis muscle (PM) and epiphallic loop (E), and the principal penis pilaster (**Fig. 148**, PT) is very long, high, and with hardened edges. The vagina (V) is very long, as is the strongly sinuated free oviduct (UV), while the spermatheca (S) is only slightly longer than normal. The penis (P) is very long and slender, kinked within a comparatively thin-walled penis sheath (PS). Entrance of the vas deferens (VD) into the sheath is at the penis head level. The radular central and lateral teeth (**Plate 47a-b**) have retained small ectocones, have a prominent anterior basal flare, and the mesocone is less elevated, less curved at the tip, and the tip itself has a sharper point than in nearly all *Westraltrachia*. *Westraltrachia limbana* (**Figs 149-150**) has the penis and vagina much shorter, the principal penis pilaster (**Fig. 158m**) is much shorter (**Table 46**), although retaining hard edges, and the radular teeth are more modified (**Plate 47d-f**). None of the other Oscar Ranges species have a principal penis pilaster that begins to approach the size shown by *W. rotunda,* and are easily recognised by this feature.

Holotype

WAM 152.80, Sta. WA-258, east bank of Brooking Gorge near entrance, north-west of Fitzroy Crossing, South-east Kimberley, Western Australia (1:100,000 'Fitzroy Crossing' map sheet 4061, grid reference 688:054). Collected by Alan Solem and Carl Christensen 26 November 1976. Height of shell 9.6 mm, diameter 14.2 mm, H/D ratio 0.676, whorls 5⅝, umbilicus with a narrow lateral crack.

Paratopotypes

WAM 153.80, WAM 154.80, FMNH 199459, FMNH 199460, FMNH 200208, 21 live, 125 dead adults, 35 live juveniles from the type locality.

Paratypes

Sta. WA-260, north-north-east of Kundra Bore, Oscar Ranges, west of Fitzroy Crossing ('Leopold Downs' 3962 – 511:112) (5 live, 103 dead adults, 3 live juveniles, WAM 167.80, WAM 169.80, FMNH 199479, FMNH 200233); Sta. WA-259, 1.5 km north-west of Two Mile Bore, Oscar Ranges, west of Fitzroy Crossing ('Cunningham' 3961 – 573:057) (24 live, 186 dead adults, 28 live, 2 dead juveniles, WAM 162.80, WAM 166.80, FMNH 199587, FMNH 200235); Sta. WA-261, 6.7 km east-south-east Two Mile Bore, Oscar Ranges, west of Fitzroy Crossing ('Cunningham' 3961 – 628:013) (3 live, 99 dead adults, 12 live juveniles, WAM 156.80, WAM 172.80, FMNH 199467, FMNH 200207); Sta. WA-267, limestone gully 1 km west of WA-261, Oscar Ranges, near Fitzroy Crossing ('Cunningham' 3961 – 634:014) (9 live, 192 dead adults, 2 live, 2 dead juveniles, WAM 155.80, WAM 160.80, FMNH 199463, FMNH 200203); Sta. WA-268, 6.2 km west of WA-261, Oscar Ranges, Fitzroy Crossing ('Fitzroy Crossing' 4061 – 679:034) (2 live, 52 dead adults, 2 live, 3 dead juveniles, WAM 163.80, WAM 165.80, FMNH 199501, FMNH 200221); Sta. WA-585, east side of entrance to Brooking Gorge, talus above flood level, Oscar Ranges, west of Fitzroy Crossing ('Fitzroy Crossing' 4061 – 688:054) (14 live, 6 dead adults, WAM 159.80, WAM 170.80, FMNH 200233, FMNH 204722); Sta. WA-257, west side Brooking Gorge, 0.7 km west of road fork, Oscar Ranges, west of Fitzroy Crossing ('Fitzroy Crossing' 4061 – 688:053) (20 live, 396 dead adults, 41 live, 8 dead juveniles, WAM 164.80, WAM 171.80, FMNH 199486-7, FMNH 200235); Sta. WA-584, valley just south of entrance to Brooking Gorge, Oscar Ranges, west of Fitzroy Crossing ('Fitzroy Crossing' 4061 – 689:045) (1 live, 38 dead adults, WAM 158.80, FMNH 204719-20); Sta. WA-255, hills by creek at Giekie Gorge Ranger Station, Giekie Gorge National Park, near Fitzroy Crossing ('Fitzroy Crossing' 4061 – 861:964) (235 dead adults, WAM 168.80, FMNH 199592); Sta. WA-256, hills south of Giekie Gorge Ranger Station, Giekie Gorge National Park, Fitzroy Crossing ('Fitzroy Crossing' 4061 – 861:964) (10 live, 42 dead adults, 7 live, 7 dead juveniles, WAM 156.80, WAM 161.80, FMNH 199463, FMNH 200230).

Distribution limits in Oscar Ranges

Westraltrachia rotunda has a known range of about 38.5 km from north-north-east of Kundra Bore (WA-260) south-south-east to the mouth of Giekie Gorge, north of Fitzroy Crossing. There is a distance of 11 km between WA-260 north-west to the gap at Twelve Mile Bore (WA-262) in the Oscar Ranges that has not been surveyed for land snails, giving a possible range of almost 50 km for this species. Almost certainly, colonies will be found in shaded nooks of the Giekie Range, providing a northeastward range extension.

Diagnosis

Shell near average in size, 11.5-17.7 mm (mean 14.15 mm) in diameter, with 4 to 5¼ + (mean 4⅝ +) almost normally coiled whorls. Apex and spire moderately and almost evenly elevated, usually slightly rounded above, body whorl descending slightly just before aperture **(Fig. 146b),** height of shell 6.9-11.4 mm (mean 9.05 mm), H/D ratio 0.527-0.757 (mean 0.639). Apical whorls **(Plate 23c)** with remnants of micro-riblets and growth striae, postapical sculpture of micro-riblets and relatively fine growth lines at irregular intervals. Shell periphery **(Fig. 146b)** obtusely rounded, never distinctly angulated in adult, juveniles with a moderate angulation. Lip strongly reflected **(Figs 146a-c),** columellar section rolled over umbilicus, which is sometimes narrowly open (23.8%), normally with a lateral crack (75.3%), or rarely closed (0.9%). Growth pattern unusual in that whorl cross-sectional area increases more rapidly and aperture is proportionately larger than in other *Westraltrachia.* Shell colour light to dark yellow-brown, no white peripheral zone, but base of shell slightly to distinctly lighter than spire and periphery. Based on 1,562 measured adults.

Genitalia **(Figs 147-148)** with massive penis muscle (PM) and large epiphallic loop (E) whose arms are tightly bound by fibers. Principal penis pilaster **(Fig 148,** PT) extending half length of penis, high, sinuated, thin, with sections of upper edge hardened at nearly regular intervals. Other weak longitudinal, low pilasters present on wall alongside main pilaster, base of penis with simple longitudinal pilasters. Penis (P) very long, slender, kinked within rather thick-walled penis sheath (PS). Vas deferens (VD) entering penis sheath almost opposite head of penis. Vagina (V) very long, spermatheca (S) typical, fastened to base of prostate-uterus by fibers, free oviduct (UV) much longer than spermatheca, and curved or sinuated.

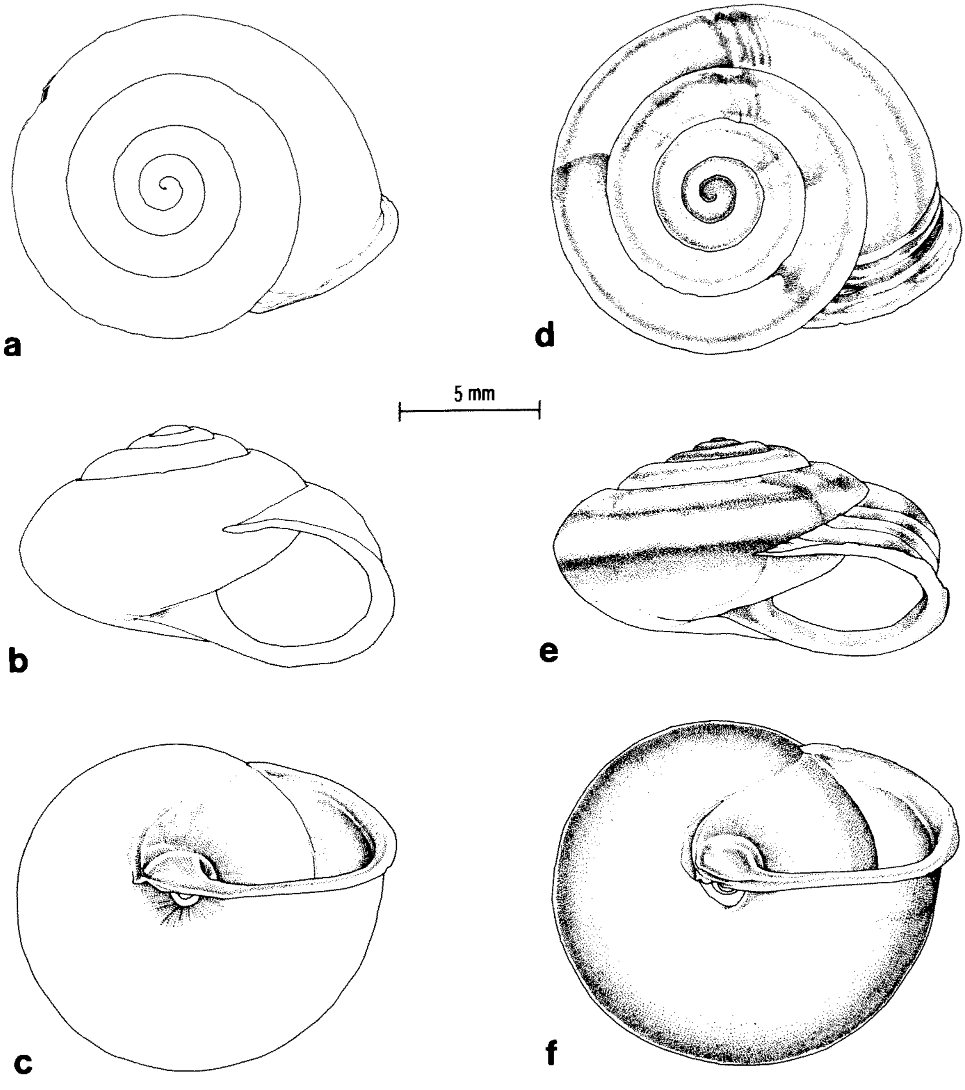


Fig. 146: Shells of *Westraltrachia rotunda* and *W. limbana:* (a-c) holotype of *Westraltrachia rotunda,* Sta. WA-258, Brooking Gorge, west of Fitzroy Crossing, WAM 152.80; (d-f) holotype of *Westraltrachia limbana,* Sta. WA-266, west of Fossil Downs Homestead, east of Fitzroy Crossing, WAM 173.80. Scale line equals 5 mm. Drawings by Linnea Lahlum.

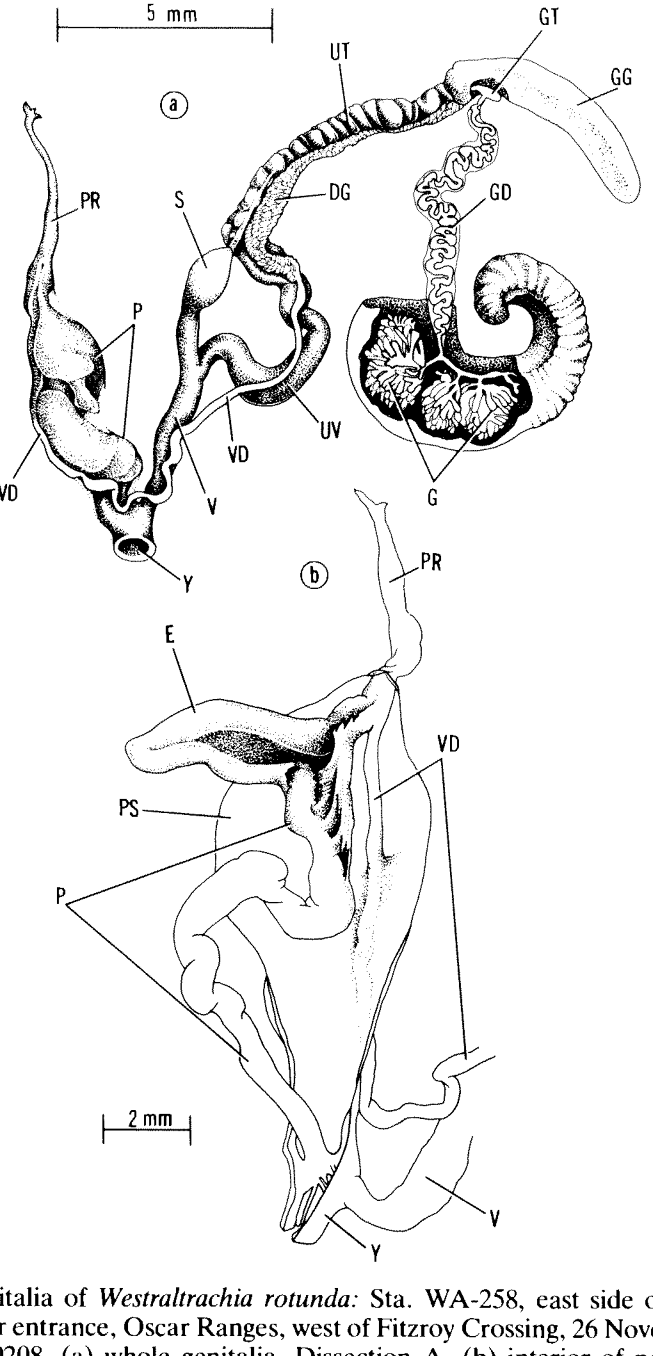


Fig. 147: Genitalia of *Westraltrachia rotunda:* Sta. WA-258, east side of Brooking Gorge, near entrance, Oscar Ranges, west of Fitzroy Crossing, 26 November 1976, FMNH 200208, (a) whole genitalia, Dissection A, (b) interior of penis sheath, Dissection B. Scale lines as marked. Drawings by Marjorie M. Connors.

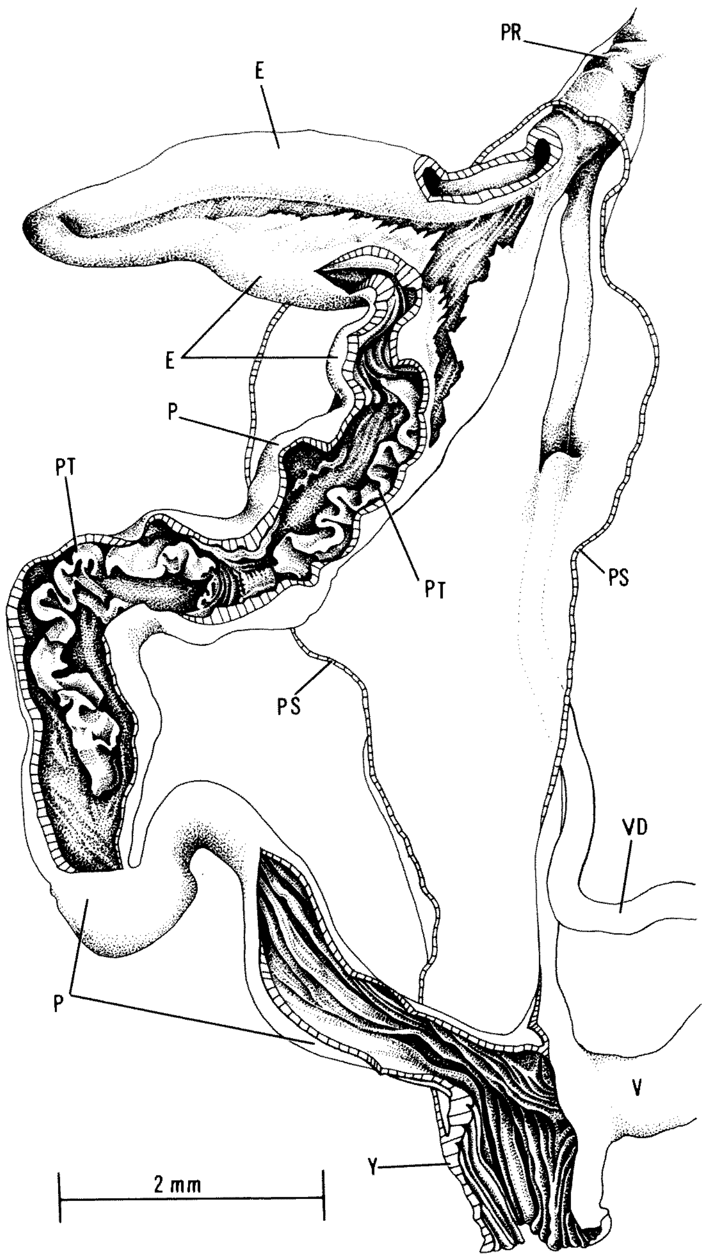


Fig. 148: Penis interior of *Westraltrachia rotunda:* Sta. WA-258, east side Brooking Gorge, near entrance, Oscar Ranges, west of Fitzroy Crossing, 26 November 1976, FMNH 200208, Dissection B. Scale line equals 2 mm. Drawings by Marjorie M. Connors.

Jaw **(Plate 31c-d)** typically camaenid, with a variable number of very prominent vertical ribs. Radula with typical marginal teeth **(Plate 47c)**, early ones elevated at about a 45° angle, outer marginals with cusps almost parallel to the basal membrane. Central and lateral teeth **(Plate 47a-b)** only slightly modified from typical camaenid pattern in having the ectocones reduced, the mesoconal tip slightly curved and a little blunted, thus contrasting greatly with most other *Westraltrachia*.

Discussion

Throughout most of its known range, *Westraltrachia rotunda* is grossly sympatric with *W. limbana*. Live or recently dead examples can be readily identified to species by the features listed above in the Comparative remarks. Genital differences are summarised above in **Table 46.** Worn or long dead and dirt encrusted individuals, which form the bulk of routine field samples, are difficult to separate. Indeed, neither Laurie Price nor I recognised in the field that we were taking two species. In part this reflected our choice of microhabitat for sampling. We went first to talus on the side of gullies shaded by larger trees, and this is the preferred habitat for live *W. rotunda.* Dead specimens from this microhabitat were a mixture of both species, and **Table 61** gives a breakdown of our collecting from this niche. During our 1980 field work, we learned that *W. limbana* can be found alive in the thinner talus present on more open slopes. Often such sites are located above the shaded talus that we had torn apart in our search for snails. Dead specimens of the latter species had washed down into the shaded talus, and we were sampling thanatocoenoses in 1976. Dead material seen on the more open slopes in 1980 was almost only *W. limbana,* but time did not permit quantitative sampling.

The two species are micro-allopatric in terms of preferred habitat, but often sympatric within a 10 metre radius. Whether *Westraltrachia limbana* is actually excluded by *W. rotunda* is unknown. The latter species has a generalised jaw **(Plate 31c-d)** and radula **(Plate 47a-c)**, plus the most generalised penis pilaster **(Fig. 148,** PT) within the entire genus, while the former has a more modified radula **(Plate 47d-f)** and a probably slightly modified jaw **(Plate 31a-b)**. *Westraltrachia rotunda* has the feeding apparatus of a generalised camaenid that uses dead plant parts, while *W. limbana* shows indications of the seepage face film feeding adaptation that becomes the normal structure in species of *Westraltrachia* that live west of Windjana Gorge, and is partly developed among those species that are sympatric with *Quistrachia monogramma* (Ancey, 1898) in the western Oscar and eastern Napier Ranges. Within the shaded talus, *W. rotunda* often is quite abundant. We have no data on population density for either species, and none is apt to be gathered easily, as most colonies are isolated in the wet season by black mud plains. Dry season collecting produced few live individuals of either species **(Table 61)**. Thus I can only speculate that perhaps *W. rotunda* is a 'wet era' relict that floods the shaded talus niche by sheer numbers, whereas *W. limbana* is better adapted to the more open talus with seepage faces providing occasional supplementary food.

Local variation in *Westraltrachia rotunda* is summarised in **Table 60.** Except for material from Sta. WA-257, on the west side of Brooking Gorge, wherever more than a few specimens are tabulated, the live adults are significantly smaller than dead material from the same station. The exception involves a very well shaded and moist niche, and may well be a buffered habitat. Differences between and among dead

Table 60: Local Variation in *Westraltrachia rotunda*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
WA-260, Kundra Bore, FMNH 200233	5L	8.98 ± 0.301 (8.1 – 9.8)	14.07 ± 0.232 (13.4 – 14.8)	0.639 ± 0.021 (0.581 – 0.703)
WA-260, FMNH 199479	103D	8.86 ± 0.068 (7.4 – 10.9)	13.87 ± 0.089 (11.8 – 16.1)	0.639 ± 0.002 (0.591 – 0.688)
WA-259, NW Two Mile Bore, FMNH 200235	24L	8.36 ± 0.160 (7.6 – 11.15)	12.70 ± 0.193 (11.5 – 15.7)	0.658 ± 0.006 (0.610 – 0.710)
WA-259, FMNH 199587	186D	9.13 ± 0.051 (6.9 – 11.3)	14.27 ± 0.067 (11.5 – 16.8)	0.640 ± 0.002 (0.551 – 0.712)
WA-267, 1 km W of WA-261, FMNH 200203	9L	8.37 ± 0.133 (7.95 – 9.0)	13.10 ± 0.127 (12.55 – 13.85)	0.639 ± 0.009 (0.611 – 0.685)
WA-267, FMNH 199463	192D	8.75 ± 0.040 (7.4 – 10.3)	13.71 ± 0.054 (12.0 – 16.2)	0.638 ± 0.002 (0.543 – 0.707)
WA-261, SE Two Mile Well, FMNH 200230	3L	8.98 ± 0.192 (8.6 – 9.2)	13.80 ± 0.275 (13.3 – 14.25)	0.651 ± 0.005 (0.646 – 0.661)
WA-261, FMNH 199467	99D	9.47 ± 0.068 (7.8 – 11.3)	14.17 ± 0.075 (12.2 – 15.9)	0.668 ± 0.003 (0.601 – 0.736)
WA-268, 6.2 km W of WA-261, FMNH 199501	52D	9.27 ± 0.089 (8.3 – 11.2)	14.12 ± 0.109 (12.2 – 15.8)	0.657 ± 0.004 (0.587 – 0.721)
WA-257, W side Brooking Gorge, FMNH 200217	20L	9.11 ± 0.163 (7.9 – 10.4)	14.14 ± 0.148 (12.65 – 15.35)	0.644 ± 0.007 (0.585 – 0.688)
WA-257, FMNH 199486	396D	9.01 ± 0.033 (7.3 – 11.1)	14.16 ± 0.040 (12.1 – 16.7)	0.636 ± 0.002 (0.531 – 0.729)
WA-585, E side Brooking Gorge, FMNH 204721	14L	9.11 ± 0.146 (8.0 – 10.0)	13.68 ± 0.140 (12.7 – 14.35)	0.666 ± 0.008 (0.606 – 0.700)
WA-585, FMNH 204722	6D	9.36 ± 0.213 (8.7 – 10.0)	14.10 ± 0.277 (13.4 – 15.1)	0.664 ± 0.008 (0.644 – 0.692)
WA-258, E side Brooking Gorge, FMNH 199460	126D	8.97 ± 0.063 (7.1 – 10.9)	13.79 ± 0.071 (11.8 – 15.9)	0.650 ± 0.003 (0.578 – 0.727)
WA-584, S of Brooking Gorge, FMNH 204719	38D	9.86 ± 0.110 (8.5 – 11.4)	14.73 ± 0.147 (12.95 – 16.5)	0.670 ± 0.006 (0.579 – 0.757)
WA-255, Giekie Gorge, FMNH 199592	235D	9.13 ± 0.037 (7.7 – 10.9)	14.79 ± 0.050 (12.7 – 17.7)	0.617 ± 0.002 (0.527 – 0.684)
WA-256, Giekie Gorge, FMNH 200207	10L	8.76 ± 0.140 (8.35 – 9.7)	13.75 ± 0.159 (13.3 – 15.0)	0.637 ± 0.005 (0.622 – 0.672)
WA-256, FMNH 200871	41D	9.06 ± 0.086 (7.8 – 10.3)	14.64 ± 0.092 (13.5 – 15.7)	0.619 ± 0.004 (0.565 – 0.680)

Table 60: Local Variation in *Westraltrachia rotunda* (continued)

Station	Number of Adults Measured	Mean and Range of: Whorls	Umbilical States
WA-260, Kundra Bore, FMNH 200233	5L	4¾ − (4½ + − 4⅞)	3 open, 2 cracked
WA-260, FMNH 199479	103D	4¾ − (4⅜ − − 5⅛ +)	22 open, 81 cracked
WA-259, NW Two Mile Bore, FMNH 200235	24L	4½ + (4¼ − − 5 −)	11 open, 13 cracked
WA-259, FMNH 199587	186D	4¾ (4¼ + − 5¼ +)	29 open, 157 cracked
WA-267, 1 km W of WA-261, FMNH 200203	9L	4½ (4¼ − 4¾ −)	9 cracked
WA-267, FMNH 199463	192D	4⅝ (4¼ − 5¼)	21 open, 170 cracked, 1 closed
WA-261, SE Two Mile Well, FMNH 200230	3L	4½ + (4½ − 4¾ −)	3 cracked
WA-261, FMNH 199467	99D	4¾ + (4½ − − 5¼ −)	6 open, 93 cracked
WA-268, 6.2 km W of WA-261, FMNH 199501	52D	4⅝ + (4¼ + − 5)	3 open, 49 cracked
WA-257, W side Brooking Gorge, FMNH 200217	20L	4½ + (4¼ − 4¾)	10 open, 10 cracked
WA-257, FMNH 199486	396D	4⅝ − (4 − 5¼ −)	132 open, 264 cracked
WA-585, E side Brooking Gorge, FMNH 204721	14L	4½ + (4¼ − 4¾)	9 cracked, 5 closed
WA-585, FMNH 204722	6D	4½ + (4⅜ − 4¾)	6 cracked
WA-258, E side Brooking Gorge, FMNH 199460	126D	4½ + (4⅛ + − 5⅛)	35 open, 91 cracked
WA-584, S of Brooking Gorge, FMNH 204719	38D	4⅞ − (4⅜ − − 5⅛)	7 open, 20 cracked, 11 closed
WA-255, Giekie Gorge, FMNH 199592	235D	4¾ − (4¼ − 5¼ +)	79 open, 156 cracked
WA-256, Giekie Gorge, FMNH 200207	10L	4⅝ − (4⅜ − 4¾)	6 open, 4 cracked
WA-256, FMNH 200871	41D	4¾ (4⅜ − − 5¼ ±)	8 open, 33 cracked

material from the sampled populations is basically exceeded by the within Station live-dead differential. Under these circumstances, I am not inclined to attribute any significance to the minor size variation. There are significant differences in the relative condition of the umbilical opening **(Table 60)**, but the reasons for this are unknown.

The name *rotunda* comes from the Latin 'rotundus' or round and refers to the apparent shell shape. The absence of the white peripheral zone gives this species a misleading globose look compared with the other *Westraltrachia,* and I had christened it "brown round" during initial phases of sorting and study. It actually is less globose than *Westraltrachia porcata* **(Fig. 143e)** or *W. woodwardi* (Fulton, 1902) **(Figs 111b, e h),** but the name stuck.

Table 61: Proportionate Occurrences of *Westraltrachia limbana* and *W. rotunda*

	Adult Specimens of:				Juvenile Specimens of:	
	W. limbana		*W. rotunda*		*W. limbana*	*W. rotunda*
Station	**Live**	**Dead**	**Live**	**Dead**	**Live**	**Live**
WA-260	–	–	5	103	–	3
WA-259	–	186	24	186	–	28
WA-261	–	11	3	99	–	12
WA-267	–	–	9	192	–	2
WA-268	–	7	2	52	–	2
WA-585	1	6	14	6	–	–
WA-257	–	1	20	396	–	41
WA-258	–	–	21	125	3	35
WA-584	–	–	1	38	–	–
WA-255	–	–	–	235	–	–
WA-256	–	63	10	42	–	7
WA-266	4	237	–	–	–	–

WESTRALTRACHIA LIMBANA SP. NOV.

(Plates 23d-f, 31a-b, 47d-f; Figs 146d-f, 149, 150, 158m)

Comparative remarks

Westraltrachia limbana **(Figs 146d-f)** has a weakly angulated periphery, nearly closed umbilicus, a relatively low spire, normal colour pattern, and is slightly larger than average. It is grossly sympatric with *W. rotunda* **(Figs 146a-c),** which differs in its smaller size, more elevated spire, rounded periphery, and monochrome brownish-yellow colouration without any white peripheral zone. *Westraltrachia recta* **(Figs 151a-c)** is much smaller **(Table 47),** very high spired, and with more prominent colour. *Westraltrachia pillarana* **(Figs 151d-f)** from further east, is conchologically very similar except for a slightly more open umbilicus, but shows significant anatomical differences, while to the west, *W. tropida* **(Figs 141d-f)** is much more strongly carinated and with a more open umbilicus. Anatomically, *W. limbana* **(Figs 149, 150)** has a very massive penis muscle (PM) that surrounds the large epiphallic loop, and there is a fairly large principal penis pilaster **(Fig. 158m).** The vagina (V) is short, but the spermatheca (S) is rather long, and the free oviduct (UV) is moderately longer than the spermatheca and curved. The penis (P) is long and slender, kinked within the penis sheath (PS), whose basal wall is noticeably thickened. Entrance of the vas deferens (VD) into the penis sheath occurs opposite the penis head. The sympatric *W. rotunda* **(Figs 147, 148)** differs most obviously **(Table 46)** in its very long vagina, free oviduct, and penis, plus the very large principal penis pilaster **(Fig. 148,** PT). *Westraltrachia recta* **(Figs 152a-b)** has the penis extremely shortened, although the epiphallic loop seems unchanged from normal size, the vagina is very short, although the spermatheca and free oviduct are very long, and the principal penis pilaster **(Fig. 158n)** is reduced in size. *Westraltrachia pillarana* **(Figs 153-154)** shows great reduction of the penis muscle, a very long, kinked penis, very long vagina, long spermatheca, but greatly shortened free oviduct (UV). Its penis pilaster **(Fig. 158o)** is short and very broad.

Holotype

WAM 173.80, Sta. WA-266, limestone gulley 3.7 km west-south-west of Fossil Downs Homestead, east of Fitzroy Crossing, South-east Kimberley, Western Australia (1:100,000 'Fitzroy Crossing' map sheet 4061, grid reference 905:910). Collected by Alan Solem, Laurie Price, and Carl Christensen 29 November 1976. Height of shell 8.55 mm, diameter 15.1 mm, H/D ratio 0.566, whorls 5 –, umbilicus with a narrow lateral crack.

Paratopotypes

WAM 174.80, WAM 175.80, FMNH 199485, FMNH 200201, 4 live, 236 dead adults from the type locality.

Paratypes

Sta. WA-259, 1.5 km north-west of Two Mile Bore, Oscar Ranges, west of Fitzroy Crossing ('Cunningham' 3961 – 573:057) (186 dead adults, WAM 177.80, FMNH 199583, FMNH 200870); Sta. WA-261, 6.7 km east-south-east Two Mile Bore, Oscar Ranges, west of Fitzroy Crossing ('Cunningham' 3961 – 628:013) (11 dead adults, 1 dead juvenile, WAM 178.80, FMNH 199465); Sta. WA-268, 6.2 km east of WA-261, Oscar Ranges, north-west of Fitzroy Crossing ('Fitzroy Crossing' 4061 – 679:034) (7 dead adults, WAM 179.80, FMNH 200872); Sta. WA-585, east entrance to Brooking Gorge, talus above flood level ('Fitzroy Crossing' 4061 – 688:054) (1 live, 6 dead adults, WAM 180.80, FMNH 204723, FMNH 205379); Sta. WA-257, west side of entrance to Brooking Gorge, 0.7 km west of road fork ('Fitzroy Crossing' 4061 – 688:053) (1 dead adult, FMNH 205374); Sta. WA-258, east side of Brooking Gorge, opposite WA-257 ('Fitzroy Crossing' 4061 – 688:054) (3 live juveniles, FMNH 205373); Sta. WA-256, hills south of Giekie Gorge Ranger Station, Giekie Gorge National Park, north of Fitzroy Crossing ('Fitzroy Crossing' 4061 – 861:964) (63 dead adults, WAM 176.80, FMNH 199620, FMNH 200206); Llaramalura Creek, Fossil Downs, Margaret River (7 dead adults, 3 dead juveniles, Consett (?Carsett) Davis 20-21 June 1943).

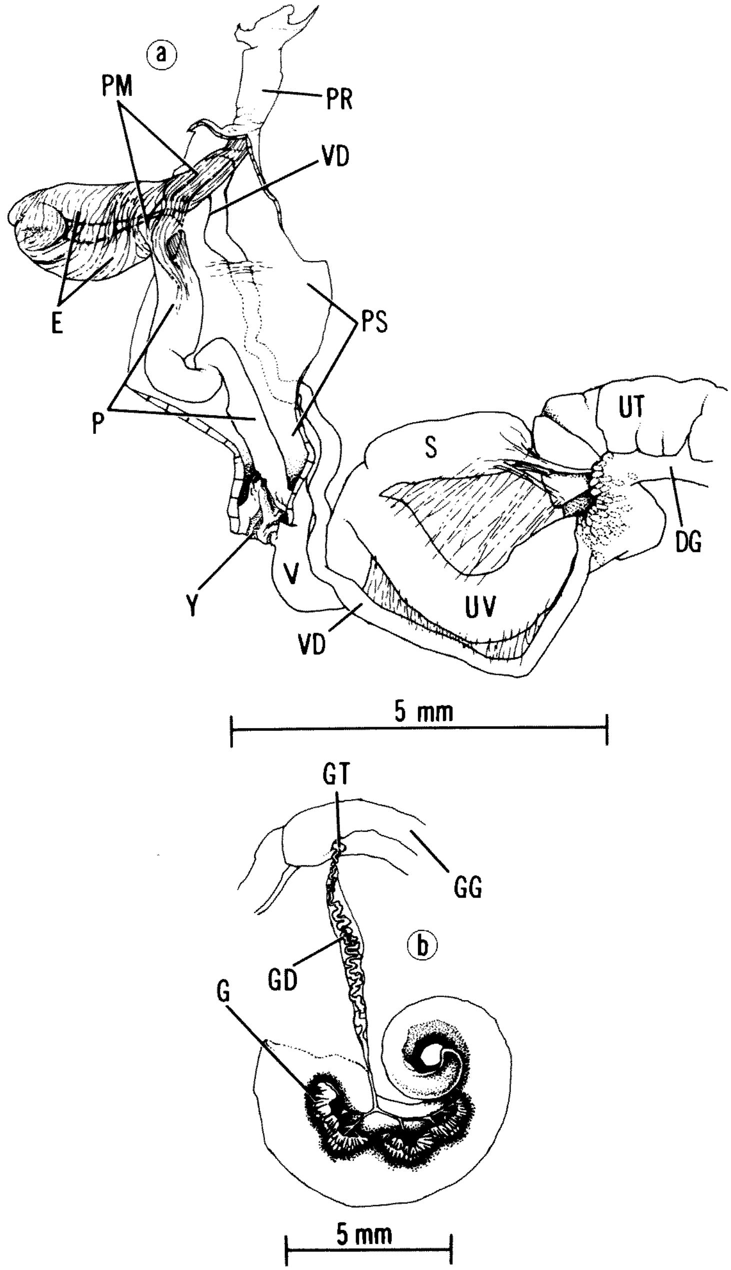


Fig. 149: Genitalia of *Westraltrachia limbana:* Sta. WA-585, east side of Brooking Gorge entrance, Oscar Ranges, west of Fitzroy Crossing, 8 May 1980, FMNH 205370, paratype, Dissection A, (a) interior of penis sheath, (b) detail of apical genitalia. Scale lines as marked. Drawings by Linnea Lahlum.

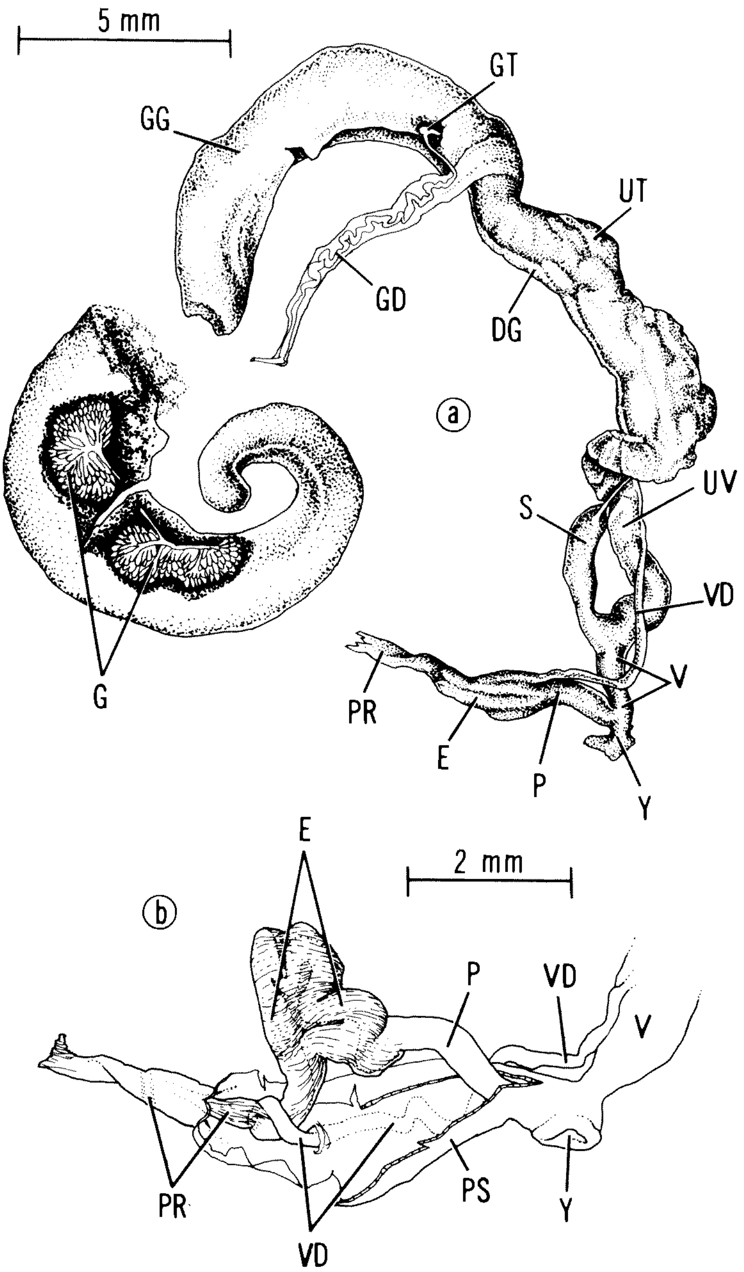


Fig. 150: Genitalia of *Westraltrachia limbana:* Sta. WA-266, 3.7 km from Fossil Downs Homestead, east of Fitzroy Crossing, 29 November 1976, FMNH 200201, paratopotypes, (a) whole genitalia, Dissection A, (b) interior of penis sheath, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

Distribution limits in Oscar and neighbouring ranges

Positive records extend from near Two Mile Bore (WA-259) east to outcrops on the north bank of the Margaret River, near Fossil Downs Station homestead, east of Fitzroy Crossing – a total air distance of about 36.5 km. It is about 8 km further north-west to WA-260 (south-east of Twelve Mile Bore), where both *Westraltrachia rotunda* and *W. tropida* have been collected sympatrically. A potential air distance range of about 45 km is indicated. North-east extension into the Giekie Range is probable, but eastward of Fossil Downs there is only the mud and lateritic plains of the Margaret River basin, while to the south, the next bit of exposed limestone, the Limestone Billy Hills, about 24 km south-east of Fitzroy Crossing, is inhabited by *W. recta*. The exact location of Llaramalura Creek, Fossil Downs Station is unknown to me. Both *W. recta* and *W. limbana* were collected there in June 1943.

Diagnosis

Shell somewhat larger than average, 12.2-18.0 mm (mean 15.24 mm) in diameter, with 4½ to 5⅞+ (mean 5+) normally coiled whorls. Apex and spire moderately and evenly elevated, at most slightly rounded above, body whorl descending very slightly before aperture **(Fig. 146e)**, height of shell 6.25-11.75 mm (mean 8.60 mm), H/D ratio 0.473-0.695 (mean 0.564). Apical whorls **(Plate 23d-f)** typical, postapical sculpture of weak irregular growth lines, microscopic periostracal folds visible on fresh specimens. Shell periphery weakly angulated **(Fig. 146e)**. Lip very strongly expanded, partly to nearly covering umbilicus **(Fig. 146f)**, which varies from partly open (34.5%) or normally a lateral crack (63.0%), to occasionally closed (2.5%). Shell colour typical, variegated brown and yellow-brown spire, white peripheral zone and shell base, darker brown above and below peripheral zone. Based on 512 measured adults.

Genitalia **(Figs 149-150)** with massive penis muscle (PM) and prominent epiphallic loop (E). Principal penis pilaster **(Fig. 158m)** much shorter than in *Westraltrachia rotunda* **(Fig. 148)**, retaining hard edges on part of length. Penis (P) long, slender, kinked within penis sheath (PS), that has comparatively thick-walled basal section. Vas deferens (VD) entering penis sheath opposite top of penis. Vagina (V) rather short, spermatheca (S) of normal length, free oviduct (UV) distinctly curved, longer than spermatheca.

Jaw **(Plate 31a-b)** with very prominent vertical ribs. Radula **(Plate 47d-f)** with typical marginal teeth, central and laterals without ectocones, mesoconal shaft distinctly elevated, tip of mesocone bluntly rounded, strongly curved, but teeth not noticeably narrowed.

Discussion

Westraltrachia limbana has a range that is almost synchronous with that of *W. rotunda*. The latter species ranges slightly further west to Sta. WA-260, north-west of Kundra Bore, while *W. limbana* has been taken near the Margaret River on Fossil Downs Station (WA-266), slightly further east than the Fitzroy River bank limit known for *W. rotunda*. The apparent ecological preference difference between the two species has been discussed above under *W. rotunda*. Range extension to the north-east is possible, but I doubt that there will be significant eastward range extension with further collecting effort.

There is moderate local variation in shell size and shape **(Table 62)**, but too few localities are represented to permit meaningful speculation on the reasons for these shifts, or the variation in umbilical openess. The comparatively limited live collected material, five adults and three juveniles, reflects the fact that in 1976 we were looking in the wrong place to find live material, and that in 1980, collecting in this part of the Kimberley was very poor.

The name *limbana* is taken from the Latin 'limbus' or fringe, referring to the occurrence of this species in a dryer, less felicitous habitat, than that of its near sympatric species *Westraltrachia rotunda*.

Table 62: Local Variation in *Westraltrachia limbana*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
WA-259, NW Two Mile Bore, FMNH 200870	184D	8.49 ± 0.045 (6.6-10.5)	15.35 ± 0.056 (13.6-17.7)	0.553 ± 0.002 (0.473-0.649)
WA-261, SE Two Mile Bore, FMNH 199465	11D	10.42 ± 0.192 (9.35-11.75)	16.55 ± 0.229 (15.05-17.3)	0.630 ± 0.008 (0.596-0.683)
WA-268, 6.2 km E, WA-261, FMNH 200872	7D	9.66 ± 0.313 (8.5-10.7)	15.01 ± 0.299 (13.6-16.0)	0.643 ± 0.012 (0.594-0.695)
WA-585, Brooking Gorge, FMNH 204723	6D	8.52 ± 0.196 (7.7-8.9)	13.40 ± 0.210 (12.7-14.2)	0.636 ± 0.011 (0.606-0.679)
WA-256, Giekie Gorge Ranger Station, FMNH 199620	62D	8.86 ± 0.073 (7.8-10.8)	14.87 ± 0.090 (13.4-16.4)	0.596 ± 0.004 (0.527-0.682)
WA-266, Fossil Downs, FMNH 200201	4L	8.83 ± 0.133 (8.55-9.1)	15.44 ± 0.155 (15.05-15.8)	0.56 ± 0.006 (0.555-0.581)
WA-266, FMNH 199485	237D	8.49 ± 0.046 (6.25-10.3)	15.26 ± 0.065 (12.2-18.0)	0.556 ± 0.002 (0.485-0.654)

Station	Number of Adults Measured	Mean and Range of: Whorls	Umbilical States
WA-259, NW Two Mile Bore, FMNH 200870	184D	5⅛ + (4¾ − − 5⅞ +)	21 open, 153 cracked,10 closed
WA-261, SE Two Mile Bore, FMNH 199465	11D	5 (4¾ + − 5¼ −)	9 cracked, 2 closed
WA-268, 6.2 km E, WA-261, FMNH 200872	7D	4⅞ − (4½ − 5¼ −)	7 cracked
WA-585, Brooking Gorge, FMNH 204723	6D	4⅞ − (4⅝ − 5 +)	2 open, 3 cracked, 1 closed
WA-256, Giekie Gorge Ranger Station, FMNH 199620	62D	5 − (4⅝ − − 5¼ +)	14 open, 48 cracked
WA-266, Fossil Downs, FMNH 200201	4L	5 − (4¾ − 5⅛)	1 open, 3 cracked
WA-266, FMNH 199485	237D	5 + (4¾ − − 5⅜ +)	138 open, 98 cracked, 1 closed

WESTRALTRACHIA RECTA SP. NOV.

(Plates 24a, 32a, 48a-b; Figs 151a-c, 152, 158n)

Comparative remarks

Westraltrachia recta **(Figs 151a-c)** has by far the smallest and most elevated shell within the genus **(Table 47)**, a rounded periphery, and the colour pattern is unusual in that it has an exceptionally wide peripheral white zone with the brownish markings on each side much more sharply delineated than is usual. Only *W. turbinata* **(Figs 117a-c)** from the vicinity of Yammera Gap, Napier Ranges comes close in shell shape, but its open umbilicus **(Table 47)** and near monochrome light colouration contrast immediately with the narrow to closed umbilicus and nearly typical colour pattern of *W. recta*. Neighbouring species, *W. limbana* from Fossil Downs Station (WA-266) **(Figs 146d-f)**, and *W. pillarana* from the Pillara Range, Home Range, and Virgin Hills **(Figs 151d-f)**, both have angulated peripheries, less elevated spires, and are significantly larger in size. Anatomically, *W. recta* **(Figs 152a-b)** has a much shortened penis (P) and vagina (V), quite long spermatheca (S) and free oviduct (UV), while retaining a very large epiphallic loop (E). The penis muscle (PM) is large, and the vas deferens (VD) enters the penis sheath (PS) above the penis head. The principal penis pilaster **(Fig. 158n)** is shortened and strongly sinuated, but apparently without hard edges. *Westraltrachia limbana* **(Figs 149-150)** has a much longer penis, more massive penis muscle, the epiphallic loop is compacted, and the principal penis pilaster **(Fig. 158m)** is much, much larger and retains hard edges. *Westraltrachia pillarana* **(Figs 153-154)** has a very long penis and vagina, greatly reduced penis muscle and epiphallic loop, and the principal penis pilaster **(Fig. 158o)** is much larger and broader.

