Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae)

VII
Taxa from Dampierland through the Nullarbor

by

Alan Solem

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

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G. Alan Solem
1931–1990

This is the last in the series of seven monographs on western and central Australian camaenid land snails by Alan Solem, concluding what was a joint project of the Western Australian Museum and the Field Museum of Natural History, Chicago.

At the time of Alan Solem's death the manuscript was well progressed, but by no means ready for publication. As any author knows, it is the final details in drawing a publication together that are particularly demanding and time-consuming. It was only through the considerable efforts and dedication of much time by Shirley Slack Smith, George Kendrick, Mark Harvey and Ann Ousey of the Western Australian Museum and Linnea Lahlum, formerly of the Field Museum, Margaret Baker, Dorothy Karall, and John Slapcinsky of the Field Museum, that this final monograph has been completed. That this could not be to the standard that would have been achieved by the author they readily acknowledge. That they have been prepared to undertake this demanding task is an indication of their respect and affection for Alan Solem and of the great importance they placed on completing this series.

Alan Solem first became actively involved with the land snails of Western Australia on a reconnaissance field trip in 1974. This led to the *Western Australian Field Program* of 1976-77, a major inter-disciplinary expedition supported by the National Science Foundation, the Field Museum, Chicago, William and Janice Street and the Western Australian Museum. As many as 30 people, mainly specialists from all around the world, were in the field at one time and significant advances were made to knowledge of the State's fauna.

Alan Solem was to make seven subsequent field trips to Australia, the last being in 1989. In the resultant series of monographs on the Camaenidae of Western and Central Australia he reviewed 404 species in 58 genera. Most of these taxa were new (257 species and 28 genera) and all holotypes and most paratypes, as well as some non-type material, were distributed among relevant Australian museums.

The monographs are far more than superb descriptive works based on detailed study of anatomy and morphology. They also incorporate aspects of evolution, biogeography and ecology, and demonstrate the existence of an extensive and apparently unique arid zone land snail radiation in Australia. Undoubtedly the most significant body of work on Australian land snails, through this monograph series Alan Solem has set the standard for future workers and left a great legacy to malacology in Australia.

The Western Australian Museum pays tribute to Alan Solem, long-time Research Associate and friend.

P.F.Berry

Records of the Western Australian Museum Supplement No. 50, 1997

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

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TAXA FROM DAMPIERLAND THROUGH THE NULLARBOR

ALAN SOLEM*†

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INTRODUCTION

This is the seventh, and final, monograph reviewing the camaenid land snails of Western and central Australia. It covers those taxa living: 1) along the south coast between roughly Norseman, Western Australia and Yalata, South Australia (these species may extend for an unknown distance north of the transcontinental rail line); 2) in a northwest arc inland from the Norseman-Kalgoorlie area across to Mt Magnet, Yalgoo, Mullewa, and Geraldton on the west coast; and 3) ranging from just south of Shark Bay to the north tip of Dampier Land, with an inland radiation through much of the Pilbara.

The humid southwest corner of Western Australia, from just south of Geraldton diagonally to Esperance and then west to Augusta, has no camaenids, and probably never has been inhabited by this group. This region has an extensive radiation of the bulimulid genus *Bothriembryon* Pilsbry, 1894 (see monographs by Pilsbry 1900: 1–19 and Iredale 1939: 17–36), a moderate radiation of both Charopidae and Punctidae, plus assorted Pupillidae (see Solem 1986), Succineidae, and one Rhytididae.

The area surveyed thus is a boomerang-shaped, mainly coastal, dry-country arc from Dampier Land to the Great Australian Bight, which serves to complete basic geographic coverage of the camaenids from the western two-thirds of Australia. Its camaenid fauna consists of three separate lineages that show certain unitary convergent features. The pleurodontid genus *Rhagada*, which ranges from the Mitchell Plateau in the monsoonal part of the Kimberley to the very arid area of Shark Bay (**Map 36**), overlaps there with the Red Centre to Flinders–Gawler Ranges sinumelonid lineage. They also are joined by a third lineage, represented by *Quistrachia* (**Map 44**) from the Kimberley and Pilbara. Conchological convergences in this area are so extensive that I have been unable to devise a workable key that will distinguish members of these three groups on shell features. Both sinumelonids and *Rhagada* in this region show extensive alterations in their genital structures, reflecting apparent adaptations to reproduction in an area with sporadic, aseasonal precipitation patterns (see Summary Discussion).

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† Deceased 26/2/1990.

The previous parts of this series covered the following regions.

Parts I through V (Solem 1979, 1981a, 1981b, 1984, 1985b) reviewed species from the Kimberley, recognizing 137 endemic species (98 new) in 23 genera (11 new). It was predicted (Solem 1985b: 976) that "... at least a doubling of species numbers will occur when other parts of the Kimberley are explored for land snails." Seven additional species were described by Solem (1988a); the remarkable *Cristilabrum kessneri* from the Jeremiah Hills (Solem 1989b) is another recent discovery; about 50 new species and two new genera were collected during a helicopter survey of mainland rain forest patches in June 1987; and a joint Western Australian Museum, Australian Museum, and Field Museum of Natural History expedition to islands of the Kimberley coast in July 1988 collected several additional new taxa. Material from both of these surveys will be described subsequently, but the Kimberley fauna is now known to consist of more than 186 species in 25 genera (**Table 168**). To place this in perspective, the total endemic non-camaenid land snail fauna of the Kimberley consists (Solem, 1989a) of 30 species in 20 genera belonging to 10 families. None of the non-camaenid genera and only five of the species (*Georissa obesa* Solem, 1989, *Gyliotrachela napierana* Solem, 1981, *G. ningbingia* Solem, 1981, *Pilsbrycharopa tumidus* [Odhner, 1917], and *Westracystis lissus* [E. A. Smith, 1894]) are restricted to the Kimberley, whereas **NONE** of the camaenid species and only six of the genera (*Hadra* Albers, 1860, *Rhagada* Albers, 1860, *Xanthomelon* von Martens, 1860, *Torresitrachia* Iredale, 1939, *Quistrachia* Iredale, 1939 and *Setobaudinia* Iredale, 1933) have been recorded from other parts of Australia.

Taxa from the Red Centre were reviewed in Part VI (Solem 1993), with 65 species (39 new) in 12 genera (three new) and two subfamilies (Sinumeloninae and Pleurodontinae). The current centre of diversity for the Sinumeloninae lies in the Red Centre, with the next greatest assemblage between the North West Cape and Geraldton, then southeast to Norseman and east to Yalata, South Australia. The third area of sinumelonid abundance lies in the Gawler Range-Eyre Peninsula–Flinders Range area of South Australia. The only other Australian Pleurodontinae belong to the genus *Rhagada* (**Map 36**), which ranges along the west coast from the Mitchell Plateau to Shark Bay, then inland in the Pilbara (see below).

Although not a part of the series, the monograph of the camaenids from southeastern South Australia (Solem 1992), which reviewed 54 species (19 new) in 10 genera (four new) and two subfamilies (Camaeninae and Sinumeloninae), is an integral portion of this project. The Camaeninae include nearly all of the larger sized camaenids from the Eastern States, one Kimberley genus (*Damochlora* Iredale, 1938), and many extralimital relatives in the area from the Solomon Islands to China. They have not been found in the southwestern portions of Australia.

The present review (Part VII) covers 48 species (23 new) in nine genera (four new). Both the Sinumeloninae and Pleurodontinae are well represented. In addition, one genus (*Quistrachia*) of unknown subfamily affinity ranges (**Map 44**) from the Oscar Ranges in the South Kimberley to near Shark Bay, plus having an isolated record in western Queensland (Black Mt., near Boulia).

The sections of Western Australia omitted from this monograph appear to be without land snails, such as the Great Sandy Desert. The current eastern records in the Pilbara region are marked by the Oakover River, followed by a major geographic gap through the Gibson Desert east to the Rawlinson Ranges and Warburton on the fringes of the

Red Centre (see Part VI). No collecting for land snails has been attempted in this region. The existence of scattered, isolated colonies is highly probable. Similarly, further south, the vast region between Mt Magnet and Kalgoorlie east through the Great Victoria Desert to the Everard Ranges is malacologically unexplored. This region probably will not yield significant numbers of species or individuals.

PREVIOUS STUDIES

The source of specimens belonging to the Dampier Land and Eighty Mile Beach species now known as *Rhagada dringi* (Pfeiffer, 1846), *R. reinga* (Pfeiffer, 1846), and *Quistrachia leptogramma* (Pfeiffer, 1846) is unknown. In contrast, the Shark Bay *R. torulus* (Férussac, 1819) was first noted at Bernier Island on the 29 June 1801 by Péron, then collected during 12–27 September 1818 by members of the ship's company of the "Uranie". This vessel was shipwrecked in the Falklands, with only a few specimens being salvaged and eventually reaching France (Iredale 1939: 3).

Other early descriptions include *Plectorhagada plectilis* (Benson, 1853), *P. carcharias* (Pfeiffer, 1864) and *R. convicta* (Cox, 1870). There were no significant new records in the first monograph of Australian land snails (Cox 1868). *Rhagada richardsoni* (E. A. Smith, 1874) was collected by the crew of the "Erebus" and "Terror", while *R. elachystoma* (von Martens, 1878) was collected during the voyage of the "Gazelle".

The comprehensive summary of all Western Australian land snails by E. A. Smith (1894) was followed by a few descriptions (Tate 1894, 1899; Preston 1908, 1914). Completing the short list of publications are the innovative and still useful check list of Hedley (1915), generic novelties introduced by Iredale (1933), the nomenclatural lists of the entire Australian land snail fauna by Iredale (1937a, 1937c, 1938), the monographic checklist of South Australian and Red Centre taxa by Iredale (1937b) and, finally, the conchological monograph of all Western Australian land snails by Iredale (1939). Several new species were named in this report (*Pleuroxia abstans*, *P. elfina*, *Sinumelon kalgum*, *S. vagente*, *Plectorhagada rovina*, *Rhagada perprima*). The only subsequent papers are the description of *Strepsitaurus rugus* (Cotton, 1953), a compilation of all Australian genera (Burch 1976), comments on Shark Bay fossil occurrences of *Rhagada torulus* (see Kendrick 1978) and a check list of all camaenid species compiled by Richardson (1985).

Prior to this series of monographs, no data on anatomical structures of Western Australian camaenids were available. The early notes of Hedley (1889, 1896) on Queensland and Red Centre species were very helpful. The few data on classification were basically modifications of the world summary by Pilsbry (1895). Nearly all papers concerning Australian land snails were simple conchological descriptions (i.e. Cotton & Godfrey 1932; Clench & Archer 1937). Thus a usable framework of classification and phylogeny did not exist at the start of these studies.

MATERIALS AND METHODS

Except for the materials taken by the Elder Exploring Expedition (Bednall 1892), the Horn Expedition to Central Australia (Tate 1894, 1896), and the South Australian

Government North-west Expedition (Hedley 1905), most of which were marginal to the area surveyed, the specimens available consist of types and historical material in various museum collections, and lots collected opportunistically by malacological and non-malacological staff of the Western Australian Museum. Many specimens were bleached bones that had weathered out of dunes or washed down from piles of limestone rubble. Occasional live-collected material was found "wandering about after rains the night before".

My own collecting in this region consisted of an initial survey from Geraldton to Port Hedland in 1974, and a fairly intensive survey of the Nullarbor to Norseman area in 1979. Subsequently I made only quick stops to obtain specimens from restricted populations that would permit study of seasonality in genital structures while "going to or coming from" the Kimberley.

The dates of my collecting and station numbers are:

STATIONS	DATES	COLLECTORS
WA–13 through WA–56	16 Jan. 6 Feb. 1974	A. Solem & L. Price
WA–165 through WA–189	23 Sept. 1976 11 May 1977	A. Solem & various colleagues
WA–403 through WA–421	24 Mar. 1977 25 Apr. 1977	L. Price & C. Christensen
WA–718 through WA–724	23 June 1980 29 June 1980	A. Solem, L. Price, B. Duckworth
WA–949 through WA–963	7 June 1983 13 June 1983	A. Solem, B. Duckworth
WA–964, WA–1058 through WA-1061	12 May 1984 14 June 1984	A. Solem & various colleagues
WA–1067 through WA–1092	20 May 1989 9 June 1989	A. Solem & V. Huff

The 1974 field work was sponsored by the Field Museum of Natural History; the remaining trips by grants from the National Science Foundation and private donors.

Because much of the collecting has been casual, and my own efforts along the west coast have been focused on repeated sampling from the same populations rather than extensive survey work, the range data presented here must be amplified by much additional collecting effort. Some taxa, such as the species of *Quistrachia* (**Maps 44–46**), do have quite restricted ranges. Others, such as *Plectorhagada* (**Maps 28–32**) and *Rhagada* (**Maps 36–43**) may show sharper boundaries or possible overlap zones when more detailed surveys are completed.

All material that I collected was shipped to the Field Museum of Natural History, Chicago for processing and study. All adult specimens in each lot were measured for shell height, diameter, umbilical width and whorl count, then Height/Diameter and

Diameter/Umbilicus ratios calculated. Live and dead examples from the same station were analyzed separately. Means, ranges, standard deviations and standard errors of the means were calculated for each lot of specimens. Nearly all of this painstaking work was accomplished by Temporary Assistant Beth S. Morris during several periods of employment at the Field Museum. *Pleuroxia bethana* (p. 1480) is named in recognition of her invaluable assistance. Summaries of adult size and shape variation were prepared for each species and compiled into the "Range of Variation" tables. Where the material warranted such presentation, data on individual populations are presented in "Local Variation" tables for single species.

Dissection of several individuals from one population and then a few individuals of other populations were carried out by the author using a Leitz dissecting microscope. Illustrators Linnea Lahlum, Elizabeth A. Liebman and Marjorie M. Connors used their considerable skills and a Wild M5 dissecting microscope with drawing tube to communicate the often subtle anatomical and shell features that characterise the species and genera, and thus enable identification without comparative collections.

Buccal masses were removed from all dissected individuals, macerated in KOH, cleaned of debris by a few seconds immersion in a sonic cleaner, then mounted with rubber cement on a metal stub by the author, coated with gold, and studied with a Cambridge S4–10 Scanning Electron Microscope (hereafter SEM). The assistance over the years of Beth S. Morris, Valerie Connor-Jackson, Patricia Johnson and Victoria B. Huff in aspects of preparation, picture labelling and calculating published magnifications from mounted photographs was essential.

Mounting and labelling of the many **Figures** and **Plates** were carried out by Associate Dorothy Karall and by Linnea Lahlum.

Manuscript was composed on a Toshiba T–250 microcomputer, provided by the late Frederick K. Leisch. Invaluable help in proofing the text, and in producing the final **Tables**, was given by Collection Manager Victoria B. Huff.

The systematic analysis involved neither cladistics nor phenetics. Three morphologically very distinctive lineages are present in the area surveyed. Two of these, the pleurodontid genus *Rhagada* Albers, 1860 and the genus *Quistrachia* Iredale, 1939, which is of unknown subfamily position, are present in the west and/or southwest Kimberley, then range south through the Pilbara to the approximate level of Shark Bay, maintaining a basically near-coastal presence. The Sinumeloninae are a Red Centre-Flinders Range-Gawler Range-Eyre Peninsula-Nullarbor complex, with examples of the wide-spread genera *Sinumelon* and *Pleuroxia* along the Great Australian Bight and in the area near Geraldton, plus a radiation of restricted endemics from the south end of Shark Bay through the North West Cape. There are major and unusual convergences in the genital systems of both *Rhagada* and the restricted endemic Sinumeloninae in the Shark Bay to North West Cape areas. These correlate with the change in preciptitation from a predictable wet season (Kimberley and south coast of Australia) to very limited and nearly aseasonal precipitation in the Shark Bay to North West Cape area. The reason for the extensive convergence in shell form and colour in this area is unknown. The basic data are presented in the species and generic accounts, the basic significance is discussed below, and full implications will be developed elsewhere.

After completion of the basic revisionary studies, specimens were selected for permanent deposition in Australian museums. Holotypes of new species have been deposited in the Western Australian Museum, Perth. Synoptic sets of paratypes and nontype material have been deposited in the South Australian Museum, Adelaide; Australian Museum, Sydney; Queensland Museum, Brisbane; and Museum of Victoria, Melbourne. The remaining material has been retained in the Field Museum of Natural History, Chicago. The lengthy task of selecting, labelling and sending these materials has been directed by Collection Manager Margaret Baker, with the assistance of Victoria B. Huff and Beth S. Morris.

Abbreviations are used throughout the text to indicate the repository of listed specimens. They are:

AM Australian Museum, Sydney

BMNH British Museum (Natural History), London

FMNH Field Museum of Natural History, Chicago

MV Museum of Victoria, Melbourne

QM Queensland Museum, Brisbane

SAM South Australian Museum, Adelaide

WAM Western Australian Museum, Perth

Zurich Zoologisches Museum der Universität Zürich.

Catalogue numbers are given where possible, so that, in the future, assemblage by a scientist of a complete series, if needed, will be aided.

To save space, directional words are abbreviated hereafter as W, N, E, S, SW, SSE, etc., and states as NT (Northern Territory), SA (South Australia) and WA (Western Australia).

ACKNOWLEDGEMENTS

The contributions of current FMNH staff members Margaret Baker, Linnea Lahlum and Victoria B. Huff, Associate Dorothy Karall, and former staff members Elizabeth A. Liebman, Valerie Connor-Jackson, Patricia Johnson and Marjorie M. Connors have been listed above. Staff of the Division of Photography provided enlargements of the SEM photographs, and recorded mounted **Figures** and **Plates** for lecture use.

Major financial support of these studies has been provided by National Science Foundation research grants DEB 75–20113, DEB 78–21444, BSR 81–19208 and BSR 85–00212 to Field Museum of Natural History, Alan Solem, Principal Investigator. The Cambridge S4–10 Stereoscan was provided to the FMNH by National Science Foundation grant BMS 72–02149, Alan Solem, Principal Investigator. Continuing gifts over the years from Mrs. Arthur T. Moulding and the late Arthur T. Moulding have greatly aided the field work, and often provided short term support for Beth S. Morris. Recently, gifts from Mrs. Charlotte Lindar-Gorbunoff have enabled completion of the statistical work by Ms Morris.

Bridging funding for Illustrator Linnea Lahlum, provided by Dr. Elizabeth-Louise Girardi and Mrs. Arthur T. Moulding, permitted completion of the illustrations for this monograph, and are gratefully acknowledged. Without this timely help the quality of this report would have been considerably diminished.

For assistance in the field, the co-operation of Field Associate Laurie Price, Carl C. Christensen, Victoria B. Huff, Laurel Keller, Barbara Duckworth and of many station owners is acknowledged. The treatment of the Nullarbor taxa would have been impossible without the co-operation of Fred and Jan Aslin, not only during the 1979 field work but subsequently in verifying localities and providing cave numbers. Curator Emeritus of Fossil Mammals at FMNH, William S. Turnbull, the late Priscilla Turnbull, and Research Associate E. Lundelius collected specimens in 1964 from the North West Cape that excited my interest in this fauna. Such species as *Strepsitaurus cardabius*, *S. williami*, *S. ningaloo*, *Quistrachia waroorana*, and *Q. lefroyi* are a permanent recognition of their help.

The unstinting co-operation of malacological curators and private collectors in Australia, who allowed access to collections, generously provided long term loan of types, and helped in many other ways, was essential to the successful completion of this study. Fred E. Wells, Shirley Slack-Smith, Winston Ponder, John Stanisic, Wolfgang Zeidler, Brian J. Smith, Fred and Jan Aslin, Vince Kessner and C. C. Lu have been of great help to me. At home, Sylvia, Laurie, Jan and even Star supported completion of the final manuscript in several ways.

SYSTEMATIC REVIEW

On the basis of overall genital structure, the camaenids living in this region fall into three distinct groups – several genera belonging to the subfamily Sinumeloninae (**Map 49**); the numerous species of *Rhagada* Albers, 1860 which belong to the Pleurodontinae (**Map 36**); and the several species of *Quistrachia* Iredale, 1939 (**Map 44**) which cannot yet be assigned to a subfamily unit. The anatomical differences are marked. It is not possible to indicate direction of character change, and no ancestor-descendant relationship can be proposed among these three lineages. Basic delineation of the two subfamilies has been given by Solem (1992, 1993). A summary of the diagnostic structural features of the genitalia, as found in the taxa reviewed below, follows:

Subfamily Sinumeloninae – stimulatory surfaces of penis (P) chamber with complex soft pilasters; verge (PV) rarely present and secondary; sperm transferred in loose mass; epiphallus (E) normally entering penis apex, with a short and blunt-tipped caecum (EC), occasionally reduced or lost, when entering sheath below apex the epiphallus usually is attached to or tunnels along inner wall of sheath; penial retractor muscle (PR) normally inserting on penis-epiphallic junction; spermatheca (S) with short shaft, never long and kinked; penis sheath (PS) thin, sometimes lost, epiphallus entering medially or apically; head of animal without head wart.

Subfamily Pleurodontinae – surface of penis chamber with little or no stimulatory structures; verge (PV) normally large (size reduced in drier areas) and with an external sperm groove; sperm transferred in a small compact mass with long tail (**Fig. 404b**); epiphallus (E) long, coiled, with a long and tapered caecum (EC); penial retractor muscle (PR) inserting on epiphallus, usually well above penis apex; spermatheca (S) medium to long, usually kinked or coiled, head ranging from low on prostate-uterus (**Fig. 404a**) to medially (Solem 1985b: 914, fig. 233a); no penis sheath, but a sheet of fibrous tissue may link epiphallus and penis; head of animal with exposed head wart between and just behind ommatophores (**Figs 405c, 409c**, etc.).

Quistrachia – surface of penis chamber minutely pustulose, a narrow bifurcated or fused main pilaster of varying length; no verge; sperm transferred in a compact mass (**Fig. 441a**); epiphallus absent or barely differentiated from vas deferens, no caecum developed; vas deferens (VD) enters base of thick walled penis sheath (PS) at peni-oviducal angle, then ascends free of the sheath wall; penial retractor muscle (PR) free in top of sheath, inserting at or near penis-vas junction; spermatheca (S) very short, neither kinked nor coiled; penis sheath (PS) large; head of animal without head wart.

These clear structural differences in the basic genital system, except for the head wart, require dissection to observe, and are not easily seen by the casual collector. They thus are of little practical use in identification. The situation also is complicated by environmental factors.

The mid-west coast of Western Australia presents the harshest environment from which camaenid land snails have been recorded. Not only is the total amount of annual rainfall considerably reduced (**Table 166**) from that of the Kimberley (up to 1,500 mm) or the Perth area (mean annual 875 mm), but instead of having a defined and predictable wet season of a few months (Summer in the N, Winter in the S), the precipitation basically is aseasonal and certainly unpredictable. Droughts of a year or more are not unusual, and drenchings of 50–100 mm in a single night occur every few years.

The Kimberley camaenids have a clear pattern of four year genital maturation and seasonal variations (Solem & Christensen 1984), keyed to the predictable wet season. The Shark Bay through North West Cape taxa must be ready to reproduce whenever it rains, since a chance may not come again for a year or more. In both the sinumelonid genera and the pleurodontid genus *Rhagada*, the genital system has become fundamentally altered, with enormous increase in the size of the albumen gland (both for food storage and to permit maximal reproductive effort "at an instant"), lack of seasonal size change in the ovotestis, reduction in the prostate-uterus, shortening and simplification of the terminal genitalia, and size reduction in the penis and verge complex. These changes can be tracked in *Rhagada* as occurring gradually through the succession of species from the Kimberley S to Shark Bay, and in sinumelonids as genera and species shift in the arc from the Nullarbor to Norseman, NW to Geraldton, and then N to the North West Cape. In the latter area, there are striking convergences in these structures, but the basic difference in overall genital patterns for the two groups remains obvious. Somewhat surprisingly, *Quistrachia*, which also extends from the S Kimberley to Shark Bay, does not show these patterns of change, although these species pass through the same rainfall gradient as do the species of *Rhagada*.

Convergence in shell shape and colour has occurred in the Shark Bay to North West Cape area, producing easily confused species. Such cross-subfamily sympatric or near sympatric pairs as *Plectorhagada scolythra* (**Figs 390d–f**) and *Quistrachia lefroyi* (**Figs 433d–f**) in the North West Cape area or *Rhagada torulus* (Férussac, 1819) (**Figs 403a–e**) and *Quistrachia warroorana* (**Figs 433a–c**) from just S of Warroora Homestead, defy production of a key adequate to distinguish even slightly worn examples. In the latter area, *Plectorhagada carcharias* (Pfeiffer, 1864) also has many shape and colour similarities. The reasons for these convergences are unknown. The existence of these convergences offers an interesting set of problems for evolutionary biologists.

SUBFAMILY SINUMELONINAE SOLEM, 1992

This subfamily is confined to the central and southern portions of Australia (**Map 49**). Cited records for W Queensland require confirmation and probably are based on convergent taxa. The genus *Sinumelon* Iredale, 1930 provides nearly continuous distribution (**Map 24**) from the Red Centre to the Flinders Ranges and into western New South Wales, then into the Eyre Peninsula, W to the Nullarbor and into WA as far as Norsemen, before angling NW to near Geraldton. *Pleuroxia* Ancey, 1887 (**Map 19**) has a similar pattern, but shows major range disjunctions. It may be a polyphyletic unit, but available data do not answer this question.

The Flinders Ranges of SA (Solem 1992) has the restricted endemic genera *Micromelon* Solem, 1992 (monotypic) and *Lacustrelix* Iredale, 1937 (three species). The Red Centre (Solem 1993) has the restricted endemic genera *Granulomelon* Iredale, 1933 (four species), *Basedowena* Iredale, 1937 (nine species), *Minimelon* Solem, 1993 (monotypic), *Tatemelon* Solem, 1993 (four species), *Eximiorhagada* Iredale, 1933 (monotypic) and *Montanomelon* Solem, 1993 (two species).

The Nullarbor to Geraldton area has five species of *Pleuroxia* (**Maps 19–21**) and five species of *Sinumelon* (**Maps 25–27**), plus a series of restricted endemic genera. *Falspleuroxia* (**Map 29**) is found just short of Shark Bay, and has one described and possibly a second species; *Plectorhagada* Iredale, 1933 (**Maps 28–32**), from the S end of Shark Bay to just S of Cape Range, and then inland along the Ashburton and Gascoyne Rivers, has six species. The North West Cape has three restricted endemic genera, *Strepsitaurus*, with five species (**Maps 33–34**), and two monotypic genera – *Promonturconchum* and *Caperantrum* (**Map 35**).

The W coast taxa show great enlargement of the albumen gland (GG, **Figs 369a, 384a, 385, 387a, 391a, 392a, 393a, 396a, 400a, 401a**) and some show size reduction of the terminal genitalia, which is reversed in the Cape Range taxa. The following artificial key to the genera will work only for adults in which the sculpture can be observed in detail. It will not work for juveniles or worn individuals.

KEY TO THE GENERA OF SINUMELONINAE

1. At least upper spire with prominent ribs and/or pustules 2
   No crenulated ribs and at most scattered pustules or malleated shell surface 5

2. Major ribs crenulated and with dense pustules 3
   Major ribs simple or anastomosing 4

3. Shell more globose; parietal wall with callus, never a free lip; periphery rounded; Scrubby Range through Shark Bay ... *Plectorhagada* Iredale, 1933 (p. 1574)
   Shell more depressed; parietal lip usually free; periphery angulated; North West Cape to Cardabia Station .... *Strepsitaurus* gen. nov. (p. 1611)

4. Simple radial ribs only .... *Falspleuroxia* gen. nov. (p. 1561)
   Anastomosing radial ribs .... *Pleuroxia* Ancey, 1887 (p. 1470)

5. North West Cape 5
Geraldton SE through Nullarbor .... *Sinumelon* Iredale, 1930 (p. 1519)

6. Whorls increase rapidly in width (**Fig. 399a**) ....
.... *Promonturconchum superbum* sp. nov. (p. 1647)
Whorls tightly coiled (**Fig. 399d**) .... *Caperantrum polygyrum* sp. nov. (p. 1657)

GENUS *PLEUROXIA* ANCEY, 1887
(= *ANGASELLA* A. ADAMS, 20 APRIL 1864, NOT *ANGASIELLA* CROSSE, 1 JANUARY 1864)
(+ *ANGASIETTA* IREDALE, 1939 AND *GANTOMIA* IREDALE, 1939)

See Solem (1992, 1993) for generic descriptions.

Type species: *Helix cyrtopleura* Pfeiffer, 1862 by original designation.

Nomenclatural matters

A full discussion concerning the availability of older generic names has been published previously (Solem, 1992; 1993).

Comparative remarks

The sculpture of low to very prominent radial ribs (**Plates 177–178**), plus the low spire (**Figs 372Ab, 374b, e**) and open umbilicus (**Figs 372Ac, 372Bf, 374c, f**), combine to immediately separate the WA species of *Pleuroxia* (**Figs 368A, 368B, 370A, 370B, 372A, 372B, 374, 375**) from the often sympatric species of *Sinumelon*, which are characterised by their globose shape (**Figs 377–379**), smooth to malleated shell surface (**Plates 183–184**), closed or nearly closed umbilici, and greatly inflated body whorls. The very small (**Table 136**) Norseman area *Sinumelon jimberlanensis* (**Figs 377a–b**) has weak radial sculpture and is globose in shape. Between Geraldton and the North West Cape *Plectorhagada* Iredale, 1933 and species of *Strepsitaurus* can be confused because of their radial sculpture, but the anastomosing, usually diagonally oriented, radial sculpture and generally closed umbilicus easily differentiate them. Anatomically, the very complex and massive pilasters within the penis chamber and reduced penis sheath of the WA *Pleuroxia* (**Figs 369b, 371b, 373b, 376b**) contrast with the generally simpler pilasters and much more substantial penis sheath found in the WA species of *Sinumelon* (**Figs 380–385**).

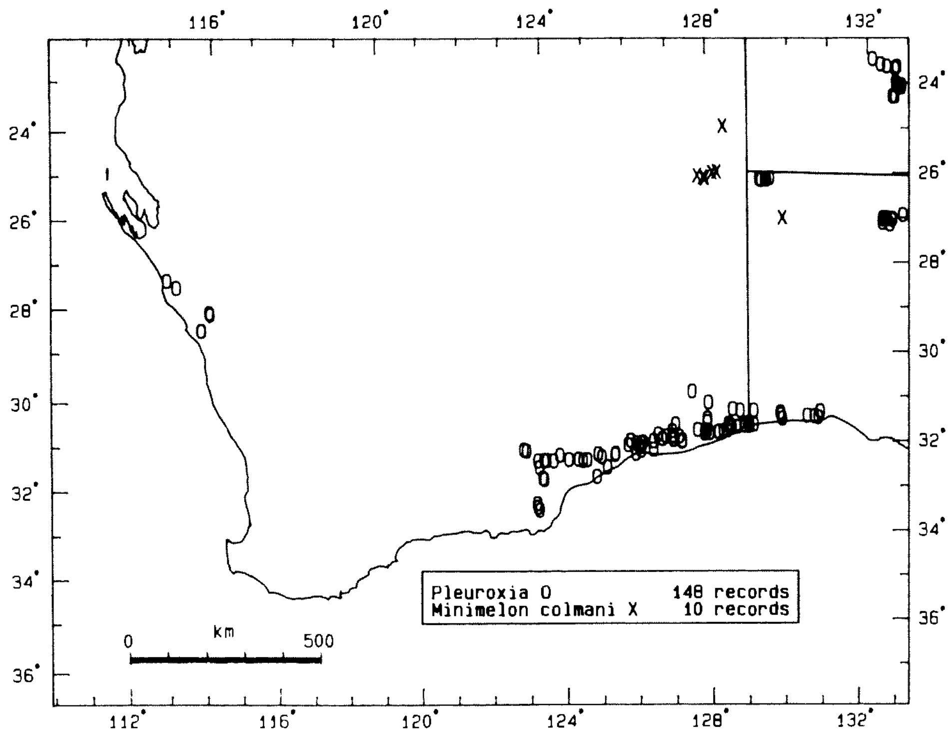
Previous studies

Tate (1894, 1899) described *Pleuroxia oligopleura* (Tate, 1894) and *P. polypleura* (Tate, 1899). No additional data were recorded until Iredale (1938: 106–107) presented a check list of all Australian land snail taxa. This was followed (Iredale, 1939: 54–57) by a monograph of the Western Australian land snail fauna in which both new generic (*Angasietta, Gantomia*) and new specific level names (*elfina, commenta, numba, abstans*) were proposed. Taxa living in the Flinders Ranges of SA, *Pleuroxia cyrtopleura* (Pfeiffer, 1862), *P. phillipsiana* (Angas, 1873), and *P. italowiana* Solem, 1992, plus the one species recorded from the Barrier Ranges of NSW, *Pleuroxia* *hinsbyi* (Gude, 1916), have been reviewed recently by Solem (1992). The Red Centre species, *P. adcockiana* (Bednall, 1894) from the MacDonnell to James Ranges, NT; *P. everardensis* (Bednall, 1892) from the Everard Ranges, SA; *P. carmeena* Solem, 1993 from the S Everard Ranges; and *P. radiata* (Hedley, 1905) from the Mann and Tomkinson Ranges, SA have been monographed by Solem (1993). Several taxa placed in *Pleuroxia* by Iredale (1938) belong to other genera and have been (Solem, 1992, 1993) or are being reallocated. The "*Pleuroxia*" type shell evolved independently in several parts of Australia. Until dissection revealed these convergences, lumping into a broadly defined genus was a logical action. Richardson (1985) presented a useful literature compilation, but made no taxonomic innovations.

Distribution and comparative ecology

The five species reviewed here are all "rock sealers", as are the Flinders Range taxa (Solem, 1992). In contrast, most of the Red Centre species are "free sealers" (Solem, 1993).

The sporadic distribution of *Pleuroxia* in both WA and the Red Centre (**Map 19**) contrasts with the nearly continuous distribution of *Sinumelon* (**Map 24**). Thus most *Pleuroxia* have allopatric ranges.



Map 19: Records of *Pleuroxia* and *Minimelon colmani* in the Red Centre, Nullarbor and WA.

Pleuroxia abstans Iredale, 1939, from the Murchison River on the W coast (**Map 20**), possibly is extinct. So far, only long-dead examples have been collected. *P. bethana* sp. nov., from the Murchison and Greenough River basins near Geraldton and Mullewa (**Map 20**), has an allopatric range that may be extended as far east as Paynes Find. The remaining three species, *P. elfina* Iredale, 1939 (**Maps 20–22**), *P. polypleura* (Tate, 1899) (**Maps 22, 23**) and *P. oligopleura* (Tate, 1894) (**Maps 21, 23**), show a mosaic distribution between Nullarbor, SA on the E and just W of Newman Rock, NW of Balladonia, WA to the W. *P. elfina* and *P. oligopleura* have been collected sympatrically at one station, WA–539, near the Eyre Highway 33.4 km W of Caiguna. *P. elfina* is wood-associated at this station, although rock-associated further E, but *P. oligopleura* is always rock-associated. They are thus ecologically and micro-geographically separated at this station.

The eastern Nullarbor Plain limit for *Pleuroxia* seems to be Nullarbor, SA, where *P. elfina* is common (**Map 20**). Collecting further E near Yalata and Ivy Tank has produced negative records for *Pleuroxia*, although both *Sinumelon nullarboricum* (Tate, 1879) (**Map 26**) and *Bothriembryon* sp. were collected. *P. elfina* is common near Nullarbor itself, then replaced by *P. polypleura* around Koonalda (**Map 22**). No *Pleuroxia* were found near Wigunda, SA. *P. elfina* occurs again from 12.9 km E of the SA border up to and around Wilson Bluff, then has been collected along the edge of the Hampton Scarp from Eucla, WA to at least 128°35'E (WA–527). In the area W of Eucla, *P. polypleura* is common INLAND (**Map 22**) of the Hampton Scarp (WA–499, Weebubbie Cave, 6N2) and at stations WA–500–503. It does reach the Hampton Scarp at Kuthala Pass (WA–524), and also is found considerably inland along the Mundrabilla–Forrest track (WA–529, WA–532). The next records for *P. polypleura* are along the Eyre Highway at WA–490–494, between Madura 6 Mile South Cave (6N62), S of Madura, and Cocklebiddy Cave (6N48), WNW of Cocklebiddy (**Map 22**). Quite probably *P. polypleura* has an extensive inland range, but collecting in this area has been minimal.

Pleuroxia oligopleura (**Maps 21, 23**) ranges from just W of Knousley Tank (WA–526) along the Hampton Scarp W to Madura (WA–495), with one short inland extension near Mundrabilla (WA–534). There is a gap in its distribution from Madura until it reappears well inland some 33.4 km W of Caiguna (WA–539) and also at Cardanumbi Rock Hole, 11.5 km E of Caiguna (types of *commenta* Iredale, 1939).

Further into WA, *P. elfina* (**Maps 20–22**) has an isolated inland record at Dingo Donga Sink (6N160) W of Madura; an isolated coastal record at Twilight Cove S of Cocklebiddy; and then begins a probably nearly continuous range W from WA–539, W of Caiguna, to just W of Newman Rock and then S to Juranda Rock Hole and Pine Hill along the Balladonia–Cape Arid track. Specimens also were collected in mid–1989 from the ruins of Deralinya Homestead (33°03'S, 123°23'E) slightly further W. It was not possible to include this record in **Maps 20–22**.

The S coast taxa thus show a mixture of occurrences along the Hampton Scarp and inland. Much more field work is needed to work out details of their distribution and variation.

Discussion

The species reviewed below show a diversity of structure and possible affinities. *Pleuroxia abstans* Iredale, 1939 (**Figs 368Aa–c**) has the expanded lip, shape, and

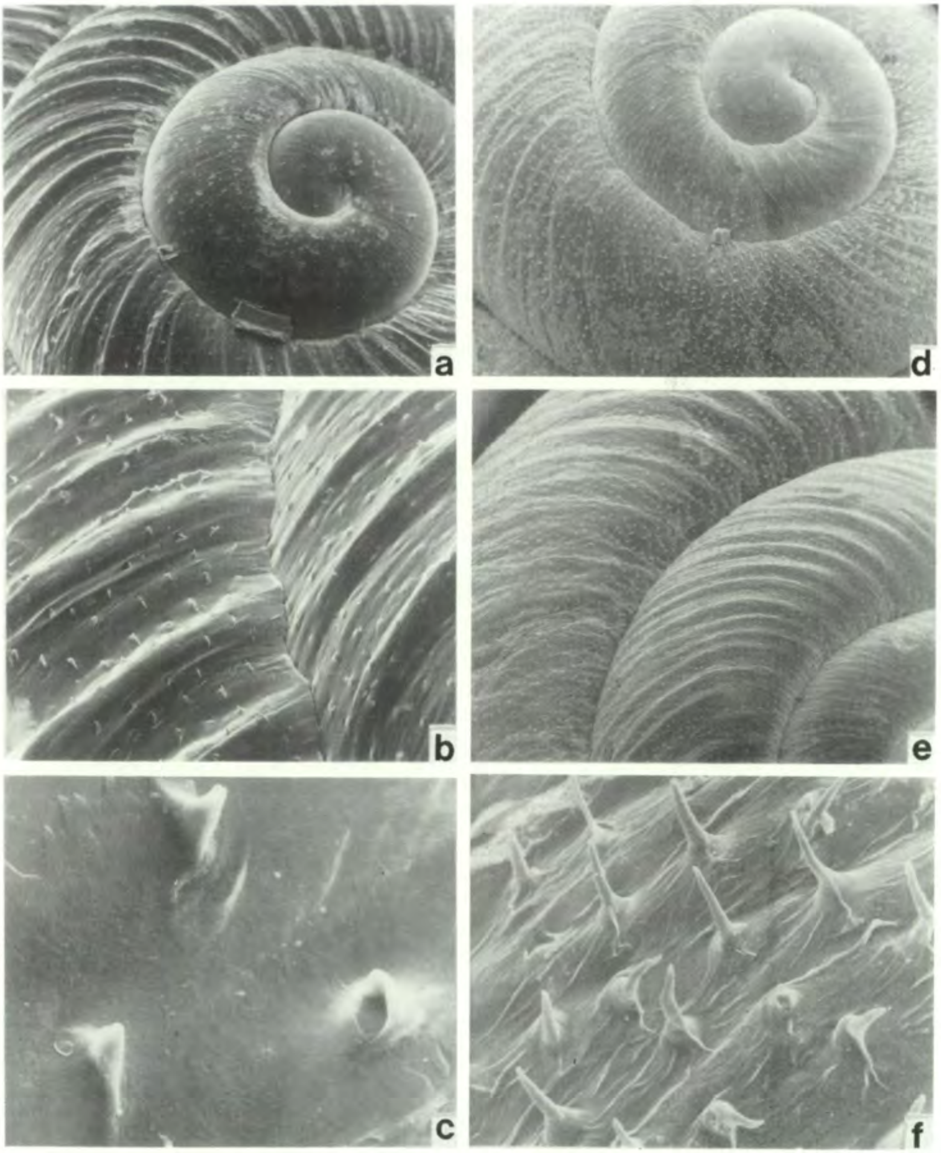


Plate 177: Shell sculpture of *Pleuroxia bethana* sp. nov. and *P. elfina* Iredale, 1939: (a–c) *P. bethana*. WA–949, near Ellendale Pool, SE of Geraldton, WA. FMNH 212457. a is apex and early spire at 19,.7X. b is sculpture on mid-spire at 46.5X. c is detail of mid-spire setae at 380X; (d–f) *P. elfina*. WA–487, near Balladonia Motel airstrip, Nullarbor fringes, WA. FMNH 204142. d is apex to mid-spire at 16.6X. e is mid- and lower spire at 16.5X. f is detail of mid-spire setae at 155X.

Table 132: Range of variation in *Pleuroxia.*

Taxon	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
P. abstans	3	5.27 (5.2-5.45)	10.40 (9.9-10.85)	0.507 (0.498-0.525)	3⅞+ (4⅛+-4¼)	2.73 (2.45-3.15)	3.79 (3.33-4.24)
P. bethana	56	8.14 (6.7-10.5)	12.17 (10.25-15.45)	0.668 (0.602-0.761)	4⅛+ (3¾-–4½+)	1.68 (1.0-2.2)	7.46 (5.59-12.8)
P. elfina	583	8.46 (5.6-11.55)	14.28 (10.15-18.65)	0.593 (0.482-0.723)	4⅜– (3⅞+-4¾+)	2.17 (1.2-3.15)	6.58 (4.22-14.0)
P. polypleura	906	8.45 (5.3-11.30)	14.44 (10.4-18.50)	0.584 (0.477-0.701)	4¼+ (3½+-5–)	2.17 (1.2-3.55)	6.71 (4.32-10.9)
P. oligopleura	492	7.64 95.15-11.4)	14.95 (11.35-18.5)	0.510 (0.404-0.675)	4¼+ (3¾+-4⅝–)	2.74 1.7-3.75)	5.56 (3.73-8.81)

basic type of radial shell sculpture found in the Red Centre *P. radiata* (Hedley, 1905) (Solem 1993: pl. 96d–e, figs 259a–c), while *P. bethana* sp. nov. (**Figs 368Bd–f, Plate 177a–c**) has the shell shape, reduced lip reflection, and simple radial sculpture of the Red Centre species *P. adcockiana* (Bednall, 1894), *P. everardensis* (Bednall, 1892) and *P. carmeena* Solem, 1988 (see Solem 1993: plts 95–96). The latter species differ most obviously in having red spiral colour bands that are lacking in *P. bethana*. *P. elfina* Iredale, 1939 has very low and smoothly rounded radial ribs (**Plate 177d–f**), while *P. polypleura* (**Plate 178a–c**) and *P. oligopleura* (**Plate 178d–f**) have higher, sharp edged, sometimes anastomosing ribs that are exactly equivalent to those found in the Flinders Ranges species, *P. cyrtopleura* (Pfeiffer, 1862) and *P. phillipsiana* (Angas, 1873) (see Solem 1992: pls 48–49, figs 71a–d, 72a–c).

The penial structures are equally varied. While *P. bethana* (**Fig 369b**) has comparatively simple pilasters, roughly equivalent to those found in *P. phillipsiana* and *P. italowiana* (see Solem 1992: figs 75c, 76d), with partial retention of the U-pilaster that also is common to the Red Centre species (Solem 1993), the structures in *P. elfina*, *P. polypleura* and *P. oligopleura* are altered. The latter three species have a massive pilaster structure inside the penis chamber, and the length of the terminal genital organs vary greatly (**Figs 371, 373, 376**). Undoubtedly much of this latter variation reflects the facts of occurrence: mostly on well isolated and quite small limestone exposures, which means small population size and much opportunity for genetic drift and founder-effect phenomena to have happened.

It is quite possible that *P. abstans* and *P. bethana* are separately derived from Red Centre taxa, while the Nullarbor taxa will relate more closely to the Flinders Ranges taxa. Add to this complication the fact that, in the Red Centre, species of *Granulomelon* Iredale, 1933 (see Solem 1993) are, in part, the shape, sculptural, and aestivation equivalents of the southern *Pleuroxia*, but anatomically are modified. Clearly there is much to learn about the relationships among the scattered radiations of *Pleuroxia*.

Pleuroxia (**Map 19**) is one of only three Australian Camaenidae genera that I have recognised as showing major disjunct distributions. *Hadra* Albers, 1861 involves a Queensland genus with several species and a still undissected species from the Prince Regent River area, W Kimberley, WA, *Hadra wilsoni* Solem (1979: 139–141) (**Map 50**). Convergence may be involved in both situations but current material is not adequate to work out these problems. The third situation involves the presence of *Quistrachia* in both western Queensland and the Napier Range to Carnarvon area of WA (**Map 53**). (**Editor's note**: There was an indication in Dr. Solem's manuscript for this monograph that he intended to publish on a new species of *Quistrachia* from Black Mountain, near Boulia in Queensland. However, after his death no trace could be found of a manuscript or other solid reference to the specimens he was going to describe. Therefore we are left with some enigmatic references to a W Queensland *Quistrachia*.)

KEY TO THE SPECIES OF *PLEUROXIA*

1. Shell more globose (**Fig. 368Be**); lip of adult expanded only on columellar wall; radial ribs simple, microsculpture widely spaced (**Plate 177a–c**); Kalbarri, Geraldton, Mullewa areas .... *Pleuroxia bethana*, sp. nov. (p. 1480)

Shell with low spire (**Figs 368Ab, 370Ab, 370Be, 372Ab, 372Be, 374b, e**); umbilicus wider (**Table 132**) 2

2. Murchison River, W coast; small, widely umbilicated; lip widely expanded (**Figs 368Aa–c**) .... *Pleuroxia abstans* Iredale, 1939 (p. 1477)

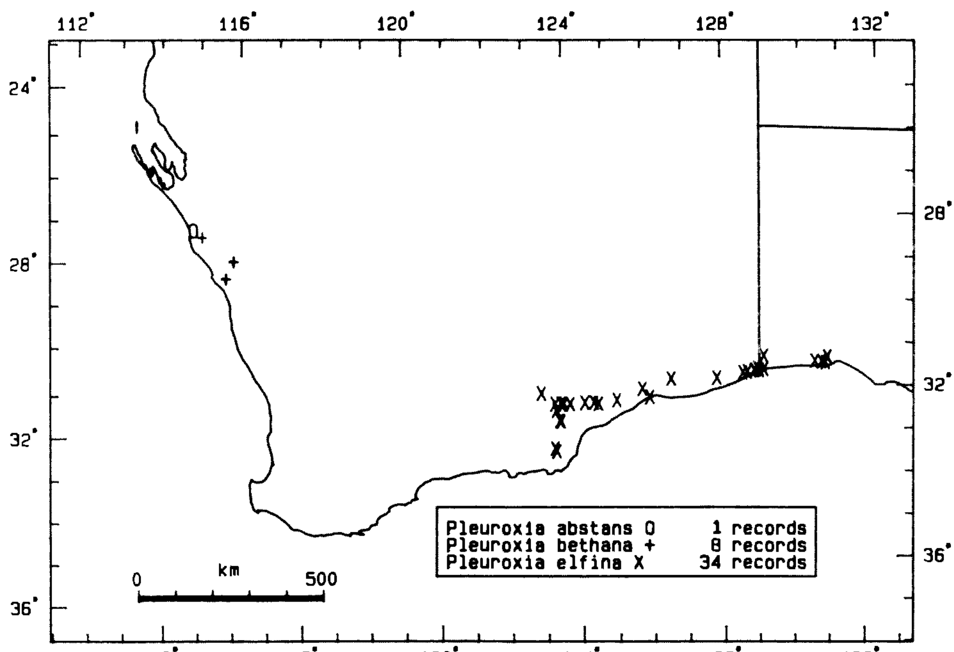
   Newman Rock and Pine Hill E to Nullarbor, SA; shell much larger, narrowly umbilicated; lip expansion variable 3

3. Radial ribs absent until midspire, then low and rounded (**Plate 177d–e**), rarely anastomosing .... *Pleuroxia elfina* Iredale, 1939 (p. 1489)

   Radial ribs present on early spire, higher and narrower (**Plate 178a–b, d–e**), often anastomosing 4

4. Spire higher (**Figs 372Ab, 372Be**); ribs more crowded (**Figs 372Aa–c, 372Bd–f**); umbilicus narrower (**Table 132**) .... *Pleuroxia polypleura* (Tate, 1899) (p. 1497)

   Spire lower (**Figs 374b, e, 375b**); ribs more widely spaced (**Figs 374–375**); umbilicus wider (**Table 132**) .. *Pleuroxia oligopleura* (Tate, 1894) (p. 1511)



Map 20: Records of *Pleuroxia abstans*, *P. bethana* and *P. elfina* in the Nullarbor and WA.

PLEUROXIA ABSTANS IREDALE, 1939

(Figs 368Aa–c; Maps 20, 27)

Pleuroxia abstans Iredale, 1939, *Jour. Roy. Soc. Western Austr.*, **25:** 56–57, pl. III, fig. 22 – on chalk, Murchison House, Gantheaume Bay, Western Australia; Burch, 1976, *Jour. Malac. Soc. Austr.*, **3** (3): 136; Richardson, 1985, *Tryonia*, **12:** 252.

Comparative remarks

Pleuroxia abstans Iredale, 1939, known only from Gantheaume Bay, Kalbarri National Park, WA (**Maps 20, 27**), is small (mean diameter 10.40 mm), low spired (**Fig. 368Ab**, mean H/D ratio 0.507), widely umbilicated (**Fig. 368Ac**, mean D/U ratio 3.79), with heavy radial sculpture (**Figs 368Aa–c**) and prominent micropustulations on both apex and spire. Its body whorl periphery is noticeably angulated (**Fig. 368Ab**). The neighbouring (**Maps 20, 27**) *P. bethana* sp. nov. has a more globose shape (**Fig. 368Be**), is larger (mean diameter 12.17 mm), more elevated (mean H/D ratio 0.668), narrowly umbilicated (**Fig. 368Bf**, mean D/U ratio 7.46), with narrow radial ribs and scattered pustulations (**Plate 177b–c**), and a very weakly expanded lip. *Plectorhagada gascoynensis* (E. A. Smith, 1894) from the Gascoyne River and the *Strepsitaurus* series from the Cape Range (**Maps 33–34**) differ (**Figs 389, 394, 395**) in their heavy microsculpture and tortuously anastomosing ribbing. The Red Centre species *Pleuroxia radiata* (Hedley, 1905) (Solem 1993: figs 259a–c) from the Mann and Tomkinson Ranges, SA, is perhaps most similar in general appearance but has much more prominent radial sculpture, a much narrower umbilicus and a reduced parietal lip. It also has a much higher mean whorl count (4 3/8–) at almost identical adult size (mean whorl count 3 7/8+) as in *P. abstans*. The anatomy of *P. abstans* is unknown.

Lectotype

WAM 833.32, on chalk, Murchison House, Murchison River, Western Australia; 27°39'S, 114°14'E. Height of shell 5.2 mm, diameter 9.9 mm, H/D ratio 0.525, whorls 3 7/8+, umbilical width 2.6 mm, D/U ratio 3.81.

Paralectotypes

WAM 834–841.32, AM C.106541, 3 DA, 8 DJ from the type locality.

Material studied

WESTERN AUSTRALIA: banks of Murchison River, 0.5–1 mile from mouth (George Buick! Buick 18040, 1 DA, 1 DJ).

Range

Known only from near the Murchison River mouth, WA (**Maps 20, 27**).

Diagnosis

Shell small, diameter 9.9–10.85 mm (mean 10.40 mm), with 3 7/8+ to 4 1/4 (mean 4 1/8) rather loosely coiled whorls. Apex and spire modestly elevated (**Fig. 368Ab**), shell height 5.2–5.45 mm (mean 5.27 mm), H/D ratio 0.498–0.525 (mean 0.507). Body whorl flattened laterally below, producing a high, obtusely rounded to angulated

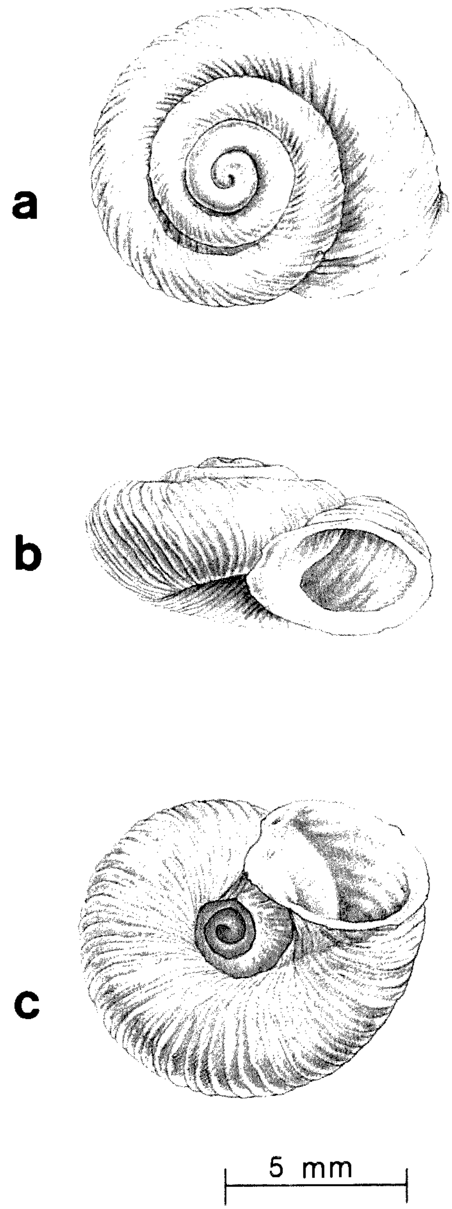


Fig. 368A: Shell of *Pleuroxia abstans* Iredale, 1939: (a–c) Murchison House, Gantheaume Bay, WA. Paratopotype. AM C.106541. Scale line equals 10 mm. Drawings by Linnea Lahlum.

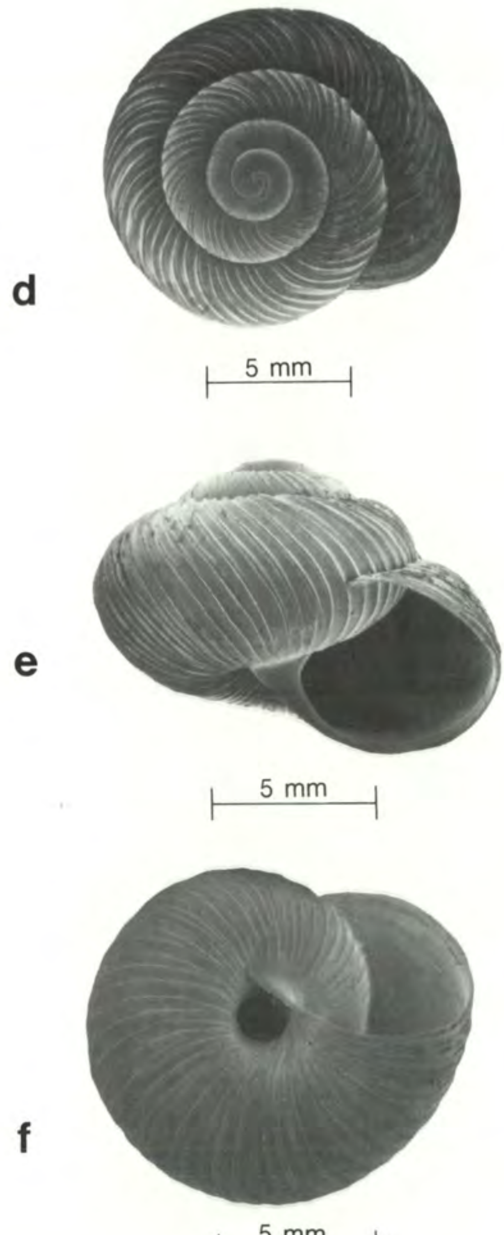


Fig. 368B: Shell of *Pleuroxia bethana*, sp. nov.: (d–f) WA–11, Ellendale Pool, SE of Geraldton, WA. Holotype. WAM 225.84. Scale lines as marked.

periphery. Shell apex with traces of large, dense micropustulations, that become slightly larger, but scattered in spacing on spire and body whorl. Macrosculpture of low, crowded, sometimes anastomosing ribs (**Figs 368Aa–c**), microsculpture eroded on most examples. Umbilicus (**Fig. 368Ac**) widely open, last whorl decoiling more rapidly, width 2.45–3.15 mm (mean 2.73 mm), D/U ratio 3.33–4.24 (mean 3.79). Body whorl moderately descending behind aperture. Lip reflexed, expanded, parietal edge appressed, but with thick callus. Colour unknown. Based upon three worn adults.

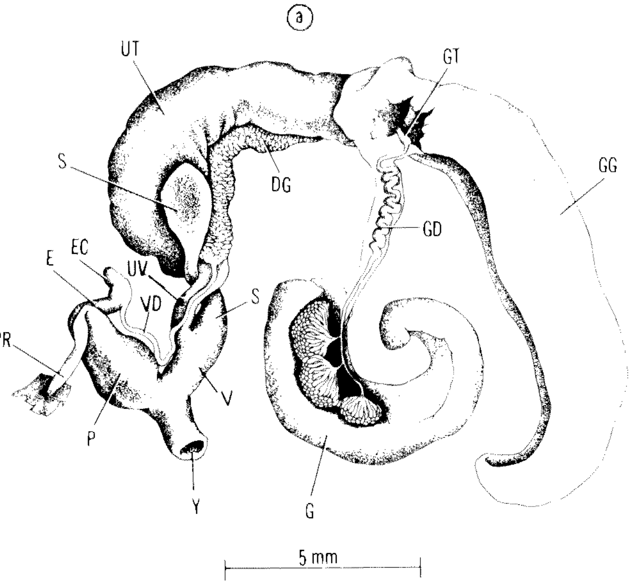
Discussion

The few examples of *Pleuroxia abstans* Iredale, 1939 are subfossil and partly to mostly worn. No trace of colour was left and the surface condition was such that I made no SEM photographs. Since fresh examples of *Pleuroxia bethana* sp. nov. were taken from the nearby Ross Graham Lookout cliffs (WA–12), I suspect that *P. abstans* is an extinct species, equivalent to the dune fossil *Strepsitaurus cardabius* found from *Ningaloo* S to Gnaraloo Station. Iredale (1939: 55) introduced the subgeneric name *Gantomia* for this species. His description was marginally valid in a nomenclatural sense but there are no characters in the shell of *P. abstans* that do not agree with most *Pleuroxia* species. Thus I have chosen not to use his subgeneric name.