Holotype

WAM 102.80, Sta. WA-254, Limestone Billy Hills, north-west of Pillara Range, east of Fitzroy Crossing, South-east Kimberley, Western Australia (1:100,000 'Fitzroy Crossing' map sheet 4061, grid reference 914:709). Collected by Alan Solem and Carl Christensen 24 November 1976. Height of shell 9.8 mm, diameter 12.7 mm, H/D ratio 0.772, whorls 4⅞ – , umbilicus with a lateral crack.

Paratopotypes

WAM 13.80, WAM 104.80, FMNH 199590, FMNH 199591, FMNH 200205, 1 live, 113 dead adults, 2 live juveniles from the type locality.

Paratypes

Llaramalura Creek, Fossil Downs, Margaret River, near Fitzroy Crossing, South-east Kimberley (7 dead adults, 1 dead juvenile, AM C.95257 collected by Consett (? Carsett) Davis 20-21 June 1943).

Distribution limits

Westraltrachia recta has been taken from a 150 metre long ridge in the Limestone Billy Hills at Sta. WA-254. Consensus decision of all collectors on both days limited collecting to this ridge. A museum record from Llaramalura Creek, Fossil Downs Station indicates that the range will be expanded by further collecting, although I could not discover this Creek on any map.

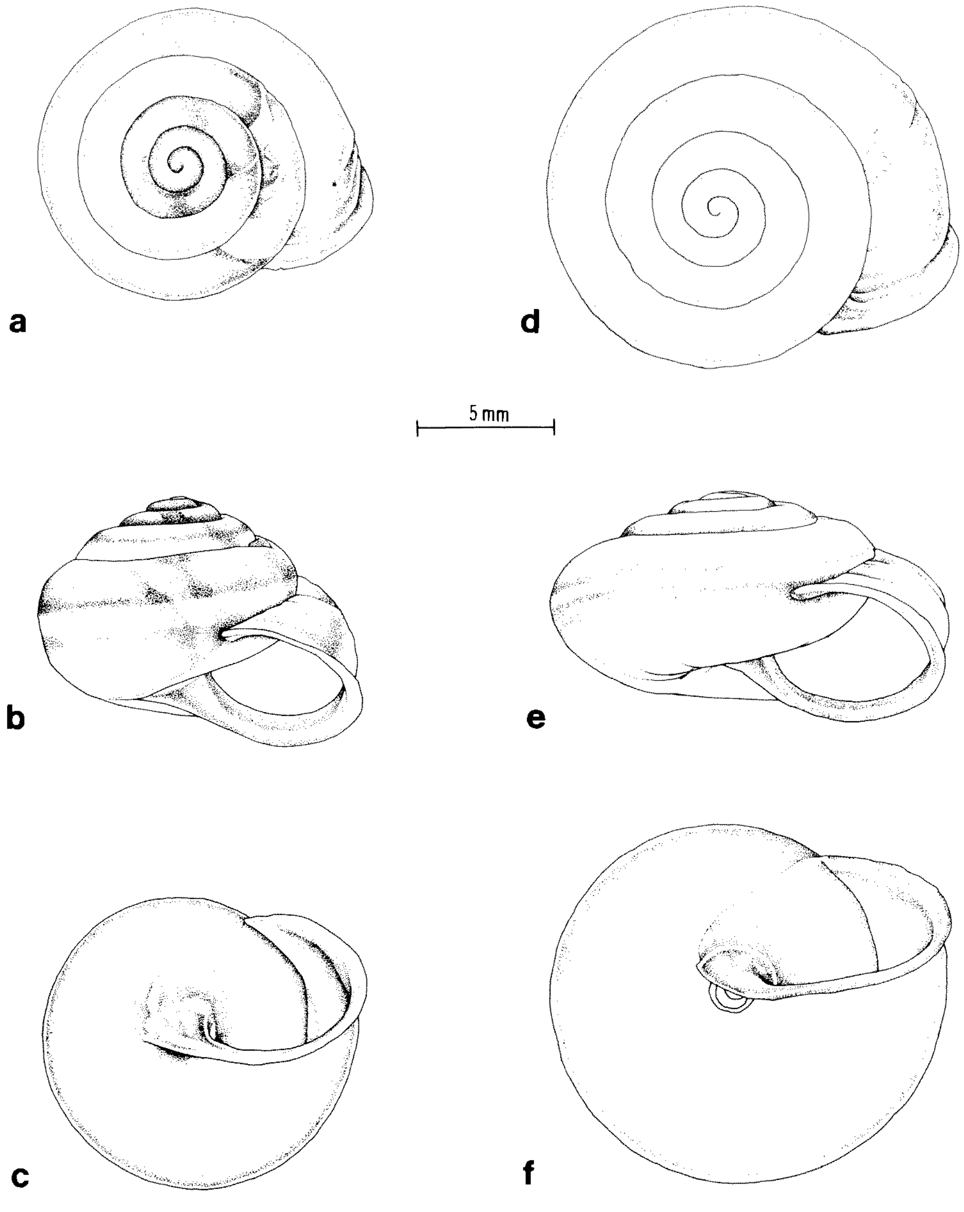


Fig. 151: Shells of *Westraltrachia recta* and *W. pillarana:* (a-c) holotype of *Westraltrachia recta,* Sta. WA-254, Limestone Billy Hills, east of Fitzroy Crossing, WAM 102.80; (d-f) holotype of *Westraltrachia pillarana,* Sta. WA-253, Emanuels Bore, Pillara Range, east of Fitzroy Crossing, WAM 105.80. Scale line equals 5 mm. Drawings by Linnea Lahlum.

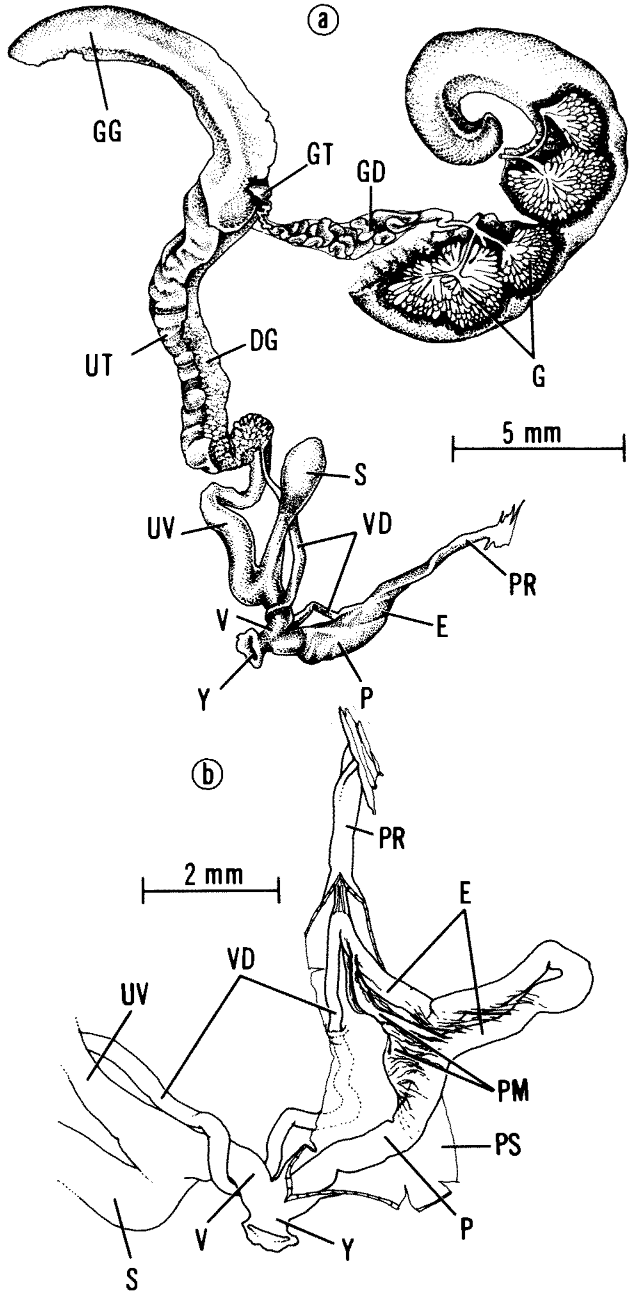


Fig. 152: Genitalia of *Westraltrachia recta:* Sta. WA-254, Limestone Billy Hills, 29 November 1976, FMNH 200205, (a) whole genitalia, (b) interior of penis sheath. Scale lines as marked. Drawings by Linnea Lahlum.

Table 63: Local Variation in *Westraltrachia recta* and *W. pillarana*

Locality	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
W. recta Fossil Downs, AM C.95257	7D	10.62 ± 0.269 (9.9 – 11.9)	12.83 ± 0.230 (12.35 – 13.8)	0.827 ± 0.013 (0.790 – 0.869)
WA-254, Limestone Billy Hills, FMNH 199591	45D	9.76 ± 0.114 (7.55 – 11.75)	12.66 ± 0.104 (10.9 – 14.75)	0.770 ± 0.006 (0.677 – 0.863)
WA-254, FMNH 199590	68D	9.70 ± 0.084 (8.35 – 11.3)	12.70 ± 0.080 (11.55 – 14.6)	0.764 ± 0.005 (0.669 – 0.853)
W. pillarana WA-250, Pillara Spring, FMNH 199468	107D	9.04 ± 0.074 (7.2 – 11.7)	14.50 ± 0.091 (12.35 – 18.1)	0.624 ± 0.003 (0.546 – 0.693)
WA-253, Emanuels Bore, FMNH 200228	12D	8.90 ± 0.202 (7.95 – 10.2)	14.80 ± 0.204 (13.5 – 15.9)	0.602 ± 0.012 (0.553 – 0.675)
WA-251, Menyous Gap, FMNH 199575	28D	9.00 ± 0.124 (7.8 – 10.75)	15.38 ± 0.140 (13.9 – 16.9)	0.585 ± 0.007 (0.528 – 0.650)
1 mi SE Timmy's Bore, WAM 462.77	8D	9.45 ± 0.258 (8.6 – 10.4)	15.38 ± 0.434 (13.75 – 17.1)	0.611 ± 0.009 (0.563 – 0.640)
WA-252, Mt Pierre Creek, Home Range, FMNH 199588	36D	9.16 ± 0.114 (7.9 – 11.0)	14.76 ± 0.134 (12.9 – 17.25)	0.621 ± 0.007 (0.557 – 0.767)
S. side Virgin Hills, WAM 454.77	16D	8.46 ± 0.119 (7.55 – 9.1)	14.56 ± 0.113 (13.75 – 15.8)	0.581 ± 0.010 (0.508 – 0.655)
WA-588, Bob's Bore, Virgin Hills, FMNH 204731	17D	8.01 ± 0.166 (6.85 – 9.2)	14.04 ± 0.202 (12.15 – 15.45)	0.570 ± 0.007 (0.524 – 0.631)
WA-588, FMNH 204730	29L	7.89 ± 0.108 (6.8 – 8.75)	13.88 ± 0.094 (13.0 – 14.75)	0.568 ± 0.006 (0.502 – 0.631)
WA-587, Bob's Bore, Virgin Hills, FMNH 204728	95D	8.50 ± 0.066 (7.2 – 9.8)	14.31 ± 0.072 (12.3 – 15.75)	0.594 ± 0.003 (0.511 – 0.668)
WA-587, FMNH 204727	17L	7.90 ± 0.128 (7.0 – 8.95)	13.77 ± 0.111 (13.2 – 14.6)	0.573 ± 0.007 (0.530 – 0.625)

Table 63: Local Variation in *Westraltrachia recta* and *W. pillarana* (continued)

Locality	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
W. recta Fossil Downs, AM C.95257	7D	4⅞ (4¾ – 5⅛)	100% cracked	
WA-254, Limestone Billy Hills, FMNH 199591	45D	4⅞ (4¼ – – 5¼ +)	4.4% open, 75.6% cracked, 20.0% closed	
WA-254, FMNH 199590	68D	4⅞ (4⅝ – 5⅜)	14.7% open, 64.7% cracked, 20.6% closed	
W. pillarana WA-250, Pillara Spring FMNH 199468	107D	5⅛ (4½ + – 5⅝ –)	0.75 ± 0.028 (0.3 – 1.6)	22.4 ± 0.883 (9.49 – 48)
WA-253, Emanuels Bore, FMNH 200228	12D	5 – (4½ + – 5⅜ –)	1.07 ± 0.074 (0.7 – 1.4)	14.6 ± 1.070 (1.05 – 20.6)
WA-251, Menyous Gap, FMNH 199575	28D	5 – (4¾ – 5⅜)	1.06 ± 0.047 (0.7 – 1.7)	15.2 ± 0.622 (8.77 – 24.1)
1 mi SE Timmy's Bore, WAM 462.77	8D	5⅛ – (4¾ – 5⅜)	1.15 ± 0.108 (0.9 – 1.7)	14.0 ± 0.991 (9.41 – 17.2)
WA-252, Mt Pierre Creek, Home Range, FMNH 199588	36D	5⅛ – (4¾ – 5½)	1.05 ± 0.042 (0.5 – 1.7)	14.8 ± 0.582 (8.9 – 26.6)
S side Virgin Hills, WAM 454.77	16D	4⅞ – (4⅝ – 5⅛ –)	1.24 ± 0.056 (0.95 – 1.8)	12.0 ± 0.484 (8.25 – 15.3)
WA-588, Bob's Bore, Virgin Hills, FMNH 204731	17D	4¾ + (4½ – 5 +)	1.20 ± 0.059 (0.8 – 1.7)	12.1 ± 0.588 (8.53 – 17.6)
WA-588, FMNH 204730	29L	4⅞ – (4½ – – 5⅛)	1.17 ± 0.043 (0.8 – 1.6)	12.3 ± 0.509 (8.59 – 18.4)
WA587, Bob's Bore, Virgin Hills, FMNH 204728	95D	5 – (4½ – 5⅜ +)	1.20 ± 0.024 (0.6 – 1.75)	12.4 ± 0.305 (7.43 – 25.3)
WA-587, FMNH 204727	17L	4⅞ – (4⅝ – – 5 +)	1.21 ± 0.058 (0.85 – 1.8)	11.7 ± 0.529 (7.78 – 15.9)

Diagnosis

Shell very small, 10.9-14.75 mm (mean 12.70 mm) in diameter, with 4¼ – to 5¼ + (mean 4⅞) tightly coiled whorls. Apex and spire strongly and almost evenly elevated, somewhat rounded above, body whorl descending slightly just before aperture **(Fig. 151b)**, height of shell 7.55-11.9 mm (mean 9.78 mm), H/D ratio 0.669-0.869 (mean

0.791). Apical whorls **(Plate 24a)** with radial growth lines, postapical whorls with fine radial micro-riblets and relatively heavy irregular growth lines. Shell periphery **(Fig. 151b)** rounded, without trace of angulation. Lip strongly expanded, columellar section rolled over and nearly covering umbilicus **(Fig 151c)**, which is rarely open (10.5%), sometimes closed (21.2%), and normally consists of a lateral crack (69.3%). Colour typical, except that peripheral white zone is wider, brown markings on each side of zone rather sharply delineated, and spire relatively lightly variegated. Based on 121 measured adults.

Genitalia **(Figs 152a-b)** with prominent penis muscle (PM) and long epiphallic loop (E). Principal penis pilaster **(Fig. 158n)** short, apically broad, tapering anteriorly, without hard edges. Penis (P) very short. Penis sheath (PS) with basal part of wall thickened. Vas deferens (VD) entering penis sheath above head of penis. Vagina (V) short, spermatheca (S) with rather long shaft, free oviduct (UV) quite long and sinuated.

Jaw **(Plate 32a)** typically camaenid, with very prominent vertical ribs. Marginal teeth of radula typical, central and lateral teeth **(Plate 48a-b)** without ectocones, mesoconal shaft slightly elevated, tip bluntly rounded and slightly curved, degree of rounding and curvature exaggerated in **Plate 48a** because worn teeth were photographed.

Discussion

Two trips were made into the Limestone Billy Hills in an effort to obtain some live material of *Westraltrachia recta*. The result was one live adult and two live juveniles after about eight person-hours on nearly barren slopes in mid-day sunlight. The area is without tree cover and only scattered low brush provided minimum shade for snails. This station (WA-254) presented as inhospitable a 'positive' snail locality as we have sampled in the entire Kimberley.

Current maps do not include the name Llaramalura Creek near Fossil Downs Station, and its precise locality is unknown to me. The specimens are subfossil, and distinctly more elevated than the type populations **(Table 63)**, but probably conspecific. Material of *W. limbana* was taken at the same station.

The name *recta*, from the Latin 'rectus', upright or proper, refers whimsically both to the high-spired shell and the typical *Westraltrachia* anatomy, despite the almost rhagadoid shell appearance.

WESTRALTRACHIA PILLARANA SP. NOV.

(Plates 24b, 32b, 48c-e; Figs 151d-f, 153, 154, 158o)

Comparative remarks

Westraltrachia pillarana **(Figs 151d-f)** has a weakly angulated periphery, narrowly open umbilicus, normal colour pattern, relatively low spire, and is average in size and shape **(Table 47)**. *Westraltrachia recta*, from the Limestone Billy Hills to the east **(Figs 151a-c)**, immediately differs in its small size **(Table 47)**, rounded periphery, closed umbilicus and wide peripheral white zone. *Westraltrachia ascita* **(Figs 155d-f)** also has a rounded periphery, more open umbilicus, and is much smaller in size **(Table 47)**, but differs most obviously in its very prominent shell microsculpture **(Plate 25a, c, d)**. The most similar species are *W. limbana* **(Figs 146d-f)**, which differs in umbilicus and proportions, and *W. lievreana* **(Figs 143a-c)**, which differs in its nearly monochrome colouration and many details of anatomical structure. Anatomically, *W. pillarana* **(Figs 153-154)** has both the epiphallic loop (E) and the penis muscle (PM) greatly reduced, the penis (P) generally long, slender, and kinked, the penis sheath (PS) with rather thick wall, and the vas deferens (VD) entering the sheath at the penis mid-point or above. The principal penis pilaster **(Fig. 158o)** is short and quite broad, strongly sinuated. The vagina (V) generally is quite long, spermatheca usually long and bound by fibers to base of prostate-uterus, and the free oviduct (UV) does not differ significantly in length from the spermatheca. *Westraltrachia ascita* **(Figs 156a-b)** has a huge glandular-muscle bulge on the penis-epiphallus head, the entire penis complex shortened, and the principal penis pilaster **(Fig. 158p)** shorter and narrower. *Westraltrachia limbana* **(Figs 149-150)** has a larger epiphallic loop and penis muscle, much larger and longer principal penis pilaster that retains hard edges **(Fig. 158m)**, and the vagina is much shorter. *Westraltrachia lievreana* **(Figs 144a-b)** has a proportionately enormous epiphallic loop, very small and slightly sinuated principal pilaster **(Fig. 158k)**, and very short vagina.

Holotype

WAM 105.80, Sta. WA-253, gulches 0.5 km west of Emanuels Bore, Pillara Range, east of Fitzroy Crossing, South-east Kimberley, Western Australia (1:100,000 'Fitzroy Crossing' map sheet 4061, grid reference 992:643). Collected by Alan Solem, Laurie Price, and Carl Christensen 24 November 1976. Height of shell 9.0 mm, diameter 15.45 mm, H/D ratio 0.583, whorls 4¾+, umbilical width 0.85 mm, D/U ratio 18.2.

Paratopotypes

WAM 106.80, FMNH 200228-9, 3 live, 11 dead adults, 2 dead juveniles from the type locality.

Paratypes

Pillara Range: Sta. WA-250, gulches 1 km south-east of Pillara Spring ('Fitzroy Crossing' 4061 – 953:681) (107 dead adults, 1 live juvenile, WAM 113.80, FMNH 199468, FMNH 200593); Sta. WA-251, east side Menyous Gap ('Fitzroy Crossing' 4061 – 998:667) (28 dead adults, WAM 108.80, FMNH 199575).

Home Range: one mile south-east of Timmy's Bore ('Fitzroy Crossing' 4061 – *ca.* 080:570) (8 dead adults, WAM 462.77, collected by George Kendrick 2 August 1967); Sta. WA-252, gulch south of bore west of Mount Pierre Creek ('Fitzroy Crossing' 4061 – 115:566) (36 dead adults, WAM 107.80, FMNH 199588).

Virgin Hills: hills one mile south of Virgin Creek Bore, south side ('Bruten' 4060 – *ca.* 013:470) (1 dead adult, WAM 448.77 collected by K. G. Buller and George Kendrick 17 July 1967); "The Sphinx", south side of Virgin Hills ('Bruten' 4060 – 069:505) (16 dead adults, 1 dead juvenile, WAM 454.77 collected by George Kendrick 1 August 1967); Sta. WA-588, south face of Virgin Hills, 1 km west of Bob's Bore ('Bruten' 4060 – 080:504) (29 live, 17 dead adults, 7 live juveniles, WAM 111.80-112.80, FMNH 204730-1); Sta. WA-587, south face of Virgin Hills, just north of Bob's Bore ('Bruten' 4060 – 087:500) (17 live, 95 dead adults, 4 live juveniles, WAM 109.80-110.80, FMNH 204727-8).

Distribution limits

Westraltrachia pillarana has a known south-east to north-west range of 20 km between WA-250 in the Pillara Range and WA-252 in the Home Range, which might be extended to 25 km if all exposed rocks areas are inhabitable. On the east, its range extends south through the Virgin Hills to just south of Virgin Creek Bore, a distance of about 10 km, although much of this area is open plains and thus snail free habitat.

Diagnosis

Shell of average size, 12.15-18.1 mm (mean 14.48 mm) in diameter, with 4½ – to 5⅝ – (mean 5) normally coiled whorls. Apex and spire moderately and evenly elevated, rarely rounded above, body whorl descending slightly before aperture **(Fig. 151e)**, height of shell 6.8-11.7 mm (mean 8.70 mm), H/D ratio 0.502-0.767 (mean 0.601). Apical whorls **(Plate 24b)** typical, postapical sculpture without unusual features. Shell periphery **(Fig 151e)** slightly to moderately angulated. Lip strongly reflected, moderately expanded, columellar section rolled. Umbilicus **(Fig. 151f)** narrowly open, umbilical width 0.3-1.8 mm (mean 1.04 mm), D/U ratio 7.43-48 (mean 15.8). Colour typical, peripheral zone and shell base white, spire variegated, brownish zones above and below periphery. Based on 368 measured adults.

Genitalia **(Figs 153-154)** with great reduction of the penis muscle (PM) and shortening of the epiphallic loop (E). Principal penis pilaster **(Fig. 158o)** broad, strongly sinuated, without hard edges. Penis sheath (PS) with rather thick walls, vas deferens (VD) entering sheath at or above mid-point of penis. Penis (P) generally long, kinked, differentiation into epiphallic and penis sections obscured by reduction in penis muscle. Vagina (V) variable in length, from quite long **(Fig. 153a)** to somewhat shorter **(Fig. 154a)**. Spermatheca (S) long **(Figs 153a, 154a)** to short **(Fig. 154b)**, free oviduct (UV) slightly shorter **(Fig. 153a)** to longer **(Fig. 154b)** than spermatheca.

Jaw **(Plate 32b)** typically camaenid, with prominent vertical ribs. Radula with typical marginal teeth **(Plate 48e)**, multicuspid, varying in cusp angle from 45° (early) to parallel to basal membrane (outer). Central and lateral teeth **(Plate 48c-d)** without ectocones, anterior flare prominent, basal plate interlock system typical, mesoconal shaft angle increased slightly, mesoconal cusp bluntly rounded and very slightly curved.

Discussion

Westraltrachia pillarana has a rather extensive geographic range **(Fig. 162)** that is basically continuous through the Pillara and Home Ranges, then patchy among the isolated knobs of the Virgin Hills. To the south, it is replaced by *W. ascita*, which extends south-east to Sta. WA-370, near Lloyd Hill in the Laidlaw Ranges, which in turn is replaced to the east in the Laidlaw and Lawford Ranges by *W. ampla*. To the west, *W. recta* replaces it in the Limestone Billy Hills. The actual boundary between *W. pillarana* and *W. ascita* occurs near Virgin Creek Bore **(Fig. 162)**, as K. G. Buller and George Kendrick collected one long dead and broken adult (WAM 448.77) of the former and seven long dead and weathered adults (WAM 452.77) of the latter 'ca one mile south' on 17 July 1967. The specimen of *W. pillarana* was barely identifiable, and the question as to which is extant at this location (if either) remains to be determined.

Size and shape variation is comparatively minor **(Table 63)**. Specimens from Sta. WA-250 do have a narrower umbilicus. The samples from near Bob's Bore, collected

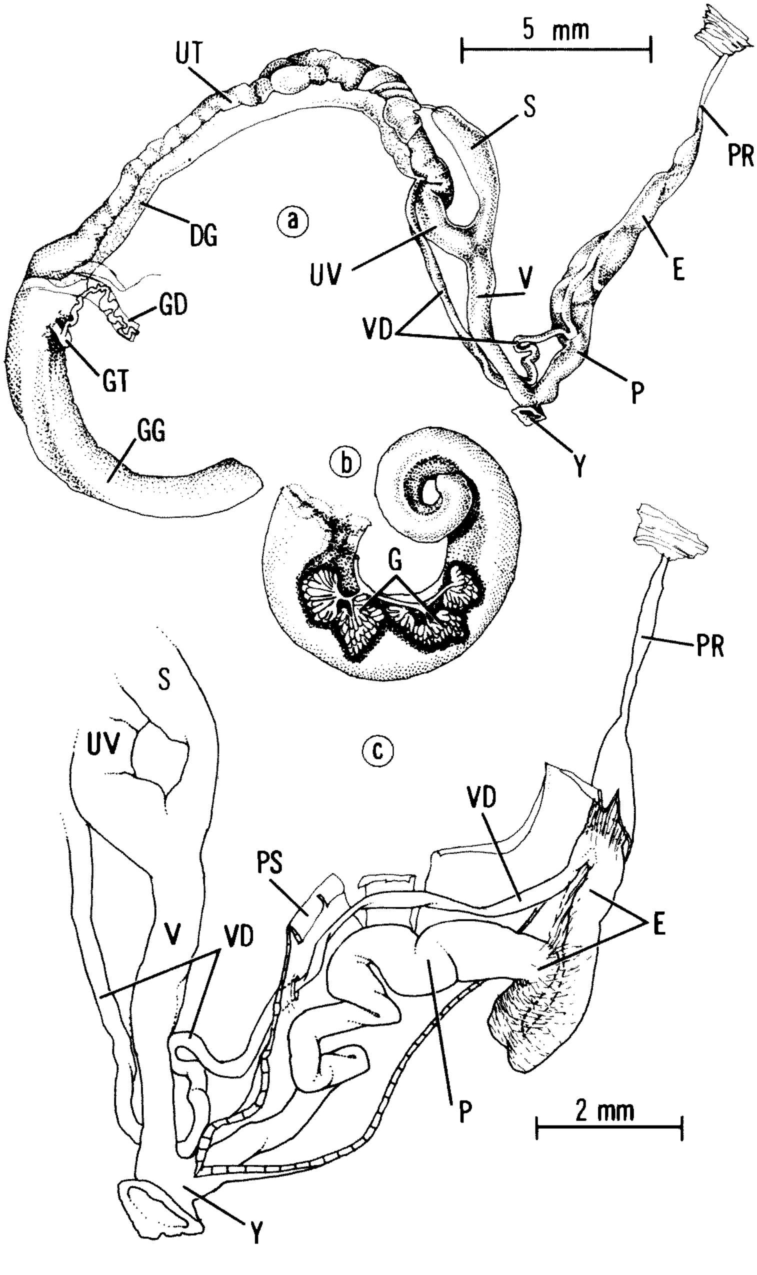


Fig. 153: Genitalia of *Westraltrachia pillarana:* Sta. WA-253, Emanuels Bore, Pillara Range, east of Fitzroy Crossing, 24 November 1976, FMNH 200229, paratopotypes, Dissection A, (a) whole genitalia, (b) ovotestis, (c) interior of penis sheath. Scale lines as marked. Drawings by Linnea Lahlum.

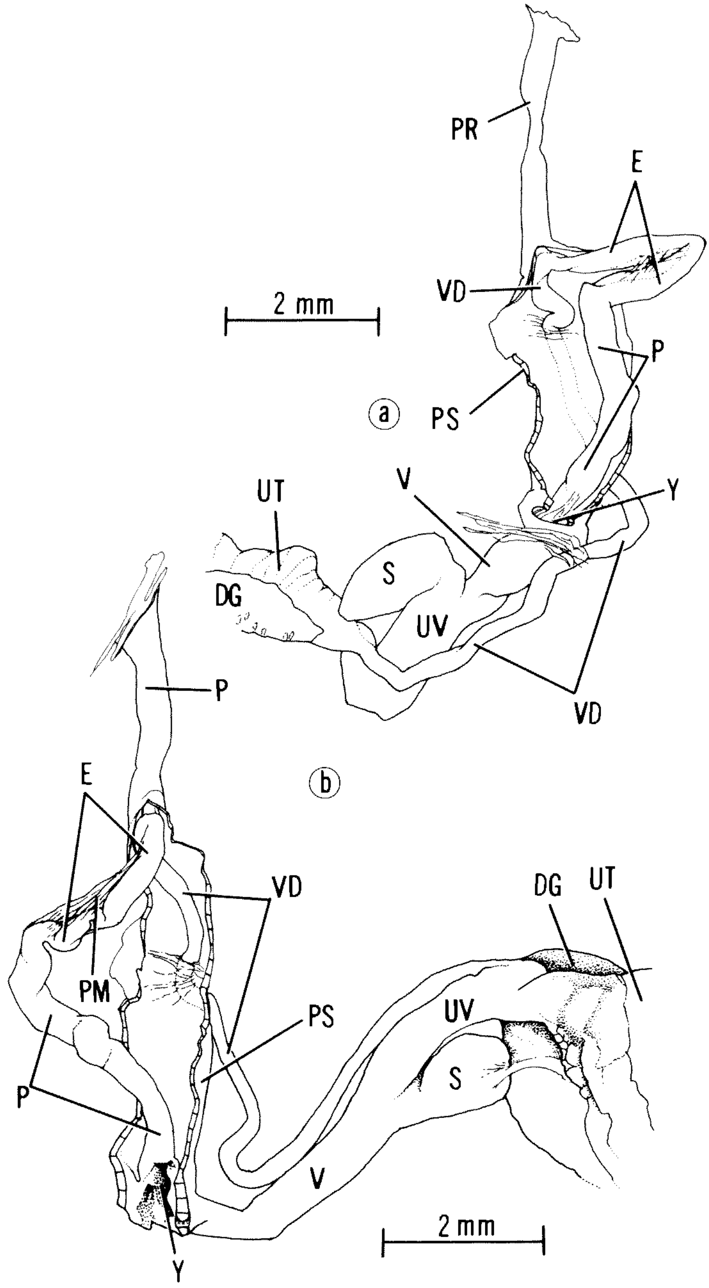


Fig. 154: Interior of penis sheath in *Westraltrachia pillarana:* Sta. WA-587, Virgin Hills, east of Fitzroy Crossing, 9 May 1980, FMNH 204727, paratypes, (a) Dissection A, (b) Dissection B. Scale lines equal 2 mm. Drawings by Linnea Lahlum.

in 1980, included a number of live examples. At Sta. WA-587, the live adults were clearly smaller than dead adults, but the difference at WA-588 is not significant.

At both of the Stations near Bob's Bore, a high percentage of live adults were taken under bushes in very thin talus, rather than in deeper talus near the rock outcrops. All individuals taken live at this time were unusual in having multiple epiphragms, a maximum of 14 counted from a single shell during processing. This probably correlates with both the more exposed aestivation site and the stations being on the absolute southern fringes of snail inhabitable area.

Observed anatomical variation **(Figs 153-154)** was greater than found in other species of *Westraltrachia,* and may correlate with the non-continuous nature of colonies within the range of *W. pillarana.* Dissection A **(Fig. 154a)** from Sta. WA-587, is of an individual that was both retracted into the shell and had the terminal genitalia slightly everted. The short and thick vagina (V), twisted spermatheca (S) and apparently shortened penis (P) may thus be in part artifacts of death and perspective, but may be indicative of actual variation. This set of material did not relax properly and proved difficult to dissect. There is much more agreement between Dissection B **(Fig. 154b)** from Sta. WA-587 and the specimen from Sta. WA-250 **(Fig. 153b)** in terms of penis complex structures.

All dissected *Westraltrachia pillarana* agree in having massive reduction of the penis muscle **(Figs 153b, 154a-b).** Indeed, there are no strands of muscle directly connecting the strands that still bind the arms of the epiphallic loop together with the penial retractor muscle (PR). The epiphallic loop itself appears reduced in size. I consider this to be an independent experiment in reduction of complexity in this region. It contrasts with the patterns found in the neighbouring *W. ascita* **(Fig. 156b)** and the related genera from the East Kimberley and Northern Territory (see *Ordtrachia* and *Exiligada* Iredale, 1939, **Figs 167-170, 173, 175).**

The name *'pillarana'* is taken from the Range where the type specimens were collected.

WESTRALTRACHIA ASCITA SP. NOV.

(Plates 25, 32e, 49; Figs 155d-f, 156, 158p)

Comparative remarks

Westraltrachia ascita **(Figs 155d-f)** is immediately recognisable by its only slightly angulated periphery, tightly coiled whorls, open umbilicus, very small size, and microsculpture of fine periostracal projections **(Plate 25a, c, d).** This microsculpture is duplicated only by *W. froggatti froggatti* (Ancey, 1898) and *W. f. complanata* **(Plate 20c-f),** but these taxa differ in their flat sided whorls, very sharply angulated periphery, more loosely coiled whorls, and massive reflected lip **(Figs 122a-f).** *Westraltrachia ampla* **(Figs 155a-c),** from the Emanuel, Laidlaw and Lawford Ranges, has normal coiling, is narrowly umbilicated at most, averages 5.6 mm more in diameter, and lacks the microsculpture. *Westraltrachia pillarana* **(Figs 151d-f),** from the Virgin Hills, Pillara and Home Ranges, lacks the microsculpture, is very narrowly umbilicated, significantly larger **(Table 47),** and has typical colour pattern on the shell.

Anatomically, *W. ascita* **(Figs 156a-b)** has a reduced epiphallic loop (E). The penis muscle (PM) is separated from the penial retractor muscle (PR) and has begun to fuse with a glandular zone on the penis-epiphallic junction. The principal penis pilaster **(Fig. 158p)** is short, broad, strongly sinuated, high and narrow. The penis (P) is very short and slender. The vagina (V) is of medium length, the spermatheca (S) rather long, and the free oviduct (UV) is slightly longer than the spermatheca. The changes in the penis muscle and the very short penis are the diagnostic features. Comparisons are thus limited to neighbouring taxa. *Westraltrachia pillarana* **(Figs 153-154)** has a greatly reduced penis muscle, the penis is much longer and kinked within the sheath, and the principal penis pilaster **(Fig. 158o)** is much larger and thicker. *Westraltrachia ampla* **(Figs 157a-b)** has a massive penis muscle and a medium sized epiphallic loop, the penis is much longer and kinked, and the free oviduct is proportionately much longer. The principal penis pilaster **(Fig. 158q)** is narrow, tightly sinuated and much longer.

Holotype

WAM 149.80, Sta. WA-370, 3.4 km north of Lloyd Hill summit, west side of Laidlaw Range, east of Fitzroy Crossing, South-east Kimberley, Western Australia (1:100,000 'Bohemia' map sheet 4160, grid reference 852:359). Collected by Laurie Price and Carl Christensen 13 February 1977. Height of shell 6.35 mm, diameter 11.8 mm, H/D ratio 0.538, whorls 4⅝+, umbilical width 1.55 mm, D/U ratio 7.61.

Paratopotypes

WAM 150.80, WAM 151.80, FMNH 199164, FMNH 200182, 1 live, 112 dead adults, 6 live juveniles from the type locality.

Paratypes

Hills *ca.* 1 mile south of site of Virgin Creek Bore, Virgin Creek (7 dead adults, WAM 452.77 collected by K. G. Buller and George Kendrick 17 July 1967); *ca.* 3 miles south-east from site of Virgin Creek Bore, Gogo Station (20 dead adults, WAM 446.77, FMNH 205371, collected by K. G. Buller and George Kendrick 18 July 1967); hills 3.1 miles south from site of Virgin Creek Bore, Gogo Station (13 dead adults, WAM 451.77, FMNH 205372 collected by K. G. Buller July 1967); Prices Hill, Gogo Station (10 dead adults, WAM 453.77 collected by K. G. Buller 13 July 1963); Emanuel Creek, Gogo Station (5 dead adults, WAM 447.77 collected by D. Cliff and George Kendrick 7 August 1967); Sadler Ridge, ¼ mile south of Long's Well, Gogo Station ('Bruten' 4060 – *ca.* 128:386) (8 dead adults, WAM 459.77 collected by K. G. Buller and George Kendrick 21 July 1967).

Distribution limits

Dead specimens of *Westraltrachia ascita* **(Fig. 162)** have been taken from near Virgin Creek Bore, south of the Virgin Hills, to near Lloyd Hill summit in the Laidlaw Range (Sta. WA-370), an air distance of about 21 km. The only live material is from WA-370, which leaves open the question as to the actual range of extant populations.

Diagnosis

Shell very small, 10.35-15.4 mm (mean 12.59 mm) in diameter, with 4⅜ to 5½ (mean 4⅞+) tightly coiled whorls. Apex and spire moderately and evenly elevated, rarely rounded above, last whorl descending moderately just before aperture **(Fig. 155e),**

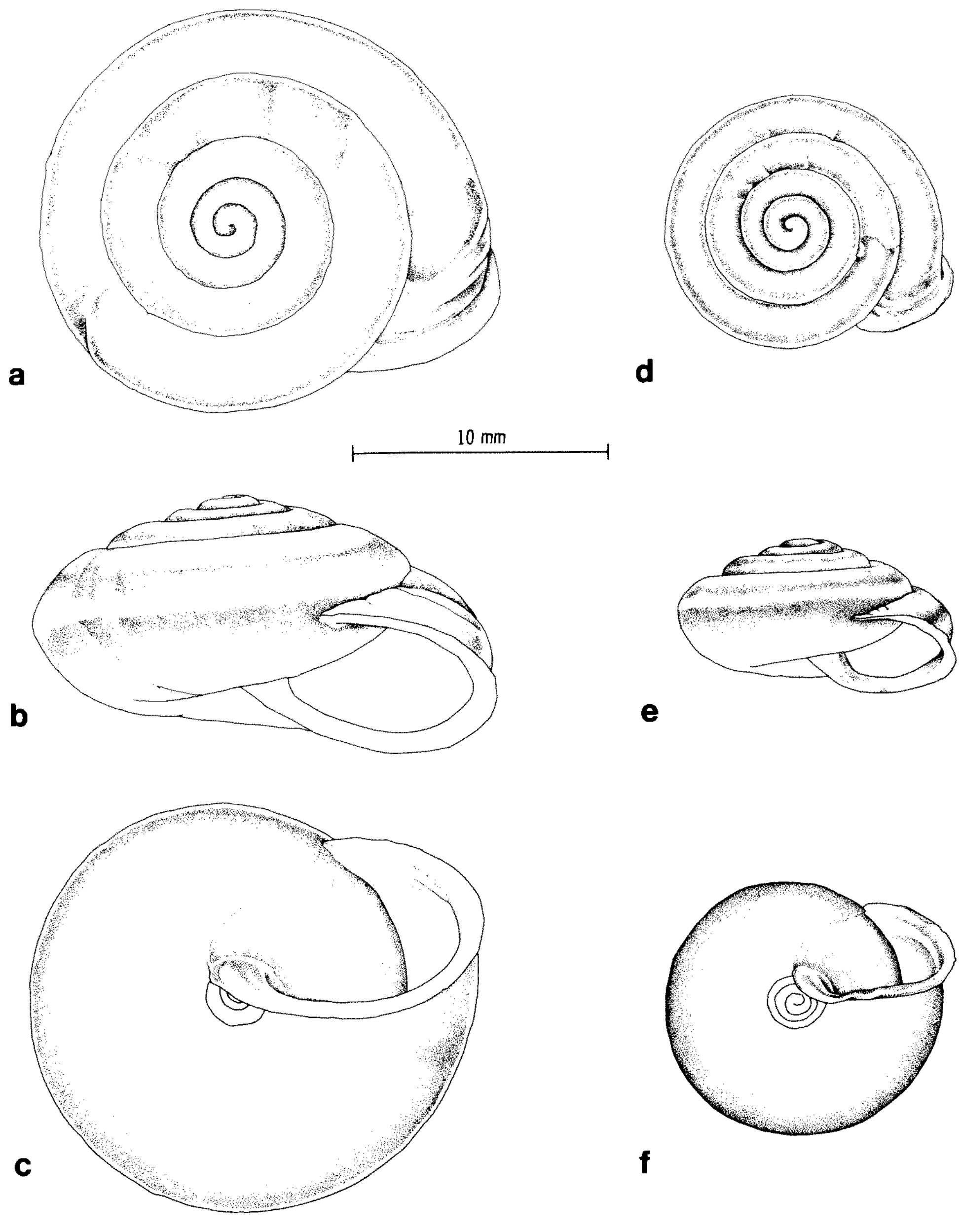


Fig. 155: Shells of *Westraltrachia ampla* and *W. ascita:* (a-c), holotype of *Westraltrachia ampla*, Sta. WA-369, west side Laidlaw Range, WAM 93.80; (d-f) holotype of *Westraltrachia ascita*, Sta. WA-370, north of Lloyd Hill summit, west side Laidlaw Range, WAM 149.80. Scale line equals 10 mm. Drawings by Linnea Lahlum.

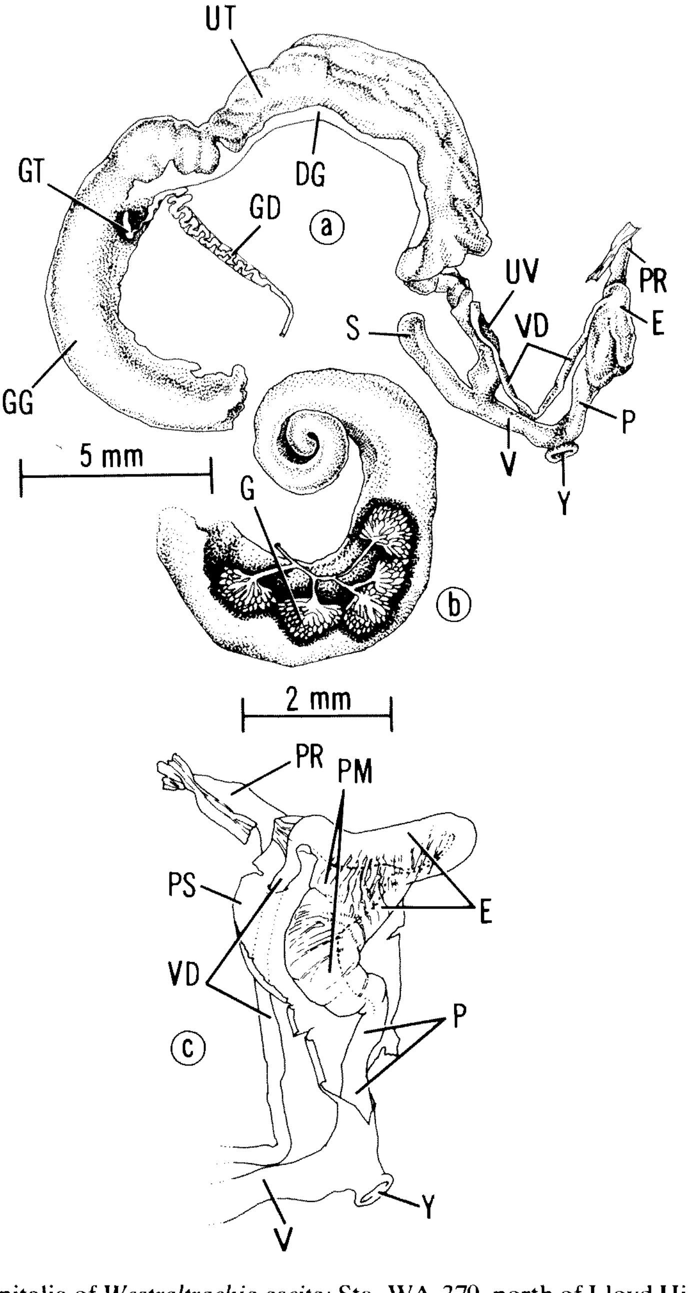


Fig. 156: Genitalia of *Westraltrachia ascita:* Sta. WA-370, north of Lloyd Hill, Laidlaw Range, 13 February 1977, FMNH 200182, Dissection A, (a) whole genitalia, (b) ovotestis, (c) interior of penis sheath. Scale lines as marked. Drawings by Linnea Lahlum.

height of shell 5.65-8.8 mm (mean 6.88 mm), H/D ratio 0.485-0.603 (mean 0.544). Apical whorls (**Plate 25a-b**) typical. Postapical sculpture (**Plate 25a c-d**) of fine radial growth striae on which is superimposed rows of pointed periostracal extensions, which rise on top of dense pustulations in the calcareous shell layers. Microsculpture reduced or absent below periphery or on shell base. Shell periphery at most obtusely angulated (**Fig. 155b**), sometimes rounded, never keeled. Lip strongly and narrowly expanded, columellar section slightly rolled. Umbilicus moderately open, partly covered by columellar lip, umbilical width 0.8-2.0 mm (mean 1.40 mm), D/U ratio 6.11-16.9 (mean 9.30). Colour pattern altered in that periostracum, when present, is relatively dark and gives a monochrome appearance. When the periostracum is partly worn off, the normal pattern appears except that spire variegation is reduced, and the brown zones around the white periphery are rather sharply delineated. Based on 177 measured adults.

Genitalia (**Figs 156a-b**) with penis muscle (PM) separated from penial retractor muscle (PR) and partly fused into a glandular zone on the penis-epiphallic junction. Epiphallic loop somewhat reduced. Principal penis pilaster (**Fig. 158p**) short, very broad, strongly sinuated, narrow. Penis very short, not kinked within very thin-walled penis sheath (PS). Vas deferens (VD) entering sheath near apex. Vagina (V) medium in length, spermatheca (S) long, only slightly exceeded in length by free oviduct (UV).

Jaw (**Plate 32e**) typically camaenid, with very prominent vertical ribs. Radula with typical marginal teeth (**Plate 49d**) and latero-marginal transition (**Plate 49c).** Central and lateral teeth (**Plate 49a-b**) without ectocones, anterior basal flare and row interlock system prominent. Mesoconal shaft elevated above 60° angle, tip slightly curved and bluntly rounded.