PLEUROXIA BETHANA SP. NOV.
(Plates 177a–c, 179a–e; Figs 368Bd–f, 369a–b; Maps 20, 27)

Comparative remarks

Pleuroxia bethana sp. nov., from the Murchison River mouth S to Bindoo Hill and Ellendale Pool, SE of Geraldton, WA (**Maps 20, 27**), is characterised by its lack of a reflected lip except on the columellar margin (**Figs 368Bd–f**), brownish-yellow spire colouration, narrow umbilicus (mean D/U ratio 7.46), and crowded radial sculpture (**Plate 177a–b, Figs 368Bd–f**). The Red Centre species *P. adcockiana* (Bednall, 1894), *P. everardensis* (Bednall, 1892), and *P. carmeena* Solem, 1988 (see Solem 1993) are most similar in size and shape, but differ in having two red spiral colour bands, simpler and less prominent radial sculpture, and prominent apical sculpture of dense micropustulations. *P. abstans* Iredale, 1939, subfossil in Kalbarri National Park (**Maps 20, 27**), has a broadly expanded lip and much wider umbilicus (**Figs 368Aa–c**), broad and less crowded radial ribs, is smaller (mean diameter 10.40 mm), and is much less elevated (mean H/D ratio 0.507). *P. elfina* Iredale, 1939, from the S coast and Nullarbor areas (**Maps 20–22**), is about the same size, but is less elevated and more widely umbilicated (**Table 132**), the lip is expanded, although still narrow, the microsculpture is much denser, and the radial ribs are less prominent (**Plate 177d–f**). The much larger (**Table 132**) Nullarbor species, *P. polypleura* (Tate, 1899) (**Maps 22, 23, 25**) and *P. oligopleura* (Tate, 1894) (**Maps 21, 23**), have much stronger radial ribbing (**Plate 178a–f**), more expanded shell lips (**Figs 372Aa–c, 372Bd–f, 374a–f**), and are less elevated. Anatomically (**Figs 369a–b**), the greatly enlarged albumen gland (GG), shortened free oviduct (UV) and vagina (V) are the most obvious features separating it from the otherwise very similar *P. elfina* (**Figs 371a–b**). The Nullarbor species *P. polypleura* (**Figs 373a–b**) and *P. oligopleura* (**Figs 376a–d**) differ most obviously in the specialisations of their penial chamber wall sculpture and penis elongation.



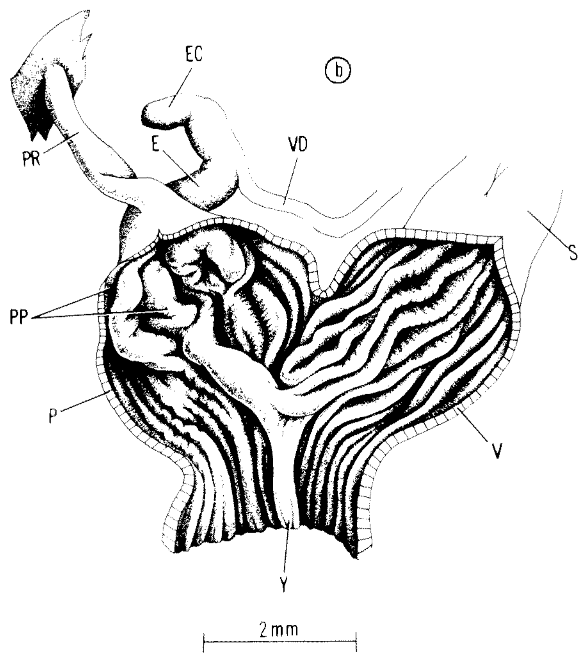


Fig. 369: Genitalia of *Pleuroxia bethana* sp. nov.: WA-11, Ellendale Pool, SE of Geraldton, WA. 2 February 1974. FMNH 182545, Dissection C, (a) whole genitalia; (b) interior of penis and vagina. Scale lines as marked. Drawings by Elizabeth A. Liebman.

Holotype

WAM 225.84, Sta. WA–11, cliffs above W bank of Ellendale Pool, near Lookout Hill, SSE of Geraldton, Western Australia; 28°50'S, 114°58'E. Collected 2 February 1974 by Alan Solem and Laurie Price. Height of shell 9.3 mm, diameter 12.6 mm, H/D ratio 0.738, whorls 4 1/4, umbilical width 1.65 mm, D/U ratio 7.63.

Paratopotypes

WAM 226.84, WAM 227.84, WAM 229.84, WAM 230.84, WAM 231.84, WAM 232.84, SAM D17709–13, FMNH 182269, FMNH 182409, FMNH 182545, FMNH 182748, FMNH 199388, FMNH 199714, FMNH 199757–8, FMNH 200355, FMNH 212457–8, 27 LA, 13 DA, many LJ, many DJ and broken individuals from the type locality (WA–11, WA–164, WA–949).

Paratypes

WESTERN AUSTRALIA: Bangemall Creek, W of Tallering Peak, NNE of Mullewa (29 August 1968, WAM 129.94, 3 DA, 11 DJ); Ross Graham Lookout, Kalbarri National Park (WA–12, WAM 130.94, FMNH 182662, 5 DA, 4 DJ); 0.9 km upstream from windmills at Noondamura Pool, Greenough River, N of Bindoo Hill, NW of Mullewa (WA–1067, 20 May 1989, FMNH 221712, 7 LA); near Bindoo Hill (WA–420, WA–1061, ESE of Northampton, WAM 228.84, WAM 233.84, SAM D17714, FMNH 199761, FMNH 199363, FMNH 211995, 8 LA, 3 DA, 5 LJ, 5 DJ).

Range

Although most known localities of *Pleuroxia bethana* sp. nov., are from the drainage of the Greenough River (Tallering Peak, Bindoo Hill, Ellendale Pool) inland of Geraldton, the records from Kalbarri National Park near the mouth of the Murchison River slightly to the N, suggest a probably much wider distribution (**Maps 20, 27**). Eastward extension of the range to near Paynes Find would not be surprising.

Diagnosis

Shell relatively small, diameter 10.25–15.45 mm (mean 12.17 mm), with 3 3/4– to 4 1/2+ (mean 4 1/8+) normally coiled whorls. Apex and spire moderately and evenly elevated (Fig. 368Be), shell height 6.7–10.5 mm (mean 8.14 mm), H/D ratio 0.602–0.761 (mean 0.668). Body whorl rounded, without trace of keel or angulation. Shell apex (**Plate 177a**) with traces of elongated pustulations. Upper and mid-spire with scattered low setae (**Plate 177c**), very scarce on body whorl. Macrosculpture of narrow, high, crowded radial ribs, sometimes anastomosing (**Figs 368Bd–f**, **Plate 177a–b**). Umbilicus (**Fig. 368Bf**) narrow to very narrow, partly closed by columellar lip reflection, width 1.0–2.2 mm (mean 1.68 mm), D/U ratio 5.59–12.8 (mean 7.46). Body whorl at most slightly descending behind aperture. Palatal and basal lips not expanded or reflected (**Figs 368Bd–f**), at most slightly thickened, columellar lip expanded. Parietal wall with at most a thin callus. Colour light yellow–brown above, base lighter in tone. Based on 56 measured adults.

Genitalia (**Figs 369a–b**) with very large albumen gland (GG). Talon (GT) and hermaphroditic duct (GD) typical. Prostate (DG) and uterus (UT) relatively short. Spermatheca (S) with base of shaft swollen, then wrapped partly around short and slender free oviduct (UV). Spermathecal head expanded at base of prostate-uterus,

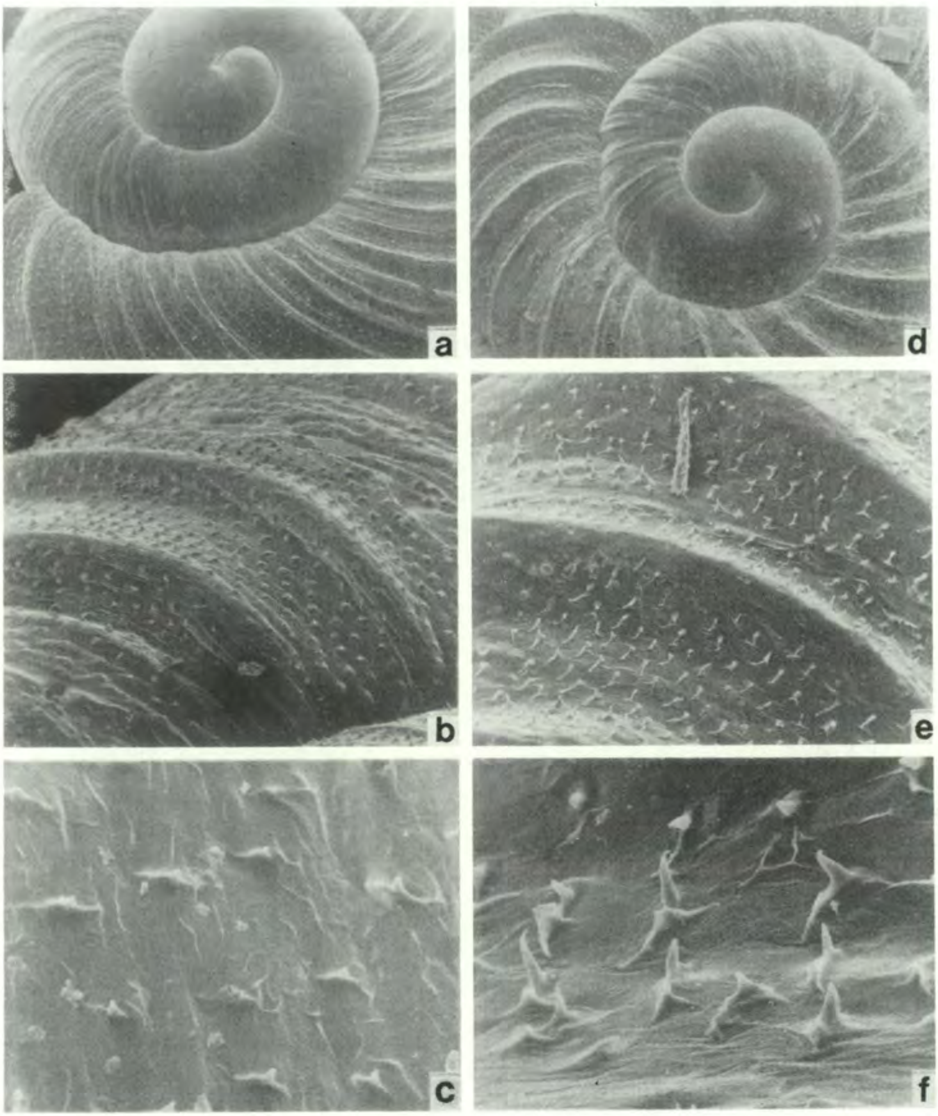


Plate 178: Shell sculpture of *Pleuroxia polypleura* (Tate, 1899) and *P. oligopleura* (Tate, 1894): (a–c) *P. polypleura*. WA–499, rim of Weebubbie Cave (6N2), WNW of Eucla, WA. FMNH 204250. a is apex and early spire at 17.4X. b is late spire at 39X. c is vertical view of late spire setae at 190X; (d–f) *P. oligopleura*. WA–535, gully above Mundrabilla Homestead, Nullarbor, WA. FMNH 204462. d is apex and early spire at 15.7X. e is early and mid-spire showing wear on rib tops at 66.5X. f is setae in mid-spire inter-rib area at 260X.

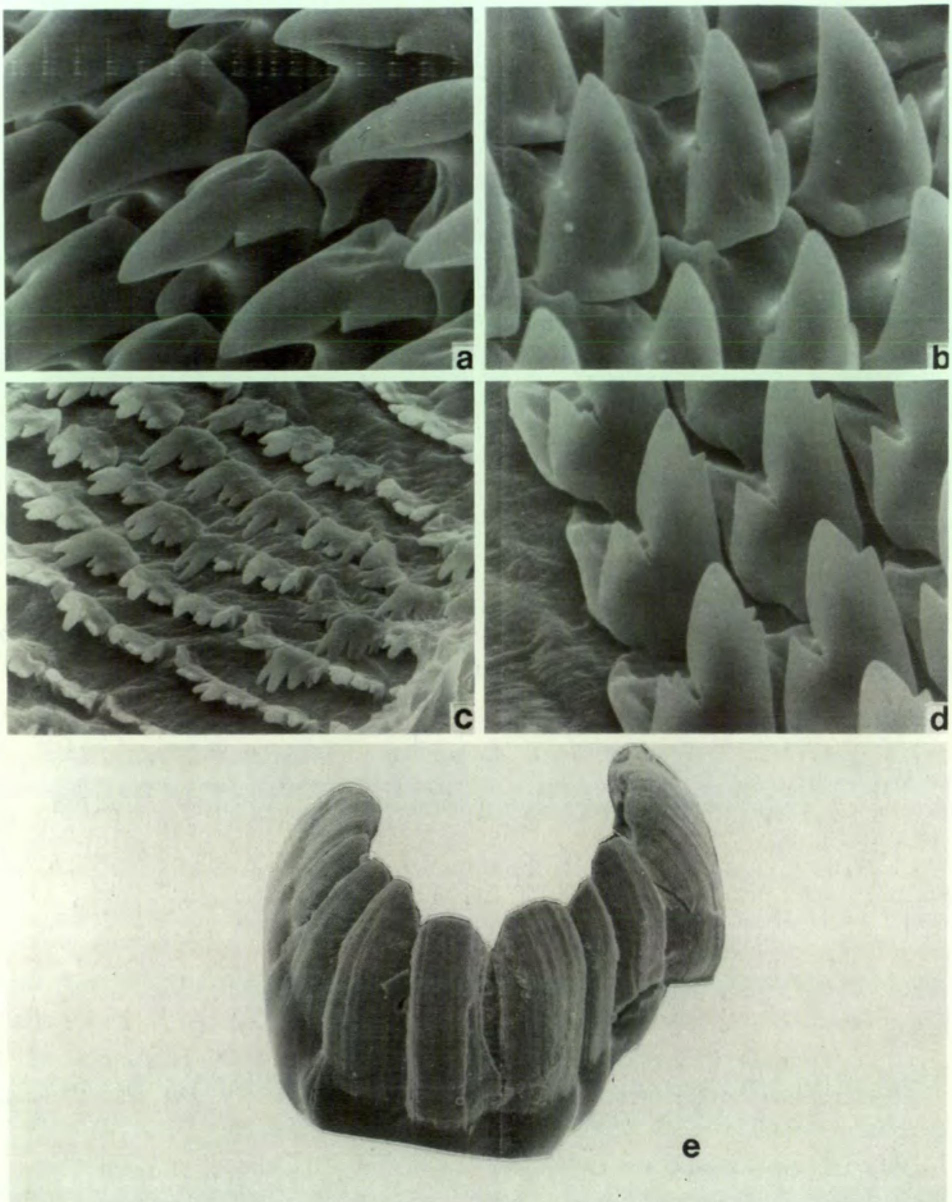


Plate 179: Radular teeth and jaw of *Pleuroxia bethana* sp. nov. WA–11, cliff above Ellendale Pool, SE of Geraldton, WA. 2 February 1974. FMNH 182545, Dissection A: (a) central and early lateral teeth at 1325X; (b) anterior view of central and early lateral teeth at 1325X; (c) outermost marginal teeth at 670X; (d) anterior view of early marginal teeth at 1325X; (e) jaw at 135X.

bound to latter by fibres. Vas deferens (VD) very slender, joining large epiphallic caecum (EC) laterally. Epiphallus thick, entering penis chamber through foliated pilasters around pore (EP) after receiving insertion of penial retractor muscle (PR). Penis sheath reduced to a very thin membrane appressed to surface of penis (P) (not shown in **Fig. 369b**). Penis (P) short, internally with complex folds on upper wall, one of which descends to atrium (Y) and branches up into the short vagina (V).

Central teeth of radula (**Plate 179a–b**) with massive basal ridges, sharp pointed cusp with very prominent ectocones. Early lateral teeth (**Plate 179a–b**) with prominent ectocone, which becomes an increasingly large to abrupt latero-marginal transition. Early marginal teeth showing small endocone (**Plate 179d**) which may be split; outer marginal teeth (**Plate 179c**) multicuspid. Jaw (**Plate 179e**) with very broad ribs.

Discussion

Pleuroxia bethana is at the known southern limit (**Maps 20, 27**) of camaenids along the W coast of Australia. Detailed collecting between Geraldton and Paynes Find undoubtedly will discover many additional colonies but this should remain the "last camaenid" before the *Bothriembryon* and charopid-punctid radiations burgeon in the humid SW region.

It also shows the greatest degree of predation I have seen for any Australian land snail. At Ellendale Pool, which has been visited several times over the years to collect samples for study of genital seasonality, more than 90% of the shells encountered have "bites" taken out of their shell. These are not located at a special place along the shell periphery in relation to the aperture. A portion of the body whorl just behind the aperture, a portion of the spire, part of the shell base, the initial portion of the body whorl – all have been torn away on some individuals. Darrell Kitchener, Mammalogist at WAM, was kind enough in 1983 to examine 75 broken specimens to see if "single bite marks" could be recognised. On 15 shells he measured bite width, which ranged from 2.1–4.9 mm (mean 3.58 mm). It was not possible to indict a particular species as predator, since several small rodents in the area could have produced bite marks within this size range. None of the lizards or snakes found in this area would produce such a mark. Birds can be eliminated since the shells are found scattered throughout rock talus to a depth of at least two feet. The snails are not taken to a "den" or nest and eaten there but apparently are consumed "as found". Since *P. bethana* aestivates sealed to rock or wood, the predator must enter the talus and pry them loose. A bitten shell still attached to a rock was seen for the first time in 1989 near Bindoo Hill. Predation either must be during activity periods of the snail or by the predator pulling the aestivating snails loose. Epiphragms of live snails were not heavily calcified. It was very easy to pull the snails off the rocks.

Only a few sets contained sufficient numbers of adults for statistical analysis (**Table 133**). There is some variation in umbilical width, but otherwise the specimens are very similar in size and shape.

This species is dedicated, as a token of appreciation, to Beth S. Morris, whose persistent labours in measuring and processing Australian land snails, then carrying out statistical analyses, first as a student, then as an Technical Assistant, have contributed so very much to completion of these studies.

Table 133: Local variation in *Pleuroxia bethana* and *Pleuroxia elfina*.

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Pleuroxia bethana							
Western Australia							
Ellendale Pool							
WA-11, 2.II.74	10L	8.11±0.178 (6.89-8.8)	11.97±0.205 (10.85-12.75)	0.678±0.009 (0.616-0.704)	4 1/4- (3 7/8+-4 3/8-)	1.77±0.053 (1.5-2.1)	6.81±0.162 (6.11-7.67)
WA-164, 19.IV.77	7L	8.58±0.303 (7.6-9.75)	12.61±0.226 (12.0-13.4)	0.680±0.015 (0.632-0.755)	4 1/4+ (4+-4 1/2+)	1.83±0.082 (1.55-2.1)	6.97±0.369 (5.72-8.26)
WA-949, 7.VII.83	6L	7.76±0.244 (6.8-8.5)	11.53±0.315 (10.25-12.4)	0.673±0.004 (0.661-0.687)	4 1/8 (4−-4 1/4)	1.63±0.084 (1.35-1.9)	7.13±0.258 (6.45-8.23)
WA-949, 7.VII.83	6D	7.24±0.188 (6.7-7.9)	11.26±0.179 (10.65-11.95)	0.643±0.013 (0.602-0.694)	4 1/8− (4−-4 1/8+)	1.87±0.039 (1.75-2.05)	6.03±0.109 (5.59-6.37)
Bindoo Hill							
WA-1061 14.VI.84	8L	7.81±0.184 (7.1-8.4)	11.79±0.262 (10.65-12.9)	0.663±0.009 (0.629-0.663)	4+ (3 3/4+-4 1/4+)	1.33±0.059 (1.05-1.55)	9.00±0.383 (7.51-10.5)
Pleuroxia elfina							
South Australia							
WA-512, Murrawijinie Cave (N-9), FMNH 204347	13L	10.18±0.145 (9.05-11.1)	15.94±0.138 (15.1-16.65)	0.639±0.009 (0.568-0.675)	4 1/2 (4 3/8+-4 3/4)	2.23±0.067 (1.7-2.6)	7.22±0.197 (6.11-8.88)
WA-511, Murrawijinie Cave (N-7), FMNH 204346	25L	10.15±0.110 (9.1-11.15)	16.15±0.172 (14.05-17.5)	0.629±0.005 (0.586-0.701)	4 1/2 (4 3/8−-4 5/8+)	2.22±0.058 (1.55-2.6)	7.37±0.177 (6.08-9.61)
WA-511, FMNH 204341	14D	10.70±0.142 (9.95-11.55)	17.08±0.252 (15.5-18.65)	0.627±0.005 (0.598-0.655)	4 1/2+ (4 3/8−-4 3/4+)	2.41±0.086 (1.95-3.15)	7.17±0.182 (5.91-8.38)
WA-517, doline N-122, FMNH 204368	24L	9.45±0.083 (8.58-10.7)	15.19±0.118 (14.1-16.25)	0.623±0.007 (0.562-0.723)	4 1/2− (4 1/4+-4 5/8+)	2.27±0.037 (1.9-2.6)	6.73±0.094 (6.06-7.61)
WA-517, FMNH 204369	16D	9.48±0.123 (8.5-10.45)	15.70±0.179 (14.6-16.9)	0.604±0.007 (0.553-0.657)	4 3/8+ (4 1/4+-4 5/8−)	2.34±0.058 (1.8-2.65)	6.76±0.170 (5.94-8.35)

Table 133: Local variation in *Pleuroxia bethana* and *Pleuroxia elfina* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
WA-518, Nullarbor, SA, FMNH 204376	13D	10.23±0.139 (9.6-11.2)	16.95±0.232 (15.7-18.5)	0.604±0.007 (0.570-0.669)	4½− (4¼+-4⅝−)	2.48±0.061 (2.2-3.05)	6.87±0.156 (6.04-7.75)
WA-519, N-163 doline, FMNH 204377	83L	8.78±0.062 (6.85-9.8)	14.48±0.077 (13.15-16.15)	0.606±0.004 (0.517-0.702)	4⅜− (4⅛−-4¾)	1.90±0.029 (1.3-2.8)	7.70±0.117 (4.85-10.9)
WA-519, FMNH 204378	59D	9.28±0.072 (8.45-11.4)	15.19±0.094 (13.75-17.25)	0.612±0.004 (0.555-0.701)	4⅜ (4+-4⅝+)	2.08±0.039 (1.5-2.75)	7.44±0.138 (5.91-10.0)
WA-521, SA, FMNH 204389	10D	7.11±0.138 (6.35-7.65)	12.66±0.251 (11.4-13.95)	0.562±0.007 (0.533-0.590)	4¼+ (4⅛−-4½−)	2.43±0.111 (2.0-3.05)	5.26±0.158 (4.61-5.99)
WA-504, 16 Mile, FMNH 204295	7L	7.00±0.479 (6.5-7.95)	12.43±0.238 (11.95-12.75)	0.563±0.032 (0.521-0.625)	4¼− (4⅛+-4¼+)	2.41±0.105 (2.25-2.6)	5.18±0.138 (4.90-5.34)
WA-504, FMNH 204294	22D	7.14±0.082 (6.5-7.8)	12.96±0.133 (11.65-14.45)	0.552±0.008 (0.501-0.615)	4¼+ (4⅛−-4½−)	2.46±0.069 (1.8-3.0)	5.34±0.130 (4.43-6.74)
6 mi NE Wilson Bluff, WAM 317.74	17D	6.81±0.071 (6.35-7.33)	12.03±0.137 (10.95-13.3)	0.567±0.007 (0.516-0.631)	4⅛+ (4−-4½+)	2.20±0.064 (1.65-2.7)	5.53±0.146 (4.44-7.00)
0.5km E of border, SA, AM C. 132229	17D	6.83±0.116 (6.0-7.7)	12.03±0.136 (11.05-13.0)	0.567±0.006 (0.537-0.615)	4¼ (4-4½)	2.35±0.051 (1.9-2.75)	5.11±0.105 (4.33-6.24)
WA-522, Wilson Bluff, FMNH 204397	11L	6.68±0.130 (6.1-7.4)	12.61±0.139 (11.95-13.5)	0.530±0.007 (0.482-0.560)	4⅛ (4-4¼)	2.43±0.65 (2.15-2.8)	5.21±0.119 (4.47-5.80)
WA-522, Wilson Bluff, FMNH 204398	27D	6.84±0.079 (6.1-7.6)	12.6±0.120 (11.45-13.9)	0.543±0.004 (0.508-0.589)	4¼− (3⅞+-4½−)	2.50±0.047 (2.0-3.05)	5.08±0.090 (4.34-6.55)
Western Australia							
Eucla Pass, top of, 24.XII.52, WAM 285.74	6D	6.81±0.217 (6.05-7.45)	12.58±0.236 (12.0-13.55)	0.541±0.013 (0.502-0.579)	4¼+ (4⅛+-4⅜+)	2.36±0.106 (2.05-2.75)	5.38±0.217 (4.68-6.15)

Table 133: Local variation in *Pleuroxia bethana* and *Pleuroxia elfina* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
WA-528, Eucla, FMNH 204434	13D	6.69±0.135 (5.8-7.7)	13.01±0.195 (12.05-14.55)	0.514±0.007 (0.479-0.578)	4$\frac{1}{8}$+ (4–-4$\frac{1}{4}$+)	2.30±0.074 (1.8-2.85)	5.71±0.151 (4.81-6.74)
WA-527, Najoda Rock Hole, FMNH 204426	20L	7.73±0.083 (7.15-8.7)	13.77±0.153 (12.9-15.4)	0.562±0.006 (0.520-0.609)	4$\frac{1}{4}$+ (4$\frac{1}{8}$+-4$\frac{5}{8}$–)	2.41±0.052 (2.1-3.0)	5.75±0.120 (4.90-6.96)
WA-527, FMNH 204425	11D	7.23±0.158 (6.5-8.1)	13.35±0.112 (12.75-14.0)	0.541±0.012 (0.482-0.607)	4$\frac{1}{4}$– (4+-4$\frac{3}{8}$–)	2.35±0.064 (2.0-2.6)	5.72±0.176 (5.12-6.9)
WA-537, Dingo Donga (N-160), FMNH 204494	56L	9.31±0.078 (8.0-10.55)	15.22±0.084 (13.95-16.6)	0.611±0.005 (0.541-0.702)	4$\frac{3}{8}$– (4+-4$\frac{5}{8}$+)	1.94±0.036 (1.1-2.4)	8.01±0.169 (6.3-14.0)
WA-538, Dingo Donga (N-160), FMNH 204493	31L	9.49±0.094 (8.5-10.75)	15.58±0.119 (14.2-17.1)	0.609±0.005 (0.564-0.673)	4$\frac{3}{8}$– (4$\frac{1}{8}$+-4$\frac{5}{8}$+)	2.00±0.053 (1.45-2.60)	7.95±0.213 (6.37-10.6)
Twilight Cove, WAM 276.74	22D	8.00±0.105 (7.2-9.1)	13.03±0.098 (11.85-14.0)	0.614±0.007 (0.556-0.676)	4$\frac{3}{8}$+ (4$\frac{1}{4}$-4$\frac{1}{2}$+)	2.18±0.043 (1.85-2.6)	6.04±0.133 (5.02-7.66)
WA-539, Caiguna, FMNH 204502	5D	6.24±0.170 (5.8-6.65)	10.69±0.185 (10.15-11.2)	0.584±0.012 (0.553-0.607)	4$\frac{1}{4}$+ (4$\frac{1}{8}$+-4$\frac{3}{8}$+)	1.90±0.061 (1.8-2.15)	5.66±0.193 (4.92-6.00)
WA-541, Balladonia, FMNH 204514	7D	5.98±0.163 (5.6-6.85)	10.94±0.151 (10.2-11.4)	0.547±0.014 (0.499-0.615)	4$\frac{1}{8}$– (4–-4$\frac{3}{8}$+)	1.89±0.050 (1.75-2.1)	5.81±0.150 (5.20-6.28)
WA-94, Balladonia, FMNH 182515	5L	6.83±0.087 (6.6-7.1)	12.32±0.252 (11.7-13.2)	0.556±0.013 (0.523-0.590)	4$\frac{1}{8}$+ (4$\frac{1}{8}$–-4$\frac{1}{4}$–)	2.59±0.143 (2.1-2.9)	4.81±0.250 (4.22-5.73)
Charlina Rocks, WAM 1114.81	5D	7.08±0.251 (6.5-7.8)	11.64±0.306 (11.0-12.45)	0.610±0.025 (0.570-0.708)	4$\frac{1}{8}$+ (4-4$\frac{3}{8}$–)	2.18±0.057 (2.0-2.3)	5.35±0.232 (4.94-6.20)
WA-543, Juranda FMNH 204546	4L	7.35±0.273 (6.75-7.85)	12.59±0.423 (11.55-13.55)	0.584±0.015 (0.546-0.611)	4$\frac{1}{4}$– (4$\frac{1}{8}$+-4$\frac{1}{4}$+)	2.12±0.096 (1.95-2.3)	5.96±0.132 (5.68-6.32)
WA-543, FMNH 204545	12D	7.79±0.144 (7.2-8.75)	13.41±0.233 (12.1-14.65)	0.582±0.009 (0.532-0.630)	4$\frac{1}{8}$+ (3$\frac{7}{8}$+-4$\frac{1}{4}$–)	2.06±0.090 (1.4-2.5)	6.62±0.246 (5.75-8.78)

PLEUROXIA ELFINA IREDALE, 1939

(Plates 177d–f, 180a–f; Figs 370Aa–c, 370Bd–f, 371a–c; Maps 20–22)

Comparative remarks

Pleuroxia elfina Iredale, 1939, from the Nullarbor Plain as far east as Nullarbor, SA (130°55'E) and extending a short distance W of Newman Rock, WA (123°05'E) (**Maps 20–22**), is characterised by its weak radial sculpture (**Plate 177d–e**) that does not develop until the mid-spire and only is prominent on the lower spire and body whorl, dense and high setae (**Plate 177e–f**) and usually narrowly expanded lip. *P. polypleura* (Tate, 1899) and *P. oligopleura* (Tate, 1894), from the Nullarbor area (**Maps 21–23, 25**), have narrower and much more prominent ribs, their radial sculpture starts on the upper spire (**Plates 178a–b, d–e**) and they have much more widely spaced setae. *P. bethana* sp. nov., from near Geraldton and Mullewa on the W coast (**Maps 20, 27**), has crowded, prominent ribs (**Plate 177a–b**, **Figs 368Bd–f**), a narrower umbilicus and more globose shape (**Table 132**). *P. abstans* Iredale, 1939, from the Murchison River mouth on the W coast (**Maps 20, 27**), is even smaller (**Table 132**) and less elevated (**Figs 368Aa–c**), with a well expanded lip, stronger and more widely spaced sculpture and a wider umbilicus. Anatomically (**Figs 371a–b**), the higher position of the spermathecal head (S), smaller albumen gland (GG), and very complex penis chamber sculpture separate *P. elfina* from *P. bethana* (**Figs 369a–b**). *P. polypleura* (**Figs 373a–b**) and *P. oligopleura* (**Figs 376a–b**) differ most obviously in their specialised penis chamber sculpture and often elongated penes.

Holotype

WAM 8880, Newman Rocks (*sic*), E of Fraser Range, Western Australia. Holotype of *Pleuroxia polypleura elfina* Iredale, 1939. Height of shell 7.8 mm, diameter 13.15 mm, H/D ratio 0.593, whorls 4 1/4, umbilical width 2.2, D/U ratio 5.98.

Paratypes

WAM 8880, AM C.64849, 7 DA from the type locality.

Material studied

SOUTH AUSTRALIA: Murrawijinie Cave (September 1947, MV F3061, 1 DA); Murrawijinie Cave # 3, 5N9 (WA–512, NNW of Nullarbor, WAM 264.84, WAM 265.84, AM, FMNH 204347–8, 13 LA, 4 DA, 15 LJ, 1 DJ); Murrawijinie Cave # 1, 5N7 (WA–511, WAM 266.84, WAM 267.84, AM, FMNH 2043341, FMNH 204346, 25 LA, 14 DA, 24 LJ, 9 DJ); Doline 5N122, W of Nullarbor (WA–517, 1.3 km S of Eyre Highway, WAM 268.84, WAM 269.84, AM, FMNH 204368–9, 24 LA, 16 DA, 32 LJ, 6 DJ); SSW of Nullarbor (WA–518, WAM 270.84, SAM D17723, AM, FMNH 204376, 13 DA, 9 DJ); 5N163 doline, NW of Nullarbor (WA–519, WAM 271.84, WAM 272.84, AM, FMNH 204377–8, 83 LA, 59 DA, 10 LJ, 21 DJ); lookout 12.9 km E of Border Village (WA–521, under limestone rocks, WAM 234.84, SAM D17715, AM, FMNH 204389–90, 9 DA, 1 DJ); Allen's Cave, 5N145 (WA–504, SSE of Sixteen Mile Tank, WAM 235.84, WAM 236.84, SAM D17716, AM, FMNH 204294–5, 3 LA, 22 DA, 4 LJ, 10 DJ); 12.9 km E of Border Village (WA–521, WAM 234.84, SAM D17715, FMNH 204390, 1 LA, 3 DA, 1 LJ, 7 DJ); Wilson Bluff (6 miles NE of, November 1966, WAM 317.74, 17 DA, 11 DJ; 1.2 miles E of cairn, November 1966,

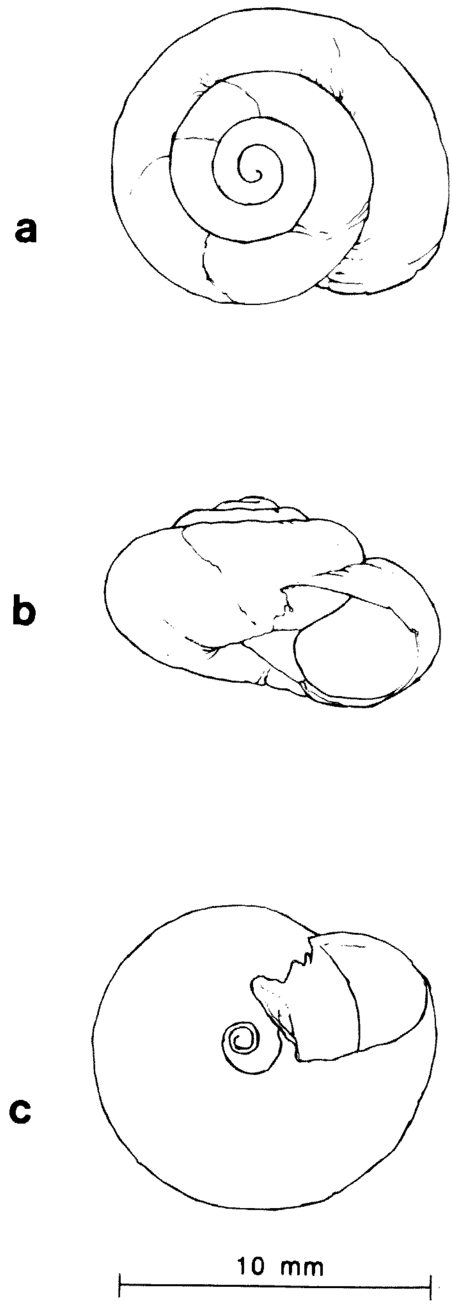


Fig. 370A: Shells of *Pleuroxia elfina* Iredale, 1939: (a–c) Newman Rock, E of Fraser Range, WA. Paratopotype of *Pleuroxia polypleura elfina* Iredale, 1939. AM C.64849. Scale line equals 10 mm. Drawings by Linnea Lahlum.

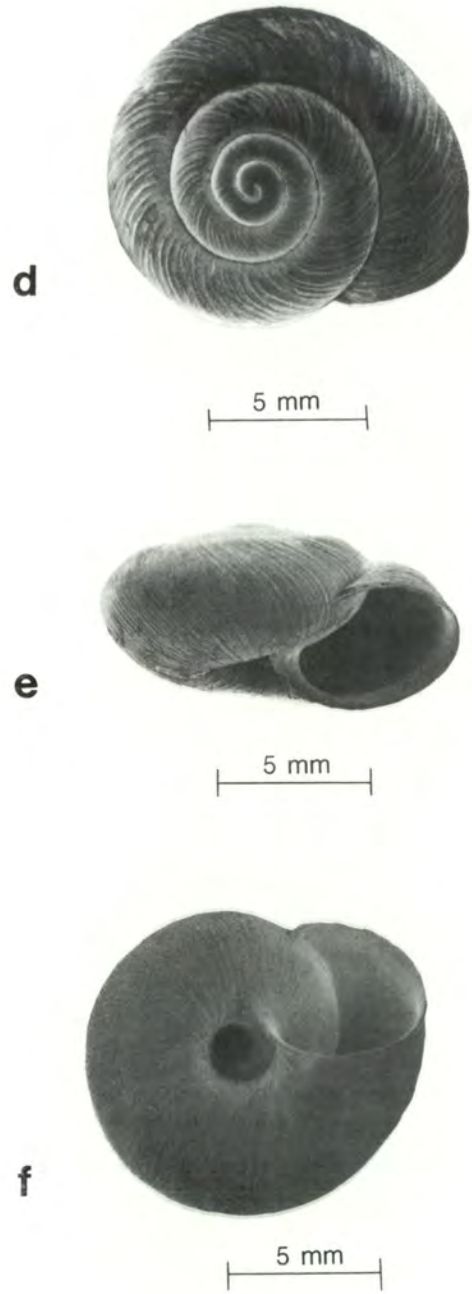
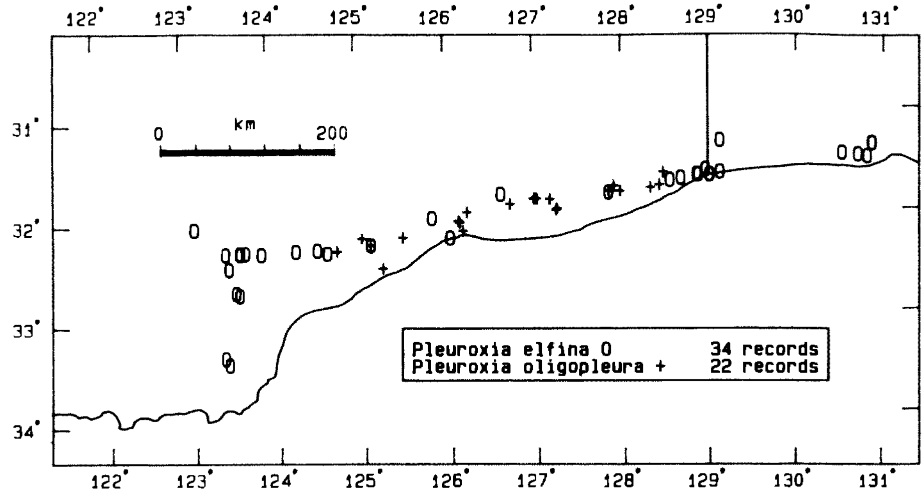


Fig. 370B: Shells of *Pleuroxia elfina* Iredale, 1939: (d–f) 6 miles NE of Wilson Bluff, Nullarbor, SA. WAM 317.84. Scale lines as marked.



Map 21: Distribution of *Pleuroxia elfina* and *P. oligopleura*.

WAM 291.74, 2 DA; 0.5 km E of SA border, 21 November 1981, AM C.132229, 17 DA, 33 DJ; WA–522, at trig, WAM 237.84, WAM 238.84, AM, FMNH 204397–8, 11 LA, 27 DA, 7 LJ, 5DJ).

WESTERN AUSTRALIA: 1.6 km W of Border Motel, 24 August 1974, WAM, 2 DA); Eucla, top of the pass (24 December 1952, WAM 285.74, 6 DA, 10 DJ; below crest of Eucla Pass (WA–498, gully on scarp, WAM 276.84, FMNH 204236–8, 4 DA, 3 DJ); WSW of Eucla (WA–528, WAM 279.84, AM, FMNH 204434, 13 DA, 10 DJ); Najoda Rock Hole (WA–527, ENE of Eucla, WAM 280.84, WAM 294.84, FMNH 204425–6, 11 LA, 20 DA, 3 LJ, 6 DJ); 300 m S of Kelly Cave, 6N165, NW of Mundrabilla (WAM, 2 DA); Mundrabilla Station (1 January 1976, WAM 29.87, 18 DA, 15 DJ); Dingo–Donga sink, 6N160, WNW of Madura (WA–538, WAM 297.84, WAM 298.94, AM, FMNH 204493–4, 31 LA, 56 DA, 28 LJ, 14 DJ); Twilight Cove (5 November 1966, WAM 276.74, 22 DA, 21 DJ); John Eyre Motel, Caiguna (WA–539, 33.4 km W of, WAM 239.84, WAM 240.84, SAM D17717, FMNH 204502–4, 1 LA, 5 DA, 4 LJ, 7DJ); E of Balladonia Homestead (WA–540, 64.5 km E of, FMNH 204515, 2 DJ; WA–541, 38.3 km E of, WAM 241.84, SAM D17718, AM, FMNH 204524, 7 DA, 7 DJ); Afghan Rock (WA–95, FMNH 182289, 1 DJ); Balladonia Roadhouse area (WA–94, WAM 242.84, WAM 243.84, SAM D17719, AM, FMNH 182515, FMNH 182720, FMNH 182291, FMNH 182296, 5 LA, 2 DA, 3 LJ, many DJ; WA–487, WAM 244.84, SAM D17720, AM, FMNH 204137–8, FMNH 204141–2, 2 LA, 4 DA, 13 DJ); Balladonia–Cape Arid track (WA–542, 46.1 km S of Eyre Highway, FMNH 204538, 1 DA, 1 DJ); 18 km NE of Charlina Rocks (WAM 1114.81, 5 DA, 2 DJ); Booanya Rock (MV, ex C. J. Gabriel, 1 DA); Junana Rock (WAM 308.74, 5 DA); Juranda Rockhole (WA–543, WAM 247.84, WAM 248.84, SAM D17721–2, AM, FMNH 204545–6, WAM 308.74, 4 LA, 13 DA, 7 LJ, 39 DJ; WA–544, WAM 245.84, FMNH 204556–7, 3 LA, 3 DA, 4 LJ, 7 DJ); Pine Hill, 48 miles S of Nanambinia (17

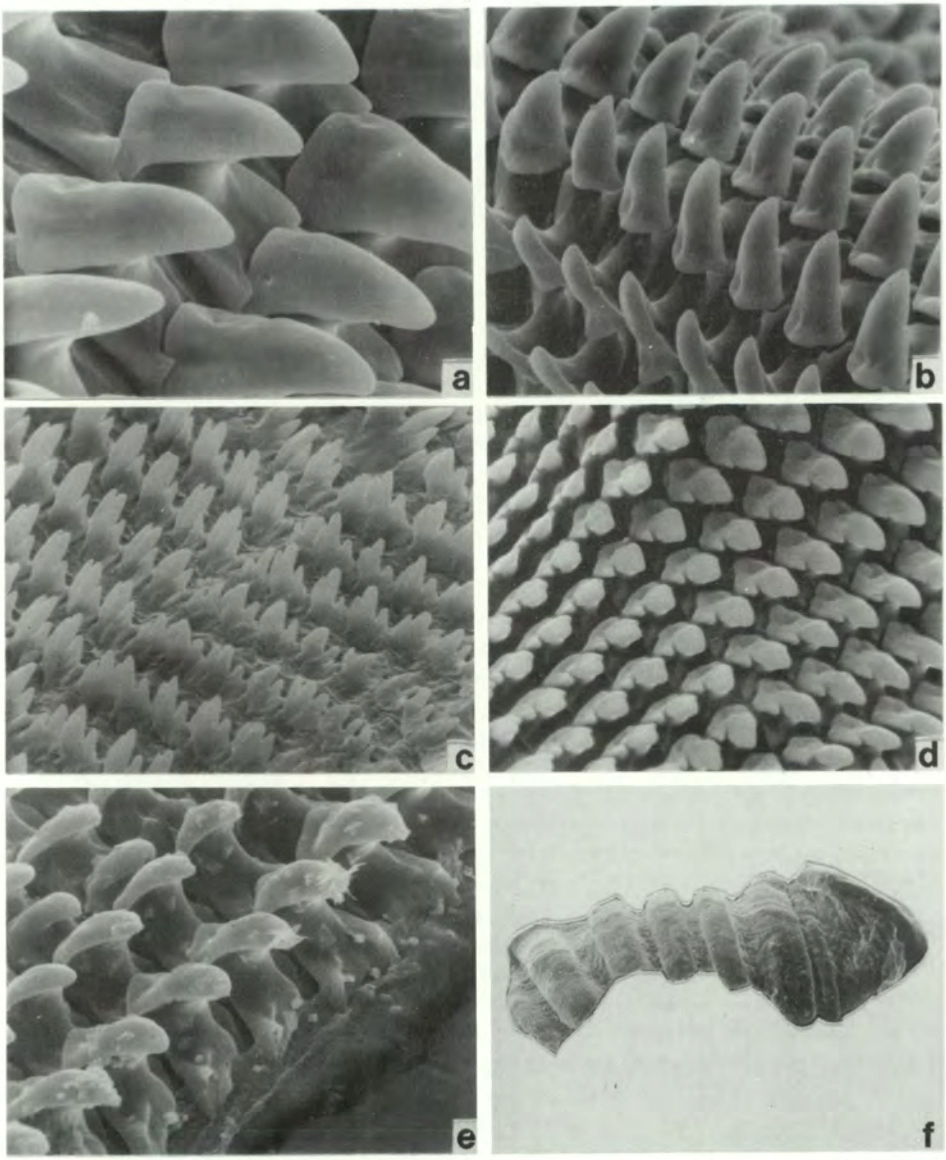


Plate 180: Radular teeth of *Pleuroxia elfina* Iredale, 1939: (a–c) WA–94, N of Balladonia Hotel-Motel, WA. 21 March 1974. FMNH 182515, Dissection A: a is central and early laterals at 130X; b is anterior view of central and early laterals at 670X; c is anterior view of marginals at 650X; (d–f) WA–543, Juranda Rock Hole, S of Balladonia, WA. 16 June 1979. FMNH 204546, Dissection A: d is latero-marginal transition at 510X. e is central and early laterals 740X. f is jaw at 81X.

December 1962, WAM, 3 DA); 7.5 km WNW of Newman Rock (WA–486, WAM 246.84, FMNH 204123–4, 1 DA, 2 LJ, 3 DJ); ruins of Deralyina Homestead (WA–1091, 9 June 1989, FMNH 221779–80, FMNH 221786, 31 LA, 41 DA).

Range

Pleuroxia elfina Iredale, 1939 has been collected (**Maps 20–22**) from 7.5 km WNW of Newman Rock (WA–486), E of the Fraser Range, SE as far as Juranda Rock Hole (WA–543, WA–544) and Pine Hill on the Cape Arid track, then along the Eyre Highway at scattered localities as far E as Nullarbor, SA (WA–511, WA–512). The east-west range is thus about 740 km, and the distance from Newman Rock SSE to Juranda Rockhole is about 145 km. The eastern part of this range is not continuous. There is an initial node of abundance near Nullarbor, SA, which is interrupted (**Map 22**) slightly to the west near Koonalda, SA by populations of *P. polypleura* (Tate, 1899). Populations of *P. elfina* resume near the WA–SA border from 12.9 km E (WA–521) to 1.6 km W, followed by records along the Hampton Scarp near Eucla (WA–498, WA–528), then W to near Najoda Rock Hole (WA–527). It is then replaced by *P. oligopleura* (**Map 21**). There are a few records near Madura (WA–538), and Mundrabilla, plus an isolated record from Twilight Cove, S of Cocklebiddy. The probably continuous range starts at 33.4 km W of Caiguna (WA–539), where it is sympatric with *P. oligopleura* (Tate, 1894), and continues W to near Newman Rock just off the Eyre Highway, Deralyina Homestead ruins, and then SW to Pine Hill on the Cape Arid track.

Diagnosis

Shell variable in size, diameter 10.15–18.65 mm (mean 14.28 mm), with 3 7/8+ to 4 3/4+ (mean 4 3/8–) normally coiled whorls. Apex and spire slightly and evenly elevated (**Figs 370Ab, 370Be**), shell height 5.6–11.25 mm (mean 8.46 mm), H/D ratio 0.482–0.723 (mean 0.593). Body whorl rounded, without trace of keel or angulation. Shell apex (**Plate 177d**) with traces of weak elongated pustulations. Periostracal setae (**Plate 177d–f**) developed on early spire, continuing on lower spire and body whorl, moderate elongated pustulations present. Mid-spire with low, rounded radial ribs, becoming more prominent on lower spire and body whorl (**Plate 177d–e**). Umbilicus (**Figs 370Ac, 370Bf**) open, regularly decoiling, only slightly narrowed by columellar lip reflection, width 1.2–3.15 mm (mean 2.17 mm), D/U ratio 4.22–14.0 (mean 6.58). Body whorl moderately to strongly descending behind aperture (**Figs 370Ab, 370Be**). Palatal and basal lips narrowly expanded and reflected (**Figs 370Aa–c, 370Bd–f**), rarely thickened, columellar lip slightly more expanded. Parietal wall with a thin callus. Colour brownish-yellow, base of shell lighter. Based on 583 measured adults.

Genitalia (**Figs 371a–c**) with normal sized albumen gland (GG), rest of apical and pallial genitalia typical. Spermatheca (S) with thick base, shaft wrapped around free oviduct, base of expanded head well above free oviduct (UV) origin, extending to mid-portion of prostate-uterus. Vagina (V) shorter than free oviduct, relatively slender. Vas deferens (VD) very slender, merging laterally with small epiphallic caecum (EC). Epiphallus (E) slender, entering penis (P) apically through foliated pilasters after receiving insertion of penis retractor muscle (PR). Penis sheath reduced to a thin membrane attached to penis (not shown in **Fig. 371b**). Penis short and nearly globular (**Fig. 371c**) to intermediate in length (**Figs 371a–b**), internally (**Fig. 371b**) with complex pilasters on chamber wall, one of which reflexes up into vagina.

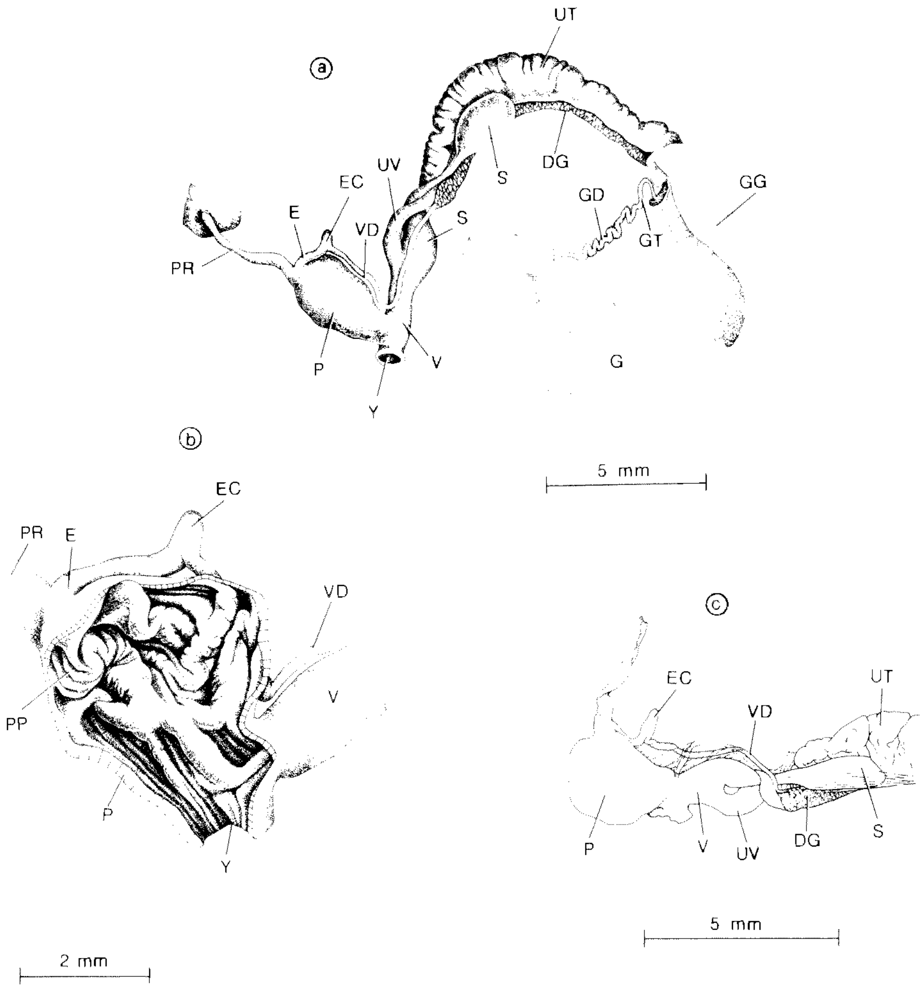


Fig. 371: Genitalia of *Pleuroxia elfina* Iredale, 1939: (a–b) WA–94, salt bushes, N of Balladonia Hotel-Motel (Eyre Highway), WA. 21 February 1974. FMNH 182515, Dissection B. (a) whole genitalia; (b) interior of penis; (c) WA–512, Murrawijinie Cave #3 (5N9), Nullarbor, SA. 9 June 1979. FMNH 204347, Dissection A, terminal genitalia. Scale lines as marked. Drawings a–b by Elizabeth A. Liebman, c by Linnea Lahlum.

Central teeth of radula (**Plate 180a–b, e**) without trace of ectocones, basal ridges massive, cusp tip slightly curved, blunt. Early laterals (**Plate 180a–b, e**) without trace of ectocones, anterior flare moderate, cusp tips curved and bluntly rounded, with large basal ridge. Latero-marginal transition (**Plate 180d**) abrupt, ectoconal cusp prominent only on last laterals. Marginals (**Plate 180c**) highly variable in cusp structure. Jaw (**Plate 180f**) with few and wide vertical ridges.

Discussion

Pleuroxia elfina Iredale, 1939 extends significantly further W into WA (**Map 20**) than do either *P. polypleura* (Tate, 1899) (**Map 22**) or *P. oligopleura* (Tate, 1894) (**Map 21**). In the Balladonia-Juranda Rock Hole region, *P. elfina* is associated with fallen trees or large branches. It aestivates sealed to the still solid upper walls of decay cavities. At the same stations, the large *Sinumelon kalgum* Iredale, 1939 inhabits the litter under shrubs or the rotten litter remains under older logs. *Bothriembryon dux* (Pfeiffer, 1861) sometimes is found in the same cavities as *P. elfina*, aestivating in the wood chips and debris at the bottom of the holes. W of Caiguna (WA–539), *P. elfina* is found in litter around logs and tree trunks, while *P. oligopleura* (Tate, 1894) is strictly rock-associated. Further E, on the Nullarbor fringes, *P. elfina* is rock-associated, as are the other *Pleuroxia*.

Size variation among populations is substantial (**Table 133**) and geographic in nature. The easternmost populations from Murrawijinie Caves (WA–511–512) and Nullarbor (WA–517–519), SA are large (mean diameters 14.48–17.08 mm), elevated (mean H/D ratio over 0.600), averaging 4 1/2 whorls, and rather narrowly umbilicated (mean D/U ratios 6.73–7.70). In contrast, the populations around the WA–SA border are smaller (mean diameters 12.03–13.01 mm), with lower spires (mean H/D ratios 0.514–0.567), with 4 1/8 to 4 1/4 whorls, and a wider umbilicus (mean D/U ratios 5.08–5.53). The isolated population from Najoda Rock Hole (WA–527) is intermediate in size and elevation, while the Dingo Donga (WA–538) shells are larger, higher spired, and narrowly umbilicated. Caiguna and Balladonia shells are small and widely umbilicated, with intermediate spire elevation. The Pine Hill, Charlinna Rocks and Juranda Rock Hole specimens are small but variable in spire height and umbilical width.

Penis structure was checked in a number of populations from western (WA–94, WA–504, WA–543), eastern (WA–511–512, WA–517, WA–519), and isolated (WA–527, WA–538) portions of the range. Most had the penis slightly elongated and with moderately massive internal pilasters, as in the illustrated Balladonia (WA–94, **Figs 371a–b**) example, but some of the SA material had a shorter, globose penis (**Fig. 371c**) with more massive internal pilasters. Penis length in all dissected material ranged from 3.9–4.6 mm (mean 4.19 mm).

The size range of *P. elfina* and *P. polypleura* overlaps (**Tables 132–134**) for some populations, especially in regard to shell diameter. Juvenile examples of the two species are easily separated by the presence of strong radial ribbing on the upper spire in *P. polypleura* and its absence in *P. elfina* (**Plates 177d–e, 178a–b**). Adults are distinguished by the more widely expanded lip (**Figs 370A, 370B, 372A, 372B**) and the generally higher H/D ratio of the former (**Table 132**). As mentioned below, the original description of *P. polypleura* may have been based on a mixture of *elfina* and *polypleura*.

PLEUROXIA POLYPLEURA (TATE, 1899)

(Plate 178a–c, 182a–d; Figs 372Aa–c, 372Bd–f, 373a–f; Maps 22, 23, 25)

Helix cyrtopleura Tate, 1879 (not Pfeiffer, 1862), *Trans. Proc. Phil. Soc., Adelaide,* **2:** 126; Hedley, 1895, *Proc. malac. Soc. London,* **1:** 260 – Eucla, WA.

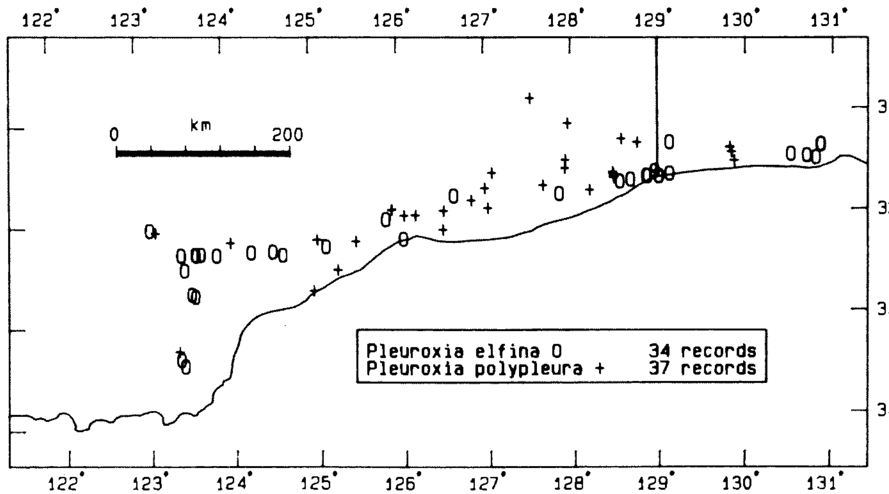
Angasella polypleura Tate, 1899, *Trans. Roy. Soc. South Austr.,* **23:** 246–247, pl. VI, figs 2a–c – Bunda Plateau, Great Australian Bight, SA.

Pleuroxia polypleura (Tate), Iredale, 1937, *South Austr. Nat.*, **18** (2): 48; Iredale, 1938, *Austr. Zool.*, **9** (2): 106; Iredale, 1939, *Jour. Roy. Soc. Western Austr.*, **25:** 55, pl. III, fig. 27 – road between Madura and Mundrabilla, WA; Richardson, 1985, Tryonia, **12:** 254.

Pleuroxia commenta Iredale, 1939, *Jour. Roy. Soc. Western Austr.*, **25:** 55, pl. III, fig. 26 – Hampton Tablelands, WA (Charles Barrett!).

Comparative remarks

Pleuroxia polypleura (Tate, 1899), from near Koonalda, SA and sporadically W as far as the John Eyre Motel, Caiguna, WA and N at least as far as Old Homestead Cave (6N83) (WA–532) on the Forrest-Mundrabilla track (**Maps 22, 23, 25**), differs from *P. oligopleura* (Tate, 1894) in its higher spire (compare **Figs 372Ab, 372Be, 374b, e**), narrower umbilicus (**Figs 372Ac, 372Bf, 374c, f**), thinner and less expanded lip (**Figs 372A, 372B, 374**) with only a thin callus on the parietal wall, and finer, generally more crowded radial ribs (**Figs 372A, 372B, 374, Plate 178a–b, d–e**). The two species are very similar in diameter and whorl counts (**Table 132**). *Pleuroxia elfina* Iredale, 1939 inhabits the same general area (**Maps 20–22**) but differs most obviously in its reduced radial ribbing (**Figs 370Bd–f, Plate 177d–e**). *P. abstans* Iredale, 1939 from



Map 22: Comparative distribution of *Pleuroxia elfina* and *P. polypleura*.

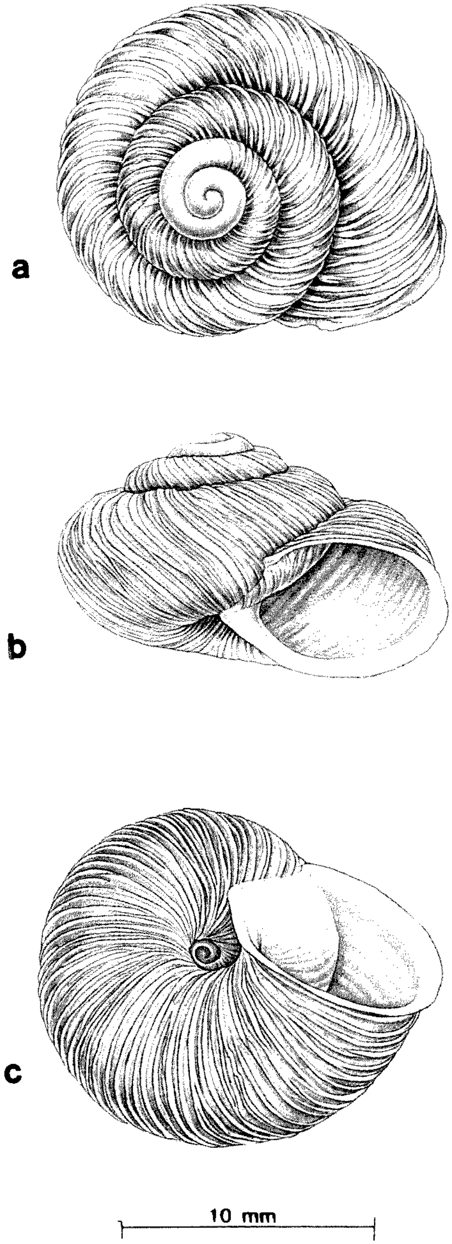


Fig. 372A: Shells of *Pleuroxia polypleura* (Tate, 1899): (a–c) doline of Cocklebiddy Cave (6N48), near Caiguna, Nullarbor, WA, WAM 272.74. Scale lines equal 10 mm. Drawings by Linnea Lahlum.

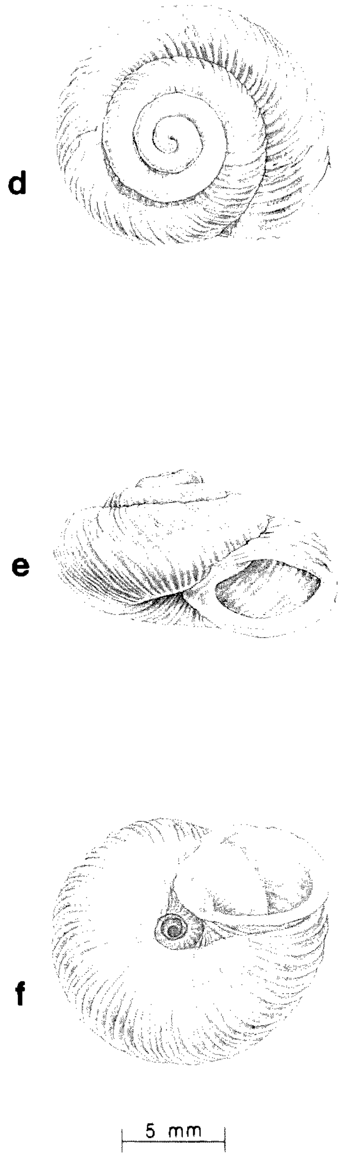


Fig. 372B: Shells of *Pleuroxia polypleura* (Tate, 1899): (d–f) Hampton Tableland, WA. Holotype of *Pleuroxia commenta* Iredale, 1939, AM C.56600. Scale lines as marked.

the Murchison River mouth N of Geraldton (**Maps 20, 27**) is very small and widely umbilicated (**Table 132**) with a much lower spire and broadly expanded lip (**Figs 368Aa–c**), while *P. bethana* sp. nov., from Kalbarri National Park to W of Mullewa and through the Greenough River basin (**Maps 20, 27**), is more globose and smaller (**Table 132**), the lip is often not expanded (**Figs 368Bd–f**). Its main shell sculpture (**Plate 177a–c**) is more sharply defined and the microsculpture is much more widely spaced. Anatomically (**Figs 373a–f**), the usually very long penis (P) with massive wall pilasters, long epiphallus that reaches midway down the penis and having part of the prostate-uterus wrapped around the spermathecal shaft, immediately separate *P. polypleura* from *P. bethana* (**Figs 369a–b**) and *P. elfina* (**Figs 371a–b**), which have short and very globose penes. *P. oligopleura* (**Figs 376a–d**) has a penis that is variable in length but generally much shorter than the penis of *P. polypleura*, the spermathecal head (S) extends further up the prostate-uterus and the epiphallus (E) is shorter.

Types

Lectotype of *Helix polypleura* Tate, 1899. SAM D15539, Bunda Plateau, South Australia. Height of shell 11.1 mm, diameter 18.2 mm, H/D ratio 0.610, whorls 4 3/8, umbilical width 2.70 mm, D/U ratio 6.74.

Type lot of *Helix polypleura* Tate, 1899. AM C.4365, AM C.112576, 8 DA, 2 DJ from the type locality.

Holotype of *Pleuroxia commenta* Iredale, 1939. AM C.56600, Hampton Tablelands, Western Australia. Height of shell 7.3 mm, diameter 12.0 mm, H/D ratio 0.608, whorls 4 1/8, umbilical width 1.8 mm, D/U ratio 6.67.

Paratypes of *Pleuroxia commenta* Iredale, 1939. AM C.64844, 2 DA, 1 DJ from Nullarbor Plains, WA.

Material studied

SOUTH AUSTRALIA: N of Koonalda (September 1947, MV F3053, 14 LA, 2 DA, 1 DJ); 5N150 doline, SSE of Koonalda (WA–506, WAM 273.84, FMNH 204311, 1 DA, 5 DJ); base of doline, Koonalda Cave, 5N4 (WA–508, FMNH 204318, 3 LA); rim of Giants Head Doline, 5N178, Koonalda (WA–507, WAM 274.84, WAM 275.84, AM, FMNH 204316–7, 22 LA, 15 DA, 34 LJ, 5 DJ).

WESTERN AUSTRALIA: near Weebubbie Cave (6N2), N of Eucla (14 September 1985, WAM, 7 DA, 2 DJ); rim of Weebubbie Cave, N–2 (WA–499, WAM 277.84, WAM 278.84, FMNH 204250, FMNH 204254, 9 LA, 27 DA, 3 LJ, 30 DJ); Kutowalla Doline, 6N44, Eucla (WA–502, rim of, WAM 281.84, WAM 282.84, AM, FMNH 204270–1, 21 LA, 22 DA, 10 LJ, 4 DJ); Winbirra Cave, 6N45, W of Eucla (WA–503, WAM 283.84, WAM 284.84, AM, FMNH 204282–3, 10 LA, 34 DA, 6 LJ, 2 DJ); on road between Madura and Mundrabilla (15 December 1926, WAM 12016, 2 DA, 2 DJ); Eucla Basin, doline (5 October 1966, WAM 310.74, 3 DA, 1 DJ); Abrakurrie Cave, 6N3 (1 November 1966, WAM 270.74, 3 DA, 2 DJ); Abrakurrie Cave, 6N3 (WA–501, rim to bottom of doline, WAM 285.84, WAM 286.84, AM, FMNH 204266–7, 20 LA, 12 DA, 24 LJ, 3 DJ); Chowilla Landslip, 6N17 (WA–500, rim of, WAM 287.84, WAM 288.84, AM, FMNH 204258–9, 29 LA, 28 DA, 30 LJ, 11 DJ); Kuthala Pass, N of Mundrabilla Roadhouse (WA–524, WAM 289.84, WAM 290.84, AM, FMNH 204401–2, 4 LA,

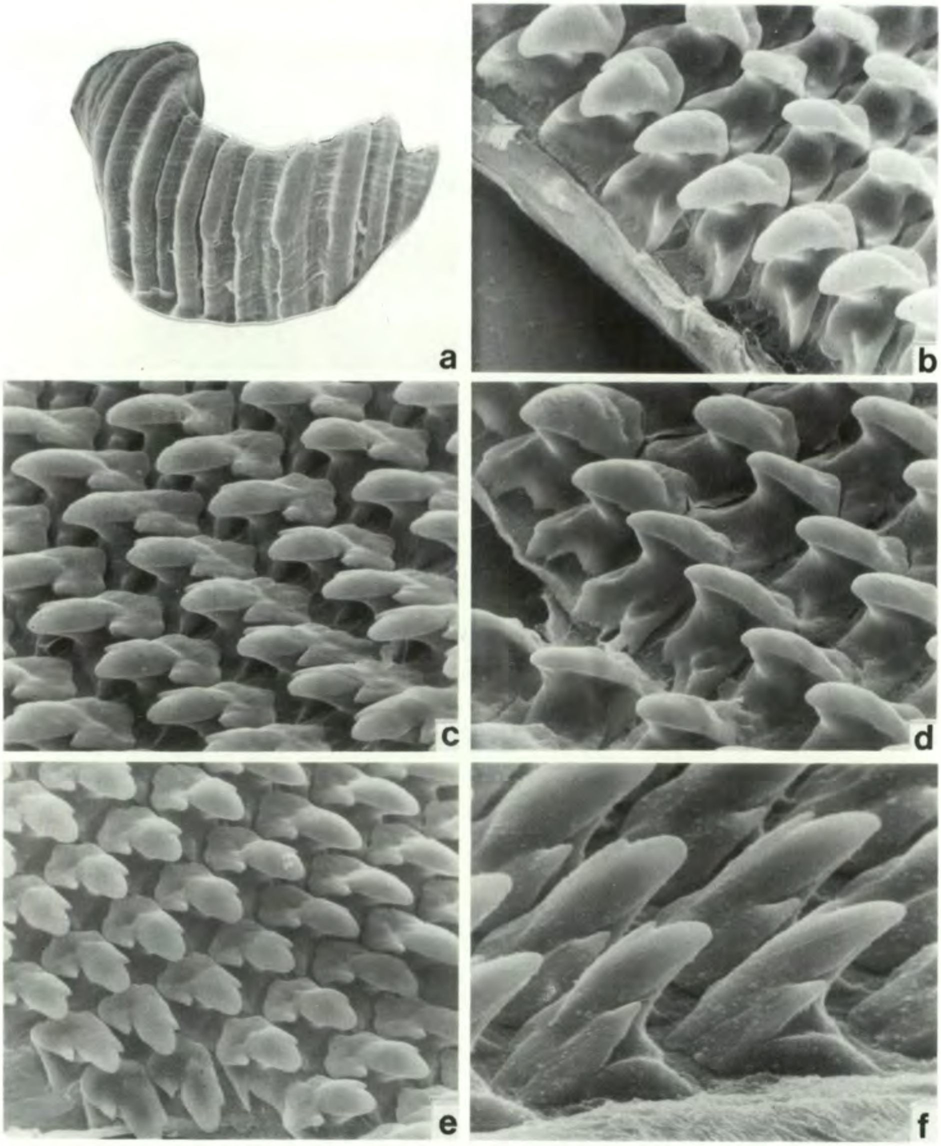


Plate 181: Radular teeth and jaw of *Pleuroxia oligopleura* (Tate, 1894). WA–359, 33.4 km W of John Eyre Motel, Caiguna, WA. FMNH 204500: (a) Dissection A, jaw at 77X; (b) Dissection A, central and early laterals at 630X; (c) Dissection C, lateromarginal transition at 730X; (d) Dissection C, central and early laterals at 750X; (e) Dissection B, latero-marginal transition at 565X; (f) Dissection B, early marginals at 1250X.

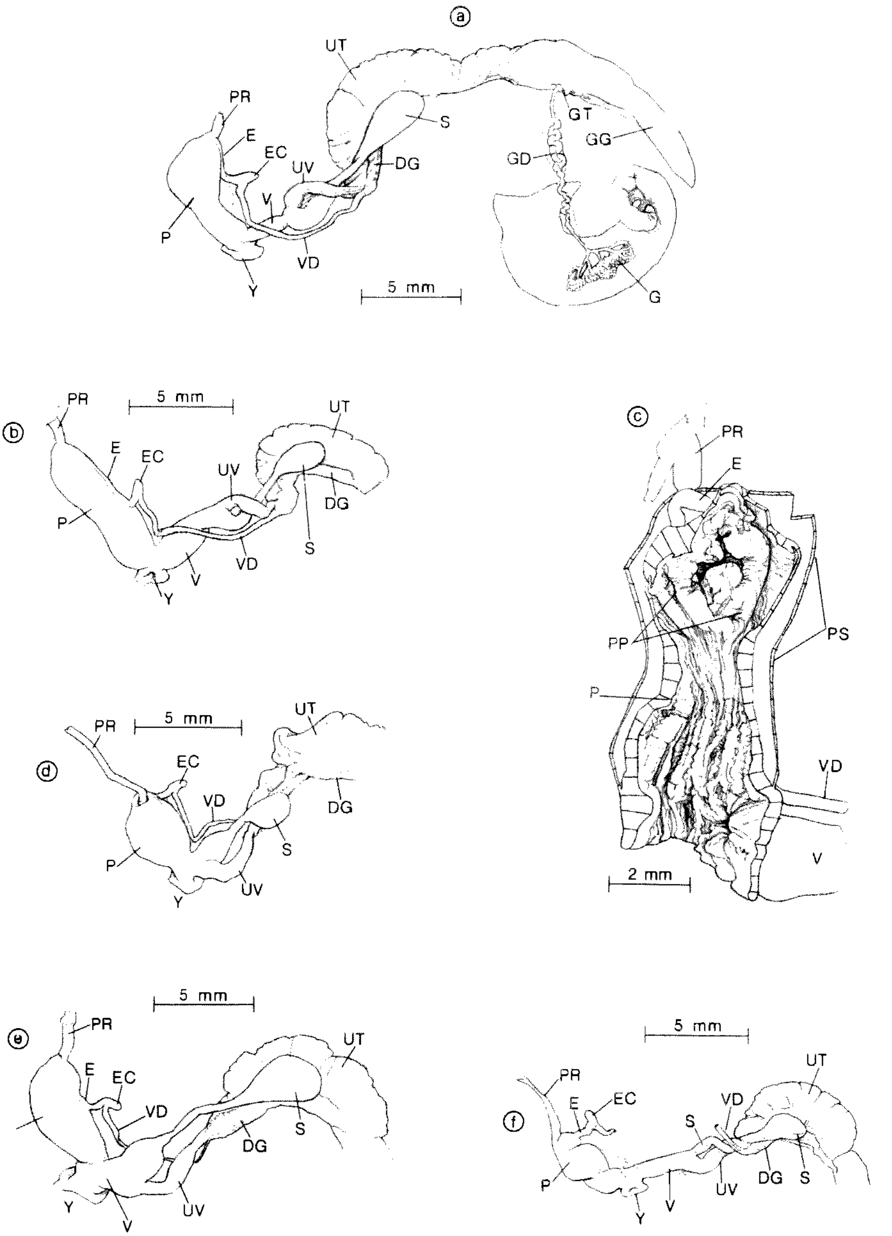


Fig. 373: Genitalia of *Pleuroxia polypleura* (Tate, 1899): (a) WA–507, Giants Head Doline (5N178), N of Koonalda, SA. 8 June 1979. FMNH 204317, Dissection A. whole genitalia; (b–c) WA–490A, S rim of Cocklebiddy Cave (6N48), WA. 4 June 1979. FMNH 204175. b is terminal genitalia, Dissection A, c is penis interior, Dissection B; (d) WA–491, E of Cocklebiddy, WA. 4 June 1979. FMNH 204182, Dissection A, terminal genitalia; (e) WA–492, Moonera Tank Cave (6N53), WA. 4 June 1979. FMNH 204189, Dissection A, terminal genitalia; (f) WA–494, Madura Cave (6N62), WA. 5 June 1979. FMNH 204204, Dissection A, terminal genitalia. Scale lines as marked. Drawings by Linnea Lahlum.

5 DA, 12 LJ, 6 DJ); *ca.* 75 km S of Forrest on Forrest-Mundrabilla track (4 September 1979, MV, 9 DA, 2 DJ); Old Homestead Cave, 6N83 (2 July 1966, WAM, 2 DA; WA–532, WAM 291.84, WAM 292.84, AM, FMNH 204448–9, 23 LA, 7 DA, 5 LJ, 2 DJ); Forrest track, 31.8 km N of Mundrabilla Homestead (WA–529, WAM 293.84, SAM D17724, AM, FMNH 204437, 35 DA, 33 DJ); Madura 6 Mile South Cave, 6N62 (WA–494, WAM 295.84, WAM 286.84, AM, FMNH 204204–5, 43 LA, 19 DA, 24 LJ, 6 DJ; 29 December 1961, WAM 325.74, 14 DA; 4 January 1976, WAM, 3 DA); 10 miles W of Madura along Eyre Highway (29 May 1967, WAM 365.74, 1 DA); in cave near Madura (August 1967, WAM 333.74, 1 DA, 1 DJ); on road between Madura and Mundrabilla (15 December 1926, WAM 12026, 2 DA, 2 DJ); "8 miles N Cave", Madura (2 November 1966, WAM 284.74, WAM 375.74, 1 LA, 20 DA); Mullamullang Cave, 6N37 (28 August to 2 September 1966, WAM 292.74, 9 DA); Mullamullang doline, 6N37, near Madura (19 May 1978, WAM 1159.81, 10 DA; 31 August 1966, WAM 271.74, 2 DA, 12 DJ); 20 miles N of Madura (29 July 1967, WAM 376.74, 6 DA 3 DJ); near Madura Cave (29 December 1961, WAM 325.74, 8 DA, 6 DJ); Moonera Tank Cave, 6N53, WSW of Madura (WA–492, WAM 299.84, AM, FMNH 204189–90, 58 LA, 2 DA, many LJ); 360 m N of Eyre Highway, W of Madura (WA–493, camp site, WAM 300.84, FMNH 204193, 5 DA, 1 DJ); 6N91 Cave, E of Cocklebiddy (WA–491, WAM 450.87, WAM 451.87, AM, FMNH 204182–3, 69 LA, 16 DA, many LJ, 9 DJ); doline of Cocklebiddy Cave 6N48 (4 November 1968, WAM 272.74, 12 DA, 7 DJ; 8 January 1972, AM C.95832, 23 LA); Cocklebiddy Cave (6N48) (WA–490A, upper S rim of cave, WAM 452.87, WAM 453.87, AM, FMNH 204174–5, 37 LA, 63 DA, many LJ, 14 DJ; WA–490B, W side, *ca.* halfway down doline, WAM 454.87, WAM 455.87, AM, FMNH 204176, FMNH 204180, 14 LA, 36 DA, 12 LJ, 16 DJ; WA–490C, cave mouth at N end, WAM 456.87, AM, FMNH 204181, 16 LA, 24 LJ); 36.6 miles E of Caiguna, S side Eyre Highway (28 March 1967, WAM 367.74, 3 LA); 5.9 km E of Caiguna (WA–489, WAM 457.87, SAM D17725, AM, FMNH 204167, FMNH 204170–1, 51 DA, 70 DJ); scrub behind John Eyre Motel, Caiguna (WA–488, WAM 458.87, SAM D17726, AM, FMNH 204157, 14 DA, 18 DJ).

Range

Pleuroxia polypleura (Tate, 1899) has been collected (**Maps 22, 23, 25**) between the vicinity of Koonalda, SA (129°53'29"E) and the John Eyre Motel at Caiguna, WA (125°29'E), a total distance of about 440 km. The northernmost record is from Old Homestead Cave 6N83 (WA–532, 31°09'S) along the Mundrabilla–Forrest–track. The above range is not continuous. *P. polypleura* was not found at the many stations made between Yalata and Koonalda, SA, thus its eastern limit at Koonalda probably is accurate. *P. polypleura* is common in the Koonalda area (WA–506–508) but then absent from Koonalda to near the WA–SA border. In WA it is common inland of the Hampton Scarp near Weebubbie Cave (WA–499) N of Eucla; inland of Knousley Tank (WA–500–503) at about 128°30'E and then inland of Mundrabilla (WA–529, WA–532) along the Forrest Track. Along the Hampton Scarp itself between Eucla and Knousley Tank it is replaced (**Map 22**) by *P. elfina* and then from Knousley Tank to Madura (**Map 23**) by *P. oligopleura*, except for the one record at Kuthala Pass (WA–524). It is common in the area from Madura W to Cocklebiddy Cave (WA–491, 6N91) and Caiguna (WA–488).

Table 134: Local variation in *Pleuroxia polypleura.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
South Australia							
N of Koonalda, IX.47 MVF 3053	14L	7.98±0.127 (7.35-9.0)	13.98±0.134 (13.0-14.85)	0.570±0.006 (0.523-0.609)	4 3/8– (4 1/8-4 1/2–)	2.36±0.037 (2.2-2.6)	5.95±0.088 (5.48-6.41)
WA-507, Giants Head Cave (N-178), FMNH 204317	22L	8.28±0.122 (7.25-9.7)	14.26±0.140 (12.75-15.75)	0.581±0.007 (0.531-0.650)	4 3/8+ (4 1/4–-4 5/8–)	2.20±0.063 (1.4-2.76)	6.60±0.208 (5.44-10.1)
WA-507, FMNH 204316	15D	8.27±0.118 (7.45-9.05)	14.20±0.207 (12.75-15.45)	0.583±0.007 (0.548-0.627)	4 3/8+ (4 1/4+-4 5/8)	2.21±0.096 (1.65-2.8)	6.57±0.246 (5.19-8.55)
Western Australia							
Weebubbie Cave, 14.IX.65, WAM	7D	7.51±0.199 (6.6-8.1)	13.68±0.063 (13.4-13.85)	0.549±0.014 (0.478-0.585)	4 1/4 (4+-4 1/2–)	2.37±0.089 (2.0-2.6)	5.82±0.236 (5.15-6.83)
WA-499, Weebubbie Cave, FMNH 204254	9L	6.87±0.127 (6.3-7.4)	12.98±0.181 (12.2-13.65)	0.530±0.010 (0.488-0.589)	4+ (3 7/8–-4 1/4+)	2.35±0.054 (2.0-2.55)	5.54±0.11 (5.14-6.26)
WA-499, FMNH 204250	27D	6.86±0.071 (6.2-7.7)	12.71±0.131 (11.4-14.3)	0.540±0.004 (0.497-0.591)	4 1/8– (3 7/8+-4 1/4–)	2.32±0.038 (1.85-2.7)	5.16±0.102 (4.54-7.2)
WA-502, Kutowalla doline, FMNH 204270	21L	7.66±0.129 (6.75-8.8)	13.3±0.153 (12.3-14.9)	0.576±0.007 (0.496-0.651)	4 1/8+ (3 7/8+-4 1/4+)	2.17±0.057 (1.75-2.8)	6.21±0.164 (4.81-7.53)
WA-502, FMNH 204271	22D	7.64±0.154 (6.55-8.95)	13.22±0.132 (12.05-14.1)	0.578±0.024 (0.495-0.687)	4 1/4 (4+-4 1/2)	2.23±0.054 (1.8-2.65)	5.99±0.124 (4.96-7.19)
WA-503, Winbirra Cave (N-45), FMNH 204282	10L	6.69±0.118 (6.05-7.15)	12.44±0.165 (11.55-13.4)	0.538±0.011 (0.496-0.612)	4+ (3 3/4+-4 1/4+)	2.19±0.093 (1.6-2.5)	5.76±0.237 (4.79-7.13)
WA-503, FMNH 204283	34D	6.58±0.088 (5.3-7.6)	12.17±0.157 (10.4-14.5)	0.541±0.006 (0.489-0.608)	4 (3 3/4+-4 3/8+)	2.07±0.056 (1.55-2.95)	5.98±0.125 (4.60-7.44)
WA-501, Abrakurrie Cave, FMNH 204266	20L	7.52±0.095 (6.8-8.45)	12.82±0.154 (11.6-14.8)	0.587±0.008 (0.520-0.648)	4 1/4– (4 1/8–-4 5/8–)	2.10±0.070 (1.6-2.8)	6.21±0.184 (4.66-2.74)

Table 134: Local variation in *Pleuroxia polypleura* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
WA-501, FMNH 204267	12D	7.71±0.131 (7.05-8.5)	13.12±0.240 (11.75-14.7)	0.588±0.007 (0.559-0.635)	4¼– (4⅛–-4¼+)	1.94±0.057 (1.6-2.35)	6.81±0.171 (5.65-7.58)
WA-500, Chowilla (N-17), FMNH 204258	29L	7.38±0.115 (6.25-8.75)	13.06±0.138 (11.95-15.15)	0.565±0.006 (0.485-0.628)	4⅛+ (3⅞+-4⅜+)	2.11±0.052 (1.65-2.65)	6.29±0.153 (4.81-7.86)
WA-500, FMNH 204259	28D	7.79±0.086 (6.9-8.6)	13.65±0.132 (12.3-15.6)	0.571±0.005 (0.511-0.630)	4⅛+ (4+-4⅜–)	2.19±0.056 (1.45-2.85)	6.34±0.149 (5.01-8.85)
75km S of Forrest, NMV	9D	8.60±0.288 (7.4-10.2)	15.40±0.306 (13.7-16.5)	0.557±0.010 (0.530-0.619)	4¼– (4–-4⅜+)	2.30±0.122 (1.8-2.9)	6.81±0.314 (5.32-7.89)
WA-532, Old Homestead Cave (N-83), FMNH 204448	23L	7.65±0.101 (6.75-8.9)	13.59±0.093 (12.85-14.4)	0.563±0.006 (0.522-0.649)	4⅛ (4+-4¼–)	2.14±0.045 (1.5-2.6)	6.41±0.143 (5.50-8.53)
WA-532, FMNH 204449	7D	7.72±0.138 (7.25-8.35)	14.16±0.169 (13.55-14.95)	0.546±0.008 (0.502-0.564)	4⅛+ (4+-4¼+)	2.30±0.092 (2.0-2.75)	6.22±0.254 (5.10-7.15)
WA-529, Forrest Road, FMNH 204437	35D	9.03±0.113 (7.4-10.15)	15.23±0.134 (14.05-17.6)	0.593±0.005 (0.527-0.671)	4⅜– (4+4⅝+)	2.78±0.053 (2.1-3.55)	5.53±0.098 (4.50-6.74)
WA-494, Madura, 6mi S (N-62), FMNH 204204	43L	6.91±0.065 (6.05-7.85)	12.53±0.005 (11.65-13.85)	0.552±0.005 (0.481-0.653)	4⅛ (3⅞–-4⅜+)	2.21±0.033 (1.75-2.8)	5.73±0.089 (4.32-7.28)
WA-494, FMNH 204205	19D	7.37±0.131 (6.45-8.65)	12.87±0.157 (12.0-14.25)	0.572±0.006 (0.528-0.616)	4⅛+ (4+-4¼+)	1.94±0.071 (1.2-2.4)	6.83±0.317 (5.14-10.9)
Madura, 8 mile N, 2.XI.66, WAM 284.74	20D	8.76±0.123 (7.75-10.0)	14.67±0.216 (12.8-16.5)	0.598±0.006 (0.532-0.638)	4¼ (4⅛–-4⅜+)	1.92±0.056 (1.45-2.5)	7.74±0.204 (6.17-9.44)
Mullamullang Cave, VIII.66, WAM 272.74	9D	7.95±0.261 (6.8-8.95)	14.79±0.202 (13.95-15.95)	0.537±0.015 (0.477-0.594)	4⅜– (4¼–-4⅝–)	2.69±0.123 (2.2-3.35)	5.58±0.252 (4.77-6.94)
Mullamullang doline, 19.V.78, WAM 1159.81	10D	9.11±0.105 (8.3-9.5)	15.03±0.169 (14.3-16.0)	0.607±0.008 (0.559-0.636)	4⅜– (4+-4⅝)	1.91±0.064 (1.65-2.25)	7.96±0.260 (6.68-9.21)

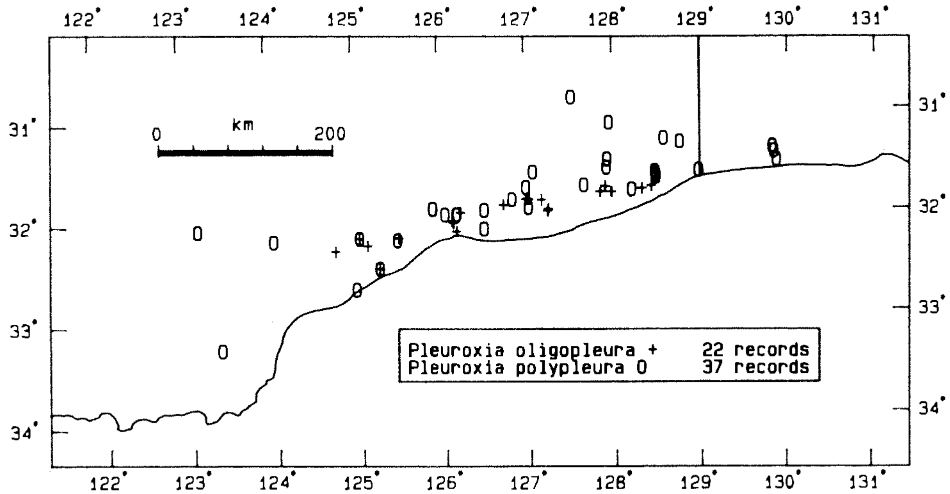
Table 134: Local variation in *Pleuroxia polypleura* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
WA-492, Moonera Tank Cave (N-53), FMNH 204189	58L	9.36±0.070 (8.15-10.5)	15.55±0.094 (14.15-17.35)	0.603±0.004 (0.542-0.661)	$4\frac{3}{8}$− ($4\frac{1}{8}$−$4\frac{5}{8}$+)	2.00±0.037 (1.5-2.6)	7.92±0.142 (6.20-10.6)
Cocklebiddy Cave, 4.XI.68, WAM 272.74	12D	9.40±0.162 (8.45-10.3)	15.23±0.172 (14.45-16.3)	0.618±0.008 (0.578-0.660)	$4\frac{3}{8}$− ($4\frac{1}{4}$−$4\frac{1}{2}$−)	2.06±0.073 (1.65-2.65)	7.47±0.188 (6.17-8.77)
WA-491, N-91 Cave, FMNH 204182	69L	8.96±0.072 (7.65-10.8)	14.96±0.090 (13.65-18.15)	0.599±0.004 (0.524-0.684)	$4\frac{3}{8}$− (4+-$4\frac{3}{4}$−)	2.14±0.031 (1.6-2.6)	7.08±0.100 (5.6-8.93)
WA-491, FMNH 204183	16D	9.13±0.119 (8.25-9.75)	15.33±0.162 (14.25-16.75)	0.595±0.006 (0.546-0.625)	$4\frac{3}{8}$− (4+-$4\frac{5}{8}$+)	2.14±0.065 (1.7-2.6)	7.26±0.197 (5.82-8.48)
WA-490A, Cocklebiddy Cave, FMNH 204175	37L	9.90±0.076 (8.8-10.7)	16.15±0.100 (15.1-17.3)	0.613±0.005 (0.548-0.692)	$4\frac{3}{8}$− ($4\frac{1}{8}$+-$4\frac{5}{8}$+)	2.09±0.043 (1.65-2.8)	7.83±0.140 (5.74-9.41)
WA-490A, upper S rim, FMNH 204174	63D	9.88±0.074 (8.6-11.15)	15.98±0.094 (14.35-17.7)	0.618±0.003 (0.563-0.668)	$4\frac{3}{8}$+ ($4\frac{1}{8}$+-$4\frac{3}{4}$−)	2.06±0.026 (1.55-2.55)	7.83±0.098 (6.10-9.81)
WA-490B, W side, FMNH 204180	14L	9.56±0.155 (8.6-10.55)	15.90±0.140 (14.8-16.6)	0.601±0.008 (0.552-0.675)	$4\frac{3}{8}$ ($4\frac{1}{4}$−$4\frac{5}{8}$+)	2.10±0.064 (1.5-2.5)	7.68±0.239 (6.53-10.3)
WA-490B, FMNH 204176	36D	9.91±0.092 (8.9-11.1)	16.13±0.128 (14.65-17.85)	0.615±0.005 (0.572-0.701)	$4\frac{3}{8}$ ($4\frac{1}{8}$+-$4\frac{5}{8}$+)	2.05±0.037 (1.7-2.6)	7.92±0.126 (6.34-9.50)
WA-490C, mouth of, FMNH 204181	16L	10.08±0.089 (9.55-10.7)	16.39±0.156 (14.9-17.4)	0.616±0.008 (0.562-0.689)	$4\frac{3}{8}$− ($4\frac{1}{4}$−$4\frac{1}{2}$−)	2.08±0.045 (1.75-2.3)	7.91±0.134 (7.22-8.97)
WA-489, 5.9km E of Caiguna FMNH 204170	35D	8.25±0.095 (7.2-9.85)	14.46±0.117 (13.35-15.9)	0.570±0.005 (0.505-0.629)	$4\frac{3}{8}$− ($3\frac{1}{2}$+-$4\frac{5}{8}$−)	2.34±0.040 (1.55-2.85)	6.25±0.212 (5.08-9.02)
WA-489, FMNH 204171	13	8.34±0.114 (7.65-8.9)	14.62±0.177 (13.8-15.95)	0.571±0.009 (0.535-0.640)	$4\frac{3}{8}$ ($4\frac{1}{4}$−$4\frac{5}{8}$−)	2.20±0.115 (1.45-3.0)	6.86±0.351 (5.09-9.92)
WA-488, John Eyre Motel, FMNH 204157	14D	8.02±0.110 (7.1-9.05)	14.19±0.204 (12.9-15.55)	0.566±0.007 (0.524-0.608)	$4\frac{3}{8}$− ($4\frac{1}{8}$+-$4\frac{5}{8}$−)	2.30±0.088 (2.0-3.15)	6.25±0.176 (4.92-7.07)

Diagnosis

Shell variable in size, diameter 10.4–18.50 mm (mean 14.44 mm), with 3 1/2+ to 5– (mean 4 1/4+) normally coiled whorls. Apex and spire usually moderately elevated (**Figs 372Ab, 372Be**), shell height 5.3–11.30 mm (mean 8.45 mm), H/D ratio 0.477–0.701 (mean 0.584). Body whorl rounded, sometimes with slight lateral compression below periphery. Shell apex (**Plate 178a**) nearly smooth, retaining traces of weak elongated pustules and ridgelets. Spire and body whorl (**Figs 372Aa–c, 372Bd–f, Plate 178b**) with low, prominent radial ribs, variable in spacing among populations, sometimes anastomosing. Microsculpture (**Plate 178b–c**) of fine setae arising from often angled bases. Umbilicus (**Figs 372Ac, 372Bf**) open, last whorl decoiling only slightly more rapidly, partly narrowed by reflexion of columellar lip, width 1.2–3.55 mm (mean 2.17 mm), D/U ratio 4.32–10.9 (mean 6.71). Body whorl usually moderately descending behind aperture. Basal and palatal lips narrowly reflected, thin, columellar lip more expanded. Parietal wall with at most a thin callus, never thickened or free. Colour light brownish, darker on spire, rib tops whitened by erosion, shell base lighter. Based on 906 measured adults.

Genitalia (**Figs 373a–f**) with apical portions typical. Head of spermatheca (S) extending past midpoint of prostate-uterus, lower part of latter wrapped around spermathecal shaft. Free oviduct (UV) usually short. Vagina (V) highly variable in length, usually fairly slender. Vas deferens (VD) slender, merging with small epiphallic caecum (EC) laterally. Epiphallus (E) rather long, extending usually to or below midpoint of penis, entering penis sheath (PS) part way to apex. Penis sheath with relatively thick walls. Penis (P) variable in length (3.6–6.8 mm) and shape, from short and globose (rarely) (**Fig. 373d**) to very long (**Figs 373b–c**), internally (**Fig. 373b**) with massive pilasters.



Map 23: Comparative distribution of *Pleuroxia oligopleura* and *P. polypleura*.

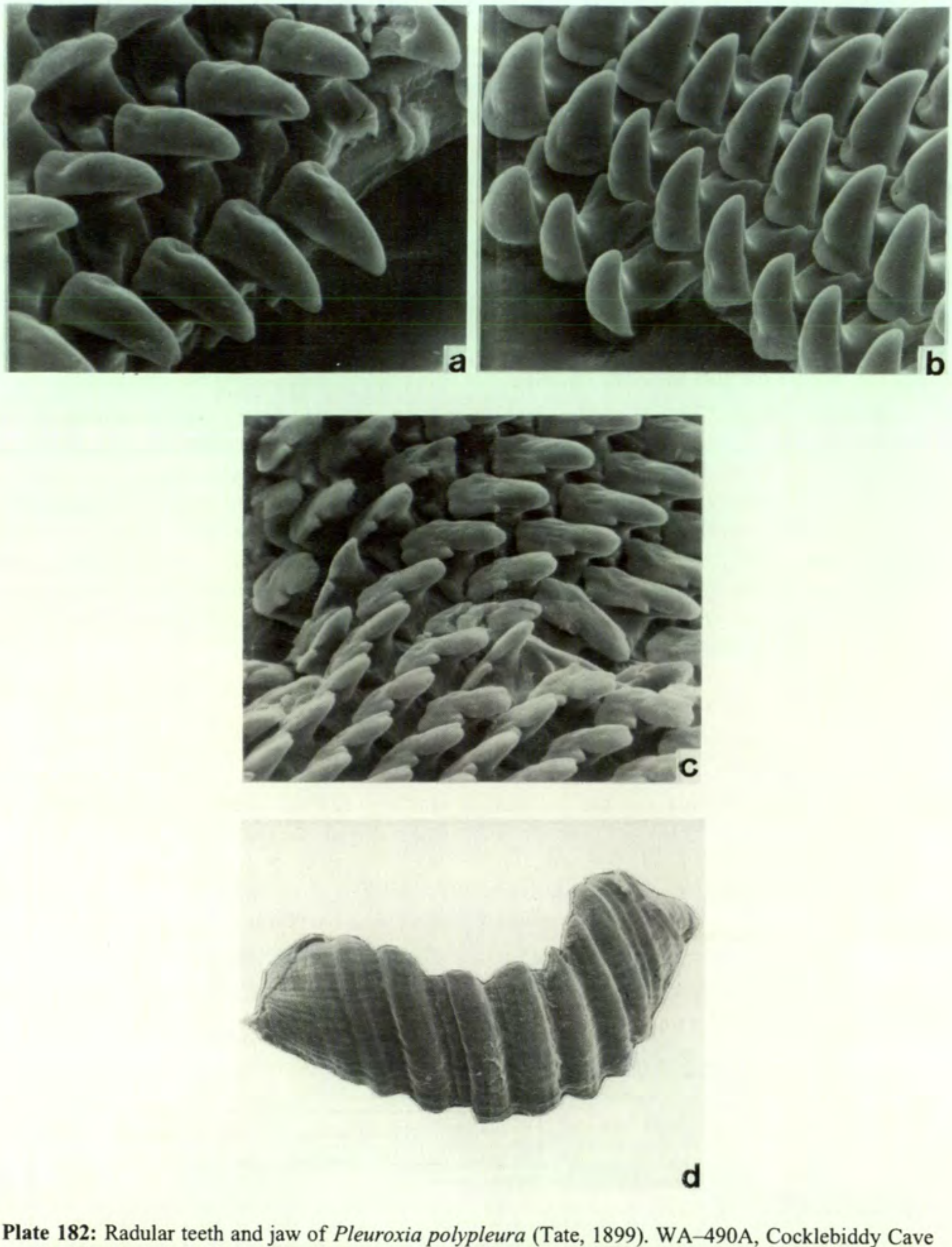


Plate 182: Radular teeth and jaw of *Pleuroxia polypleura* (Tate, 1899). WA–490A, Cocklebiddy Cave (6N48), Nullarbor, WA. 4 June 1979. FMNH 204175: (a–c) Dissection C. a is slightly worn central and early laterals at 640X. b is anterior view of unworn central and early laterals at 530X. c is latero-marginal transition at 495X; (d) Dissection A. d is jaw at 51X.

Central teeth of radula (**Plate 182a–b**) without ectocones, basal ridges massive, cusp tip curved and bluntly rounded. Early lateral teeth (**Plate 182a–b**) with at most weak ectocone, anterior flare small, cusp tip curved and bluntly rounded. Lateromarginal transition (**Plate 182c**) abrupt, ectoconal prominence developing on late laterals. Jaw (**Plate 182d**) with few broad vertical ribs that are reduced on side margins.

Discussion

Just as *Pleuroxia oligopleura* (Tate, 1894) from the Nullarbor and *P. cyrtopleura* (Pfeiffer, 1862) from the Flinders Ranges are morphologically equivalent, *P. polypleura* (Tate, 1899) (**Figs 372Aa-c, 372Bd–f**) and *P. phillipsiana* (Angas, 1873) from the Flinders Ranges (Solem 1992: figs 72a–c) share a higher spire, more crowded sculpture, narrower umbilicus and wider geographic range than the other pair of species. The reasons for these parallel developments are unknown.

Pleuroxia polypleura often is locally abundant and variation in a number of samples is summarised in **Table 134**. Larger sized populations, averaging more than 14.4 mm in diameter and more than 4 3/8 whorls, are found inland of Mundrabilla on the Forrest track, and then from 8 miles N of Madura through Cocklebiddy Cave (WA–490A–C) and 6N91 (WA–491) Cave. These populations also tend to have relatively narrow umbilici and high spires. There are two exceptions. The inland population at Old Homestead Cave (6N83, WA–532) on the Forrest-Mundrabilla Homestead track has slightly reduced mean diameters (13.59 and 14.16 mm, whorl count 4 1/8 to 4 1/8+) and shells from Madura Cave (6N62, WA–494) are very small in size (mean diameters 12.53 and 12.87 mm, whorl count 4 1/8 and 4 1/8+). Only the Winbirra Cave (6N45, WA–503) specimens average smaller in size than the latter. The inland population along the Forrest track is from a highly exposed site and the local occurrence of smaller sized adults does not surprise me. I have no explanation as to why the Madura Cave examples should be smaller.

The areas around Koonalda, SA and then near Eucla, WA and NW above the Hampton Scarp, are inhabited by smaller individuals with mean diameters 12.17–14.26 mm and 4 to 4 3/8+ mean whorl counts. These specimens also tend to be slightly more widely umbilicated and with somewhat reduced H/D ratios (**Table 134**). They thus approach *P. oligopleura* in appearance.

The few samples from near Caiguna (WA–488, WA–499) are intermediate in size (mean diameter 14.19–14.62 mm, whorl count 4 3/8– or 4 3/8), with slightly lower spires (mean H/D ratios 0.566–0.571), more open umbilici (mean D/U ratios 6.25–6.86), and more widely spaced sculpture than the Cocklebiddy examples (**Table 134**). None of these specimens was collected alive. They were found either dead on the ground (WA–488) or inside large tree stumps (WA–489). It is possible that they may be a different species, but until live collected material is available for dissection, they are best placed in *P. polypleura*.

There is an interesting difference between the two size groupings in regard to allochronic variation. With only two exceptions, all of the populations with larger sized shells have the mean diameter of dead adults significantly larger (difference between means is greater than the sum of the two standard errors) than those of live adults collected in 1979. On the upper S rim of Cocklebiddy Cave (WA–490A,

Table 134), the LIVE adults are 0.17 mm larger but the sum of the standard errors is 0.194 mm. Specimens from partway down the doline on the W side of Cocklebiddy Cave (WA–490B, **Table 134**) have the live adults a bit larger in diameter, 0.23 mm, with the sum of standard errors being 0.268.

The populations with smaller mean shell diameters tend to have LIVE adults somewhat larger (**Table 134**). At Weebubbie Cave (WA–499) the difference is 0.27 mm (sum of standard errors 0.312); and at Winbirra Cave (6N45, WA–503) the difference is 0.27 mm (sum of standard errors 0.322). At both Giants Head Doline (5N178, WA–507) in SA and Kutowalla Doline (6N83, WA–502) in WA, the means are essentially identical. Only at Abrakurrie Cave (WA–501) in WA do the DEAD adults average slightly, but not significantly, larger (mean difference 0.30 mm, sum of standard errors 0.394). At Old Homestead Cave (WA–532), the northernmost locality, where shell size is reduced, the dead adults are significantly larger (mean difference 0.57 mm, sum of standard errors 0.262) and at Madura Cave (6N62, WA–494), the dead adults are significantly larger (mean difference 0.34 mm, sum of standard errors 0.162).

Specimens were dissected from a number of populations (WA–507–8, WA–499, WA–500–3, WA–532, WA–494, WA–492, WA–491 and WA–490A) between Koonalda, SA and Cocklebiddy Cave in WA to see if there are differences in the genitalia paralleling those found in *Pleuroxia oligopleura* (Tate, 1894). As shown in Fig. 373a–f, the penis (P) and vagina (V) are generally long but can be short and globose (**Fig. 373d**) and thus approximate the condition seen in *P. oligopleura* (**Figs 376a–d**). A more dependable difference is the pattern of the lower portion of the prostate-uterus wrapping around the spermathecal shaft (S) in *P. polypleura*, whereas this rarely occurs in any examples of *P. oligopleura* (**Figs 376a–d**). Penis length in all dissected material ranged from 3.8–8.25 mm (mean 5.3 mm).

The identity of the type specimen is uncertain. It and the "Nullarbor Plains" cotypes are bleached "bones" and the sculpture could be interpreted as being either that of *P. elfina* or *P. polypleura*. It may well be that Tate had a mixture of the two species before him and used examples of *polypleura* for the base and side views (Tate 1899: pl. VI, figs 2a, 2b) and an example of *P. elfina* for the top view (Tate *ibid.*, pl. VI, fig. 2c). The lectotype is large for most *polypleura* populations, but the original base and side view illustrations are of this species. I follow a conservative course and use the name in its traditional sense.

Despite the initial confusion between *Pleuroxia polypleura* and the Flinders Range *Pleuroxia cyrtopleura* (Pfeiffer, 1862), there is only one named synonym. *Pleuroxia commenta* Iredale, 1939, from the Hampton Tablelands of WA (**Figs 372Bd–f**), is based on a specimen from one of the smaller-in-diameter populations discussed above, while the Bunda Plateau type lot examples of *P. polypleura* agree better with the larger-in-diameter populations. Since the smaller shells occur in the middle of the species range and there are no sculptural or genital differences between these size groups *commenta* is considered to be a subjective synonym. *Pleuroxia elfina* Iredale, 1939 originally was described as a subspecies of *polypleura*, based on very worn and bleached specimens. It differs in sculpture, shell proportions and anatomy and thus has been treated above as a full species.

PLEUROXIA OLIGOPLEURA (TATE, 1894)

(Plates 178d–f, 181a–f; Figs 374a–f, 375a–c, 376a–d; Maps 21, 2)

Hadra oligopleura Tate, 1894, *Trans. Roy. Soc. South Austr.*, **18:** 193 – Eyre's Sandpatch, 160 miles west from Eucla, Western Australia.

Angasella oligopleura (Tate), Tate 1896, *Rep. Horn Sci. Exped. Cent. Austr., Zool.*, p. 219, pl. XIX, figs 29a–b – Flinders Ranges, South Australia (transposition of locality with that of *Sinumelon wilpenensis* [Tate, 1894], figs 28a–b); Ludbrook 1978, *Geol. Survey of Western Aust., Bull.*, **125:** 194–195 – Roe Plains (nomenclatural notes).

Angasella lemani Gude, 1916, *Proc. malac. Soc. London*, **12** (1): 41–42, 3 figs – Cape Borda, Kangaroo Island, South Australia (error).

Pleuroxia oligopleura (Tate), Iredale 1937, *South Austr. Nat.*, **18** (2): 48–49; Iredale 1938, *Austr. Zool.*, **9** (2): 106; Iredale, 1939 *Jour. Roy. Soc. Western Austr.*, **25:** 56, pl. III, fig. 28; also published as Burch 1976, *Jour. malac. Soc. Austr.*, **3** (3): 136; Richardson 1985, *Tryonia*, 12: 254.

Pleuroxia lemani (Gude), Iredale 1937, *South Austr. Nat.*, **18** (2): 49; Iredale 1938, *Austr. Zool.*, **9** (2): 107; Richardson 1985, *Tryonia*, **12**: 253.

Pleuroxia oligopleura numba Iredale, 1939, *Jour. Roy. Soc. Western Austr.*, **25:** 56 – Cardanumbi, west of Eyre, Western Australia; also published as Richardson 1985, *Tryonia*, **12:** 254.

Comparative remarks

Pleuroxia oligopleura (Tate, 1894), known from the Hampton Tableland W of Eucla to about 34 km W of Caiguna, WA (**Maps 21, 23**)has a very low spire (**Figs 374b, e, 375b**), wider umbilicus (**Figs 374c, f, 375c**), very strong and comparatively widely spaced radial ribbing (**Plate 178d–e, Figs 374, 375**) and slightly larger size (**Table 132**) when compared with *P. polypleura* (Tate, 1899) (see **Figs 372Aa–c, 372Bd–f, Plate 178a–b**). *P. abstans* Iredale, 1939, from the Murchison River mouth on the W coast, WA (**Map 20**), has a broadly reflected lip, much wider umbilicus, more crowded radial sculpture (**Figs 368Aa–c**) and is much smaller (**Table 132**). *P. bethana* sp. nov., from the Geraldton–Mullewa area near the W coast, WA (**Map 20**), has crowded radial ribbing, globose shape, a narrow umbilicus and only columellar lip reflection (**Figs 368Bd–f, Plate 177a–b**). *P. elfina* Iredale, 1939, from near Newman Rock to Nullarbor, SA (**Maps 20–22**), has greatly reduced radial ribbing present only on the lower spire and body whorl (**Plate 177d–e**), a higher spire, often similar umbilicus but only weak lip reflection (**Figs 370Aa–c, 370Bd–f**). Anatomically (**Figs 376a–d**), the massive and complex penial chamber pilasters immediately separate *P. oligopleura* from *P. elfina* (**Figs 371a–b**), the other Nullarbor species that normally has a globose penis. *P. polypleura* (**Figs 373a–d**) usually is immediately separable by its long penis (P).

Holotypes

Hadra oligopleura Tate, 1894. SAM D13606. Eyre's Sand Patch, 160 miles W of

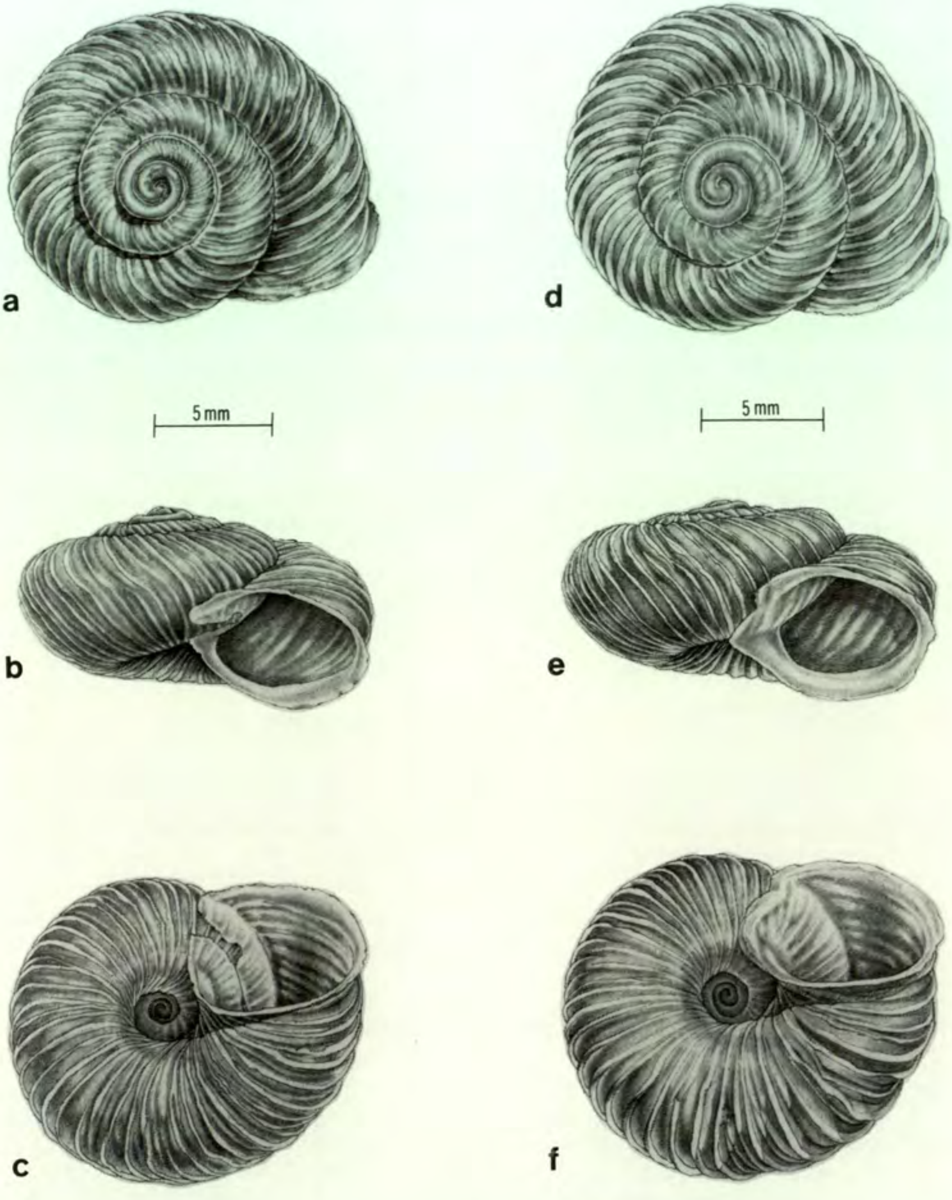


Fig. 374: Shells of *Pleuroxia oligopleura* (Tate, 1894): (a–c) Eyre's Sand Patch, 160 miles W of Eucla, WA. Paratype of *Helix oligopleura* Tate, 1894, AM C.4364; (d–f) 70 mile tank, E of Balladonia, Nullarbor, WA, Paratype of *Pleuroxia oligopleura numba* Iredale, 1939. AM C.64846. Scale lines equal 10 mm. Drawings by Linnea Lahlum.

Eucla, Western Australia. Height of shell 8.45 mm, diameter 14.8 mm, H/D ratio 0.571, whorls 4 1/4+, umbilical width 2.9 mm, D/U ratio 5.10.

Angasella lemani Gude, 1916. National Museum of Wales 77.34. Cape Borda, Kangaroo Island, South Australia. Height of shell 9.75 mm, diameter 15.5 mm, H/D ratio 0.629, whorls 4 5/8, umbilical width 2.45 mm, D/U ratio 6.33.

Pleuroxia oligopleura numba Iredale, 1939. WAM 8881. Cardanumbi (Rock Hole), W of Caiguna, Western Australia. 32°17'S, 125°36'E. Height of shell 9.55 mm, diameter 17.4 mm, H/D ratio 0.549, whorls 4 5/8+, umbilical width 2.8 mm, D/U ratio 6.21.

Paratopotypes

Hadra oligopleura Tate, 1894. SAM D15541, AM C.4364, AM C.64843, 6 DA, 1 DJ from the type locality.

Pleuroxia oligopleura numba Iredale, 1939. AM C.64687, 2 DA from the type locality.

Paratypes

Pleuroxia oligopleura numba Iredale, 1939. AM C.64846, 2 DA from 70 Mile Tank, E of Balladonia, Western Australia.