Discussion

Westraltrachia ascita, at optical levels of examination, very closely approaches the shell appearance of species assigned to the Red Centre genus *Semotrachia* Iredale, 1933. The latter genus, under SEM study, has periostracal extensions as pointed hairs (Solem, In preparation), and very different genital anatomy, but the convergence in shell appearance is remarkable.

Local variation in *Westraltrachia ascita* (**Table 64**) is fairly substantial in respect to diameter and umbilical size, with the single Lawford Range sample (WA-370) being smaller and more widely umbilicated. The Sadler Ridge sample is intermediate, and the largest specimens come from an unspecified locality along Emanuel Creek. Only one live adult and six live juveniles are known, all from near Lloyd Hill, Lawford Range. More field work in the Virgin Hills through Emanuel Range area is required to determine whether the eastern records are based on extinct or extant populations.

Dissection of the single live collected adult established that *Westraltrachia ascita* belongs in this genus, and provided important evidence as to the direction of character changes in the evolution of the penis muscle-epiphallic loop complex. The separation of the penis muscle from the penial retractor muscle, amalgamation of the penis muscle into a muscle-glandular area in the penis-ephiphallic junction, and start in reduction of the epiphallic loop itself are clearly intermediate between the typical conditions of *Westraltrachia* and the major alterations found in *Ordtrachia* and *Exiligada* Iredale, 1939. This is discussed in detail elsewhere (p. 698).

Table 64: Local Variation in *Westraltrachia ascita*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
Hills 1 mi S of Virgin Bore, WAM 452.77	7	7.15 ± 0.216 (6.5 – 8.0)	12.81 ± 0.246 (12.3 – 13.75)	0.557 ± 0.007 (0.528 – 0.584
3 mi SE of Virgin Bore, WAM 446.77	20	7.23 ± 0.119 (6.3 – 8.05)	13.07 ± 0.159 (12.1 – 14.85)	0.553 ± 0.005 (0.514 – 0.594)
Hills 3.1 mi S of Virgin Creek Bore, WAM 451.77	13	7.51 ± 0.115 (6.7 – 8.1)	13.91 ± 0.199 (12.7 – 15.1)	0.540 ± 0.005 (0.515 – 0.563)
Prices Hill, WAM 453.77	10	7.18 ± 0.143 (6.65 – 8.0)	13.13 ± 0.261 (12.2 – 14.5)	0.547 ± 0.007 (0.496 – 0.580)
Emanuel Creek, WAM 447.77	5	8.20 ± 0.185 (7.7 – 8.8)	14.58 ± 0.256 (13.85 – 15.4)	0.563 ± 0.011 (0.536 – 0.603)
Sadler Ridge, WAM 459.77	8	7.20 ± 0.106 (6.75 – 7.65)	13.31 ± 0.277 (12.3 ± 14.25)	0.542 ± 0.006 (0.519 ± 0.573)
WA-370, Lawford Range, FMNH 199164	113	6.62 ± 0.037 (5.65 – 7.7)	12.15 ± 0.116 (10.35 – 14.0)	0.541 ± 0.002 (0.485 – 0.591)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
Hills 1 mi S of Virgin Bore, WAM 452.77	7	4 7/8 + (4 3/4 – 5 1/8)	1.34 ± 0.108 (0.95 – 1.6)	10.0 ± 0.987 (7.69 – 14.4)
3 mi SE of Virgin Bore, WAM 446.77	20	5 – (4 5/8 – 5 1/4)	1.34 ± 0.058) (0.8 – 1.75)	10.15 ± 0.538 (7.41 – 16.9)
Hills 3.1 mi S of Virgin Creek Bore, WAM 451.77	13	5 1/8 (5 – 5 3/8)	1.40 ± 0.077 (0.9 – 1.7)	10.34 ± 0.589 (8.38 – 14.4)
Prices Hill, WAM 453.77	10	5 + (4 7/8 – – 5 3/8)	1.34 ± 0.081 (0.95 – 1.8)	10.02 ± 0.509 (7.69 – 12.8)
Emanuel Creek, WAM 447.77	5	5 1/4 (5 1/8 – – 5 3/8)	1.23 ± 0.124 (0.9 – 1.6)	12.38 ± 1.304 (9.22 – 15.9)
Sadler Ridge, WAM 459.77	8	5 + (4 7/8 – 5 1/2 –)	1.47 ± 0.060 (1.2 – 1.65)	9.15 ± 0.355 (7.46 – 10.6)
WA-370, Lawford Range, FMNH 199164	113	4 7/8 – (4 3/8 – 5 1/8)	1.43 ± 0.022 (0.9 – 2.2)	8.79 ± 0.140 (6.11 – 13.2)

The very high elevation of the mesoconal cusp on the central and lateral teeth of the radula **(Plate 49a-b)**, combined with the rounding and slight curvature of the tip, suggest that this species makes use of the seasonal seepage face films on the limestone exposures.

The name *ascita* comes from the Latin 'ascitus' for alien, foreign, or strange, and refers to the unusual microsculpture, shell shape, and general form of this species in comparison with other *Westraltrachia*.

WESTRALTRACHIA AMPLA SP. NOV.

(Plates 24c, 32c-d, 50; Figs 155a-c, 157, 158q)

Comparative remarks

Westraltrachia ampla **(Figs 155a-c)** has an obtusely angulated periphery, barely open to cracked umbilicus, normal colour pattern, is very large **(Table 47),** and with typical sculpture. The neighbouring *W. ascita* **(Fig. 155d-f)** is one of the smallest species, has very distinctive microsculpture **(Plate 25a, c-d),** an open umbilicus, and much tighter whorl coiling. *Westraltrachia pillarana* **(Figs 151d-f)** agrees in shape, umbilicus, colour, and coiling pattern, but averages 3.7 mm less in size, and shows many anatomical differences. The other large species are *W. woodwardi* (Fulton, 1902) **(Figs 111a-i)** from west of Barker Gorge in the Napier Range, and *W. oscarensis* (Cox, 1892) **(Figs 136a-f)** from the eastern Napier and western Oscar Ranges. The former differs in its globose shape, closed umbilicus, white colour on the lower spire and body whorl, plus the very broadly expanded shell lip; the latter in its rounded periphery, at times almost purplish colour, and many anatomical features. Anatomically, *W. ampla* **(Figs 157a-b)** has a very large penis muscle (PM) and reduced epiphallic loop (E), the principal penis pilaster **(Fig. 158q)** is narrow, long, highly convoluted, and without hard edges. Penis (P) long, slender, slightly kinked, base of penis sheath (PS) with slightly thicker wall. Entrance of vas deferens (VD) into penis sheath opposite head of penis. Vagina (V) slightly longer than average, spermatheca (S) relatively long, free oviduct (UV) much longer than spermatheca and strongly curved. *Westraltrachia ascita* **(Figs 156a-b)** has the penis muscle greatly altered, and the penis very short. *Westraltrachia pillarana* **(Figs 153-154)** has a very long penis and vagina, greatly reduced epiphallic loop and penis muscle, plus a much broader and larger principal penis pilaster. *Westraltrachia oscarensis* (Cox, 1892) **(Figs 137a-c)** has a much longer penis, huge epiphallic loop, extremely long vagina, and the principal penis pilaster **(Fig. 158h)** is reduced to a narrow, low, slightly sinuated ridge. *Westraltrachia woodwardi* (Fulton, 1902) **(Figs 112-114)** has a very different principal penis pilaster, which retains hard edges, and quite different relative sizes of the genital organs. Both of the Napier Range taxa differ dramatically in the structure of their central and lateral teeth **(Plates 33, 34, 41).**

Holotype

WAM 93.80, Sta. WA-369, 1.4 km east-south-east of Lloyd Hill Summit, west side of Laidlaw Range, South-east Kimberley, Western Australia (1:100,000 'Bohemia' map sheet 4160, grid reference 863:321). Collected by Carl Christensen and Roger Buick 13 February 1977. Height of shell 10.8 mm, diameter 18.5 mm, H/D ratio 0.584, whorls 5⅛−, umbilical width 1.25 mm, D/U ratio 14.8.

Paratopotypes

WAM 94.80, FMNH 199163, FMNH 200270, 43 dead adults, 1 live juvenile from the type locality.

Paratypes

Laidlaw Range, geographic sequence north to south; Sta. WA-371, 2.0 km north-north-east of Lloyd Hill summit, west side of Laidlaw Range, 100 km east of Fitzroy Crossing ('Bohemia' 4160 – 857:342) (14 dead adults, WAM 97.80, FMNH 199165); Sta. WA-372, east slope of Lloyd Hill, west side of Laidlaw Range ('Bohemia' 4160 – 851:325) (28 dead adults, WAM 92.80, FMNH 199166); Sta. WA-368, 2.0 km north-north-west of Ross Hill, east side of Laidlaw Range ('Bohemia' 4160-870:322) (39 dead adults, WAM 95.80, FMNH 199161). Lawford Range, geographic sequence north to south: Sta. WA-367, south-west side of Galeru Gorge, west side of Lawford Range, 110 km east of Fitzroy Crossing ('Bohemia' 4160 – 922:393) (5 dead adults, WAM 91.80, FMNH 199160); Sta. WA-366, canyon 4.9 km south of Galeru Gorge, west side of Lawford Range ('Bohemia' 4160 – 908:349) (56 dead adults, 5 live juveniles, WAM 100.80, FMNH 199159, FMNH 200276); Sta. WA-365, *ca.* 1 km downstream from Jones Spring, canyon west side of Lawford Range ('Bohemia' 4160 – 896:285) (22 dead adults, WAM 88.80, FMNH 199158); Sta. WA-363, slope below entrance to Nardji Cave, Lawford Range ('Bohemia' 4160 – 902:277) (57 dead adults, WAM 98.80, FMNH 199152); Sta. WA-364, narrow gorge where Mimbi Creek enters east side of Lawford Range ('Bohemia' 4160 – 915:279) (36 dead adults, WAM 90.80, FMNH 199156); Sta. WA-282, Mimbi Creek, south-south-west of Nardji Cave, Lawford Range ('Bohemia' 4160 – 908:273 est.) (6 dead adults, WAM 101.80, FMNH 199497); Sta. WA-374, vicinity of cave, Mimbi Creek, south-east side of Lawford Range ('Bohemia' 4160 – 905:269) (7 dead adults, WAM 99.80, FMNH 199319).

Emanuel Range, geographic sequence east to west: Sta. WA-375, south-east side of Emanuel Range, 2.0 km north of Great Northern Highway, 100 km east of Fitzroy Crossing ('Bohemia' 4160 – 887:244) (60 dead adults, WAM 96.80, FMNH 199168); Sta. WA-249, 0.5 km west of Pinnacles Creek, Great Northern Highway, 11.1 km east of Give & Take Creek ('Bruten' 4060 – 158:245 est.) (30 dead adults, WAM 89.80, FMNH 199469); near Cave Spring, Bugle Gap, south end of Emanuel Range (4 live, 39 dead adults, WAM 438.77, WAM 609.79, FMNH 198764 collected by George Kendrick 22 June 1966); Emanuel Range, 5 km north of Bugle Gap (4 dead adults, WAM 460.77 collected by George Kendrick 28 June 1966); Bugle Gap, Lawford Ranges, out from Christmas Creek (7 dead adults, WAM 463.77 collected by George Kendrick 25 July 1963).

Distribution limits

Westraltrachia ampla (**Fig. 162**) ranges from Galeru Gorge (WA-367) at the north end of the Lawford Range south to near the south-east tip of the Emanuel Range (WA-375), then east to the Pinnacles (WA-249, WA-589) and as far north on both sides of the Laidlaw Ranges as WA-371. It is replaced at WA-370 by *W. ascita,* and it is unknown which species lives on the north and north-east perimeter of the Laidlaw Range between WA-370 and WA-368. The total known north-south range of *W. ampla* is about 15 km, the east-west range varies from 5-8 km.

Diagnosis

Shell very large, 11.3-21.2 mm (mean 18.19 mm) in diameter, with 4½+ to 5¾ – (mean 5½+) normally coiled whorls. Apex and spire moderately and almost evenly elevated, slightly rounded above, body whorl normally descending a bit just before

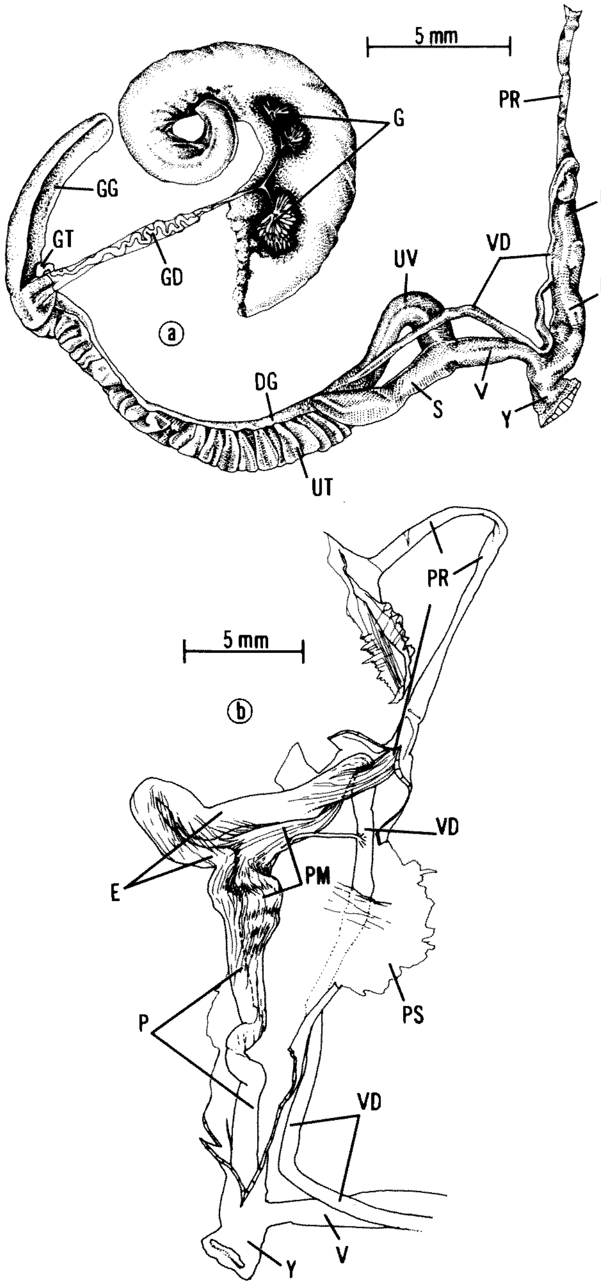


Fig. 157: Genitalia of *Westraltrachia ampla:* Cave Spring, Bugle Gap, Emanuel Range, 28 May 1966, WAM 609.79, (a) whole genitalia, Dissection A, (b) interior of penis sheath, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

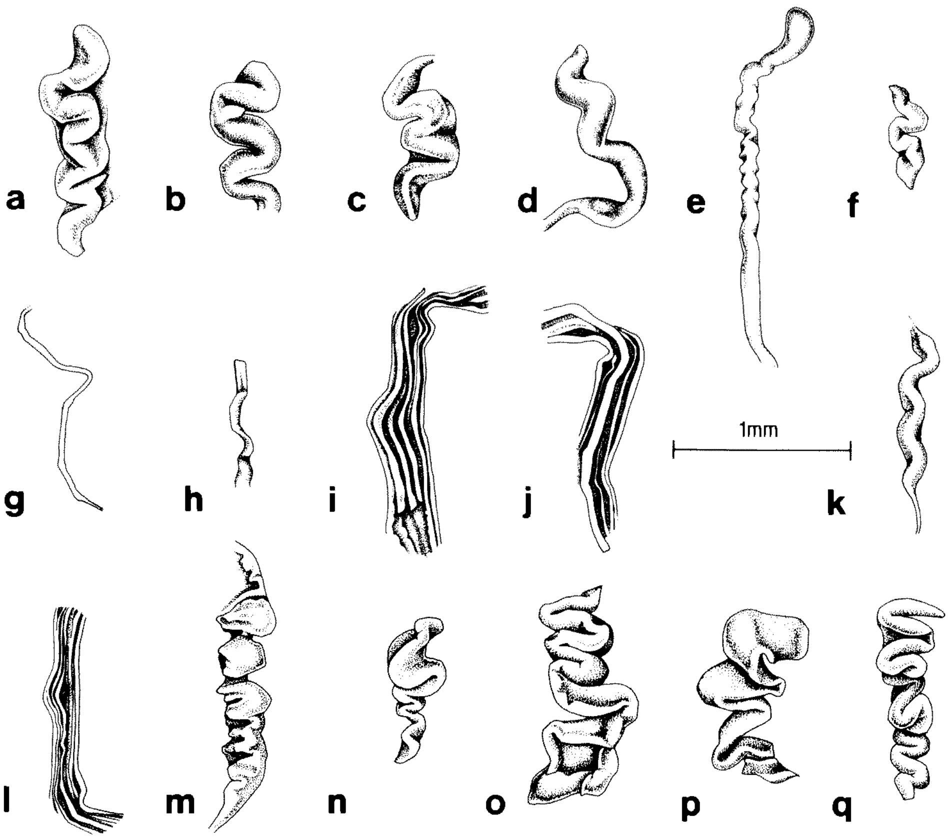


Fig. 158: Comparative size and shape of principal penial pilasters or that region in species of *Westraltrachia:* (a) *W. commoda* (Iredale, 1939), Sta. WA-325, FMNH 200103, Dissection A, 18 December 1976; (b) *W. turbinata,* Sta. WA-281, FMNH 199871, Dissection A, 6 December 1976; (c) *W. inopinata,* Sta. WA-339, FMNH 200157, Dissection B, 23 December 1976; (d) *W. froggatti complanata,* Sta. WA-359, FMNH 200153, Dissection C; (e) *W. derbyi* (Cox, 1892), Sta. WA-194, FMNH 200056, Dissection A, 5 December 1976; (f) *W. alterna* Iredale, 1939, Sta. WA-275, FMNH 199930, Dissection A, 3 December 1976; (g) *W. cunicula,* Sta. WA-274, FMNH 199886, Dissection B, 3 December 1976; (h) *W. oscarensis* (Cox, 1892), Sta. WA-356, FMNH 200165, Dissection B, 1 January 1977; (i) *W. subtila,* Sta. WA-265, FMNH 200216, Dissection A, 28 November 1976; (j) *W. instita,* Sta. WA-264, FMNH 200224, Dissection B, 28 November 1976; (k) *W. lievreana,* Sta. WA-263, FMNH 200223, Dissection B, 28 November 1976; (l) *W. porcata,* Sta. WA-711, FMNH 205311, Dissection A, 19 June 1980; (m) *W. limbana,* Sta. WA-585, FMNH 205370, Dissection A, 8 May 1980; (n) *W. recta,* Sta. WA-254, FMNH 200205, Dissection A, 29 November 1976; (o) *W. pillarana,* Sta. WA-253, FMNH 200229, Dissection A, 24 November 1976; (p) *W. ascita,* Sta. WA-370, FMNH 200182, Dissection A, 13 February 1977; (q) *W. ampla,* Cave Spring, Emanuel Range, WAM 609.79, Dissection B, 28 May 1966. Drawings by Linnea Lahlum.

aperture (**Fig. 155b**), height of shell 7.5-14.9 mm (mean 11.26 mm), H/D ratio 0.505-0.749 (mean 0.619). Apical whorls (**Plate 24c**) typical, postapical whorls with irregular growth lines and remnants of micro-riblets. Shell periphery (**Fig. 155b**) normally obtusely angulated, rarely almost rounded. Lip strongly expanded and reflected, columellar section partly rolled over umbilical opening. Degree of umbilical opening geographically variable, overall 84% partly open, 16% with opening reduced to a lateral crack. Colour typical, although darker markings generally reduced in intensity. Based on 454 measured adults.

Genitalia (**Figs 157a-b**) with massive penis muscle (PM) that extends well down side of penis (P), epiphallic loop (E) partly reduced. Principal penis pilaster (**Fig. 158q**) relatively long, slender, tightly convoluted, without hard edges. Penis (P) long and slender, kinked within penis sheath (PS), which has its basal wall slightly thickened. Vas deferens (VD) entering sheath opposite head of penis. Vagina (V) slightly longer than average, spermatheca (S) long, free oviduct (UV) curved.

Jaw (**Plate 32c-d**) typically camaenid, with very prominent vertical ribs. Radula with typical marginal teeth (**Plate 50d**) and latero-marginal transition (**Plate 50c, e**). Central and lateral teeth (**Plate 50a-b**) without ectocones, somewhat narrowed, greatly elevated mesoconal shaft, with bluntly rounded and slightly curved mesoconal tip.

Discussion

Numerous dead specimens of *Westraltrachia ampla* have been taken at localities in the Laidlaw Range, Lawford Range, and the south-east section of the Emanuel Range. In the north-west corner of the Laidlaw Range, Sta. WA-370, it apparently is replaced by *W. ascita,* which also is found further west in the Virgin Hills, on Sadler Ridge, and Prices Hill. In the Virgin Hills, Home Range and Pillara Range, it is replaced by the smaller *W. pillarana.* In 1977, a few live juveniles were taken at WA-369, in the Laidlaw Range, and WA-366 in the Lawford Range. No live adults were taken, and the anatomical study had to be based on material collected by G. Kendrick in 1966 (WAM 609.79).

Size and shape variation in more than 400 adults is summarised in **Table 65.** With the exception of a few dead shells picked up in the flood-plain of Mimbi Creek (WA-282) by Laurel Keller, they are quite uniform in size and shape. The Mimbi Creek sample is distinctly dwarfed in size, the reduction occurring by change in whorl count to 4¾, compared with a more normal range of 5 to 5¼+ for other populations. The reason for this dwarfing effect is unknown.

Despite the comparative lack of live collected material, evidence that the alteration in central and lateral teeth (**Plate 51a-b**) is feeding associated comes from observations of snail feeding tracks on seepage faces at WA-374 in the Lawford Range on 13-14 February by Carl C. Christensen (personal communication). *Westraltrachia ampla* is the only camaenid present at this locality and photographs of the feeding track show typical scrape marks.

The name *ampla,* from the Latin 'amplus', meaning large, refers to the very large size of the shell when compared with other species of *Westraltrachia.*

Table 65: Local Variation in *Westraltrachia ampla*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
Laidlaw Range				
WA-371, 2 km NNE Lloyd Hill, FMNH 199165	14D	11.09 ± 0.302 (7.5—12.3)	17.48 ± 0.503 (11.3 – 18.85)	0.636 ± 0.006 (0.597 – 0.664)
WA-372, E slope of Lloyd Hill, FMNH 199166	28D	10.88 ± 0.173 (9.25 – 12.9)	17.24 ± 0.144 (15.25 – 19.3)	0.631 ± 0.008 (0.551 – 0.741)
WA-369, 1.4 km ESE Lloyd Hill, FMNH 199163	44D	11.43 ± 0.100 (9.8 – 13.1)	18.31 ± 0.102 (17.2-19.8)	0.625 ± 0.006 (0.542 – 0.716)
WA-368, 2 km NNW Ross Hill, FMNH 199161	39D	11.37 ± 0.104 (9.9 – 12.7)	18.05 ± 0.112 (16.75 – 19.45)	0.630 ± 0.005 (0.570 – 0.695)
Lawford Range				
WA-367, SW side Galeru Gorge, FMNH 199160	5D	12.85 ± 0.820 (10.0 – 14.9)	19.37 ± 0.401 (17.95 – 20.4)	0.661 ± 0.030 (0.557 – 0.730)
WA-366, 4.9 km S of Galeru FMNH 199159	56D	10.62 ± 0.100 (9.0 – 12.1)	17.71 ± 0.103 (16.15 – 19.1)	0.601 ± 0.005 (0.505 – 0.692)
WA-365, 1 km from Jones Spring, FMNH 199158	22D	11.28 ± 0.146 (10.4 – 13.0)	18.61 ± 0.222 (16.9 – 20.4)	0.607 ± 0.007 (0.531 – 0.675)
WA-363, Nardji Cave, FMNH 199152	57D	11.96 ± 0.106 (9.9 – 13.8)	19.41 ± 0.108 (17.85 – 21.2)	0.616 ± 0.004 (0.547 – 0.682)
WA-364, Mimbi Creek, FMNH 199156	36D	11.08 ± 0.171 (9.45 – 13.25)	18.10 ± 0.202 (16.0 – 20.2)	0.612 ± 0.007 (0.514 – 0.699)
WA-282, Mimbi Creek, FMNH199467	6D	9.64 ± 0.357 (8.9 – 11.3)	14.94 ± 0.391 (13.7 – 16.5)	0.645 ± 0.010 (0.621 – 0.685)
WA-374, Mimbi Creek, FMNH 199319	7D	12.52 ± 0.093 (12.1 – 12.85)	19.33 ± 0.228 (18.3 – 20.1)	0.648 ± 0.006 (0.621 – 0.661)
Emanuel Range				
WA-375, SE side, FMNH 199168	60D	10.45 ± 0.071 (8.9 – 11.55)	17.36 ± 0.111 (14.85 – 19.5)	0.603 ± 0.003 (0.551 – 0.650)
WA-249, 0.5 km W Pinnacles Creek, FMNH 199469	30D	11.25 ± 0.156 (9.55 – 13.5)	18.24 ± 0.119 (17.1 – 19.9)	0.617 ± 0.008 (0.528 – 0.707)
Cave Spring, Bugle Gap, WAM 438.77	39D	12.29 ± 0.135 (10.8 – 14.2)	19.12 ± 0.140 (17.25 – 21.1)	0.643 ± 0.006 (0.567 – 0.749)
Bugle Gap, WAM 463.77	7D	12.31 ± 0.221 (11.55 – 13.0)	19.49 ± 0.267 (18.4 – 20.4)	0.632 ± 0.013 (0.569 – 0.675)
Cave Spring, Bugle Gap, WAM 609.79	4L	12.55 ± 0.241 (12.15 – 13.25)	18.40 ± 0.238 (17.7 – 18.7)	0.683 ± 0.014 (0.650 – 0.709)

Table 65: Local Variation in *Westraltrachia ampla* (continued)

Station	Number of Adults Measured	Mean and Range of: Whorls	Umbilical Width	D/U Ratio
Laidlaw Range				
WA-371, 2 km NNE Lloyd Lloyd Hill, FMNH 199165	14D	5⅛+ (5–5⅜)	10 open, 4 cracked	
WA-372, E slope of Lloyd Hill, FMNH 199166	28D	5⅛ (4⅞–5½)	20 open, 8 cracked	
WA-369, 1.4 km ESE Lloyd Hill, FMNH 199163	44D	5¼ (5–5¾–)	40 open, 4 cracked	
WA-368, 2 km NNW Ross Hill, FMNH 199161	39D	5¼+ (5– –5⅝)	34 open, 5 cracked	
Lawford Range				
WA-367, SW side Galeru Gorge, FMNH 199160	5D	5⅛ (4¾– –5⅜)	1 open, 4 cracked	
WA-366, 4.9 km S of Galeru Gorge, FMNH 199159	56D	5¼– (4⅞– –5⅝)	54 open, 2 cracked	
WA-365, 1 km from Jones Spring, FMNH 199158	22D	5+ (4¾– –5⅜)	17 open, 5 cracked	
WA-363, Nardji Cave, FMNH 199152	57D	5⅛+ (4⅝–5½)	50 open, 7 cracked	
WA-364, Mimbi Creek, FMNH 199156	36D	5– (4⅝+ –5⅜)	26 open, 10 cracked	
WA-282, Mimbi Creek, FMNH 199467	6D	4¾ (4½+ –5⅜+)	2 open, 4 cracked	
WA-374, Mimbi Creek, FMNH 199319	7D	5⅛+ (5– –5⅜+)	5 open, 2 cracked	
Emanuel Range				
WA-375, SE side, FMNH 199168	60D	5⅛ (4¾–5½)	58 open, 2 cracked	
WA-249, 0.5 km W Pinnacles Creek, FMNH 199469	30D	5⅛ (5– –5⅜–)	25 open, 5 cracked	
Cave Spring, Bugle Gap, WAM 438.77	39D	5⅛+ (4⅞– –5⅝–)	31 open, 8 cracked	
Bugle Gap, WAM 463.77	7D	5¼– (5–5⅜–)	6 open, 1 cracked	
Cave Spring, Bugle Gap, WAM 609.79	4L	5¼– (4¾–5 53/8)	4 open	

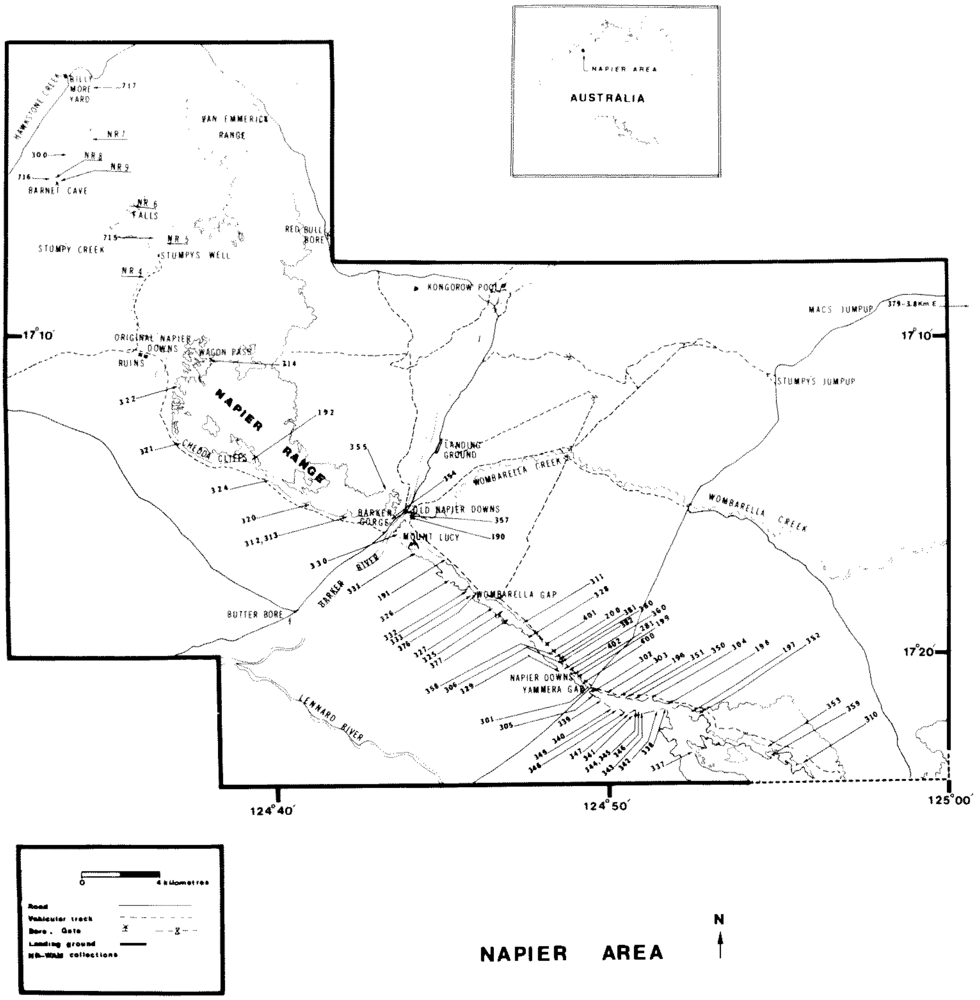


Fig. 159: Collecting stations in the north-west Napier Range, east of Derby. Drafted by Elizabeth Lizzio.

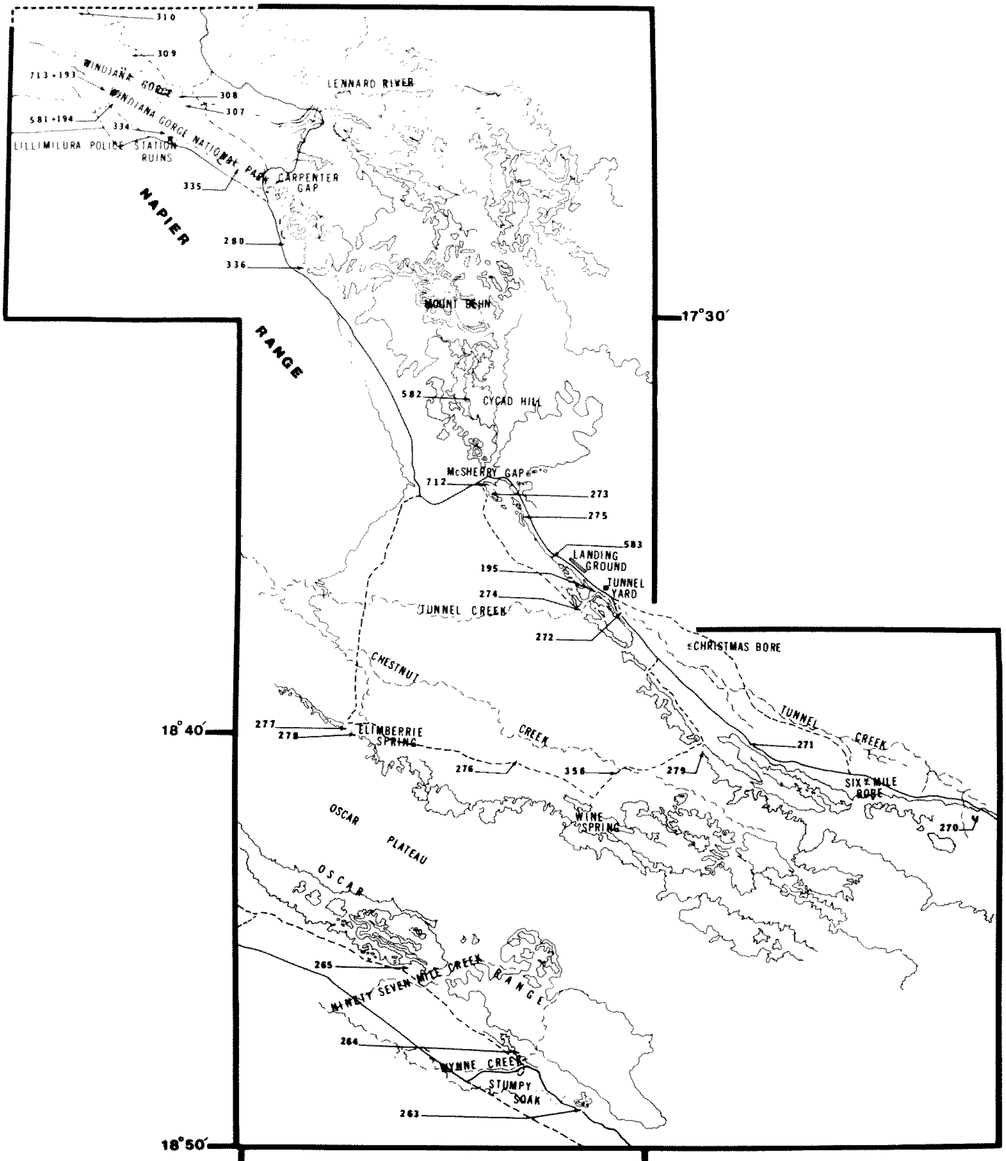


Fig. 160: Collecting stations in the south-east Napier Range, east of Derby. Drafted by Elizabeth Lizzio.

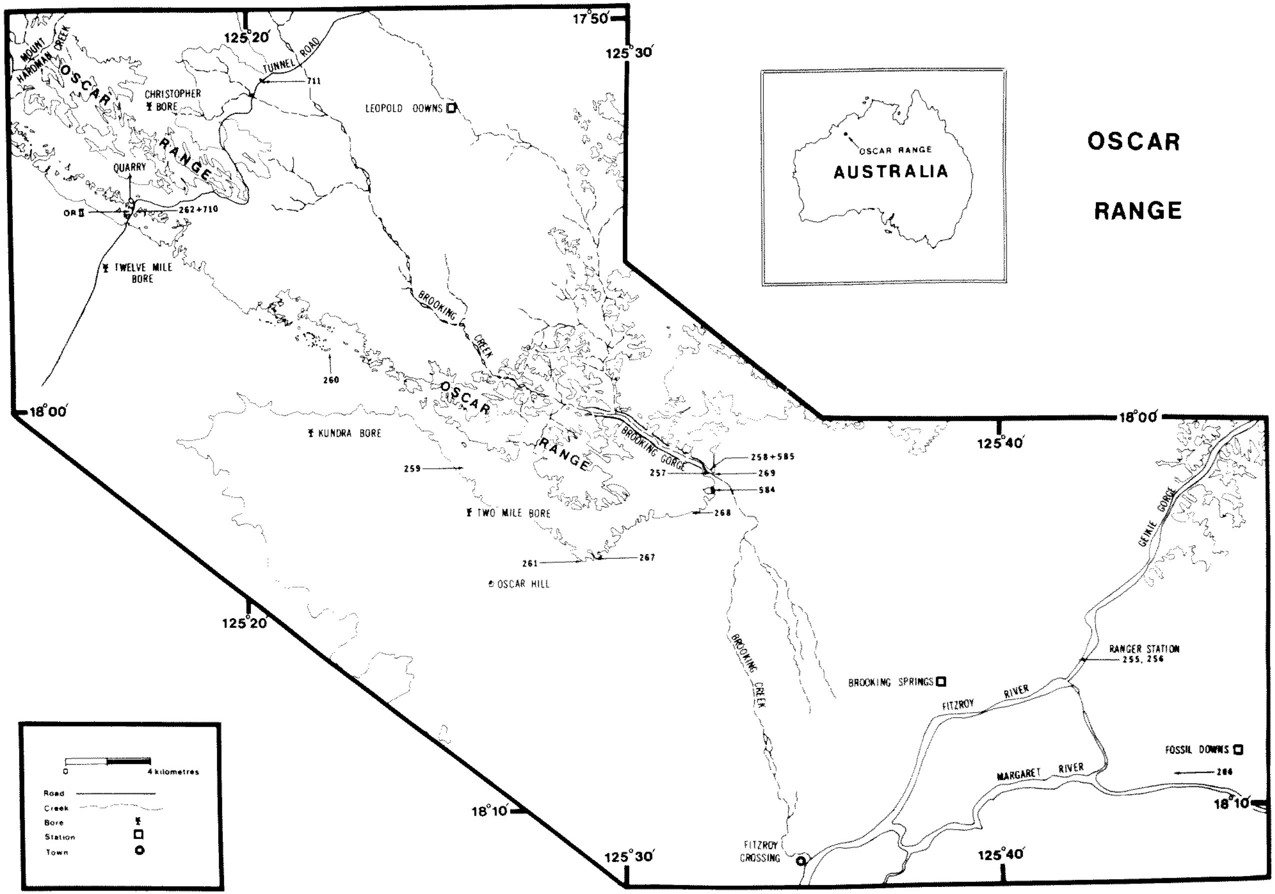


Fig. 161: Collecting stations in the Oscar Range, north-west of Fitzroy Crossing. Drafted by Linnea Lahlum.

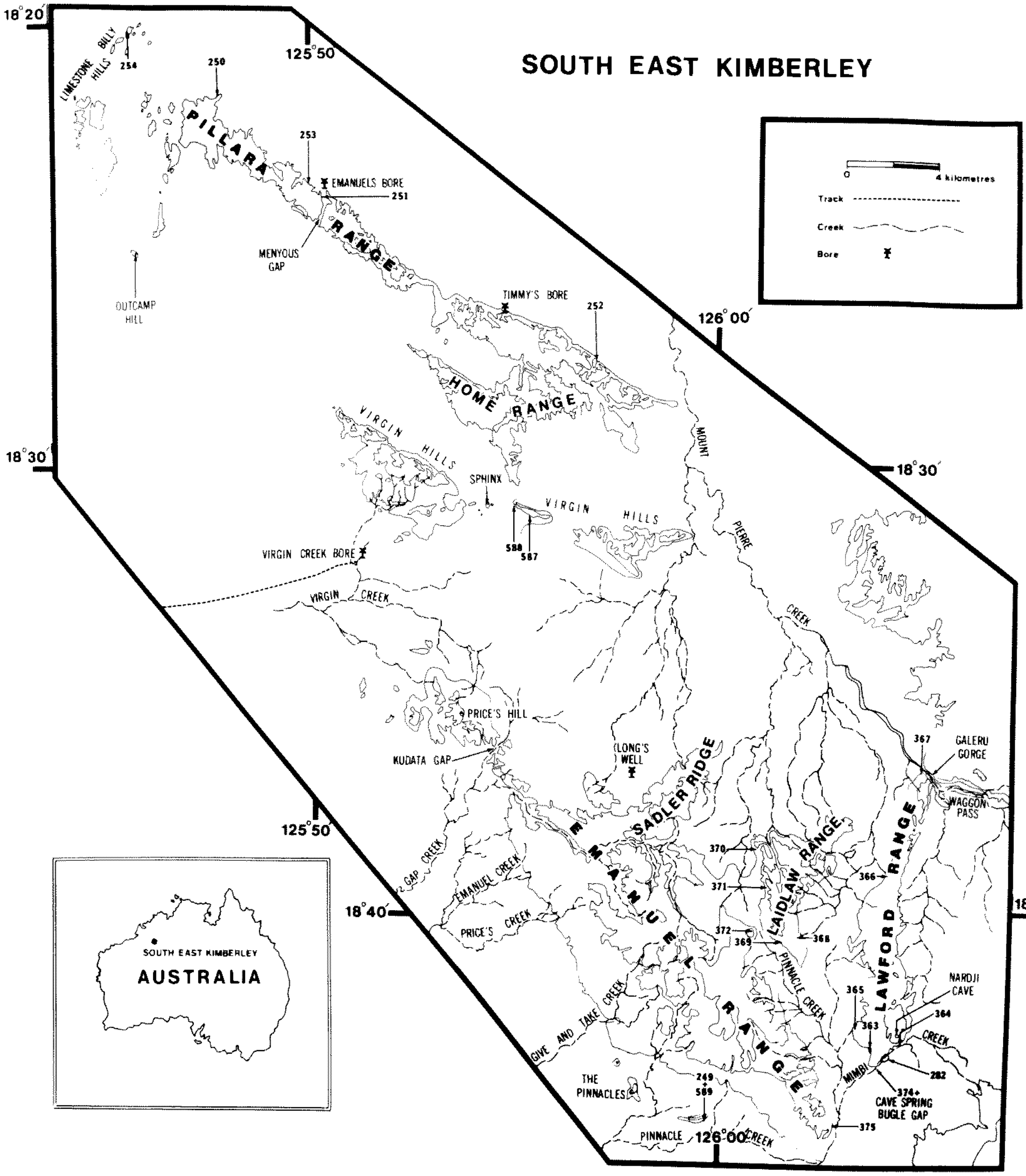


Fig. 162: Collecting stations to the east of Fitzroy Crossing in the south-east Kimberley. Drafted by Linnea Lahlum.

GENUS *MOULDINGIA* NEW GENUS

Shell very small, apex and spire usually flat, body whorl descending moderately, descent accelerated just before aperture **(Figs 163b, e)**. Umbilicus broadly open, last whorl decoiling more rapidly **(Figs 163c, f)**, only partly covered by reflection of columellar lip. Apical whorls with quite prominent pustules, fewer in *occidentalis* **(Plate 52a, b)** than *orientalis* **(Plate 53a, b)**, with a secondary sculpture of vague radial ridgelets on last portion. Postapical sculpture complex, with irregularly spaced, very large and high, protractive radial ribs **(Figs 163a-f, Plates 52a, c, 53a, c, d)** continuing to aperture. Microsculpture **(Plates 52-53)** of very prominent and densely packed periostracal extensions, varying considerably in shape. Sculpture greatly reduced in umbilicus, slightly reduced below periphery. Body whorl generally strongly deflected just behind aperture, variable individually. Lip rather strongly expanded and reflected, detached from parietal wall in *occidentalis* **(Figs 163b, c)**, reduced to a thin parietal callus in *orientalis*. Shell periphery moderately (*orientalis*, **Fig. 163e**) to strongly (*occidentalis*, **Fig. 163b**) protruded as a thread-like keel. Whorls strongly rounded, sutures of spire deeply impressed, prominent supraperipheral and subperipheral sulci **(Figs 163a-f)**. Shell colour monochrome, light yellow-brown, without flammulations. Genitalia **(Figs 164-165)** with normal seasonal variability. Entrance of hermaphroditic duct (GD) into talon (GT) subterminal **(Figs 164c, 165b)**. Ovotestis (G), albumen gland (GG), prostate (DG) and uterus (UT) typical of complex. Free oviduct (UV) distinctly longer than spermatheca (S), but former not sinuated **(Figs 164b, 165a)** as in many *Westraltrachia* **(Figs 116a, 130a)**. Shaft of spermatheca very short, head attached by connective tissue strands to prostate-uterus. Vagina (V) very long, almost equal in length to penis sheath **(Figs 164a, 165a)**, slender, without unusual internal structures. Terminal male genitalia enclosed in a sheath, that is very thin-walled in *occidentalis* **(Fig. 164d)**, much thicker in *orientalis* **(Fig. 165c)**. Vas deferens (VD) a thin tube, reflexing at peni-oviducal angle, entering penis sheath **(Figs 164d, 165c)** from one-third to more than half-way up sheath. Penial retractor muscle (PR) long, originating on base of diaphragm, entering apex of penis sheath and attaching to reflexed junction of vas deferens and epiphallus (E). A strand of the penial retractor muscle extends part way along epiphallus in *orientalis* **(Fig. 165c)**, sometimes terminal in *occidentalis* **(Fig. 164d)**. Epiphallus (E) elongated and complexly folded within penis sheath, gradually increasing in diameter to junction with penis **(Figs 164d, 165c)**, internally with simple longitudinal pilasters. Penis-epiphallus junction marked by a lateral protrusion in the coiled tube **(Fig. 165d)**, internally with complex pilasters. Penis (P) slender, with muscular walls, lower two-thirds in *orientalis* **(Fig. 165c)** bound to wall of sheath, free of wall in *occidentalis* **(Fig. 164d)**. Interior of penis **(Fig. 165d)** with a few apical pilasters that are narrow and zigzagged, lower portion with simple longitudinal pilasters. Atrium (Y) short, without unusual features. Jaw **(Plate 58h, i)**, with vertical ribs reduced in prominence, variable in number. Radula **(Plate 59)** with mesoconal tips of central and lateral teeth blunt, thickened, and slightly curved, marginal teeth without unusual features.

Type species: *Mouldingia occidentalis* sp. nov.