Material studied

WESTERN AUSTRALIA: W of Eucla (WA–526, halfway up scarp, W of Knousley Tank, NE of Hearder Tower, WAM 249.84, WAM 250.84, AM, FMNH 204419–21, 53 LA, 7 DA, 17 LJ, 2 DJ); W of Yakcoorga Rock Hole, E of Mundrabilla (WA–525, scarp base, WAM 251.84, WAM 252.84, AM, FMNH 204410–1, 20 LA, 34 DA, 5 LJ, 13 DJ); 40 miles W of Eucla (8 September 1965, WAM, 5 DA, 1 DJ); gully behind Mundrabilla microwave tower (WA–497, WAM 253.84, WAM 254.84, AM, FMNH 204221, FMNH 204225, 30 LA, 41 DA, 13 LJ, 11 DJ); Forrest track from Mundrabilla Homestead, 9.8 km N of scarp edge (WA–534, WAM 255.84, AM, FMNH 204454, 43 DA, 44 DJ); base of scarp, gully above Mundrabilla Homestead (WA–535, WAM 256.84, WAM 257.84, AM, FMNH 204462–3, 10 LA, 25 DA, 19 LJ, 13 DJ); 10.2 km S of Eyre Highway, E of Madura, Roe Plains (WA–496, WA–536, FMNH 204216, FMNH 204469, 1 DA, 1 DJ); Moodini Pass, E of Madura (WA–537, WAM 258.84, WAM 259.84, AM, FMNH 204476–7, 56 LA, 9 DA, 21 LJ, 3 DJ); Hampton Scarp, 16 miles E of Madura (30 October 1966, WAM 143.68, 5 DA); 1.5 miles E of bend from Pass, Madura (10 May 1966, WAM 269.74, 1 DA); Madura Pass (30 October 1966, WAM 141.68, WAM 362.74, 28 LA, 5 DA, 5 DJ); Hampton Scarp behind Old Madura Hotel (1 October 1966, WAM, 4 DA); lower end Madura Pass (30 October 1966, WAM 362.74, 18 LA, 10 LJ); E side Madura Pass crest (WA–495, gully N of road, WAM 260.84, WAM 261.84, AM, FMNH 204209–10, 7 LA, 30 DA, 7 LJ, 11 DJ); above Madura Hotel (7 December 1971, AM C.91797, 10 LA, 15 LJ); Madura (MV F21944, 14 LA, 3 LJ); 8 miles E of Cocklebiddy (30 October 1966, WAM 311.74, 11 DA, 9 DJ); Cocklebiddy to Pannikin Plain Cave (6N49) (8 January 1972, AM C.95832, 15 LA, 8 LJ); Cocklebiddy Roadhouse (20 May 1978, WAM 1164.81, 4 DA, 2 DJ); 33.4 km W of John Eyre Motel, Caiguna (WA–539, WAM 262.84, WAM 263.84, AM, FMNH 204500–1, 14 LA, 5 DA, 22 LJ, 4 DJ); 41 miles W of Caiguna

(25 November 1969, WAM 323.74, 9 DA, 3 DJ); 96 miles E of Balladonia (MV F28284, 10 DA).

Range

Specimens referred here to *Pleuroxia oligopleura* (Tate, 1894) have been collected from approximately 66 km W of Caiguna (*ca.* 124°45'E) to just W of Knousely Tank (WA–526, 128°26'23"E), about 42.5 km W of Eucla, WA (**Maps 21, 23**). These colonies are about 355 km apart. A number of collecting stops have been made to the E without finding additional colonies, although populations referred to *P. elfina* Iredale, 1939 and *P. polypleura* (Tate, 1899) are common. The area W of Caiguna is not good snail habitat. Colonies in this area probably are scattered and small in size, but a range extension is probable. The northernmost locality, WA–534, Forrest Track above Mundrabilla, lies only a few km inland, whereas *P. polypleura* was taken much further N along the Forrest Track (WA–532, Old Homestead Cave, 6N83). The range of *P. oligopleura* is not continuous. The eastern limit, near Knousley Tank, is confirmed by extensive collecting from there to the WA border and into SA. It is common along the Hampton Scarp from W of Knousley Tank (WA–526) to Madura and then replaced from Madura W to Caiguna by *P. polypleura*. Near its western limit it is sympatric with *P. elfina* although with habitat differences.

Diagnosis

Shell fairly large, diameter 11.35–18.5 mm (mean 14.95 mm), with 3 3/4+ to 4 5/8+ (mean 4 1/4+) normally coiled whorls. Apex and spire at most slightly elevated (**Figs 374b, e, 375**b), shell height 5.15–11.4 mm (mean 7.65 mm), H/D ratio 0.404–0.675 (mean 0.510). Body whorl often compressed laterally below periphery, producing a strongly rounded and elevated periphery, rarely somewhat angulated in juveniles. Shell apex (**Plate 178d**) initially smooth, lower portion with irregular growth lines. Spire and body whorl (**Plate 178d–f, Figs 374–375**) with very prominent, often anastomosing radial ribs, microsculpture (**Plate 178e–f**) of crowded setae arising from seentially triangular bases. Umbilicus (**Figs 374c, f, 375c**) open, variable in width, last whorl decoiling more rapidly, partly closed by reflection of columellar lip, width 1.7–3.75 mm (mean 2.74 mm), D/U ratio 3.73–8.88 (mean 5.56). Body whorl slightly to moderately descending behind aperture. Basal and palatal lips reflected and thickened, columellar section more expanded (**Figs 374–375**). Parietal wall with callus of varying thickness, sometimes lip edge continuous but never free of wall. Colour on spire brownish, lighter on body whorls, ribs tending to white possibly by erosion, shell base lighter in tone. Based on 492 measured adults.

Genitalia (**Figs 376a–d**) with slightly enlarged albumen gland (GG), remaining apical and pallial organs typical. Spermatheca (S) with base greatly enlarged, narrowing abruptly to shaft wrapped around free oviduct (UV) and base of prostate–uterus, expanded head of spermatheca bound to mid-section of prostate-uterus by fibres. Free oviduct (UV) relatively short, slender, entering spermathecal-vaginal channel laterally. Vagina (V) short, swollen. Vas deferens (VD) slender, merging with small epiphallic caecum laterally. Epiphallus (E) short, entering very thin-walled penis sheath (PS) apically, receiving insertion of penial retractor muscle (PR) before entering penis (P) through comparatively small foliated pilasters (**Fig. 376b**). Penis sheath (PS) very thin-walled, appressed to penis walls. Penis variable in length from short and

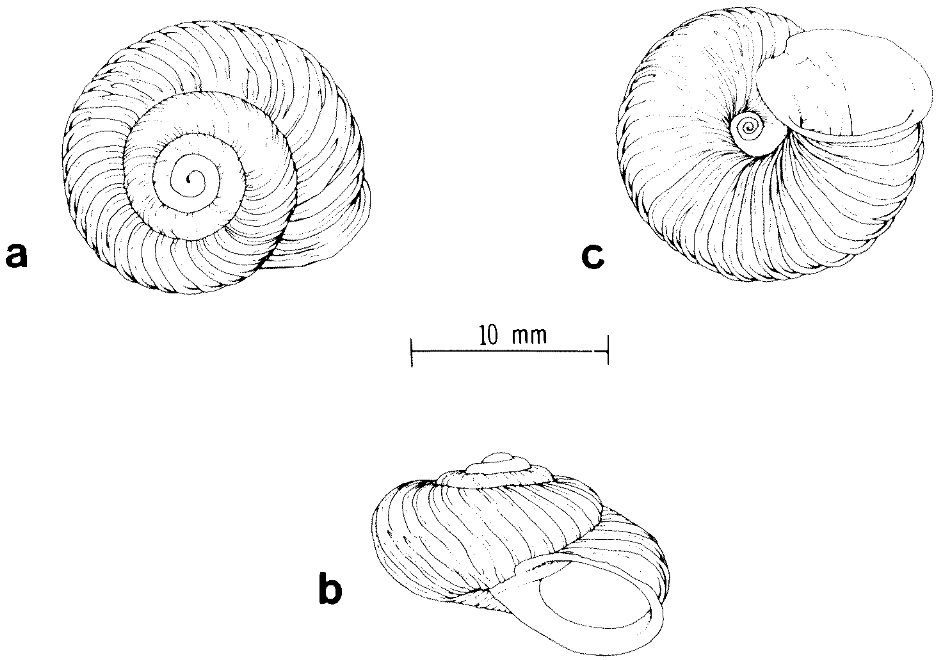


Fig. 375: Shell of *Pleuroxia oligopleura* (Tate, 1894): Cape Borda, Kangaroo Island, SA (error), Holotype of *Angasella lemani* Gude, 1916. National Museum of Wales 77.34, ex Tomlin collection. Scale line equals 10 mm. Drawings by Linnea Lahlum.

globular (3.9–4.6 mm long) to quite elongated (5.0–6.3 mm long), internally with massive pilasters on wall below entrance of epiphallus, with major pilasters confined to upper portion of elongated penes.

Central teeth of radula (**Plate 181b, d**) with at most a slight trace of ectocones, basal ridges massive, cusp tip slightly curved and bluntly rounded. Early lateral teeth (**Plate 181b, d**) with moderately variable anterior flair, curved and bluntly rounded cusp tips. Lateromarginal transition abrupt (**Plate 181c, e**), ectocone prominent on laterals well before transition. Early marginals (**Plate 181f**) with high endocone, slender ectocone tending to split. Outer marginals with cusps subequal, variable in splitting. Jaw (**Plate 181a**) with very narrow and crowded vertical ribs.

Discussion

Pleuroxia oligopleura is the exact counterpart of the Flinders Range *P. cyrtopleura* (Pfeiffer, 1862) in shell form and sculpture (compare **Figs 374–375** with Solem 1992: figs 71a–d), but the two species are very different in details of shell form and in genital anatomy (compare **Figs 376a–b** and Solem 1992: figs 74a–b). Both species are rock sealers and occur essentially within the ranges of, but not microsympatrically with, higher spired species with more crowded shell sculpture – *P. polypleura* (Tate, 1899) along the Eyre Highway (**Figs 372Aa–c, 372Bd–f**) and *P. phillipsiana* (Angas, 1873) in the Flinders Range (Solem 1992: figs 72a–c).

Table 135: Local variation in *Pleuroxia oligopleura.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
WA-526, W of Eucla, FMNH 204420	53L	8.00±0.064 (7.05-9.0)	15.37±0.088 (13.7-16.9)	0.521±0.004 (0.478-0.636)	$4\tfrac{3}{8}-$ ($4\tfrac{1}{8}+-4\tfrac{1}{2}+$)	2.59±0.040 (1.9-3.35)	6.00±0.087 (4.68-7.81)
WA-526, FMNH 204419	9D	8.37±0.141 (7.9-8.8)	15.51±0.213 (14.8-16.55)	0.540±0.011 (0.497-0.588)	$4\tfrac{3}{8}-$ ($4\tfrac{1}{8}+$ $-4\tfrac{3}{8}+$)	2.92±0.105 (2.55-3.4)	5.34±0.144 (4.87-5.91)
WA-525, Yakcoorga, FMNH 204411	20L	7.70±0.084 (7.15-8.25)	15.00±0.180 (13.3-16.7)	0.514±0.005 (0.476-0.551)	$4\tfrac{1}{2}$ ($4\tfrac{1}{4}--5\tfrac{5}{8}-$)	2.83±0.056 (2.45-3.2)	5.32±0.095 (4.73-6.55)
WA-525, FMNH 204410	34D	7.43±0.080 (6.7-8.9)	15.15±0.142 (13.9-16.9)	0.490±0.004 (0.455-0.551)	$4\tfrac{3}{8}-$ ($4\tfrac{1}{8}+-4\tfrac{1}{2}+$)	2.84±0.048 (2.1-3.5)	5.39±0.090 (4.23-7.13)
WA-497, Mundrabilla, FMNH 204221	30L	7.12±0.086 (6.2-8.25)	14.50±0.131 (13.25-15.75)	0.491±0.006 (0.444-0.581)	$4\tfrac{1}{4}$ ($4\tfrac{1}{8}--4\tfrac{3}{8}+$)	2.94±0.073 (2.15-3.75)	5.01±0.117 (4.00-6.44)
WA-497, FMNH 204225	41D	7.26±0.077 (6.25-8.2)	14.93±0.104 (13.75-16.8)	0.487±0.005 (0.413-0.577)	$4\tfrac{1}{4}$ ($3\tfrac{7}{8}+-4\tfrac{1}{2}-$)	2.92±0.057 (2.2-3.7)	5.18±0.094 (4.06-6.64)
WA-535, FMNH 204462	25D	7.66±0.108 (6.6-9.0)	15.09±0.122 (14.15-16.3)	0.508±0.006 (0.427-0.575)	$4\tfrac{3}{8}$ ($4\tfrac{1}{8}+-4\tfrac{5}{8}+$)	2.98±0.082 (1.7-3.55)	5.34±0.175 (4.36-8.59)
WA-535, Mundrabilla, FMNH 204463	10L	7.17±0.139 (6.3-7.7)	14.56±0.183 (13.8-15.55)	0.493±0.012 (0.404-0.532)	$4\tfrac{1}{4}$ ($4+-4\tfrac{1}{2}+$)	2.79±0.108 (2.3-3.35)	5.29±0.214 (4.39-6.37)
WA-534, Forrest track, FMNH 204454	43D	7.15±0.081 (5.9-8.3)	14.82±0.110 (13.3-16.6)	0.482±0.004 (0.410-0.543)	$4\tfrac{1}{8}+$ ($3\tfrac{3}{4}+-4\tfrac{1}{2}+$)	3.06±0.46 (2.5-3.6)	4.87±0.061 (4.19-5.96)
WA-537, Moodini Pass, FMNH 204477	56L	6.56±0.070 (5.15-7.9)	13.14±0.082 (12.05-14.3)	0.499±0.005 (0.428-0.584)	$4\tfrac{1}{8}+$ ($3\tfrac{3}{4}+-4\tfrac{1}{2}-$)	2.62±0.037 (2.0-3.25)	5.07±0.065 (4.15-6.80)
WA-537, FMNH 204476	9D	6.69±0.105 (6.25-7.2)	13.26±0.144 (12.35-13.9)	0.505±0.010 (0.470-0.549)	$4\tfrac{1}{8}+$ ($4+-4\tfrac{3}{8}$)	2.47±0.061 (2.3-2.85)	5.39±0.119 (4.62-5.77)

Table 135: Local variation in *Pleuroxia oligopleura* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Madura, MVF 21944	18L	6.76±0.116 (5.75-7.5)	13.37±0.173 (11.35-14.35)	0.506±0.007 (0.467-0.563)	$4\frac{1}{8}$+ ($3\frac{3}{4}$+-$4\frac{3}{8}$)	2.69±0.065 (2.25-3.2)	5.01±0.121 (4.44-6.12)
Madura Pass, 30.X.66 WAM 362.74	13L	7.88±0.158 (6.9-8.85)	15.45±0.170 (14.55-16.65)	0.510±0.010 (0.453-0.578)	$4\frac{1}{4}$+ ($4\frac{1}{4}$−-$4\frac{1}{2}$−)	2.72±0.129 (2.05-3.6)	5.83±0.268 (4.22-7.39)
WA-495, Madura Pass, FMNH 204209	7L	8.39±0.157 (7.95-9.15)	15.58±0.296 (14.5-16.55)	0.540±0.016 (0.486-0.597)	$4\frac{3}{8}$ ($4\frac{1}{4}$+$4\frac{5}{8}$−)	2.60±0.170 (2.0-3.3)	6.11±0.330 (4.99-7.58)
WA-495, FMNH 204210	30D	8.16±0.107 (7.15-9.45)	15.87±0.142 (14.6-17.65)	0.515±0.006 (0.436-0.582)	$4\frac{3}{8}$− ($4\frac{1}{8}$−-$4\frac{5}{8}$−)	2.68±0.066 (1.8-3.6)	6.03±0.141 (4.88-8.38)
Madura Hotel, AM C.91797	10L	7.78±0.127 (7.15-8.55)	15.65±0.218 (14.55-16.9)	0.498±0.009 (0.459-0.551)	$4\frac{3}{8}$ ($4\frac{1}{4}$+-$4\frac{1}{2}$+)	2.70±0.153 (1.75-3.6)	5.97±0.367 (4.36-8.88)
Cocklebiddy, 30.X.66, WAM 311.74	11D	9.29±0.207 (8.2-10.35)	16.32±0.230 (15.2-17.55)	0.569±0.009 (0.518-0.608)	$4\frac{3}{8}$+ ($4\frac{1}{4}$−-$4\frac{5}{8}$+)	2.42±0.095 (2.05-2.09)	6.85±0.290 (5.43-8.37)
Cocklebiddy, 8.I.72, AM C.95832	15L	9.23±0.336 (6.7-11.4)	15.58±0.294 (13.1-17.6)	0.590±0.014 (0.497-0.675)	$4\frac{3}{8}$+ ($4\frac{1}{4}$-$4\frac{1}{2}$)	2.27±0.086 (1.75-2.95)	7.01±0.309 (5.09-8.8)
WA-539, Caiguna, FMNH 204500	14L	9.39±0.128 (8.5-10.05)	17.01±0.173 (15.85-18.05)	0.553±0.008 (0.490-0.581)	$4\frac{3}{8}$ ($4\frac{1}{4}$+-$4\frac{1}{2}$+)	2.54±0.079 (2.0-3.3)	6.78±0.189 (5.30-7.94)
WA-539, Caiguna, FMNH 204501	5D	9.15±0.195 (8.8-9.85)	17.34±0.221 (16.7-17.85)	0.528±0.012 (0.491-0.554)	$4\frac{3}{8}$+ ($4\frac{1}{4}$+-$4\frac{3}{8}$+)	2.65±0.211 (2.1-3.4)	6.71±0.553 (5.02-8.47)
41 miles W of Caiguna, WAM 323.74	9D	9.82±0.119 (9.5-10.5)	17.34±0.199 (16.7-18.5)	0.567±0.008 (0.517-0.596)	$4\frac{1}{2}$− ($4\frac{3}{8}$−-$4\frac{1}{2}$+)	2.64±0.087 (2.25-3.1)	6.61±0.215 (5.49-7.61)

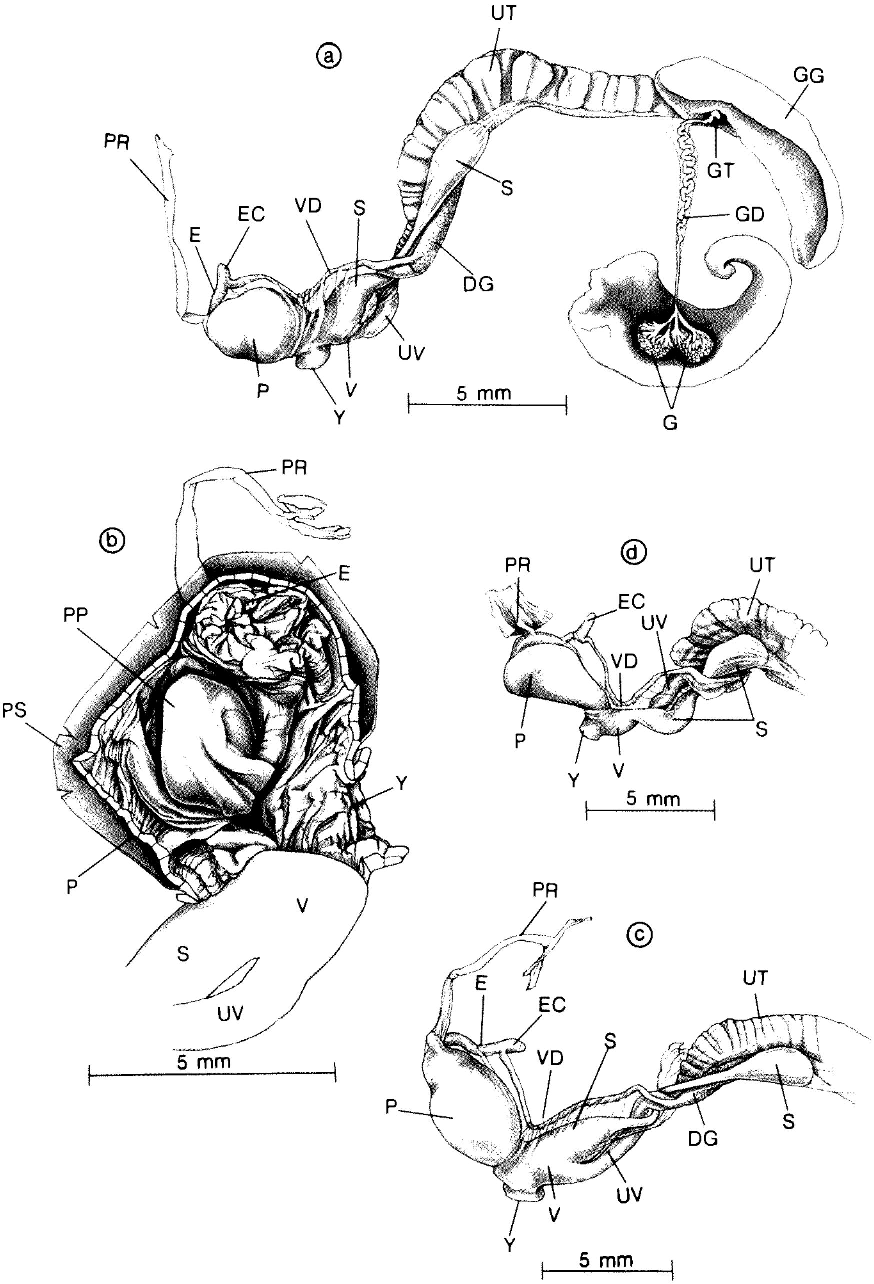


Fig. 376: Genitalia of *Pleuroxia oligopleura* (Tate, 1894): (a–b) WA–539, W of Caiguna, WA. 15 June 1979. FMNH 204500. (a) whole genitalia, Dissection C; (b) penis interior, Dissection B; (c) lower end Madura Pass, WA. 30 October 1966. WAM 362.74, Dissection B, terminal genitalia; (d) WA–526, Knousley Tank, W of Eucla, WA. 12 June 1979. FMNH 204420, Dissection A, terminal genitalia. Scale lines as marked. Drawings by Linnea Lahlum.

Shell variation is fairly extensive (**Table 135**) and has some geographic pattern. The eastern samples (WA–526, Knousley Tank and WA–525, Yakcoorga Rock Hole) are average in size and umbilical width. At both stations the dead adults are slightly but not significantly larger than the live adults. Material from Mundrabilla and the lower part of the Forrest Track (WA–497, WA–534, WA–535) average a little bit smaller in diameter and are a little more widely umbilicated but the most noticable change is that the difference between live and dead adults has increased, reaching statistical significance. The Moodini Pass examples are the smallest in size, with little difference between live and dead adults. The Madura samples come from a number of slightly different stations and were collected in several different years. As a result, it is not possible to assess the meaning of observed variation. Most of them are of medium size and somewhat more narrowly umbilicated, the exception being the unlocalised Madura set (MV F21944), the shells being small and widely umbilicated. Both Cocklebiddy samples are high-spired and narrowly umbilicated with some increase in shell diameter and whorl count. The largest shells were taken near Caiguna. They show almost significant size differences between live and dead adults, are rather narrowly umbilicated, but have a proportionately lower spire than is seen in the Cocklebiddy specimens.

Clearly additional collecting is needed. There are geographic changes in size and shell shape present, but not enough to warrant subspecific designations.

Specimens were dissected from a number of localities (WA–495, WA–497, WA–525–6, WA–535, WA–537, WA–539, and several sets from Madura Pass). Three figured examples indicate the variation: 1) W of Caiguna (WA–539, **Figs 376a–b**) the penes are long and with a slender lower portion; 2) intermediate length examples are from near Madura Pass (WAM 362.74, **Fig. 376c**); and 3) globose penes without a slender lower portion are found near Knousley Tank (WA–526, **Fig. 376d**) at the eastern range limit. The penis length varies from 3.9–6.3 mm long (mean 4.95 mm), but the internal pilaster pattern seems to remain basically the same. By far the longest penes (5.6–6.3 mm long) were found in specimens from near Mundrabilla (WA–535, WA–537). The pattern of variation, which is shared with *P. polypleura* (Tate, 1899), has been discussed above.

Label errors have resulted in a modest synonymy for this species. The initial illustrations (Tate, 1896: pl. XIX, figs 29a–b) carried the locality data for the Flinders Range *Sinumelon wilpenensis* (Tate, 1894), which was, in turn, credited incorrectly to Eyre's Sand Patch. This error was first corrected by Iredale (1937b: 49, 50). *Pleuroxia lemani* Gude, 1916 was based on a single shell from the Cox collection that had been mixed in with some *Glyptorhagada bordaensis* (Angas, 1880). On the basis of wear, apertural debris and shell details, it has been identified (Solem 1992) as a mislabelled type lot specimen of *P. oligopleura*. The subspecies, *Pleuroxia oligopleura numba* Iredale, 1939, is based on the large, high-spired examples found near Caiguna, whereas the type examples agree more closely with the Madura and Cocklebiddy specimens.

GENUS *SINUMELON* IREDALE, 1930
(+ *NOTOBADISTES* COTTON & GODFREY, 1932)

Sinumelon Iredale, 1930, *Victorian Nat.*, **47** (7): 120 – type species: *Helix nullarborica*

Tate, 1879; Iredale 1937, *South Austr. Nat.*, **18** (2): 40–46 – review of Red Centre and South Australian species; Iredale 1938, *Austr. Zool.*, **9** (2): 103–105 – check list of Australian species, description of some New South Wales taxa; Iredale 1939, *Jour. Roy. Soc. Western Austr.*, **25:** 52–54 – review and description of Western Australian species; Richardson 1985, *Tryonia*, **12:** 276–278 – check list of species; Solem 1992, *Rec. South Austr. Mus. Monograph Series, No.* **2:** 1–425 – monograph of taxa from southeastern South Australia; Solem 1993, *Rec. Western Austr. Mus., Suppl.*, **43:** 1067-1079 – monograph of Red Centre species.

Notobadistes Cotton & Godfrey, 1932, *South Austr. Nat.*, **13** (4): 171 – type species: *Helix bitaeniata* Cox, 1868.

Shell medium to very large in size, often variable, adult diameters 10–35 mm, whorl counts 3 3/4 to 6. Spire normally well elevated, lower in *S. jimberlanensis*. Apical sculpture with vestiges of weak radial ridglets to smooth (**Plate 184a**), lower spire and body whorl with radial ridglets of varying prominence (**Plates 183a–b, 184a, c–d**) and weak (**Plate 184b**) to very prominent micropustulations (**Plate 184d–e**). Spire and body whorl of *S. nullarboricum* (**Plate 183c–e**) with prominent malleations. Body whorl rounded, descending moderately *S. jimberlanensis*, *S. vagente*, *S. kalgum*, *S. nullarboricum*) to sharply (*S. tarcoolanum*) behind aperture. Umbilicus closed or a narrow lateral crack (*S. vagente*, *S. kalgum*, *S. tarcoolanum*), to generally narrowly open (*S. nullarboricum*, *S. jimberlanensis*). Columellar lip slightly expanded and reflected over umbilicus. Lip white, narrowly expanded except in *S. nullarboricum* (**Figs 377c–d**), usually thickened internally. Shell colour greenish yellow (*S. vagente*), yellow–brown *(S. jimberlanensis*), with a reddish suffusion to spiral red band (*S. tarcoolanum*), or usually white (*S. kalgum*, *S. nullarboricum*).

Live adults aestivate loose in litter under bushes, in rock rubble or crevices, with a flexible, uncalcified epiphragm.

Genitalia (**Figs 380a–b, 381a–b, 382a–d, 383a–b, 384a–b, 385**) typical of Sinumeloninae. Free oviduct (UV) and shaft of spermatheca (S) twisted around each other, head of spermatheca bound to lower portion of prostate-uterus. Vagina (V) very short (*S. jimberlanensis*, *S. nullarboricum*), medium (*S. tarcoolanum*, *S. kalgum*), or elongated (*S. vagente*). Free oviduct short (*S. jimberlanensis*, *S. kalgum*, *S. vagente*) or long (*S. tarcoolanum*, *S. nullarboricum*). Epiphallic caecum (EC) short, situated just before epiphallus (E) enters wall of penis sheath (PS). Epiphallus enclosed in wall of penis sheath for part of length, exiting near-apically and partly circling penial retractor muscle (PR) before entering apex of penis (P) through either foliated pilaster (*S. vagente* **Fig. 384b**, *S. kalgum* **Fig. 382b**) or simple continuation of epiphallic pilasters (*S. tarcoolanum* **Fig. 383b**, *S. nullarboricum* **Fig. 381c**, *S. jimberlanensis* **Fig. 380b**). Penial retractor muscle attached to epiphallus-penis junction. Penis sheath variable in wall thickness. Penis variable in size and shape, elongated and cylindrical in *S. nullarboricum* (**Fig. 381a**) and *S. vagente* (**Figs 384a, 385**), elongated and tapering in *tarcoolanum* (**Fig. 383a**), shorter and kinked within penis sheath in *S. kalgum* (**Fig. 382a, c**), nearly globose in *S. jimberlanensis* (**Fig. 380a**). Penis chamber wall sculpture varied. Main pilaster (PP) large and U-shaped with unequal arms (*S. vagente* **Fig. 384b**, *S. kalgum* **Fig. 382b**), large and with corrugated edge (*S. tarcoolanum* **Fig. 383b**), reduced and simple (*S. nullarboricum* **Fig. 381c**), or reduced to size of other ridges (*S. jimberlanensis* **Fig. 380b**). Accessory ridges and corrugated folds ranging from weak (*S. vagente* **Fig. 384b**) to very prominent (*S. jimberlanensis* **Fig. 380b**, *S. nullarboricum* **Fig. 381c**).

Table 136: Local variation in *Sinumelon.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
S. jimberlanensis	31	10.88 (8.2-14.55)	14.42 (12.05-17.4)	0.760 (0.608-0.839)	4¼+ (3⅞–4½+)	1.43 (0.7-2.3)	11.0 (6.15-23.4)
S. nullarboricum	908	13.79 (11.3-18.6)	17.00 (12.2-22.1)	0.852 (0.724-1.051)	4⅝+ (4¼+-5¼–)	1.42 (closed-2.85)	11.2 (6.84-closed)
S. kalgum	246	21.03 (14.95-25.8)	23.80 (17.35-27.75)	0.884 (0795-1.088)	5⅛+ (4⅛+-5⅝–)	0.37 (closed-2.1)	mostly closed
S. tarcoolanum	210	24.13 (18.75-28.2)	26.20 (20.45-31.05)	0.921 (0.807-1.052)	5⅜– (4¾+-5¾+)	0.54 (closed-3.6)	mostly closed
S. vagente	88	16.97 (13.3-22.8)	19.68 (16.55-24.65)	0.862 (0.774-1.005)	4¾ (4⅜+-5⅛+)	0.63 (closed-1.75)	mostly closed

Table 137: Local variation in *Sinumelon vagente*, *S. jimberlanensis* and *S. tarcoolanum*.

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
Sinumelon vagente							
Eduga River banks, E of Gullewa, WAM	8D	18.67±0.449 (16.1-19.85)	21.78±0.493 (19.6-23.7)	0.857±0.011 (0.821-0.903)	$4\frac{7}{8}+$ ($4\frac{3}{4}$-$5\frac{1}{8}$)	closed or crack	
Fields Find, WAM 374.74	12L	17.30±0.246 (15.75-18.7)	20.25±0.257 (18.25-21.6)	0.854±0.007 (0.818-0.902)	$4\frac{3}{4}$ ($4\frac{1}{2}$-5+)	closed or crack	
Fields Find, WAM 387.74	11L	16.10±0.272 (14.9-17.8)	18.43±0.231 (17.35-19.85)	0.873±0.007 (0.838-0.912)	$4\frac{5}{8}+$ ($4\frac{1}{2}-$-$5\frac{1}{8}-$)	closed or crack	
Fields Find, WAM	9D	16.96±0.261 (15.85-18.0)	19.22±0.348 (17.95-21.3)	0.883±0.011 (0.836-0.923)	$4\frac{3}{4}+$ ($4\frac{5}{8}$-$4\frac{7}{8}$)	closed or crack	
Rothsay Mine, Yalgoo Dist., WAM	14D	14.60±0.216 (13.3-16.0)	17.55±0.239 (16.55-19.2)	0.832±0.010 (0.774-0.906)	$4\frac{1}{2}+$ ($4\frac{3}{8}$-$4\frac{3}{4}$)	closed or crack	
Sinumelon jimberlanensis							
Western Australia							
WA-483, FMNH 204109	7L	10.33±0.119 (9.9-10.85)	13.59±0.275 (12.4-14.4)	0.761±0.012 (0.715-0.800)	$4\frac{3}{8}-$ ($4\frac{1}{4}-$-$4\frac{3}{8}+$)	1.55±0.124 (0.95-2.0)	9.18±0.953 (6.98-14.3)
WA-484, FMNH 204112	5D	11.29±0.351 (10.35-12.5)	15.60±0.350 (14.65-16.6)	0.724±0.018 (0.679-0.785)	$4\frac{3}{8}$ ($4\frac{1}{4}-$-$4\frac{1}{2}-$)	1.72±0.037 (1.65-1.8)	9.07±0.312 (8.32-10.1)
Sinumelon tarcoolanum							
South Australia							
E of Ooldea, NMV F28298	10D	25.78±0.315 (24.5-27.55)	27.84±0.249 (26.85-29.0)	0.926±0.012 (0.875-1.006)	$5\frac{1}{2}-$ ($5\frac{1}{4}+$-$5\frac{3}{4}$)	closed	
Yarrina Hill, SAM	5D	24.86±0.507 (23.4-26.1)	26.85±0.535 (25.8-28.8)	0.926±0.009 (0.906-0.956)	$5\frac{1}{2}-$ ($5\frac{1}{4}$-$5\frac{5}{8}$)	closed	
Wallinippie, NMV 3205	9D	24.19±0.358 (22.8-26.1)	25.61±0.286 (24.1-26.7)	0.946±0.019 (0.854-1.052)	$5\frac{1}{8}+$ (5–-$5\frac{3}{8}$)	closed	

Table 137: Local variation in *Sinumelon vagente*, *S. jimberlanensis* and *S. tarcoolanum* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Mt. Wallaby, FMNH 212617	19D	24.95±0.291 (21.7-26.9)	27.13±0.262 (24.2-28.7)	0.920±0.008 (0.838-0.972)	5½− (5¼+-5¾+)	closed	
Wallala Hill, Sta. 22, FMNH 212618	50D	24.66±0.144 (21.9-26.75)	26.15±0.106 (24.5-27.8)	0.943±0.004 (0.875-1.002)	5⅜	1.17±0.048	23.6±0.639
Wallala Hill, Sta. 22, FMNH 212622	9L	25.15±0.491 (23.5-28.1)	26.08±0.301 (25.0-27.4)	0.964±0.011 (0.924-1.036)	5⅜ (5⅛+-5½+)	1.09±0.061 (0.98-1.42)	24.5±1.230 (18.0-27.4)
Yarlbrinda Hill, FWA 2956	9D	24.24±0.423 (22.4-26.3)	26.70±0.397 (25.45-28.6)	0.908±0.013 (0.858-0.988)	5⅜ (5¼−-5⅝−)	1.09±0.050 (1.0-1.38)	25.0±1.212 (18.58-28.6)
Lake Everard Station, FWA 2957	17D	24.51±0.236 (22.5-25.9)	26.58±0.213 (25.25-28.25)	0.922±0.010 (0.821-0.988)	5⅜ (5⅛+-5½+)	1.09±0.045 (1.0-1.74)	24.96±0.781 (15.15-28.3)
89 miles N of Cook, WAM	12D	21.80±0.353 (20.3-22.8)	24.54±0.268 (23.2-26.4)	0.888±0.011 (0.851-0.943)	5¼+ (5⅛−-5½)	closed	
N Nullarbor, near "The Dip", WAM 86.1397	11D	26.13±0.362 (23.9-28.2)	27.83±0.388 (26.7-31.05)	0.939±0.007 (0.893-0.974)	5⅜+ (5¼−-5⅝)	closed	
100 miles N of Cook, WAM	6D	23.43±0.343 (22.05-24.5)	25.93±0.507 (24.1-27.4)	0.904±0.011 (0.855-0.937)	5¼+ (5⅛-5⅜)	closed	
105 miles N of Cook, WAM	5D	23.59±0.428 (22.5-24.85)	26.15±0.541 (24.35-27.6)	0.902±0.009 (0.872-0.924)	5¼− (5+-5⅜−)	closed	
Western Australia							
Goddard's Creek, NW Cundeelee, WAM	8D	22.61±0.263 (21.3-23.85)	26.27±0.300 (25.0-27.4)	0.861±0.011 (0.835-0.908)	5⅜+ (5+-5⅝+)	closed	
Yindi Station, WAM 4678.68	9D	23.03±0.590 (18.75-24.7)	26.38±0.650 (22.1-28.35)	0.873±0.008 (0.835-0.905)	5¼− (5-5⅜)	closed	

Jaw with prominent vertical ribs medially, that are variable in width and prominence, becoming greatly reduced on side margins. Central and lateral teeth of radula (**Plates 185–187**, Solem 1992: plt. 64c) with moderate anterior flare, typical to elevated cusp shaft angle, cusp tip not (*S. tarcoolanum*) to strongly curved (*S. jimberlanensis*, *S. vagente*), ectocone absent (*S. tarcoolanum*, *S. kalgum*, *S. vagente*), small (*S. jimberlanensis*) or very prominent (*S. nullarboricum*) on early laterals, appearing or enlarging on late laterals, endocone appearing at or about lateromarginal transition. Marginals typical, lateromarginal transition slow to abrupt.

Type species: *Helix nullarborica* Tate, 1879.

Comparative remarks

The globose shape, large aperture, lack of prominent radial ribbing, nearly smooth apex, and comparatively large size combine to separate *Sinumelon* from other genera in this region. It is most apt to be confused with the Cape Range monotypic genus *Promonturconchum superbum* (**Figs 399a–c**), which differs in its proportionately larger aperture, strongly reflected lip, lack of pustulations, larger size and yellow-brown periostracal colouration. The smaller *Pleuroxia*, *Falspleuroxia* and *Plectorhagada* in the Nullarbor to Shark Bay region differ in having moderate to very strong apical sculpture and generally very prominent radial ribs on at least the early spire, are much smaller and usually very different in shell shape. Some of the West Coast *Quistrachia* (**Figs 433, 440, 447**) are similar in shape but have proportionately smaller apertures, less elevated spires and very different genitalia.

The malleated shell sculpture of *Sinumelon nullarboricum* (Tate, 1879) (**Plate 183c–e**) is unusual. This feature is not known in other *Sinumelon* but occurs sporadically in helicoid land snails in most parts of the world and also in a number of bulimulid taxa. There is no obvious ecological correlation.

The variation in penial chamber wall sculpture found in the WA species is basically matched, probably independently, by patterns seen in both Flinders-Gawler (Solem 1992) and Red Centre (Solem 1993) species of *Sinumelon*.

Previous studies

Scattered description by Tate (1879, 1894), unidentifiable records (specimens could not be located) in the Elder Expedition report (Bednall 1892), a checklist (Iredale 1938: 103–105), a descriptive review (Iredale 1939: 52–54), and a nomenclatural check list (Richardson 1985) comprise the literature prior to the detailed revisions of Gawler-Flinders (Solem 1992: 1–338) and Red Centre (Solem 1993: 1067-1079) taxa. The latter two publications should be used in conjunction with this report.

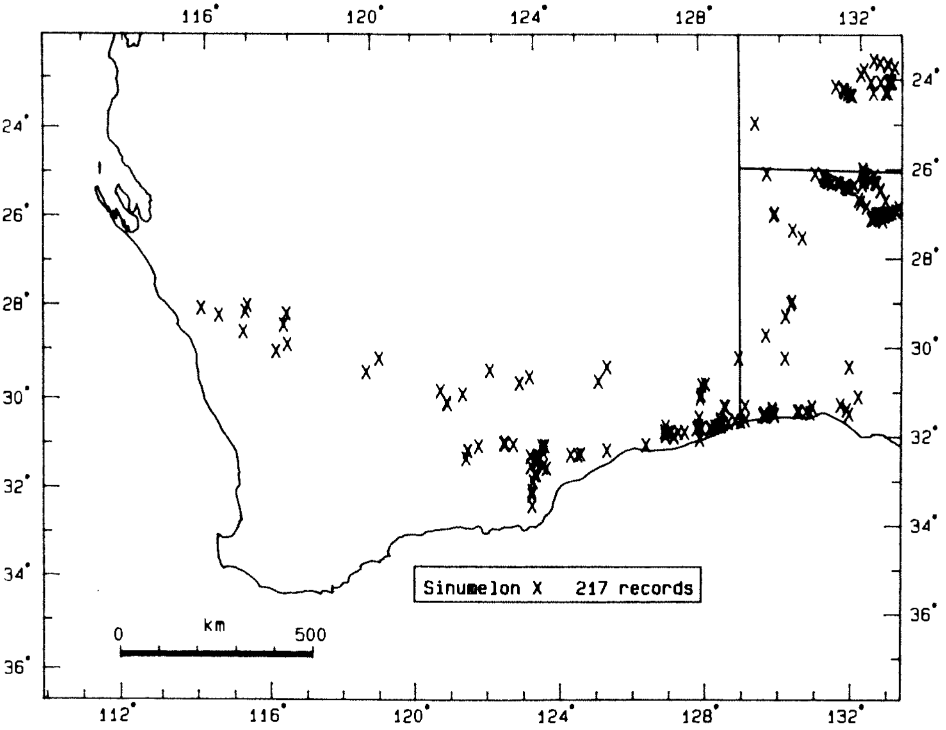
No anatomical or variational data on WA species have been presented previously.

Distribution and comparative ecology

Map 24 summarises the currently available records for *Sinumelon* in WA and adjacent portions of the NT and SA. Gaps in distribution, such as between the Eyre Highway and the rail line to the north, or in the central western region are areas in which no collections of land snails have been made. Similarly, the area in northern SA between the Birksgate Range and from N of Cook has not been explored for land snails. I anticipate that *Sinumelon* will have an essentially continuous range of isolated small colonies from the Red Centre to the Nullarbor coast, and then W through the goldfields and wheat belt to at least Bindoo Hill, inland of Geraldton. Ranges of the individual species show only minor overlap. *S. kalgum* and *S. jimberlanensis* (**Map 25**) are allopatric; *S. vagente* and *S. kalgum* (**Map 26**) are separated by a collecting gap; *S. tarcoolanum* and *S. kalgum* (**Map 26**) probably have partial overlap inland; and only *S. kalgum* and *S. nullarboricum* (**Map 26**), which are very different in size (**Table 136**), have actual or near microsympatric records along the Balladonia-Cape Arid Track. The last two species have been collected together at "Emu Hole, 4 miles S of Nanambinia Homestead", plus there are mosaic records in this region.

All WA *Sinumelon* are "free sealers", with a flexible mucoid epiphragm. They often inhabit the same rock ledges or rock piles as do specimens of *Pleuroxia*. The latter are limited to these rocky areas or the rotting inside of fallen tree trunks, since they aestivate sealed to a rock or wood surface, but the *Sinumelon* can and do lie loose in litter under salt bush or at the base of rock piles. Thus a colony of *Pleuroxia* at a particular station may occupy a significantly smaller area through its aestivation restriction than *Sinumelon* at the same station.

Known species ranges (**Maps 25–26**) are basically allopatric, although *S. tarcoolanum* and *S. kalgum* may overlap and there is one microsympatric record for *S. kalgum* and *S. nullarboricum* (**Map 26**). *S. jimberlanensis* (**Map 25**) and *S. vagente* (**Map 26**) have the smallest ranges; *S. kalgum* is intermediate (**Maps 25–26**); while *S.*



Map 24: Distribution of *Sinumelon* in the Red Centre, Nullarbor and WA.

tarcoolanum (**Map 26**, Solem 1992: figs 126, 139) has a very large inland range and *S. nullarboricum* (**Map 26**) has a large near coastal range.

Size variation is quite extensive in *S. nullarboricum* (**Table 138**), less so in the other species (**Tables 137, 139**). The change in whorl counts is proportionately less than the change in shell diameter, which suggests that more than simple timing of growth cessation is involved in this variation.

The following key will work for live collected adults but not for juveniles or worn examples.

KEY TO THE WESTERN AUSTRALIAN *SINUMELON*

1. Shell surface not malleated on spire and body whorl 2
   Shell surface malleated on spire and body whorl (**Plate 183c**) ....
   .... *Sinumelon nullarboricum* (Tate, 1879) (p. 1531)

2. Umbilicus closed or a narrow lateral slit; spire strongly elevated (**Figs 378, 379**) 3
   Umbilicus narrowly open (**Fig. 377b**); spire less elevated (**Fig. 377a**) ....
   .... *Sinumelon jimberlanensis*, sp. nov. (p. 1526)

3. Mt. Manning E to Gawler Range, SA; shell very large; mean whorl counts over 5
   4
   Geraldton SW to Paynes Find, WA; colour greenish-yellow; diameter about 20 mm; whorl count about 4 3/4 ..... *Sinumelon vagente* Iredale, 1939 (p. 1557)

4. Inland areas, Yindi, WA to Gawler Ranges, SA; body whorl descending abruptly behind lip (Fig. 379b); spire with reddish suffusion ....
   .... *Sinumelon tarcoolanum* Solem, 1992 (p. 1555)
   Balladonia to Mt Manning, WA; body whorl not descending abruptly behind lip (**Figs 378a, c**); shell white in colour, no reddish suffusion ....
   .... *Sinumelon kalgum* Iredale, 1939 (p. 1543)

SINUMELON JIMBERLANENSIS SP. NOV.

(Plates 183a, 185a-c; Figs 377a–b, 380a–b; Map 25)

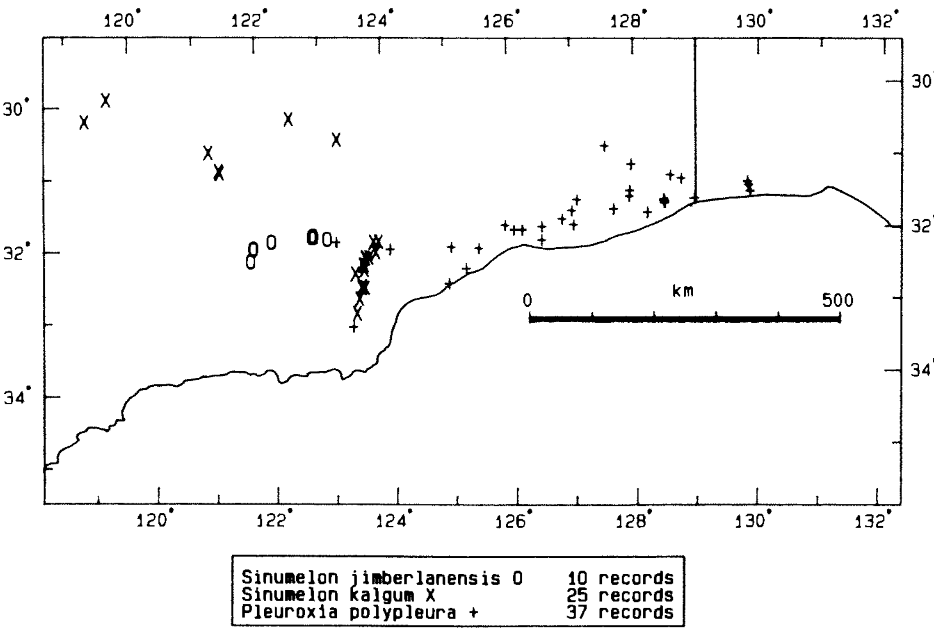
Comparative remarks

Sinumelon jimberlanensis, found between Norseman and the N edges of the Fraser Range, WA (**Map 25**), is the smallest (mean diameter 14.42 mm, **Table 136**) species of *Sinumelon* in WA, although examples of *S. nullarboricum* (Tate, 1879) overlap in diameter. Its low spire (**Fig. 377a**, mean H/D ratio 0.760), low whorl count (mean whorls 4 1/4+), open umbilicus (Fig. 377b, mean D/U ratio 11.0), dark yellow-brown colour and shell sculpture of vague radial ribs and irregular pustulations (**Plate 183a**) combine to separate *S. jimberlanensis*. The malleated shell sculpture (**Plate 183c–e**), higher spire (**Fig. 377c**, mean H/D ratio 0.852), greater diameter (mean 17.00 mm) and increased whorl count (mean 4 5/8+) of *S. nullarboricum* are diagnostic, although the umbilici of the two species are very similar. Both *S. kalgum*

Iredale, 1939 (**Figs 378b, d**) and *S. vagente* (**Fig. 378f**) have the umbilici at most a narrow crack, are much larger, higher spired, with an increased whorl count (**Table 136**) and fresh examples show a microsculpture of dense pustulations (**Plates 183b, 184c–e**). The extremely large and high spired *S. tarcoolanum* Solem, 1992 (**Table 136**) also has a much higher whorl count and lacks the radial sculpture. Anatomically (**Figs 380a–b**), *S. jimberlanensis* has a very short vagina (V) and penis complex, with the free oviduct (UV) short and thick. The penis chamber (**Fig. 380b**) has the main pilaster (PP) corrugated and reduced in prominence, with accessory ridges and corrugated folds enlarged. *S. kalgum* (**Figs 382a, b**) shares the short penis (P) but the vagina is much longer and the penis chamber main pilaster is very large and U-shaped, with the accessory ridges and corrugated folds reduced in size. The tapered penis and long free oviduct of *S. tarcoolanum* (**Fig. 383a**), cylindrical penes and slender free oviducts of *S. nullarboricum* (**Figs 381a–c**) and *S. vagente* (**Figs 384a–b, 385**) readily distinguish those species. The penis chamber sculpture of *S. jimberlanensis* (**Fig. 380b**) is similar to the patterns found in the South Australian species *S. wilpenensis* Solem (1992: fig. 92b) from the South Flinders Range and *S. gawleri* Solem (1992: fig. 100b) from the Gawler Range but, as discussed above, they probably are independently derived.

Holotype

WAM 751.87, WA–483, mid to upper two-thirds of N slope, Jimberlana Hill, E of Norseman, Western Australia (1:250,000 'Norseman' map sheet SI 51–2 – 4837:0246, *ca.* 32°09'24"S, 121°48'39"E). Collected by A. Solem, F. and J. Aslin 2 June 1979.



Map 25: Comparative distribution of *Sinumelon jimberlanensis*, *S. kalgum* and *Pleuroxia polypleura*.

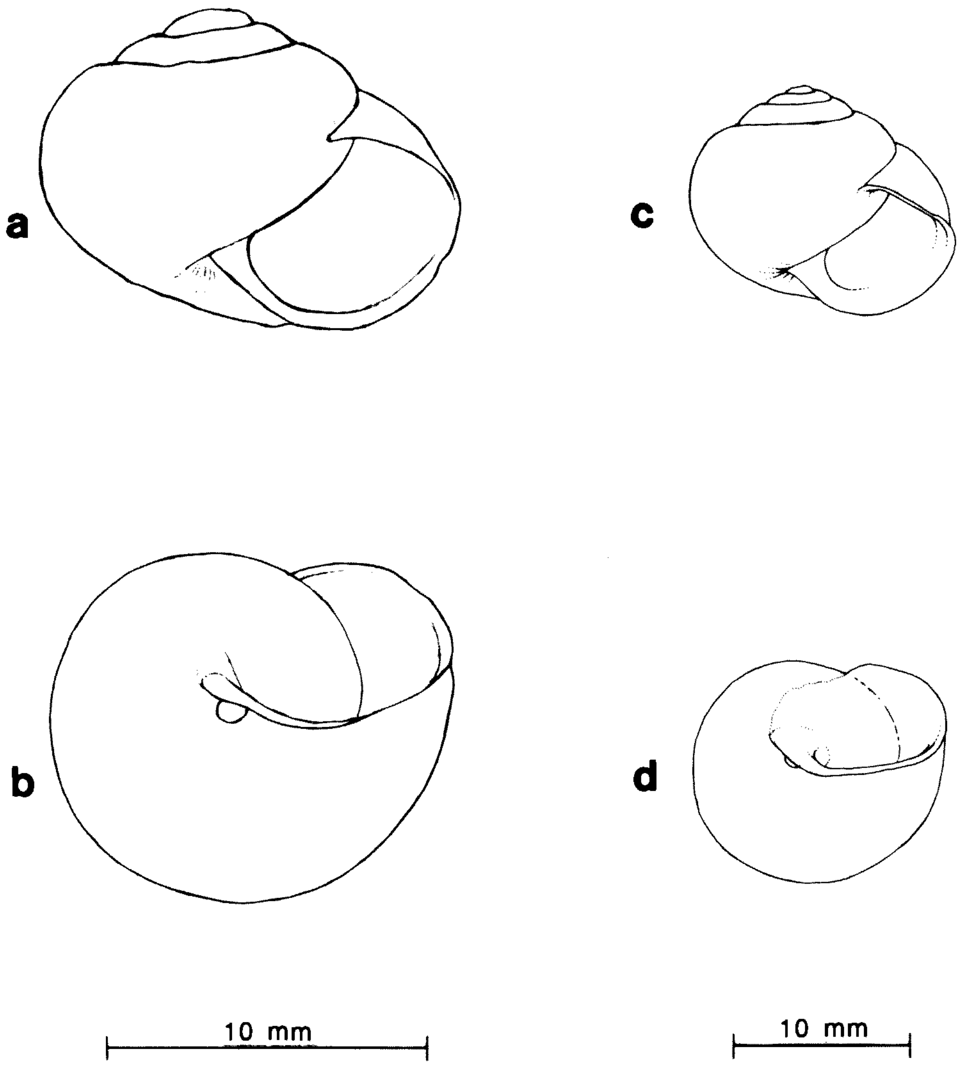


Fig. 377: Shells of *Sinumelon jimberlanensis* sp. nov. and *S. nullarboricum* (Tate, 1879): (a–b) Paratype of *Sinumelon jimberlanensis*. WA–485A, N of Fraser Range Homestead, E of Norseman, WA> FMNG 20-4122; (c–d) *S. nullarboricum*. Paratype of *Sinumelon datum* Iredale, 1939. AM C.64840. Scale line equals 10 mm. Drawings by Margaret Baker (a–b) and Elizabeth A. Liebman (c–d).

Height of shell 11.1 mm, diameter 14.3 mm, H/D ratio 0.776, whorls 4 3/8+, umbilical width 2.1 mm, D/U ratio 6.81.

Paratopotypes

WAM 893.87, AM C.200,707, SAM D18226, FMNH 204108–9, 6 LA, 27 LJ, 9 DJ from the type locality.

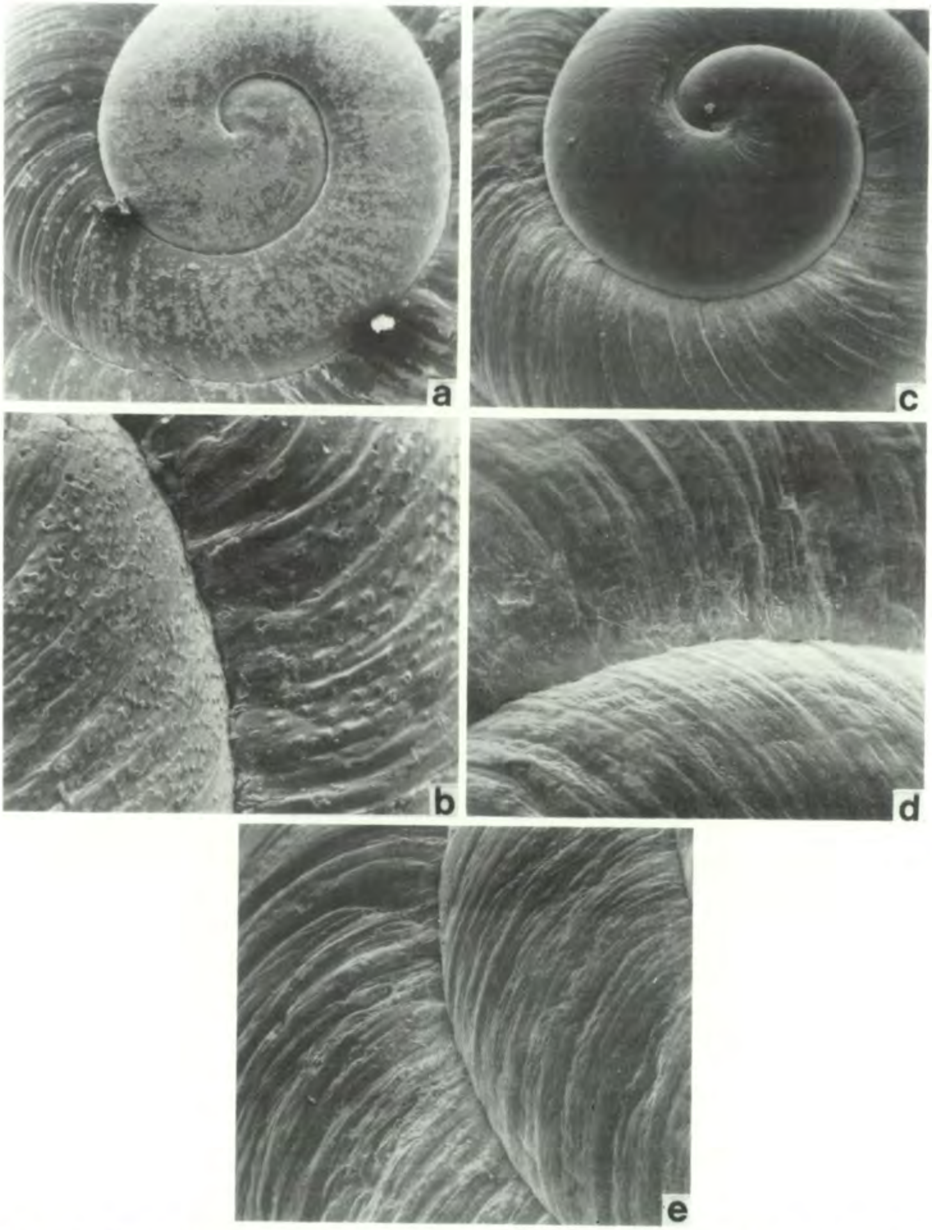


Plate 183: Shell sculpture of *Sinumelon jimberlanensis* sp. nov., *S. vagente* Iredale, 1939 and *S. nullarboricum* (Tate, 1879): (a) *S. jimberlanensis*. WA–96, Fraser Range fringes, 63.25 miles E of Norseman, WA. FMNH 182259. a is apex and early spire at 19.1X; (b) *S. vagente*. Gullewa, near old Shanandar Mine, WA. WAM 245.74. b is sculpture on lower spire at 21.6X; (c–e) *S. nullarboricum*. WA–501, Abrakurrie Cave, Nullarbor, WA. FMNH 204263. c is apex and early spire at 20.5X. d is part of lower spire and body whorl at 19.2X. e is near end of body whorl at 18.8X.

Paratypes

WESTERN AUSTRALIA: Jimberlana Hill, Norseman (WA–97, FMNH 182280, 7 DJ); Beacon Hill, Norseman (S. M. Slack-Smith 2 January 1977, WAM 125.94, 4 DA, 32 DJ); base of Mt Deans to Esperance Highway, *ca.* 15.7 km S of Eyre Highway junction (WA–484, FMNH 204112–3, WAM 894.87, AM C.200,708, SAM D18227, QM 45002, MV F.60097, 5 DA, 1 LJ, 28 DJ); *ca.* 5 km N of Norseman (S. M. Slack-Smith! 17 December 1978, WAM 1117.81, 2 DA, 1 DJ); 24 miles E of Norseman (G. M. Storr! 8 December 1962, WAM 267.74, 1 DA, 3 DJ); 63.25 miles E of Norseman (WA–96, edge of Fraser Range along old Eyre Highway, WAM 895.87, FMNH 182259, FMNH 182663, 4 DA, 6 DJ; WA–485, WA–485a, 103.8 km E of Norseman, rocky ledges on both sides of old Eyre Highway, FMNH 204116–8, FMNH 204122, 3 DA, 11 LJ, 20 DJ); Fraser Range Station (P. Cawthorn, 24 December 1961, WAM 1115.81, 2 DA, 1 DJ); 79 miles E of Norseman (10 November 1969, MV F.75301, 2 LJ).