Comparisons

The extremely prominent radial ribs, protruded keel, flat or nearly flat spire, prominent sulci, deflected aperture with widely expanded lip, and pustulose

Table 66: Range of Variation in Genera Related to *Westraltrachia*

Taxon	Number of Adults Measured	Mean and Range of: Shell Height	Shell Diameter	H/D Ratio
Mouldingia occidentalis	317	3.83 (3.1 – 4.8)	9.41 (8.1 – 10.8)	0.399 (0.330 – 0.506)
M. orientalis	557	4.10 (2.9 – 5.65)	9.85 (8.0 – 11.8)	0.423 (0.318 – 0.585)
Ordtrachia septentrionalis	74	7.90 (6.7 – 9.2)	13.00 (11.1 – 14.75)	0.608 (0.537 – 0.685)
O. australis	530	7.64 (6.5 – 9.1)	14.32 (12.5 – 16.5)	0.534 (0.450 – 0.627)
O. grandis	289	7.38 (6.1 – 10.1)	17.03 (14.0 – 22.2)	0.434 (0.347 – 0.523)
O. intermedia	468	4.61 (3.6 – 6.4)	8.76 (7.3 – 10.9)	0.536 (0.431 – 0.698)
Exiligada negriensis Iredale, 1939	201	13.21 (9.9 – 17.25)	19.26 (16.05 – 24.5)	0.677 (0.539 – 0.824)
Prototrachia sedula	69	8.35 (7.2 – 10.5)	15.56 (13.6 – 17.3)	0.536 (0.495 – 0.604)

Taxon	Number of Adults Measured	Mean and Range of: Whorls	Umbilical Width	D/U Ratio
Mouldingia occidentalis	317	3¾+ (3½– – 4+)	2.71 (1.85 – 3.85)	3.52 (2.64 – 4.92)
M. orientalis	557	4+ (3⅝ – 4⅜+)	2.86 (1.9 – 3.9)	3.49 (2.55 – 5.11)
Ordtrachia septentrionalis	74	4⅞+ (4⅜+ – 5⅜)	0.89 (0.4 – 1.85)	16.3 (7.38 – 36)
O. australis	530	5¼– (4⅝+ – 5¾+)	1.48 (0.35 – 2.7)	10.4 (5.56 – 39)
O. grandis	289	5⅛+ (4¾ – 5¾)	1.97 (0.7 – 3.7)	9.20 (5.51 – 23.1)
O. intermedia	468	4¼– (3⅞ – 4¾+)	1.90 (1.2 – 2.8)	4.70 (3.17 – 7.36)
Exiligada negriensis Iredale, 1939	201	5⅛– (4⅜– – 5¾)	1.07 (0.25 – 2.9)	21.9 (7.93 – 80)
Prototrachia sedula	69	5⅜– (5– – 5¾)	1.31 (0.55 – 2.1)	12.8 (7.71 – 26.3)

microsculpture found in *Mouldingia* are a combination of shell features not duplicated by any other Kimberley land snail. The absence of any prominent nodes in the aperture immediately separates *Mouldingia* from the North Kimberley *Baudinella* Thiele, 1931 and *Setobaudinia* Iredale, 1933, or Queensland taxa such as *Trozena* Iredale, 1938. An undescribed genus from west of Barker Gorge in the Napier Ranges agrees in shape, major ribbing, and approximate size with *Mouldingia,* but lacks the shell microsculpture and is very different in anatomy (Solem, unpublished). The series of genera clustered around the *Pleuroxia* Ancey, 1887 complex, that range through much of southern and central Australia, share the ribs and sometimes the microsculpture, but differ radically in anatomy.

The anatomy of *Mouldingia* is fully consistent with it being a member of the *Westraltrachia* complex. It differs most noticeably in having the penis-epiphallus junction marked by a simple bulge in the tube **(Fig. 165d),** rather than extended into a large loop; the penial retractor muscle attaching directly **(Fig. 164d)** to the vas-epiphallus junction or with only a modest lateral extention along the epiphallus, rather than extending as a penis muscle **(Fig. 113);** and retaining fairly simple, multiple pilasters within the upper penis chamber **(Fig. 165d),** rather than the complex, enlarged pilasters found in most species of *Westraltrachia* **(Fig. 158).**

Two species are known: *Mouldingia occidentalis* has been collected at a few stations in the vicinity of McSherry Gap in the eastern Napier Ranges **(Fig. 160,** Stations WA-273, WA-275, WA-712) and *Mouldingia orientalis* is known from some isolated limestone hillocks near the south-west corner of Lake Argyle on Lissadell Station **(Fig. 179,** Stations WA-247, WA-248, WA-590). It is quite probable that the flooding of Lake Argyle resulted in drowning other colonies of *M. orientalis.*

This remarkably disjunct range is quite unusual. Although the shells differ obviously only in the parietal lip condition, the anatomical changes are striking and suggest that these has been a fairly long period of isolation. Fairly intensive collecting has been done in the Oscar-Laidlaw Range area without discovering any *Mouldingia.* It is tempting to speculate that accidental dispersal by birds was originally responsible for this disjunction. Both species are free sealers, lying loose on the soil surface during aestivation, and both occur quite abundantly at their known stations. Transport as gut contents or stuck to the foot or body of the bird would be viable possibilities. If minor limestone exposures exist directly west of Lake Argyle, and to the north of the Napier-Laidlaw arc, these are possible sites for additional species or colonies.

The known species are easily identified:

KEY TO THE SPECIES OF *MOULDINGIA*

1. Parietal lip a thin, attached callus; penis sheath with thick walls; penis attached to sheath; south-west corner of Lake Argyle .... *Mouldingia orientalis* sp. nov.

   Parietal lip detached from wall, strongly expanded; penis sheath with very thin walls; penis not attached to sheath; near McSherry Gap, eastern Napier Ranges *Mouldingia occidentalis* sp. nov.

For many years Mr. and Mrs. Arthur T. Moulding of Winnetka, Illinois have provided generous support for my research and activities of the Division of Invertebrates, Field Museum of Natural History. It is my pleasure to dedicate this genus to Mrs. Mary B. Moulding and her late husband, Arthur T. Moulding.

MOULDINGIA OCCIDENTALIS SP. NOV.

(Plates 52, 58i, 59a-b: Figs 163a-c, 164)

Comparative remarks

Mouldingia occidentalis is slightly smaller and with a lower mean whorl count than *M. orientalis* **(Table 66)**, but differs most obviously in having the parietal lip free of the penultimate whorl, thickened, and strongly reflexed **(Figs 163b, e)**. No other Napier Range camaenid has equivalent radial ribbing and keel protrusion. The keeled *Westraltrachia froggatti* (Ancey, 1898) lacks all radial ribbing, while an undescribed genus from west of Barker Gorge has radial ribbing, but a rounded periphery and no microsculpture between the major ribs. Genital differences of *M. occidentalis* include the very thin wall of the penis sheath, absence of fibers binding the penis to the sheath wall, and simple insertion of the penial retractor on the vas-epiphallus junction **(Figs 164a-d)**. These features contrast with the thick sheath wall, heavy fibers binding the penis to the sheath, and lateral extension of the penial retractor muscle down along the epiphallus found in *M. orientalis* **(Figs 165a-d)**.

Holotype

WAM 512.80, Sta. WA-273, 0.8 km east of McSherry Gap, south side of eastern Napier Ranges, Kimberley District, Western Australia (1:100,000 'Leopold Downs' map sheet 3962 – 563:232). Collected by Alan Solem, Carl Christensen, and Laurie Price 3 December 1976. Height of shell 3.7 mm, diameter 9.35 mm, H/D ratio 0.396, whorls 3⅞, umbilical width 2.5 mm, D/U ratio 3.74.

Paratopotypes

WAM 549.80, WAM 551.80, WAM 552.80, WAM 554.80, FMNH 199202, FMNH 199474, FMNH 199919, FMNH 200179, 140 live and 44 dead adults from the type locality.

Paratypes

Sta. NRII-34, north corner of McSherry Gap (19 live, 8 dead adults, WAM 277.80, WAM 296.80); Sta. NRII-35, inside west corner McSherry Gap (42 live, 72 dead adults, WAM 278.80, WAM 295.80, WAM 297.80); Sta. NRXXIV, just south of McSherry Gap (2 live, 48 dead adults, WAM 838.75, WAM 839.75); Sta. WA-712, 100 m east of McSherry Gap ('Leopold Downs' 3962 – 228:566) (59 live, 94 dead adults, WAM 550.80, WAM 553.80, FMNH 205315-6); Sta. NRXIX, about 2.2 km south of McSherry Gap ('Leopold Downs' 3962 – 228:566) (59 live, 94 dead adults, WAM west of Tunnel Creek turnoff, north side Napier Range ('Leopold Downs' 3962 – 554:244) (25 live adults, WAM 555.80, FMNH 199929).

Diagnosis

Shell small, 8.1-10.8 mm (mean 9.41 mm) in diameter, with 3½ – to 4+ (mean 3¾+) normally coiled whorls. Apex and spire almost flat, rarely slightly protruding, body whorl descending moderately until just before aperture, where it becomes abruptly deflected, height of shell 3.1-4.8 mm (mean 3.83 mm), H/D ratio 0.330-0.506 (mean 0.399). Apical sculpture **(Plate 52a, b)** of very prominent pustules, sharp pointed when unworn, with secondary radial undulations on later sections. Postapical whorls **(Plate 52a, c, d, Figs 163a-c)** with high, sharply defined, protractive radial ribs that become somewhat reduced on shell base and are almost absent in the umbilicus. Microsculpture of very dense pustulations that overlay the major sculpture and have the characteristic shape of a "U"-cone when unworn (**Plate 52c, d**). Shell periphery sharply protruded into a thread-like keel (**Fig. 163b**), with very prominent supra- and subperipheral sulci. Body whorl descending moderately, sharply just behind aperture. Lip broadly reflexed and expanded, parietal section equally expanded, free of and elevated above parietal wall, only slightly reflected over umbilicus on columellar margin. No internal lip nodes. Umbilicus widely open (**Fig. 163c**), last whorl decoiling more rapidly, umbilical width 1.85-3.85 mm (mean 2.71 mm), D/U ratio 2.64-4.92 (mean 3.52). Based on 317 measured adults.

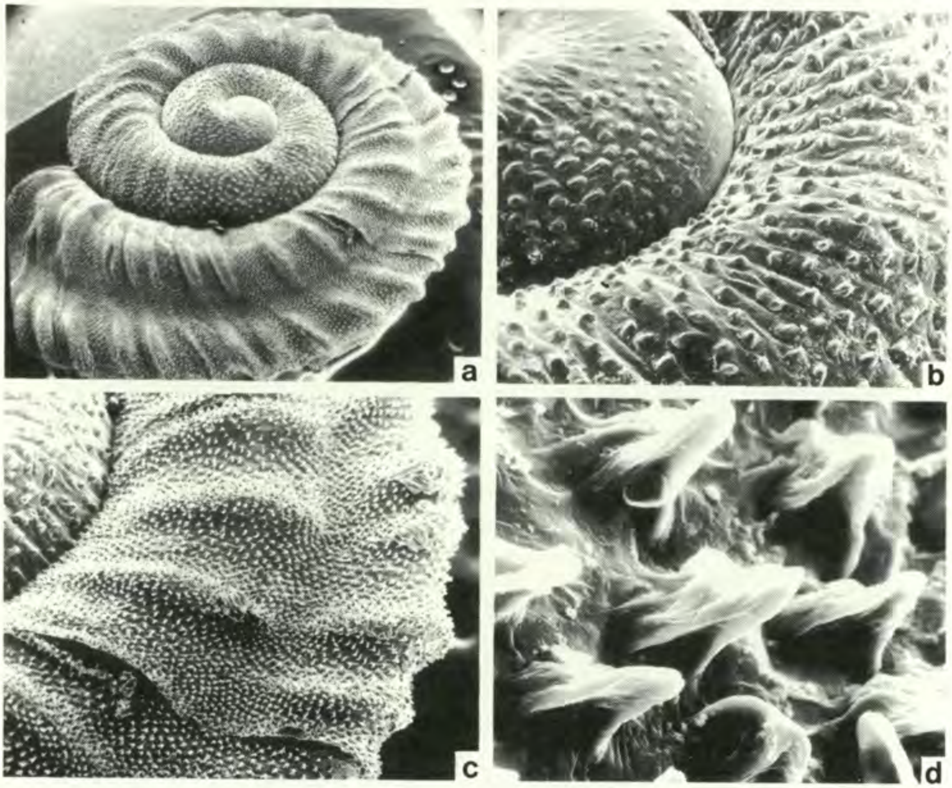


Plate 52: Shell sculpture of *Mouldingia occidentalis:* (a-d) FMNH 199919, Dissection A, Sta. WA-273, 0.8 km east of McSherry Gap, Napier Range, 5 December 1976, (a) apex and early spire at 13.5X, (b) detail of apical sculpture at 67X, (c) detail of early spire at 36X, (d) detail of spire projections at 650X.

Genitalia (**Fig. 164**) with vas deferens (VD) entering fairly low on thin walled penis sheath, reflexing apically to join epiphallus (E). Penis (P) not attached to wall of sheath, junction with epiphallus indicated externally by a small lateral bulge, upper portion of penis chamber with small, zigzagged pilasters, lower part of chamber with simple pilasters. Vagina (V) very long, almost equal in length to penis, spermatheca (S) short with slightly expanded head, free oviduct (UV) slightly longer, but not noticeably sinuated. Apical genitalia without unusual features.

Jaw **(Plate 58i)** with reduced vertical ribs. Radular teeth **(Plate 59a-b)** unusual only in slight thickening and curvature of mesoconal tip.

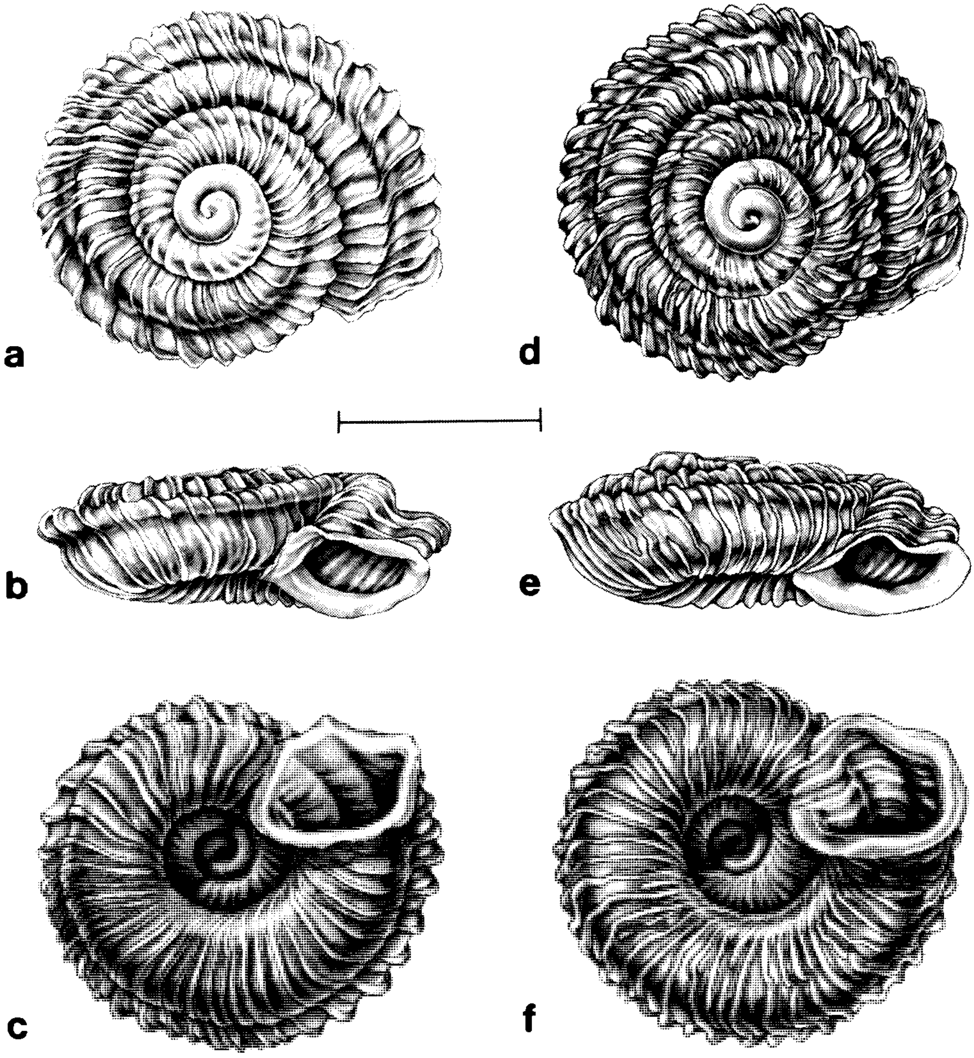


Fig. 163: Shells of *Mouldingia:* (a-c) *M. occidentalis,* Sta. WA-273, McSherry Gap, Napier Range, 1 January 1977, WAM 512.80, holotype; (d-f) *M. orientalis,* Sta. WA-248, Lissadell Homestead, near Lake Argyle, 17 November 1976, WAM 513.80, holotype. Scale line equals 5 mm. Drawings by Linnea Lahlum.

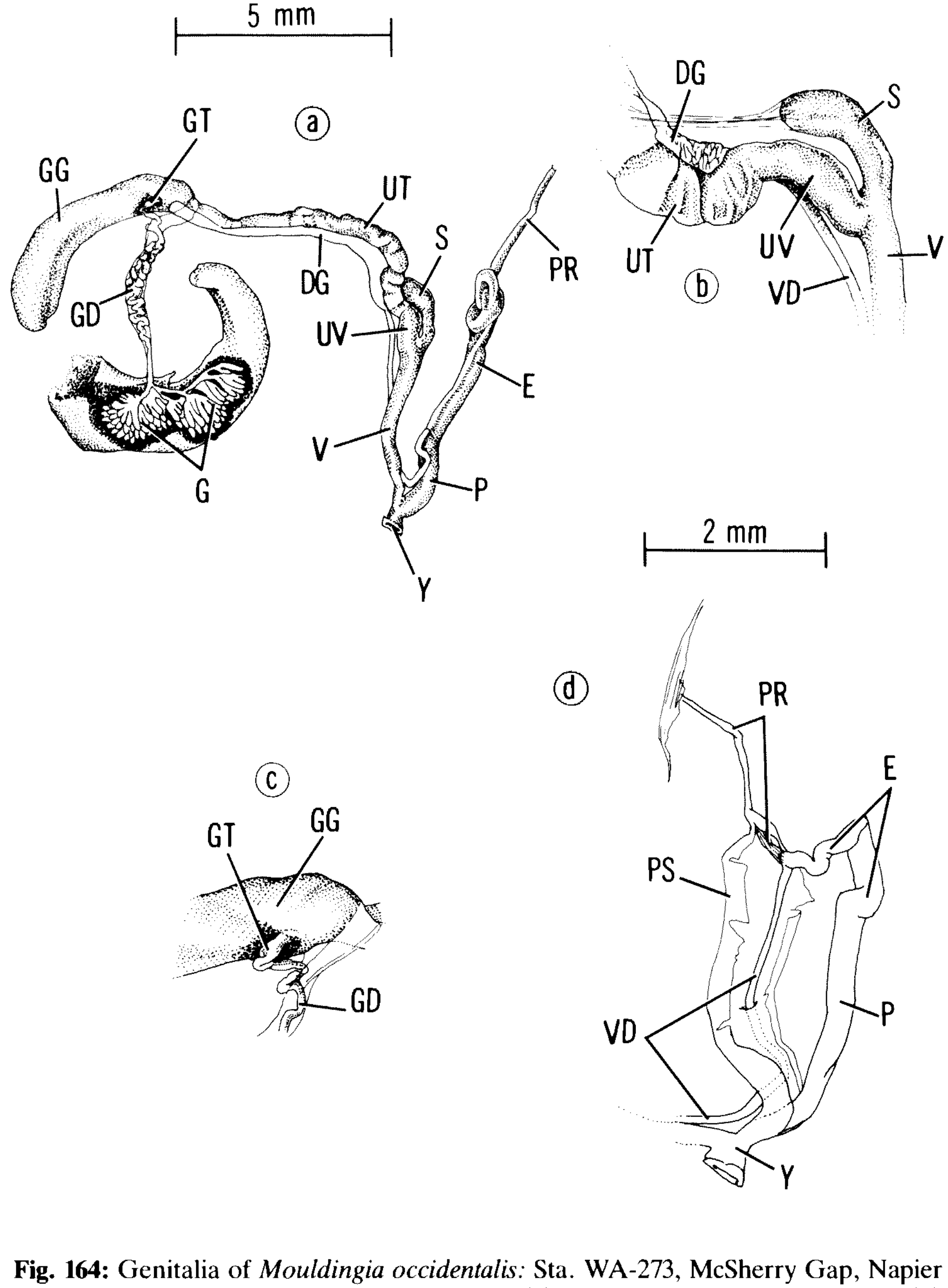


Fig. 164: Genitalia of *Mouldingia occidentalis:* Sta. WA-273, McSherry Gap, Napier Range, 3 December 1976, FMNH 199919, (a) whole genitalia, Dissection A, (b) detail of terminal female genitalia, Dissection A, (c) detail of talon, (d) penis complex, Dissection C. Scale lines as marked. Drawings by Linnea Lahlum.

Table 67: Local Variation in *Mouldingia*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
M. occidentalis				
WA-273, FMNH 199919	109(L)	3.71 ± 0.029 (3.1 − 4.8)	9.30 ± 0.041 (8.3 − 10.45)	0.399 ± 0.003 (0.330 − 0.497)
WA-273, FMNH 200179	31(L)	3.73 ± 0.055 (3.15 − 4.4)	9.14 ± 0.068 (8.3 − 9.85)	0.410 ± 0.008 (0.330 − 0.506)
WA-275, FMNH 199929	25(L)	3.75 ± 0.051 (3.3 − 4.45)	9.38 ± 0.093 (8.35 − 10.25)	0.400 ± 0.006 (0.343 − 0.473)
NRII-35, WAM 278.80	42(L)	4.31 ± 0.555 (3.3 − 4.4)	9.53 ± 0.058 (8.8 − 10.3)	0.392 ± 0.004 (0.330 − 0.447)
NRII-35, WAM 297.80	70(D)	3.86 ± 0.039 (3.1 − 4.5)	9.57 ± 0.045 (8.8 − 10.8)	0.430 ± 0.004 (0.333 − 0.486)
M. orientalis				
WA-248, FMNH 200333	209(L)	4.14 ± 0.027 (3.15 − 5.45)	9.91 ± 0.033 (8.3 − 11.8)	0.418 ± 0.003 (0.318 − 0.527)
WA-248, FMNH 199720	42(D)	4.29 ± 0.067 (3.6 − 5.65)	9.89 ± 0.095 (8.3 − 11.7)	0.434 ± 0.007 (0.364 − 0.585)
WA-247, FMNH 199577	122(D)	4.12 ± 0.035 (2.9 − 5.05)	9.77 ± 0.055 (8.0 − 11.3)	0.452 ± 0.030 (0.338 − 0.558)
WA-590, FMNH 204737	24(D)	4.19 ± 0.091 (3.4 − 4.9)	9.92 ± 0.135 (8.9 − 11.0)	0.424 ± 0.010 (0.328 − 0.540)
WA-590, FMNH 204736	160(L)	3.98 ± 0.026 (3.3 − 4.7)	9.82 ± 0.033 (8.7 − 10.7)	0.406 ± 0.003 (0.321 − 0.490)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
M. occidentalis				
WA-273, FMNH 199919	109(L)	3¾ (3½− −4+)	2.684 ± 0.036 (2.1 − 3.45)	3.53 ± 0.031 (2.80 − 4.45)
WA-273, FMNH 200179	31(L)	3¾− (3½− −3⅞+)	2.57 ± 0.052 (2.0 − 3.3)	3.59 ± 0.062 (2.79 − 4.50)
WA-275, FMNH 199929	25(L)	3¾+ (3½−4+)	2.65 ± 0.068 (1.85 − 3.15)	3.59 ± 0.092 (2.98 − 4.92)
NRII-35, WAM 278.80	42(L)	3⅞− (3¾− −4)	2.80 ± 0.036 (2.3 − 3.35)	3.42 ± 0.042 (2.70 − 4.02)

Table 67: Local Variation in *Mouldingia* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
NRII-35, WAM 297.80	70(D)	3¾ (3½ – 4)	2.75 ± 0.029 (2.1 – 3.3)	3.49 ± 0.035 (2.69 – 4.50)
M. orientalis				
WA-248, FMNH 200333	209(L)	4 + (3¾ + – 4⅜)	2.96 ± 0.025 (1.9 – 3.9)	3.39 ± 0.026 (2.55 – 4.86)
WA-248, FMNH 199720	42(D)	4⅛ – (3⅞ – 4⅜)	2.93 ± 0.056 (2.25 – 3.65)	3.41 ± 0.057 (2.79 – 4.29)
WA-247, FMNH 199577	122(D)	4 (3⅝ – 4⅜)	2.82 ± 0.035 (1.9 – 3.7)	3.52 ± 0.046 (2.58 – 5.11)
WA-590, FMNH 204737	24(D)	4⅛ + (3¾ + – 4⅜ +)	2.63 ± 0.046 (2.2 – 3.0)	3.79 ± 0.059 (3.23 – 4.43)
WA-590, FMNH 204736	160(L)	4⅛ – (3¾ – 4⅜ –)	2.76 ± 0.019 (2.2 – 3.3)	3.57 ± 0.022 (2.93 – 4.50)

Discussion

Mouldingia occidentalis has a known range of only 2.2 km, extending from McSherry Gap in the eastern Napier Range south-east. It has not been collected at Cycad Hill only 3.4 km to the north-west, or at Sta. WA-583, located 2.5 km south-east of Sta. WA-275 **(Fig. 160)**. The unsampled intervening areas are rolling hills without rock exposures visible from the road to the north-west and barren looking cliffs without talus accumulation south-east. Thus, I do not anticipate a significant range extension to be made by more intensive collection activity.

It is sympatric with *Westraltrachia alterna* Iredale, 1939 and *Quistrachia monogramma* (Ancey, 1898), both of which are significantly larger in shell diameter. During aestivation we could detect no clear difference in aestivation site, all being found in talus-litter accumulations on shady slopes or in crevices at the cliff base. All three species were loose in the soil with calcareous epiphragm secreted across the aperture. The reduced vertical ribbing on the jaw of *W. occidentalis* **(Plate 58i)** may be indicative that it, as well as *Westraltrachia alterna,* is involved in a feeding resource shift to algal-fungal blooms because of sympatry with *Quistrachia* (see Solem. In Press-A for a discussion of this phenomenon).

Size variation among the few populations of *Mouldingia occidentalis* is minimal **(Table 67)**, probably reflecting measurement error as much as anything.

The name *occidentalis* refers to the western position of this species within the range of the genus.

MOULDINGIA ORIENTALIS SP. NOV.

(Plates 53, 58h, 59c-e; Figs 163d-f, 165)

Comparative remarks

Mouldingia orientalis is slightly larger and with a greater whorl count than *M. occidentalis* **(Table 66)**, but differs most obviously in that the lip is attached to the parietal wall and reduced to a thin callus **(Fig. 163e)**. The peripheral keel is less protruded and sometimes the apex is slightly protrudant **(Fig. 163e)**. Shell differences from other Kimberley camaenids have been covered in the Comparative remarks about *M. occidentalis* (see above). In the genitalia, the most obvious differences are the thicker walls of the penis sheath **(Fig. 165c)**, having the penis bound to the wall of the sheath by connective tissue fibers, and the lateral extention of the penial retractor muscle (PR) along the epiphallus (E).

Holotype

WAM 513.80, Sta. WA-248, large limestone hill 3.3 km west of Lissadell Homestead, south-west corner of Lake Argyle, south of Kununurra, Western Australia (1:100,000 'Lissadell' map sheet 4664 – 490:572). Collected by Alan Solem and Carl C. Christensen 17 November 1976. Height of shell 3.85 mm, diameter 9.75 mm, H/D ratio 0.395, whorls 4⅛, umbilical width 2.7 mm, D/U ratio 3.61.

Paratopotypes

WAM 556.80, WAM 558.80, WAM 559.80, FMNH 199609, FMNH 199719-20, FMNH 200333, 209 live and 1,019 dead adults from the type locality in 1976-7, and WAM 557.80, FMNH 204735-7, 160 live and 25 dead adults (Sta. WA-590) from the type locality in 1980.

Paratypes

Sta. WA-247, ca 200 metres east of Sta. WA-248, Lissadell Station (122 dead adults, WAM 560.80, FMNH 199577).

Diagnosis

Shell small, 8.0-11.8 mm (mean 9.85 mm) in diameter, with 3⅝ to 4⅞+ (mean 4+) normally coiled whorls. Apex and spire sometimes emergent **(Fig. 163e)**, usually flat, body whorl descending moderately until just before aperture, where it reflexes abruptly, height of shell 2.9-5.65 mm (mean 4.10 mm), H/D ratio 0.318-0.585 (mean 0.423). Apical sculpture **(Plate 53a, b)** more crowded than in *M. occidentalis,* but the same in structure. Postapical whorls **(Plate 53c-f, Figs 163d-f)** with same sculpture as *M. occidentalis,* except that the sculpture is less reduced on the shell base and in the umbilicus.Microsculpture without unusual features. Shell periphery protruded into a thread-like keel that is less prominent than the keel found in *M. occidentalis* **(Figs 163b, e)**, supraperipheral sulcus very prominent, subperipheral sulcus weak. Body whorl reflexing sharply just before aperture. Lip broadly expanded and reflected, except on parietal wall where it is reduced to a thin callus **(Fig. 163e)**, only slightly encroaching upon umbilicus by reflection of columellar margin. No internal lip nodes. Umbilicus widely open **(Fig. 163f)**, last whorl decoiling more rapidly, umbilical width 1.9-3.9 mm (mean 2.86 mm), D/U ratio 2.55-5.11 (mean 3.49). Based on 557 measured adults.

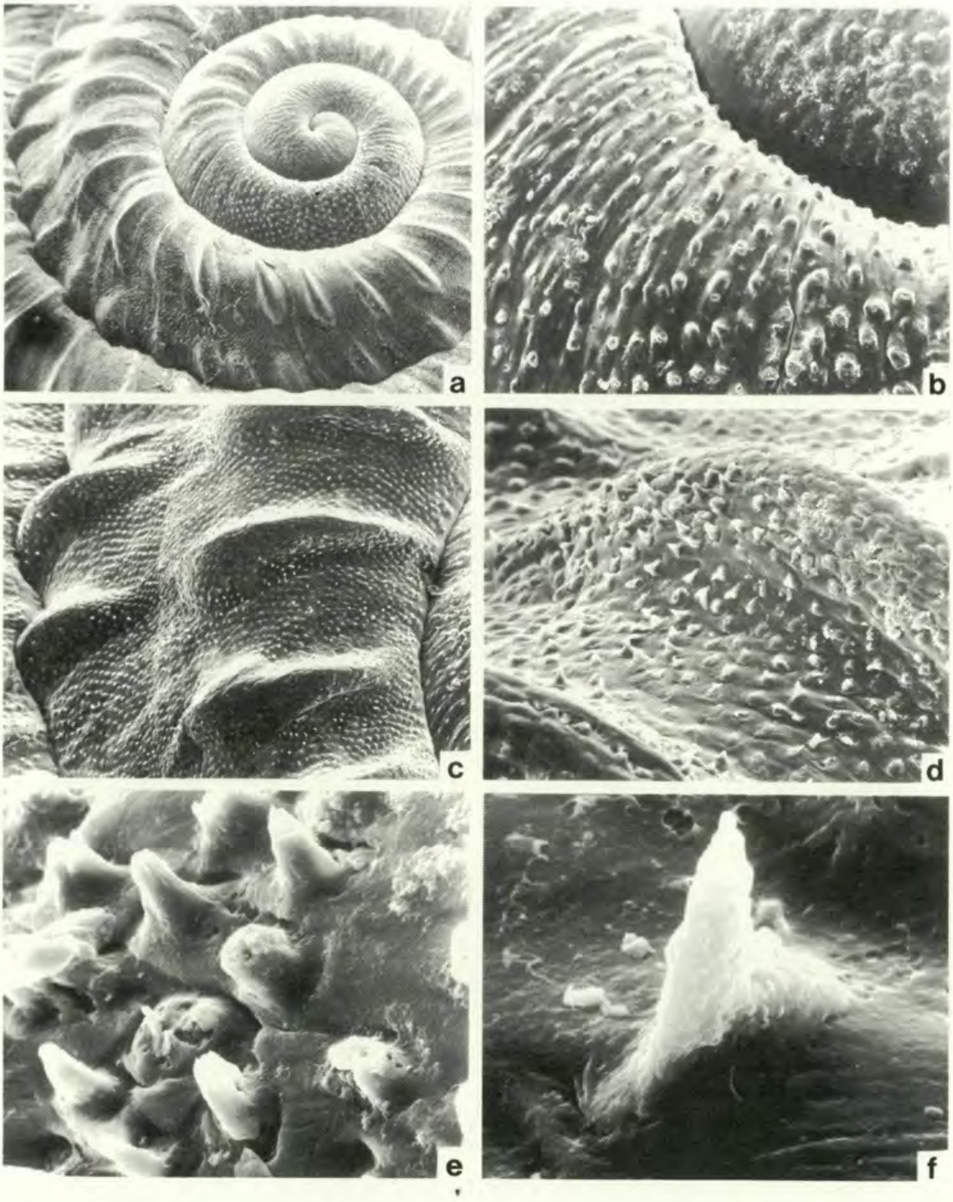


Plate 53: Shell sculpture of *Mouldingia occidentalis:* (a-f) FMNH 200333, Sta. WA-248, 3.3 km west of Lissadell Homestead, south of Lake Argyle, 17 November 1976, (a) apex and spire at 14.8X, (b) detail of apical sculpture at 76X, (c) early spire sculpture at 36X, (d) detail of a single radial rib at 139X, (e) detail of crowded micro-projections at 685X, (f) single micro-projection at 1,320X.

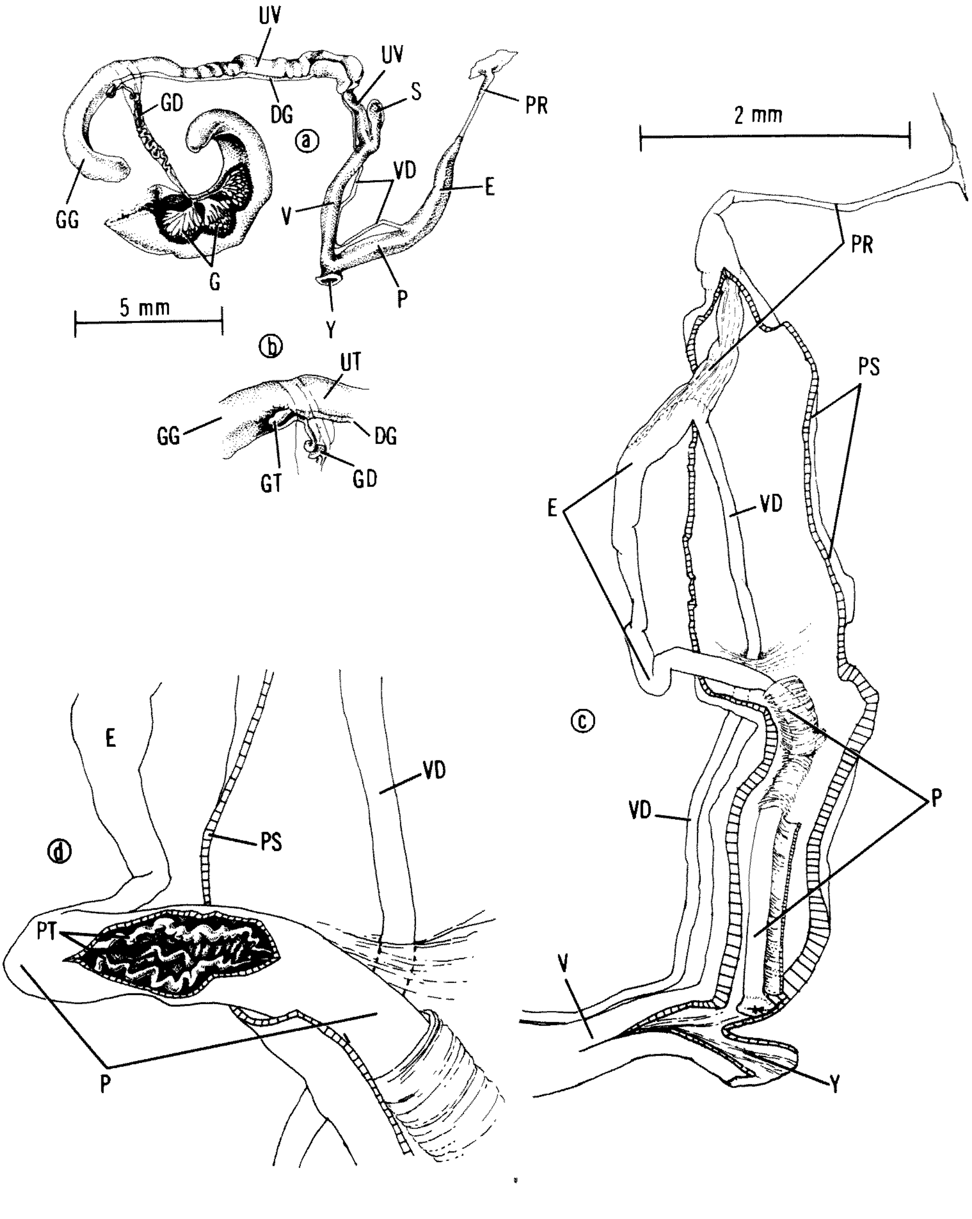


Fig. 165: Genitalia of *Mouldingia orientalis:* Sta. WA-248, Lissadell Homestead, near Lake Argyle, 17 November 1976, FMNH 200333, (a) whole genitalia, Dissection C, (b) detail of talon-carrefour region, Dissection C, (c) penis sheath opened, Dissection B, (d) apical pilasters in penis, Dissection B, Scale lines as marked. Drawings by Linnea Lahlum.

Genitalia **(Fig. 165)** with vas deferens (VD) entering about midway up penis sheath (PS), which is thick walled basally, becoming thinner in epiphallic section. Most of penis (P) bound to wall of sheath by fibers, epiphallic junction indicated by a lateral bulge **(Fig. 165d)**. Penis interior typical, with several zigzagged apical pilasters **(Fig. 165d**, PT). Penial retractor muscle extending downward along epiphallus **(Fig. 165c)**. Terminal female and apical genitalia without unusual features.

Jaw **(Plate 58h)** typical camaenid in structure with prominent vertical ribs. Radular teeth **(Plate 59c-e)** the same as in *M. occidentalis*, mesoconal tip of central and lateral teeth blunt and curved.

Discussion

Mouldingia orientalis was extremely abundant in a small cliff base talus. Initial burrowing produced more than 900 dead adults, but not a single live example. A lateral shift of less than 0.5 m opened up an aestivation pocket, and 209 live adults were collected in less than 15 minutes. A second colony was located a few hundred metres east, but no specimens were found at Sta. WA-246 on the shore of Lake Argyle **(Fig. 179)**. A number of limestone hillocks were drowned by the flooding of Lake Argyle and in all probability additional colonies vanished in the process. I know of no nearby, still exposed limestone masses that could harbor additional colonies, and conversations with the staff of Lissadell also were unproductive. The entire range of *Mouldingia orientalis* is thus less than 0.5 km.

Because of the very large number of individuals taken, and the slight variation in size among stations **(Table 67)**, no attempt was made to measure all adult examples.

Mouldingia orientalis is sympatric with *Exiligada negriensis* Iredale, 1939, although only dead examples of the latter have been taken on Lissadell Station. On the basis of live collections elsewhere, the latter species probably is not rock associated, and thus may be microallopatric locally.

The name *orientalis* refers to the eastern location of this species within the range of the genus.

GENUS *ORDTRACHIA* NEW GENUS

Shell variable in size, quite small *(intermedia)* to large *(grandis)*, apex and spire moderately and evenly elevated, at most slightly rounded above **(Figs. 166, 171, 172)**, body whorl descending slightly just before aperture, except *intermedia* **(Fig. 172b)** where the preapertural descension is increased. Umbilicus widely open *(intermedia* **Fig. 172c)** to almost closed by reflection of columellar lip *(septentrionalis,* **Fig. 166c)**. Apical sculpture usually of fine radial riblets **(Plates 54a-b, 55a-b, 56a-b)**, prominent rows of short raised radial ridgelets only in *intermedia* **(Plate 56d-e)**. Postapical sculpture usually macroscopically smooth **(Figs 166, 171)**, prominent, protractive radial ribs present only in *intermedia* **(Figs 172a-c)**. Microsculpture of low, blunt pustules *(septentrionalis,* **Plate 54c-d)**, "V"-shaped periostracal ridges *(australis,* **Plate 55c-d)**, reduced "V"-shaped scattered periostracal ridges *(grandis,* **Plate 56c)**, or a dense coat of pointed periostracal projections *(intermedia,* **Plate 56d-f)**. Sculpture reduced on shell base and in umbilicus for all species except *grandis,* which has reduced sculpture over entire shell. Body whorl slightly deflected just behind aperture in all species except *intermedia* **(Fig. 172b),** where it occurs earlier and is greater. Lip strongly expanded and reflexed, outer edge rolled, reduced to a thin callus on parietal wall **(Figs 166c, f, 171c, 172c).** Internal lip nodes occasionally in *intermedia*. Shell periphery weakly **(Figs 166b, 172b)** to strongly **(Figs 166e, 171b)** protruded as a thread-like keel, sulci weak except for supraperipheral in *intermedia* **(Fig. 172b).** Whorls of spire relatively flat in *australis* **(Fig. 166e)** and *grandis* **(Fig. 171b),** more strongly rounded in species with weaker keels, *septentrionalis* **(Fig. 166b)** and *intermedia* **(Fig. 172b).** Shell colour monochrome light yellow brown in *intermedia*, a weakly variegated pattern of brownish and yellow flammulations in remaining species, shell base lighter to white in all species. Genitalia **(Figs 167-170, 173)** with normal seasonal variations. Hermaphroditic duct (GD) entering subterminally or laterally into talon (GT). Ovotestis (G) with clumps well separated. Albumen gland (GG) proportionately quite large in both *septentrionalis* **(Fig. 167a)** and *intermedia* **(Fig. 173a).** Prostate (DG) and uterus (UT) typical. Free oviduct (UV) ranging from much longer than spermatheca (S) and strongly sinuated *(septentrionalis*, **Fig. 167a** and *intermedia*, **Fig. 173a)** to shorter than spermatheca and only slightly sinuated *(australis*, **Fig. 168a).** Spermatheca very short *(intermedia*, **Fig. 173a),** intermediate in length *(grandis*, **Fig. 169a),** to long *(septentrionalis*, **Fig. 167a** and *australis*, **Fig. 168a).** Vagina (V) very short in *septentrionalis* with base of spermatheca swollen **(Fig. 167a),** longer in other species. Atrium (Y) very short. Terminal male genitalia enclosed in a thin-walled sheath (PS) that is at most slightly thickened basally. Vas deferens (VD) entering sheath at or slightly above head of penis (P), continuing to apex where it reflexes and becomes epiphallus (E). Penial retractor muscle (PR) attaching to head of epiphallus, continuing as grossly expanded penis muscle-glandular zone on side opposite to vas deferens **(Figs 167b, 168b, 169b, c, 173b)** down to penis apex. Epiphallic region thus consisting of large muscle-gland outer portion and very narrow tube **(Figs 168b, 169c).** Base of epiphallus and head of penis with a lateral, thin-walled, glandular outpocket that is most clearly differentiated in *intermedia* **(Fig. 173b).** Penis with thick walls, internally with weak, simple longitudinal pilasters. Jaw **(Plate 58c-g)** typically camaenid. Radular teeth **(Plates 60-62)** modified only in having mesocones of central and laterals bluntly tipped with some curvature, ectocones and occasionally endocone fairly prominent. Marginal teeth typical.

Type species: *Ordtrachia septentrionalis* sp. nov.

Comparisons

The variable shell sculpture, shape, and size of species assigned to *Ordtrachia* make conchological generic characterisation difficult. The key feature of the genus is a unique modification to the terminal male genitalia. The penis muscle (PM) and epiphallic loop of *Westraltrachia* has shrunken into a thickened area on the outer margin of the epiphallus, producing a glandularised-muscular area that finds no direct parallel in any other camaenid lineage. This feature is shared with *Exiligada* Iredale, 1939 **(Figs 175b, d),** a sympatric genus easily separated by its globose shell that lacks a keel and its tendency to aestivate by burrowing under vegetation, rather than living in talus as does *Ordtrachia*. Discussion of the direction of character changes that led to this feature is presented below on p. 697.

The presence of a thread-like keel on the shell of *Ordtrachia* **(Figs 166b, e, 171b, 172b)** is shared with *Mouldingia* **(Figs 163b, e),** and *Prototrachia sedula* **(Fig. 176b).** The sulci and strong radial ribs of *O. intermedia* made us field identify this species as a *Mouldingia*. That genus differs in its genitalia, which has a comparatively short penis-epiphallus whose junction is marked only by a slight bend, lacks the epiphallic muscle-glandular zone of *Ordtrachia*, and has the penial retractor muscle (PR) either attach simply to the vas-epiphallic junction **(Fig. 164d)** or extend slightly down the epiphallus **(Fig. 165c)**. The micropustulations are of the same type found in *Mouldingia* **(Plates 52, 53)**, *Westraltrachia froggatti* (Ancey, 1898) **(Plate 20f)**, and *W. ascita* **(Plate 25)**.

Thus shell features are shared within the entire complex of genera, but there is a unique directional change in the genitalia that has a coherent geographic range. It has been used to define *Ordtrachia*.

Four species are known: *Ordtrachia septentrionalis* from a 1.4 km stretch along the new Duncan Highway near the current Rosewood Station turnoff **(Fig. 179,** Sta. WA-242, WA-594, WA-707), where it lives under isolated limestone boulders in open savannah country that floods during the wet season, and The Rock Wall, 7.6 km west on the Old Duncan Highway; *O. grandis* found in a 6.7 km stretch of the new Duncan Highway from 8.4-15.1 km south of the Behn River Crossing **(Fig. 179,** Sta. WA-244, WA-595, WA-598, WA-597, WA-596), and formerly taken in quantity from a limestone wall (The Rock Wall, **Fig. 179)** at the former Rosewood turnoff on the Old Duncan Highway; *O. australis* from a cliff area 5.4 km south of the current Rosewood turnoff on the new Duncan Highway and 11.6 km north of the Behn River crossing **(Fig. 179,** Sta. WA-245, WA-600); and *O. intermedia* that is sympatric with *O. grandis* at Sta. WA-244, WA-595, WA-597, WA-598 **(Fig. 179)**, but also has been taken at Sta. WA-708, much further south on the Duncan Highway, about 43.5 km north of the Nicholson River (17° 41′ S, 128° 49′ E).

The new Duncan Highway still is closed for several months each year because of damage from severe wet season flooding and sections of the Old Duncan Highway were covered by the flooding of Lake Argyle. Undoubtedly the local ranges of *Ordtrachia* are affected by the annual torrents swirling past and over the limestone exposures with which they are directly associated. No specimens have been taken alive or recently dead other than immediately around limestone rocks.

A key to shell features follows:

KEY TO THE SPECIES OF *ORDTRACHIA*

1. Shell with strong radial ribs; diameter under 11 mm .... *Ordtrachia intermedia* sp. nov.
   Shell without strong radial ribbing 2
2. Umbilicus nearly closed **(Fig. 166c)**; peripheral keel obtuse, whorls of spire rounded **(Fig. 166b)** .... *Ordtrachia septentrionalis* sp. nov.
   Umbilicus at least slightly open **(Figs. 166e, 171c)**; peripheral keel acutely angled **(Figs 166e, 173b)** 3
3. Micropustulations prominent; spire higher, mean H/D ratio 0.534 .... *Ordtrachia australis* sp. nov.
   Micropustulations obscure; spire lower, mean H/D ratio 0.434 .... *Ordtrachia grandis* sp. nov.

The name *Ordtrachia* refers to the geographic location of this genus within the Ord River drainage, its survival of the Ord River project's flooding of Lake Argyle (although many colonies probably vanished through this event), and the fact that it is related to both *Westraltrachia* Iredale, 1933 and *Prototrachia* from a nearby area in the Northern Territory.

ORDTRACHIA SEPTENTRIONALIS SP. NOV.

(Plates 54, 58d-e, 60a-d; Figs 166a-c, 167)

Comparative remarks

Ordtrachia septentrionalis is most readily recognised by its combination of nearly closed umbilicus **(Fig. 166b),** almost rounded and weakly keeled periphery, prominent micropustulations, but absence of radial ribs, and comparatively high spire (mean H/D ratio 0.608). *Ordtrachia intermedia* **(Fig. 172)** is much smaller (mean diameter 8.76 mm compared with 13.00 for *septentrionalis),* has a widely open umbilicus, and very prominent radial ribs. Both *O. grandis* and *O. australis* have sharply keeled peripheries, are much lower in profile (mean H/D ratios, respectively, 0.434 and 0.534), and have less prominent micropustulations. The shortened vagina (V) and thickened base of the spermatheca **(Fig. 167a,** S) in *O. septentrionalis* are the obvious genital differences from other species of *Ordtrachia.*

Holotype

WAM 514.80, Sta. WA-707, scattered limestone rocks in open field, just west of new Duncan Highway, 1.4 km south of current Rosewood Station turnoff, south of Kununurra, Northern Territory (1:100,000 'Newry' map sheet 4765 – 031:789). Collected by Alan Solem, Laurie Price and Barbara Duckworth 16 June 1980. Height of shell 8.05 mm, diameter 12.75 mm, H/D ratio 0.631, whorls 5⅛, umbilical width 0.95 mm, D/U ratio 13.4.

Paratopotypes

WAM 563.80, WAM 564.80, FMNH 205295-6, 10 live and 22 dead adults, 6 live and 13 dead juveniles from the type locality.

Paratypes

Sta. WA-242, new Duncan Highway at current Rosewood Station turnoff, southwest corner ('Newry' 4765 – 033:800) (29 dead adults, WAM 561.80, FMNH 199610); Sta. WA-594 (= WA-242) (1 live, 5 dead adults, WAM 562.80, FMNH 204754-5); at the former Rosewood Station turnoff from old Duncan Highway by The Rock Wall (7 dead adults, WAM 427.77, WAM 431.77, WAM 433.77 collected between 24 June 1966 and 8 June 1967).

Diagnosis

Shell of medium size, 11.1-14.75 mm (mean 13.00 mm) in diameter, with 4⅜+ to 5⅜ (mean 4⅞+) normally coiled whorls. Apex and spire moderately and evenly elevated, slightly rounded above, body whorl descending slightly just before aperture, height of shell 6.7-9.2 mm (mean 7.64 mm), H/D ratio 0.537-0.685 (mean 0.608). Apical sculpture **(Plate 54a-b)** of very fine radial riblets. Postapical whorls with at most weak irregular radial growth lines, plus a dense pattern of prominent pustulations **(Plate 54c-d)** that are greatly reduced to absent below periphery. Shell periphery **(Fig. 166b)** with a thread-like keel, but whorl profile rounded and usually no sulci present. Body whorl descending slightly just before aperture. Lip strongly reflexed and rolled, expanded, columellar reflection nearly covering umbilicus **(Fig. 166c)**, lip reduced to a thin callus on parietal wall. No internal lip nodes. Umbilicus a lateral crack to narrowly open **(Fig. 166c)**, umbilical width 0.4-1.85 mm (mean 0.89 mm), D/U ratio 7.38-36 (mean 16.3). Based on 74 measured adults.

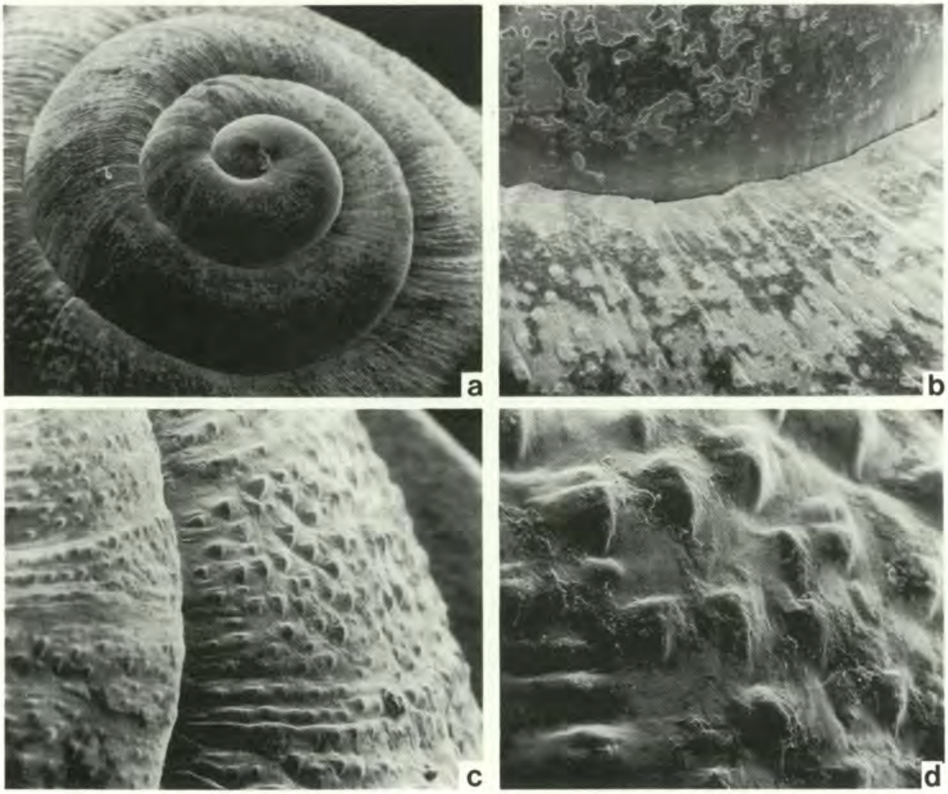


Plate 54: Shell sculpture of *Ordtrachia septentrionalis:* (a-d) FMNH 199610, Sta. WA-242, Duncan Highway at Rosewood turnoff, south-west corner, 15 November 1976, juvenile, (a) apex and early spire at 14.0X, (b) detail of apex at 69X, (c) detail of sculpture on early spire at 35X, (d) detail of projections on body whorl at 125X.

Genitalia **(Fig. 167)** with hermaphroditic duct (GD) entering talon (GT) laterally. Albumen gland (GG) proportionately large, prostate (DG) and uterus (UT) without unusual features. Free oviduct (UV) long, strongly sinuated, entering at right angles into spermathecal-vaginal junction. Spermatheca long, base grossly enlarged **(Fig.**

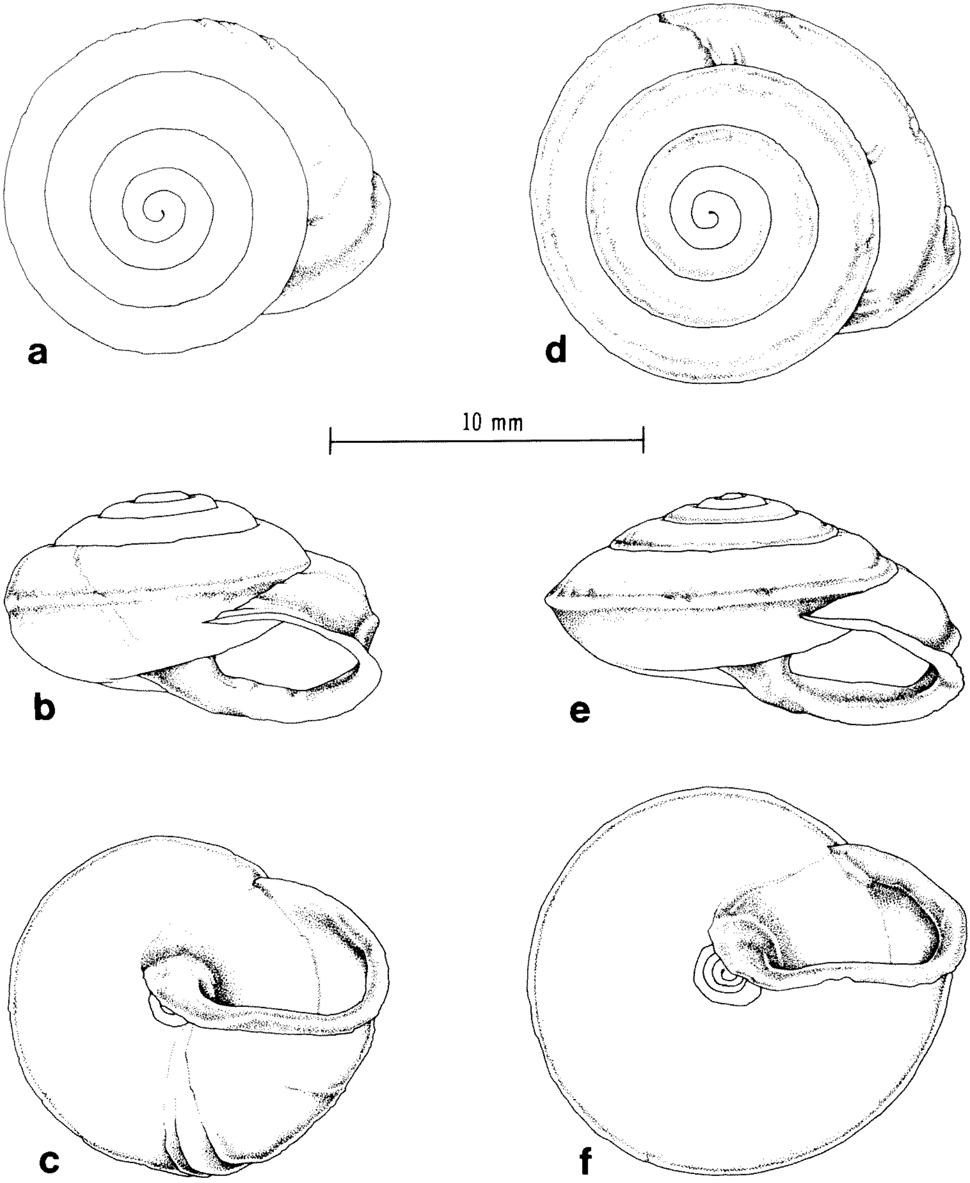


Fig. 166: Shells of *Ordtrachia septentrionalis* and *O. australis:* (a-c) *O. septentrionalis,* Sta. WA-707, 1.4 km south of Rosewood turnoff, Duncan Highway, south of Kununurra, Northern Territory, 16 June 1980, WAM 514.80, holotype; (d-f) *O. australis,* Sta. WA-245, 11.6 km north of Behn River, Duncan Highway, south of Kununurra, 16 November 1976, WAM 515.80, holotype. Scale line equals 10 mm. Drawings by Linnea Lahlum.

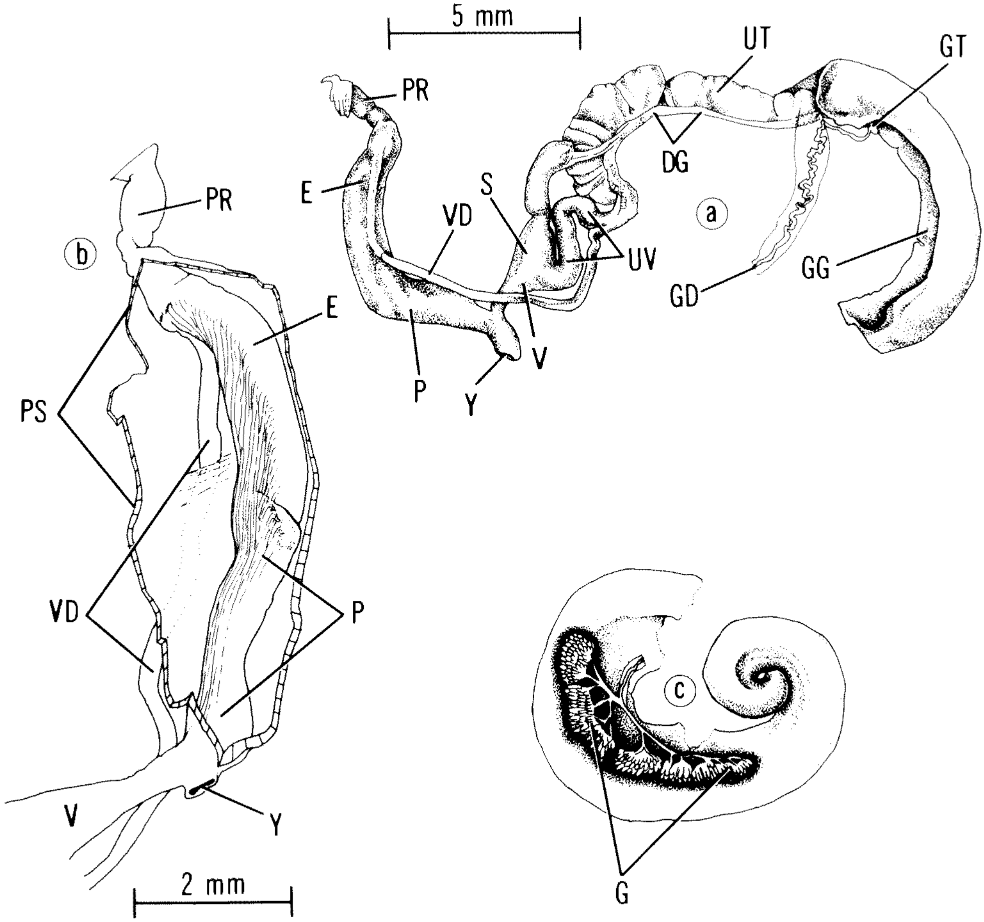


Fig. 167: Genitalia of *Ordtrachia septentrionalis:* Sta. WA-707, 1.4 km south of Rosewood turnoff, Duncan Highway, south of Kununurra, Northern Territory, 16 June 1980, FMNH 205295, (a) whole genitalia, Dissection B, (b) penis chamber, Dissection A, (c) ovotestis, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

167a), head attached to prostate-uterus by strands of connective tissue. Vagina very short. Vas deferens (VD) entering rather thick-walled penis sheath **(Fig. 167b,** PS) above midpoint and slightly above penis-epiphallic junction, reflexing apically to enter epiphallus (E) with outer side (twisted inward in **Fig. 167b)** containing fused muscle-glandular zone, base with thin glandular pocket (stippled in **Fig. 167b).** Penis (P) short, not bound to wall of sheath, thick walled, internally with simple longitudinal pilasters.

Jaw **(Plate 58d-e)** with strong vertical ribs that vary in number. Radular teeth **(Plate 60a-d)** with prominent side cusps and bluntly tipped, curved mesocone on laterals and central, marginals typical.

Discussion

Ordtrachia septentrionalis has a known range of only 1.4 km along the new Duncan Highway just south of the Rosewood Station road turnoff (**Fig. 179**). In several low areas along this stretch, on both sides of the road, scattered limestone boulders and blocks are exposed in open savannah plains. The blocks vary from a few inches to several feet in diameter, but rarely project more than a few inches above ground level. Accumulations of mud and leaves testify that flooding is a frequent wet season event. Six separate collecting visits to this region enabled finding a total of 11 live adults and 6 live juveniles. All were taken west of the new Duncan Highway, although the rock exposures on the east side were 'better looking' snail shelter.

The next noticed limestone exposure, 4 km further south, is the type locality of *O. australis*. *Exiligada negriensis* Iredale, 1939 is not recorded this far north on the east side of Lake Argyle.

Insignificant shell variation was noted among allochronic or allopatric samples (**Table 68**), the differences not exceeding probable measurement error.

Table 68: Local Variation in *Ordtrachia septentrionalis* and *O. australis*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
O. septentrionalis				
WA-242, FMNH 199610	29(D)	8.16 ± 0.113 (6.8 – 9.2)	13.03 ± 0.142 (11.1 – 14.75)	0.626 ± 0.006 (0.569 – 0.685)
WA-594, FMNH 204755	5(D)	7.72 ± 0.153 (7.2 – 8.05)	12.60 ± 0.179 (11.9 – 12.95)	0.613 ± 0.007 (0.599 – 0.637)
WA-707, FMNH 205295	10(L)	8.06 ± 0.147 (7.45 – 9.0)	13.39 ± 0.186 (12.3 – 14.0)	0.602 ± 0.009 (0.557 – 0.639)
WA-707, FMNH 205296	23(D)	7.57 ± 0.116 (6.7 – 8.5)	12.98 ± 0.135 (11.8 – 14.3)	0.583 ± 0.006 (0.537 – 0.623)
Rosewood turnoff, Old Duncan Hwy., WAM: 427.77, 431.77, 433.77	7(D)	7.80 ± 0.206 (7.0 – 8.6)	12.63 ± 0.210 (11.8 – 13.4)	0.617 ± 0.010 (0.593 – 0.664)
O. australis				
WA-245, FMNH 200173	82(L)	7.71 ± 0.050 (6.55 – 8.95)	14.29 ± 0.061 (13.1 – 15.65)	0.540 ± 0.003 (0.482 – 0.606)
WA-245, FMNH 199622	296(D)	7.72 ± 0.030 (6.45 – 9.1)	14.31 ± 0.036 (12.5 – 15.7)	0.540 ± 0.002 (0.450 – 0.627)
WA-600, FMNH 204778	4(L)	7.33 ± 0.293 (6.8 – 8.0)	14.94 ± 0.716 (13.4 – 16.5)	0.492 ± 0.008 (0.482 – 0.515)
WA-600, FMNH 204777	148(D)	7.46 ± 0.041 (6.65 – 8.8)	14.34 ± 0.052 (12.75 – 15.9)	0.520 ± 0.002 (0.453 – 0.602)
22 km SW of Nicholson, NMV	8(D)	7.55 ± 0.076 (7.25 – 7.8)	14.56 ± 0.171 (13.55 – 15.2)	0.519 ± 0.006 (0.490 – 0.546)

Table 68: Local Variation in *Ordtrachia septentrionalis* and *O. australis* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
O. septentrionalis				
WA-242, FMNH 199610	29(D)	4⅞ – (4¾ + – 5⅛)	0.92 ± 0.054 (0.5 – 1.85)	15.4 ± 0.859 (7.60 – 24.6)
WA-594, FMNH 204755	5(D)	4⅞ – (4¾ – – 4⅞ +)	0.73 ± 0.100 (0.4 – 1.0)	18.9 ± 3.39 (12.7 – 32)
WA-707, FMNH 205295	10(L)	5 (4⅝ – 5¼)	1.14 ± 0.112 (0.7 – 1.7)	12.6 ± 1.20 (7.94 – 18.7)
WA-707, FMNH 205296	23(D)	5 + (4¾ – – 5⅜)	0.71 ± 0.041 (0.4 – 1.15)	19.8 ± 1.24 (11.3 – 36)
Rosewood turnoff, Old Duncan Hwy., WAM: 427.77, 431.77, 433.77	7(D)	5 (4¾ – – 5⅛)	1.136 ± 0.123 (0.8 – 1.6)	11.9 ± 1.21 (7.38 – 15.4)
O. australis				
WA-245, FMNH 200173	82(L)	5¼ – (4¾ – 5⅝ –)	1.48 ± 0.033 (0.8 – 2.1)	10.1 ± 0.245 (6.59 – 18.9)
WA-245, FMNH 199622	296(D)	5¼ – (4⅝ + – 5⅝)	1.54 ± 0.020 (0.6 – 2.7)	9.77 ± 0.137 (5.56 – 25.7)
WA-600, FMNH 204778	4(L)	5⅜ (5 + – 5⅝)	2.18 ± 0.075 (2.1 – 2.4)	6.87 ± 0.385 (6.24 – 7.99)
WA-600, FMNH 204777	148(D)	5¼ + (4⅞ – – 5¾ +)	1.33 ± 0.032 (0.35 – 2.4)	11.8 ± 0.351 (6.03 – 39)
22 km SW of Nicholson, NMV	8(D)	5¼ (5⅛ – – 5⅜)	1.58 ± 0.136 (1.1 – 2.3)	10.0 ± 0.880 (6.44 – 13.5)

Because of the limited live material obtained and the striking difference in the vagina-spermatheceal region **(Fig. 167b)**, only two specimens were dissected for this project.

The name *septentrionalis* refers to the fact that this is the northernmost species of *Ordtrachia.*

ORDTRACHIA AUSTRALIS SP. NOV.

(Plates 55, 58g, 60e-f; Figs 166d-f, 168)

Comparative remarks

Ordtrachia australis differs from *O. septentrionalis* in having a sharply protruded peripheral keel **(Figs 166b, e)**, which increases the shell diameter and reduces the H/D ratio **(Table 66)**, more open umbilicus **(Figs 166c, f)**, and in having a much longer, more slender vagina **(Fig 168a**, V), no enlargement of the spermatheceal base (S), a higher entrance of the vas deferens (VD) into the penis sheath **(Fig. 168b,** PS), and a shorter epiphallus **(Fig. 168b, E).** *Ordtrachia grandis* is much larger in size, has a greatly reduced H/D ratio, wider umbilicus (see **Fig. 171, Table 66),** and the shell microsculpture is greatly reduced in prominence. *Ordtrachia intermedia* **(Fig. 172)** is immediately differentiated by its much smaller size, prominent radial ribbing, rounded periphery with prominent supraperipheral sulcus, and widely open umbilicus.

Holotype

WAM 515.80, Sta. WA-245, just west of new Duncan Highway, 11.6 km north of Behn River Crossing, 5.4 km south of Rosewood Station turnoff, south of Kununurra, Northern Territory (1:100,000 'Newry' map sheet 4765 – 003:760). Collected by Alan Solem and Carl C. Christensen 16 November 1976. Height of shell 7.7 mm, diameter 14.5 mm, H/D ratio 0.531, whorls 5-¼, umbilical width 1.3 mm, D/U ratio 11.2.

Paratopotypes

WAM 565.80, WAM 566.80, FMNH 199622, FMNH 200173, 82 live and 295 dead adults, 5 live juveniles from the original 1976 collection, and WAM 567.80, WAM 568.80, FMNH 204777-8, 4 live and 148 dead adults, 5 live juveniles from 1980 collecting (Sta. WA-600 = WA-245).

Diagnosis

Shell of medium size, 12.5-16.5 mm (mean 14.32 mm) in diameter, with 4⅝+ to 5¾+ (mean 5¼–) normally coiled whorls. Apex and spire moderately and almost evenly elevated, slightly rounded above, body whorl descending slightly just before aperture **(Fig. 166e),** height of shell 6.5-9.1 mm (mean 7.65 mm), H/D ratio 0.450-0.627 (mean 0.534). Apical sculpture **(Plate 55a)** of very fine radial riblets. Postapical whorls **(Plate 55b-d)** with weak irregular growth lines overlaid with a dense, rather coarse microsculpture of pustulations, that are greatly reduced to absent below periphery. Shell periphery **(Fig. 166e)** with a protruded thread-like keel, some examples with distinct supra- or subperipheral sulci. Body whorl descending just before aperture. Lip strongly reflexed and rolled, expanded, columellar section about half covering umbilicus **(Fig. 166f).** No internal lip nodes. Umbilical width quite variable, 0.35-2.7 mm (mean 1.48 mm), normally about half open, D/U ratio 5.56-39 (mean 10.4). Based on 530 measured adults.

Genitalia **(Fig. 168)** with hermaphroditic duct (GD) entering side of talon **(Fig. 168c,** GT). Albumen gland (GG) of normal size, prostate (DG) and uterus (UT) without unusual features. Free oviduct (UV) slightly sinuated, shorter than spermatheca **(Fig. 168a,** S), which is attached to prostate-uterus by connective tissue strands. Vagina (V) long. Vas deferens (VD) entering penis sheath **(Fig. 168b,** PS) above head of penis (P), approximately one-third of way from sheath apex. Penial retractor muscle (PR) arising from base of diaphragm, inserting on vas deferens-epiphallic junction. Epiphallus (E) short, most of volume a muscle-glandular zone that lies on outside of organ, internal tube minute **(Fig. 168b,** drawing with epiphallus twisted to show basal patch, twisting omitted apically) opening into a thin-walled glandular sac at head of penis. Penis (P) not bound to wall of sheath, longer than epiphallus, thick walled, internally with simple longitudinal pilasters.

Jaw **(Plate 58g)** with a few strong vertical ribs. Radular teeth **(Plate 60e-f)** typical of genus, with blunt, curved mesoconal cusp and prominent side cusps on central and laterals.

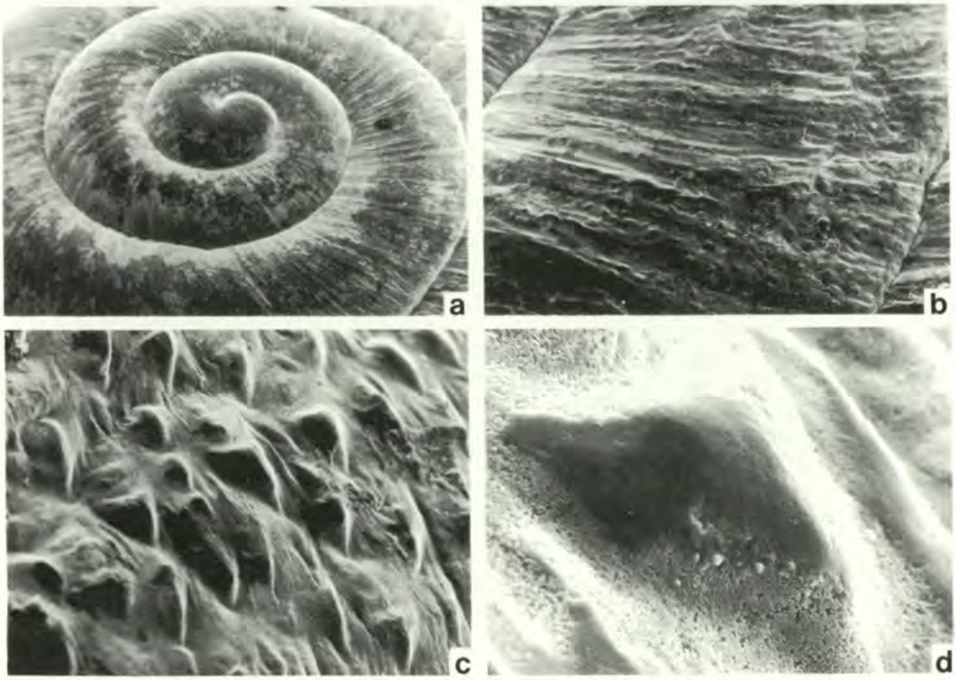


Plate 55: Shell sculpture of *Ordtrachia australis:* (a-d) FMNH 200173, Sta. WA-245, 11.6 km north of Behn River crossing, Duncan Highway, 16 November 1976, juvenile, (a) apex and spire at 14.7X, (b) detail of mid-spire at 35X, (c) detail of body whorl at 139X, (d) single projectionn on body whorl at 660X.

Discussion

Ordtrachia australis is known from only the one colony, Sta. WA-245 (= WA-600), occupying a short cliff area 5.4 km south of the current Rosewood Station road turnoff and 11.6 km north of the Behn River crossing, just west of the new Duncan Highway. This is an isolated exposure **(Fig. 179)** and neither topographic nor geologic maps of the region suggest possible locations for additional colonies. This is the only camaenid found at this locality. *Ordtrachia septentrionalis* is 4 km (Sta. WA-707) and 5.4 km north (Sta. WA-242 and WA-594). *Ordtrachia grandis* lives 20 km south (WA-244) and in the The Rock Wall **(Fig. 179)** about 7.6 km west. The only intermediate positive collecting Station, WA-243 and WA-599, yielded only dead examples of *Exiligada negriensis* Iredale, 1939 on visits in 1976 and 1980.

The difference in shell height and then H/D ratio **(Table 68)** shown between dead material collected in 1976 (Sta. WA-245) and 1980 (Sta. WA-600) is an artifact of measurement. The angle at which the shell is oriented to record the shell height parameter is subject to individual judgement, and the sets were measured by two different people. This is not allochronic variation.

The name *australis,* referring to a southern geographic location, was selected before I was aware that *Ordtrachia intermedia* was a member of this genus and when I was confused as to the identity of *O. grandis.* Although this is not the southernmost species of *Ordtrachia,* the name has been retained as a permanent reminder not to jump to conclusions as to affinities or ranges of species. After writing the above, a set of eight dead adults (NMV), from a creek bed (probably Calico Creek), along Duncan Highway 22 km south-west of the Buchanan-Duncan Highway junction at Nicholson, collected by A.C. Beauglehole 23 May 1976 was uncovered. In size and shape **(Table 68)** they are identical to *O. australis,* but too worn for certain classification. If confirmed, this record would be the southernmost for the genus, and the name thus more appropriate.

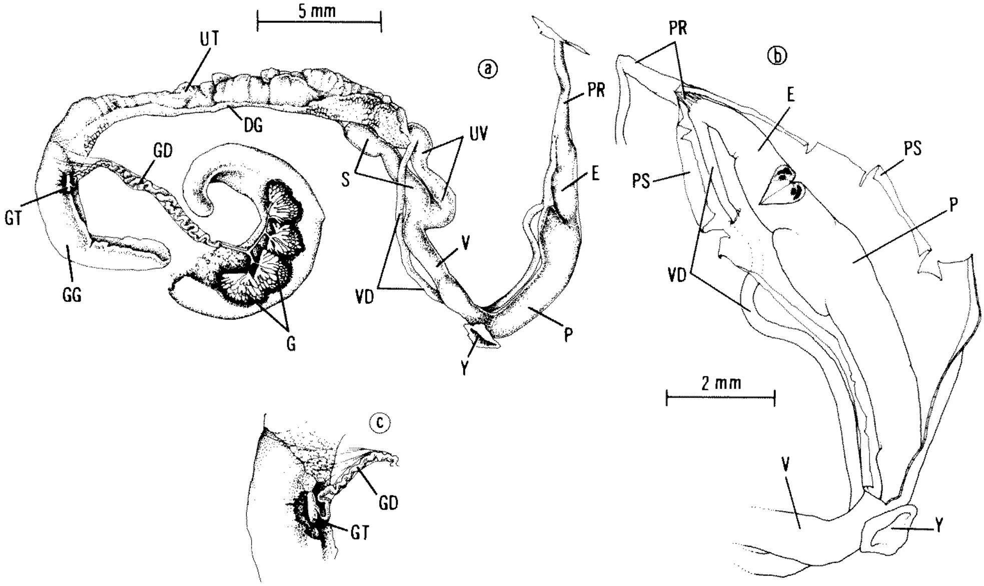


Fig. 168: Genitalia of *Ordtrachia australis:* Sta. WA-245, 11.6 km north of Behn River, Duncan Highway, south of Kununurra, 16 November 1976, FMNH 200173, Dissection B, (a) whole genitalia, (b) detail of talon, (c) penis complex. Scale lines as marked. Drawings by Linnea Lahlum.

ORDTRACHIA GRANDIS SP. NOV.

(Plates 56a-c, 58c, 61; Figs 169-171)

Comparative remarks

Ordtrachia grandis is the largest **(Table 66)** and most depressed **(Fig. 171b)** member of the genus. It also has the micropustulations greatly reduced in prominence **(Plate 56a-c)**. The genitalia **(Figs 169-170)** has a long vagina (V), moderate swelling of the spermathecal base (S), and relatively long penis-epiphallus that must be partly coiled within the penis sheath (PS). *Ordtrachia septentrionalis* has very prominent micropustulations **(Plate 54c)**, a much more globose shell with reduced keel and nearly closed umbilicus **(Figs 166b, c)**, very short vagina **(Fig. 167a**, V), long free oviduct (UV), grossly expanded spermatheca base (S), and proportionately shorter penis-epiphallus **(Fig. 167b)**. *Ordtrachia intermedia* differs in its strong radial ribs **(Figs 172a-c)**, much smaller size **(Table 66)**, widely open umbilicus, prominent shell microsculpture **(Plate 56d-f)**, enlarged albumen gland **(Fig. 173a**, GG), long free oviduct (UV), and shorter penis-epiphallic tube **(Fig. 173b)**. *Ordtrachia australis* is most similar in size **(Table 66)** and shape, but differs in its narrower umbilicus **(Fig. 166c)**, much more prominent microsculpture **(Plate 55b-d)**, and shorter penis-epiphallus tube **(Fig. 168b)**. *Prototrachia sedula* is smaller, less strongly keeled **(Fig. 176b)**, has very different microsculpture **(Plate 57b-e)**, and the genitalia differs radically in penis structure **(Fig. 178)** and vaginal length **(Fig. 177a)**.

Holotype

WAM 516.80, Sta. WA-244, cliffs west of Duncan Highway, 8.4 km south of Behn River Crossing, south of Kununurra, Western Australia (1:100,000 'Lissadell' map sheet 4664 – 937:599). Collected by Alan Solem and Carl C. Christensen 16 November 1976. Height of shell 7.5 mm, diameter 8.95 mm, H/D ratio 0.439, whorls 5⅛–, umbilical width 2.05 mm, D/U ratio 8.34.

Paratopotypes

WAM 569.80, WAM 570.80, FMNH 199628, FMNH 199959, 8 live and 425 dead adults from the type locality.

Paratypes

Limestone wall (The Rock Wall) at the former Rosewood Station turnoff, Old Duncan Highway (30 dead adults, WAM 430.77, WAM 432.77, WAM 435.77, collected 16 August 1966, 18 June 1966, 29 May 1970, respectively); 14 miles south of Rosewood turnoff on Old Duncan Highway (6 dead adults, WAM 467.77 collected in 1970 by W.H. Butler); Sta. WA-595, cliffs west of new Duncan Highway, 9.0 km south of Behn River crossing ('Lissadell' 4664 – 933:583) (1 live juvenile, 57 dead adults, WAM 571.80, FMNH 204756, FMNH 204758); Sta. WA-598, edge of old gravel pit, 10.8 km south of Behn River crossing ('Lissadell' 4664 – 923:570) (2 live, 32 dead adults, WAM 573.80, FMNH 204771-2); Sta. WA-597, limestone cliffs west of new Duncan Highway, 14.3 km south of Behn River crossing ('Lissadell' 4664 – 912:540) (1 live juvenile, 45 dead adults, WAM 572.80, FMNH 204765-6); Sta. WA-596, south end of limestone hills west of new Duncan Highway, 15.1 km south of Behn River crossing ('Lissadell' 4664 – 912:532) (9 dead adults, WAM 574.80, FMNH 204761).

Diagnosis

Shell large, but variable, 14.0-22.2 mm (mean 17.03 mm) in diameter, with 4¾ to 5¾ (mean 5⅛+) normally coiled whorls. Apex and spire moderately and evenly elevated **(Fig. 171b)**, rarely rounded above, body whorl descending very slightly before aperture, height of shell 6.1-10.1 mm (7.38 mm), H/D ratio 0.347-0.523 (mean 0.434). Apical sculpture **(Plate 56a-b)** of very fine radial riblets. Postapical whorls with irregular radial

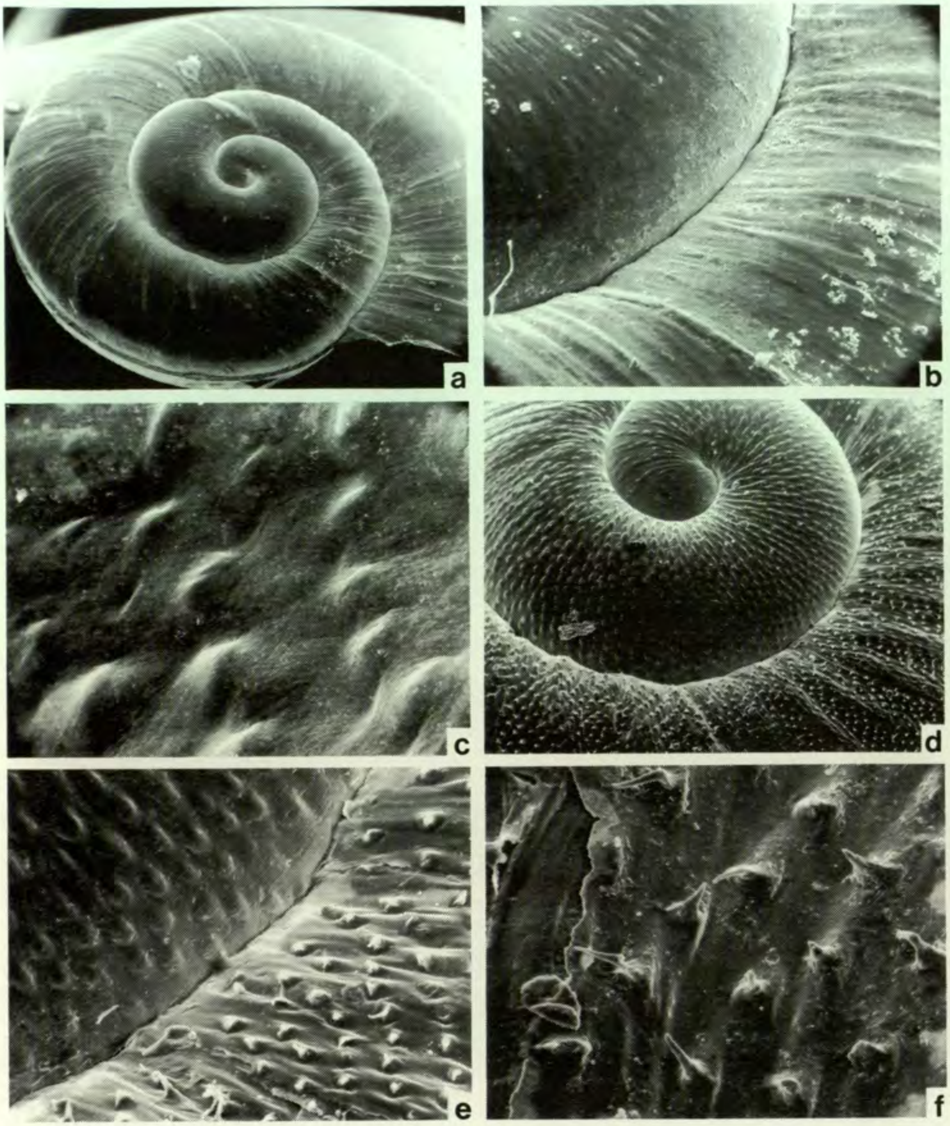


Plate 56: Shell sculpture of *Ordtrachia grandis* and *O. intermedia:* (a-c) *O. grandis,* FMNH 199959, Sta. WA-244, 8.4 km south of Behn River crossing, west of Duncan Highway, 16 November 1976, (a) Dissection A, apex and early spire at 13.1X, (b) Dissection A, detail of apex and early spire at 65X, (c) Dissection B, detail of body whorl projections at 120X; (d-f) *O. intermedia,* FMNH 204764, Sta. WA-597, 14.3 km south of Behn River crossing, 13.4 km north of Spring Creek Station turnoff from Duncan Highway, 13 May 1980, juvenile, (d) apex and early spire at 34X, (e) detail of apex and early spire at 138X, (f) detail of spire projections at 330X.

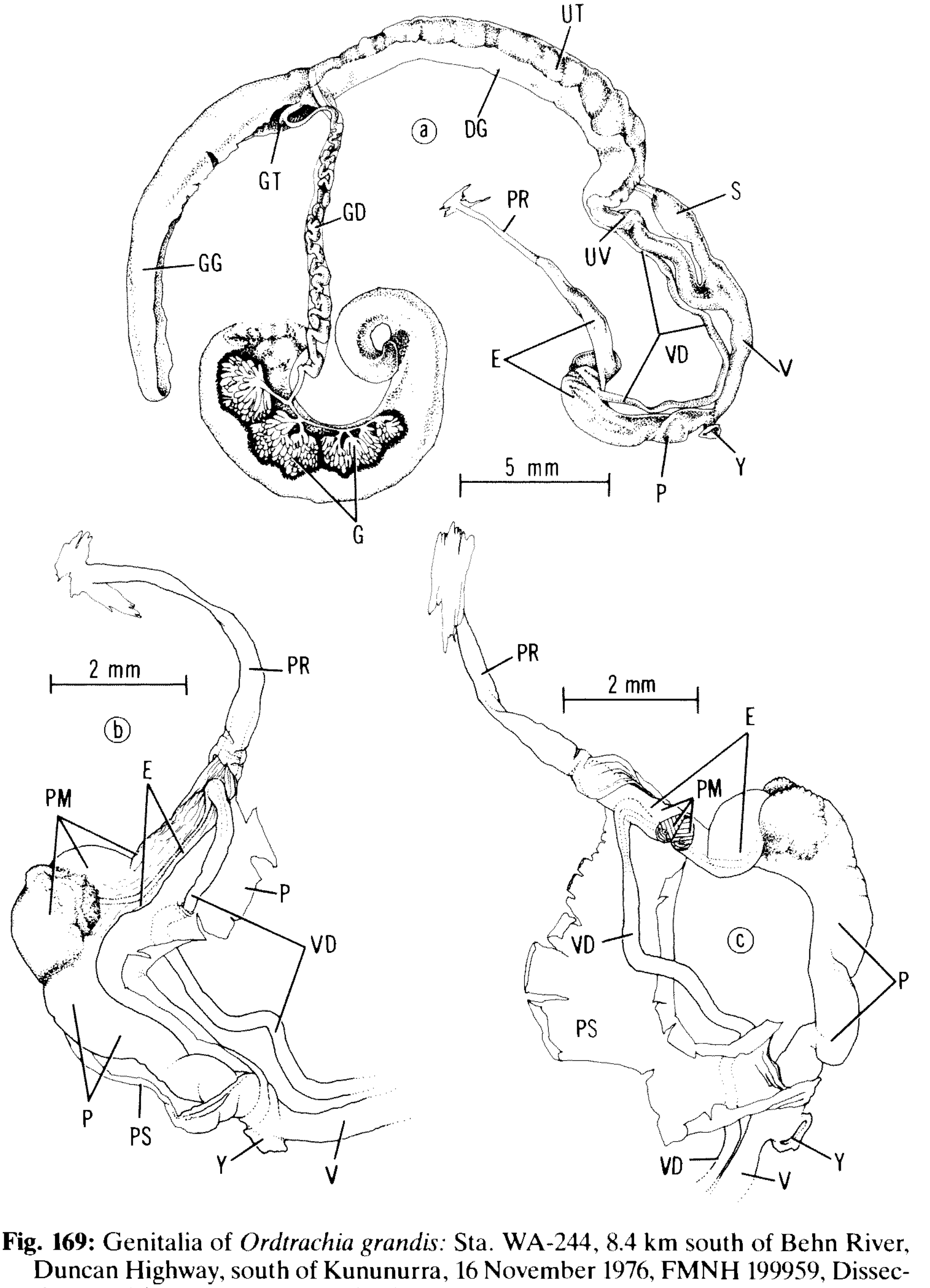


Fig. 169: Genitalia of *Ordtrachia grandis:* Sta. WA-244, 8.4 km south of Behn River, Duncan Highway, south of Kununurra, 16 November 1976, FMNH 199959, Dissection B, (a) whole genitalia, (b-c) penis sheath opened. Scale lines as marked. Drawings by Linnea Lahlum.

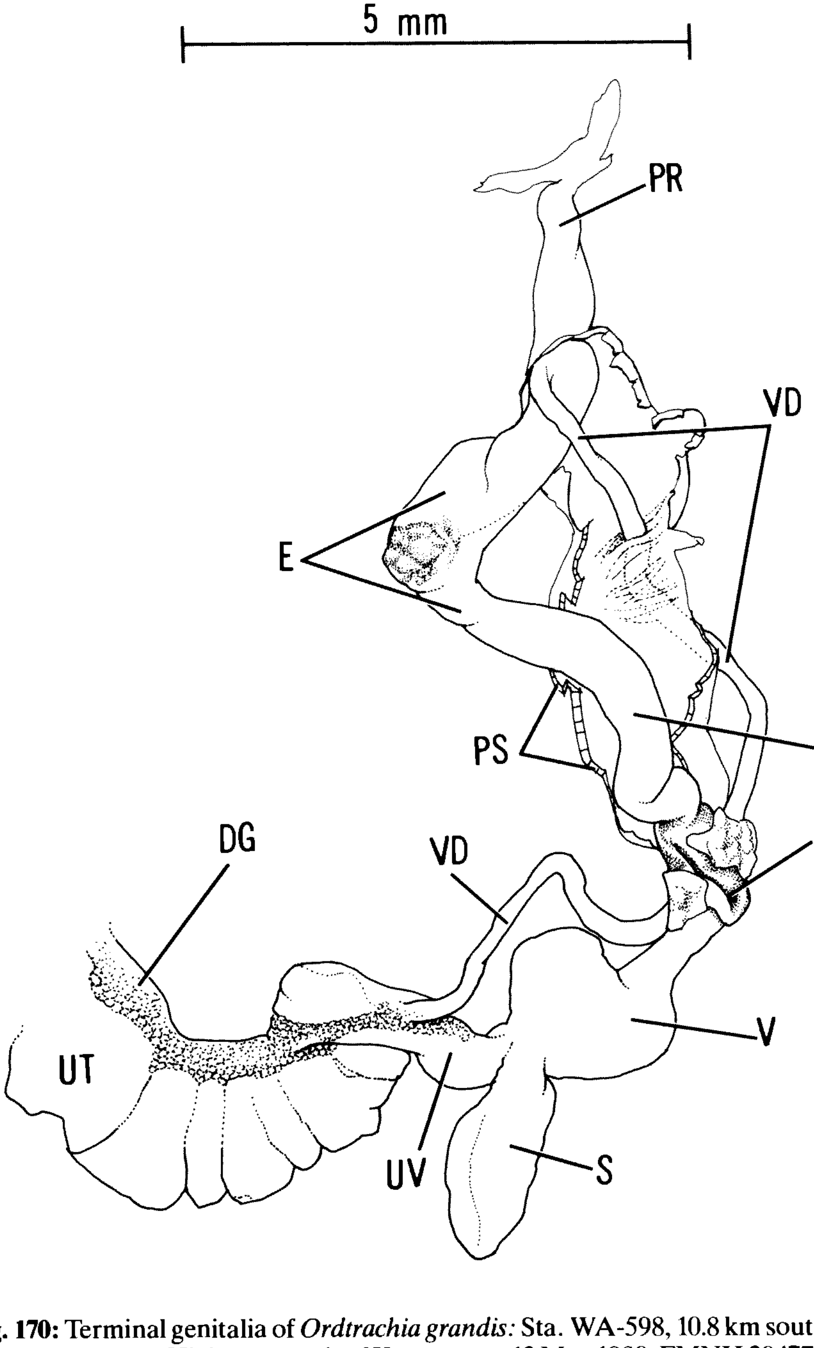


Fig. 170: Terminal genitalia of *Ordtrachia grandis:* Sta. WA-598, 10.8 km south of Behn River, Duncan Highway, south of Kununurra, 13 May 1980, FMNH 204772, Dissection A. Scale line equals 5 mm. Drawing by Linnea Lahlum.