Range

Collections of *Sinumelon jimberlanensis* (**Map 25**) have been made during hurried trips along the Esperance and Eyre Highways, from 5 km N to 16 km S of Norseman and from Mt Deans and Jimberlana Hill, Norseman to the N tip of the Fraser Range and slightly beyond (if the "79 miles [= 126.5 km] E of Norseman" record cited above is accurate). The confirmed E-W range is about 105 km and the N-S range near Norseman is only 21 km. Adequate survey work undoubtedly will extend these distances.

Diagnosis

Shell very small, adult diameter 12.05–17.4 mm (mean 14.42 mm), whorls 3 7/8– to 4 1/2+ (mean 4 1/4+). Spire relatively low (**Fig. 377a**), shell height 8.2–14.55 mm (mean 10.88 mm), H/D ratio 0.608–0.839 (mean 0.760). Body whorl rounded, descending relatively little behind aperture (**Fig. 377a**). Apex with only weak traces of wrinkles even in juveniles, usually worn in adults, upper spire with weak irregular radial ridges, scattered and varied micropustulations (**Plate 183a**), lower spire with dense micropustulations much as in *S. vagente* (**Plate 183b**). Umbilicus (**Fig. 377b**) narrow, at most slightly narrowed by lip expansion, width 0.7–2.3 mm (mean 1.43 mm), D/U ratio 6.15–23.4 (mean 11.00). Lip weakly expanded on columellar margin, not on basal or palatal margins, slightly thickened internally, white. Spire and body whorl dark yellow-brown, shell base lighter in tone. Based on 31 measured adults.

Genitalia (**Figs 380a–b**) with very short vagina (V), free oviduct (UV) thickened, spermatheca (S) with shaft circling free oviduct. Vas deferens (VD) entering epiphallus (E) about midway up penis (P), epiphallic caecum (EC) short, blunt tipped. Penis and penial retractor muscle (PR) short. Penis sheath (PS) with relatively thick wall, epiphallus circling penial retractor muscle. Penis chamber with main pilaster (PP) reduced in prominence, other ridges enlarged.

Central and lateral teeth of radula (**Plate 185 a–b**) with moderate anterior flare, normal cusp shaft angle, weak ectocone and curved cusp tip with sharp point. Lateromarginal transition typical. Jaw (**Plate 185c**) typical.

Discussion

Sinumelon jimberlanensis inhabits crevices in rock outcrops or the depths of huge boulder jumbles. It has been collected dead in very limited numbers on several occasions but the only significant number of live examples were taken from Jimberlana Hill, just E of Norseman late one afternoon during and just after heavy showers. Both it and a still undescribed species of *Bothriembryon* were common crawling in the open but by the next morning had retreated back into the rock jumbles, again becoming out of reach. Seven live adults and 27 live juveniles were collected in about 30 minutes on the slopes, with the *Sinumelon* more common near lightly vegetated crevices and the *Bothriembryon* more widely dispersed and abundant.

So few adults were collected that variation in only two sets is summarised in **Table 137**. The dead adults from the slopes of Mt Deans (WA–484) are larger in size than the live adults from Jimberlana Hill (WA–483). No geographic size pattern could be detected among the remaining scattered adults.

The name *jimberlanensis* is taken from the type locality, Jimberlana Hill, Norseman.

SINUMELON NULLARBORICUM (TATE, 1879)
(Plates 183c–e, 186a–e; Figs 377c–d, 381a–c; Map 26)

Helix nullarborica Tate, 1879, *Proc. Phil. Soc. Adelaide,* **1878–9:** 126, 133, plt. VI, figs 1a, b – Bunda Plateau, Nullarbor Plain, South Australia.

Helix (*Xanthomelon*) *nullarborica* Tate, Pilsbry 1890, *Man. Conch.,* (2) **6:** 181, pl. 40, figs 96–97.

Thersites (*Badistes*) *nullarborica* (Tate), Pilsbry 1894, *Man. Conch.,* (2) **9:** 131 – citation in check list.

Sinumelon nullarboricum (Tate), Iredale 1930, *Victorian Nat.,* **47:** 120 – as type of a new genus, *Sinumelon*.

Notobadistes nullarborica (Tate), Cotton & Godfrey 1932, *South Aust. Nat.*, **13:** 173–174.

Sinumelon nullarboricum (Tate), Iredale 1937, *South Aust. Nat.,* **18** (2): 42 – citation in a check list; Iredale 1938, *Australian Zool.,* **9** (2): 103 – citation in a check list; Iredale 1939, *Jour. Roy. Soc. Western Aust.*, **25:** 53, plt. III, fig. 19 – Eucla, WA; Burch 1976, *Jour. malac. Soc. Aust.*, **3:** 136 – checklist; Ludbrook 1978, *Geol. Survey Western Aust.,* **125:** 194 – Nullarbor and Roe Plains; Richardson 1985, *Tryonia*, **12:** 277 – checklist.

Sinumelon datum Iredale, 1939, *Jour. Roy. Soc. Western Aust.,* **25:** -X-53, plt. III, fig. 18 – Eucla and Madura, WA; Richardson 1985, *Tryonia*, **12:** 276 – check list.

Thersites (*Sinumelon*) *nullarborica* (Tate), Zilch 1960, *Hand. Palaozool.,* **6** (2): 617, fig. 2163 – synopsis of genera.

Comparative remarks

Sinumelon nullarboricum (Tate, 1879), found primarily near the coast between Colona Homestead, SA (31°38'S, 132°04'E) and Juranda Rockhole on the Balladonia-Cape Arid Track, WA (33°27'S, 123°26'38"E) (**Map 26**), is relatively small (mean diameter 17.00 mm), with a moderately elevated spire (**Fig. 377c**, mean H/D ratio 0.852), usually narrowly

Table 138: Local variation in *Sinumelon nullarboricum.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
South Australia							
WA-203, FMNH 171630	11D	13.60±0.231 (12.05-14.55)	15.15±0.277 (13.45-16.45)	0.898±0.010 (0.858-0.981)	$4\frac{1}{2}$ ($4\frac{3}{8}-$ – $4\frac{5}{8}+$)	0.81±0.035 (0.65-1.05)	19.1±0.951 (14.5-23.9)
WA-516 FMNH 204362	12D	13.44±0.241 (12.3-15.25)	15.14±0.267 (13.75-16.95)	0.888±0.007 (0.840-0.927)	$4\frac{5}{8}+$ ($4\frac{1}{2}-$ – $4\frac{7}{8}-$)	1.30±0.083 (1.05-1.85)	12.1±0.776 (7.63-16.0)
WA-511, FMNH 204339	5D	15.29±0.364 (14.8-16.75)	18.16±0.254 (17.7-19.0)	0.842±0.013 (0.805-0.882)	$4\frac{5}{8}+$ ($4\frac{1}{2}+$ – $4\frac{3}{4}+$)	1.50±0.063 (1.35-1.7)	12.25±0.643 (10.6-14.1)
WA-510, FMNH 204333	7L	14.42±0.323 (13.4-15.8)	16.98±0.347 (15.7-18.15)	0.849±0.009 (0.803-0.879)	$4\frac{1}{2}+$ ($4\frac{3}{8}-$ – $4\frac{3}{4}-$)	1.10±0.077 (0.95-1.5)	15.9±1.030 (11.4-19.1)
WA-510, FMNH 204334	5D	15.51±0.595 (14.2-17.55)	17.89±0.365 (16.95-19.0)	0.867±0.025 (0.797-0.924)	$4\frac{3}{4}+$ ($4\frac{5}{8}-$ – $5+$)	1.60±0.084 (1.35-1.75)	11.3±0.450 (10.2-12.6)
WA-520, FMNH 204385	8L	14.94±0.245 (14.1-16.3)	17.67±0.133 (17.25-18.2)	0.845±0.011 (0.811-0.894)	$4\frac{5}{8}$ ($4\frac{1}{2}-$ – $4\frac{3}{4}+$)	1.69±0.104 (1.25-2.1)	10.8±0.693 (8.45-14.5)
WA-509, FMNH 204327	14D	14.91±0.206 (13.65-16.3)	17.69±0.253 (16.45-19.7)	0.844±0.012 (0.775-0.915)	$4\frac{5}{8}$ ($4\frac{3}{8}+$ – $4\frac{3}{4}$)	1.53±0.099 (1.1-2.25)	12.0±0.656 (8.38-15.7)
WA-509, FMNH 204328	14L	15.12±0.144 (14.2-16.15)	17.68±0.145 (17.0-18.6)	0.855±0.006 (0.791-0.878)	$4\frac{5}{8}$ ($4\frac{1}{4}+$ – $4\frac{3}{4}+$)	1.25±0.074 (0.7-1.75)	14.9±1.010 (10.0-24.9)
WA-505, FMNH 204304	19L	14.94±0.167 (13.35-16.2)	17.0±0.161 (15.95-18.1)	0.880±0.010 (0.788-0.955)	$4\frac{3}{4}-$ ($4\frac{1}{2}+$ – $4\frac{7}{8}+$)	1.54±0.042 (1.1-1.9)	11.2±0.303 (9.31-14.5)
WA-505, FMNH 204303	61D	14.82±0.105 (12.75-16.75)	17.13±0.081 (15.9-18.6)	0.865±0.004 (0.770-0.940)	$4\frac{3}{4}$ ($4\frac{1}{2}-$ – $5\frac{1}{8}-$)	1.55±0.030 (1.0-2.25)	11.3±0.211 (7.73-15.8)
WA-506, FMNH 204312	58L	14.61±0.076 (13.55-16.2)	17.23±0.088 (15.7-18.85)	0.848±0.004 (0.792-0.920)	$4\frac{5}{8}+$ ($4\frac{3}{8}+$ – $4\frac{7}{8}-$)	1.65±0.033 (1.0-2.15)	10.7±0.233 (8.31-17.1)
WA-508, FMNH 204326	14L	14.38±0.266 (12.75-16.6)	16.90±0.224 (15.6-18.15)	0.851±0.011 (0.811-0.959)	$4\frac{1}{2}+$ ($4\frac{3}{8}+$ – $4\frac{3}{4}+$)	1.31±0.055 (0.95-1.7)	13.2±0.565 (9.65-17.2)

Table 138: Local variation in *Sinumelon nullarboricum* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
WA-521, FMNH 204387	8D	15.69±0.451 (14.0-17.6)	18.08±0.411 (16.3-19.9)	0.867±0.013 (0.817-0.930)	$4\frac{3}{4}$ ($4\frac{1}{2}$+-$4\frac{7}{8}$+)	1.54±0.113 (1.15-2.1)	12.2±0.887 (9.44-15.9)
WA-504, FMNH 204302	28L	13.92±0.163 (12.4-16.9)	16.87±0.136 (15.35-19.05)	0.825±0.006 (0.749-0.886)	$4\frac{1}{2}$+ ($4\frac{3}{8}$–-$4\frac{3}{4}$+)	1.47±0.041 (0.85-1.9)	11.7±0.365 (9.41-19.4)
Wilson Bluff, WAM 384.74	9L	13.15±0.199 (12.45-14.4)	16.20±0.308 (15.1-17.45)	0.813±0.013 (0.748-0.879)	$4\frac{3}{4}$– ($4\frac{1}{2}$+-$4\frac{7}{8}$–)	1.05±0.085 (0.9-1.7)	15.9±0.780 (10.2-18.2)
Wilson Bluff, WAM	17D	14.35±0.275 (12.2-16.6)	17.63±0.298 (15.7-21.0)	0.814±0.010 (0.767-0.909)	$4\frac{3}{4}$ ($4\frac{3}{8}$-$5\frac{1}{8}$–)	closed or crack	
Western Australia							
Lookout Hill, ENE Reid, WAM 1202.81	30D	15.02±0.156 (13.35-17.4)	16.46±0.179 (14.85-19.2)	0.913±0.005 (0.849-0.954)	$4\frac{3}{4}$– ($4\frac{3}{8}$-$4\frac{7}{8}$+)	closed or crack	
Eucla, WA, WAM	7D	12.52±0.332 (11.3-14.1)	13.61±0.290 (12.2-14.4)	0.920±0.015 (0.872-0.983)	$4\frac{1}{2}$+ ($4\frac{3}{8}$-$4\frac{3}{4}$)	closed	
WA-498, FMNH 204234	9L	14.13±0.263 (12.7-15.15)	17.45±0.156 (16.85-18.15)	0.810±0.016 (0.724-0.893)	$4\frac{5}{8}$ ($4\frac{5}{8}$-$5\frac{1}{4}$–)	1.93±0.092 (1.35-2.25)	9.22±0.504 (8.02-12.4)
WA-528, FMNH 204435	16L	15.32±0.158 (14.3-16.75)	18.18±0.151 (17.25-18.9)	0.843±0.007 (0.776-0.893)	$4\frac{3}{4}$+ ($4\frac{5}{8}$–-5–)	1.52±0.070 (0.95-1.9)	12.3±0.626 (9.41-18.8)
WA-527, FMNH 204428	6L	13.80±0.367 (12.35-14.45)	16.78±0.312 (15.9-17.75)	0.823±0.020 (0.773-0.908)	$4\frac{3}{4}$ ($4\frac{1}{2}$+-$4\frac{7}{8}$–)	1.62±0.093 (1.3-1.9)	10.5±0.595 (9.30-13.0)
WA-502, FMNH 204278	48L	13.85±0.103 (12.4-15.25)	16.31±0.105 (14.9-18.25)	0.849±0.004 (0.791-0.905)	$4\frac{5}{8}$ ($4\frac{3}{8}$–-$4\frac{3}{4}$+)	1.40±0.032 (0.9-1.9)	12.0±0.317 (8.42-18.5)
WA-502, FMNH 204279	5D	14.31±0.103 (13.95-14.55)	16.25±0.285 (15.65-17.3)	0.882±0.014 (0.842-0.919)	$4\frac{5}{8}$ ($4\frac{3}{8}$+-$4\frac{3}{4}$+)	1.42±0.087 (1.3-1.75)	11.6±0.693 (9.24-13.4)
WA-503, FMNH 204280	8L	13.15±0.419 (11.95-15.75)	16.12±0.304 (14.85-17.75)	0.815±0.013 (0.770-0.886)	$4\frac{1}{2}$– ($4\frac{1}{4}$+-$4\frac{3}{4}$+)	1.42±0.109 (0.75-1.7)	12.0±1.294 (9.16-20.8)

Table 138: Local variation in *Sinumelon nullarboricum* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
WA-500, FMNH 204256	7L	13.52±0.184 (13.0-14.45)	17.04±0.262 (16.0-17.8)	0.795±0.014 (0.750-0.844)	4½ (4¼+-4⅝+)	1.82±0.113 (1.45-2.15)	9.58±0.633 (7.77-12.2)
WA-501, FMNH 204262	50L	13.91±0.090 (12.4-15.1)	16.44±0.078 (15.45-17.55)	0.847±0.005 (0.766-0.933)	4⅝− (4¼+-4⅞+)	1.77±0.036 (1.25-2.5)	9.44±0.185 (6.97-13.1)
WA-501, FMNH 204263	14D	14.82±0.241 (13.3-16.3)	17.53±0.357 (15.1-20.3)	0.847±0.009 (0.800-0.907)	4⅝+ (4½−-4⅞−)	1.79±0.116 (1.3-2.85)	10.2±0.539 (6.84-13.2)
WA-500, FMNH 204255	9D	14.09±0.251 (13.2-15.75)	17.24±0.278 (16.1-18.5)	0.818±0.010 (0.754-0.856)	4⅝− (4½−-4¾+)	1.93±0.068 (1.7-2.3)	9.01±0.279 (7.83-10.7)
WA-526, FMNH 204418	31L	14.24±0.125 (12.8-15.75)	16.70±0.109 (15.65-17.8)	0.853±0.006 (0.771-0.918)	4⅝ (4⅜+-4⅞+)	1.39±0.046 (1.0-1.9)	12.4±0.409 (8.58-17.2)
WA-525, FMNH 204416	5L	15.22±0.230 (14.5-15.75)	18.75±0.132 (18.45-19.2)	0.812±0.017 (0.773-0.851)	4¾ (4⅜+-5+)	1.83±0.130 (1.5-2.3)	10.5±0.733 (8.25-12.6)
WA-524, FMNH 204407	23L	13.73±0.192 (11.6-15.2)	16.96±0.182 (14.75-18.9)	0.810±0.007 (0.742-0.890)	4⅝+ (4⅜−-5+)	1.57±0.040 (1.1-1.8)	11.0±0.311 (8.28-15.1)
WA-497, FMNH 204224	40L	15.26±0.154 (13.35-17.1)	18.09±0.141 (16.3-20.0)	0.843±0.006 (0.766-0.905)	4⅝+ (4¼+-5+)	1.40±0.042 (0.75-1.95)	13.3±0.412 (8.91-21.7)
WA-497, FMNH 204226	6D	16.12±0.702 (13.6-18.6)	19.50±0.929 (15.75-22.1)	0.828±0.012 (0.781-0.863)	4¾+ (4½+-4⅞+)	1.54±0.182 (1.15-2.35)	13.3±1.181 (8.36-16.6)
WA-532, FMNH 204447	5D	14.99±0.362 (14.3-16.4)	16.44±0.396 (15.6-17.9)	0.912±0.010 (0.882-0.935)	4¾− (4⅝−-4¾+)	1.38±0.062 (1.25-1.6)	12.0±0.369 (11.1-13.3)
WA-529, FMNH 204438	6D	15.19±0.451 (13.8-16.7)	16.44±0.388 (15.3-17.9)	0.925±0.029 (0.830-1.051)	4⅝+ (4⅜+-4⅞−)	1.24±0.076 (0.9-1.45)	13.5±0.820 (10.8-16.9)
WA-535, FMNH 204460	35L	15.17±0.139 (13.3-16.6)	18.29±0.135 (16.8-20.05)	0.830±0.007 (0.746-0.929)	4¾+ (4½−-5⅛−)	1.73±0.057 (1.05-2.35)	11.0±0.360 (7.43-16.0)
ca.31 miles E of Madura, WAM 247.74	17D	13.99±0.198 (12.45-15.15)	16.97±0.164 (16.3-18.7)	0.825±0.011 (0.761-0.916)	4¾ (4½+-5+)	1.55±0.061 (1.2-2.0)	11.2±0.469 (8.47-14.5)

Table 138: Local variation in *Sinumelon nullarboricum* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
WA-536, FMNH 204472	5D	14.08±0.184 (13.4-14.5)	15.58±0.436 (14.7-16.75)	0.905±0.019 (0.851-0.962)	4½ (4⅜–-4⅝+)	1.13±0.137 (0.9-1.6)	14.5±1.462 (10.3-18.3)
WA-537, FMNH 204473	17L	15.43±0.239 (13.55-17.4)	18.54±0.221 (17.05-20.45)	0.832±0.008 (0.771-0.891)	4¾+ (4⅝–-5⅛+)	1.68±0.072 (1.05-2.3)	11.4±0.486 (8.17-17.1)
WA-494, FMNH 204200	42L	14.93±0.118 (13.6-16.85)	17.94±0.116 (16.5-19.4)	0.833±0.004 (0.776-0.893)	4¾– (4⅜+-4⅞+)	1.56±0.044 (1.1-2.15)	11.9±0.373 (7.67-16.9)
6 miles S Madura Cave, WAM 339.76	10L	13.47±0.179 (12.75-14.55)	16.60±0.220 (15.2-17.35)	0.812±0.008 (0.779-0.855)	4⅝– (4⅜+-4¾+)	1.58±0.062 (1.2-1.9)	10.7±0.416 (8.36-13.1)
WA-494, FMNH 204201	22D	15.13±0.222 (13.5-17.25)	18.01±0.226 (16.05-20.15)	0.841±0.009 (0.764-0.926)	4¾ (4½–-5⅛–)	1.52±0.066 (1.05-2.2)	12.2±0.517 (8.74-17.5)
WA-495, FMNH 204211	6D	14.74±0.274 (14.0-15.5)	17.47±0.298 (16.8-18.8)	0.845±0.017 (0.788-0.911)	4¾+ (4⅝+-4⅞+)	1.64±0.126 (1.2-2.0)	11.1±1.064 (8.83-15.6)
WA-495, FMNH 204212	6L	14.46±0.342 (13.6-16.05)	17.20±0.283 (16.55-18.45)	0.840±0.008 (0.822-0.868)	4¾ (4⅝+-4¾+)	1.66±0.104 (1.4-2.1)	10.6±0.640 (8.03-12.1)
ca. 10 miles E of Madura, WAM 380.74	11D	13.87±0.205 (12.7-15.2)	15.29±0.172 (14.3-15.95)	0.908±0.009 (0.869-0.968)	4⅝+ (4½-4⅞)	1.07±0.044 (0.9-1.3)	14.5±0.565 (12.2-17.7)
21 miles E of Madura, WAM 250.74	11D	14.19±0.223 (13.15-15.5)	15.82±0.331 (14.25-17.85)	0.899±0.016 (0.833-1.008)	4⅝+ (4½+-4⅞–)	1.18±0.073 (0.9-1.75)	13.7±0.735 (9.47-18.9)
ca. 25 miles W of Madura, MLM 2630	14D	14.12±0.211 (13.0-15.45)	15.56±0.160 (14.6-16.45)	0.908±0.013 (0.830-0.992)	4¾ (4½–-5⅛–)	1.06±0.053 (0.8-1.5)	15.1±0.692 (10.2-18.7)
WA-493, FMNH 204194	5D	13.81±0.260 (13.1-14.6)	15.74±0.251 (15.05-16.6)	0.877±0.008 (0.860-0.907)	4¾+ (4¾+-4⅞–)	1.08±0.029 (1.0-1.2)	14.6±0.443 (13.3-15.7)
41 miles W of Caiguna, WAM 251.74	10D	13.40±0.252 (12.4-15.0)	15.27±0.134 (14.6-15.95)	0.877±0.010 (0.821-0.940)	4⅝– (4⅜+-4¾+)	1.22±0.065 (0.95-1.6)	12.8±0.640 (10.1-16.5)
WA-544, FMNH 204555	9D	12.83±0.274 (11.8-14.6)	14.21±0.283 (13.2-16.15)	0.903±0.006 (0.882-0.943)	4⅝– (4⅜+-4¾+)	0.774±0.065 (0.5-1.05)	19.5±1.799 (13.2-28)

open umbilicus (**Fig. 377d**), reduced whorl count (mean 4 5/8+), and malleated surface on the spire and body whorl (**Plate 183c–e**). *S. kalgum* Iredale, 1939, which partly overlaps in distribution along the Balladonia-Cape Arid track (**Map 26**), is much larger (mean diameter 23.80 mm), with an increased whorl count (mean whorls 5 1/8+), umbilicus generally closed or a narrow lateral crack, is white in colour and lacks (**Plate 184c**) the malleated surface sculpture. The very small (mean diameter 14.42 mm) *S. jimberlanensis*, from Norseman E to the Fraser Range (**Map 25**), has a reduced whorl count (mean 4 1/4+), open umbilicus (**Fig. 377b**), yellow-brown periostracum, moderate radial ridging plus weak micropustulations (**Plate 183a**) and a lowered spire (**Fig. 377a**, mean H/D ratio 0.760). *S. vagente* Iredale, 1939, from inland near Geraldton (Bindoo Hill) E at least to Paynes Find, WA (**Map 26**), is larger (mean diameter 19.68 mm), with a basically closed umbilicus (**Figs 378b, d**), yellow-green periostracum, and with a microsculpture of large pustulations (**Plate 183b**). The very large (mean diameter 26.20 mm) *S. tarcoolanum* Solem, 1992, from inland near Yindi E to the W end of the Gawler Range, SA (**Map 26**), has a generally closed umbilicus, reddish spire suffusion, high spire (**Fig. 379b**, mean H/D ratio 0.921) and increased whorl count (mean 5 3/8–). Anatomically (**Figs 381a–c**), *S. nullarboricum* has a very short vagina (V), long and slender free oviduct (UV), cylindrical penis complex, small epiphallic caecum (EC), reduced main pilaster (PP) and enlarged accessory ridges in the penis chamber. *S. vagente* (**Figs 384a–b**) has a similar-shaped penis, but the vagina is much longer, the main pilaster enlarged and simplified and the free oviduct is much shorter. *S. jimberlanensis* (**Figs 380a–b**) has an extremely short penis and vagina and the penis chamber sculpture is greatly altered, while *S. kalgum* (**Figs 382a–d**) has a short penis, long vagina, short free oviduct and altered penis chamber wall sculpture. *S. tarcoolanum* (**Figs 383a–b**) has a tapering penis with complexly altered pilasters, a long free oviduct and a medium length vagina.

Holotype of *Helix nullarboricum* Tate, 1879

SAM D13602, Bunda Plateau, South Australia. Height of holotype 17.4 mm, diameter 19.2 mm, H/D ratio 0.906, whorls 4 5/8, umbilical width 1.35 mm, D/U ratio 14.2.

Holotype of *Sinumelon datum* Iredale, 1939

WAM 8878, Eucla, Western Australia. Height of holotype 12.65 mm, diameter 17.0 mm, H/D ratio 0.744, whorls 4 5/8, umbilical width 2.0 mm, D/U ratio 8.50.

Paratopotypes of *Helix nullarboricum* Tate, 1879

SAM D15542, 3 DA from the type locality.

Paratopotypes of *Sinumelon datum* Iredale, 1939

WAM 8878, AM C.64840, 5 DA, 1 DJ from the type locality.

Paratype of *Sinumelon datum* Iredale, 1939

WAM 8879, Madura, Western Australia. 1 DA.

Material studied

SOUTH AUSTRALIA: 35 miles N of Colona, Nullarbor Plain (WA–203, W. Turnbull! 1964, FMNH 171630, 11 DA, 9 DJ); 2 km E of Yalata turnoff from Eyre Highway (WA–516, FMNH 204361–2, 2 LA, 12 DA, 4 LJ, 5 DJ); 25 miles from Karanda Station (Kirsch

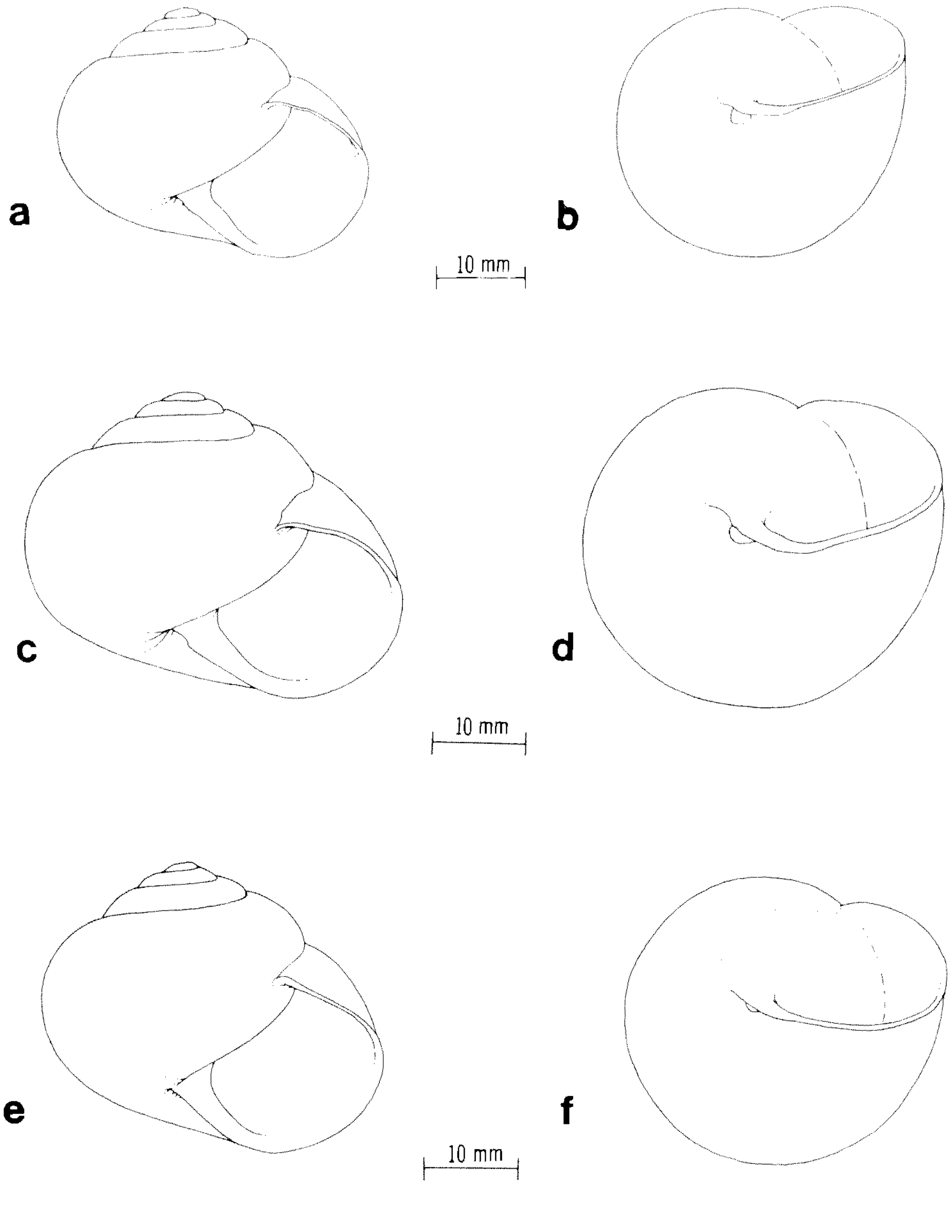


Fig. 378: Shells of *Sinumelon kalgum* Iredale, 1939 and *S. vagente* Iredale, 1939: (a–d) *S. kalgum*. a–b Holotype of *Sinumelon kalgum* Iredale, 1939. Hannans, Kalgoorlie, WA. AM C.3171; c–d Holotype of *Sinumelon lennum* Iredale, 1937. Boulder, WA. AM C.64841; (e–f) Holotype of *Sinumelon vagente* Iredale, 1939. Scale lines equal 10 mm. Drawings by Elizabeth A. Liebman.

& Douglas! 4 January 1965, WAM 378.74, 3 DA); 17 miles E of Ivy Tanks, 1 mile N of Eyre Highway (D. G. Williams! 18 June 1971, SAM, 2 DA); 26 miles W of Waltabie Shed Tanks, Eyre Highway (D. L. Serventy! 2 August 1952, SAM, 3 DA, 1 DJ); Murrawijinie Cave # 3, N–9 (WA–512, FMNH 204350, 2 DA); Murrawijinie Cave # 1, N–7 (WA–511, FMNH 204339, 5 DA, 1 DJ); doline N–122, W of Nullarbor Roadhouse (WA–517, FMNH 204371, 4 DA); campsite WSW of Nullarbor (WA–518, FMNH 204375, 1 DA, 2 DJ); Wigunda Cave, N–147, S of Eyre Highway (WA–510, FMNH 204333–4, 7 LA, 5 DA, 2 LJ); N–163 doline, NW of Nullarbor (WA–519, FMNH 204380, 1 LA, 1 LJ); N–148 doline, WNW of Nullarbor (WA–520, WAM 929.87, SAM D18256, FMNH 204385–6, 8 LA, 8 LJ); WNW of Wigunda Microwave Tower, SE of Koonalda (WA–509, WAM 933.87, SAM D18255, FMNH 204327–8, 14 LA, 14 DA, 13 LJ, 4 DJ); Clay Dam Cave, N–16, SSE of Koonalda (WA–505, WAM 937.87, WAM 938.87, SAM D18259, AM, QM, MV, FMNH 204303–4, 19 LA, 61 DA, 5 LJ, 5 DJ); N–150 doline, SSE of Koonalda (WA–506, WAM 932.87, SAM D18254, QM, MV, FMNH 204312, 58 LA); Giant's Head Cave, N–178 (WA–507, rim of, FMNH 204314, 1 LA, 1 LJ); Koonalda Cave, N–4 (WA–508, base of doline, FMNH 204325–6, 14 LA, 1 DA, 1 LJ); on cliffs, E of SA/WA border (5 September 1979, MV, 4 DA); outlook 12.9 km E of Border Village (WA–521, FMNH 204387–8, 8 DA, 1 LJ, 2 DJ); Wilson Bluff at trig, S of Border Village (WA–522, FMNH 204395, 1 LJ); N–145 or N–146 doline, SSE of 16 Mile Tank (WA–504, WAM 936.87, SAM D18258, AM, QM, MV, FMNH 204301–2, 28 LA, 3 DA, 23 LJ, 1 DJ); Wilson Bluff (A. E. Cockbain & G. W. Kendrick! 31 October 1966, WAM 384.74, 9 LA; G. W. Kendrick! 1 November 1966, WAM, 17 DA, 5 DJ).

WESTERN AUSTRALIA: Lookout Hill, 89 km ENE of Reid (30°05'26"S, 128°48'21"E, Bill Cleverly!, WAM 1202.81, 30 DA, 9 DJ); Eucla (pre-1940, SAM, 7 DA); below Eucla Pass crest, W side (WA–498, FMNH 204234–5, 9 LA, 4 DA, 4 LJ); WSW of Eucla side of scarp (WA–528, FMNH 204435, 16 LA, 3 DA); ENE of Najoda Rock Hole E of Eucla (WA–527, FMNH 204427–8, 6 LA, 1 DJ); Kutowalla doline, W of Eucla N–34 (WA–502, WAM 935.87, SAM D18257, AM, QM, MV, FMNH 204278–9, 48 LA, 5 DA); Winbirra Cave, N–45 W of Eucla (WA–503, FMNH 204280–1, 8 LA, 2 DA, 4 LJ, 1 DJ); Chowilla Landslip, N–17 WNW of Eucla (WA–500, FMNH 204255–6, 7 LA, 9 DA, 11 LJ, 3 DJ); Abrakurrie Cave, N–3 W of Eucla (WA–501, WAM 934.87, SAM D18256, AM, QM, MV, FMNH 204262–3, 50 LA, 14 DA, 2 DJ); NE of Hearder Tower (WA–526, WAM 931.87, SAM D18253, AM, QM, MV, FMNH 204418, 31 LA, 4 LJ); W of Yakcoorga Rock Hole (WA–525, FMNH 204416–7, 5 LA, 2 DA); Kuthala Pass, N of Mundrabilla Roadhouse (WA–524, WAM 930.87, SAM D18252, AM, MV, QM, FMNH 204407, 23 LA, 6 LJ); gully behind tower, E of Mundrabilla (WA–497, WAM 940.87, SAM D18262, AM, QM, MV, FMNH 204224, FMNH 204226, 40 LA, 6 DA, 1 DJ); camp 6 km E of WA–497, Mundrabilla (FMNH 204233, 1 DA); on Mundrabilla–Forrest Track (WA–531, FMNH 204445–6, 1 DA, 3 DJ); Old Homestead Cave, N–83, Mundrabilla-Forrest Track (WA–532, FMNH 204447, 5 DA, 4 DJ); 31.8 km N of Mundrabilla Homestead, Mundrabilla-Forrest Track (WA–529, FMNH 204438, 6 DA, 3 DJ); Forrest Track N of Mundrabilla Homestead (WA–534, FMNH 204459, 4 DA, 1 DJ); near Mundrabilla Homestead (WA–535, WAM 927.87, SAM D18250, AM, QM, MV, FMNH 204460–1, 35 LA, 4 DA, 1 DJ); Boondaroo Station, Ponton Creek, near W boundary fence (R. Savage & D. Ride! 18 August 1967, WAM 273.74, 2 DA, 5 DJ); 30–32 miles E of Madura (22 December 1967, WAM 247.74, 17 DA, 37 DJ); Roe Plains, E of Madura (WA–536, FMNH 204472, 5 DA, 7 DJ); Moodini Pass (WA–537, E of Madura, WAM

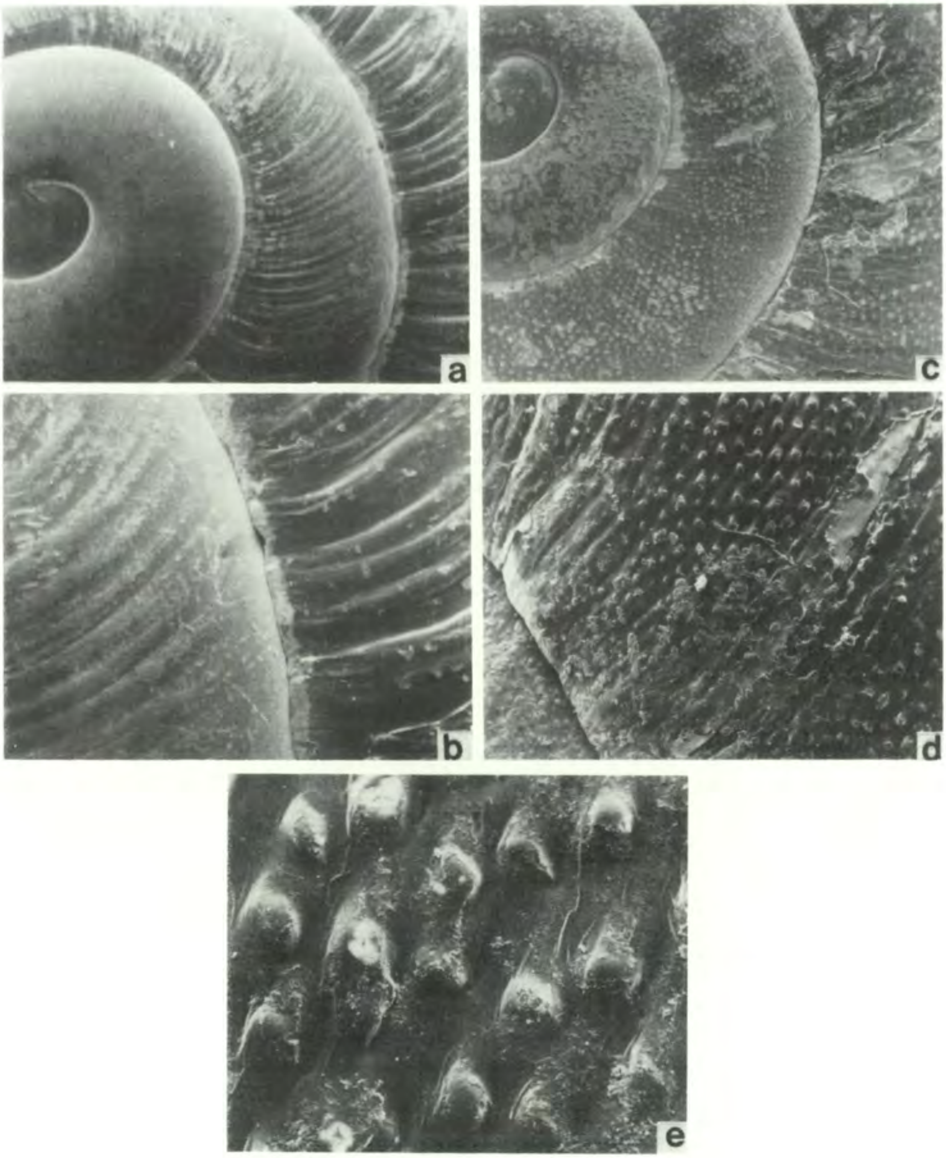


Plate 184: Shell sculpture of *Sinumelon tarcoolanum* Solem, 1992 and *S. kalgum* Iredale, 1939: (a–b) *S. tarcoolanum*. Malbooma Outstation, near Tarcoola, SA. FMNH 198765. a is apex and spire at 17.7X. b is lower spire at 44X; (c–e) *S. kalgum*. WA–482, 16 miles SE of Coolgardie, WA. FMNH 204104. c is apex and spire at 16.1X. d is detail of lower spire at 20.6X. e is detail of body whorl at 105X.

928.87, FMNH 204473–5, 17 LA, 2 DA, 4 LJ); Roe Plains, 16.6 km E of Madura (WA–496, FMNH 204219, 1 DA, 1 DJ); Horseshoe Cave (J. Lowry! 1 November 1968, WAM 275.74, 16 DJ); Madura Cave (J. Lowry! 27 October 1968, WAM 1553.70, 1 DA, 6 DJ); 6 mile S, Madura Cave doline, J. Lowry! 27 October 1968, WAM 5286.68, 4 LA; 6 Mile S Cave entrance doline, 28 March 1967, WAM 339.76, 10 DA, 16 DJ; WA–494, 6 Mile S Cave doline, WAM 939.87, SAM D18261, AM, QM, MV, FMNH 204200–1, 42 LA, 22 DA, 13 LJ, 8 DJ); Madura Pass (WA–495, E side of crest, FMNH 204211–2, 6 LA, 6 DA, 5 LJ, 4 DJ); *ca.* 10 miles E of Madura (WAM 380.74, 2 DA); 21 miles E of Madura (A. G. Nichols! 1970's, WAM 250.74, 11 DA, 17 DJ); *ca.* 25 miles W of Madura (G. F. Mees! 7 February 1975, 14 DA); campsite W of Madura (WA–493, FMNH 204194, 5 DA, 4 DJ); 43 miles W of Cocklebiddy (A. R. Main! 12 February 1959, WAM 243.74, 2 DA); 41 miles W of Caiguna (B. G. Muir & M. Archer! 25 November 1969, WAM 251.74, 10 DA, 2 DJ); Wonberna Rocks, Balladonia Hstd. (G. M. Storr! 11 December 1962, WAM 254.74, 1 DA); E of Balladonia (WA–540, FMNH 204516, 3 DA, 2 DJ); Emu Rock Hole, 4 miles S of Nanambinia Homestead (D. L. Serventy! 7 August 1952, SAM, 1 DA); 12 miles S of Balladonia Homestead (G. M. Storr! 8 December 1962, WAM 264.74, 2 DA, 5 DJ); N of Juranda Rockhole (WA–543, FMNH 204553, 1 DJ); Juranda Rockhole, E side (WA–544, WAM 941.87, SAM D18263, FMNH 204554–5, 3 LA, 9 DA, 3 LJ, 8 DJ).

Range

Sinumelon nullarboricum (Tate, 1879) has been collected as far E as Yalata (WA–516, 31°30'57"S, 131°50'41"E) and Colona (31°38'S, 132°04'E), SA, and as far W as Juranda Rockhole (WA–544, 33°26'57"S, 123°26'38"E), WA (**Map 26**). Most of the records are either near the Eyre Highway or along the Balladonia-Cape Arid road. There are very few inland records (**Map 26**), in part because no collecting has been done, and in part because records such as "89 km ENE of Reid" could not be given accurate coordinates. The known E-W distribution thus is about 825 km but no meaningful N-S estimate can be presented.

Diagnosis

Shell medium in size, adult diameter 12.2–22.1 mm (mean 17.00 mm), whorls 4 1/4+ to 5 1/4– (mean 4 5/8+). Spire moderately elevated (**Fig. 377c**), shell height 11.3–18.6 mm (mean 13.79 mm), H/D ratio 0.724–1.051 (mean 0.852). Body whorl rounded, descending moderately behind aperture (**Fig. 377c**). Apex nearly smooth, weak wrinkles developed on later portion, spire with combination of irregular radial ridges, micropustulations and prominent malleations (**Plate 183c–e**). Umbilicus a narrow crack (**Fig. 377d**) to narrowly open. Lip moderately expanded, partly reflected over umbilicus, white, moderately thickened internally. Colour very light yellow-brown, often worn to white colour. Based on 908 measured adults.

Genitalia (**Figs 381a–c**) with very short vagina (V), free oviduct (UV) long and slender, shaft of spermatheca (S) circling free oviduct. Epiphallic caecum (EC) short, opposite mid-section of penis complex. Epiphallus (E) partly circling penial retractor muscle (PR). Penis sheath (PS) with thin wall. Penis (P) with medium sized, U-shaped, main pilaster (PP), accessory ridges and pilasters prominent.

Central and early lateral teeth of radula (**Plate 186a, c**) with prominent anterior flare, pointed basal support ridge, normal cusp shaft angle, bluntly rounded and

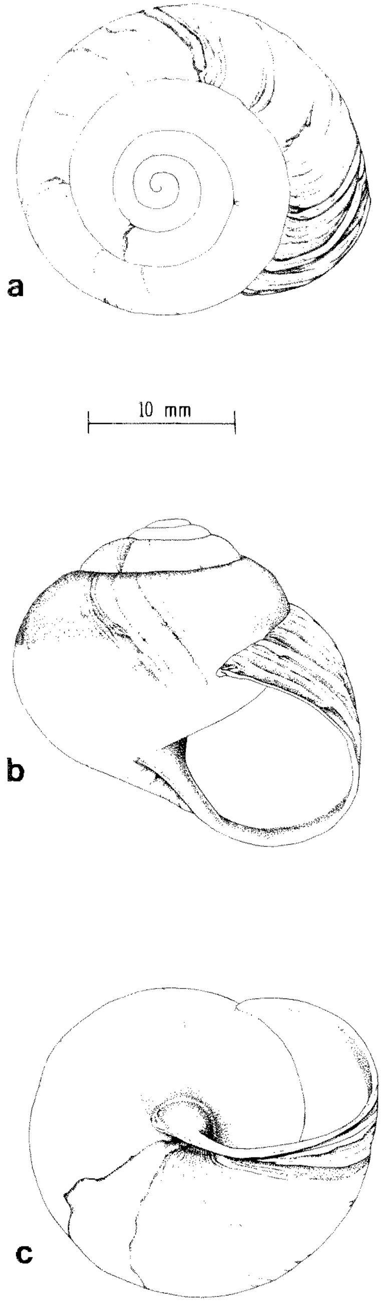


Fig. 379: Shell of *Sinumelon tarcoolanum* Solem, 1992: Holotype. Malbooma Outstation, Tarcoola, SA. SAM D17073. Scale line equals 10 mm. Drawings by Linnea Lahlum. (From Solem, 1992: figs 82a–c).

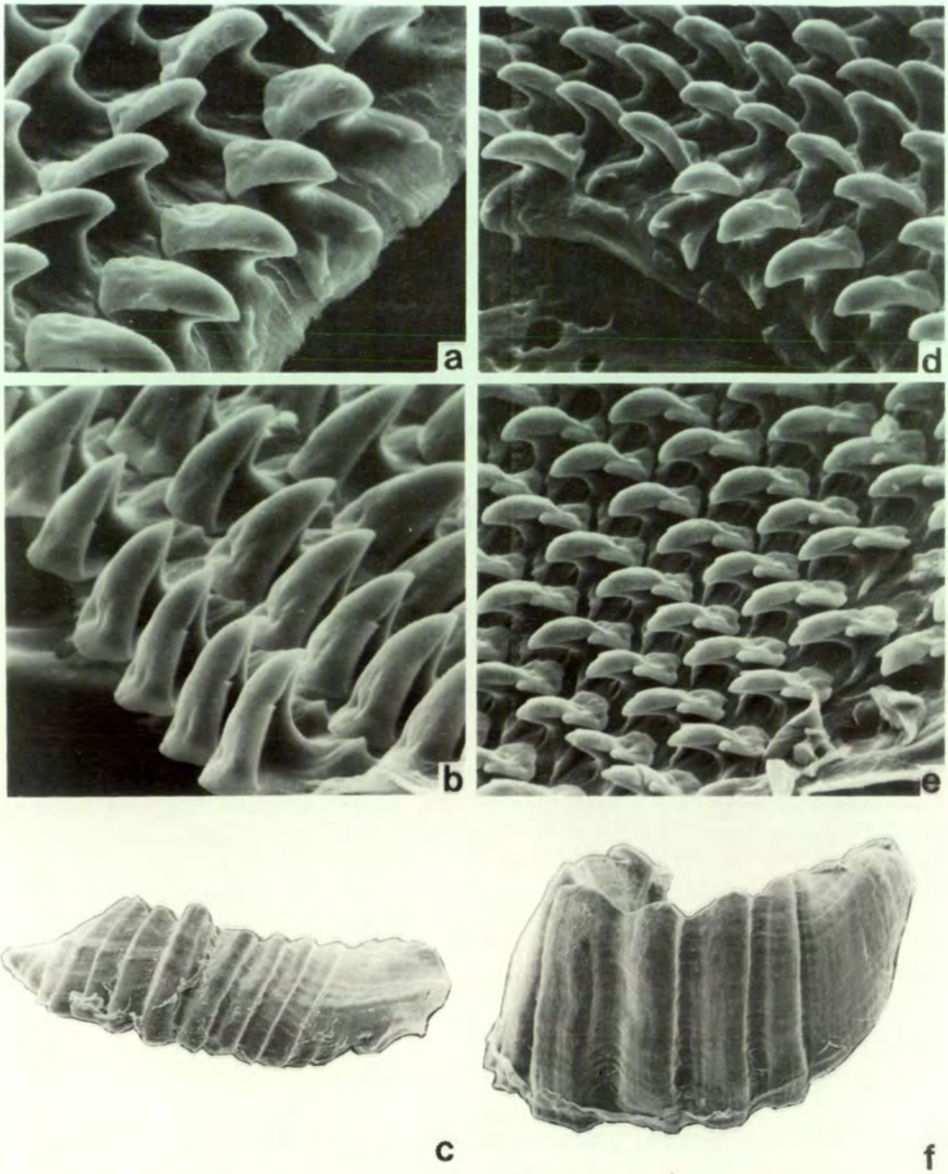
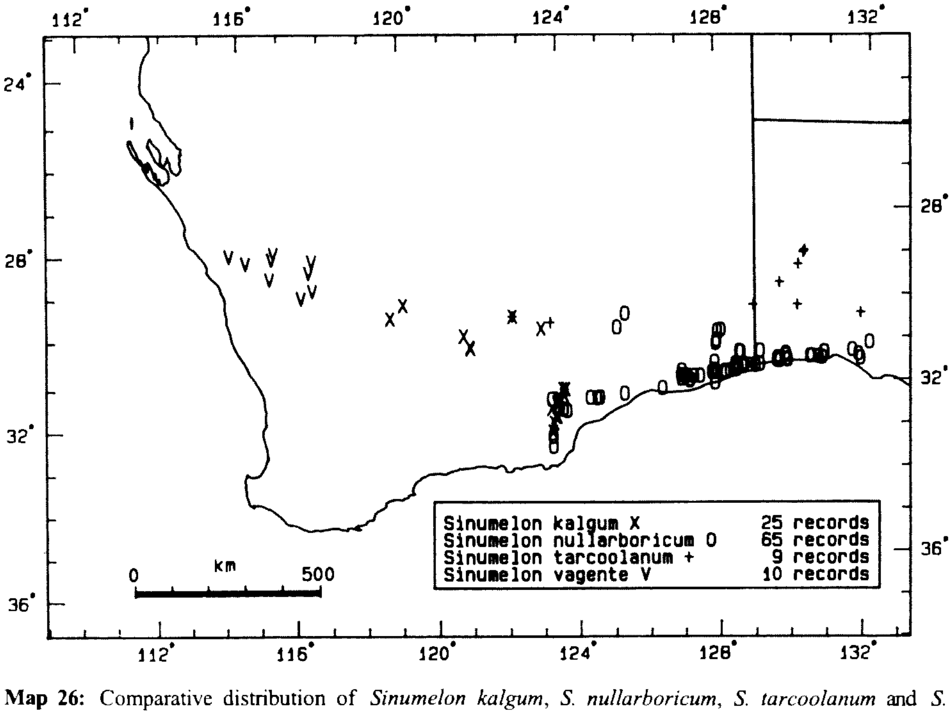


Plate 185: Radular teeth and jaws of *Sinumelon jimberlanensis* sp. nov. and *S. vagente* Iredale, 1939: (a–c) *S. jimberlanensis*. WA–483, Jimberlana Hill, Norseman, WA. 2 June 1979. FMNH 204109, Dissection B. a is central and early laterals at 660X. b is anterior view of central and early laterals at 720X. c is jaw at 61X; (d–e) *S. vagente*. Fields Find, SE of Yalgoo, WA. 29 January 1968. WAM 507.74, Dissection A. d is central and early laterals at 460X. e is latero-marginal transition at 465X; (f) *S. vagente*. WA–1061, Bindoo Hill, Greenough River drainage, E of Geraldton, WA. 14 June 1984. FMNH 211993, specimen #2. f is jaw at 53X.

Sinumelon lennum mutuum Iredale, 1939, *Jour. Roy. Soc. Western Aust.*, **25**: 54 – Madura, WA (probable label error).

Comparative remarks

Sinumelon kalgum Iredale, 1939, which ranges from Balladonia Station on the Eyre Highway (123°52'E) S to at least Heinsman Rock (33°07'S) on the Cape Arid road, and then NW to Norseman, Kalgoorlie and on to Mt. Manning (119°39'E, 30°01'S), WA (**Maps 25–26**), is very large (mean diameter 23.80 mm), with a strongly elevated spire (**Figs 378a, c**, mean H/D ratio 0.884), high whorl count (mean 5 1/8+) and often very thick, white shell. Fresh examples show a microsculpture of dense pustulations (**Plate 184c–e**). Two much smaller species with reduced whorl counts (**Table 136**), *S. jimberlanensis* Solem, this paper and *S. nullarboricum* (Tate, 1879), are easily recognised. The more inland species *S. tarcoolanum* Solem, 1992 (**Map 26**) is larger, with a higher whorl count, more elevated spire (**Table 136**) and often has reddish colouration. *Sinumelon vagente* Iredale, 1939, found from Geraldton E to Paynes Find (**Maps 26, 27**), is smaller (mean diameter 19.68 mm), with a reduced whorl count (mean 4 3/4), generally greenish-yellow in colour and has larger micropustules. Anatomically (**Figs 382a–d**), the thickened vagina (V), short free oviduct (UV), very short penis complex with the penis (P) kinked inside the penis sheath (PS) combines with the enlarged main pilaster (PP) to easily distinguish *S. kalgum*. The only other WA species with a shortened penis, *S. jimberlanensis* (**Figs 380a–b**), has an extremely short vagina and the penis chamber wall sculpture is completely different.



Map 26: Comparative distribution of *Sinumelon kalgum*, *S. nullarboricum*, *S. tarcoolanum* and *S. vagente*.

somewhat curved cusp tip. Late laterals (**Plate 186b, c**) with enlarged anterior flare and ectocone, cusp tip curvature increased and basal plate shortened. Endocone first appears on outermost laterals. Marginals without unusual features. Jaw (**Plate 186d, e**) quite variable in rib width and numbers.

Discussion

Sinumelon nullarboricum (Tate, 1879) is the most variable species of WA *Sinumelon* (**Table 138**). Mean diameters of populations range from 13.61 mm (unlocalised Eucla set) to 19.50 mm (WA–497, E of Mundrabilla, WA). Both the easternmost and westernmost populations have smaller diameters but do not show significant changes in whorl counts. The pattern of size relationship between live and dead examples from the same station is not consistent. Material taken in different years cannot be assumed to be from precisely the same locality, but the 1979 collections were made from quite restricted areas and thus can be compared as to size differences. Dead shells were substantially larger than live adults at WA–510 (Wigunda Cave, SA), WA–501 (Abrakurrie Cave, WA), WA–497 (E of Mundrabilla, WA) and WA–495 (crest of Madura Pass, WA), but essentially the same at WA–509 (near Wigunda Microwave Tower, SA), WA–505 (Clay Dam Cave, SA), WA–502 (Kutowalla Doline, WA) and WA–494 (Madura 6 Mile South Cave). Some of these localities showing different size patterns are very close together, indicating that local conditions must influence size. As would be anticipated, populations with a smaller mean diameter tend to have an increased H/D ratio but are at most slightly different in whorl count.

A more detailed analysis of size variation in relation to variation in the Nullarbor *Pleuroxia* will be presented elsewhere as part of a *commentary* on covariation patterns of sympatric species in several parts of Australia.

Sinumelon datum Iredale (1939: 53) was based on a few examples from Eucla. The holotype, WAM 8878, is 17.0 mm in diameter and the largest paratype, AM C.64840, which probably is the figured example, is 17.7 mm in diameter (although the type description gives the diameter as 19 mm). The three smaller specimens in AM C.64840 are 13.6, 14.05 and 15.15 mm in diameter. The largest one probably is the shell figured by Iredale (1939: plt. III, fig. 19) as *Sinumelon nullarboricum* (Tate, 1879), since it contains a second label in Iredale's script reading "*Sinumelon nullarboricum* Tate, Eucla, Sth West Aust". This is yet another situation in which Iredale apparently used small and large individuals from the same museum lot to recognise two species. *S. datum* is based on a slightly larger, more depressed example of *S. nullarboricum* and thus is reduced to synonymy.

SINUMELON KALGUM IREDALE, 1939

(Plates 184c-e, 187a–d; Figs 378a–d, 382a–d; Maps 25–26)

Sinumelon kalgum Iredale, 1939, *Jour. Roy. Soc. Western Aust.*, **25:** 53–54, plt. III, fig. 25 – Hannans, Kalgoorlie and Lake Kalgoorlie, WA; Richardson 1985, *Tryonia*, **12:** 277 – citation in check list.

Sinumelon lennum Iredale, 1939, *Jour. Roy. Soc. Western Aust.*, **25:** 54, plt. III, fig. 21 – Boulder, WA; Richardson 1985, *Tryonia*, **12:** 277 – citation in check list.

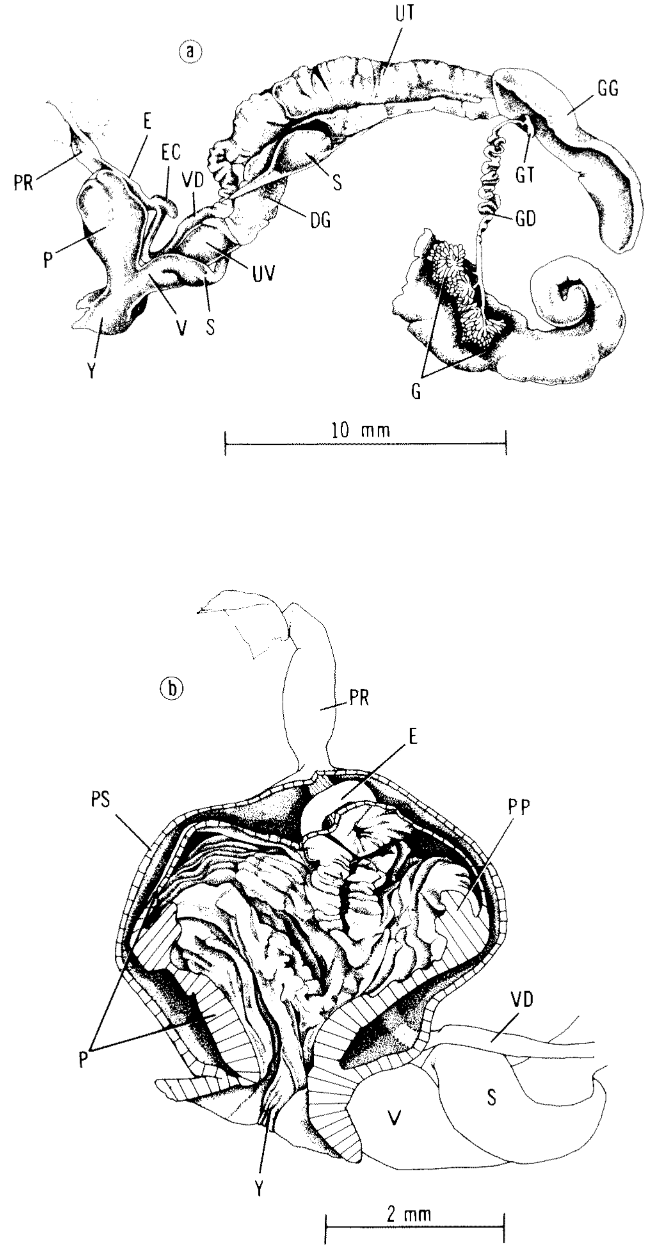


Fig. 380: Genitalia of *Sinumelon jimberlanensis* sp. nov.: WA–483, Jimberlana Hill, Norseman, WA. 2 June 1979. FMNH 204109: (a) whole genitalia, Dissection A; (b) interior of penis, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum.

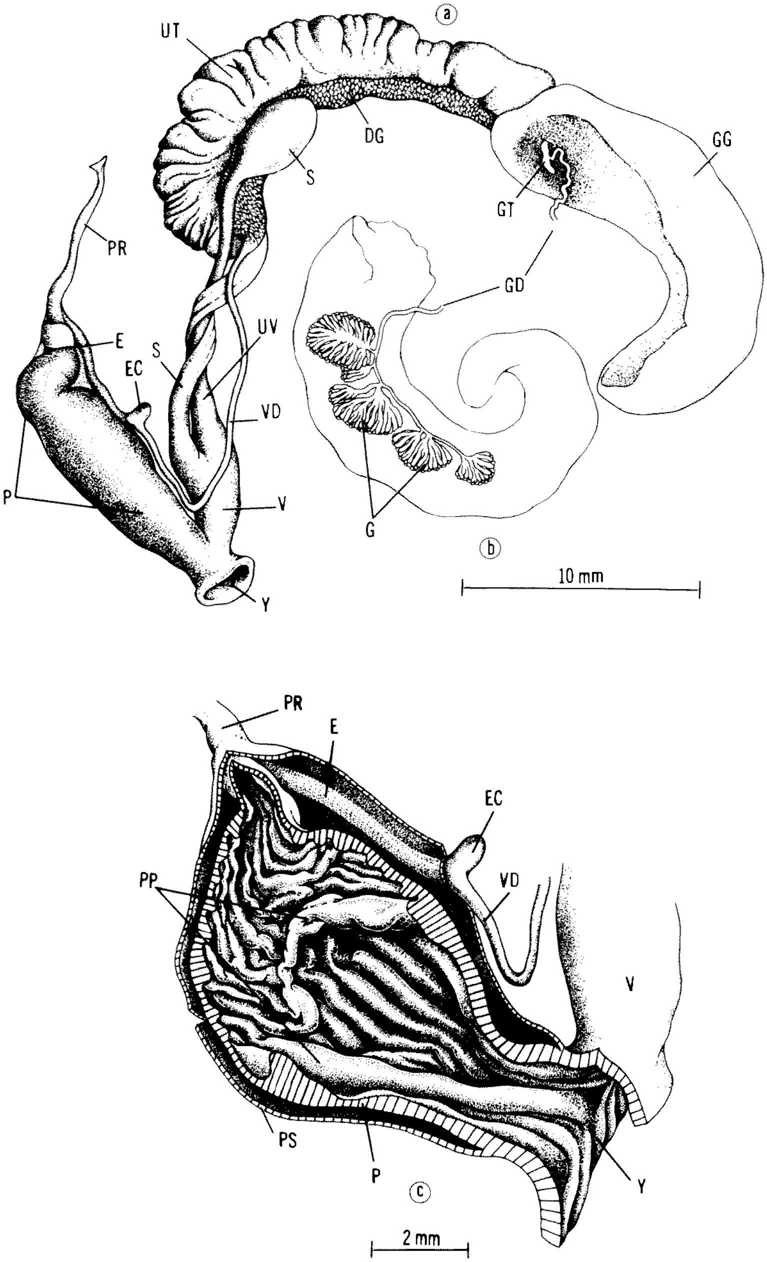


Fig. 381: Genitalia of *Sinumelon nullarboricum* (Tate, 1879): Madura Cave doline, in roots of saltbush, 6 miles S of Madura, Nullarbor, WA. 27 October 1968. WAM 5286.68: (a) whole genitalia, Dissection A; (b) ovotestis, Dissection A; (c) interior of penis, Dissection B. Scale lines as marked. Drawings by Elizabeth A. Liebman.

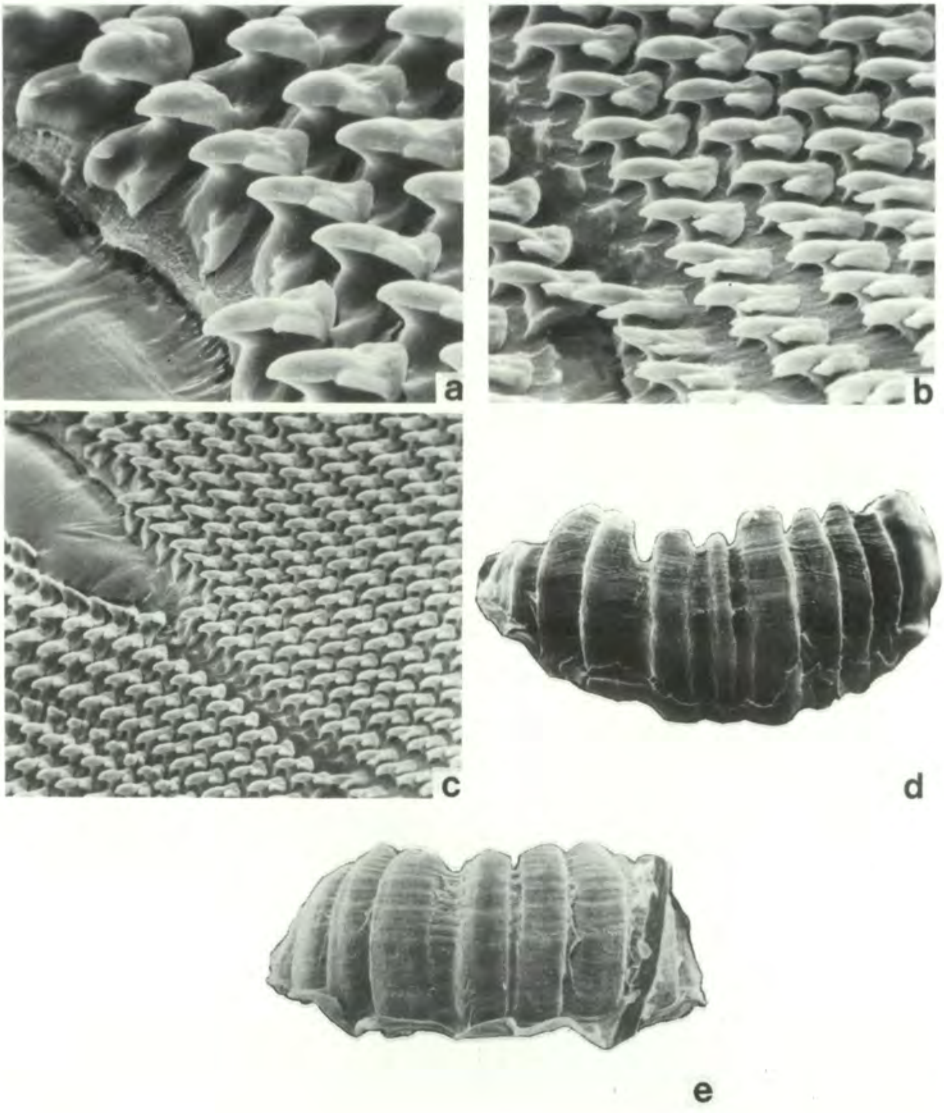


Plate 186: Radular teeth and jaws of *Sinumelon nullarboricum* (Tate, 1879): (a–d) Madura Cave, 6 miles S of Madura, Nullarbor, WA. 27 October 1968. WAM 5286.68, Dissection A. a is central and early laterals at 680X. b is lateromarginal transition at 450X. c is part row at 190X. d is jaw at 54X; (e) Wilson Bluff, Nullarbor, SA. 31 October 1968. WAM 384.74, Dissection B. e is jaw at 71X.

Table 139: Local variation in *Sinumelon kalgum*.

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
WA-95, FMNH 182519	6D	21.16±0.516 (20.2-23.1)	23.18±0.435 (21.7-24.55)	0.913±0.017 (0.850-0.954)	5− ($4\frac{3}{4}$+-$5\frac{1}{4}$−)	closed or crack	
WA-95, FMNH 182309	11D	20.54±0.311 (18.95-22.4)	22.88±0.255 (21.55-24.1)	0.898±0.010 (0.854-0.952)	$5\frac{1}{8}$ ($4\frac{3}{4}$+-$5\frac{3}{8}$−)	closed or crack	
Israelite Bay road, WAM 1200.81	9D	19.88±0.370 (18.8-22.1)	22.24±0.207 (21.4-23.05)	0.893±0.012 (0.850-0.976)	$5\frac{1}{8}$+ ($4\frac{7}{8}$-$5\frac{1}{2}$+)	closed	
Deralinya Hstd, WAM 1201.81	5D	19.57±0.456 (17.85-20.4)	22.42±0.237 (21.7-23.2)	0.873±0.016 (0.823-0.911)	5+ ($4\frac{7}{8}$+-$5\frac{1}{8}$)	closed or crack	
WA-94, FMNH 182324	31D	22.69±0.240 (19.75-24.6)	25.50±0.187 (22.85-27.6)	0.890±0.006 (0.814-0.957)	$5\frac{3}{8}$− ($5\frac{1}{8}$+-$5\frac{5}{8}$−)	closed or crack	
WA-94, FMNH 182477	17D	22.30±0.208 (21.3-25.1)	25.83±0.091 (25.05-27.75)	0.863±0.006 (0.818-0.917)	$5\frac{1}{8}$+ ($4\frac{7}{8}$-$5\frac{3}{8}$)	closed or crack	
WA-94, FMNH 182461	5D	22.05±0.626 (20.7-24.15)	24.65±0.307 (24.0-25.45)	0.894±0.021 (0.847-0.956)	$5\frac{1}{8}$ (5-$5\frac{3}{8}$−)	closed or crack	
WA-487, FMNH 204129	6L	22.6±0.420 (20.95-23.6)	26.05±0.342 (24.65-27.1)	0.867±0.011 (0.827-0.897)	$5\frac{1}{4}$+ ($5\frac{1}{8}$+-$5\frac{1}{2}$−)	closed or crack	
WA-487, FMNH 204140	12D	22.87±0.336 (21.4-25.8)	25.92±0.260 (24.35-27.4)	0.883±0.011 (0.818-0.940)	$5\frac{1}{4}$ ($5\frac{1}{8}$-$5\frac{5}{8}$−)	closed or crack	
WA-487, FMNH 204128	6D	22.44±0.326 (21.55-23.4)	25.98±0.252 (24.85-26.6)	0.864±0.013 (0.829-0.902)	$5\frac{1}{4}$ ($5\frac{1}{8}$+-$5\frac{3}{8}$−)	closed or crack	

Table 139: Local variation in *Sinumelon kalgum* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Emu Hole, Nanambia SAM	5D	22.00±0.582 (20.3-23.65)	24.36±0.514 (22.8-25.7)	0.903±0.011 (0.879-0.937)	$5\frac{1}{8}$ ($5+$-$5\frac{1}{4}$)	closed	
Coragina Rock, WAM	13D	20.58±0.312 (18.1-22.5)	22.8±0.312 (21.0-24.6)	0.903±0.007 (0.862-0.951)	$5\frac{1}{4}$ (5-$5\frac{1}{2}$)	closed	
Yadadinia Rockhole, WAM 603.79	7D	19.47±0.843 (17.55-24.05)	21.77±0.254 (20.95-22.8)	0.893±0.034 (0.831-1.088)	$5\frac{1}{8}-$ ($4\frac{7}{8}+$-$5\frac{1}{4}-$)	closed or crack	
Heinsman Rock, WAM	8D	20.12±0.257 (19.1-21.2)	22.93±0.225 (22.2-23.9)	0.878±0.008 (0.838-0.913)	5+ ($4\frac{7}{8}+$-$5\frac{1}{8}$)	closed	
WA-542, FMNH 204533	28D	20.45±0.189 (18.7-22.6)	22.74±0.157 (21.4-24.8)	0.899±0.006 (0.813-0.959)	$5\frac{1}{4}-$ ($4\frac{3}{4}+$-$5\frac{3}{8}-$)	closed or crack	
Yiridi Station, WAM 171/6-1956	6D	22.65±0.450 (21.05-23.9)	26.08±0.430 (24.9-27.35)	0.869±0.013 (0.835-0.910)	$5\frac{3}{8}$ ($5\frac{1}{4}+$-$5\frac{1}{2}+$)	0.89±0.312 (0.0-1.9)	
Yarri near Edjudina, WAM	6D	18.76±0.262 (17.9-19.75)	21.89±0.389 (20.7-23.1)	0.857±0.011 (0.827-0.903)	5− ($4\frac{3}{4}$-$5\frac{1}{8}$)	closed or crack	
Edujudina Station, WAM	9D	19.01±0.176 (18.4-19.7)	22.35±0.335 (20.75-23.4)	0.852±0.013 (0.795-0.916)	$4\frac{7}{8}+$ ($4\frac{3}{4}$-$5\frac{1}{4}$)	closed or crack	
Kalgoorlie, NMV F28297	5D	18.73±1.341 (13.65-20.9)	22.36±1.509 (16.55-25.3)	0.837±0.012 (0.810-0.881)	5 ($4\frac{5}{8}+$-$5\frac{3}{8}$)	1.66±0.160 (1.1-2.05)	14.2±2.102 (9.19-21.1)

Holotype of *Sinumelon kalgum* Iredale, 1939

AM C.3171, Hannans, Kalgoorlie, Western Australia. Height of holotype 15.4 mm, diameter 18.65 mm, H/D ratio 0.650, whorls 5–.

Holotype of *Sinumelon lennum* Iredale, 1939

AM C.64841, Boulder, Western Australia. Collected by W. D. Campbell. Height of holotype 18.55 mm, diameter 22.45 mm, H/D ratio 0.826, whorls 5.

Holotype of *Sinumelon lennum mutuum* Iredale, 1939

WAM 8879, Madura, Western Australia (probable label error). Height of holotype 20.2 mm, diameter 25.0 mm, H/D ratio 0.808, whorls 5+.

Material studied

WESTERN AUSTRALIA: Afghan Rock, Balladonia Station (WA–95, WAM 925.87, FMNH 182309, FMNH 182519, 6 LA, 11 DA, 4 LJ, 3 DJ; G. M. Storr! 8 December 1962, WAM, 9 DA, 10 DJ); 22 km N from Balladonia on track to Zanthus (M. Kriewaldt! 1965, WAM, 1 DA, 1 DJ); scrub just N of Balladonia Hotel-Motel (WA–94, WAM 922.87, SAM D18247, AM, QM, MV, FMNH 182324, FMNH 182461, FMNH 182661, FMNH 182477, 5 LA, 28 DA, 16 DJ; WA–487, scrub at S end of Balladonia Roadhouse airstrip, WAM 923.87, WAM 924.87, SAM D18248, FMNH 204128–9, FMNH 204140, 6 LA, 18 DA, 4 LJ, 1 DJ); 16 miles S of Balladonia Motel (W. H. Butler! 17 February 1970, WAM 1540.70, 5 DA); 20 miles N of Balladonia Hotel on Zanthus track (W. H. Butler! 12 August 1967, WAM, 2 DA, 4 DJ); 86 miles S of Zanthus, near Eastern Dam (K. Thiess! 19 May 1971, WAM 6 DA, 1 DJ); 85 miles S of Zanthus (K. Thiess! 19 May 1971, WAM, 1 DA); 15 miles W of Zanthus, on Zanthus-Kalgoorlie Road (K. Lance! 29 August 1975, WAM 1157.81, 1 DA, 3 DJ); 6 miles W of Coonana (G. M. Storr! 9 November 1963, WAM, 1 DA, 1 DJ); 6 miles E of Noondoonia (G. M. Storr! 10 December 1962, WAM, 3 DA); Balladonia (Matthews! 7 September 1968, WAM, 1 DA); 16 miles S of Balladonia (W. H. Butler! 17 February 1970, WAM 452.70, 3 DA); Heinsman Rock (D. Merrilees & G. M. Storr! 16 December 1962, WAM 14 DA, 1 DJ); Israelite Bay road (W. G. & M. H. Henderson! 19 May 1978, WAM 1200.81, 9 DA); Deralinya Homestead, N of Israelite Bay (W. G. & M. H. Henderson! 17 May 1978, WAM 1201.81, 5 DA, 9 DJ); Cape Arid track, 46.1 km S of Balladonia (WA–542, WAM 926.87, SAM D18249, AM, QM, MV, FMNH 204533, FMNH 204537, 3 LA, 28 DA, 3 DJ); near Guralia Rock Hole (S. B. Bennett! October 1968, WAM, 9 DA, 1 DJ; T. Darragh, M. Archer, G. W. Kendrick! 6 March 1969, WAM, 1 DA); 7 miles S of Balladonia Hotel (G. M. Storr! 9 December 1962, WAM, 18 DA, 5 DJ); Guralia Rock Hole (G. W. Kendrick! 2 October 1976, WAM, 2 DA, 1 DJ); Yadadinia Rockhole, 12 km SW of Balladonia Motel-Hotel (W. H. Cleverley! 16 April 1074, WAM 603.79, 7 DA, 12 DJ; WAM, 2 DA, 2 DJ); 18 km NE of Charlina Rock (W. K. Youngson! 15 October 1979, WAM 1193.81, 3 DA); Emu Hole, 4 miles S of Nanambinia Homestead (D. L. Serventy! 7 August 1952, SAM, 5 DA); 8 miles S of Nanambinia (G. M. Storr! 14 December 1962, WAM, 21 DA, 1 DJ); 9 miles S of Nanambinia (A. R. Main! 4 December 1959, WAM 1168.81, 2 DA); Booanya Rocks, 28 miles S of Balladonia (A. M. Crocker! May 1967, WAM 233.67, 2 DA, 2 DJ; G. M. Storr! 13 December 1962, WAM 25 DA, 20 DJ); Coragina Rock, 18 miles S of Nanambinia Homestead (G. M. Storr! 16 December 1962, WAM, 13 DA, 11 DJ); Heinsman Rock (D. Merrilees, G. M. Storr! 16 December

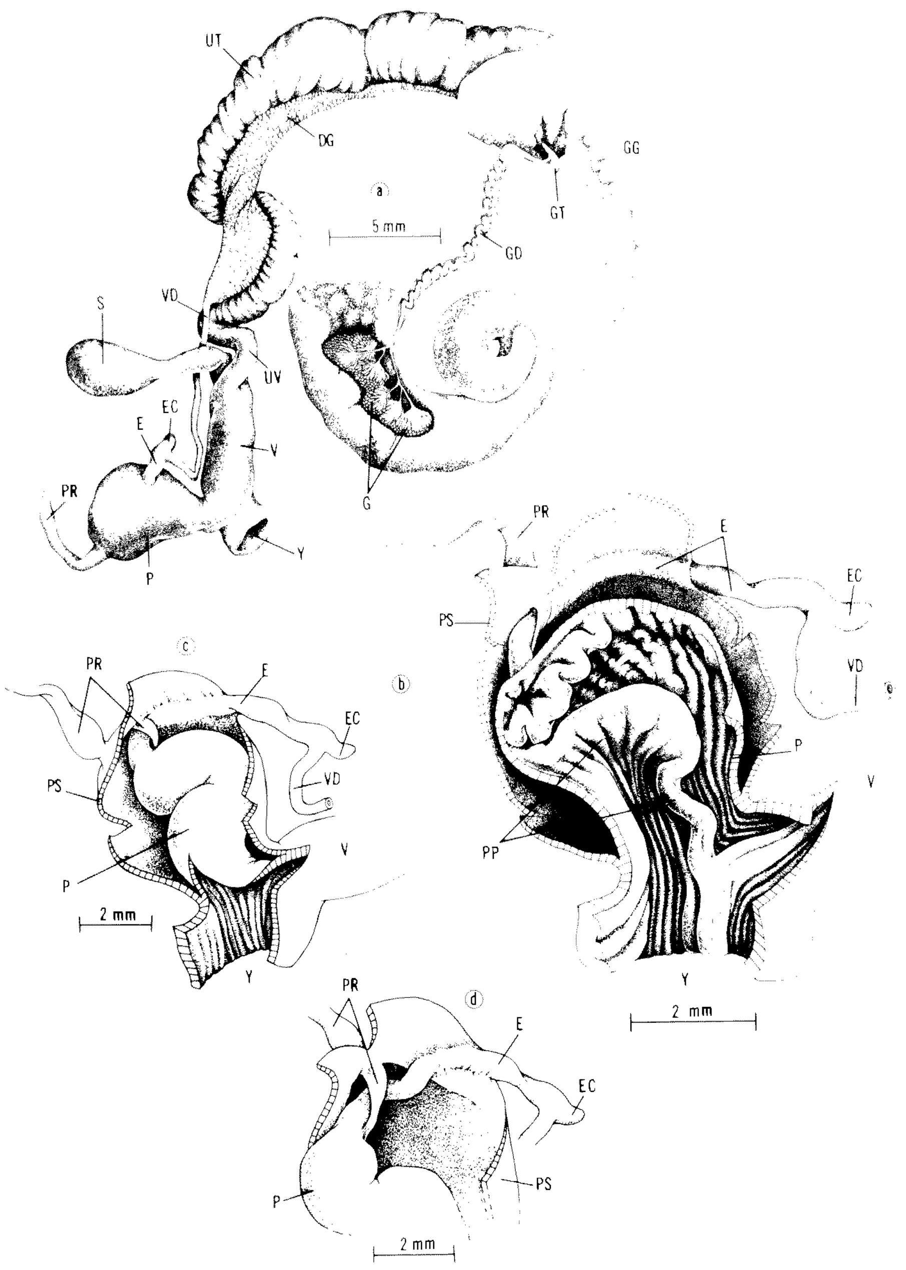


Fig. 382: Genitalia of *Sinumelon kalgum* Iredale, 1939: WA–94, saltbush area just N of Balladonia Hotel–Motel, near Balladonia Station, fringe of Nullarbor, WA. 21 February 1974. FMNH 182461, Dissection B: (a) whole genitalia; (b) interior of penis; (c) opened penis sheath (PS) showing coiling of penis (P); (d) attachment of penial retractor muscle (PR). Scale lines as indicated. Drawings by Elizabeth A. Liebman.

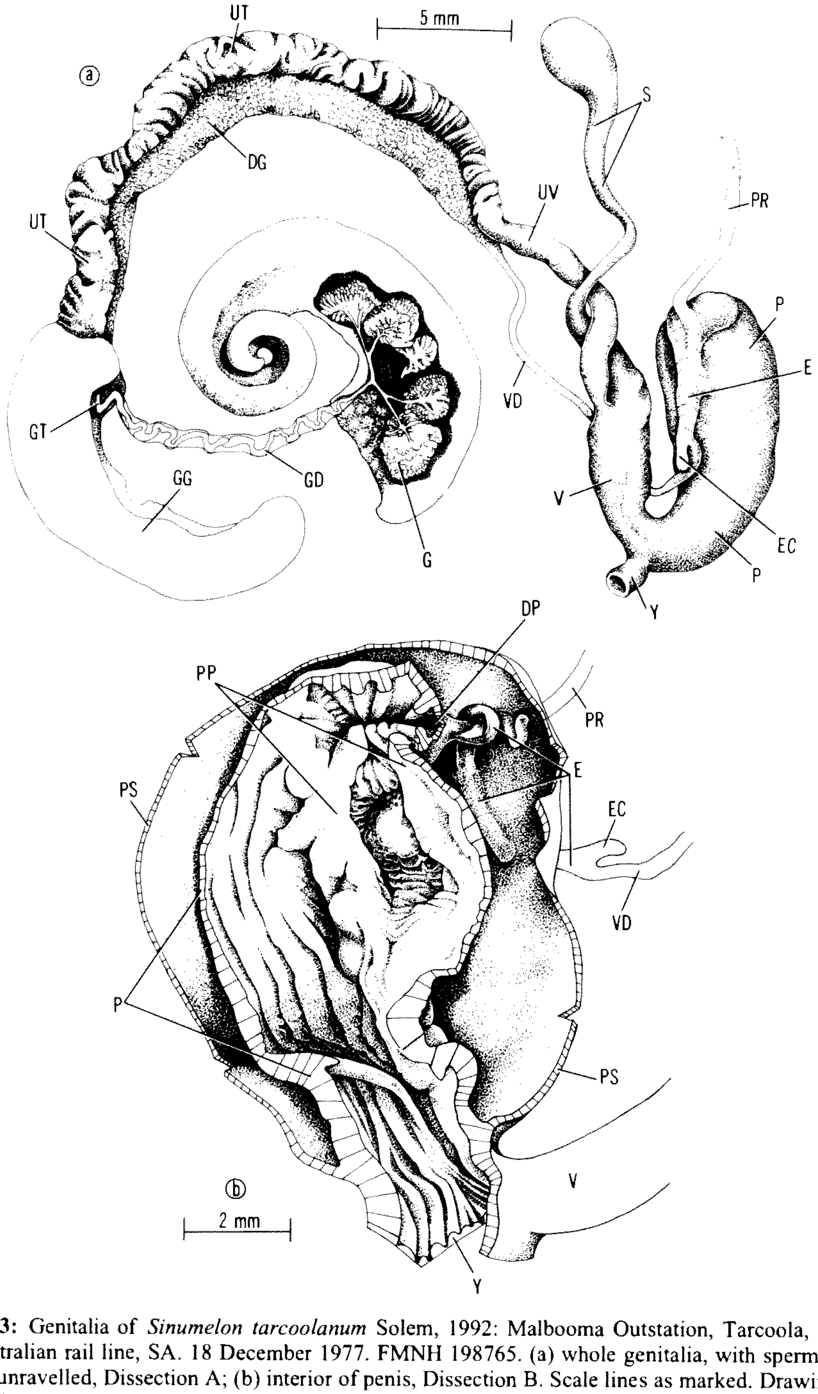


Fig. 383: Genitalia of *Sinumelon tarcoolanum* Solem, 1992: Malbooma Outstation, Tarcoola, Trans-Australian rail line, SA. 18 December 1977. FMNH 198765. (a) whole genitalia, with spermatheca (S) unravelled, Dissection A; (b) interior of penis, Dissection B. Scale lines as marked. Drawings by Marjorie M. Connors. (From Solem, 1992: figs 83a–b).

1962, WAM, 8 DA, 8 DJ; W. H. Cleverley! 13 April 1976, WAM, 4 DA, 1 DJ); 43 miles N of Pine Hill (A. R. Main! 16 December 1952, WAM 1166.81, 1 DA); near Deralinya Homestead ruins (WA–1091, 9 June 1989, FMNH 221778, 18 LA, 5 LJ); Yindi Station (N. Maddigan! 3 September 1956, WAM 171/6–1956, 6 DA); Yarri, near Edjudina (A. M. & M. J. Douglas! 22 August 1974, WAM, 6 DA; Bob Hunter! June 1983, WAM, 2 DA); Edjudina Station, Eastern Goldfields (P. N. Chalmer! 31 March 1980, WAM, 9 DA, 3 DJ); *ca.* 16 miles SE of Coolgardie (WA–482, FMNH 204104, 5 DJ); by Koolgardie-Kambalda road (N. Sammy! 22 April 1973, WAM 268.74, 2 DA, 1 DJ); Norseman (WAM 87.70, 2 DA); Pink Lake, 16–17 miles W of Cundeelee (L. Kwitko! 19 January 1974, WAM, 1 DA); Kanowna, Eastern Goldfields (M. J. Douglas! 21 August 1974, WAM, 1 DA); Kalgoorlie (H. E. Hill! June 1904, MV F28297, MV F28299, MV F28300, 8 DA; 8 miles W of, D. L. Serventy! 9 August 1952, SAM, 3 DA, 2 DJ; Lake Gidgie, 8 miles N of, WAM 151.35, 1 DA); Coolgardie (12 miles N of, W of Kurrawang Lakes, 1965, WAM 68.1209 (fossil), WAM 68.1210 (fossil), 4 DA); Mt. Manning Range (1.5 km S of SE peak, A. A. Burbidge! September 1980, WAM 1.82, 1 LA).

Range

Sinumelon kalgum Iredale, 1939 has been collected as far S as Heinsman Rock on the Balladonia-Cape Arid track and is common from there to N of Balladonia (**Maps 25–26**). It probably extends inland to the Zanthus-Coonana-Yarri-Edjudina axis, although material from these regions is so worn and battered that it is impossible to give positive identifications. The records then extend W to Norseman, Kalgoorlie, Coolgardie and finally to the Mt Manning Range (29°58'S, 119°38'E). Most inland records are based solely on very worn examples and need to be confirmed by dissection, since *S. tarcoolanum* and *S. vagente* may partly overlap the range of *S. kalgum* (**Maps 25–26**). See discussion above.

Diagnosis

Shell large, adult diameter 17.35–27.75 mm (mean 23.80 mm), with 4 1/8+ to 5 5/8– (mean 5 1/8+) whorls. Apex and spire elevated (**Figs 378a, c**), shell height 14.95–25.8 mm (mean 21.03 mm), H/D ratio 0.795–1.088 (mean 0.884). Body whorl rounded, descending sharply just behind aperture (**Figs 378a, c**). Apex and early spire (**Plate 184c**) with dense micropustulations that become more prominent and widely spaced (**Plate 184d–e**) on lower spire and body whorl. Vague radial ridges present, last portion of shell usually with many rugosities and growth pauses. Umbilicus (**Figs 378b, d**) usually a narrow lateral crack, rarely moderately open. Lip weakly expanded, often thickened internally. Shell normally thick. Colour white, some inland populations with light yellow-brown periostracum. Based on 246 measured adults.

Genitalia (**Figs 382a–d**) with thickened vagina (V), short free oviduct (UV), spermatheca (S) wrapped around free oviduct. Penis complex usually short, epiphallic caecum (EC) short, located below middle of penis. Epiphallus (E) entering wall of penis sheath (PS) about at middle, emerging into sheath chamber below apex. Penial retractor muscle (PR) partly circling epiphallus before inserting on penis apex. Penis (P) kinked within sheath, internally (**Fig. 382b**) with high main pilaster (PP) that curves above, well developed wall sculpture around epiphallic pore (EP).

Central and lateral teeth of radula (**Plate 187a**) with very prominent anterior flare,

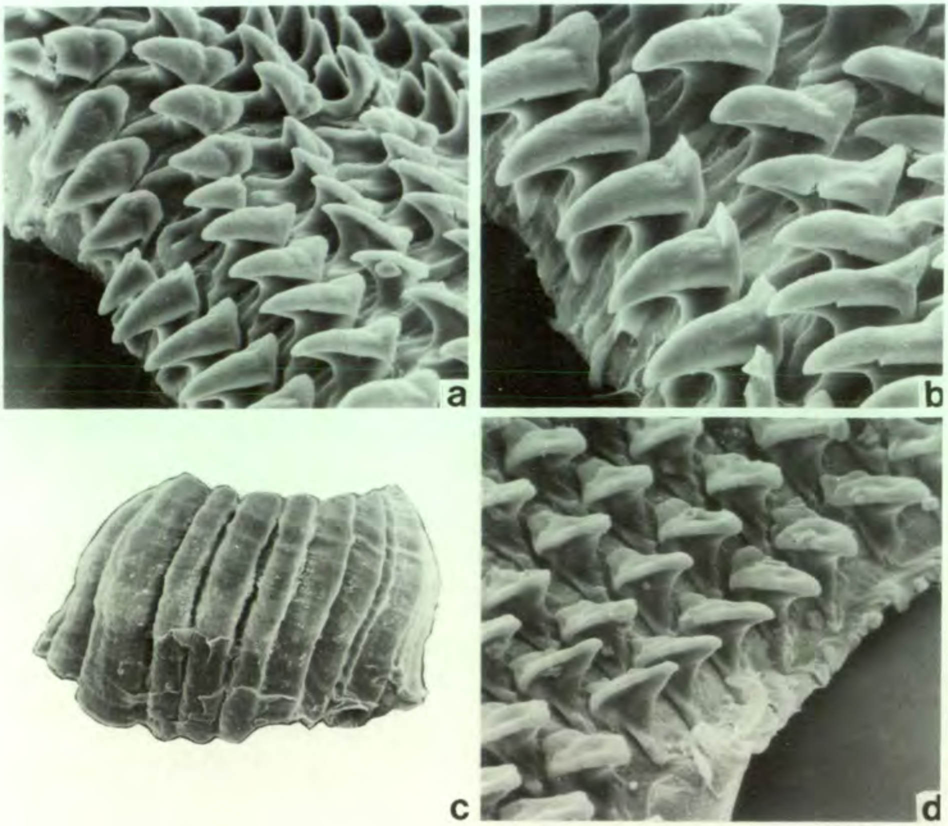


Plate 187: Radular teeth and jaw of *Sinumelon kalgum* Iredale, 1939: (a–c) WA–95, Afghan Rock, Balladonia Station, WA. 21 February 1974. FMNH 182519. a is central and early laterals at 395X. b is late laterals at 580X. c is jaw at 58X; (d) WA–94, scrub just N of Balladonia Hotel-Motel, WA. 21 February 1974. FMNH 182461, Dissection E. d is late laterals at 410X.

typical cusp shaft angle, with curved cusp tip and blunt tip. Mid-laterals (**Plate 187b**) with enlarged anterior flare, small ectocone and more curved cusp tip. Lateromarginal transition (**Plate 187d**) and jaw (**Plate 187c**) typical.

Discussion

Typical adult examples of *Sinumelon kalgum* Iredale, 1939 are readily recognised by their white colour, unexpanded lip, sharp descension of the body whorl and relatively high spire. The reddish colour suffusion, larger size and reduced micropustulations of *S. tarcoolanum* will separate fresh examples. The latter has a generally inland range (**Map 26**) that extends E as far as the Gawler Ranges of SA, whereas *S. kalgum* (**Maps 25–26**) has a more southern and western range. In the areas near Yindi and Edjudina, long dead or juvenile examples have been collected that cannot be identified with certainty. "First impression" identifications have been retained but study of live-collected examples will be required to work out the inland distributional limits.

The figured genitalia (**Figs 382a–d**) is from a partly retracted individual and thus the length of the penis complex is artificially shortened.

Size and shape variation in local populations (**Table 139**) is moderate, with no clear geographic pattern. The higher spire and larger size (**Table 137**) of *S. tarcoolanum* is consistent among local populations.

SINUMELON TARCOOLANUM SOLEM, 1992
(Plate 184a–b; Figs 379a–c, 383a–b; Map 26)

Sinumelon tarcoolanum Solem, 1992, *Rec. South Austr. Mus. Monograph Series, No.***2**: 1–425, figs 82a–c, 83a–b, 126, 139, plts 58a–b, 64a–f, 72a – NW Gawler Range to rail line, SA and W into WA.

Comparative remarks

Sinumelon tarcoolanum, which ranges from the W end of the Gawler Ranges, SA to at least 168 km N of Cook, SA and then W to near Yindi, WA (**Map 26**), is the largest (**Table 136**) species from WA, although some individuals of both *S. vagente* Iredale, 1939 and *S. kalgum* Iredale, 1939 overlap in size. Its very large diameter (mean 26.20 mm), high H/D ratio (mean 0.921), increased whorl count (mean 5 3/8–), greatly reduced micropustulations (**Plate 184a–b**) and normal presence of a reddish spire suffusion that often becomes a supraperipheral spiral band on the body whorl (**Fig. 379b**), differentiate it from the other WA species. The malleated surface sculpture (**Plate 183c–e**), slightly open umbilicus (**Fig. 377d**) and small size (**Table 136**) of *Sinumelon nullarboricum* (Tate, 1879); very small (mean diameter 14.42 mm) size (**Table** 136) and weak micropustulations (**Plate 183a**) of *S. jimberlanensis* easily separate those species. *S. vagente*, from Bindoo Hill, inland of Geraldton to Paynes Find and Mt Singleton, WA (**Map 26**), is much smaller (mean diameter 19.68 mm), with a lower spire (mean H/D ratio 0.862), reduced whorl count (mean whorls 4 3/4), prominent micropustulations (**Plate 183b**) and lacks any red markings. *S. kalgum*, which ranges (**Map 25**) from Mt Manning and Johnson Rocks (*ca.* 119°40'E, 29°49'S) SE to near Balladonia (123°52'E, 32°27'S) and then S to Pine Hill on the Cape Arid track, WA, is smaller (mean diameter 23.80 mm), with a lower spire (mean H/D ratio 0.884) at a slightly lower whorl count (mean 5 1/8+) and also lacks the colouration that is characteristic of *S. tarcoolanum* (**Figs 379a–c**). Differences from strictly South Australian species have been given in Solem (1992). Anatomically (**Figs 383a–b**), the medium length and tapered penis complex of *S. tarcoolanum* is most similar to that of *S. vagente* (**Fig. 384a**) but differs internally (compare **Figs 383b, 384b**) by its corrugated main pilaster and large accessory ridges, while the latter has a simple main pilaster (PP) and reduced accessory ridges. The short, almost globose penis complexes of *S. kalgum* (**Fig. 382a**) and *S. jimberlanensis* (**Fig. 380a**) and the long, nearly cylindrical penis complex of *S. nullarboricum* (**Figs 381a–c**), in which the main pilaster is greatly reduced in prominence, provide obvious differences. For South Australian species differences see Solem (1992).

Holotype

SAM D17073, under Milk Bush (*Sarcostema australe*), just W of Malbooma Outstation house, NW of Tarcoola, SA. 30°41'S, 134°10'30"E. Collected by Fred and Jan Aslin 18 December 1977. Height 21.1 mm, diameter 22.9 mm, H/D ratio 0.926, whorls 5–.

Paratopotypes

SAM D17074, FMNH 198765, 3 LA, 17 LJ from the type locality. FWA 2926 contains some adults and a number of juveniles. This 'type lot' material was seen after completion of the species description.

Paratypes

See Solem (1992) for the many South Australian records.

Material studied

SOUTH AUSTRALIA: Cook (25 miles N of, WAM, J. Dell! 10 May 1970, 1 DA; 85 miles N of, WAM, J. Dell! 10 May 1970, 2 DA, 2 DJ; 89 miles N of, WAM, G. M. Storr! 4 September 1968, 12 DA; 99 miles N of (J Dell and party! 10 May 1970, WAM, 2 DA, 2 DJ); 100 miles N of (WAM 3 September 1968, 6 DA, 1 DJ; 105 miles N of, WAM, J. Dell! 19 May 1970, 5 DA); Maralinga, N of RR, SAM, A. A. Eatts!, 1 DA, 1 LJ, 2 DJ); N fringe of Nullarbor near "The Dip", 29°45'S, 129°40'E, WAM 86.1397 (fossil), A. J. Carlisle! 5 August 1986, 11 DA, 1 broken.

WESTERN AUSTRALIA: Reid ("Lookout Hill", 89 km ENE of, WAM 1203.81, 30°05'26"S, 128°48'21" E, Bill Cleverly!, 1 DA); Goddard Creek, 14 km NW of Cundeelee (30°43'S, 123°26'E, WAM, W. H. Butler! 23 January 1959, 8 DA, 2 broken); Yindi, Kurnalpi District (30°32'S, 122°42'E, WAM, Gill Chapman! June 1972, 4 DA); Yindi Station (WAM 4678.68, Mike Kriewaldt! 1967, 9 DA, 3 broken).

Range

Sinumelon tarcoolanum has been collected from Yindi Station, WA (*ca.* 122°40'E) to the W end of the Gawler Ranges, SA (*ca.* 135°20'E, see Solem, 1992: figs 126, 139). It has been found inland as far as 105 miles (= 168 km) N of Cook, SA and between 29°45'S and 30°43'S in WA. Probably many additional isolated inland colonies exist but no malacological collecting activity has taken place between the Trans-Australia Railway line and Warburton area of the Red Centre. The known range thus covers approximately 1,225 km E to W, with a N-S known range in SA of perhaps 450 km from the SW Gawler Range to the furthest record N of Cook. Lack of collecting in WA above the rail line prevents any accurate measure of N-S range in this region (**Map 26**).

Diagnosis

Shell very large, adult diameter 20.45–31.05 mm (mean 26.20 mm), whorls 4 3/4+ to 5 3/4+ (mean 5 3/8–). Spire very strongly elevated (**Fig. 379b**), shell height 18.75–28.2 mm (mean 24.13 mm), H/D ratio 0.807–1.052 (mean 0.921). Body whorl rounded, descending moderately just behind aperture (**Fig. 379b**). Apex usually eroded (**Plate 184a**), sometimes traces of fine wrinkles and pustulations visible, lower spire

(**Plate 184b**) with prominent radial ridging, no micropustulations. Umbilicus (**Fig. 379c**) closed or at most a narrow lateral crack. Lip not expanded, thickened internally, columellar portion usually covering umbilical crack. Lip and aperture white, spire and body whorl above periphery with reddish suffusion, which may concentrate into a supraperipheral red colour band on the body whorl in some individuals. Based on 210 measured adults.

Genitalia (**Figs 383a–b**) with long free oviduct (UV) and spermatheca (S), vagina (V) about half length of penis (P). Epiphallic caecum (EC) slender, prominent, located below middle of penis. Penis chamber (**Fig. 383b**) with long main pilaster (PP) that becomes corrugated above and few large accessory ridges lateral to and below main pilaster; complex low corrugated folds surround epiphallic pore and cover top of penis chamber.

Radular teeth and jaw (Solem 1992: plates 64a–f, 72a) typical, central and early laterals with very high cusp shaft angles, marked anterior flare, and slight curving of the somewhat blunted cusp tip.

Discussion

Sinumelon tarcoolanum has one of the largest ranges documented for any Australian land snail. It is exceeded by some pupillids but the 1,225 km E-W range is a record for any camaenid. Unfortunately, this range is based on conchological similarity, since no live examples have been collected in WA. All the specimens from there have been picked up "dead on ground" by non-malacologists. Specimens from Malbooma Outstation near Tarcoola on the rail line and Wallala Hill, Gawler Range (FA–22) in SA were dissected (Solem 1992) and found to have the same genital structures. In view of the differences shown by the other WA species and the strong conchological agreement among populations grouped here (**Table 137**), they are kept as a single species. Differences among the WA samples in size and shape are very minor, and they agree closely with SA populations (also see Solem 1992: table 25).

SINUMELON VAGENTE IREDALE, 1939

(Plates 183b, 185d–f; Figs 378e–f, 384a–b, 385; Maps 26–27)

Sinumelon vagente Iredale, 1939, *Jour. Roy. Soc. Western Aust.*, **25:** 54, plt. III, fig. 24 – Mt Singleton, inland from Geraldton, Western Australia; also published as Richardson, 1985, *Tryonia*, **12:** 278 – citation in checklist.

Comparative remarks

Sinumelon vagente, found from Bindoo Hill inland of Geraldton E to at least Paynes Find, WA (**Maps 26–27**), is of medium size (mean diameter 19.68 mm) and whorl count (mean 4 3/4), with the umbilicus mostly closed or a lateral crack (**Fig. 378e**), elevated spire (Fig. 378e, mean H/D ratio 0.862) and without red colour markings. The apex is nearly smooth but the spire and body whorl (**Plate 183b**) have a microsculpture of dense pustulations. The malleated shell sculpture (**Plate 183c–e**) and generally open umbilicus of *S. nullarboricum* (Tate, 1879) and the always open umbilicus (**Fig. 377b**), very small size (mean diameter 14.42 mm) and low spire (**Fig. 377a**, mean H/D ratio

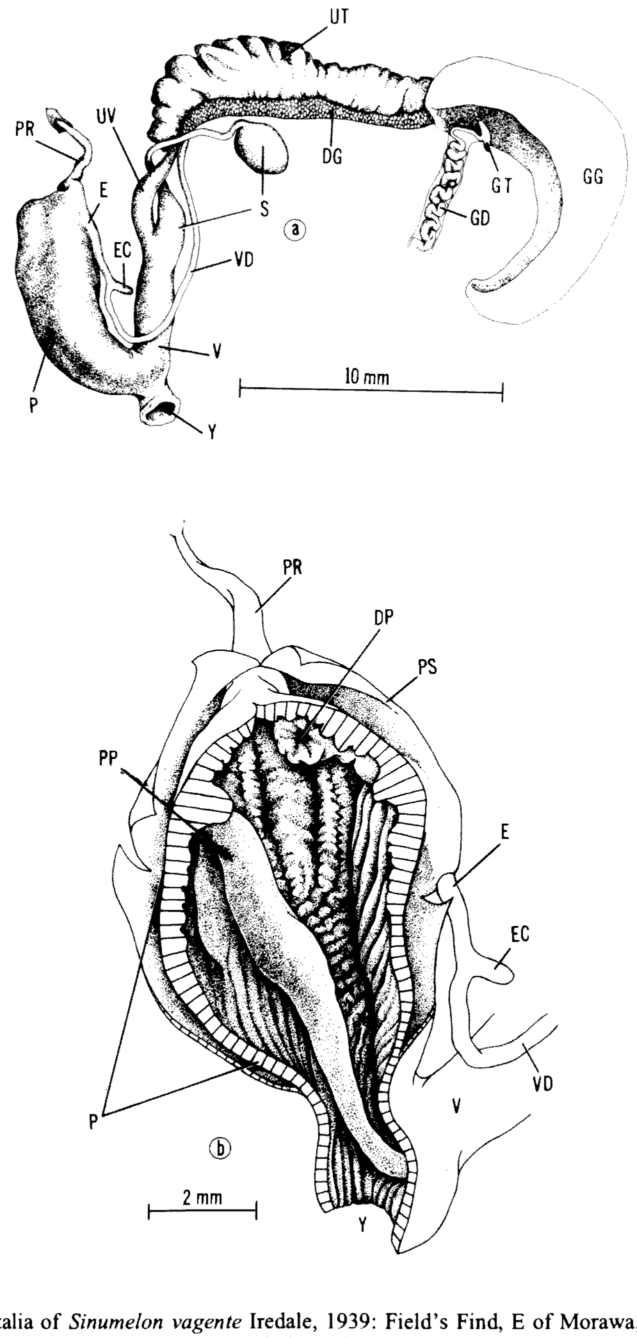


Fig. 384: Genitalia of *Sinumelon vagente* Iredale, 1939: Field's Find, E of Morawa, WA. 29 January 1968. WAM 387.74, Dissection B: (a) whole genitalia; (b) interior of penis. Scale lines as marked. Drawings by Elizabeth A. Liebman.

0.760) of *S. jimberlanensis* distinguish those two species from *S. vagente*. The very large (mean diameter 26.20 mm) *S. tarcoolanum* has a higher spire (Fig. 379b, mean H/D ratio 0.921), a much higher whorl count (mean 5 3/8–) and often a reddish spire suffusion or spiral red colour band on the body whorl. *S. kalgum* Iredale, 1939 is most similar in shape (**Table 136**) but typically is considerably larger, with a higher whorl count, thicker shell that descends more rapidly just behind the lip, and is white in colour, except near the northwestern limits of its known range, where the shell can have a greenish-yellow periostracum. Fresh examples have a microsculpture of very dense pustulations (**Plate 184c–e**). Anatomically (**Figs 382a–d**), the vagina (V) is relatively long, the penis-complex is large and cylindrical and the penis chamber has a large and relatively simple main pilaster (PP) with reduced accessory pilaster structures. *S. tarcoolanum* (**Figs 383a–b**) has a tapered penis complex, much thicker vagina, enlarged accessory pilasters, corrugated main pilaster and long free oviduct. The other species with a cylindrical penis, *S. nullarboricum* (**Fig. 381a–c**), has a very short vagina and very different penis chamber wall sculpture. In both *S. kalgum* (**Figs 382a–d**) and *S. jimberlanensis* (**Figs 380a–b**) the penis is very short, almost globular in shape and has very different penis chamber wall sculpture.

Holotype

WAM 109.44, Mt Singleton, inland from Geraldton, Western Australia; 117°19'E, 29°28'S. Collected by G. H. Bardwell 28 May 1932. Height 19.1 mm, diameter 19.95 mm, H/D ratio 0.957, whorls 4 4 7/8.

Paratypes

WAM 109.44, AM C.64842, MV F28277, 3 DA, 1 DJ from the type locality.

Material studied

WESTERN AUSTRALIA: Mt Meru, 9 miles S of Wurarga, 6 miles N of Yalgoo road (John White! 23 July 1967, WAM 337.74, 1 LA, 1 DA); 12 km N of Mullewa (Robin Roe! 9 September 1983, WAM, 2 DA); reserve E of road between Murchison River and Mullewa (Mrs R. Roe! 9 September 1983, WAM, 2 DA); along Wubin-Mullewa road, S of Morawa (O. Mueller! 1 June 1986, WAM, 1 DA, 2 DJ); Yuna Reserve, banks of Greenough River (12 May 1973, WAM, 1 DJ); 0.99 km above windmills at Noondamura Pool, Greenough River, near Bindoo Hill, NW of Mullewa (WA–1067, 20 May 1989, FMNH 221714, 3 DJ); near Bindoo Hill, E of Geraldton (WA–420, WA–1061, WAM 920.87, SAM D18246, FMNH 199364, FMNH 199762, FMNH 211992–3, 8 LA, 3 DA, 7 LJ, 1 DJ); Barong Station (John White!, WAM, 1 DA); Gullewa, near Old Shanomdor Mine (John White! 23 July 1967, WAM 245.74, WAM 355.74, 1 LA, 1 DA, 1 LJ); Ponton Creek (= Goddard's Creek) (R. Savage! 18 August 1967, WAM 1155.81, 2 DJ); Gullewa Mine (M. H. Henderson! 9 March 1967, WAM 1 DA); Ederga River banks, E of Gullewa (D. Ride & D. Merrilees! 22 September 1961, WAM, 8 DA, 3 DJ); Fossil Cliff, Irwin River (Keith Tostevin! 1970, WAM 1548.70, 1 DA); Burnerbinmah Homestead (Mrs D. Craven! 1961, WAM 244.74, 1 DA); Narndee Station (Mrs R. Fogerty! 6 May 1980, WAM, 2 DA); Thundellara Station (A. M. & M. J. Douglas! 20 June 1976, WAM, 3 LA); on top of Mt. Wardia (28°59'S, 118°13'02"E, A. Baynes! 26 April 1975, WAM, 10DJ); Fields Find (A. M. Douglas! 11 April 1965, WAM 347.74, 12 LA, 1 LJ; A. M. Douglas! 29

January 1968, WAM 387.74, 11 LA, 2 LJ; Kevin Morgan! 12 April 1972, WAM, 9 DA, 4 DJ; Mrs. F. Dodds! 11 October 1970, WAM, 4 DA); 2.3 km N of Paynes Find (WA–724, WAM 921.87, FMNH 205368–9, 1 DA, 3 LJ, 5 DJ); Paynes Find (J. B. Horner! 21 June 1976, WAM, 1 DA, WAM, 7 DA); Rothsay Mine, Yalgoo District (Kevin Morgan! April 1972, WAM, 14 DA, 6 DJ); Rothsay (Kevin Butler! 7 June 1971, WAM, 4 DA, 11 DJ); Koobabbie, between Marchagee and Coorow (Ms A. Doley! October 1985, WAM, 2 DJ); Mt. Jackson, 100 km N of Bullfinch (R. How! 14 February 1980, WAM 1118.81, 2 DJ).

Range

Sinumelon vagente has been taken as far N as Mt Meru (28°31'S) and as far S as Mt Jackson (30°12'S). The westernmost record is at Bindoo Hill (115°13'E) and the easternmost at Mt. Jackson (119°06'E). The total diagonal range is thus about 300 km. Localities are too few in number for calculating an area range (**Maps 26–27**). Extension of the range to the SE is highly probable, since no collections have been made in this region.

Diagnosis

Shell medium in size, adult diameter 16.55–24.65 mm (mean 19.68 mm), with 4 3/8+ to 5 1/8+ (mean 4 3/4–) whorls. Apex and spire elevated (**Fig. 378e**), shell height 13.3–22.8 mm (mean 16.97 mm), H/D ratio 0.774–1.005 (mean 0.862). Body whorl rounded, descending slightly behind aperture (**Fig. 378e**). Apex and early spire without radial ridging, lower spire and body whorl (**Plate 183b**) with irregular radial ridging and varied micropustulations. Umbilicus (**Fig. 378f**) a narrow lateral crack to closed. Lip only slightly expanded, white, columellar section slightly expanded. Colour yellow-brown, lighter on base, with reddish markings. Based on 88 measured adults.

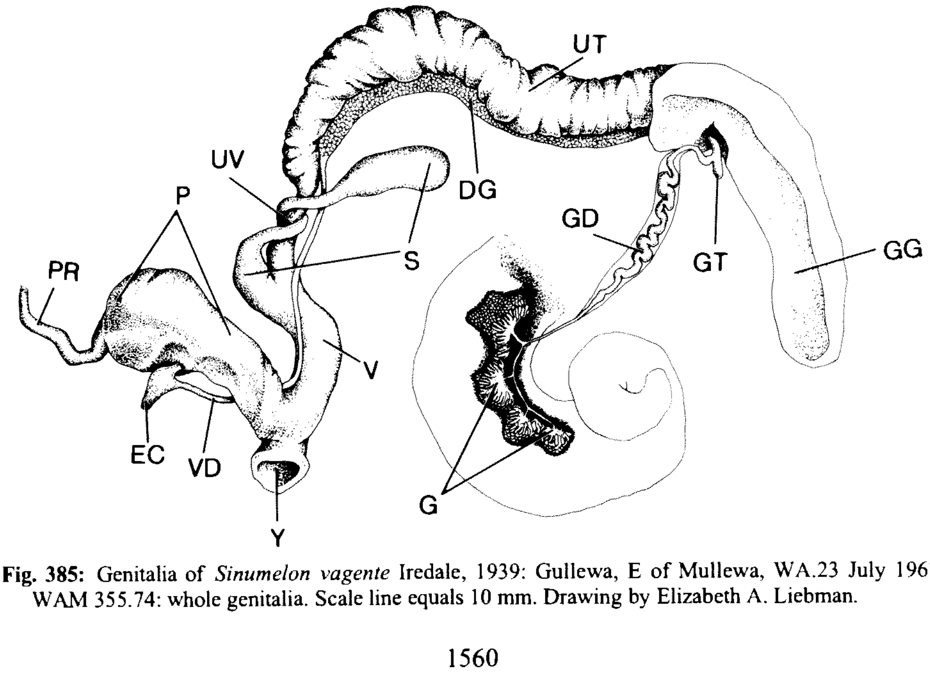


Fig. 385: Genitalia of *Sinumelon vagente* Iredale, 1939: Gullewa, E of Mullewa, WA.23 July 1967. WAM 355.74: whole genitalia. Scale line equals 10 mm. Drawing by Elizabeth A. Liebman.

Genitalia (**Figs 384a–b, 385**) with long slender vagina (V) and free oviduct (UV). Spermatheca (S) with base of shaft expanded, twisted around free oviduct. Epiphallic caecum (EC) small, located below middle of penis (P), which is large and cylindrical. Penis sheath (PS) very thin walled. Penis chamber (**Fig. 384b**) with large main pilaster (PP), small accessory ridges, and typical corrugated ridges.

Central and lateral teeth of radula (**Plate 185d**) with moderate anterior flare, high cusp shaft angle, cusp tip bluntly rounded and with moderate curvature, ectocone absent. Late laterals (**Plate 185e**) with enlarged anterior flare, prominent ectocone and trace of endocone, cusp tip remaining strongly curved. Lateromarginal transition (**Plate 185e**) abrupt, marked by increased side cusps, loss of anterior flare and reduced cusp tip curvature. Outermost marginals and jaw (**Plate 185f**) typical.

Discussion

The type lot of *Sinumelon vagente* consists of bleached and worn "bones" that retain no trace of sculpture. They agree in shape and lip features with dissected materials from Bindoo Hill and Fields Find, so that this is considered to be a single species.

Few samples contained enough specimens for analysis of variation (**Table 137**) and no geographic pattern can be detected from these limited data.

GENUS *FALSPLEUROXIA* GEN. NOV.

Shell medium in size, variable, adult diameter 14.1 to 21.2 mm, whorls 3 7/8+ to 4 3/4–, increasing fairly rapidly in width (**Figs 386c, f**). Spire moderately and evenly elevated (**Figs 387b, d**), H/D ratio 0.539–0.777. Apical sculpture (**Plate 188a, d**) smooth initially, with irregular radial growth ridgelets on later portion, spire and body whorl (**Plate 188b–d**) with low, rounded, nearly regularly spaced radial ridges that fade out below periphery. Microsculpture (**Plate 188a–d**) of low, slightly elongated pustules that are topped (**Plate 188b–c**) with low periostracal setae having wide lateral buttresses. Body whorl rounded, descending regularly and slightly for up to an eighth of a whorl behind the lip (**Figs 386b, d**). Umbilicus variable in width, usually narrow (**Figs 386c, f**), partly closed by reflected columellar lip, D/U ratio 5.94. Columellar lip slightly expanded on columellar margin, narrow and not thickened on basal and palatal margins (*overlanderensis*, **Figs 386a–c**) or not expanded at all (*F.* species, **Figs 386d–f**). Shell colour very light yellow-brown above, with narrow red spiral slightly supraperipheral band visible on lower spire and body whorl (*overlanderensis*) or unknown (*F.* species). Lip white.