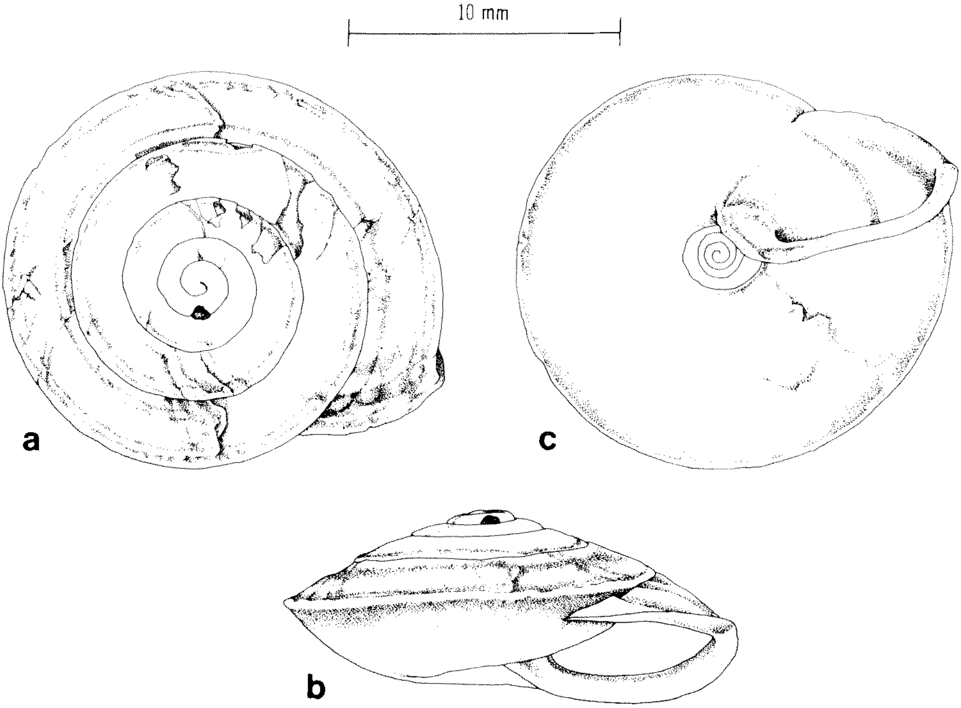


Fig. 171: Shell of *Ordtrachia grandis:* Sta. WA-244, 8.4 km south of Behn River, Duncan Highway, south of Kununurra, 16 November 1976, WAM 516.80, holotype. Scale line equals 10 mm. Drawings by Linnea Lahlum.

growth lines, occasionally small patches of remnant pustulations **(Plate 56c),** shell base without significant sculpture. Shell periphery **(Fig. 171b)** protruded into a thread-like keel, weak sulci sometimes developed. Lip strongly reflexed and rolled, reduced to a thin callus on parietal wall, columellar section expanded to partly cover umbilicus **(Fig. 171c).** No internal lip nodes. Umbilicus moderately open **(Fig. 171c),** umbilical width 0.7-3.7 mm (mean 1.97 mm), D/U ratio 5.51-23.1 (mean 9.20). Based on 289 measured adults.

Genitalia **(Figs 169-170)** with hermaphroditic duct (GD) entering talon (GT) laterally **(Fig. 169a).** Albumen gland (GG), prostate (DG), and uterus (UT) without unusual features. Free oviduct (UV) sinuated, longer than spermatheca (S), base of latter slightly enlarged. Head of spermatheca bound to prostate-uterus by fibers **(Fig. 169a).** Vagina (V) of average length. Vas deferens (VD) entering penis sheath (PS) about two-thirds of way from base, above head of penis (P), continuing to apex of sheath **(Figs 169b, c, 170).** Penial retractor muscle (PR) arising from base of diaphragm, inserting on vas-epiphallic junction. Epiphallus (E) short **(Figs 169b, c, 170),** with very large muscle-glandular structure on outer side, terminating in a thin-walled glandular sac (stippled in illustrations). Penis (P) rather long, not bound to wall of sheath, internally with simple longitudinal pilasters.

Jaw (**Plate 58c**) with prominent, narrow vertical ribs. Radular teeth (Plate 61) typical of genus, with blunt-tipped, slightly curved mesocones on the central and laterals, quite prominent side cusps. Transition from laterals to marginals (**Plate 61c-e**) occurring rapidly, marked by loss of interrow support system, increase in size of side cusps, loss of mesoconal tip curvature, greater elevation of cusp angle, shortening of tooth base, and decrease in tooth size. Marginal teeth (**Plate 61e-f**) variable in shape, cusp size, and angle of elevation.

Discussion

Ordtrachia grandis has a known range extending from the former Rosewood Station turnoff on the Old Duncan Highway in Western Australia, about 10.5 road km north of the Behn River crossing, to Sta. WA-596, about 15.1 road km south of the Behn River (**Fig. 179**). The first locality is based on pre-1971 collections along the Old Duncan Highway. Stations to the east and north-east on the new Duncan Highway (WA-707, WA-243, WA-599) have yielded only *O. septentrionalis, O. australis,* and *Exiligada negriensis* Iredale, 1939. The distance from WA-244, 8.4 km south of the Behn River, to WA-596, 15.1 km south of the Behn River, is only 6.7 km. About 2 km south-east and again at 9 km south of Mt. Quirk (**Fig. 179**), there are cliffs indicated on topographic

Table 69: Local Variation in *Ordtrachia grandis*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
Rosewood turnoff, Old Duncan Hwy., WAM: 430,77, 432.77, 435.77	30(D)	8.60 ± 0.170 (6.4 – 10.1)	20.19 ± 0.158 (18.45 – 22.2)	0.429 ± 0.007 (0.347 – 0.492)
14 mi S of Rosewood turnoff, Old Duncan Hwy., WAM 467.77	6(D)	7.26 ± 0.193 (6.7 – 8.1)	16.68 ± 0.391 (15.25 – 18.1)	0.436 ± 0.013 (0.396 – 0.479)
WA-244, FMNH 199959	8(L)	7.58 ± 0.145 (6.9 – 8.0)	17.39 ± 0.219 (16.1 – 18.2)	0.435 ± 0.005 (0.404 – 0.449)
WA-244, FMNH 199628, newly dead	50(D)	7.32 ± 0.056 (6.4 – 8.6)	17.16 ± 0.108 (15.55 – 18.6)	0.427 ± 0.003 (0.374 – 0.479)
WA-244, FMNH 199628, long dead	50(D)	7.32 ± 0.089 (6.1 – 9.0)	16.59 ± 0.121 (14.9 – 18.85)	0.441 ± 0.004 (0.381 – 0.523)
WA-595, FMNH 204756	57(D)	7.03 ± 0.054 (6.25 – 8.0)	16.92 ± 0.102 (14.95 – 18.4)	0.416 ± 0.003 (0.366 – 0.471)
WA-598, FMNH 204772	2(L)	6.70 (6.52 – 6.88)	16.49 (15.6 – 17.4)	0.407 (0.396 – 0.418)
WA-598, FMNH 204771	32(D)	7.31 ± 0.086 (6.5 – 8.65)	16.75 ± 0.130 (14.8 – 18.4)	0.437 ± 0.004 (0.393 – 0.509)
WA-597, FMNH 204765	45(D)	7.11 ± 0.061 (6.2 – 8.15)	15.74 ± 0.105 (14.0 – 16.8)	0.452 ± 0.003 (0.412 – 0.495)
WA-596, FMNH 204761	9(D)	7.86 ± 0.163 (7.3 – 8.7)	16.52 ± 0.183 (15.8 – 17.25)	0.476 ± 0.006 (0.457 – 0.510)

Table 69: Local Variation in *Ordtrachia grandis* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
Rosewood turnoff, Old Duncan Hwy., WAM: 430.77, 432.77, 435.77	30(D)	5½ − (5 − 5¾)	2.67 ± 0.075 (1.85 − 3.7)	7.79 ± 0.266 (5.51 − 11.4)
14 mi S of Rosewood turnoff, Old Duncan Hwy., WAM 467.77	6(D)	5⅛ (5 − − 5⅜ +)	2.13 ± 0.149 (1.5 − 2.5)	8.14 ± 0.856 (6.35 − 12.1)
WA-244, FMNH 199959	8(L)	5⅛ (4⅞ + − 5⅜)	2.04 ± 0.118 (1.65 − 2.6)	8.75 ± 0.514 (6.80 − 10.8)
WA-244, FMNH 199628, newly dead	50(D)	5⅛ − (4¾ − 5⅜ +)	2.15 ± 0.052 (1.5 − 2.9)	8.20 ± 0.197 (6.11 − 11.5)
WA-244, FMNH 199628, long dead	50(D)	5 + (4¾ − 5⅜ +)	2.09 ± 0.049 (1.3 − 2.8)	8.16 ± 0.199 (6.34 − 12.8)
WA-595, FMNH 204756	57(D)	5⅛ + (4¾ − 5½ −)	1.85 ± 0.049 (1.0 − 3.1)	9.50 ± 0.263 (5.70 − 16.5)
WA-598, FMNH 204772	2(L)	5 (4¾ + − 5¼ −)	2.00 (1.76 − 2.24)	8.31 (7.76 − 8.31)
WA-598, FMNH 204771	32(D)	5⅛ + (4⅞ + − 5½ +)	1.53 ± 0.080 (0.8 − 2.9)	11.9 ± 0.625 (6.35 − 21.6)
WA-597, FMNH 204765	45(D)	5⅛ + (4⅞ − − 5½ +)	1.72 ± 0.052 (0.9 − 2.4)	9.53 ± 0.309 (6.58 − 16.7)
WA-596, FMNH 204761	9(D)	5¼ (5 + − 5½ +)	1.43 ± 0.188 (0.7 − 2.6)	13.3 ± 1.85 (6.41 − 23.1)

maps that may be limestone exposures, but these have not been sampled for land snails. It is quite possible that they will contain additional populations of *Ordtrachia grandis*, giving a potential total linear range of about 23.5 km.

Ordtrachia grandis is sympatric with the much smaller, heavily ribbed, *O. intermedia* at stations WA-244, WA-595, WA-598, WA-597.

Size and shape variation is rather extensive **(Table 69).** The specimens from The Rock Wall on Rosewood Station are the largest, exceeding by up to 4 mm in mean diameter those from elsewhere. Sta. WA-244 yielded 426 dead, but only eight live adults. Measurment of 50 long dead and 50 fresh examples by A. Solem showed a clear difference, with the long dead examples being smaller in diameter and with a slightly reduced whorl count. It is hypothesised that these specimens reached adult shell growth in less favourable years than the more recent examples.

The very limited live collected materials and striking differences in anatomy restricted the number of individuals dissected. Material from Sta. WA-598 **(Fig. 170)** had the vaginal-spermathecal base area much larger than in the specimens from Sta. WA-244 **(Figs. 169b, c),** but otherwise there were no real differences noted, except the normal seasonal variation in ovotestis size, hermaphroditic duct diameter, and prostate-uterus swelling. The late dry season material (WA-244, November 1976) had all three areas enlarged in preparation for early wet season mating, while they were greatly reduced in size early in the dry season (WA-598, May 1980).

The name *grandis* refers to the large size and polished surface of the shell in comparison with other members of the genus.

ORDTRACHIA INTERMEDIA SP. NOV.

(Plates 56d-f, 58f, 62; Figs 172, 173)

Comparative remarks

Ordtrachia intermedia is immediately separable from all other *Ordtrachia* in having very prominent radial ribs **(Figs 172a-c),** a widely open umbilicus, and a nearly rounded periphery. The other *Ordtrachia* lack any trace of radial ribbing, have the umbilicus much less widely open, and have a stronger, thread-like peripheral keel **(Figs 166, 171).** *Mouldingia occidentalis* and *M. orientalis* **(Figs 163a-f)** agree in ribbing, but have nearly flat spires, much stronger sulci, and very strongly deflected body whorls. Anatomically, they differ in lacking the epiphallic muscle-glandular zone and many features of the penis-epiphallus interiors.

Holotype

WAM 517.80, Sta. WA-597, cliffs on west side of new Duncan Highway, about 14.3 km south of Behn River Crossing, south of Kununurra, Western Australia (1:100,000 'Lissadell' map sheet 4664 – 912:540). Collected by Alan Solem and Laurie Price 13 May 1980. Height of shell 4.9 mm, diameter 8.95 mm, H/D ratio 0.547, whorls 4⅜ –, umbilical width 2.2 mm, D/U ratio 4.07.

Paratopotypes

WAM 577.80, WAM 578.80, FMNH 204763-4, 74 live and 105 dead adults from the type locality.

Paratypes

Sta. WA-244, limestone ridge 0.25 km west of new Duncan Highway, 8.4 km south of Behn River crossing, south of Kununurra ('Lissadell' 4664 – 937:599) (150 dead adults, WAM 580.80, FMNH 199626); Sta. WA-595, 9.0 km south of Behn River crossing ('Lissadell' 4664 – 933:583) (1 live juvenile, 78 dead adults, WAM 575.80, FMNH 204757, FMNH 204759); Sta. WA-598, 10.8 km south of Behn River crossing ('Lissadell' 4664 – 923:570) (20 dead adults, WAM 576.80, FMNH 204773); Sta. WA-708, limestone bench and cliff above creek, ca. 2 km south of 2nd Brook Creek crossing, 43.25 km north of Nicholson River crossing ('Linnekar' 4662 – 799:488) (40 dead adults, WAM 579.80, FMNH 205297).

Diagnosis

Shell small, diameter 7.3-10.9 mm (mean 8.76 mm), with 3⅞ – to 4¾ + (mean 4¼ –) normally coiled whorls. Apex and spire strongly elevated, rounded above, body whorl descending just before aperture **(Fig. 172b),** height of shell 3.6-6.4 mm (mean 4.61 mm), H/D ratio 0.495-0.604 (mean 0.536). Apical sculpture **(Plate 56d-e)** of prominent short ridges arranged in radial rows, with secondary radial undulations on last portion of apex. Postapical sculpture of very strong radial ribs **(Figs 172a-c)**, not reduced on shell base, but greatly reduced in umbilicus, microsculpture **(Plate 56f)** of very sharp and dense periostracal projections. Shell periphery **(Fig. 172b)** with a slightly protruded keel and very prominent supraperipheral sulcus. Body whorl descending just before aperture. Lip strongly reflexed and rolled, reduced to thin callus on parietal wall, only slightly reflected over umbilicus. Some specimens with a prominent basal lip node, upper palatal lip often indented slightly by strong supraperipheral sulcus. Umbilicus widely open, width 1.2-2.8 mm (mean 1.90 mm), D/U ratio 3.17-7.36 (mean 4.70). Based on 468 measured adults.

Genitalia **(Figs 173a-c)** with hermaphroditic duct (GD) entering laterally on talon **(Fig. 173a,** GT). Albumen gland (GG) greatly enlarged, prostate (DG) and uterus (UT) without unusual features. Free oviduct **(Fig. 173a,** UV) longer than spermatheca (S), "U"-shaped. Head of spermatheca bound to prostate-uterus by connective tissue, base moderately enlarged. Vagina (V) of medium length. Vas deferens **(Fig. 173b,** VD) entering penis sheath (PS) at midpoint, opposite head of penis, continuing to apex

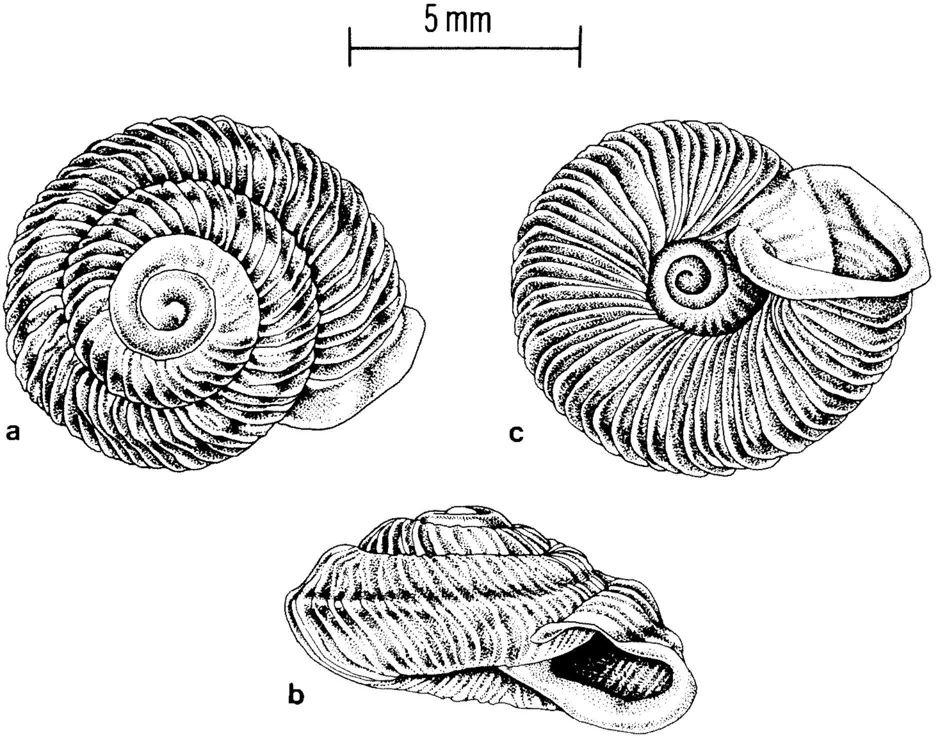


Fig. 172: Shell of *Ordtrachia intermedia:* Sta. WA-597, 14.3 km south of Behn River, Duncan Highway, south of Kununurra, 13 May 1980, WAM 517.80, holotype. Scale line equals 5 mm. Drawings by Linnea Lahlum.

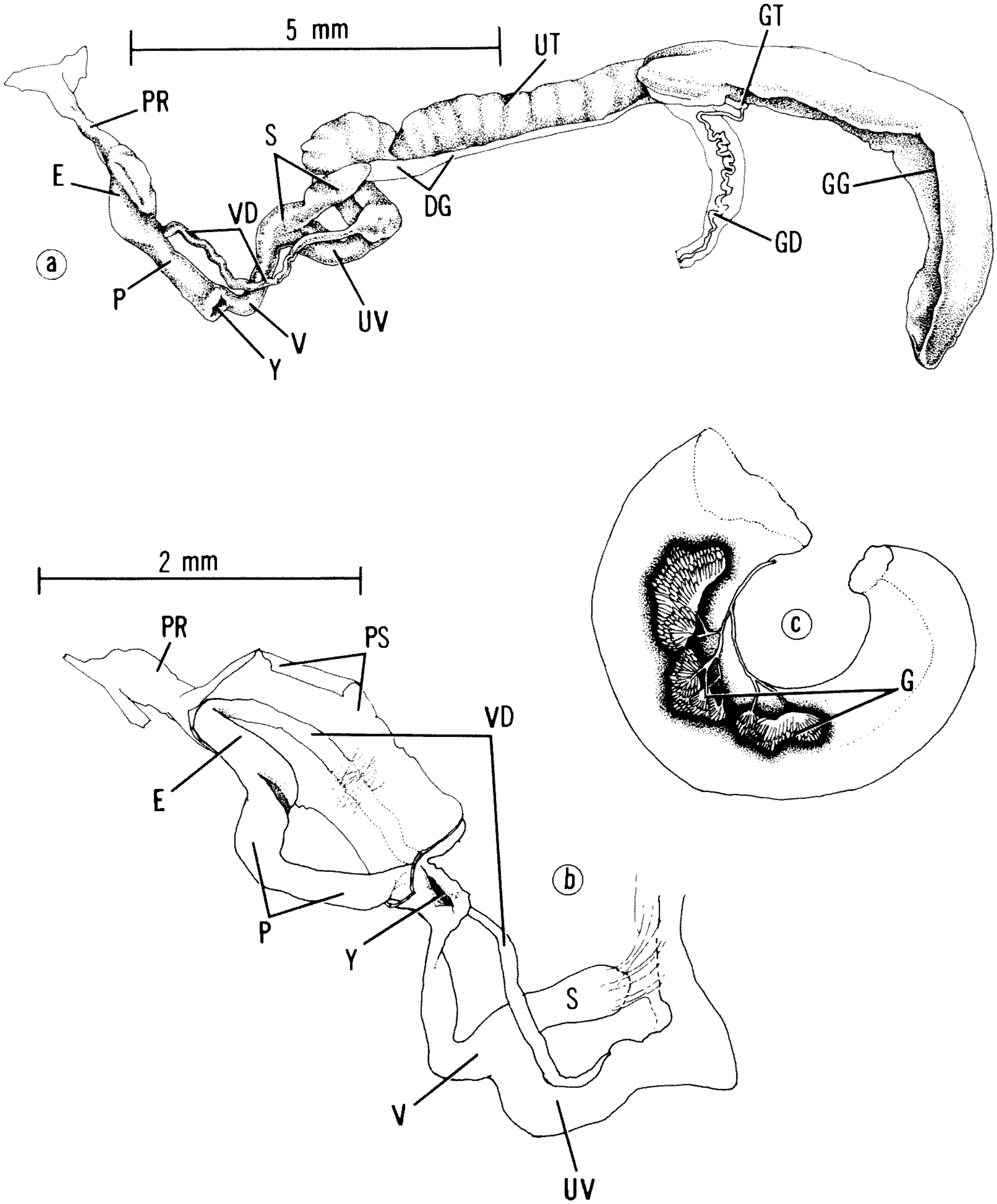


Fig. 173: Genitalia of *Ordtrachia intermedia:* Sta. WA-597, 14.3 km south of Behn River Crossing, Duncan Highway, south of Kununurra, 13 May 1980, FMNH 204764, (a) whole genitalia, Dissection B, (b) penis complex, Dissection A. Scale lines as marked. Drawings by Linnea Lahlum.

where it reflexes into epiphallus (E). Penial retractor muscle (PR) arising from base of diaphragm, attaching to vas-epiphallic junction. Epiphallus (E) short, large muscle-glandular zone on outer side, terminating in thin-walled, protruded sac. Penis (P) about twice length of epiphallus (E), not bound to wall of sheath, thick walled, internally with simple longitudinal pilasters. Atrium (Y) short, without unusual features.

Jaw **(Plate 58f)** without unusual features. Radular teeth **(Plate 62)** typical of genus except for enlarged endocones on central **(Plate 62b)** and early laterals. A part row view **(Plate 62a)** shows typical transition series.

Table 70: Local Variation in *Ordtrachia intermedia*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
WA-595, FMNH 204757	78(D)	4.40 ± 0.036 (3.8 – 5.55)	8.89 ± 0.053 (7.9 – 10.9)	0.554 ± 0.059 (0.444 – 0.583)
WA-598, FMNH 204773	20(D)	4.53 ± 0.090 (3.8 – 5.3)	8.65 ± 0.111 (7.3 – 9.5)	0.524 ± 0.007 (0.483 – 0.575)
WA-597, FMNH 204764	74(L)	4.67 ± 0.038 (4.0 – 5.4)	8.55 ± 0.050 (7.4 – 9.4)	0.546 ± 0.003 (0.473 – 0.629)
WA-597, FMNH 204763	106(D)	4.34 ± 0.029 (3.6 – 4.95)	8.66 ± 0.037 (7.6 – 9.6)	0.502 ± 0.003 (0.431 – 0.570)
WA-708, FMNH 205297	40(D)	4.82 ± 0.056 (3.9 – 5.4)	8.66 ± 0.078 (7.7 – 9.7)	0.556 ± 0.004 (0.497 – 0.612)
WA-244, FMNH 199626	150(D)	4.83 ± 0.035 (4.0 – 6.4)	8.91 ± 0.045 (7.65 – 10.5)	0.544 ± 0.003 (0.455 – 0.698)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
WA-595, FMNH 204757	78(D)	4¼ (3⅞+ – 4¾+)	1.90 ± 0.029 (1.25 – 2.4)	4.77 ± 0.077 (3.72 – 6.82)
WA-598, FMNH 204773	20(D)	4¼ (3⅞+ – 4½–)	1.74 ± 0.061 (1.2 – 2.3)	5.09 ± 0.184 (3.91 – 6.84)
WA-597, FMNH 204764	74(L)	4¼– (3⅞ – 4½)	2.05 ± 0.035 (1.5 – 2.8)	4.21 ± 0.079 (3.17 – 5.63)
WA-597, FMNH 204763	106(D)	4¼– (3⅞ – 4½+)	1.88 ± 0.029 (1.3 – 2.5)	4.72 ± 0.071 (3.54 – 6.64)
WA-708, FMNH 205297	40(D)	4¼ (3⅞ – 4½)	1.76 ± 0.034 (1.4 – 2.45)	4.97 ± 0.085 (3.71 – 5.93)
WA-244, FMNH 199626	150(D)	4¼– (3⅞ – 4⅝)	1.89 ± 0.031 (1.35 – 2.75)	4.75 ± 0.059 (3.12 – 7.36)

Discussion

Ordtrachia intermedia has a moderately extensive range. The northernmost locality (Sta. WA-244) is about 8.4 road kilometres south of the Behn River, and the southernmost locality (Sta. WA-709) is 37.2 km north of the Nicholson River, an air distance of about 120 km. All colonies lie in the east drainages of the Ord River. Undoubtedly there are many more colonies clinging to bits of exposed limestone in this region that have not been found yet. Over much of its range, *O. intermedia* is sympatric with *Exiligada negriensis* Iredale, 1939 and *O. grandis*.

Very little live material was collected, with only the one pocket at Sta. WA-597 yielding a quantity of aestivating snails. A single live juvenile was taken at Sta. WA-595.

Interpopulational size and shape variation in *Ordtrachia intermedia* is modest **(Table 70)**, with the apparent difference in shell height between live collected and dead individuals from Sta. WA-597 the result of different measuring techniques by the two people who measured these sets. Considerable individual shell variation exists in the prominence of the basal lip node and the indentation of the upper palatal wall by the supraperipheral sulcus. The holotype **(Fig. 173b)** has quite prominent protrusions, while others in the same set show only slight traces, although with equal lip expansion.

The name *intermedia* refers to the shell morphology that combines the shape of *Ordtrachia* with the ribbing and aperture of *Mouldingia* **(Figs 163a-f)**. Classification of this species in *Ordtrachia* is based upon its genital anatomy and elevated spire.

GENUS *EXILIGADA* IREDALE, 1939

Exiligada Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 68-69 – type species *Exiligada negriensis* Iredale, 1939 by original designation.

Shell large, globose, apex and spire moderately **(Fig. 174b)** to strongly **(Fig. 174e)** elevated, rounded above, body whorl descending gradually over last eighth whorl before aperture. Umbilicus narrowly open to a lateral crack **(Figs 174c, f)**. Apex **(Plate 57f)** with fine radial riblets, postapical whorls smooth or with weak, irregular growth wrinkles. Very fine micropustulations developed on lower spire and body whorl. Lip reflexed, moderately expanded, reduced to thin callus on parietal wall, columellar section reflexed to nearly cover umbilicus. No internal lip nodes. Shell periphery evenly rounded, without trace of angulation or keel, no sulci present. Whorls of spire normally rather strongly rounded. Shell colour light yellow horn on spire and body whorl, unless worn, normally with two spiral reddish-yellow bands, one peripheral, the second and usually lighter located mid upper palatal area. Sometimes bands broken up into many narrow bands that also are present on shell base (Iredale, 1939: pl. V, Fig. 2) or into many short dashes (Iredale, 1939: pl. V, Fig. 4), but often banding reduced or absent. Genitalia **(Figs 175a-d)** with ovotestis **(Fig. 175c,** G) clumps well separated in dry season examples. Hermaphroditic duct (GD) entering laterally on talon (GT). Albumen gland (GG) large, prostate (DG) and uterus (UT) without unusual features. Spermatheca (S) short, base greatly enlarged, free oviduct **(Fig. 175a,** UV) much longer and "U"-shaped. Vagina (V) short. Vas deferens **(Fig. 175b)** entering penis sheath (PS) shortly above base, continuing to sheath apex where it reflexes into epiphallus (E).

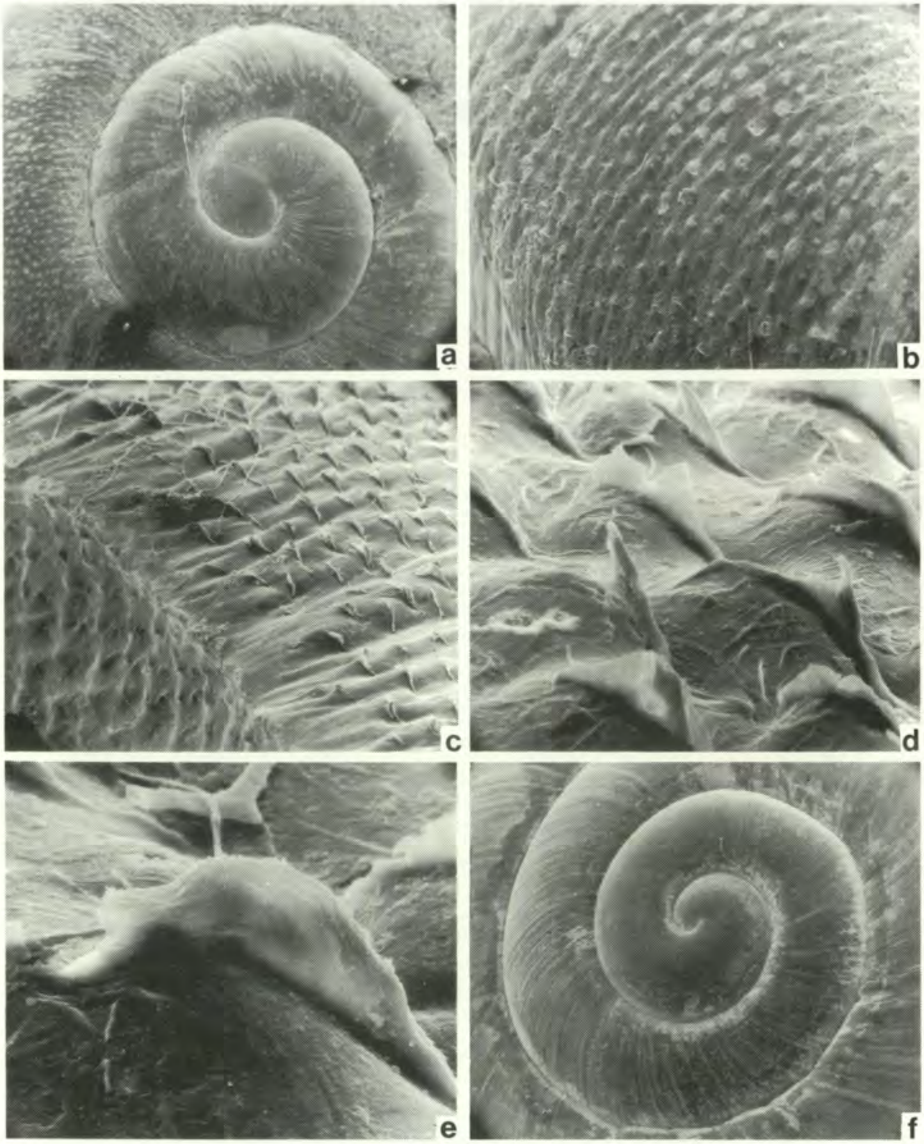


Plate 57: Shell sculpture of *Prototrachia sedula* and *Exiligada negriensis* Iredale, 1939: (a-e) *P. sedula,* FMNH 205145, Dissection B, Sta. WA-680, limestone ridges, 24.4 km east of Timber Creek Police Station, N.T., 1 June 1980, (a) apex and early spire at 20.3X, (b) detail of early spire at 66X, (c) detail of body whorl sculpture at 68X, (d) detail of projections on body whorl at 320X, (e) single broken projection on body whorl at 680X; (f) *E. negriensis* Iredale, 1939, FMNH 205303, Dissection A, Sta. WA-709, 37.2 km north of Nicholson River off Duncan Highway, N.T., 17 June 1980, apex and early spire at 13.9X.

Penis sheath with lower third of wall somewhat thickened **(Figs 175b, d)**. Penial retractor muscle (PR) arising from diaphragm, inserting on vas-epiphallic junction, with fibers continuing along epiphallus (E) to head of penis **(Fig. 175b)**. Epiphallus shorter than penis, ending in a short loop **(Fig. 175b)** bound by penis muscle (PM). Penis (P) coiled inside sheath **(Figs 175b, d)**, thick walled, internally with a large apical pilaster (PP), basally with simple longitudinal pilasters. Atrium (Y) very short. Jaw **(Plate 58b)** typically camaenid. Radular teeth **(Plate 63c-d)** with blunt tipped, curved mesocone, but no side cusps on the central and lateral teeth, marginals typical.

Type species: *Exiligada negriensis* Iredale, 1939 by original designation.

Comparisons

The presence of reddish-yellow spiral bands, more globular shape of the shell, and slight reflexion of the shell lip, combined to persuade Iredale (1939: 68-9) to place this in the new and undescribed Family Rhagadidae, but the nature of the banding and isolated geographic position led to his description of a new genus, *Exiligada* Iredale, 1939. The absence of a keel and relatively globose shape, plus absence of either major ribs or prominent microsculpture, easily separate the shell of *Exiligada* from *Ordtrachia, Prototrachia,* or *Mouldingia.*

The genitalia of *Exiligada* **(Figs 175a-d)** differ from that of *Mouldingia* **(Figs 164-5)** in having a bound portion of the epiphallic loop retained, development of a large muscle-glandular zone on the outer side of the epiphallus, a single major pilaster in the penis apex **(Fig. 175d)** instead of several zigzagged pilasters **(Fig. 165d)**, the much shorter vagina (V) (compare **Figs 164a, 165a, 175a)**, and the much longer free oviduct (UV). *Ordtrachia* is much closer in genital structure, but there is no epiphallic loop remaining, the muscle-glandular zone is even more strongly developed, and the epiphallus ends in a larger thin-walled chamber (see **Figs 167b, 168b, 169b, 173b)**. *Westraltrachia* has the epiphallic loop and penis muscle much more strongly developed, retains special penial pilasters in most species **(Figs 158a-q)**, and lacks the muscle-glandular zone on the epiphallus. *Prototrachia* has an extremely long vagina **(Fig. 177a,** V) and penis **(Fig. 177b)**, with the interior of the penis retaining a complex and generalised wall sculpture **(Fig. 178)**.

Another major difference shown by *Exiligada* is its apparent tendency to aestivate while burrowed under spinifex or shrubs, rather than shelter in talus as do other members of the *Westraltrachia* complex. Although some long dead specimens of *Exiligada negriensis* have been taken from 'a steep basalt hill between Nicholson and Halls Creek in the WA-NT border area' (WAM 437.77), other examples have been found in the vicinity of limestone exposures. Admittedly, most collecting effort in this region has been focused on limestone masses, but dead specimens of *Exiligada* have not been discovered strewn on open country surfaces in a fashion equivalent to the occurence of *Xanthomelon* shells further north in the Kimberley and Northern Territory.

Only one species, *Exiligada negriensis* Iredale, 1939, is recognised in this study. The only material available to Iredale was a single set of shells collected in 1896 by Richard Helms at "Negri outstation, about 25 miles north of Ord River Station". Iredale (1939: 68-9) selected extreme examples and named two species: *E. negriensis* for low spired, umbilicated shells with colour bands broken up into short, multiple dashes (Iredale, 1939: Plate V, Fig. 4), and *E. qualis* for higher spired shells with nearly closed umbilicus and banding of continuous stripes that are fragmented into many narrow bands and extend down onto the shell base (Iredale, 1939: Plate V, Fig. 2). Variation among the paratypes, as sorted out by Iredale, is summarised in **Table 71.** Many specimens could be placed in either segregate, and the differences between the two samples are not significant. Many of the type lot had been alive, but aestivating, when collected. Thin epiphragm remnants extend across the aperture, indicating that they were free sealers. Dermestid beetles in Sydney long since had removed the soft parts, while the set of shells was housed in a museum cabinet with loose fitting doors.

The western geographic limit of *Exiligada* is 3 km west of Lissadell Station at the south-west margin of Lake Argyle (Sta. WA-247, WA-248). The northern known limit is 2.9 km south of the Behn River crossing of the new Duncan Highway (Sta. WA-243, WA-599), while the southern limit lies on the Halls Creek-Nicholson road near the Northern Territory-Western Australia border. There are no records of *Exiligada* north of the Behn River where *Ordtrachia grandis, O. septentrionalis,* and *O. australis* occur **(Fig. 179).** *Exiligada* is thus sympatric with *Ordtrachia grandis* at Sta. WA-244, WA-598, and WA-596; also with *O. intermedia* at Sta. WA-244 and WA-598; with just *O. intermedia* at Sta. WA-708; and with *Mouldingia orientalis* at Sta. WA-247, WA-248, and WA-590. The total east-west range is about 46 km (Sta. WA-248 to WA-243) and the north-south range is about 160 km (WA-243 to Nicholson).

Despite finding many dead specimens, only four live adults have been taken in our surveys: one from under spinifex at Sta. WA-598 and three from under spinifex or scrub on a slope of small limestone fragments further south at Sta. WA-709.

EXILIGADA NEGRIENSIS IREDALE, 1939

(Plates 57f, 58b, 63c-d; Figs 174, 175)

Exiligada negriensis Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 69, plt. V, fig. 4 – Negri Outstation, twenty-five miles north of Ord River Sation, East Kimberley.

Exiligada qualis Iredale, 1939, Jour. Roy. Soc. Western Australia, **25:** 69, plt. V, fig. 2 – Negri Outstation, twenty-five miles north of Ord River Station, East Kimberley.

Comparative remarks

Exiligada negriensis Iredale, 1939 has a globose shape, tiny or closed umbilicus, neither major radial ribs nor micropustulations on the shell, often spiral colour bands or dashes, and lacks any trace of a keel or peripheral angulation. There is no East Kimberley camaenid with which it can be confused. Some of the Napier Range *Westraltrachia* and *Amplirhagada* come close in size, shape and colour, but the genital anatomy of these genera are very different, and their shells have microsculpture. Species of *Rhagada* Albers, 1861 from the Napier Range and coast regions of Western Australia agree in shape and colour, but the presence of a massive penial verge and many other differences in the terminal genitalia indicate that they are not related.

Holotype of *negriensis* Iredale, 1939

AMS C.64865, Negri Outstation, 25 miles north of Ord River Station, East Kimberley, Western Australia. Collected by Richard Helms in 1896. Height of shell

11.1 mm, diameter 21.0 mm, H/D ratio 0.529, whorls 5½ – , umbilical width 1.9 mm, D/U ratio 11.1.

Paratopotypes of *negriensis* Iredale, 1939

AMS C.64916, WAM 71.40, FMNH 198992, 13 dead adults and many juveniles from the type locality.

Holotype of *qualis* Iredale, 1939

AMS C.64866, Negri Outstation, twenty-five miles north of Ord River Station, East Kimberley, Western Australia. Collected by Richard Helms in 1896. Height of shell 13.85 mm, diameter 19.2 mm, H/D ratio 0.721, whorls 5⅛, umbilical width 0.6 mm, D/U ratio 32.

Paratopotypes of *qualis* Iredale, 1939

AMS C.64915, WAM 72.40, FMNH 198993, 16 dead adults and many juveniles from the type locality.

Measured adults

Geographical sequence roughly north to south: limestone wall north of Lissadell Homestead (1 dead adult, WAM 550.75, collected by B. R. Wilson and R. J. McKay October 1971); Sta. WA-247, 3.3 km west of Lissadell Homestead, limestone hill, south-west corner Lake Argyle ('Lissadell' 4664 – 493:574) (13 dead adults, WAM 199.80, FMNH 199580); Sta. WA-248 and WA-590, 200 metres west of Sta. WA-247, Lissadell Station ('Lissadell' 4664 – 490:572) (34 dead adults, WAM 200.80, FMNH 199608, FMNH 199721, FMNH 204734): Sta. WA-243 and WA-599, limestone hill west side of new Duncan Highway, 2.9 km south of Behn River crossing, south of Kununurra ('Lissadell' 4664 – 948:636) (36 dead adults, WAM 197.80, WAM 585.80, FMNH 199617, FMNH 204774); Sta. WA-244, limestone ridge 0.25 km west of new Duncan Highway, 8.4 km south of Behn River crossing ('Lissadell' 4664 – 937:599) (13 dead adults, WAM 198.80, FMNH 199627); Sta. WA-598, 10.8 km south of Behn River Crossing ('Lissadell' 4664 – 923:570)((1 live, 12 dead adults, WAM 586.80, FMNH 204769-70); Sta. WA-596, 15.1 km south of Behn River crossing ('Lissadell' 4664 – 912:532) (1 dead adult, FMNH 204762); Sta. WA-708, limestone cliff ca 2 km south of 2nd Brook Creek crossing, 43.25 km north of Nicholson River crossing on Duncan Highway ('Linnekar' 4662 – 799:488) (20 dead adults, WAM 587.80, FMNH 205298); Sta. WA-709, limestone exposure east of Duncan Highway, 37.2 km north of Nicholson River crossing ('Linnekar' 4662 – 832:397) (3 live, 15 dead adults, WAM 588.80, FMNH 205303-4); Ord River, East Kimberley (6 dead adults, WAM 47.54); White Mt., Ord River Station (13 dead adults, WAM 436.77, collected by A. M. Douglas and G. Kendrick 7 June 1966); west side of White Mt. (3 dead adults, WAM 450.77, collected by M. Archer 31 May 1970); steep basalt hill between Halls Creek and Nicholson, border area of N.T. and W.A. (9 dead adults, WAM 437.77, collected by C. R. Whitaker in 1973); Date Palm Creek, 25.7 km south-east of Halls Creek along Duncan Highway (1 dead adult, NMV, collected by A. C. Beauglehole 20 June 1976).

Diagnosis

Shell large, diameter 16.05-24.05 mm (mean 19.26 mm), with 4⅜ – to 5¾ (mean 5⅛ –) rather tightly coiled whorls. Apex and spire moderately to strongly elevated

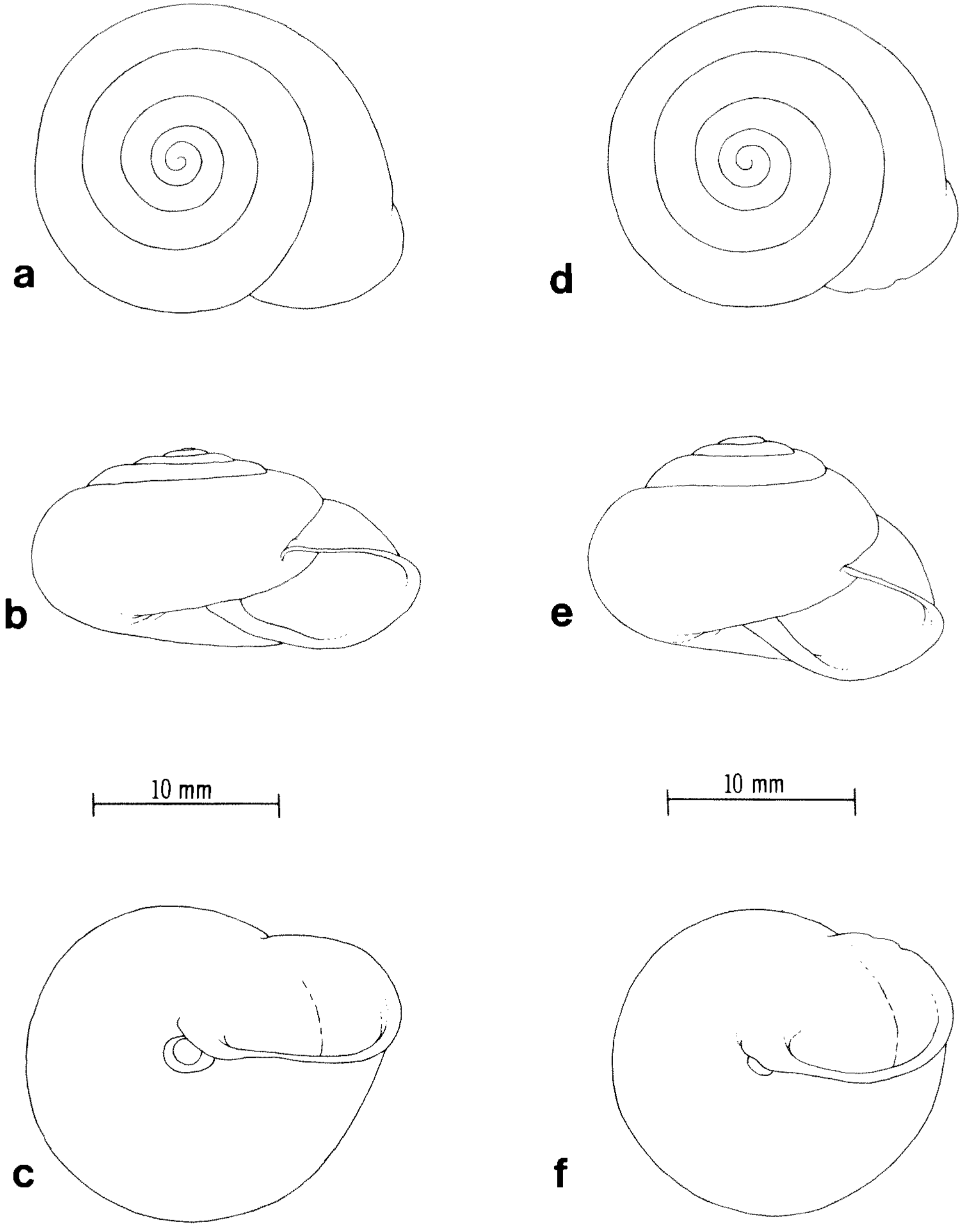


Fig. 174: Shells of *Exiligada negriensis* Iredale, 1939: (a-c) holotype, Negri Outstation, twenty-five miles north of Ord River Station, East Kimberley, AM C.64865; (d-f) holotype of *Exiligada qualis* Iredale, 1939, Negri Outstation, AM C.64866. Scale lines equal 10mm. Drawings by Elizabeth Liebman.