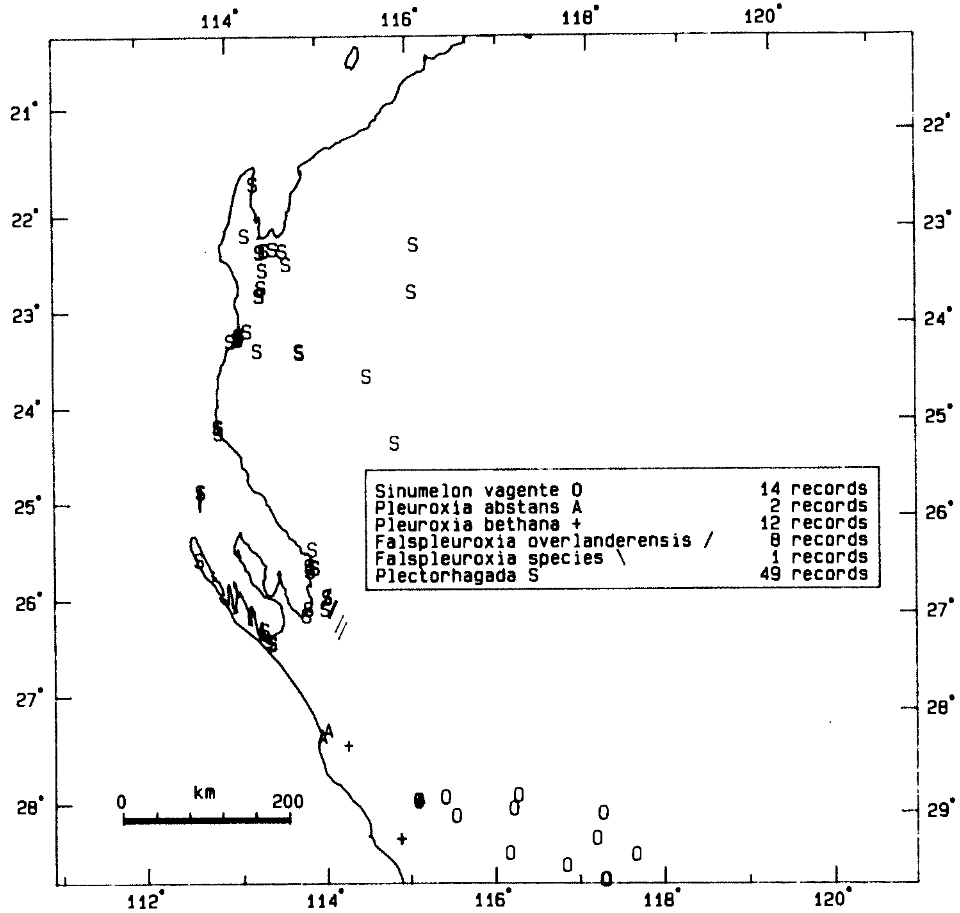
Specimens aestivate sealed by a thick chitinous rim to another shell, usually an adult example which is sealed to the underside of a limestone slab or tree root.

Genitalia (**Figs 387a–c**) with enormous enlargement of albumen gland (GG), vagina (V) very short, free oviduct (UV) and shaft of spermatheca (S) twisted around each other. Head of spermatheca just above base of prostate-uterus. Epiphallic caecum (EC) a small nub, epiphallus (E) free of penis wall, partly circling penial retractor muscle (PR) before entering penis (P) through a verge (PV). Penis short, almost globular in shape, without a sheath. Internally (**Figs 387b–c**) with a short verge and terminal pore (PVO) plus a lateral vergic stimulator (PPV) and one small pilaster (PP) on the upper chamber wall. Lower part of chamber walls smooth except for low circular ridge. Jaw (**Plate 189f**) with narrow, high vertical ribs, reduced on outer margins. Central and lateral teeth of radula (**Plate 189a**) with small anterior flare, no ectocone, high cusp shaft angle with strongly curved and bluntly rounded cusp tip, basal plate massive. Mid (**Plate 189b**) and late (**Plate 189c**) laterals with enlarged basal plate and anterior flare, latero-marginal transition (**Plate 189d**) abrupt, with ectocone and endocone developed quickly, marginals (**Plate 189e**) without unusual features.

Type species: *Falspleuroxia overlanderensis* sp. nov.

Comparative remarks

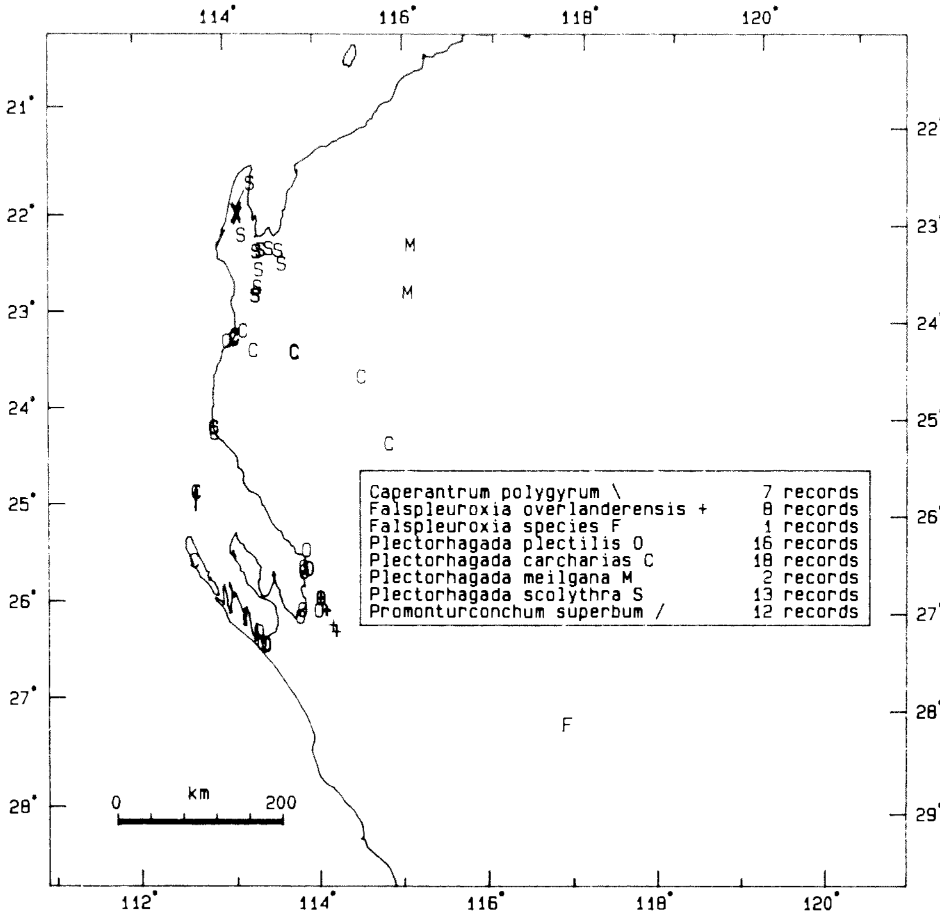
The simple radial ribs that are absent below the periphery, smooth shell apex, microsculpture of setae-surmounted pustules, narrow umbilicus and relatively low spire combine to separate *Falspleuroxia* from the neighbouring genera *Pleuroxia* and *Plectorhagada*. Both *Pleuroxia bethana*, from the Greenough River basin inland of Geraldton and the mouth of the Murchison River to the N (**Maps 20, 27**) and *Pleuroxia*



Map 27: Records of *Falspleuroxia overlanderensis*, *F.* species, *Plectorhagada*, *Pleuroxia abstans*, *Pleuroxia bethana* and *Sinumelon vagente* in the region from the North West Cape south through Geraldton, WA.

abstans Iredale, 1939 from the mouth of the Murchison River, have prominent radial ribs on the shell base, prominent apical shell sculpture (**Plate 177a**) and wider umbilici (**Figs 368Ac, 368Bf**). The species of *Plectorhagada* have a characteristically dense apical sculpture and, at least on the spire, a crenulated or crinkled sculpture of anastomosing radial ribs and dense pustules (**Plates 190–193**) that is strikingly different in aspect.

Compared with the present genus, species of *Pleuroxia* retain a thin penial sheath and have more massive and complex penial pilasters and a larger epiphallic caecum, but lack a verge (**Figs 371, 373, 376**), while the few dissected *Plectorhagada* either lack (*plectilis, carcharias*) or have a very faint remnant of (*scolythra* sp. nov.) an epiphallic caecum, lack a penis sheath, and have more standard penis chamber wall pilasters. *F. overlanderensis* sp. nov. is the only species of Sinumeloninae known to have developed a verge.



Map 28: Records of the species belonging to the sinumelonid genera *Caperantrum*, *Falspleuroxia*, *Plectorhagada* and *Promonturconchum* in the North West Cape to Shark Bay area, WA.

Thus *F. overlanderensis* sp. nov. is easily separated from other WA genera in both shell and genital features.

Distribution and comparative ecology

Map 27 summarises the known distribution of both *Falspleuroxia* and *Plectorhagada* along the W coast of WA between North West Cape and the Geraldton area. *Plectorhagada plectilis* (Benson, 1853) and *F. overlanderensis* have a narrow zone of overlap 14–15 km N of the Overlander Roadhouse on the North West Coastal Highway (**Maps 28–29**), but otherwise the species appear to be allopatric. Both *Pleuroxia* and *Sinumelon* have a distinctly more southern distribution (**Maps 20, 24, 26, 27**). The single specimen of *Falspleuroxia* species (**Map 27**) was collected in the SE fringe of the Murchison River drainage basin and is well removed from other collecting records.

Specimens of *F. overlanderensis* aestivate tightly sealed to the underside of limestone rocks or onto shells that are sealed to these rocks. The large adults may have many individuals sealed to them, whereas smaller ones rarely have other snails attached. This is not a matter of space but seems to indicate some selectivity, with larger shells (proven survivors?) selected over smaller ones. Clusters of shells sealed-together in rock rubble or at the bottom of crevices are commonly observed. They do not form the lengthy "chains" of sealed together shells (found in *Plectorhagada*.

The enormous enlargement of the albumen gland (**Fig. 387a**) in *Falspleuroxia* is partly matched by that of *Plectorhagada* (**Figs 391–393**), *Pleuroxia bethana* (**Fig. 369a**) and some *Rhagada* (**Figs 404–405**) but stands in great contrast to the situation found in taxa from other arid areas of Australia.

The name *Falspleuroxia* refers to the similarity of the shell to that found in many species of *Pleuroxia*.

KEY TO THE SPECIES OF *FALSPLEUROXIA*

SE Murchison River drainage basin; diameter about 14 mm; sculpture more crowded . ... *Falspleuroxia* species (p. 1574)

Near Overlander Roadhouse, NW Coastal Highway; diameter 14–21 mm; sculpture more widely spaced .... *Falspleuroxia overlanderensis* sp. nov. (p. 1564)

FALSPLEUROXIA OVERLANDERENSIS SP. NOV.

(Plates 188a–d, 189a–f; Figs 386a–c, 387a–c; Maps 27–29)

Comparative remarks

Falspleuroxia overlanderensis sp. nov., which has been found from about 19 km S to 15 km N of the Overlander Roadhouse, at the Shark Bay turn-off on the NW Coastal Highway, WA (**Maps 27–29**), is of medium size (mean diameter 17.04 mm), with comparativly few and rather rapidly widening whorls (mean 4 3/8–), a moderately elevated spire (**Fig. 386b**), a narrow umbilicus (**Fig. 386c**, mean D/U ratio 11.8), smooth apex (**Plate 188a, d**), basic shell sculpture of simple, low radial ribs that

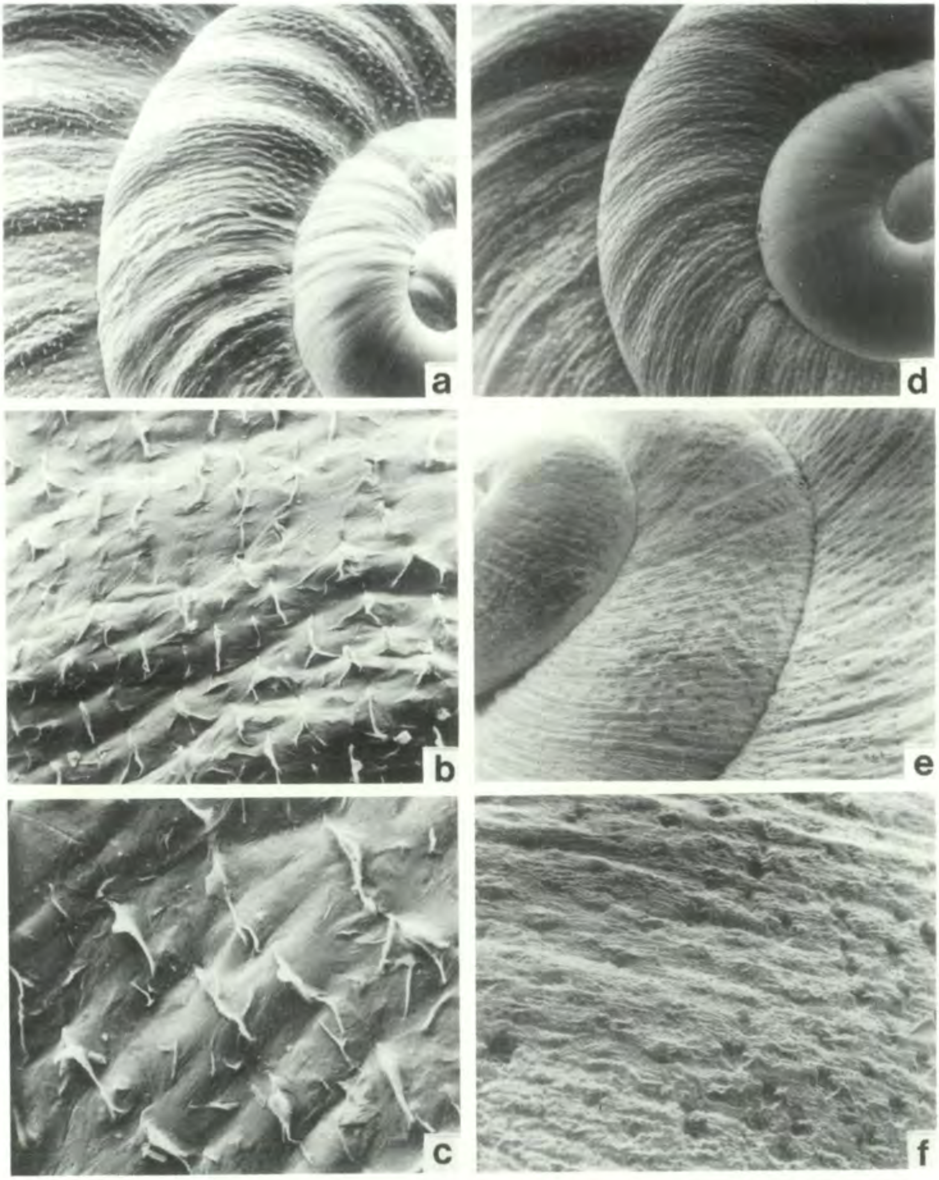


Plate 188: Shell sculpture of *Falspleuroxia*: (a–c) *F. overlanderensis* sp. nov. a–c, WA–56, 10.6 miles S of Overlander Roadhouse, North West Coastal Highway, WA. FMNH 182594. a is apex and spire at 18X. b is detail of lower spire at 89X. c is detail of lower spire microridging at 185X. (d) *F. overlanderensis* sp. nov. WA–55, 300 yards N of Overlander Roadhouse, North West Coastal Highway, WA. d is apex and spire at 20.8X; (e–f) *F.* species. Dalgaranga Hill, NW of Mt Magnet, WA. WAM 475.77. e is apex and spire at 20X. f is lower spire at 46.5X.

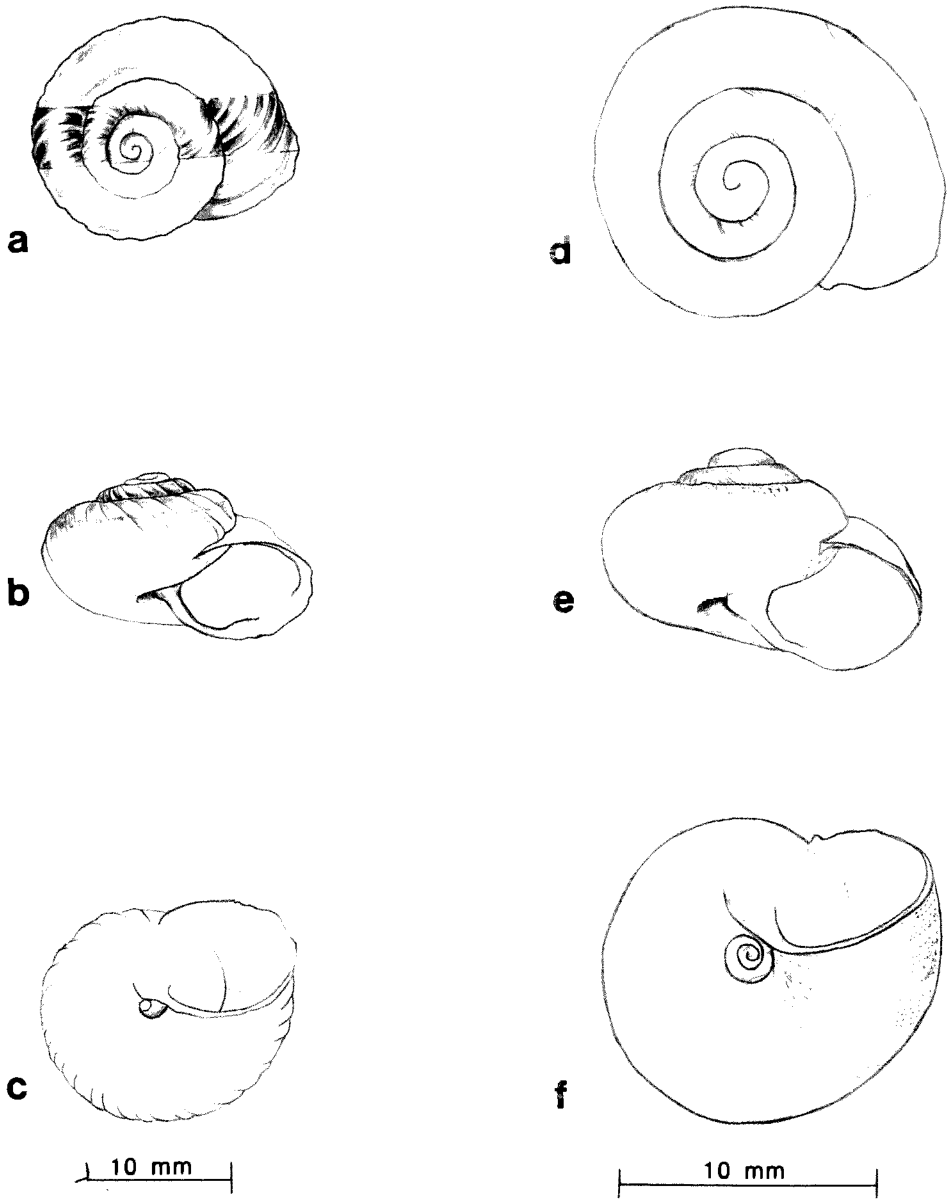
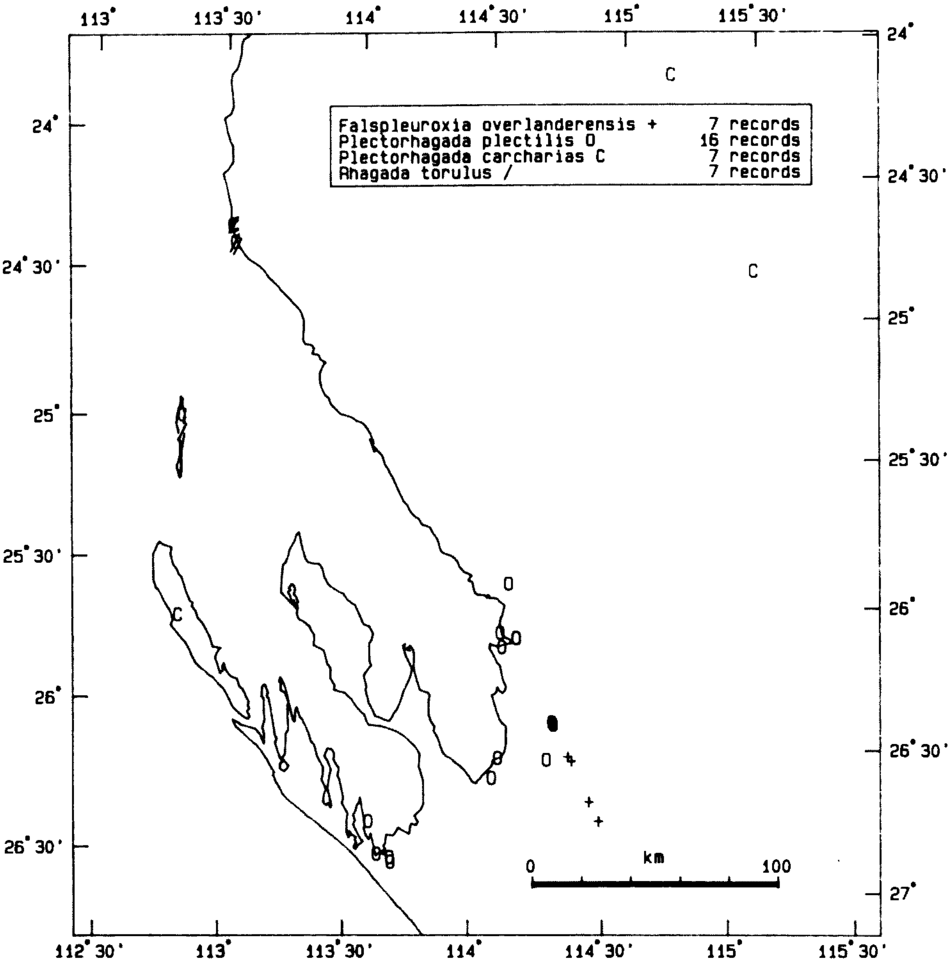


Fig. 386: Shells of *Falspleuroxia*: (a–c) Holotype of *Falspleuroxia overlanderensis* sp. nov. WAM 753.87. WA–56, 10.6 miles S of Overlander Roadhouse, North West Coastal Highway, SSE of Gladstone, WA; (d–f) *Falspleuroxia* species. WAM 475.77. About half way up slope of Dalgaranga Hill, *ca* 100 km NW of Mt Magnet, WA. Scale line equals 10 mm. Drawings by Linnea Lahlum.

Table 140: Local variation in *Falspleuroxia* and *Plectorhagada*.

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Falspleuroxia							
overlanderensis	620	11.04 (8.3-14.0)	17.04 (14.3-21.2)	0.648 (0.539-0.777)	$4\frac{3}{8}-$ ($3\frac{7}{8}+$-$4\frac{3}{4}-$)	1.52 (0.75-2.75)	11.8 (5.94-23.0)
species	1	9.40	14.10	0.667	4	1.75	8.06
Plectorhagada							
plectilis	677	13.46 (10.05-16.8)	17.04 (13.6-19.75)	0.790 (0.674-0.916)	$4\frac{5}{8}$ ($4\frac{1}{8}$-$5\frac{1}{8}+$)	closed to crack	
rovina	1	9.95	11.45	0.869	$4\frac{7}{8}$	0.85	13.5
gascoynensis	7	6.52 (4.95-7.9)	13.11 (11.0-14.7)	0.495 (0.450-0.553)	$3\frac{7}{8}+$ ($3\frac{3}{4}$-$4\frac{1}{8}+$)	2.63 (2.15-3.1)	5.07 (3.93-6.21)
carcharias	1,160	14.33 (9.9-18.3)	16.93 (12.3-20.25)	0.846 (0.665-0.986)	$4\frac{3}{4}-$ ($3\frac{7}{8}+$-$5\frac{1}{2}+$)	closed to crack	
meilgana	6	8.10 (7.35-8.8)	13.31 (10.9-15.0)	0.612 (0.577-0.674)	$4\frac{1}{8}+$ (4+-$4\frac{1}{4}$)	1.30 (1.0-1.8)	10.6 (7.67-14.2)
scolythra	375	15.29 (13.1-17.6)	18.06 (15.75-20.75)	0.847 (0.748-0.963)	$4\frac{5}{8}+$ ($4\frac{1}{4}$-$5\frac{1}{2}+$)	crack to closed	

extend only slightly beyond the periphery (**Plate 188b–c**), a moderately descending body whorl, weakly expanded shell lip and with a narrow, slightly supraperipheral, red spiral colour band visible on the lower spire and body whorl. Differences from *F.* species are discussed below. *Plectorhagada plectilis* narrowly overlaps with *F. overlanderensis* N of the Overlander Roadhouse (**Map 29**) and extends N to the Wooramel River and to the SW side of Shark Bay, WA. It is the same size (mean diameter 17.04 mm) as *F. overlanderensis* but with an increased whorl count (**Fig. 388a**, mean whorls 4 5/8), a much higher spire (**Fig. 388b**, mean H/D ratio 0.790), closed or nearly closed umbilicus (**Fig. 388c**), strong apical sculpture (**Plate 190a**) and has crenulated ribs plus prominent micropustules (**Plate 190b–c**) extending from the



Map 29: Records of *Falspleuroxia overlanderensis*, *Plectorhagada carcharias*, *P. plectilis* and *Rhagada torulus* in the Shark Bay area, WA.

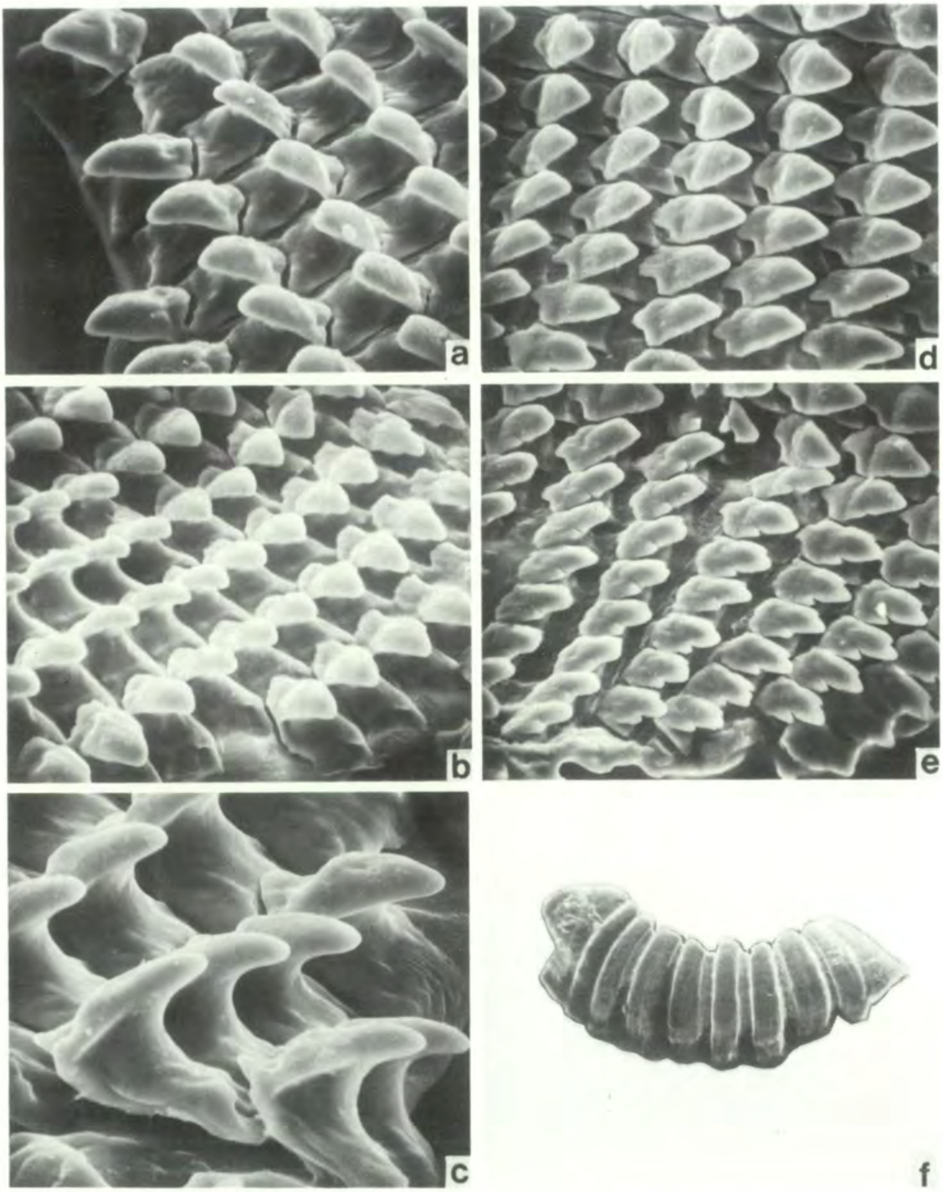


Plate 189: Radular teeth and jaw of *Falspleuroxia overlanderensis*. WA–56, 10.6 miles S of Overlander Roadhouse, North West Coastal Highway, WA. 6 February 1974. FMNH 182527: (a) Dissection B, central and early laterals at 375X; (b) Dissection B, mid- to late laterals at 350X; (c) Dissection B, early laterals at 680X; (d) Dissection B, lateromarginal transition at 335X; (e) Dissection B, early marginals at 345X; (f) Dissection C, jaw at 53.5X.

apex to just behind the lip. *Plectorhagada gascoynensis* (E. A. Smith, 1894), from somewhere in the Gascoyne District, WA, is smaller (mean diameter 13.11 mm), with greatly reduced whorl count (**Fig. 389a**, mean 3 7/8+), a very low spire (**Fig. 389b**, mean H/D ratio 0.495), widely open umbilicus (**Fig. 389c**, mean D/U ratio 5.07) and has the *plectilis* type of shell sculpture.

Anatomically (**Figs 387a–c**), F. overlanderensis is characterised by a very short vagina (V), enormous albumen gland (GG), globose penis (P) with prominent verge (PV) and an absence of both an epiphallic caecum and a penial sheath. *Plectorhagada plectilis* (**Figs 391a–b**) has the albumen gland less enlarged, also lacks the epiphallic caecum and the penis sheath but differs most obviously in lacking a verge and has the penis chamber wall dominated by a very large, U-shaped main pilaster. *Pleuroxia bethana*, from the Murchison River mouth and Greenough River basin, has (**Figs 369a-b**) a large epiphallic caecum (EC), retains a thin penis sheath and complex ridges inside the penis chamber.

Holotype

WAM 753.87, WA–56, limestone rubble just E of North West Coastal Highway, 10.6 miles S of Overlander Roadhouse, at the Shark Bay turn-off, Western Australia (1:250,000 'Yaringa' map sheet SG 50–9 – 243:691, 26°38'35"S, 114°32'56"E). Collected 6 February 1974 by A. Solem and L. Price. Height of shell 11.85 mm, diameter 18.4 mm, H/D ratio 0.644, whorls 4 3/8, umbilical width 1.7 mm, D/U ratio 10.8. Is same specimen as FMNH 182527, Dissection A, which was used to prepare anatomical figures.

Paratopotypes

WAM 915.87, SAM D18242, AM C.200,709, MV F.60049, QM 46928, FMNH 182527, FMNH 182755, FMNH 182594, FMNH 182395, 12 LA, 7 DA, 34 LJ, 9 DJ from the type collection.

Paratypes

WESTERN AUSTRALIA: 17 km S of Overlander Roadhouse WA–165, 23 September 1976, FMNH 199839, 118 LA, many LJ; WA–165, 16 April 1977, FMNH 199773, 81 LA, many LJ; WA–165, 16 December 1976, FMNH 199946, 14 LA, 52 LJ; WA–165, 9 May 1977, WAM 914.87, SAM D18241, AM C.200,710, QM 52993, MV F.59496, FMNH 199645, 43 LA, many LJ; WA–950, 7 July 1983, FMNH 212459–2, 12 LA, 16 DA, 47 LJ, 39 DJ); 16.8 km S of Overlander Roadhouse (WA–1068, 21 May 1989, FMNH 221715–6, 18 LA); 300 yards N of Overlander Roadhouse (WA–55, 6 February 1974, WAM 916.87, SAM D18243, AM C.200,711, QM 46929, MV F.60025, FMNH 182520, FMNH 182334, 1 LA, 249 DA, 3 LJ); 14 km N of Overlander Roadhouse (WA–951, 8 July 1983, FMNH 212463–4, 4 LA, 28 DA, 3 LJ, 13 DJ).

Material studied

19 km S of Overlander Roadhouse (Anne Brearley! 30 August 1982, WAM, 2 LA); 17 km S of Overlander Roadhouse (Anne Brearley! 7 September 1982, WAM, 27 LA, 51 LJ; 15 km N of Overlander Roadhouse (G. W. Kendrick! 23 August 1984, WAM, 5 DA).

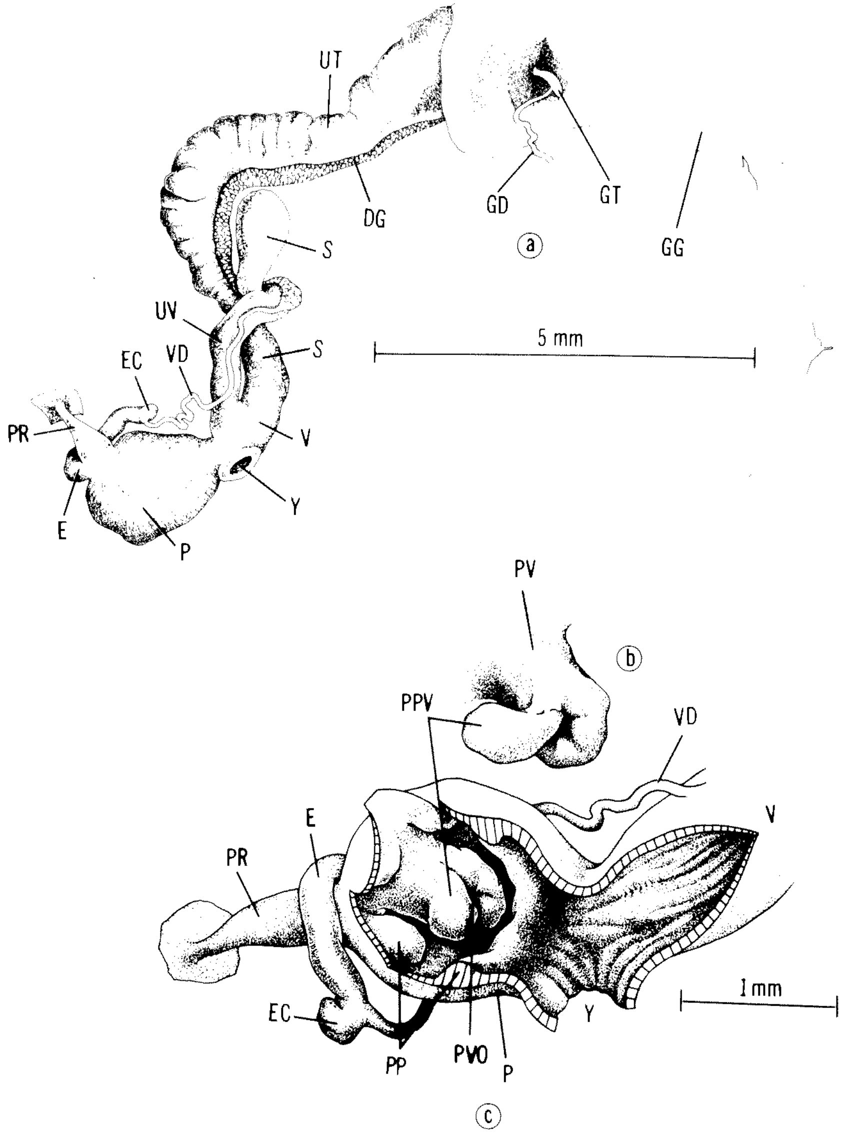


Fig. 387: Genitalia of *Falspleuroxia overlanderensis* sp. nov.: WA–56, 10.6 miles S of Overlander Roadhouse, North West Coastal Highway, WA. 6 February 1974. FMNH 182594, Dissections A & C. (a) whole genitalia except ovotestis; (b) detail of verge (PV) and vergic papilla (PPV); (c) interior of penis chamber. Scale lines as marked. Drawings by Elizabeth A. Liebman.

Table 141: Local variation in *Falspleuroxia overlanderensis.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
17 km S of Overlander, WAM	27L	11.36±0.166 (9.7-14.0)	17.43±0.156 (16.3-19.4)	0.652±0.008 (0.593-0.777)	4⅜ (4¼-4⅝+)	1.57±0.041 (1.15-2.0)	11.3±0.276 (8.69-14.2)
WA-56, FMNH 182594	9L	11.11±0.171 (10.35-11.8)	17.50±0.213 (16.4-18.25)	0.635±0.009 (0.592-0.677)	4⅜– (4¼-4⅜+)	1.64±0.11 (0.95-2.05)	11.2±0.973 (8.17-17.7)
WA-165, FMNH 199839	118L	10.95±0.064 (9.2-12.85)	17.29±0.095 (14.75-21.2)	0.634±0.003 (0.551-0.702)	4⅜– (4+-4⅝+)	1.66±0.026 (1.1-2.5)	10.7±0.177 (7.13-17.7)
WA-165, FMNH 199946	14L	11.11±0.247 (9.9-12.85)	17.79±0.271 (16.85-20.15)	0.625±0.010 (0.576-0.709)	4⅜– (4⅛+-4½+)	1.69±0.099 (0.95-2.05)	11.2±0.920 (8.19-18.6)
WA-165, FMNH 199773	81L	10.97±0.093 (8.9-12.8)	17.26±0.104 (15.2-19.7)	0.636±0.004 (0.539-0.726)	4⅜– (4–-4⅝+)	1.66±0.033 (1.05-2.75)	10.8±0.236 (6.31-17.3)
WA-165, FMNH 199645	43L	10.84±0.082 (9.8-12.0)	16.70±0.102 (14.6-18.3)	0.649±0.005 (0.594-0.706)	4⅜– (4⅛+-4½–)	1.67±0.034 (1.3-2.2)	10.2±0.228 (7.20-13.2)
WA-950, FMNH 212462	6L	11.66±0.317 (10.7-12.65)	17.39±0.458 (16.25-19.3)	0.671±0.013 (0.644-0.725)	4⅜ (4¼–-4⅝+)	1.55±0.128 (1.15-1.85)	11.6±1.024 (9.32-15.6)
WA-950, FMNH 212461	6L	10.92±0.229 (10.35-11.75)	17.12±0.244 (16.45-18.15)	0.638±0.011 (0.613-0.684)	4⅜– (4¼+-4⅜+)	1.55±0.082 (1.3-1.8)	11.2±0.726 (9.18-14.1)
WA-950, FMNH 212460	16D	10.82±0.179 (10.0-12.4)	17.37±0.248 (15.9-19.4)	0.623±0.005 (0.585-0.655)	4⅜– (4⅛+-4⅝–)	1.65±0.080 (1.1-2.4)	10.9±0.556 (7.62-16.3)
WA-55, 300 yds N of Overlander, FMNH 182334	249D	11.24±0.054 (8.6-13.4)	16.85±0.067 (14.3-20.0)	0.667±0.002 (0.582-0.755)	4⅜ (3⅞+-4¾–)	1.31±0.017 (0.75-2.05)	13.4±0.197 (7.70-23.0)
WA-951, 14 km N of Overlander, FMNH 212464	28D	9.87±0.144 (9.87-0.144)	16.26±0.194 (16.26-0.194)	0.607±0.005 (0.607-0.005)	4⅛+ (4+-4⅜+)	1.75±0.058 (1.25-2.70)	9.55±0.321 (5.95-14.0)
15 km N of Overlander, WAM	5D	9.73 (9.4-10.25)	15.97 (15.5-16.4)	0.609 (0.591-0.641)	4⅛ (4–-4⅜+)	1.42 (1.05-1.6)	11.5 (10.2-15.6)

Range

F. overlanderensis has been collected along the highway from 15 km N to 19 km S of the Overlander Roadhouse, which is located about 60 km SSE of Gladstone and 29 km E of Hamelin Pool, Shark Bay, WA (**Maps 27–29**). The known N-S range of 34 km approximates that of exposed limestone in this area. No attempt has been made to establish an E-W range for this species. At 14 and 15 km N of the Overlander Roadhouse, dead specimens of both *F. overlanderensis* and *Plectorhagada plectilis* have been collected microsympatrically.

Description

Shell medium in size, adult diameter 14.3–21.2 mm (mean 17.04 mm), with 3 7/8+ to 4 3/4– (mean 4 3/8–) whorls that increase rather rapidly in width. Apex and spire moderately and evenly elevated (**Fig. 386b**), shell height 8.3–14.0 mm (mean 11.04 mm), H/D ratio 0.539–0.777 (mean 0.648). Body whorl rounded, without trace of angulation. Shell apex (**Plate 188a, d**) smooth initially, lower portion with variable radial growth ridgelets. Spire and body whorl (**Plate 188a–d**) with low, rounded, almost regularly spaced radial ribs that end just below shell periphery and a microsculpture of fine pustules surmounted by periostracal setae with prominent lateral extensions. Umbilicus (**Fig. 386c**) narrow, partly covered by reflection of columellar lip, width 0.75–2.75 mm (mean 1.52 mm), D/U ratio 5.94–23.0 (mean 11.8). Body whorl descending gradually over last eighth (**Fig. 386b**). Palatal and basal lips reflected and narrowly expanded, columellar lip more widely expanded. Colour light yellow-brown above, lighter on base, live examples with a narrow spiral red colour band that is slightly supraperipheral and visible on lower spire and body whorl. Based on 620 measured adults.

Genitalia (**Figs 387a–c**) with huge albumen gland (GG), talon (GT) short. Prostate (DG) and uterus (UT) short. Spermatheca (S) with head next to base of prostate-uterus, shaft and free oviduct (UV) about equal in width, twined around each other. Vagina (V) short, thick. Vas deferens (VD) very slender, entering epiphallus (E) laterally. Epiphallic caecum (EC) small, epiphallus free of penis wall, partly circling penial retractor muscle (PR). Penis (P) short, globular, without trace of sheath, internally with distinct verge (PV) bearing a lateral stimulator (PPV) and with terminal vergic pore (PVO). A smaller main pilaster (PP) lies to one side of verge and a low circular ridge is just below the verge tip.

Central and early lateral teeth of radula (**Plate 189a**) with modest anterior flare, no trace of an ectocone, high cusp shaft angle, curved and bluntly rounded cusp tip, short and massive basal plate. Mid- (**Plate 189b**) and late (**Plate 189c**) laterals with longer basal plates, enlarged anterior flare, reduced cusp shaft angle and cusp tip curvature. Ectocone only appearing at lateromarginal transition (**Plate 189d**), early marginals (**Plate 189e**) with small endocone and rapidly enlarging ectocone. Jaw (**Plate 189f**) with rather narrow, high vertical ribs that are greatly reduced on lateral margins.

Discussion

The main sampled population of *Falspleuroxia overlanderensis*, located about 17 km S of the Overlander Roadhouse, was subjected to considerable and repeated disturbance by road graders between 1974 and 1985. It was not possible to sample exactly the same area during the various visits. Paratopotypic designation thus is restricted to the original sample taken in 1974. Later material from this area is cited as paratypic because there were minor shifts in the area from which samples were collected.

Despite this change in population site, no significant variation in size and shape was detected (**Table 141**) over the years. The two samples from N of the Overlander Roadhouse were noticably smaller (**Table 141**). Only dead specimens of both *F. overlanderensis* and *Plectorhagada plectilis* were found at the latter localities, their only known place of sympatry.

The name *overlanderensis* recognises that travellers' oasis, the Overlander Roadhouse, that continues to serve those who pass.

FALSPLEUROXIA SPECIES
(Plate 188e–f; Figs 386d–f; Maps 27–28)

Comparative remarks

Falspleuroxia species, from Dalgarangar Hill, NW of Mt. Magnet, WA (**Maps 27–28**), is smaller (diameter 14.1 mm), with a less expanded lip (**Figs 386d–f**) and more crowded sculpture (**Plate 188e–f**) than *Falspleuroxia overlanderensis*, which is larger (mean diameter 17.04 mm), has a more expanded shell lip (**Figs 386a–c**), and more prominent and widely spaced radial ribbing (**Plate 188a, d**). In both species the radial sculpture is absent from the shell base. Species of *Plectorhagada* (**Plates 190–193, Figs 388–390**) differ most obviously in their crenulated shell sculpture on at least the upper spire, while the widely umbilicated *Pleuroxia abstans* Iredale, 1939 and *P. bethana* (**Figs 368Ac, 368Bf**) also have prominent apical shell sculpture (**Plate 177a**). The anatomy of the present species is unknown.

Material studied

WESTERN AUSTRALIA: Dalgarangar Hill, *ca*. 100 km NW of Mt Magnet (1/2 way up slope, J. N. Masters! 4–5 September 1976, WAM 475.77, 1 DA).

Range

Only one example of *Falspleuroxia* species has been collected in the SE fringes of the upper Murchison River drainage, WA. Dalgarangar Hill (*ca.* 27°50'S, 117°06'E) is an isolated, low hill.

Discussion

The only specimen of *Falspleuroxia* species is sufficiently worn that the apical sculpture cannot be seen but enough is left of the spire and body whorl sculpture to determine that it is more crowded than in the type species.

The specimen is inadequate for description but is figured here to call attention to the presence of an unnamed camaenid in this part of WA. It is possible that it may belong to *Pleuroxia* and is only convergent with *Falspleuroxia* but without preserved specimens for dissection its identity will remain uncertain.

GENUS *PLECTORHAGADA* IREDALE, 1933
(+ *IDAMERA* IREDALE, 1939)

Plectorhagada Iredale, 1933, *Rec. Austr. Mus.*, **19** (1): 52 – subgenus of *Rhagada* Albers, 1861. Type species: *Helix plectilis* Benson, 1853; Iredale 1938, *Austr. Zool.*, **9** (2): 113 – elevated to generic rank; Iredale 1939, *Jour. Roy. Soc. Western Austr.*, **25:** 69–71 – review of species; Burch 1976, *Jour. Malac. Soc. Austr.*, **3:** 136 – citation in check list; Richardson 1985, *Tryonia*, **12:** 231–232 – citation in check list.

Idamera Iredale, 1939, *Jour. Roy. Soc. Western Austr.*, **25:** 71 – subgenus of *Plectorhagada*. Type species: *Plectorhagada rovina* Iredale, 1939.

Shell small to medium in size, variable, adult diameter 10.9 to 20.75 mm, whorls 3 3/4– to 5 7/8, coiling pattern dependent upon spire elevation, loose in *gascoynensis* (**Plate 389a**), much tighter in *rovina* (**Fig. 388d**). Spire very low in *gascoynensis* (**Fig. 389b**); very high in *rovina* (**Fig. 388e**); moderately to strongly elevated in other species, H/D ratio 0.450–0.986. Apical sculpture (**Plates 190a, d, 191a, 192a, c, 193a**) with dense to scattered, often elongated micropustules, sometimes arranged in radial rows. At least upper spire with prominent crenulated ridges (**Plates 190–193**) and large micropustules (except *scolythra*) that extend to just behind shell lip in *plectilis*, *gascoynensis*, *rovina*, and *meilgana*; are restricted to spire in *carcharias* and *scolythra*; in most species reduced in prominence below periphery. Body whorl rounded in all species except *meilgana* (**Fig. 389e**), where it is noticeably angulated; descending moderately to sharply behind lip, except in *gascoynensis* (**Fig. 389b**) and *meilgana* (**Fig. 389e**). Umbilicus closed or a narrow lateral crack in the more globose species (*plectilis*, *carcharias*, *scolythra*); narrowly open in *rovina* and *meilgana*; widely open in *gascoynensis*. Palatal and basal lips narrowly to moderately reflected and expanded, columellar lip usually wider. Parietal wall callus varying from thin to thick and elevated, lip edge always appressed to parietal wall if thickened. Shell colour unknown in *gascoynensis* and *meilgana*, light brownish suffusion on spire in others, a narrow reddish brown spiral supraperipheral band and white zone just below found in some *plectilis* and all *carcharias* and *scolythra*. Lip white.

Specimens aestivate sealed by a calcified rim to other shells and lie loose in litter or rubble in "chains" of up to 15 specimens, in the only species collected alive (*plectilis*, *carcharias*, *scolythra*). Sometimes there are several epiphragms formed by a single individual. Aestivation strategy of other species unknown but probably the same.

Genitalia (**Figs 391–393**) with moderately (*scolythra*) to greatly (*plectilis*) enlarged albumen gland (GG). Vagina (V) short to very short, free oviduct (UV) and shaft of spermatheca twisted around each other, head of spermatheca reaching just above base of prostate-uterus. Epiphallic caecum (EC) absent (*plectilis*, *carcharias*) to a small knob (*scolythra*). Vas deferens (VD) very slender, entering directly into slightly expanded head of epiphallus. Latter not circling penial retractor muscle, which inserts in an arc at point where epiphallus enters penis (P) through a simple pore. Penis globular to somewhat elongated, without an identifiable sheath. Penis chamber with a large and simple (*plectilis*), highly modified (*scolythra*) or greatly reduced (*carcharias*) U-pilaster, area of accessory ridging small (*plectilis*), large (*carcharias*) or greatly enlarged (*scolythra*).

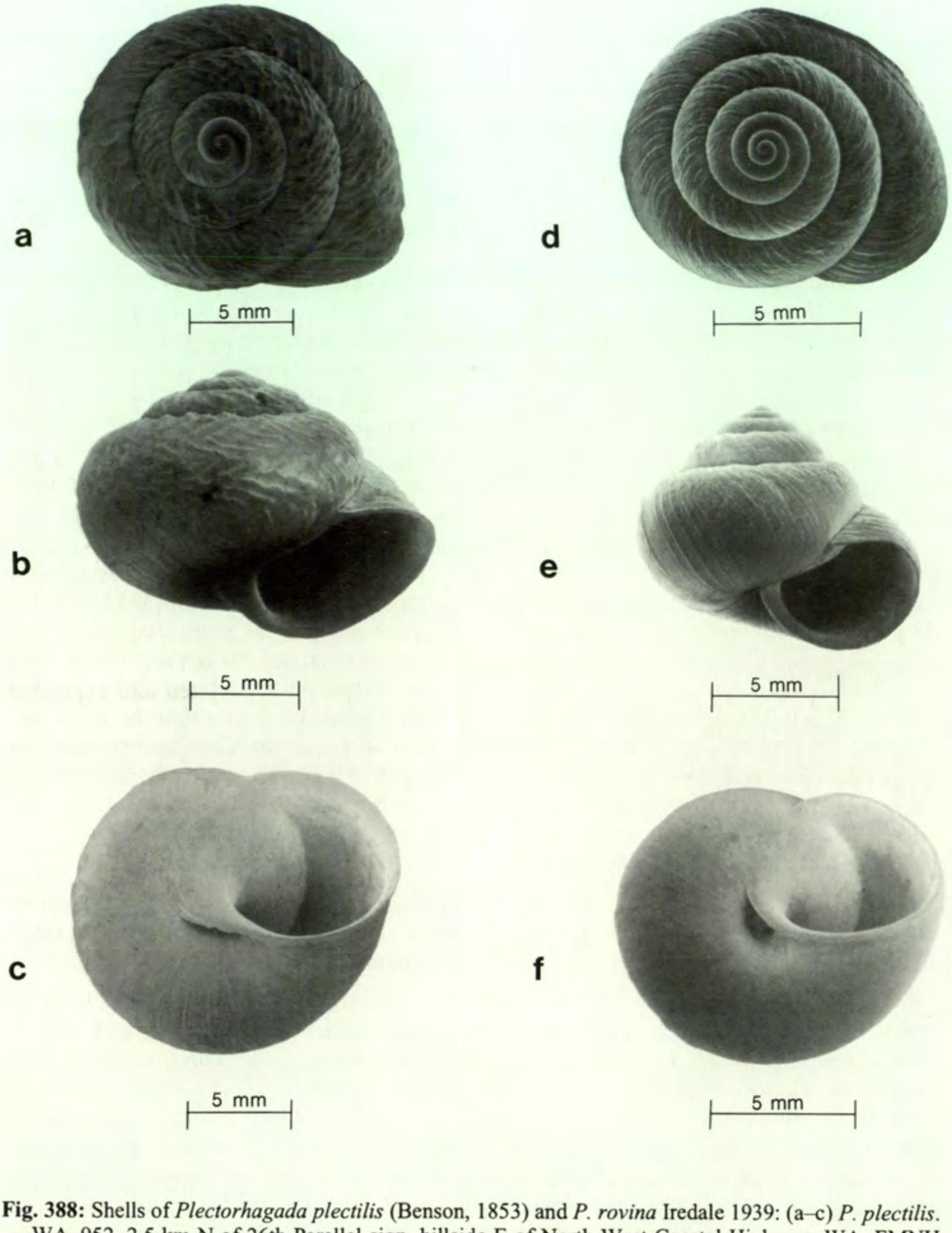


Fig. 388: Shells of *Plectorhagada plectilis* (Benson, 1853) and *P. rovina* Iredale 1939: (a–c) *P. plectilis*. WA–952, 2.5 km N of 26th Parallel sign, hillside E of North West Coastal Highway, WA. FMNH 212466; (d–f) Holotype of *Plectorhagada rovina* Iredale, 1939. Shark Bay, WA. AM C.33432. Scale lines as marked.

Jaw (**Plates 194e, 195f**) with a few broad but very low vertical ribs on central portion, greatly reduced to absent on sides. Central and early lateral teeth of radula (**Plates 194a, 195a, c**) with small anterior flare, no ectocone, short to medium basal plate, moderately elevated to very high cusp shaft angle, cusp tip curvature moderate (*carcharias*) to abrupt (*scolythra*), cusp tip itself variable among species. Lateromarginal transition (**Plate 195b, d**) abrupt, marked by first appearance of ectocone and loss of basal support ridge. Marginals (**Plates 194c, 195b, e**) without unusual features.

Type species: *Helix plectilis* Benson, 1853 by original designation.

Comparative remarks

The prominent apical pustulations and the very unusual crenulated ribbing (**Plates 190–193**) on at least the upper spire are the shell features that separate *Plectorhagada* from neighbouring genera. *Strepsitaurus* from Warroora and Cardabia stations N through the Cape Range (**Plates 196–198**) has even more striking sculpture on the postapical whorls, while *Falspleuroxia overlanderensis*, found near the Overlander Roadhouse, just at the S range limit for *Plectorhagada*, has a nearly smooth apex (**Plate 188a**) and simple radial ribs on the spire and body whorl (**Plate 188b–d**).

In other shell features, *Plectorhagada* shows great variation, from the basic *Pleuroxia* shape of *Plectorhagada gascoynensis* (E. A. Smith, 1894) (**Figs 389a–c**) and *Plectorhagada meilgana* sp. nov. (**Figs 389d–f**), to the high spired *Plectorhagada rovina* Iredale, 1939 (**Figs 399d–f**). In order of increasing globosity, *Plectorhagada plectilis* (Benson, 1853) (**Figs 388a–c**), *P. carcharias* (Pfeiffer, 1864) (**Figs 390a–c**) and *P. scolythra* (**Figs 390d–f**), closely approach taxa in both *Quistrachia* and *Rhagada* in size, form and colour.

Unfortunately, only the latter three species have been dissected. The lack (*plectilis*, *carcharias*) or great size reduction (*scolythra*) of the epiphallic caecum, lack of a verge or penis sheath and failure of the epiphallus to partly encircle the penial retractor muscle, combine to separate easily *Plectorhagada* from *Pleuroxia* or *Sinumelon*. The moderate to great enlargement of the albumen gland in *Plectorhagada* is carried even further in *Falspleuroxia*, which has a distinct verge, the epiphallus partly encircling the penial retractor muscle and very different penial pilasters (**Figs 387a–c**). *Strepsitaurus* (**Figs 396–398**) has very different penial chamber sculpture. The U-pilaster found in *Plectorhagada* varies from being a mere remnant (*carcharias*) to becoming the main structure (*plectilis*). Its counterpart is present in many other Sinumeloninae (Solem 1992, 1993).

Previous studies

Originally (Iredale 1933: 52) described as a subgenus of *Rhagada*, *Plectorhagada* was elevated to generic rank by Iredale (1938: 113) without comment. A review of the three available species names, *plectilis* Benson, 1853, *carcharias* Pfeiffer, 1864 and paleata Reeve, 1854, with synonymization of the latter two, was presented by Iredale (1939: 69–71), who also described the unlocalised *Plectorhagada rovina* and erected a new subgenus, Idamera Iredale 1939, for it. Richardson (1985: 231-232) provided a summary of literature citations for the species. As pointed out below, the holotype and only known example of *P. rovina* is so badly worn that it should not have been described, much less serve as a type species for a generic level unit.

Distribution and comparative ecology

Maps 27–32 summarise the known distribution of *Plectorhagada*. The various species range as far south as the southern tip of Shark Bay and as far N as the Rough Range near Exmouth Gulf. One species, *Plectorhagada meilgana* sp. nov., has a purely inland range, residing in the Henry River basin on Meilga and Glen Florrie Stations (**Map 28**). Two species, *Plectorhagada gascoynensis* (E. A. Smith, 1894) and *P. rovina* Iredale, 1939, are from unknown localities. The original citations of "Gascoyne District" and "Shark Bay" have not been localised by later collections.

The three globose species have allopatric ranges (**Maps 28–32**). *Plectorhagada plectilis* is found on the S side of Shark Bay and near the Overlander Roadhouse, then extends up the E shore of Shark Bay to the Wooramel River. It has not been collected on the Peron Peninsula or the large islands that form the W side of Shark Bay. *Plectorhagada plectilis* overlaps narrowly with *Falspleuroxia overlanderensis* (**Map 29**) in the area 14–15 km N of the Overlander Roadhouse but otherwise is allopatric to other camaenids. *P. carcharias* (**Maps 29–30**) appears to be be present on both Dirk Hartog and Dorre Islands on the W side of Shark Bay but has not been reported yet on Bernier Island; it then extends inland for a distance E along the Minilya River to the Kennedy Range and N from Lake Macleod and Point Quobba, N of Carnarvon to just S of Warroora Homestead. It has the largest range of any of these species and is variously sympatric or mosaically microallopatric with *Quistrachia* and *Rhagada* (see below). *Plectorhagada scolythra* (**Maps 30–32**) ranges N and E of *P. carcharias*, occupying a limited area in the Scrubby (= Giralia) and Rough Ranges just SE and S of Exmouth Gulf, also being microsympatric with *Quistrachia* and *Rhagada*. No trace of any *Plectorhagada* has been found in the area between Warroora and Ningaloo or in the Cape Range area.

Three species have been collected alive: *Plectorhagada plectilis*, *P. carcharias* and *P. scolythra*. All aestivate sealed to another shell by a calcified mucus rim. In areas of local abundance, clusters or "chains" of aestivating adult shells are frequently encountered. Juveniles will be attached to the larger shells. These chains occur in litter under bushes or in rock rubble. Rarely, younger examples will be found sealed to rocks or wood. Frequently large numbers of dead shells are found at the bottom of a boulder crevice, with live examples mingled with them near the bottom. This pattern is different from that found in *Strepsitaurus*, where the live specimens are sealed by calcified rims either to vertical rock faces overhung by spinifex or other plants or to shells sealed to the rocks; in *Falspleuroxia*, in which a mucoid seal attaches them to the underside of rock slabs; and in *Pleuroxia* which has rock-sealing habits.