(Figs 174b, e), rounded above, last whorl descending slightly over last eighth, height of shell 9.9-17.25 mm (mean 13.21 mm), H/D ratio 0.539-0.824 (mean 0.677). Apical sculpture **(Plate 57f)** of weak radial riblets. Postapical whorls with irregular radial growth wrinkles, weak micropustulations present on lower spire and body whorl. Shell periphery evenly rounded. Lip slightly expanded, moderately reflected, reduced to thin callus on parietal wall, columellar section nearly covering umbilicus **(Figs 174c, f).** No internal lip nodes. Umbilicus varying from slightly open to a narrow lateral crack, umbilical width 0.25-2.9 mm (mean 1.07 mm), D/U ratio 7.93-80 (mean 21.9). Based on 201 measured adults.

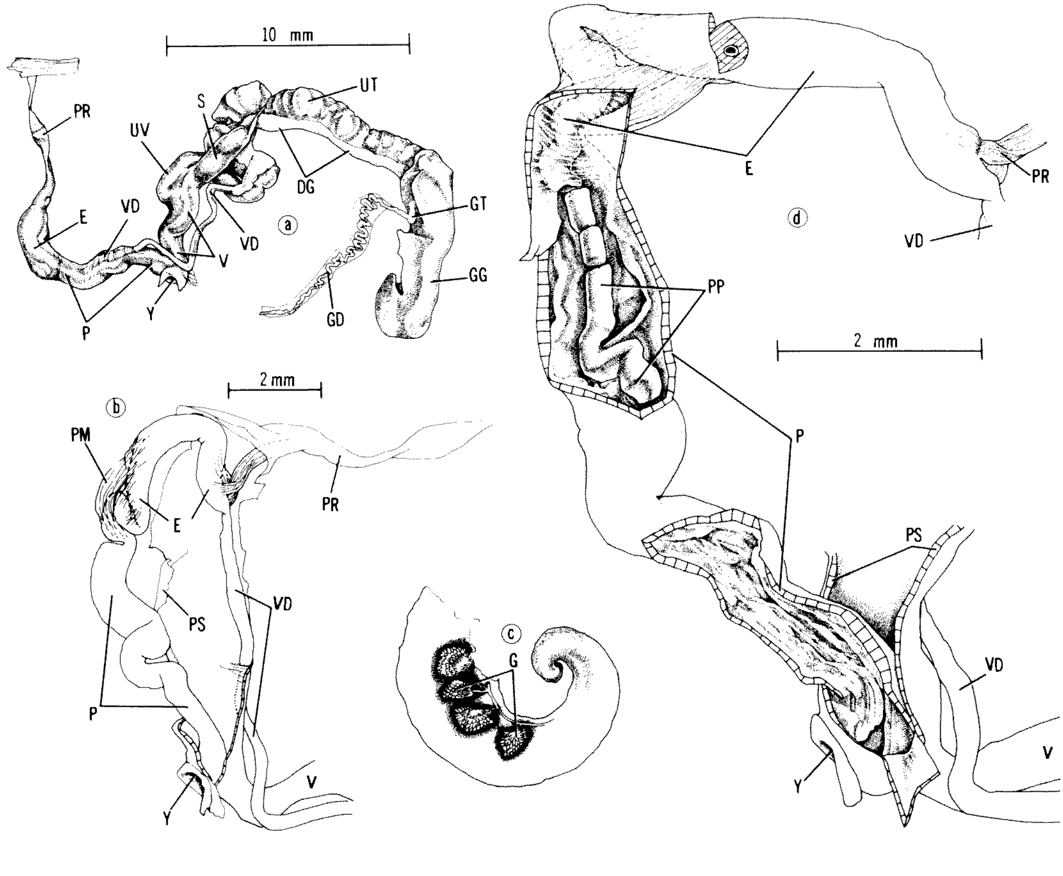


Fig. 175: Genitalia of *Exiligada negriensis* Iredale, 1939: Sta. WA-709, Duncan Highway, 37.2 km north of Nicholson River, south of Kununurra, 17 June 1980, FMNH 205303, Dissection B, (a) whole genitalia except for ovotestis, (b) opened penis sheath, (c) ovotestis, (d) interior of penis and epiphallus. Scale lines as marked. Drawings by Linnea Lahlum.

Genitalia **(Figs 175a-d)** with hermaphroditic duct (GD) entering laterally on talon (GT). Albumen gland (GG) large, uterus (UT) and prostate (DG) without unusual features. Spermatheca **(Fig. 175a,** S) short, head attached to prostate-uterus by fibers. Free oviduct **(Fig. 175a,** UV) very long, "U"-shaped, entering laterally upon expanded spermatheca-vaginal chamber. Vagina **(Fig. 175a,** V) very short. Vas deferens (VD) entering thin-walled penis sheath **(Fig. 175b,** PS) shortly above base, continuing to apex of sheath where it reflexes into epiphallus (E). Penial retractor muscle (PR) arising from base of diaphragm, attaching to vas-epiphallic junction. Epiphallus (E) long, walls with heavy muscle-glandular zone, base a thin-walled extended loop with clear muscle fibers around it **(Figs 175b, d).** Penis (P) very long, kinked to coiled within sheath **(Figs 175b, d),** which is slightly thicker in basal area. Interior of penis **(Fig. 175d)** showing a single, very large, interrupted pilaster (PP) in apical section, lower chamber with vague longitudinal ridging. Walls of penis thick.

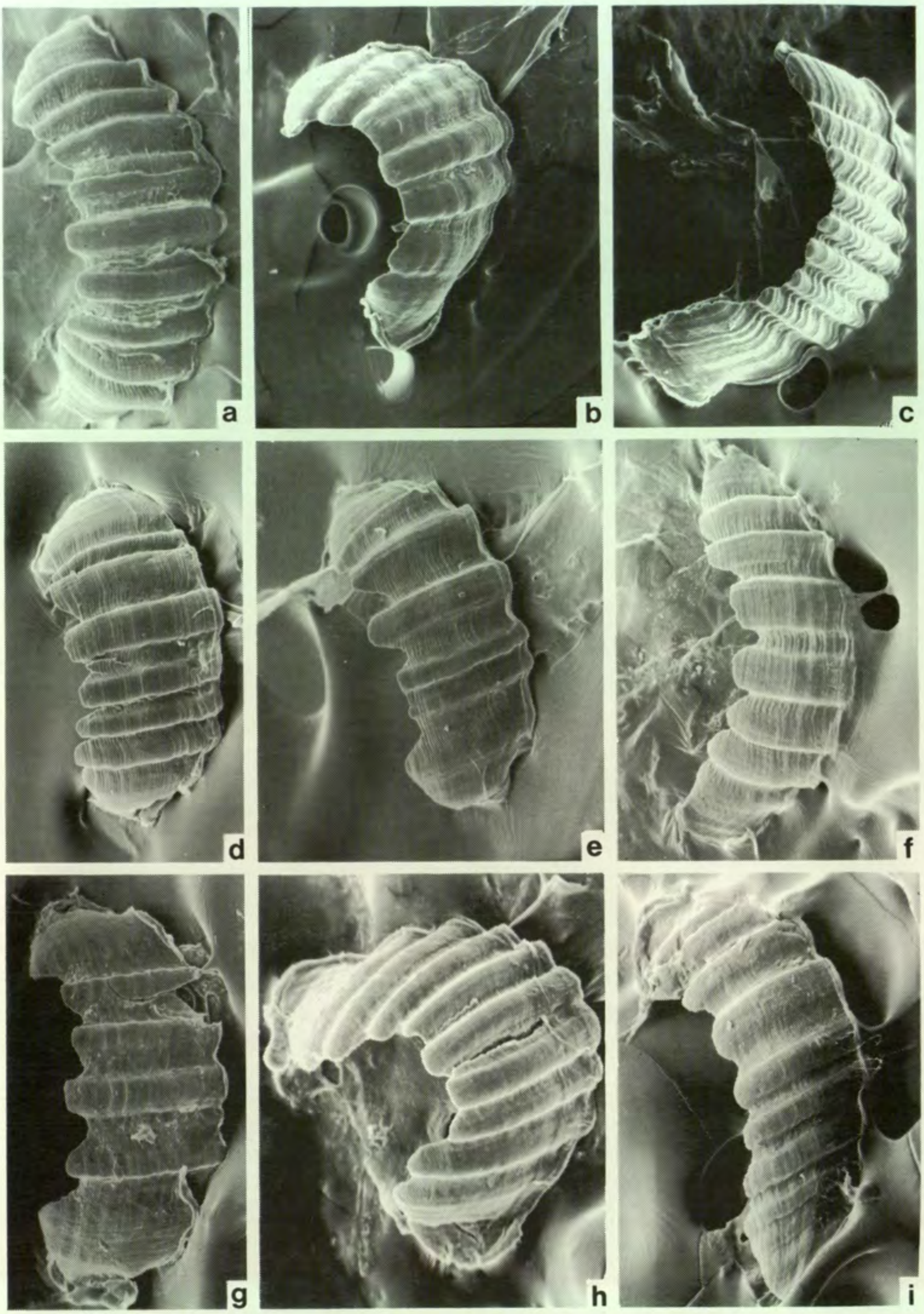
Jaw **(Plate 58b)** typically camaenid. Radular teeth **(Plate 63c-d)** lack side cusps on central and lateral teeth, mesocone bluntly tipped and curved. Marginal teeth typical.

Discussion

The exact type locality for *Exiligada negriensis* and *E. qualis* is unknown. Staff at Ord River Station did not know the location of 'Negri Outstation' and I could not find any maps on which this was shown. The Negri River, a major tributary of the Ord River, does lie about 40 km north of Old Ord River Station, and presumably the types were taken somewhere in this vicinity. No collecting stops have been made in this region during my surveys of the East Kimberley for land snails, as the terrain through which the Duncan Highway passes is unfavourable looking territory.

There is considerable variation in shell shape, colour and umbilical width among populations **(Table 71).** Southern and northern populations are smaller in size and with more open umbilici than are taxa from the more central part of the range (Sta. WA-598, WA-708, WA-709). The extent to which this indicates allochronic variation is unknown. Material was taken just south of the Behn River (Sta. WA-243, **Fig. 179)** in 1976 and then the same small rock face resampled in 1980 as Sta. WA-599. Considerably more time was spent there in 1980 during an unsuccessful attempt to find living specimens. Collecting time in the two years was not equal. Umbilical size varied greatly between the two collections, which did come from areas a few yards apart.

Too little fresh material is available to assess the meaning of colour variation. Those from east of Lake Argyle tended to have multiple colour bands, either dashes or spirals, while those from the south-west corner of Lake Argyle (Sta. WA- 247, WA-248, WA-590), when fresh enough to show pattern, tended to have two wide colour bands. Without more live collected material to dissect, the union of these populations into one species must be tentative. The synonymisation of *qualis* with *negriensis* is based on intergradation within the original set, but the possibility that more than one species of *Exiligada* is present in known material must be considered.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◀**Plate 58:** Jaws of genera related to *Westraltrachia:* (a) *Prototrachia sedula,* FMNH 205145, Dissection A, Sta. WA-680, limestone ridges, 24.4 km east of Timber Creek Police Station, N.T., 1 June 1980, at 70X; (b) *Exiligada negriensis* Iredale, 1939, FMNH 205303, Dissection A, Sta. WA-709, 37.2 km north of Nicholson River off Duncan Highway, N.T., 17 June 1980, at 47X; (c) *Ordtrachia grandis,* FMNH199959, Dissection A, Sta. WA-244, 8.4 km south of Behn River crossing, west of Duncan Highway, 16 November 1976, at 53X; (d-e) *O. septentrionalis,* FMNH 205295, Sta. WA-707, south of Rosewood turnoff, 15.6 km north of Behn River crossing on Duncan Highway, 16 June 1980, (d) Dissection A, at 62X, (e) Dissection B, at 68X; (f) *O. intermedia,* FMNH 204764, Dissection A, Sta. WA-597, 14.3 km south of Behn River crossing, 13.4 km north of Spring Creek Station turnoff from Duncan Highway, 13 May 1980, at 98X; (g) *O. australis,* FMNH 200173, Dissection A, Sta. WA-245, 11.6 km north of Behn River crossing, Duncan Highway, 16 November 1976, at 67X; (h) *Mouldingia orientalis,* FMNH 200333, Dissection A, Sta. WA-248, 3.3 km west of Lissadell Homestead, south of Lake Argyle, 17 November 1976, at 103X; (i) *M. occidentalis,* FMNH 199919, Dissection A, Sta. WA-273, east of McSherry Gap, Napier Range, 3 December 1976, at 82X.

Table 71: Local Variation in *Exiligada negriensis* Iredale, 1939

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
WA-590, FMNH 204734	26	11.30 ± 0.134 (9.9 – 13.0)	18.33 ± 0.156 (16.1 – 19.4)	0.617 ± 0.006 (0.543 – 0.672)
WA-248, FMNH 199721	8	11.88 ± 0.218 (11.1 – 12.95)	18.61 ± 0.300 (17.5 – 19.8)	0.639 ± 0.009 (0.594 – 0.677)
WA-247, FMNH 199580	13	12.49 ± 0.185 (11.2 – 13.8)	18.70 ± 0.222 (17.3 – 20.1)	0.668 ± 0.010 (0.605 – 0.728)
WA-243, FMNH 199617	11	16.14 ± 0.263 (14.95 – 17.25)	22.26 ± 0.340 (20.2 – 24.5)	0.726 ± 0.016 (0.610 – 0.780)
WA-599, FMNH 204774	25	15.33 ± 0.185 (13.9 – 17.0)	21.53 ± 0.196 (18.9 – 23.3)	0.713 ± 0.007 (0.642 – 0.782)
WA-244, FMNH 199627	13	13.0 ± 0.298 (11.65 – 14.3)	19.28 ± 0.307 (17.3 – 21.2)	0.674 ± 0.010 (0.625 – 0.739)
WA-598, FMNH 204769	12	12.62 ± 0.187 (11.6 – 13.6)	19.13 ± 0.190 (18.0 – 20.1)	0.660 ± 0.011 (0.574 – 0.731)
WA-708, FMNH 205298	20	14.20 ± 0.162 (12.95 – 15.5)	20.32 ± 0.237 (17.75 – 22.0)	0.700 ± 0.010 (0.616 – 0.811)
WA-709, FMNH 205304	15	13.28 ± 0.172 (11.9 – 14.2)	19.74 ± 0.214 (18.3 – 21.6)	0.673 ± 0.008 (0.620 – 0.731)
Ord River, WAM 47.54	6	13.24 ± 0.333 (12.4 – 14.8)	18.63 ± 0.340 (17.0 – 19.5)	0.711 ± 0.013 (0.675 – 0.759)

Table 71: Local Variation in *Exiligada negriensis* Iredale, 1939 (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
White Mt., Ord River Station, WAM 436.77	13	12.41 ± 0.201 (10.5 – 13.1)	17.65 ± 0.171 (17.1 – 19.4)	0.703 ± 0.010 (0.603 – 0.741)
between Nicholson and Halls Creek, WAM 437.77	9	14.48 ± 0.174 (13.75 – 15.5)	18.85 ± 0.079 (18.4 – 19.2)	0.768 ± 0.009 (0.724 – 0.824)
Paratypes of *E. negriensis*, AM C.64916	10	11.29 ± 0.158 (10.5 – 12.35)	19.1 ± 0.212 (17.8 – 20.3)	0.592 ± 0.009 (0.539 – 0.635)
Paratypes of *E. qualis*, AM C.64915	13	12.57 ± 0.265 (11.55 – 14.4)	18.83 ± 0.125 (18.1 – 19.4)	0.667 ± 0.012 (0.620 – 0.760)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
WA-590, FMNH 204734	26	4⅞ (4½+ – 5⅛–)	1.24 ± 0.055 (0.8 – 2.1)	15.5 ± 0.621 (8.8 – 21.9)
WA-248, FMNH 199721	8	4¾ (4⅝ – 4⅞)	1.63 ± 0.085 (1.2 – 1.95)	11.6 ± 0.548 (9.59 – 14.6)
WA-247, FMNH 199580	13	5– (4⅝ – 5⅛+)	1.56 ± 0.096 (1.1 – 2.05)	12.5 ± 0.713 (8.85 – 16.2)
WA-243, FMNH 199617	11	5⅛– (4⅞– – 5½+)	1.67 ± 0.161 (1.1 – 2.9)	14.3 ± 1.06 (7.93 – 19.7)
WA-599, FMNH 204774	25	5⅛+ (5– – 5¾–)	0.88 ± 0.063 (0.4 – 1.7)	27.6 ± 2.11 (13.4 – 60)
WA-244, FMNH 199627	13	4⅞ (4⅝ – 5¼)	0.94 ± 0.039 (0.7 – 1.2)	20.7 ± 0.876 (15.5 – 26.9)
WA-598, FMNH 204769	12	5– (4¾+ – 5¼)	0.58 ± 0.058 (0.25 – 1.05)	37.3 ± 4.522 (19.2 – 80)
WA-708, FMNH 205298	20	5¼+ (5+ – 5½+)	0.66 ± 0.048 (0.35 – 1.0)	33.4 ± 2.082 (20.6 – 51)
WA-709, FMNH 205304	15	5⅛– (4⅞– – 5¼+)	0.69 ± 0.072 (0.3 – 1.25)	32.5 ± 2.991 (16.4 – 57)
Ord River, WAM 47.54	6	5⅛ (4⅞ – 5⅜–)	0.89 ± 0.043 (0.8 – 1.0)	21.8 ± 1.034 (19.5 – 24.3)
White Mt., Ord River Station, WAM 436.77	13	5⅛ (5– – 5⅜)	1.37 ± 0.116 (0.75 – 1.9)	14.2 ± 1.286 (9.16 – 23.7)
between Nicholson and Halls Creek, WAM 437.77	9	5⅛ (5– – 5¼)	1.25 ± 0.101 (0.9 – 1.7)	15.6 ± 1.192 (11.2 – 20.9)
Paratypes of *E. negriensis*, AM C.64916	10	5⅜– (5⅛ – 5⅝)	1.21 ± 0.101 (0.6 – 1.7)	17.1 ± 1.607 (11.5 – 29.7)
Paratypes of *E. qualis*, AM C.64915	13	5⅛+ (4⅞– – 5⅝+)	0.97 ± 0.040 (0.75 – 1.2)	19.8 ± 0.845 (15.1 – 24.2)

Shell of average size, apex and spire moderately and evenly elevated, not to slightly rounded above **(Fig. 176b)**, body whorl at most descending slightly before aperture. Umbilicus narrowly open **(Fig. 176c)**, partly covered by reflexion of columellar lip. Apical sculpture **(Plate 57a-c)** initially of fine radial riblets to which, on last portion, are added periostracal projections that on spire and body whorl **(Plate 57d-e)** become crescent-shaped ridgelets oriented spirally individually, but radially in rows, reduced on shell base. Lip strongly expanded and reflexed, reduced to a thin callus on parietal wall, partly covering umbilicus, no lip node present. Shell periphery protruded into a thread-like keel **(Fig 176b)**, no sulci developed. Whorls of spire somewhat flattened. Shell colour very light yellow-horn, almost white on part of base. Genitalia **(Figs 177-8)** with hermaphroditic duct (GD) entering laterally on talon (GT). Lobes of ovotestis **(Fig. 177a, g)** well separated. Albumen gland (GG), prostate (DG) and uterus (UT) without unusual features. Free oviduct **(Fig. 177a,** UV) rather short, slender, entering laterally onto expanded chamber at base of spermatheca (S) and head of vagina (V). Spermatheca attached to prostate-uterus by connective tissue, base enlarged and with high, simple pilasters, which continue into the expanded apex of the vagina. Latter very long, coiled, slender except for apical region, internally with low, longitudinal pilasters. Vas deferens (VD) entering very thin-walled penis sheath (PS) near apex **(Fig. 177b)**, reflexing almost immediately and continuing downward to enter epiphallus (E). Latter short, with thick walls, vague longitudinal pilasters **(Fig. 178)**, no external indication of change to penis (P), internally the transition marked by sharp alteration in wall sculpture. Penis coiled within sheath, basal two-thirds very slender and with simple longitudinal pilasters, upper third **(Fig. 178)** much thicker and with complex, foliated pilasters that have hardened upper edges (indicated by vertical lines). Atrium (Y) very short. Jaw **(Plate 58a)** typically camaenid. Radular teeth **(Plate 63a-b)** typical of group, mesocone blunt tipped and curved apically, side cusps prominent. Marginals typical.

Type species: *Prototrachia sedula* sp. nov.

Comparisons

The shell of *Prototrachia sedula* **(Figs 176a-c)** is macroscopically very similar to that of the keeled *Ordtrachia* **(Figs 166, 171)** and *Westraltrachia froggatti* (Ancey, 1898) **(Figs 122a-f)**. There is a visible microsculpture that enhances the similarity, but even low level optical examination of the shell surfaces shows major differences. The simple periostracal pointed projections of *W. froggatti* **(Plate 20c-f)** and *Ordtrachia intermedia* **(Plate 56e-f)**, or the blunter pustules of *O. septentrionalis* **(Plate 54c)**, are very different from the semi-circular ridgelets of *Prototrachia sedula* **(Plate 57b-e)**. The latter also are oriented spirally, while the former are longitudinally situated. The functional aspects are probably the same, but the structure is quite different.

Elongation of the vagina (V) and penis (P) in *Prototrachia sedula* **(Figs 177a, b)** may reflect species recognition interactions with the undescribed camaenids found at the same station, but consideration of this must be deferred until the other species are reviewed. The internal wall sculpture of the penis **(Fig. 178)** is very different from that found in the East Kimberley genera *Mouldingia*, *Ordtrachia* and *Exiligada* (see **Figs 165d, 175d)**, and most species of *Westraltrachia* **Figs 158a-q)**. Only *W. rotunda* **(Fig. 148)** and, to a lesser extent, *W. woodwardi* **(Fig. 113c)**, show large foliated pilasters and retain traces of the hard edging that is so prominent in *P. sedula*. The absence of an

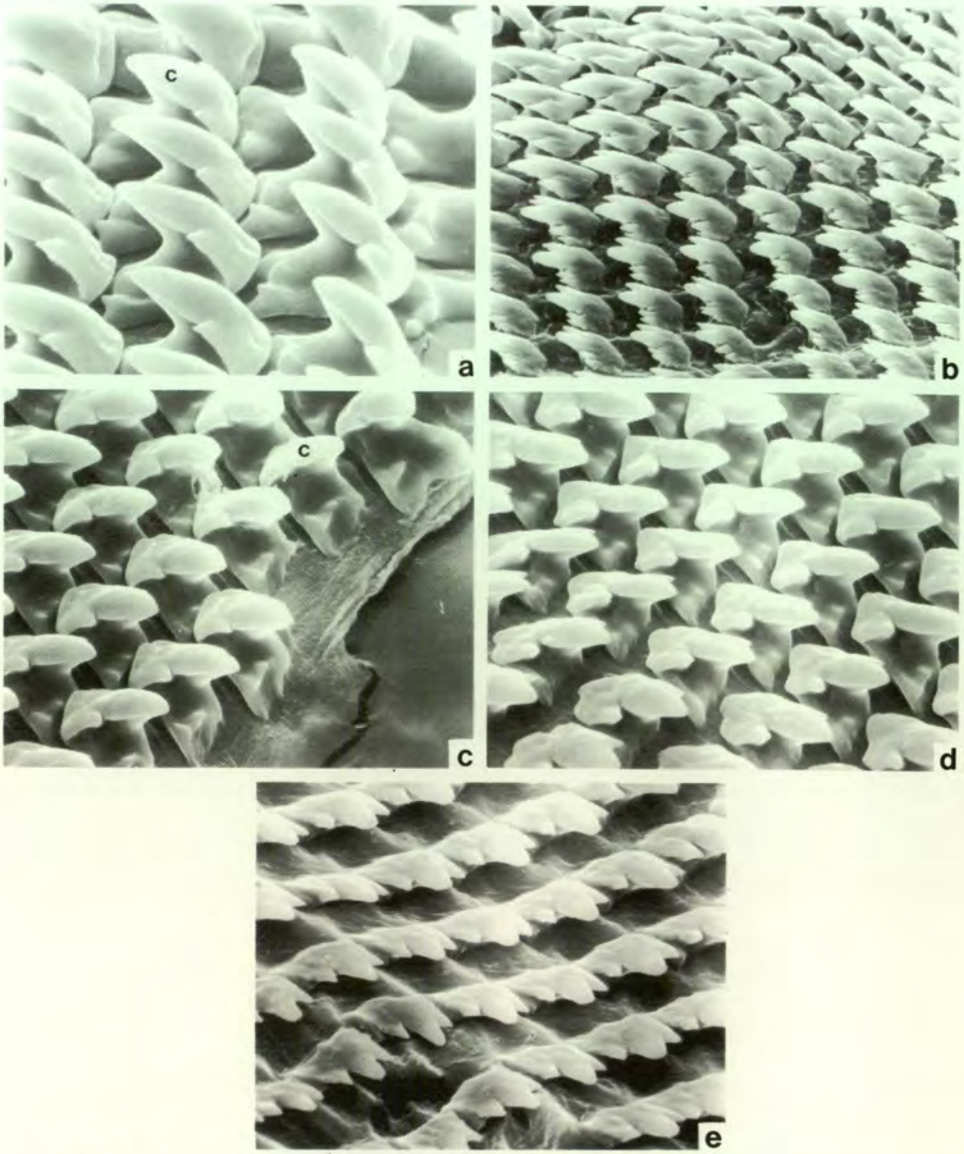

Plate 59: Radular teeth of *Mouldingia occidentalis* and *M. orientalis:* (a-b) *M. occidentalis,* FMNH 199919, Dissection A, Sta. WA-273, east of McSherry Gap, Napier Range, 3 December 1976, (a) mid-angle side view of central and laterals at 1,050X, (b) high angle top view of latero-marginal transition at 565X; (c-e) *M. orientalis,* FMNH 200333, Dissection A, Sta. WA-248, 3.3 km west of Lissadell Homestead, south of Lake Argyle, 17 November 1976, (c) mid-angle top view of central and laterals at 735X, (d) mid-angle top view of latero-marginal transition at 745X, (e) high angle top view of marginals at 725X. Central teeth indicated by a "C."

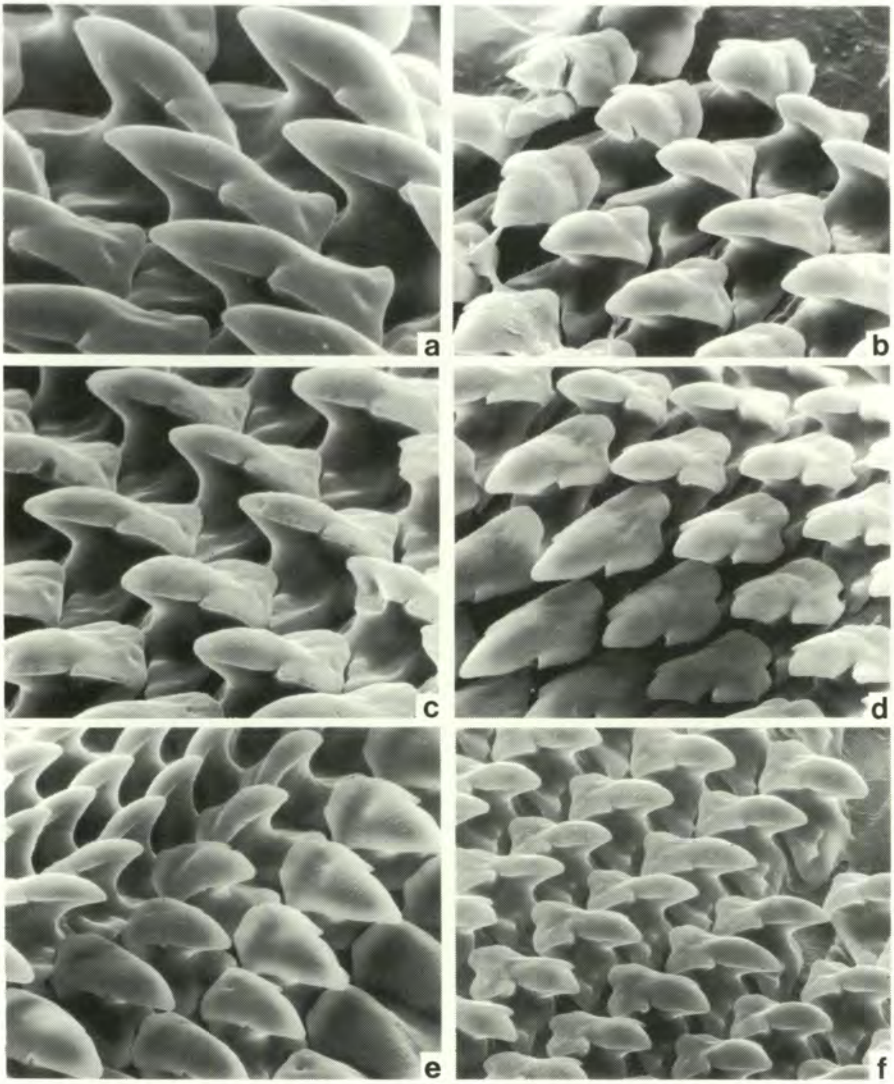

Plate 60: Radular teeth of *Ordtrachia septentrionalis* and *O. australis:* (a-d) *O. septentrionalis,* FMNH 205295, Sta. WA-707, south of Rosewood turnoff, 15.6 km north of Behn River crossing on Duncan Highway, 16 June 1980, (a) Dissection B, low angle side view of central and laterals at 1,315X, (b) Dissection A, low angle side view of central and early laterals at 720X, (c) Dissection A, mid-angle top view of latero-marginal transition at 900X, (d) Dissection A, mid-angle side view of mid-laterals at 690X; (e-f) *O. australis,* FMNH 200173, Dissection A, Sta. WA-245, 11.6 km north of Behn River crossing, Duncan Highway, 16 November 1976, (e) mid-angle top view of central and laterals at 660X, (f) high angle side view of latero-marginal transition at 650X.

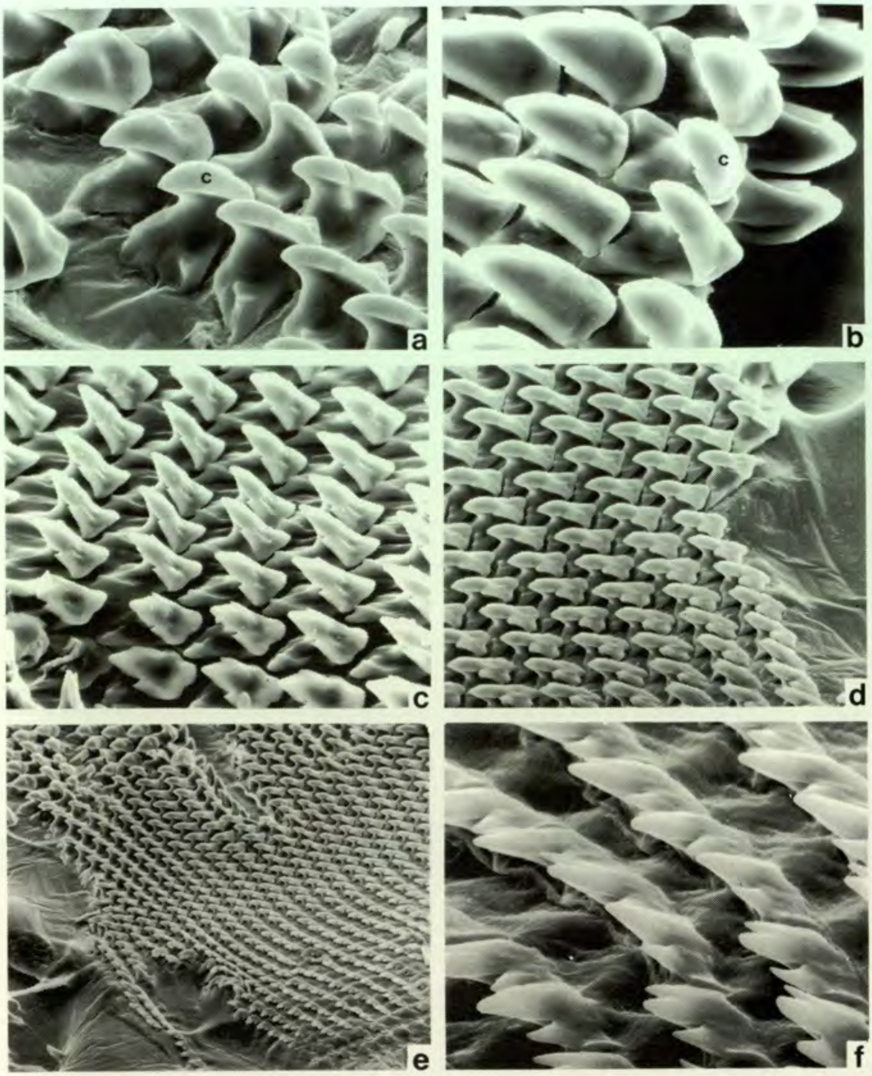

Plate 61: Radular teeth of *Ordtrachia grandis:* (a) FMNH 204772, Dissection A, Sta. WA-598, 10.8 km south of Behn River crossing, 16.9 km north of Spring Creek turnoff, Duncan Highway, 13 May 1980, mid-angle side view of central and early laterals at 630X; (b-c) FMNH 199959, Dissection A, Sta. WA-244, 8.4 km south of Behn River crossing, west of Duncan Highway, 16 November 1976, (b) low angle top view of central and laterals at 635X, (c) high angle side view of latero-marginal transition at 460X; (d-f) FMNH 204772, Dissection A, Sta. WA-598, (d) high angle side view of latero-marginal transition at 325X, (e) very high angle top view of part row at 135X, (f) mid-angle side view of mid-marginals at 985X. Central teeth indicated by a "C".

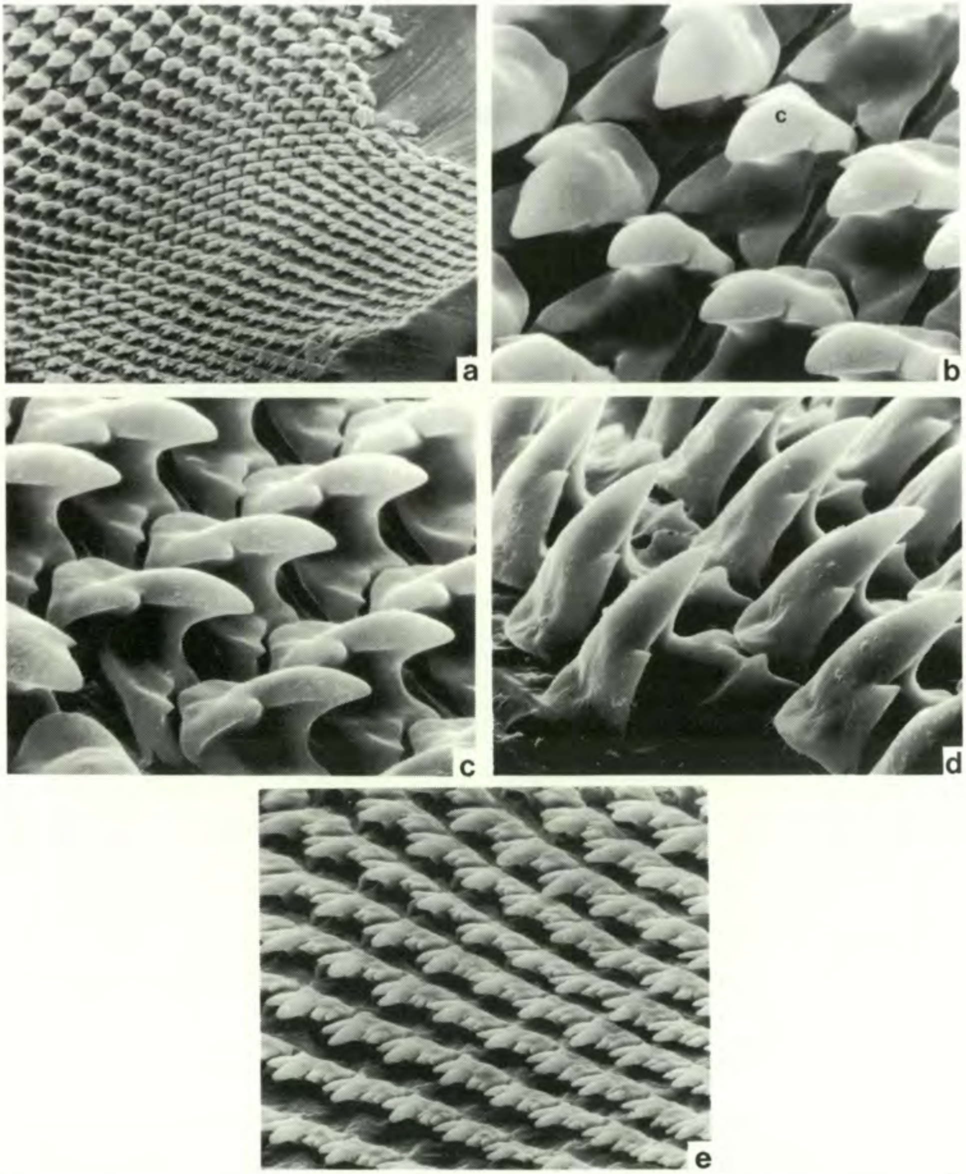

Plate 62: Radular teeth of *Ordtrachia intermedia;* (a-e) FMNH 204764, Dissection A, Sta. WA-597, 14.3 km south of Behn River crossing, 13.4 km north of Spring Creek Station turnoff from Duncan Highway, 13 May 1980, (a) very high angle top view of part row at 220X, (b) low angle posterior view of central and first laterals at 1,230X, (c) low angle side view of later laterals at 1,300X, (d) low angle side view of laterals at 1,240X, (e) high angle top view of marginals at 645X. Central teeth indicated by a "C".

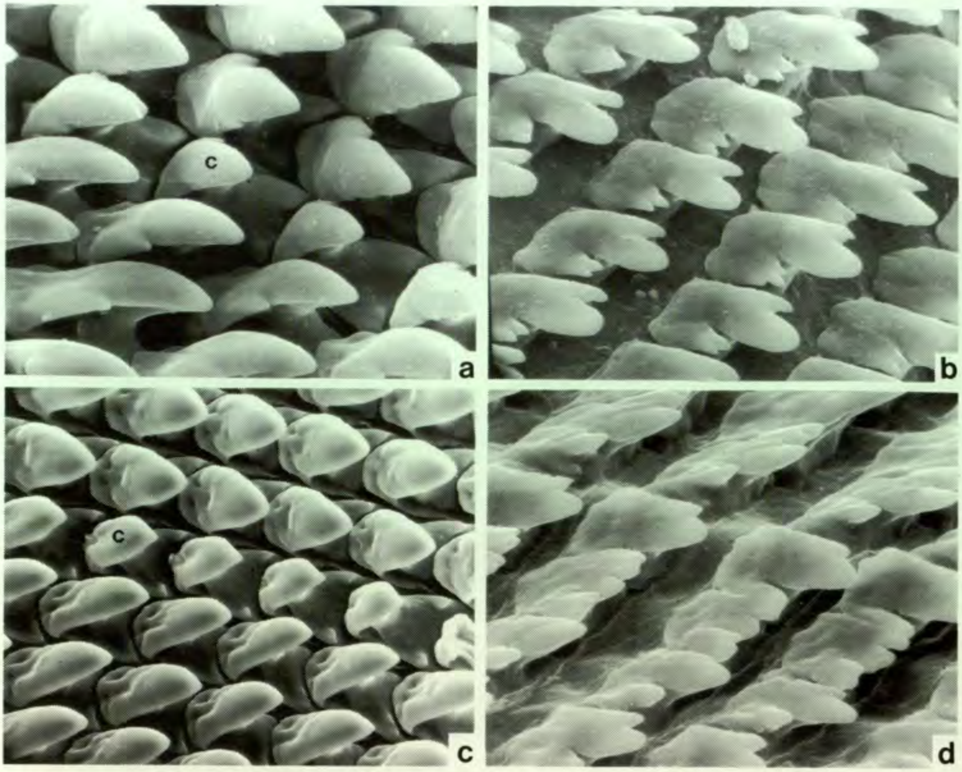

Plate 63: Radular teeth of *Prototrachia sedula* and *Exiligada negriensis* Iredale, 1939: (a-b) *P. sedula,* FMNH 205145, Dissection A, Sta. WA-680, limestone ridges, 24.4 km east of Timber Creek Police Station, N. T., 1 June 1980, (a) mid-angle side view of central and laterals at 715X, (b) mid-angle side view of marginals at 730X; (c-d) *E. negriensis* Iredale, 1939, FMNH 205303, Sta. WA-709, 37.2 km north of Nicholson River off Duncan Highway, N. T., 17 June 1980, (c) Dissection A, mid-angle top view of central and laterals at 340X, (d) Dissection B, mid-angle side view of marginals at 725X. Central teeth indicated by a "C".

epiphallic loop, penial muscle, or muscle-glandular zone on the outer side of the epiphallus in *P. sedula* separates it from any of the above genera. *Prototrachia* has a more generalised penial complex that shares features with *Prymnbriareus nimberlinus* Solem (1981b: Figs 108a-b, 109f).

Only one species of *Prototrachia* is known, and it has been collected at Sta. WA-680, the only major limestone exposure on the Victoria Highway between Kununurra, Western Australia and Katherine, Northern Territory. This is located approximately 24.4 km east of Timber Creek Police Station and 44.1 km west of the Fitzroy Station turnoff, with the coordinates 15° 45′ S, 130° 37′ E. The Victoria Highway passes through a small gap, and low cliffs are exposed near and at the tops of the slopes on each side. Two undescribed camaenids are common in the cliff area, but *Prototrachia* *sedula* lives on the lower slopes under scattered single boulders or blocks. It aestivates as a free sealer, and in selection of aestivation site agrees exactly with *Ordtrachia septentrionalis* and *O. australis* in the area north of the Behn River (**Fig. 179**). Several stops at sandstone or granitic cliffs in this section of the Northern Territory produced no land snails, and this may be a relict situation.

The name *Prototrachia* refers to its generalised genital structures compared with other members of this complex.

PROTOTRACHIA SEDULA SP. NOV.

(Plates 57a-e, 58a, 63a-b; Figs 176-178)

Comparisons

The unique pattern of micropustulations **(Plate 57a-e)** found in *Prototrachia sedula* easily separates it from any keeled *Westraltrachia* or *Ordtrachia*. It is most similar in size and shape to *Ordtrachia australis* (compare **Figs 166d-f** and **176a-c),** but the different microsculpture (compare **Plate 55** and **57a-e)** of wide pustules oriented long edge vertically in *australis* and thin semicircular projections with long edge horizontally in *sedula* can be seen at low optical magnifications. The large foliated ridges with hard upper edges inside the penis **(Fig 178),** lack of an epiphallic loop, penis muscle, or muscle-glandular zone on the epiphallus, combine to separate *P. sedula* from any other member of the *Westraltrachia* complex.

Holotype

WAM 518.80, Sta. WA-680, limestone exposures north of Victoria Highway, 24.4 km east of Timber Creek Police Station and 44.1 km west of Fitzroy Station turnoff, Northern Territory (1:100,000 'Stokes' map sheet 5066 – 722:585). Collected by Alan Solem, Barbara Duckworth and Laurie Price 14 June 1980. Height of shell 8.8 mm, diameter 15.95 mm, H/D ratio 0.552, whorls 5¼ +, umbilical width 1.9 mm, D/U ratio 8.40.

Paratopotypes

WAM 581.80, WAM 582.80, WAM 583.80, FMNH 205144-5, FMNH 205157, 22 live, 46 dead adults, 7 live, 12 dead juveniles from the type locality.

Diagnosis

Shell medium in size, 13.6-17.3 mm (mean 15.56 mm) in diameter, with 5 – to 5¾ (mean 5⅜ –) normally coiled whorls. Apex and spire moderately and evenly elevated, body whorl at most descending slightly before aperture, height of shell 7.2-10.5 mm (mean 8.35 mm) H/D ratio 0.495-0.604 (mean 0.536). Apical sculpture **(Plate 57a-b)** of fine radial riblets joined by micropustulations on later sections. Postapical whorls **(Plate 57c-e)** with minor irregular growth wrinkles and a microsculpture of semicircular periostracal ridgelets that are oriented horizontally along the whorl rather than vertically. Shell periphery slightly protruded into a thread-like keel **(Fig. 176b),** no significant sulci developed. Lip strongly expanded and reflected, reduced to a thin callus on parietal wall, columellar section partly covering umbilicus. No internal lip nodes. Umbilicus partly open, width 0.55-2.1 mm (mean 1.31 mm), D/U ratio 7.71-26.3 (mean 12.8). Based on 69 measured adults.

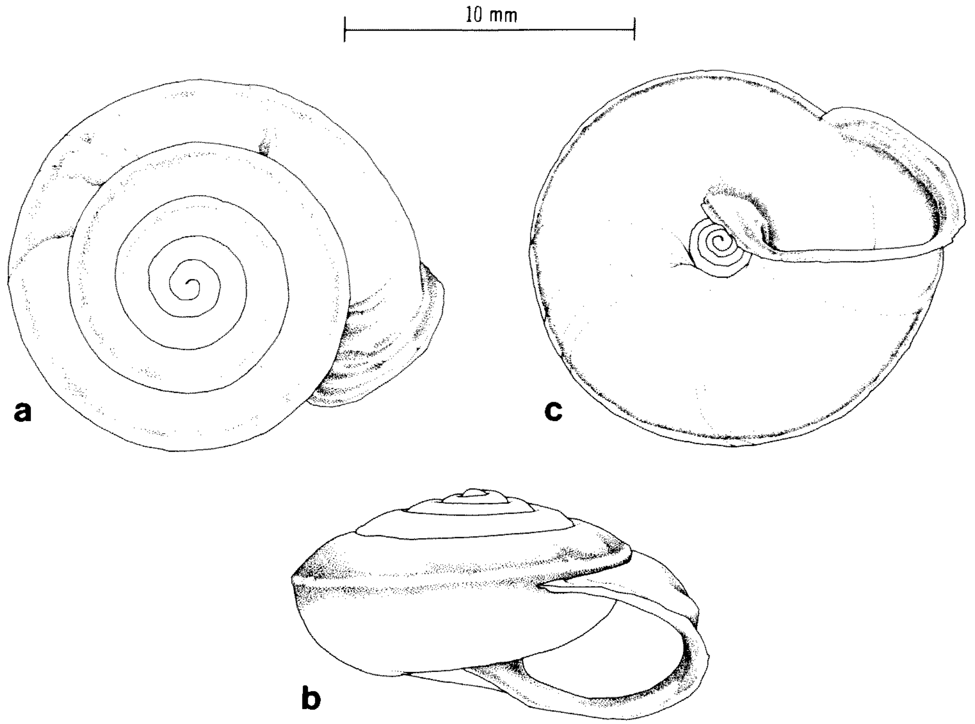

Fig. 176: Shell of *Prototrachia sedula:* Sta. WA-680, east of Timber Creek Police Station between Kununurra and Katherine, Northern Territory, 14 June 1980, WAM 518.80, holotype. Scale line equals 10 mm. Drawings by Linnea Lahlum.

Genitalia **(Figs 177-178)** with hermaphroditic duct (GD) entering laterally on talon (GT). Albumen gland (GG), prostate (DG), and uterus (UT) without unusual features. Spermatheca (S) of average length, base greatly enlarged and with high long pilasters on inner walls, extending into head of vagina (V). Free oviduct **(Fig. 177a,** UV) slender, entering laterally upon vagina-spermatheca chamber, somewhat sinuated. Vagina (V) very long, slender, coiled. Vas deferens (VD) entering thin-walled penis sheath (PS) near apex **(Fig. 177b),** receiving penial retractor muscle (PR), then reflexing downward and coiled to expanded section marking start of epiphallus (E). Interior of thick-walled epiphallus with vague longitudinal pilasters **(Fig. 178)** and glandular tissue. Penis (P) very long **(Fig. 177b)** and coiled inside sheath, lower two-thirds very slender, upper third thicker because of the high foliated pilasters inside **(Fig. 178).** Latter with hardened upper edges (indicated by lines in **Fig. 178).** The high pilasters first diminish in size, then disappear at base of enlarged section, replaced in basal two-thirds by simple longitudinal pilasters. Walls of penis thick.

Jaw **(Plate 58a)** with typical vertical ribs. Radula **(Plate 63a-b)** with marginals typical, central and laterals with prominent side cusps, mesocone with curved, rather blunt tip.

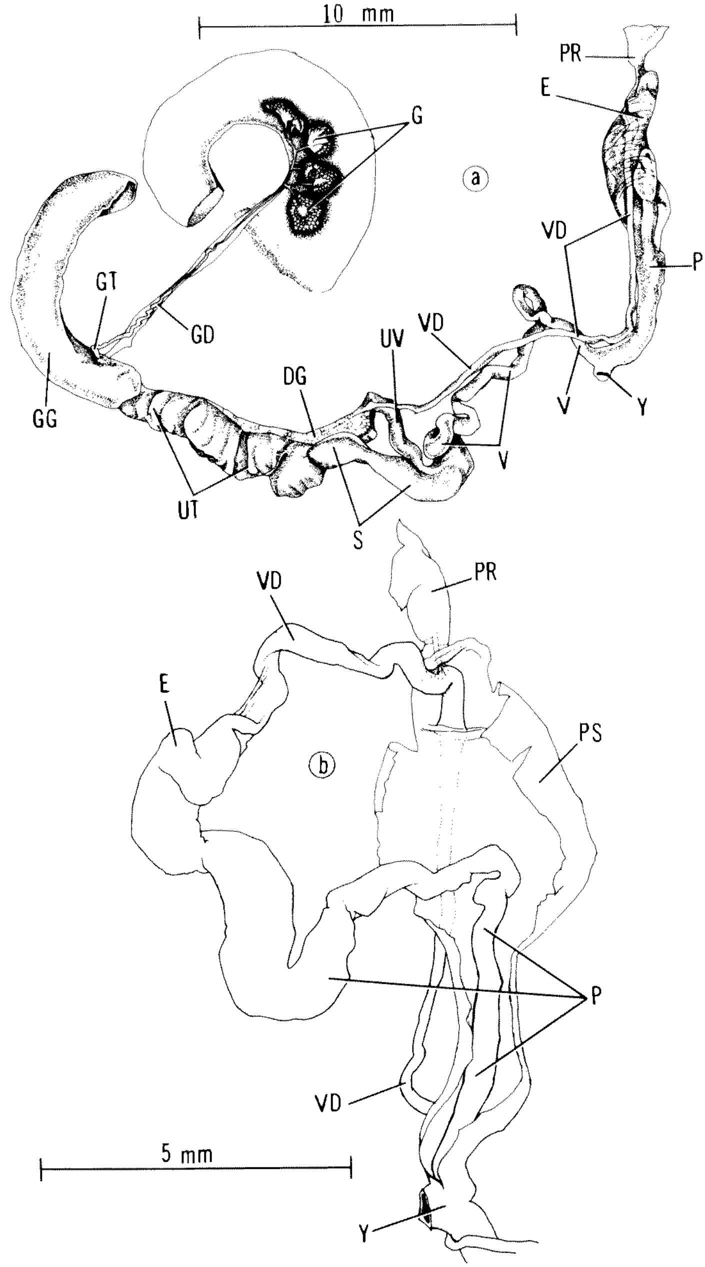

Fig. 177: Genitalia of *Prototrachia sedula:* Sta. WA-680, east of Timber Creek Police Station between Kununurra and Katherine, Northern Territory, 1 June 1980, FMNH 205145, paratopotypes, (a) whole genitalia, Dissection A, (b) penis sheath opened, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

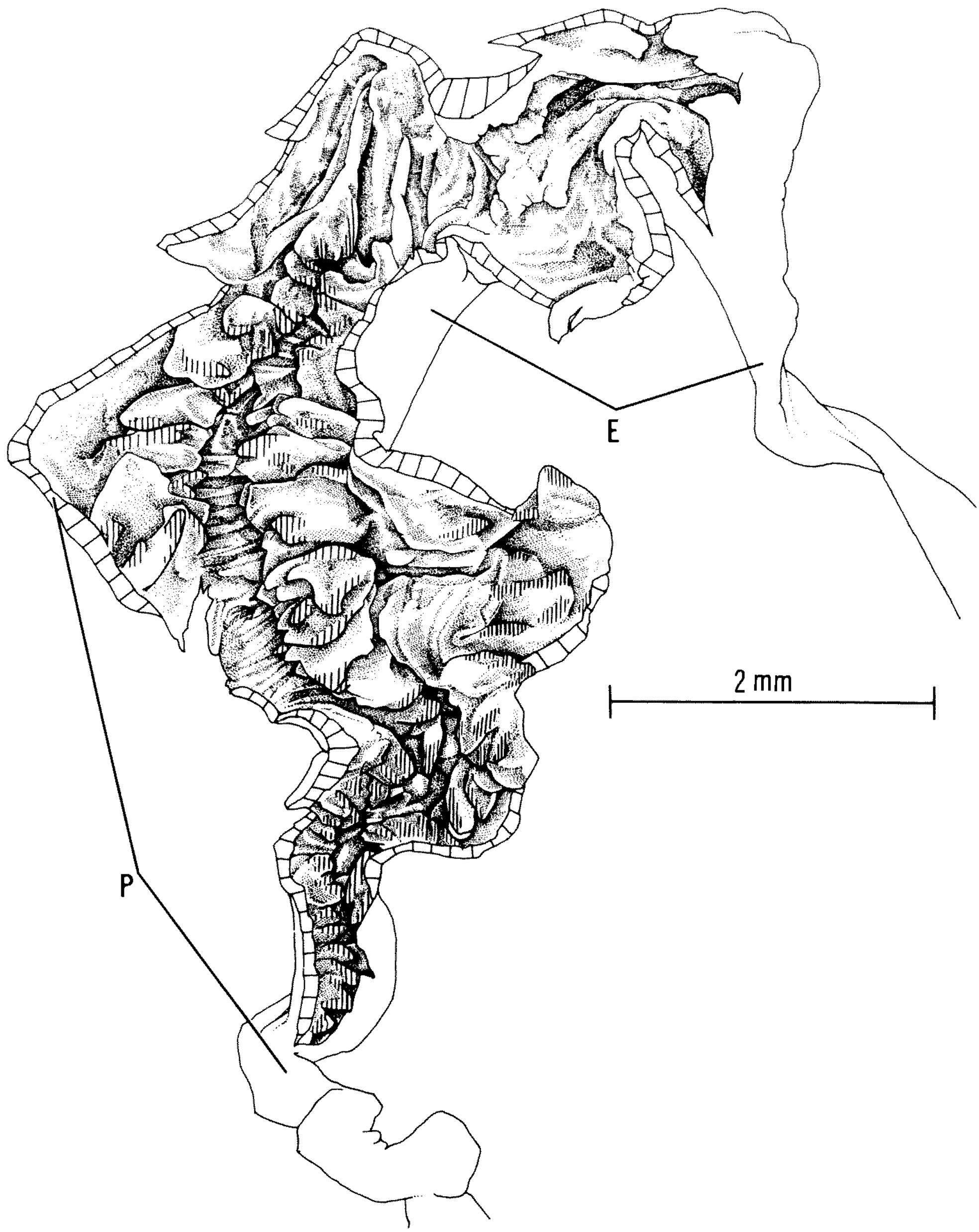

Fig. 178: Genitalia of *Prototrachia sedula:* Sta. WA-680, east of Timber Creek Police Station between Kununurra and Katherine, Northern Territory, 1 June 1980, FMNH 205145, paratopotype, interior of penis and epiphallus, Dissection B. Scale line equals 2 mm. Drawing by Linnea Lahlum.

Discussion

With the advice of rangers from the Northern Territory Conservation Commission, attempts were made to locate limestone exposures in the area between Kununurra, Western Australia and Katherine, Northern Territory. Some river bed sites, that annual flooding makes uninhabitable by land snails, were seen. A few limestone pillars in a dip located about 86 km south-west of Katherine (Sta. WA-681), sheltered two camaenids. The type locality of *Prototrachia sedula*, Sta. WA-680, was the only major exposure of inhabitable limestone located. An undescribed genus of camaenid was taken from sandstone cliffs about 11 km east of Fish Creek, Northern Territory (Sta. WA-699), but this region of the Northern Territory is not good land snail territory.

Thus finding three genera in fair abundance at Sta. WA-680 is remarkable. A *Setobaudinia* (Part V), quite small in size, was common in the rubble at the cliff bases. A large undescribed species related to an extensive radiation in the Katherine area, also was common at the cliff base and in boulder fissures. On the initial quick visit, 1 June 1980, in company with a ranger, Fred and Jan Aslin of Mt. Gambier, South Australia, and Laurie Price, we concentrated on the cliff bases and found only seven dead specimens of *Prototrachia*. A subsequent visit, 14 June 1980 by Solem, Price and Barbara Duckworth, resulted in discovering the open slope aestivation site under scattered limestone boulders and produced 22 live and 40 dead adults.

Variation among the samples **(Table 72)** is another example of "operator difference", as the two large sets that vary in mean shell height, diameter, and D/U ratio were measured by two people. The shells appear identical, it is the angle at which they were held while being measured that differed.

Table 72: Variation in Samples of *Prototrachia sedula*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio
WA-680, FMNH 205144, 1-VI-1980	7(D)	8.25 ± 0.303 (7.2 – 9.1)	15.63 ± 0.439 (14.5 – 17.3)	0.527 ± 0.009 (0.495 – 0.554)
WA-680, FMNH 205145, 14-VI-1980	22L	8.72 ± 0.135 (7.7 – 10.5)	15.87 ± 0.154 (14.9 – 17.3)	0.549 ± 0.005 (0.503 – 0.604)
WA-680, FMNH 205157, 14-VI-1980	40(D)	8.16 ± 0.089 (7.2 – 9.35)	15.37 ± 0.123 (13.6 – 16.9)	0.531 ± 0.003 (0.498 – 0.567)

Station	Number of Adults Measured	Mean, SEM and Range of: Whorls	Umbilical Width	D/U Ratio
WA-680, FMNH 205144, 1-VI-1980	7(D)	5¼ + (5+ – 5½)	1.18 ± 0.119 (0.8 – 1.65)	14.2 ± 1.51 (8.82 – 18.4)
WA-680, FMNH 205145, 14-VI-1980	22(L)	5⅜ – (5– – 5¼)	1.54 ± 0.056 (1.15 – 2.1)	10.6 ± 0.390 (7.71 – 14.4)
WA-680, FMNH 205157, 14-VI-1980	40(D)	5⅜ – (5– – 5¼ –)	1.21 ± 0.050 (0.55 – 1.9)	13.7 ± 0.691 (8.48 – 26.3)

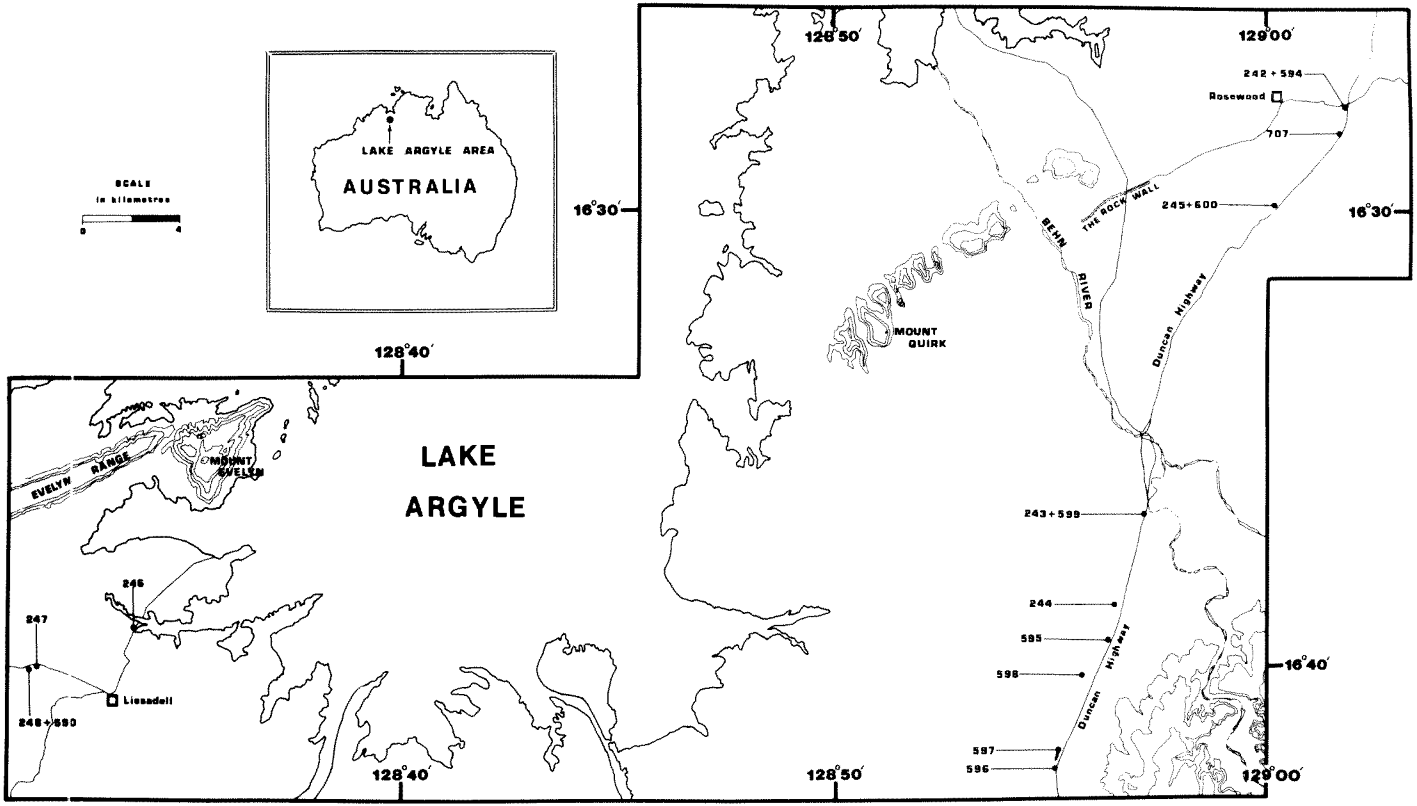

Fig. 179: Collecting stations in the vicinity of Lake Argyle. Drafted by Linnea Lahlum.

The combination of generalised penial morphology and unique periostracal microsculpture found in *Prototrachia* is indicative that evolution in this complex is mosaic and that relict situations occur. It is quite probable that there are other snail inhabited spots in this section of the Northern Territory, but it will take much effort and mining of local knowledge to discover them.

The name *sedula* characterises the efforts expended on 14 June 1980 by Price, Duckworth and Solem in determined effort to find live specimens for study. Their success provided a key to understanding the probable evolution of the *Westraltrachia* complex. Thus 'busy, active, energetic, zealous, careful, and hard-working' is an appropriate name for this snail.

PHYLOGENY OF *WESTRALTRACHIA* COMPLEX

The genera reviewed above, *Westraltrachia* Iredale, 1933, *Mouldingia, Ordtrachia, Exiligada* Iredale, 1939, and *Prototrachia,* show complex and contradictory minor changes in shell features, major changes in the terminal genitalia, and no clear geographic trends. One genus, *Westraltrachia,* becomes sympatric in the western Oscar Ranges with *Quistrachia* Iredale, 1939 and then in the central Napier Range with *Amplirhagada* Iredale, 1933. The simultaneous divergence in feeding and convergence in shell features that occurs in this zone of sympatry has been discussed elsewhere (Solem, In press-A). Here it is sufficient to note that this is a special situation, and that the jaw, radular, and shell changes found in this region have been discounted from this discussion.

Many features are mosaic in presence. Major shell radial ribs are found in both species of *Mouldingia* and *Ordtrachia intermedia,* but in no other species of this complex. Microsculpture **(Table 74)** is of multiple origins. The thin, horizontally arranged, semi-circular protrusions of *Prototrachia sedula* **(Plate 57c-e)** are very different from the scoop-shaped points found in *Westraltrachia froggatti* (Ancey, 1898) **(Plate 20d-e),** *W. ascita* **(Plate 49),** both species of *Mouldingia* **(Plates 52, 53)** plus *Ordtrachia intermedia* **(Plate 56d-f),** and the large pustules present in *Ordtrachia septentrionalis* and *O. australis* **(Plates 54, 55).** A protruded keel is found in *Westraltrachia froggatti* (Ancey, 1898), all *Ordtrachia,* both *Mouldingia,* and *Prototrachia,* but is absent from *Exiligada* and the other 19 taxa of *Westraltrachia.*

All species aestivate as free sealers. Nearly all have been taken only in the vicinity of limestone cliffs or scattered boulders. Only *Exiligada negriensis* Iredale, 1939 may differ in preferred habitat by burrowing into soil under spinifex or shrubs.

Except for *Westraltrachia rotunda* **(Plate 47a-c),** which approximates the generalised camaenid tooth structure, all species show at least a curved mesocone with blunted tip on the central and lateral teeth. In the area where *Westraltrachia* became sympatric with *Quistrachia* or *Amplirhagada,* the central and lateral radular teeth of the former became highly modified in adaptation to a different food resource, algal-fungal blooms on limestone seepage faces (Solem, In press-A, see also **Plates 33-41).** In the same region, *Westraltrachia* has the vertical ribs on the jaw first reduced, and then lost **(Plates 26-30),** as part of the same shift in food resources (Solem, In press-A).

The major change is a unique, unidirectional change within the terminal male genitalia. Evidence is quite strong as to the direction of change, and is summarised in **Table 74** and **Fig. 180.** This hypothesis is based on data obtained in part from out groups, and in part through a transformation series among the several genera involved.

Using only published evidence on other Kimberley camaenids (Solem, 1979, 1981b), there is a common pattern of adjustment in species recognition patterns under conditions of congeneric sympatry. One member of the genus will show extraordinary elongation of the penis complex, while the other member will show either shortening or no change. This has been documented for four genera in **Table 73.** It is not the only type of adjustment pattern, since *Amplirhagada,* for example, shows changes in verge length, principal pilaster armature, or wall sculpture of the penis or vagina (Solem, 1981a). The pattern of proportional changes also holds for the two grossly sympatric species of *Westraltrachia, W. limbana* and *W. rotunda* **(Table 46).**

Table 73: Sympatric Elongation of Penis in Kimberley Camaenids

Genus	Normal or short penis	Elongated penis
Xanthomelon	*prudhoensis* (Solem, 1979: 26, fig. 7)	*obliquirugosa* (Solem, 1979: 41, fig. 11e)
Ningbingia	*laurina* (Solem, 1981b: 349, fig. 84b)	*octava* (Solem, 1981b: 346, fig. 82b)
Turgenitubulus	*opiranus* (Solem, 1981b: 372, fig. 93b)	*depressus* (Solem, 1981b: 373, fig. 94b)
Cristilabrum	n. sp. (unpublished)	*simplex* (Solem, 1981b: 401, fig. 102b)

Since the elongated penis has to be folded up inside the penis sheath, such elongation frequently is accompanied by slenderisation of the organs. The penial retractor muscle arises from the base of the diaphragm, and generally is rather short **(Figs 167b, 173b, 177b).** There is little or no room within the body for elongation of the *sheath.* The penis-epiphallus must be folded inside a tube that can be lengthened very little. Space needs of muscle, digestive, and vascular organs that also occupy this area of the body prevent major widening of the penis complex. Such folding and narrowing of the penis-epiphallus will, of necessity, lead to a change in internal pilaster structure. The very elongated penial complexes of *Ningbingia, Turgenitubulus,* and *Cristilabrum* **(Table 73)** all resulted in the pilasters being reduced in size, and the stimulatory section of the main pilasters shortened quite dramatically. Comparing the large foliated pilasters of *Prototrachia sedula* **(Figs 178, 180A)** with the tiny pilasters found in most *Westraltrachia* **(Figs 158a-q)** and *Mouldingia* **(Fig. 165d),** indicates a world of difference.

There are intermediate examples, involving partial pilaster reduction. Two have been diagrammed in **Figs 180B-C).** *Westraltrachia rotunda* from the eastern Oscar Ranges has the least modified radular teeth of any member of this complex **(Plate 47a-c),** lives in well shaded gullies rather than open slopes, and has the most globose shell of any *Westraltrachia* **(Fig. 146b).** It retains a set of large pilasters within a thick

Table 74: Character States of Penis Pilasters, Epiphallic Loop, Major Radial Ribs, and Microsculpture in *Westraltrachia* Complex

Taxon	Penis main pilaster state	Epiphallic loop state	Shell ribs	Micro-sculpture type
WESTRALTRACHIA				
woodwardi	C	5	–	1
commoda	C	4	–	1
turbinata	C	4	–	1
inopinata	C	4	–	1
f. complanata	D	3-4	–	a
f. froggatti	D	4	–	a
derbyi	E	3-4	–	–
alterna	D	5	–	–
MOULDINGIA				
occidentalis	E	1	+	a
WESTRALTRACHIA				
oscarensis	E	5	–	(a)
cunicula	E	6	–	–
subtila	E	5	–	–
instita	E	5	–	–
lievreana	D	5	–	–
tropida	E	5	–	–
porcata	E	6	–	–
rotunda	B	5	–	–
limbana	C	5-6	–	–
recta	C	5	–	–
pillarana	C	6	–	–
ascita	C	6	–	a
ampla	C	6	–	–
ORDTRACHIA				
septentrionalis	F	8	–	b
australis	F	8	–	b
MOULDINGIA				
orientalis	E	2	+	a
EXILIGADA				
negriensis	F	6	–	–
ORDTRACHIA				
grandis	F	8	–	(b)
intermedia	F	7	+	a
PROTOTRACHIA				
sedula	A	PRE	–	c

Penis main pilaster states: A – large, primitive condition; B – partly reduced; C – apical remnant; D – single short, zigzagged remnant; E – several thin, zigzagged remnants; F – none.

Epiphallic loop state: PRE – primitive conditions; 1-8 – degrees of change explained in text.

Shell ribs: + – major radial ribs present; "–" – absent

Microsculpture type: 1 – fine spiral lines developed; a – simple periostracal projections; b – broad pustules; c – semi-circular projections; ( ) – reduced condition; "–" – absent.

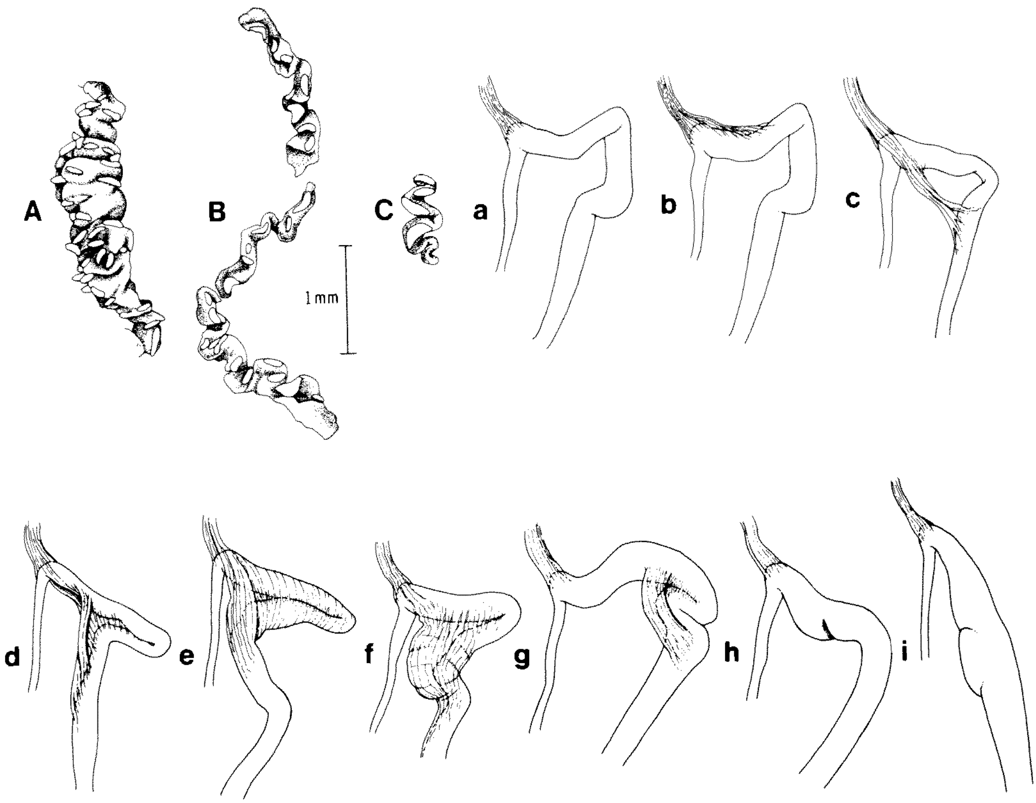

Fig. 180: Patterns of phyletic change in terminal male genitalia of *Westraltrachia* and related genera: A-C, reduction in size and armature on main pilaster, white ovals indicated hardened edges, A) primitive condition as in *Prototrachia sedula,* B) intermediate stages as in *Westraltrachia rotunda,* C) reduced stage as in *W. woodwardi.* a-i, stages in the evolution and then loss of the penis muscle and epiphallic loop: a) elongation of penis-epiphallus, probably under conditions of micro-sympatry, but no shift in strueture, as in *Mouldingia occidentalis;* b) lateral extension of penial retractor muscle along epiphallus, as in *Mouldingia orientalis;* c) extension of muscle to head of penis, with epiphallic loop projected laterally, as in *Westraltrachia derbyi;* d) some fibers connect arms of epiphallic loop and massive penis muscle extends partway down penis, as in *W. subtila;* e) loop of epiphallus bound tightly, penis muscle short, some thickening of area, as in *W. rotunda;* f) epiphallic loop decreased in size, thick muscle-glandular bulge on upper penis-lower epiphallic region, as in *W. ampla;* g) penis muscle separated from penial retractor, epiphallic loop reduced to remnant, as in *Exiligada negriensis;* h) muscle-glandular zone developed, lateral slit remnant of epiphallic loop, as in *Ordtrachia intermedia;* i) muscle-glandular zone left, no trace of epiphallic loop, lateral bulge at penis-epiphallic junction, as in *Ordtrachia australis.* Not to scale. Drawings by Linnea Lahlum.

penis **(Fig. 148)**, and the upper edges have distinct hard sections **(Fig. 180B)**. The more globose shape of the shell in *W. rotunda* increases the cross-sectional area of the whorls, providing more space for organs, and thus permitting a larger diameter penis with retention of the larger pilasters with hardened edges. *Westraltrachia woodwardi* (Fulton, 1902) from the north-west section of the Napier Range is characterised by a more globose shape **(Figs 111b, e, h)** than its neighbour, *W. commoda* (Iredale, 1939) **(Figs 115b, e)**. Retention of a comparatively large pilaster with scattered hard edge sections **(Fig. 180)** in the upper penis of *W. woodwardi* **(Fig. 113c)** also may be linked to the extra space available because of whorl globosity.

All other species of *Westraltrachia* have relatively small main pilasters in the upper penis **(Figs 158a-q)**. Inspection by optical microscope rarely revealed any presence of hardened edges. The nature of the hardening has not been investigated. They appear as white or opaque, generally smooth sections of the edge that are firm to the touch of a needle or tweezers, whereas the intervening sections of pilaster are flexible and easily torn or dented by the same needle or tweezer touch. The possibility exists that this may be seasonally variable and directly comparable to the situation found in *Torresitrachia amaxensis* Solem (1979: 59-60, 81, 83, figs 16a, b). This species has the upper portion of the penis chamber lined with high pustules that in October, just before the Summer rains start and mating can take place, are topped with 'chitinized', very sharp, anteriorly directed points. In March, near the end of the wet season, when the reproductive system shuts down to permit maximum food storage over the forthcoming dry season, the same pustules have lost their points and are soft and flexible. Additional seasonal samples of *Prototrachia sedula, Westraltrachia woodwardi,* and *W. rotunda* are needed before it will be possible to analyse the nature of the edging and whether it changes with the seasons. The whitish colour could be added calcium granules, but this has not been tested.

A sudden increase in the length of the penis-epiphallus presents practical problems of how to fold and manipulate the complex during extension before and then retraction after mating. In *Amplirhagada,* the vas deferens (Solem, 1981a: 242, Fig. 53, VD) normally is coiled in the apex of the sheath, but for an unknown period of hours or days after mating will be stretched out (*ibid.*, dissections of 5 Dec, 4 Jan, 31 Jan, 21 Mar, 3 July). In *Westraltrachia* there is the pattern of the epiphallus forming a laterally extended loop, the arms of which are bound together by muscle fibers. In addition, an extension of the penial retractor muscle (PR) has grown from its insertion at the vas-epiphallic junction along the epiphallus itself to the head of the penis proper. Typical examples of this are shown in **Figs 113, 116, 118, 119, 137** and **140.** The net effect of this change is to shorten the length of tube that must be retracted into the penis sheath, by placing much of the epiphallic length to one side.

The above examples show the completed shift, but extant species have intermediate stages and then demonstrate a further alteration that enables describing a morphocline or transformation series.

This is summarised diagrammatically in **Figs 180a-i.** The specific steps in the process are as follows:

1) initial elongation of the epiphallic-penis tube with simple direct attachment of the penial retractor muscle (PR) to the vas-epiphallic junction, as in *Mouldingia occidentalis* **(Figs 164c, 180a)**;

2) extention of the PR along the outside margin of the epiphallus (E), as in *Mouldingia orientalis* **(Figs 165c, 180b);**
3) muscle extension reaches down to the penis apex (P), attaches to it firmly as the penis muscle (PM), with the epiphallus becoming extended as a lateral loop, for example, in *Westraltrachia derbyi* **(Figs 129d, 180c).**

By this stage the muscle position has shifted so that it runs *inside* the outwardly extended epiphallic loop. This permits more compact folding than if the loop extended inwards. Strands may or may not extend to bind the two arms of the epiphallic loop together, and there is great individual variation in this feature (compare **Figs 129c, d, e, 130b, c, 131b, d, 132b, c).**

4) the PM forms a solid attachment to the penis head and extends part way down the penis, as in *Westraltrachia subtila* **(Figs 140d, 180d);**
5) the arms of the epiphallic loop become tightly compacted and bound together by fibers, the penis muscle becomes a compact mass, and the whole area thickens, as in *Westraltrachia rotunda* **(Figs 148, 180e);**
6) there is size reduction of the epiphallic loop, followed by development of a thick glandular-muscle zone on the penis-epiphallus, as in *Westraltrachia ascita* **(Figs 156c, 180f),** which is carried significantly further in *Exiligada negriensis* **(Figs 175b, 180g)** by having a separation of the penis muscle from the penial retractor;
7) epiphallic loop lost by reduction, only a slight lateral outpocket from the epiphallic base remains **(Fig. 180h),** but a residual very large muscle-glandular zone persists along the epiphallus-penis, as in *Ordtrachia intermedia* **(Fig 173b);** and
8) the outpocket is reduced to a patch, but the massive glandular-muscle zone is left **(Fig. 180i),** as in *Ordtrachia septentrionalis* **(Fig. 167b)** and *O. australis* **(Fig. 168b).**

The reduction in the epiphallic loop and growth of a muscle-glandular bulge on the epiphallus-penis is interpreted as transferring the glandular functions of the epiphallic tube to a concentrated zone, with the actual passage of the sperm transporting duct occupying an extremely small part of the cross-section **(Figs 168b, 169c),** and the total length of the duct reduced to perhaps near the original condition.

These changes are not geographically linear. **Table 74** tries to indicate the status of each species, organised west to east except for the taxa clustered around Lake Argyle, which are listed north to south. The numbers used above indicate the condition, and penis pilaster status is indicated by: 'A' – *Prototrachia* (primitive condition); 'B' – *Westraltrachia rotunda* (intermediate condition); 'C' – *W. woodwardi* (apical remnant condition); 'D' – reduced to a wavy ridge; 'E' – several slender pilasters (vestigial condition); and 'F' – no special pilasters as in *Ordtrachia* (none).

The number of exceptions to linearity suggests experimentation, and the presence of a primitive condition in *Westraltrachia woodwardi,* which has spectacularly altered shell and radular features (Solem, In press-A), suggests that this is not a very old pattern. The development of epiphallic loop loss in the taxa of open plains and small cliffs in the East Kimberley, *Ordtrachia, Exiligada,* may be climate linked, since the rainfall there is only about 500 mm annual average, compared with 725 mm in the

Napier Range, up to 1,500 mm on the north-west coast, and 1,000 mm near Kununurra (Solem, In press-A).

Finding of relict taxa in the East Kimberley and adjacent areas of the Northern Territory may provide additional evidence of experimentation, and might find the hypothesised ancestral situation, where penis elongation occurred when two closely related species of the *Westraltrachia* complex became sympatric.

I know of no equivalent set of changes among camaenid genera. The condition of complex pilaster reduction following penis elongation has been observed in several genera **(Table 73).** The subsequent development of a compacted epiphallic loop, reduction and then loss of loop, with it replaced by a muscle-glandular zone, seems to be unique. Within the context of camaenid variations, this is unidirectional, as the zoned condition is not known elsewhere within the Camaenidae or more advanced helicaceans.

The known genera show combinations of generalised and derived conditions. These are summarised in **Table 74.** On the basis of the changes in the genital structures, I consider that:

- *Prototrachia sedula,* despite its unique shell micro-sculpture, is the most generalised genus:
- *Mouldingia,* generalised in anatomy, has unusual and advanced shell form and sculpture;
- *Westraltrachia,* with the exception of *W. froggatti* and *W. ascita,* is generalised in shell features, but advanced in genital structures, with major changes in jaw, radula, shell colour, and shell shape having occurred under conditions of sympatry with *Quistrachia* and *Amplirhagada;*
- *Ordtrachia,* except for *O. intermedia* with its radial ribbing, is generalised in shell features, but highly specialised in genital structures; and
- *Exiligada* is almost as advanced in genital structure as *Ordtrachia,* but has a simple shell, probably secondarily globose, and an apparently unique shift in aestivation strategy (under vegetation instead of limestone rock associated).

These genera appear to be a well defined unit, with mosaic occurrence of shell ribbing and microsculpture **(Table 74).** I consider that the most obvious and gross changes, such as the feeding shift in Oscar and Napier Ranges *Westraltrachia* and shell size, colour and shape convergence of *W. commoda* (Iredale, 1939) and *W. woodwardi* (Fulton, 1902) with *Amplirhagada napierana* Solem, 1981 resulted from local selective pressures and should be discounted in phylogenetic analysis of intergeneric affinities. Attempts to provide a detailed phyletic tree thus will be postponed until a few additional Kimberley taxa have been reviewed. Patterns of dispersal and generic interactions must be a significant part of the evidence, but are not currently available in published form. It seems likely that both *Ordtrachia* and *Exiligada* were derived from a *Westraltrachia* ancestor; *Prototrachia* probably is close in structure to what could have been the direct ancestor of *Westraltrachia;* and *Mouldingia* is of uncertain relation to the other genera.

BIOGEOGRAPHY OF *WESTRALTRACHIA* COMPLEX

Compared with the uncertainties of phyletic analysis, these genera show a simple biogeographic pattern. Throughout their ranges they are limestone associated, with the possible minor exception of *Exiligada negriensis* Iredale, 1939. It may be able to survive in more open areas with heavy shrub or spinifex cover providing suitable aestivation sites.

The probable origin of the group would be in north-eastern or north-central Australia, with gradual dispersal by seasonal floods from limestone bit to limestone bit. Relict taxa, such as the colony of *Prototrachia,* will lie east of the Ord River drainage in the hills of the Northern Territory. The Ord River drainage today has advanced genera, *Ordtrachia* and *Exiligada,* plus one species of the problematic *Mouldingia.* This is a drier area than that occupied by *Westraltrachia,* and I suspect that the reduction in genital mass found in *Ordtrachia* and *Exiligada* is associated with drying of the climate in comparatively recent times. Loss of the epiphallic loop provided an energy saving both in building an accessory organ, and in maintaining it through dry conditions. Most colonies in the Ord River drainage yielded comparatively few live individuals, the distances between colonies are relatively great, and the total ranges of species are small. These aspects suggest relict status.

Westraltrachia is hypothesised (Solem, In press-A) to have entered the south-east Kimberley from the Ord Drainage to the Lawford Ranges. When and how the jump was made from the northward drainage of the Ord Basin to the westward drainage of the Margaret River and eventually into the Fitzroy River drainage is unknown. Sampling for land snails in the vicinity of Halls Creek in 1976 was a frustratingly negative experience, with no positive stations south of Lissadell Station and west of the Pinnacles. Essentially no collecting has been attempted yet in the Durack and Mueller Ranges west and north-west of Halls Creek. Quite possibly some taxa will be found in that area.

Once the Lawford Range had been colonised, dispersal by floods eventually west to the Oscar and Napier Ranges presents no major difficulties. In this region, the encounter with *Quistrachia* and *Amplirhagada* resulted in simultaneous divergence by *Westraltrachia* in respect to feeding, and convergence in respect to shell form, size, and colour by both *Westraltrachia* and *Amplirhagada* (Solem, In press-A).

The absence of this complex from the Ningbing Ranges north of Kununurra, near the mouth of the Ord River, is surprising – unless the Ningbing Ranges were already occupied by its endemic radiation, and the *Westraltrachia*-type genera were unable to colonise successfully because of competition from entrenched taxa. Some indication that this is a possibility is given by another situation existing in the Ningbing Ranges today. Two genera of wide north Australian distribution, *Xanthomelon* and *Torresitrachia,* are found in abundance both east and west of the main masses of the Ningbings (Solem, 1979). *Xanthomelon* aestivates by burrowing into the ground, and rarely is directly rock associated, but is much less frequently encountered in the Ningbings than in other areas. *Torresitrachia* has been found to the east of the Ningbing Ranges among granitic rock outcrops, and two dead adults were taken from the base of a boab tree located about 15 metres from an eastern limestone outcrop of the north Ningbing Ranges (Solem, unpublished), but *Torresitrachia* never has been found within the Ningbing Range itself. This could be a case of competitive exclusion, but more field study is needed.

Because all the species in this complex, except *Exiligada negriensis*, are tied to limestone exposures, and the entire hill complex on the margin of the South and East Kimberley consists of narrow raised Devonian fringing or barrier reefs, it is possible to present evidence concerning the actual linear ranges of species. The narrow nature of the exposed limestone, from less than 50 metres to a maximum of about one kilometre, means that linear species range is a reasonable indicator of total species ranges.

Table 75 summarises available data. Most species live in areas of almost continuous limestone hills. Talus or fissure aestivation sites are present every few metres, and distribution can be assumed to be essentially continuous. It is necessary to allow for local extinctions and recolonisations during bad and good years in terms of moisture supply, but this is a minor variable. In many parts of the Napier Range, collecting has been intensive enough that the transition zones between species have been identified as being less than 100-300 metres wide, and we have verified the lack of actual sympatry or mosaic distributions. In the main section of the Oscar Ranges, limestone is nearly continuous, but collecting effort has left large sections unsampled. Several species are known from single collections. For these taxa, it is possible to calculate the *maximal potential range* for each species by adding the distances on both sides to the next station from which snails have been collected and recording this sum as the potential range. Obviously, these estimated ranges will be significantly *reduced* by further collecting, since the distances between known species have been added to the range of *both* species.

Other species live in areas where the limestone is exposed as scattered islands and the intermediate plains area are snail-free zones. It is misleading to discuss actual linear ranges for these taxa.

Thus records in **Table 75** are presented as actual ranges, when transition points are known or the end of exposed limestone provide discrete limits; 'less than' a distance when the same potential range extensions have been added to two species; and 'scattered populations' when island distribution, rather than nearly continuous range, is involved. Significant range width, presence in two parallel ranges separated by open plains, or having an 'L'-shaped range, are indicated to the right of the range itself.

Median range for all twenty-nine taxa is 14 km, shown by *Westraltrachia derbyi* (Cox, 1892). Only two taxa have ranges of more than 50 km. *Ordtrachia intermedia* has populations on small bits of isolated limestone in the Ord River drainage, and the most distant colonies are 120 km apart. *Exiligada negriensis* Iredale, 1939 lives in the same region, but may be able to live in relatively open areas under bushes or aestivating by burrowing in the soil. It does not seem to be limestone restricted, and may have many scattered colonies. The east-west range of *Exiligada* is about 46 km (Sta. WA-248 to WA-243, **Fig. 179**), and the approximate north-south range is 160 km (WA-243 to Nicholson).

Most species have very short ranges. A clear distinction must be made between species ranges that are delimited by physical size of the limestone mass (L); ranges that occupy only part of a larger, continuous limestone exposure (C); and ranges that are composed of scattered limestone islands (I). The above symbols are given in **Table 75** after the range itself.

The eight ranges truncated by the size of the limestone include most of the very short ranges, with only *Westraltrachia pillarana* **(Fig. 162)** having a relatively long range. These are not relict ranges, since the species exist on isolated limestone masses that are

Table 75: Species Ranges in *Westraltrachia* and Related Genera

Species	Known or estimated range in km
Minimal Ranges	
W. porcata	0.1 L
O. australis	0.2 L
M. orientalis	0.5 L
P. sedula	0.5 L
O. septentrionalis	1.4 L
W. inopinata	2.0 C
M. occidentalis	2.2 C
Small Ranges	
W. recta	ca 5.0 L
W. turbinata	5.5 C
W. f. froggatti	5-6 C
W. alterna	5.5-7 C
Medium Ranges	
W. instita	less than 9.6 C
W. commoda	11.0 C
W. f. complanata	11-12 C
W. derbyi	14.0 C
W. ampla (scattered populations)	15.0 L (5-8 km wide)
Moderate Ranges	
W. subtila	less than 17.3 C
W. lievreana	less than 21.3 C
W. ascita (scattered populations)	21 I
W. cunicula	23.5 C
O. grandis	23.5 I
W. pillarana	25 L (at east edge in two ranges 7 km apart)
W. oscarensis	20 C (at east edge in two ranges 8 km apart, also lives in plains inbetween)
Extensive Ranges	
W. woodwardi	32.5 C
W. limbana	36.5 C (+ possible 8 km north-west extension)
W. tropida	less than 37 C
W. rotunda	38.5 C (+ possible 11 km added unsampled area)
Very Large Ranges	
O. intermedia (scattered populations, limestone restricted)	ca 120 I
E. negriensis (scattered populations, may burrow in soil)	ca 160 I (?)

many kilometres away from other exposed limestone. It is quite possible that other colonies of *Westraltrachia porcata, Ordtrachia australis, O. septentrionalis,* and *Mouldingia orientalis* may be located, changing these to 'island species', but the flooding of Lake Argyle reduced this possibility for the last three species. *Prototrachia sedula* lives on a small limestone exposure resulting from a 'V'-shaped gap through a ridge, and may indeed be the only colony.

The three 'island species' are *Westraltrachia ascita* in the south-east Kimberley, *Ordtrachia grandis* and *O. intermedia* in the Ord River drainage. In each case, limestone exposures are small and separated by plains areas, so that the species actually occupy only a small portion of the listed range.

There are 17 taxa that occupy only part of their potential habitat. The median range for these also is the 14 km range of *Westraltrachia derbyi.* Range limits for these species probably result from biological factors, presumably interactions with other species of snails. There normally are no physical barrier explanations as to why one species stops and another begins. The review of simultaneous character convergence and divergence in Napier Range camaenids (Solem, In press-A, Fig. 2) points out that wherever there is a physical gap in the Napier Range, whether a major river or less than 100 metres of dirt, species in one genus may cross the barrier, while species in another genus may be different on each side of the gap. Thus minor physical barriers cannot be used to explain the general pattern of short ranges. *Mouldingia occidentalis* is the only species of its genus in the Napier Range, is very abundant locally, but has a very small 2.2 km range.

Of the Napier Range *Westraltrachia,* the following species have at least one distributional limit occurring at the 'middle of a continuous cliff' and thus are biologically, not geographically limited: –

W. inopinata
W. turbinata
W. froggatti complanata
W. froggatti froggatti (Ancey, 1898)
W. commoda (Iredale, 1939)
W. cunicula
W. oscarensis (Cox, 1892)

The other two Napier Range species, *Westraltrachia derbyi* (Cox, 1892) and *W. woodwardi* (Fulton, 1902), can be considered to be geographically limited, since the former extends from the east bank of Windjana Gorge through the inhabitable stretch of limestone 14 km further east, while the latter's range extends from the west bank of Barker Gorge for 32.5 km north-west to the end of the Napier Range.

So far as is known, all the *Westraltrachia* living in the Oscar Ranges show 'mid-cliff' distributions. These species are: –

W. oscarensis (Cox, 1892)
W. instita
W. subtila
W. lievreana
W. tropida
W. limbana
W. rotunda

The latter two, in the Giekie Range east of Fitzroy Crossing, and in the hills on the banks of the Margaret River, may run out of area that can be inhabited, but their eastern limits will not coincide with absence of limestone. Again, all these species probably are biologically limited in range.

Full discussion of the significance of these very small species ranges will be presented later, when data from all of the Kimberley taxa is available for comparison. Here it is perhaps well to point out that many areas in the South Kimberley have exposed limestone formations significantly longer than the ranges listed here – and they have yet to be visited by malacologists. Even casual collections from such areas can produce material of great interest to science. The small ranges also provide unique opportunities for the study of species interactions.

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