Discussion of the albumen gland enlargement and the changes in terminal genital structures have been discussed above.

KEY TO THE SPECIES OF *PLECTORHAGADA*

1. Umbilicus narrowly to widely open 2
   Umbilicus a narrow lateral crack or closed 4

2. Shell periphery angulated; Henry and Ashburton River basins .... *Plectorhagada meilgana*, sp. nov. (p. 1600)
   Shell periphery rounded 3

3. Spire very low (**Fig. 389b**); umbilicus wide (**Fig. 389c**) .... *Plectorhagada gascoynensis* (E. A. Smith, 1894) (p. 1587)

Spire very high (**Fig. 388e**); umbilicus narrow (**Fig. 388f**) .... *Plectorhagada rovina* Iredale, 1939 (p. 1585)

4. Crenulated radial sculpture absent from lower spire and body whorl 5

Crenulated radial sculpture extends to just behind lip .... *Plectorhagada plectilis* (Benson, 1853) (p. 1579)

5. Scrubby Range (= Giralia Range) and Rough Range, near Exmouth Gulf .... *Plectorhagada scolythra*, sp. nov. (p. 1603)

Dirk Hartog and Dorre Islands, Shark Bay; Lake Macleod to Warroora and inland along Minilya River to Kennedy Range .... *Plectorhagada carcharias* (Pfeiffer, 1864) (p. 1589)

PLECTORHAGADA PLECTILIS (BENSON, 1853)

(Plates 190a–c, 194a–e; Figs 388a–c, 391a–b; Maps 28–29)

Helix plectilis Benson, 1853, *Ann. Mag. Nat. Hist.,* (2) **11:** 29–30 Shark's (*sic*) Bay, West Australia; Reeve, 1853, *Conch. Icon.*, **7**, *Helix*, plt. CLXXII, species 1162 – figure of type; Cox, 1864, *Cat. Austr. Land Shells,* p. 13; Pfeiffer, 1859, *Monog. Helic. viv.,* **4:** 250; Cox, 1868, *Monog. Austr. Land Shells*, p. 44, plt. IX, fig. 17 (after Reeve, 1853), plt. XX, fig. 8.

Helix paleata Reeve, 1854, *Conch. Icon.*, **7**, *Helix*, plt. CXCIX, fig. 1399 – banks of Swan River, Australia; Bacon (error); Cox, 1864, *Cat. Austr. Land Shells,* p. 16; Cox, 1868, *Monog. Austr. Land Shells*, p. 44; Tryon, 1887, *Man. Conch.,* (2) **3:** 215, plt. 49, fig. 17; Pilsbry, 1894, *Man. Conch.*, (2) **9:** 136.

Helix (*Dorcasia*) *plectilis* (Benson), Tryon, 1887, *Man. Conch.*, (2) **3:** 215, plt. 49, figs 17–18.

Helix (*Rhagada*) *plectilis* (Benson), Pilsbry, 1890, *Man. Conch.,* (2) **6:** 188–189, plt. 35, figs 16–18 – Shark Bay and Swan River, W. Australia; Smith, 1894, *Proc. Malac. Soc. London*, **1:** 90.

Thersites (*Rhagada*) *plectilis* (Benson), Pilsbry, 1894, *Man. Conch.*, (2) **9:** 136.

Rhagada plectilis (Benson), Hedley, 1916, *Jour. Roy. Soc. Western Australia*, **1:** 70 – check list citation.

Rhagada (*Plectorhagada*) *plectilis* (Benson), Iredale, 1933, *Rec. Austr. Mus.,* **19** (1): 52 – as type of new subgenus.

Plectorhagada plectilis (Benson), Iredale, 1938, *Austr. Zool.,* **9** (2): 113 – citation in check list; Iredale, 1939, *Jour. Roy. Soc. Western Austr.,* **25:** 70, plt. V, fig. 15 – review of genus; Burch, 1976, *Jour. Malac. Soc. Austr.*, **3:** 136 – citation in check list; Richardson, 1985, *Tryonia*, **12:** 231–232 – citation in check list.

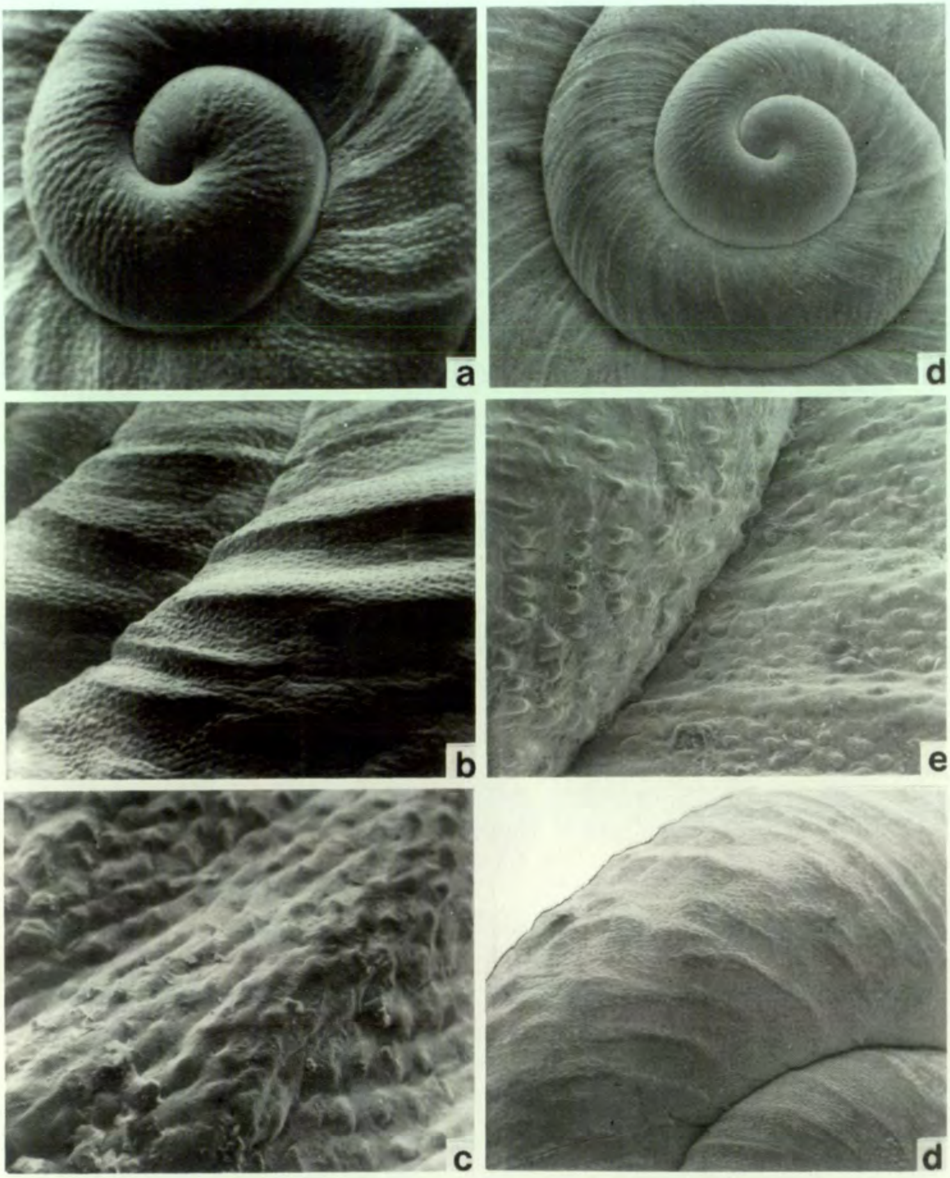


Plate 190: Shell sculpture of *Plectorhagada plectilis* (Benson, 1853) and *P. gascoynensis* (E.A. Smith, 1894): (a–c) *P. plectilis*. WA–54, 31.5 miles N of Overlander Roadhouse, North West Coastal Highway, WA. FMNH 182378. a is apex and early spire at 22.5X. b is mid-spire at 18.3X. c is microsculpture on mid-spire at 91X; (d–f) *P. gascoynensis*. Gascoyne District, Western Australia. Probably type lot. FMNH 41682. d is apex and spire at 16X. e is detail on 2nd and 3rd whorls at 77X. f is lower spire and body whorl at 15.8X.

Comparative remarks

Plectorhagada plectilis (Benson, 1853), which ranges from the Wooramel River S to a few kilometres N of the Overlander Roadhouse and then W around the southern shores of Shark Bay to beyond Tamala Station (**Map 28**), WA, is most easily recognised by its crenulated sculpture and large pustules (**Plate 190a–c**) that continue to the shell lip (although reduced on shell base), comparatively large size (mean diameter 17.04 mm), elevated spire (**Fig. 388b**, mean H/D ratio 0.790), high whorl count (**Fig. 388a**, mean whorls 4 5/8) and the umbilicus closed or reduced to a narrow lateral crack (**Fig. 388c**). *P. carcharias* (Pfeiffer, 1864), which ranges from Dirk Hartog Island off Shark Bay N to Warroora Homestead on the coast and inland to the Kennedy Range, WA (**Maps 28–31**), has the crenulated ridging and large micropustules restricted to the upper spire (**Plate 191a–d**), with the lower spire and body whorl having irregular growth ridges and very small micropustules (**Plate 191b, e**). Its (*P. carcharias*) red spiral band and lower white zone are more prominent, the shell is slightly more elevated (mean H/D ratio 0.846) and it is much more globose in appearance with less strongly rounded spire whorls (compare **Figs 388a–b, 390a–c**). Otherwise the parameters of both species and also those of *P. scolythra*, are very similar (**Table 140**). The latter species, found just S of Exmouth Gulf from the Bullara-Giralia road south to the southern parts of the Scrubby (= Giralia) Range (**Maps 28, 30–32**), is almost identical to *P. carcharias* in shell features but has finer pustulations and several anatomical differences. The genus *Strepsitaurus* gen. nov. (Cape Range to below Warroora Station, see below) has an even more rugose sculpture (**Plates 196–198, 237**) but a much lower spire, smaller size and very different genital anatomy. Anatomically (**Figs 391a–b**), the complete absence of an epiphallic caecum (EC), enlarged albumen gland (GG), short terminal female organs, absence of a penis sheath and massive U-pilaster within the penis chamber are diagnostic. *P. carcharias* (**Figs 392a–b**) also lacks the epiphallic caecum and penis sheath but has a smaller albumen gland, the U-pilaster is greatly reduced and there is a broad, accessory ridged section on the penis chamber wall. *P. scolythra* sp. nov. (**Figs 393a–b**) lacks the penis sheath, has a tiny nub of an epiphallic caecum, the U-pilaster is highly modified, there is a very complex accessory pilaster developed and the albumen gland is smaller. Differences in radular structure have been discussed above.

Type specimens

Lectotype of *Helix paleata* Reeve, 1854. BMNH 197015. Banks of Swan River, Australia (error). Collected by Bacon. Height of lectotype 10.9 mm, diameter 13.6 mm, H/D ratio 0.801, whorls 4 1/2–.

Syntype of *Helix paleata* Reeve, 1854. BMNH 197015. Banks of Swan River, Australia (error). Height of syntype 11.55 mm, diameter 14.25 mm, H/D ratio 0.810, whorls 4 5/8.

No possible type material of *Helix plectilis* Benson, 1853 was located during this study.

Material studied

WESTERN AUSTRALIA: 5 miles W of Hamelin Station (G. M. Storr! 28 August 1965, WAM 290.74, 3 DA, 1 DJ); rubbish dump 0.5 mile W of Hamelin Pool Station (B. W. Wilson & G. W. Kendrick! 2 March 1966, WAM, 6 DA, many DJ); Shark Bay

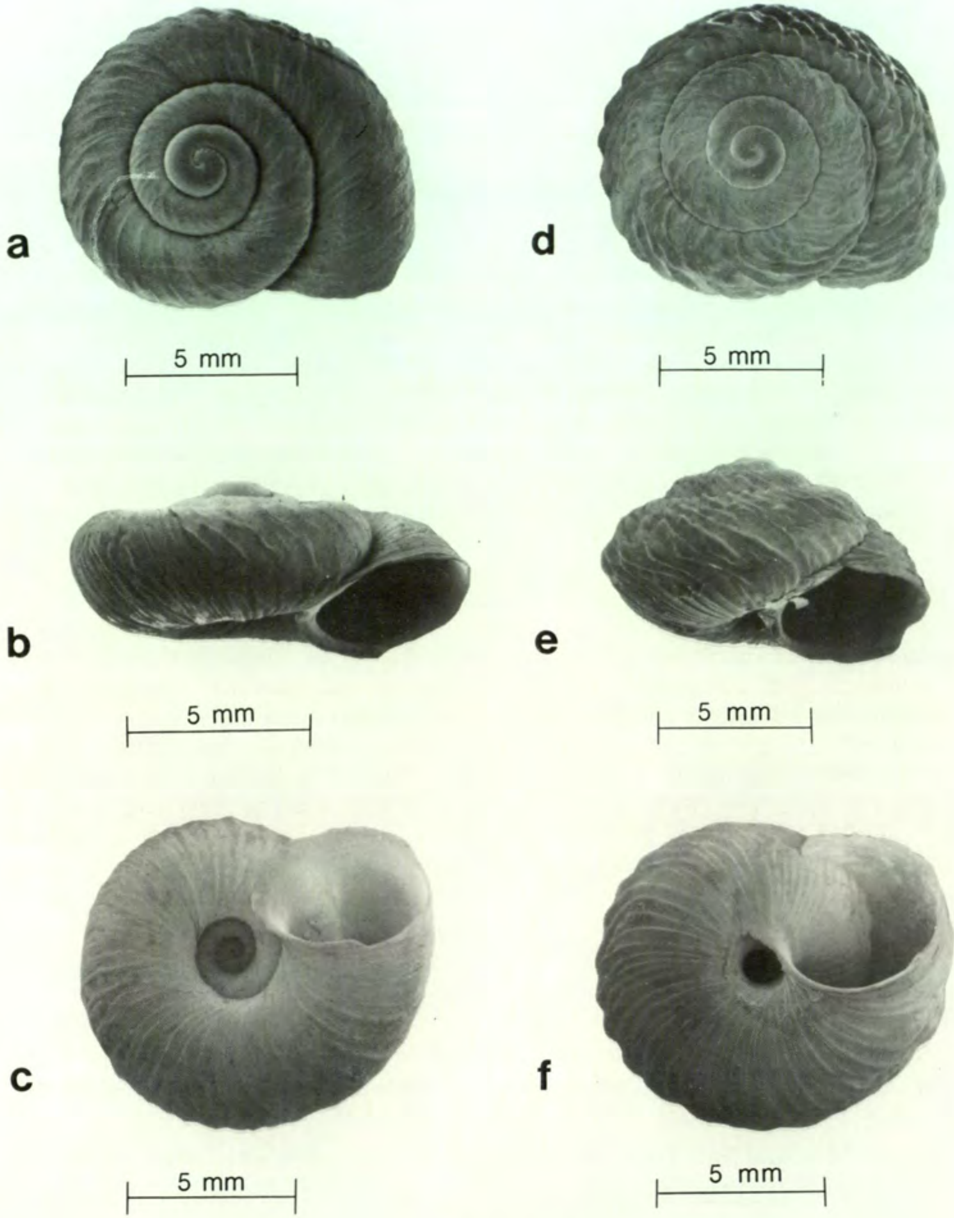


Fig. 389: Shells of *Plectorhagada gascoynensis* (E. A. Smith, 1894) and *P. meilgana* sp. nov.: (a–c) Gascoyne District, WA. FMNH 41682, probably type lot of *Helix (Trachia) gascoynensis* E. A. Smith, 1894; (d–f) Holotype of *Plectorhagada meilgana*. WAM 754.87. Old white abestos mine, *ca* 5 miles E of Meilga Station Homestead, WA. Scale lines as marked.

turnoff from NW Coastal Highway (G. M. Storr! 17 October 1962, WAM, 9 DA); Tamala Homestead, Peddigudda Mill (G. M. Storr! 12 January 1963, WAM, 6 DA); 1 km N of Tamala turnoff on road to Denham (G. W. Kendrick! 6 July 1963, WAM, 2 DA); 4 miles W of Tamala Homestead, Shark Bay (B. W. Wilson & G. W. Kendrick! 8 March 1966, WAM, 3 DA); Flint Cliff near Hamelin Pool (Henderson! 1971, WAM, 3 DA); Three Bays Island, Shark Bay (G. M. Storr! 30 August 1965, WAM, 1 DA); Gladstone, Hamelin Pool (G. W. Kendrick! 17 August 1975, WAM 1362.75, WAM 1364.75, 17 LA, 13 LJ, 15 DJ); 5 miles W of Overlander Roadhouse on Shark Bay turnoff (K. Vollprecht! 7 January 1958, WAM, 5 DA); 14 km N of Overlander Roadhouse: just E of highway (WA–951, FMNH 212465, 26 DA, 16 DJ); 15 km N of Overlander Roadhouse (G. W. Kendrick! 23 August 1984, WAM, 11 DA); 1.8 miles N of 26th Parallel sign; E of road (WA–54, WAM 918.87, WAM 919.87, SAM D18245–6, AM, QM, MV, FMNH 182378, FMNH 182406, 188 DA, many DJ; WA–166, WAM 917.87, SAM D18244, QM, AM, MV, FMNH 199643, FMNH 199770, FMNH 199884, FMNH 200183, 186 LA, many LJ; WA–952, FMNH 212466–7, 8 LA, 31 DA, 12 LJ, 14 DJ); 29 km S of Wooramel River, along NW Coastal Highway (WAM 39.87, 4 LA, 19 DA, 32 DJ); 0.5 mile W of 512 mile peg, NW Coastal Highway (20 August 1968, WAM 377.74, 26 DA, 44 DJ); Yaringa Station 28 miles N of Overlander Roadhouse (B. W. Wilson & G. W. Kendrick! 8 March 1966, WAM, 30 DA, 3 DJ); 518 mile peg, near Yaringa, NW Coastal Highway (W. Ponder! 12 January 1972, AM C.87650, 12 DA); 3 miles S of Wooramel River (WA–53, FMNH 182724, FMNH 182394, 50 DA, 1 DJ); Hutchison Embayment, Shark Bay (S. M. Slack-Smith! August 1976, WAM 38.87, 18 DA).

Range

Plectorhagada plectilis has been collected (**Maps 28–29**) in the Shark Bay region from a few km W and N of the Overlander Roadhouse up to near the Wooramel River on the mainland, W around the south end of Shark Bay past Hamelin Pool and thence W of Tamala Homestead. There are no confirmed records from the Peron Peninsula, Dirk Hartog Island, Dorre Island, or Bernier Island. The limited available materials from Dirk Hartog and Dorre Islands are tentatively assigned below to *Plectorhagada carcharias* (Pfeiffer, 1864). The N-S mainland range of *P. plectilis* on the E side of Shark Bay is thus about 60 km and the confirmed range on the W side of Shark Bay is about 17 km. The maximum E-W range would be about 90 km.

Diagnosis

Shell relatively large, adult diameter 13.6–19.75 mm (mean 17.04 mm), with 4 1/8 to 5 1/8+ (mean 4 5/8) normally coiled whorls. Apex and spire strongly and nearly evenly elevated (**Fig. 388b**), shell height 10.05–16.8 mm (mean 13.46 mm), H/D ratio 0.674–0.916 (mean 0.790). Body whorl rounded, without trace of angulation (**Fig. 388b**). Apex (**Plate 190a**) with dense elongated pustules, spire and body whorl (**Plate 190b–c**) with crenulated ridging and large micropustules often arranged in lines: both elements continue on body whorl to just behind lip above periphery, although greatly reduced on shell base. Umbilicus (**Fig. 388c**) closed or a narrow lateral crack. Body whorl descending moderately to sharply just behind lip. Palatal and basal lips reflected and narrowly expanded, columellar lip broader and often thickened. Parietal wall with a very thick callus in older specimens. Colour generally bleached from shell but a light

Table 142: Local variation in *Plectorhagada plectilis.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
WA-166, FMNH 199770	26L	13.83±0.112 (12.8-14.8)	17.49±0.109 (16.3-18.45)	0.791±0.006 (0.735-0.845)	$4\frac{5}{8}$ ($4\frac{1}{2}$–-$4\frac{7}{8}$+)	closed	
WA-166, FMNH 199884	24L	13.45±0.166 (12.15-15.15)	17.17±0.175 (16.0-19.05)	0.783±0.005 (0.728-0.821)	5– ($4\frac{3}{8}$–-$4\frac{7}{8}$+)	closed	
WA-166, FMNH 199643	37L	13.63±0.122 (12.2-15.65)	17.65±0.151 (15.8-19.5)	0.773±0.006 (0.716-0.890)	$4\frac{5}{8}$ ($4\frac{3}{8}$-5–)	closed	
WA-166, FMNH 200183	99L	13.66±0.079 (12.15-16.8)	17.40±0.085 (15.4-19.2)	0.786±0.003 (0.721-0.898)	$4\frac{5}{8}$ ($4\frac{3}{8}$–-$5\frac{1}{8}$+)	closed	
WA-54, FMNH 182406	132D	13.42±0.069 (11.05-15.3)	17.07±0.077 (14.7-19.05)	0.787±0.003 (0.704-0.894)	$4\frac{5}{8}$+ ($4\frac{3}{8}$–-5)	closed	
WA-951, FMNH 212465	26D	13.19±0.119 (11.6-14.3)	16.43±0.116 (15.05-17.75)	0.803±0.006 (0.743-0.887)	$4\frac{5}{8}$ ($4\frac{1}{2}$–-5–)	0.99±0.042 (0.62-1.54)	17.2±0.708 (10.7-27)
WA-952, FMNH 212467	8L	14.27±0.321 (13.15-16.25)	17.90±0.247 (16.8-18.8)	0.797±0.013 (0.747-0.865)	$4\frac{3}{4}$ ($4\frac{1}{2}$+-5–)	0.97±0.103 (0.53-1.41)	20.1±2.362 (13.3-33)
WA-952, FMNH 212466	31D	13.64±0.138 (12.1-15.15)	17.33±0.171 (16.0-19.7)	0.788±0.005 (0.731-0.850)	$4\frac{5}{8}$+ ($4\frac{3}{8}$+-5–)	0.94±0.048 (0.63-1.80)	19.6±0.882 (9.45-28)
WA-54, FMNH 182378	56D	13.33±0.113 (11.2-15.75)	16.90±0.116 (14.95-19.2)	0.789±0.005 (0.692-0.875)	$4\frac{5}{8}$ ($4\frac{3}{8}$–-5+)	closed	
WA-53, FMNH 182394	49D	13.00±0.116 (10.4-15.65)	16.87±0.105 (15.4-19.2)	0.771±0.005 (0.674-0.893)	$4\frac{1}{2}$+ ($4\frac{1}{4}$-$4\frac{3}{4}$+)	closed	

reddish-brown spire suffusion and a narrow red spiral supraperipheral band just above a narrow white zone visible in fresh material from some populations. Based on 677 measured adults.

Genitalia (**Figs 391a–b**) with enormous albumen gland (GG), relatively short prostate (DG) and uterus (UT). Spermatheca (S) with head lying just above base of prostate-uterus, shaft very short, thicker than short free oviduct (UV). Vagina (V) short, rather thick. Vas deferens (VD) very slender, entering slightly expanded head of epiphallus (E) about midway up penis. Epiphallus not encircling penial retractor muscle, entering penis through a simple pore with fine longitudinal pilasters emerging. Penial retractor muscle (PR) inserting in a quarter circle on junction of epiphallus and penis (P). Penis chamber (**Fig. 391b**) dominated by huge U-pilaster, with one arm continued into atrium (Y). Area between arms with low and irregular ridges.

Central and early lateral teeth of radula (**Plate 194a**) with reduced anterior flare, high cusp shaft angle, curved and broadly rounded cusp tip and shortened basal plate. Late lateral teeth (**Plate 194b**) with enlarged anterior flare and with reduced cusp shaft angle, tip curvature and degree of rounding. Basal plate slightly longer, faint ectoconal trace visible. Marginal teeth (**Plate 194c**) short, shaft angle low. Jaws (**Plate 194d–e**) with greatly reduced vertical ribs.

Discussion

Although no type material of *Plectorhagada plectilis* could be located, the original description of the shell sculpture and figures leave no doubt concerning the identity of this species. The types of *Helix paleata* (see above) agree in size and shape with the very small examples from the S end of Shark Bay and have the typical sculpture extending to just behind the shell lip. In most examples, the radial sculpture is noticeably reduced below the shell periphery. Except for differential surface wear, no variations were noted in sculpture prominence.

Shell colour varies from population to population. Examples from Gladstone, 512 mile peg and 5 miles W of Hamelin Station have a noticeable brownish-red supraperipheral spiral colour band above a narrow white zone and some brownish-red suffusion on the spire. Those from near the 26th Parallel and S end of Shark Bay rarely show any colour trace, while the dead Wooramel examples are too worn to show any colour traces.

Size variation (**Table 142**) is moderate. The northern populations near the Wooramel River and Hutchison Embayment, near the Overlander Roadhouse and around the S end of Shark Bay tend, with few exceptions, to be smaller in diameter and lower in whorl count than the more central populations on the mainland.

PLECTORHAGADA ROVINA IREDALE, 1939

(Figs 388d–f)

Plectorhagada rovina Iredale, 1939, *Jour. Roy. Soc. Western Austr.*, **25:** 70–71, plt. V, fig. 17 – Shark Bay, Western Australia; Burch, 1976, *Jour. Malac. Soc. Austr.*, **3:** 136 – check list citation; Richardson, 1985, *Tryonia*, **12:** 232 – check list citation.

Comparative remarks

Plectorhagada rovina Iredale, 1939, from "Shark Bay", WA, is based on a small (diameter 11.45 mm), high spired (**Fig. 388e**, H/D ratio 0.869), narrowly umbilicated (**Fig. 388f**, D/U ratio 13.5) shell with increased whorl count (5 7/8), worn surface showing traces of crenulated sculpture and three narrow red spiral bands on the body whorl – just below suture, mid-palatal and peripheral. In general appearance it resembles some of the small *Rhagada* and Carnarvon area *Quistrachia* but the sculpture is very different from that of those genera. The other umbilicated species, *Plectorhagada meilgana* sp. nov. from the middle Ashburton drainage and the "Gascoyne District" *P. gascoynensis* (E. A. Smith, 1894) are easily differentiated. The latter has a very wide umbilicus (**Fig. 389c**, mean D/U ratio 5.07), low spire (**Fig. 389b**, mean H/D ratio 0.495) and reduced whorl count (**Fig. 389a**, whorls 3 7/8+), while the former has an angulated body whorl (**Fig. 389e**), wider umbilicus (**Fig. 389f**, mean D/U ratio 10.6) and only moderately elevated spire (**Fig. 389e**, mean H/D ratio 0.612) with typical whorl count (**Fig. 389d**, mean whorls 4 1/8+). The anatomy is unknown.

Holotype

AM C.33432. Shark Bay, Western Australia. *Ex* John Brazier. Height of shell 9.95 mm, diameter 11.45 mm, H/D ratio 0.869, whorls 5 7/8, umbilical width 0.85 mm, D/U ratio 13.5.

Range

Plectorhagada rovina is known from a single pre-1900 collected subfossil example labelled "Shark Bay". It had been misidentified as *Helix australis* Menke, 1843, which probably is based on a mislabelled European helicellid. No exact locality is known for *P. rovina*.

Diagnosis

Shell small, adult diameter 11.45 mm, with 5 7/8 rather tightly coiled whorls (**Fig. 338d**). Apex and spire strongly and evenly elevated (**Fig. 338e**), height 9.95 mm, H/D ratio 0.869. Whorls evenly rounded, without trace of angulation. Shell apex badly worn, faint traces of radial ridglets on lower portion. Spire and body whorl with remnants of *Plectorhagada* crenulated ridging. Umbilicus narrowly open (**Fig. 338f**), blocked by soil deposits, width 0.85 mm, D/U ratio 13.5. Body whorl descending very slightly behind lip. Palatal lip not, basal lip slightly reflected, both thickened internally (**Figs 338d–f**). Columellar lip modestly expanded to partly narrow umbilicus. Ground colour unknown, early part of body whorl showing three narrow spiral red bands: upper slightly subsutural, middle is midpalatal, lower is slightly supraperipheral. Based on holotype.

Discussion

The unique example of *Plectorhagada rovina* (**Figs 338d–f**) is in too poor a condition to warrant description. Its name does exist, however, and the shell shows no sign of repaired injury that could have produced its high spire. Since the sculptural remnants on the spire and body whorl are consistent with the sculpture of other *Plectorhagada*, it has been kept provisionally in this genus. The circular aperture with slight inclination, three red spiral colour bands and thickened lip suggest possible affinity with *Rhagada* or *Quistrachia* but only new collections and study of the anatomy can resolve doubts as to its classification. The shell does have more similarities to W coast camaenids than to taxa from any other part of Australia.

PLECTORHAGADA GASCOYNENSIS (SMITH, 1894)

(Plate 190d–f; Figs 389a–c)

Helix (*Trachia*) *gascoynensis* E. A. Smith, 1894, *Proc. malac. Soc. London,* **1:** 93, plt. VII, fig. 13 – Gascoyne District, W. Australia.

Planispira gascoynensis (E. A. Smith), Pilsbry 1895, *Man. Conch.,* (2) **9:** 343 – check list citation; Hedley 1916, *Jour. Roy. Soc. Western Austr.,* **1:** 69 – check list citation.

Pleuroxia gascoynensis (E. A. Smith), Iredale 1938, *Austr. Zool.,* **9** (2): 107 – check list citation; Iredale 1939, *Jour. Roy. Soc. Western Austr.,* **25:** 56 – copy of original description and remarks; Richardson 1985, *Tryonia,* **12:** 253 – check list citation.

Comparative remarks

Plectorhagada gascoynensis (E. A. Smith, 1894), described without more detailed locality from the "Gascoyne District", WA, is easily recognised by its small size (mean diameter 13.11 mm), low spire (**Fig. 389b**, mean H/D ratio 0.495), comparatively wide umbilicus (**Fig. 389c**, mean D/U ratio 5.07) and typical crenulated sculpture on the spire and body whorl (**Plate 190e–f**). The only other umbilicated species are *Plectorhagada meilgana* from the upper Ashburton drainage (Joy Helen Mine, 23°15'S, 115°46'E and near Meilga Homestead, 22°46'S, 115°51'E) (**Map 28**), and *Plectorhagada rovina* Iredale, 1939 from "Shark Bay", WA. The former has an angulated periphery (**Fig. 389e**), much more elevated spire (**Fig. 389b**, mean H/D ratio 0.612), narrowed umbilicus (**Fig. 389f**, mean D/U ratio 10.6) and the lip is much more broadly reflected and expanded. The latter has an increased whorl count (5 7/8), very high spire (H/D ratio 0.869), narrow umbilicus (D/U +ratio 13.5) and rounded shell periphery. *Falspleuroxia* overlanderensis differs in its much larger size (mean diameter 17.04 mm), narrow umbilicus (**Fig. 386c**, mean D/U ratio 11.8) and sculpture of simple radial ribs (**Plate 188a, d**) that stop just below the shell periphery. The anatomy of *Plectorhagada gascoynensis* is unknown.

Lectotype

BMNH 91.8.8.12. Gascoyne District, Western Australia. Collected by H. P. Woodward. Height of lectotype 5.9 mm, diameter 12.3 mm, H/D ratio 0.480, whorls 3 3/4, umbilical width 2.9 mm, D/U ratio 4.24.

Syntypes

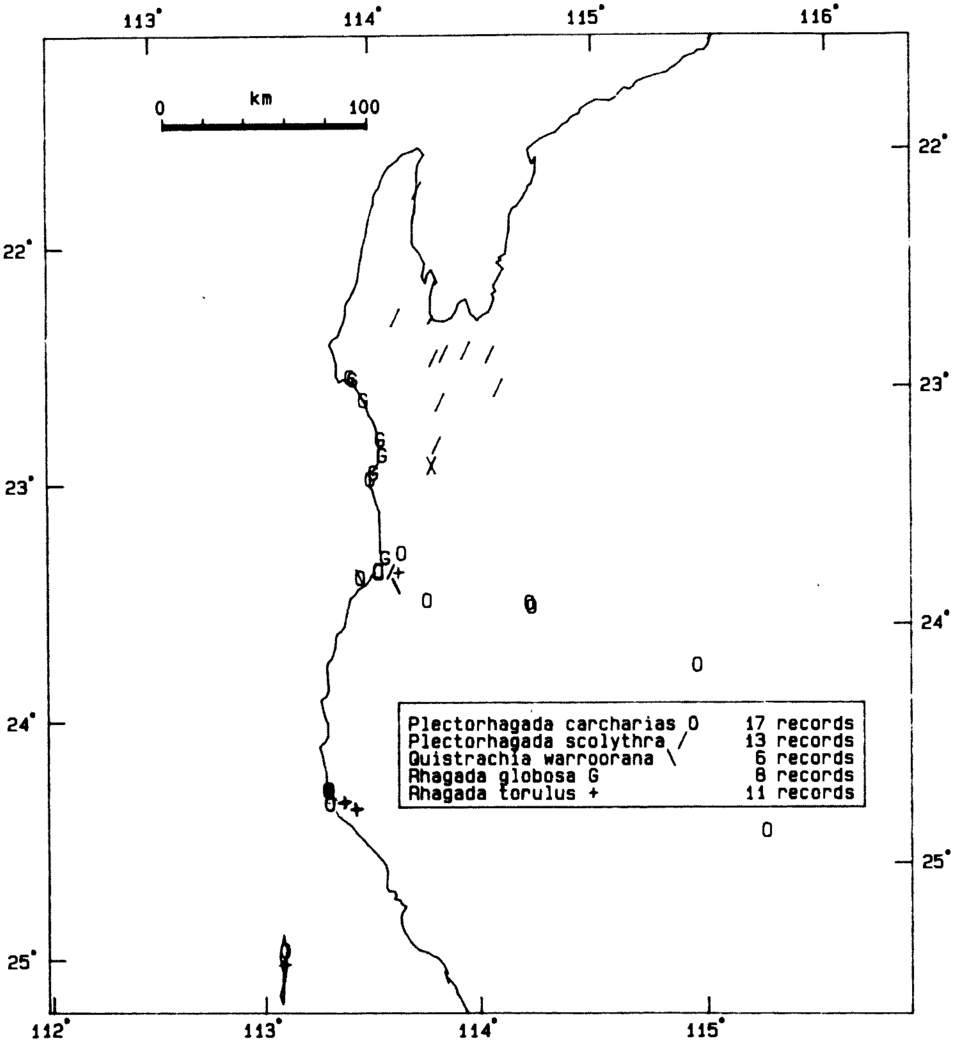
BMNH 91.8.8.13–14, MV F16728, FMNH 41682, 6 DA, 2 DJ, from the type lot.

Range

Plectorhagada gascoynensis is from the "Gascoyne District", WA and has not been recollected. It is not possible to speculate on its probable actual range.

Diagnosis

Shell small, adult diameter 11.0–14.7 mm (mean 13.11 mm), with 3 3/4 to 4 1/8+ (mean 3 7/8+) normally coiled whorls. Apex and spire slightly to moderately elevated (**Fig. 389b**), shell height 4.95–7.9 mm (mean 6.52 mm), H/D ratio 0.450–0.553 (mean 0.495). Body whorl rounded, without trace of angulation. Shell apex (**Plate 190d**) initially with elongated pustules in vague radial rows, becoming weak ridgelets on lower portion. Spire and body whorl (**Plate 190e–f**) with typical crenulated ridging and micropustules continuing onto shell base. Umbilicus (**Fig. 389c**) widely open, partly narrowed by reflection of columellar lip, last whorl decoiling more rapidly, width



Map 30: Records of *Plectorhagada carcharias*, *P. scolythra*, *Quistrachia warroorana*, *Rhagada globulus* and *R. torulus* from the North West Cape to Shark Bay area, WA.

2.15–3.1 mm (mean 2.63 mm), D/U ratio 3.93–6.21 (mean 5.07). Body whorl descending slightly behind lip. Palatal and basal lips narrowly expanded (**Figs 389a–c**), columellar lip more expanded, parietal wall with a thick to medium callus. Colour unknown as all specimens bleached. Based on 7 measured adults.

Anatomy unknown.

Discussion

Plectorhagada gascoynensis has the shape and umbilicus of *Pleuroxia* but the very different shell sculpture of *Plectorhagada*.

It is possible that the available material represents two separate collections: shells from the original material are smaller in size (diameter 11.0–13.0 mm, whorls 3 3/4) than the MV specimens (diameter 14.3–14.7 mm, whorls 4 1/8– to 4 1/8+). No notes accompany the latter specimens. They could have been larger examples retained by the original collector but only new collections of this species will solve the problem.

PLECTORHAGADA CARCHARIAS (PFEIFFER, 1864)

(Plates 191a–e, 195a–b; Figs 390a–c, 392a–b; Maps 28–31)

Helix carcharias Pfeiffer, 1864, *Proc. Zool. Soc. London*, **1863:** 528 – Shark's (*sic*) Bay, West Australia; Pfeiffer 1868, *Monog. Helic. viv.*, **5:** 322; Cox 1868, *Monog. Austr. Land Shells*, p. 45, plt. XX, fig. 12.

Helix (*Dorcasia*) *carcharias* Pfeiffer, Tryon 1887, *Man. Conch.*, (2) **3:** 217; Clessin 1881, *Nomen. Helic. viv.*, p. 187.

Helix (*Rhagada*) *carcharias* Pfeiffer, Pilsbry 1890, *Man. Conch.*, (2) **6:** 189; Smith 1894, *Proc. malac. Soc. London,* **1**: 90.

Thersites (*Rhagada*) *carcharias* (Pfeiffer), Pilsbry 1894, *Man. Conch.*, (2) **9:** 135–136, plt. 27, figs 16–18.

Rhagada carcharias (Reeve), Hedley 1916, *Jour. Roy. Soc. Western Austr.*, **1:** 69 – check list citation.

Helix carcharias Pfeiffer, 1864. In synonymy of *Plectorhagada plectilis* (Benson, 1853). Iredale, 1939, *Rec. West. Aust. Mus.* **2**(1): 70. Also published as *Jour. Roy. Soc. West. Aust.* **25**: 70.

Comparative remarks

Plectorhagada carcharias (Pfeiffer, 1864), which lives on Dirk Hartog and Dorre Islands, Shark Bay, on the mainland along the Minilya River as far E as the Kennedy Range and from Lake Macleod and Point Quobba N to near Warroora Homestead, WA (**Maps 28–31**), has the crenulated sculpture (**Plate 191a–b**) confined to the upper spire, with only small pustules and irregular growth lines present on the lower spire and body whorl (**Plate 191b, e**). It shares a closed or nearly closed umbilicus (**Fig. 390c**) with *P. plectilis* (**Fig. 388c**) and *P. scolythra* (**Fig. 390f**). The shape is more globose (compare **Figs 388b, 390b**), the spire whorls less strongly rounded and the H/D ratio (mean 0.846) higher than in *P. plectilis* from the S and E sides of Shark Bay

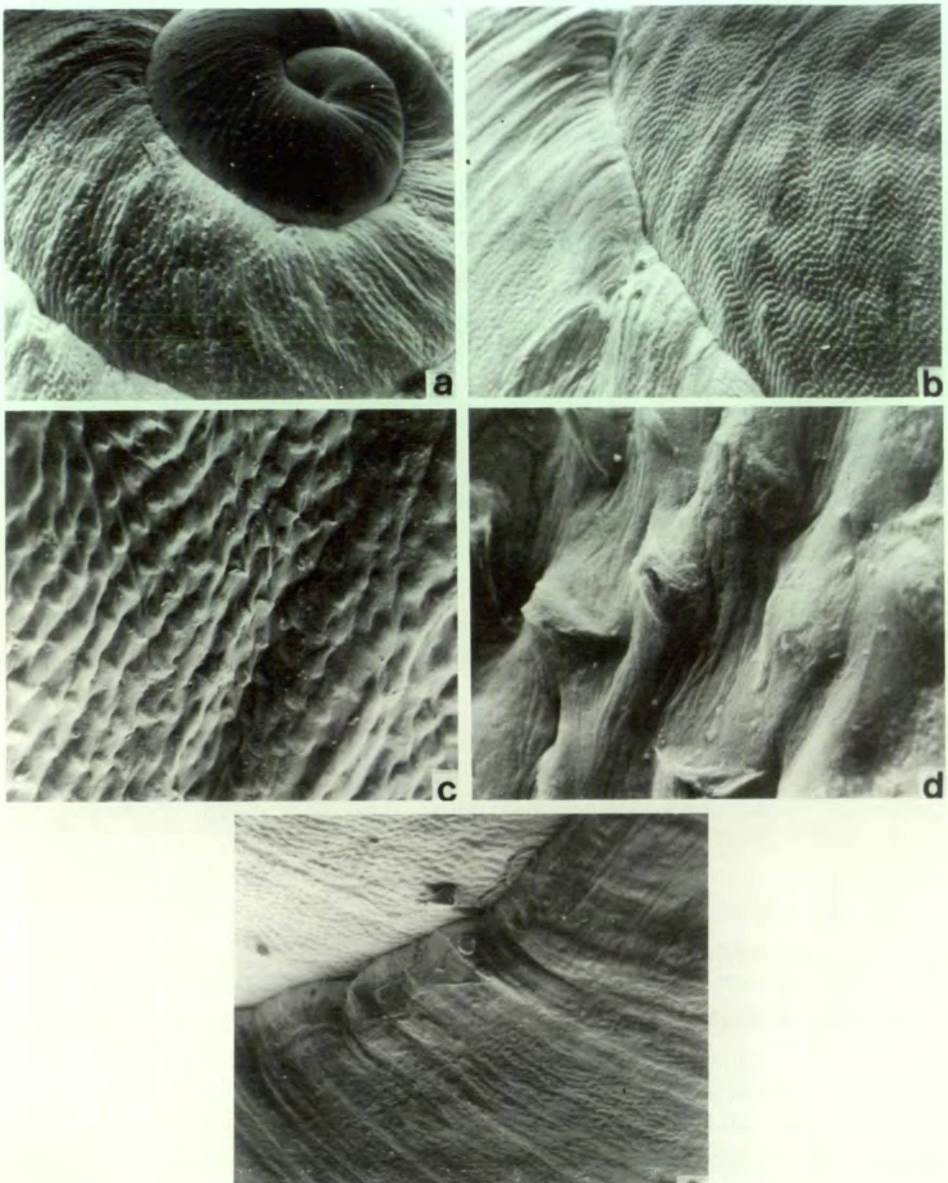


Plate 191: Shell sculpture of *Plectorhagada carcharias* (Pfeiffer, 1864): WA–47, 4.6 miles S of Warroora Homestead, Gascoyne District, WA. FMNH 182300: (a) apex and spire at 18.9X; (b) lower spire and body whorl at 19X; (c) micro-sculpture on lower spire at 96X; (d) detail of lower spire micro-sculpture at 470X; (e) lower spire and body whorl sculpture at 20.7X.

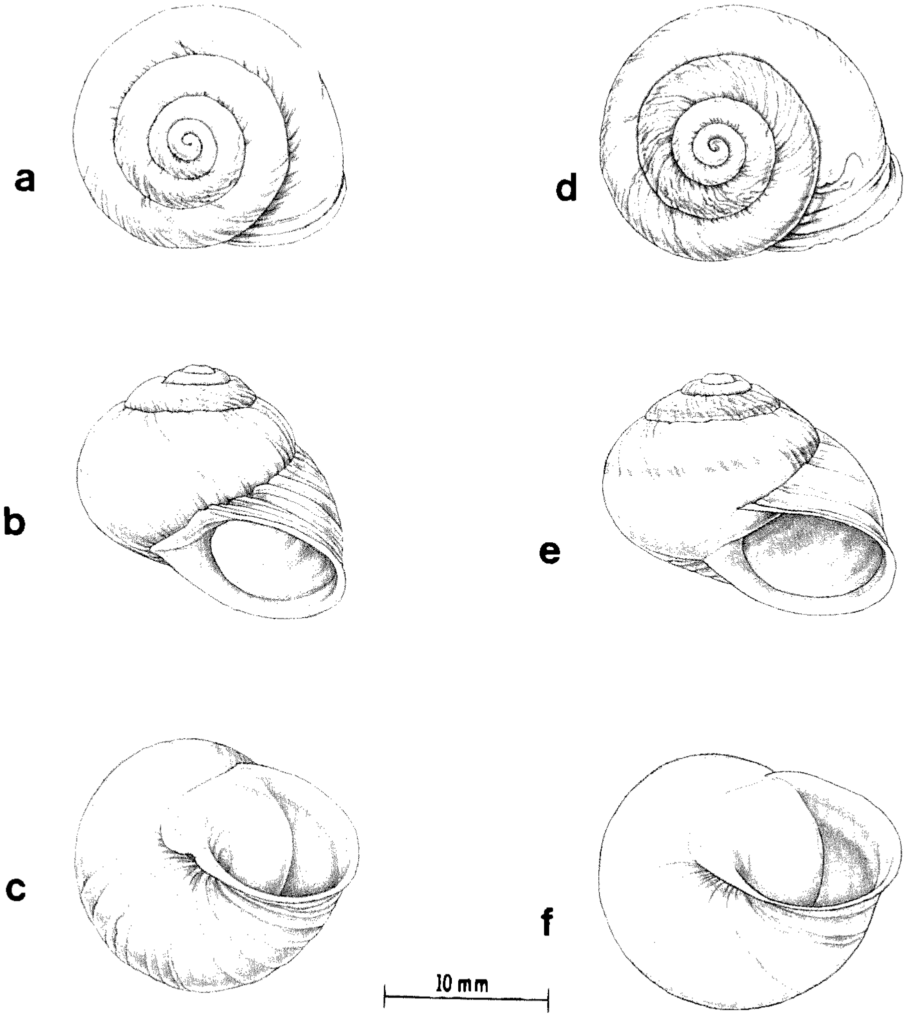


Fig. 390: Shells of *Plectorhagada carcharias* (Pfeiffer, 1864) and *P. scolythra* sp. nov.: (a–c) *P. carcharias*. WA–169, near coast, 7.3 km S of Warroora Homestead, 0.4 km S of bore, N of Carnarvon, WA. FMNH 199843, Dissection B; (d–f) Holotype of *Plectorhagada scolythra*. WAM 752.87. WA–51, 12.8 miles E of Exmouth Road from Cardabia turnoff, Scrubby Range, WA. Scale line equals 10 mm. Drawings by Linnea Lahlum.

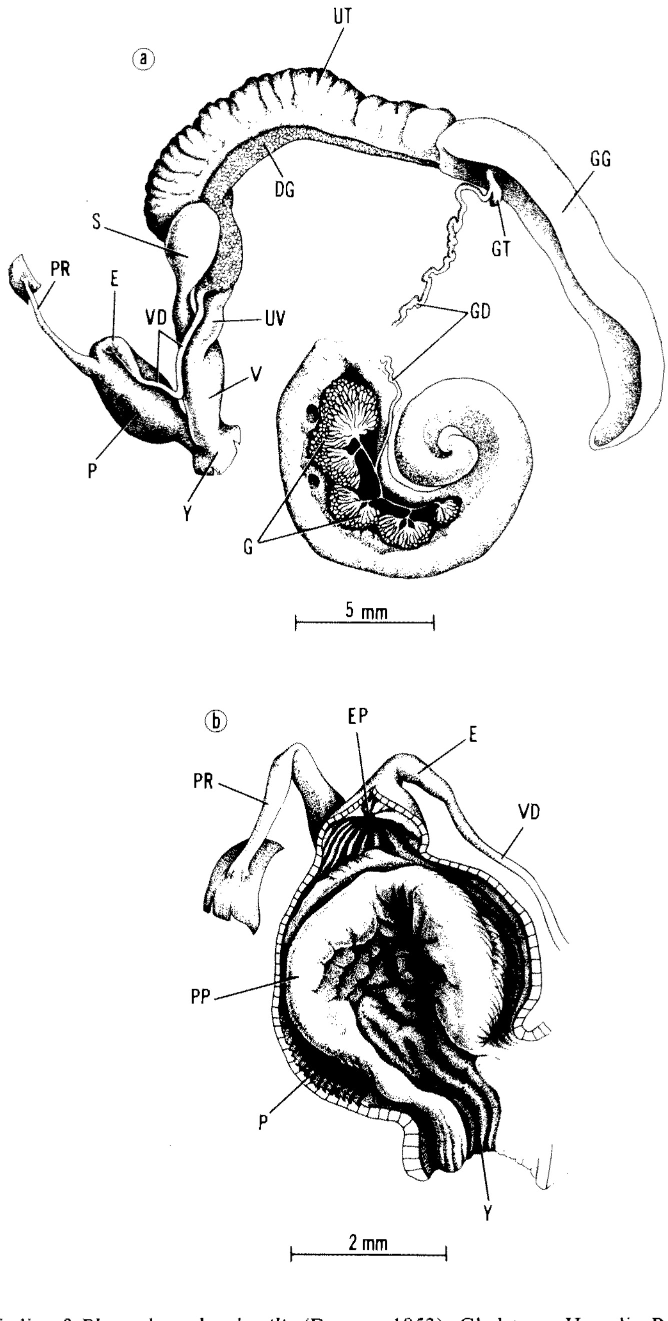
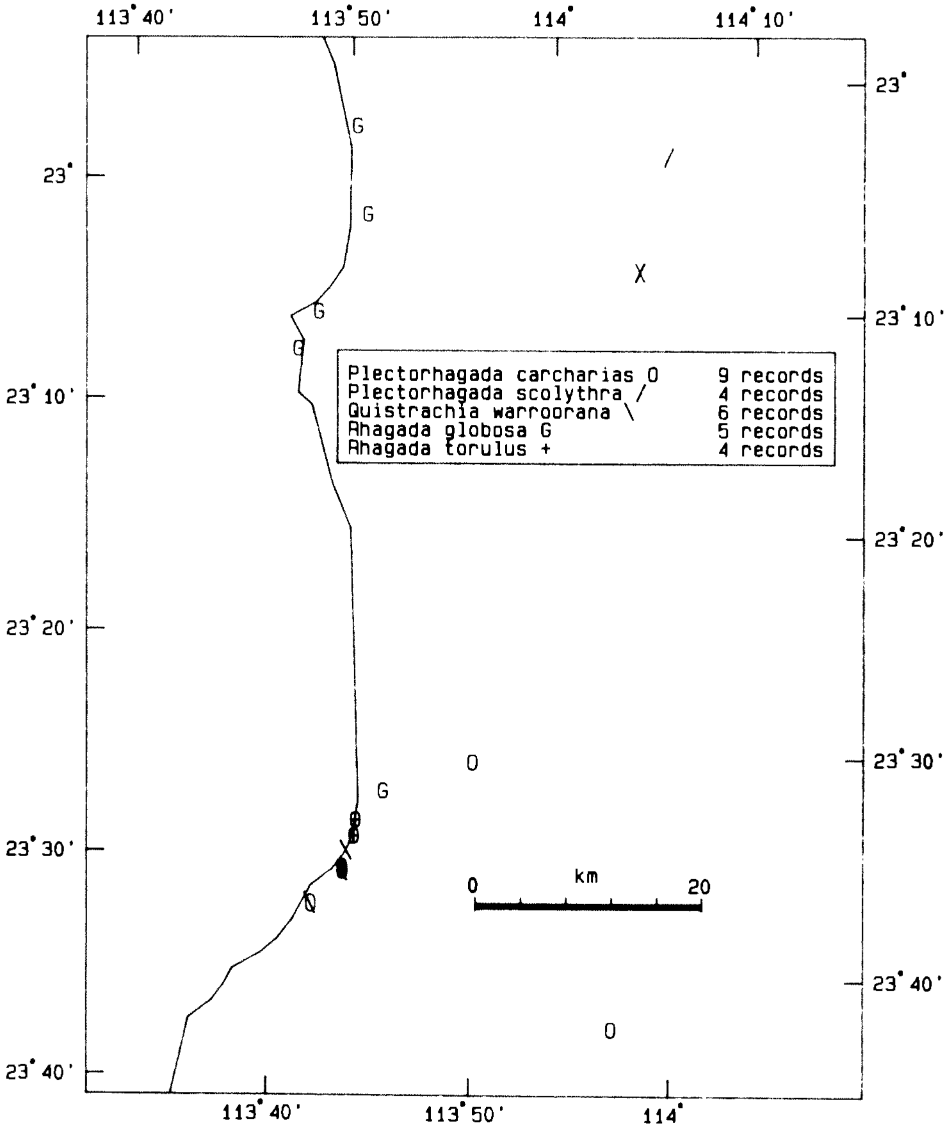


Fig. 391: Genitalia of *Plectorhagada plectilis* (Benson, 1853): Gladstone, Hamelin Pool, Shark Bay, WA. 17 August 1975. WAM 1362.75, Dissection C. (a) whole genitalia. (b) interior of penis chamber. Scale lines as marked. Drawings by Elizabeth A. Liebman.

as far N as the Wooramel River (**Maps 28–29**). *P. scolythra*, from the Scrubby Range to near the S tip of Exmouth Gulf, WA (**Maps 28, 30–32**), has finer pustulations and is slightly larger (**Table 140**) but differs primarily in radular and genital features. Species of *Strepsitaurus* from Cardabia N through the Cape Range, WA (**Maps 33–34**), differ in having very prominent rugose sculpture on the entire shell, a much lower spire (**Figs 394–395**) and an angulated body whorl. Species of *Rhagada* and *Quistrachia* (**Plates 205, 227–228**) from this region differ most obviously in the lack of



Map 31: Records of *Plectorhagada carcharias*, *P. scolythra*, *Quistrachia warroorana*, *Rhagada globosa* and *R. torulus* just S of the North West Cape, WA.

Table 143: Local variation in *Plectorhagada carcharias.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
WA-953, FMNH 212470	5D	14.13±0.310 (13.45-15.2)	16.10±0.272 (15.45-17.0)	0.877±0.011 (0.850-0.908)	$4\frac{3}{4}$ ($4\frac{5}{8}$–-5–)	0.94±0.075 (0.65-1.1)	17.7±1.700 (14.3-24.0)
WA-168, FMNH 199881	12L	14.34±0.227 (12.95-15.55)	16.99±0.199 (15.6-17.85)	0.844±0.010 (0.794-0.901)	$4\frac{5}{8}$+ ($4\frac{1}{2}$-$4\frac{7}{8}$+)	closed	
WA-168, FMNH 199740	28L	14.85±0.151 (13.5-16.7)	17.16±0.158 (15.6-18.45)	0.866±0.006 (0.807-0.948)	$4\frac{7}{8}$– ($4\frac{5}{8}$–-$5\frac{1}{8}$–)	closed	
Moogooree Station, WAM 314.74	6D	13.58±0.356 (12.7-15.15)	17.07±0.224 (16.4-18.05)	0.795±0.011 (0.765-0.837)	$4\frac{5}{8}$ ($4\frac{1}{2}$–-$4\frac{5}{8}$+)	closed	
WA-953, FMNH 212469	99L	14.03±0.085 (10.9-16.05)	16.03±0.086 (13.75-17.95)	0.876±0.004 (0.729-0.986)	$4\frac{7}{8}$– ($4\frac{3}{8}$+-$5\frac{1}{4}$+)	0.86±0.021 (0.25-1.75)	20.0±0.678 (9.06-65)
WA-168, FMNH 200177	128L	14.43±0.072 (12.1-16.7)	16.76±0.073 (15.0-18.4)	0.861±0.003 (0.772-0.941)	$4\frac{3}{4}$ ($4\frac{3}{8}$+-$5\frac{1}{8}$+)	closed	
#73, Gnargoo Ra., FMNH 199065	99D	12.49±0.082 (9.9-14.6)	15.28±0.086 (12.3-17.1)	0.818±0.003 (0.764-0.902)	$4\frac{1}{2}$– ($4\frac{1}{7}$+-$4\frac{7}{8}$–)	closed	
Wandagee, Minilya River, WAM 306.80	6D	13.39±0.393 (11.85-14.7)	16.38±0.447 (15.1-17.6)	0.818±0.016 (0.784-0.876)	$4\frac{1}{2}$ ($4\frac{1}{4}$+-$4\frac{3}{4}$)	0.64±0.207 (0.0-1.1)	
WA-48, FMNH 182361	9D	15.08±0.202 (14.35-16.1)	18.06±0.275 (17.15-19.65)	0.835±0.011 (0.784-0.888)	$4\frac{3}{4}$+ ($4\frac{5}{8}$+-$4\frac{3}{4}$+)	closed	
WA-169, FMNH 199843	32L	14.64±0.116 (13.2-15.65)	17.29±0.132 (15.4-18.22)	0.847±0.006 (0.765-0.904)	$4\frac{3}{4}$ ($4\frac{1}{2}$-$4\frac{7}{8}$+)	closed	
WA-169, FMNH 199844	18D	14.15±0.170 (13.0-15.4)	16.86±0.176 (14.45-17.9)	0.840±0.011 (0.761-0.910)	$4\frac{5}{8}$+ ($4\frac{1}{2}$-5–)	closed	
WA-169, FMNH 199875	15L	14.17±0.170 (13.4-15.8)	16.87±0.125 (16.2-17.6)	0.840±0.009 (0.791-0.899)	$4\frac{5}{8}$ ($4\frac{3}{8}$+-5–)	closed	

Table 143: Local variation in *Plectorhagada carcharias* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
WA-954, FMNH 212472	11L	15.86±0.306 (14.7-18.3)	17.9±0.248 (16.5-19.1)	0.886±0.009 (0.851-0.961)	5 1/8− (4 3/4−-5 1/2+)	0.91±0.048 (0.7-1.15)	20.1±1.130 (14.9-26)
WA-954, FMNH 212471	50D	15.10±0.131 (13.05-16.75)	17.49±0.121 (15.4-19.2)	0.863±0.005 (0.770-0.929)	4 7/8 (4 1/2+-5 1/4−)	0.81±0.024 (0.55-1.25)	22.6±0.721 (13.9-35)
WA-47b, FMNH 182393	12D	14.49±0.314 (13.05-16.55)	17.38±0.226 (16.35-18.95)	0.833±0.010 (0.794-0.903)	4 5/8+ (4 1/2-4 7/8+)	closed	
WA-47a, FMNH 182543	28L	14.84±0.117 (14.0-16.6)	17.45±0.157 (16.05-20.25)	0.852±0.006 (0.799-0.914)	4 3/4 (4 1/2+-5−)	closed	
WA-47b, FMNH 182533	80L	14.61±0.084 (12.75-16.4)	17.25±0.074 (15.6-19.2)	0.847±0.003 (0.756-0.912)	4 3/4 (4 3/8+-5 1/8+)	closed	
WA-47, FMNH 182529	82L	14.6±0.092 (13.0-16.55)	17.17±0.072 (15.55-18.9)	0.850±0.004 (0.776-0.961)	4 3/4− (4 3/8+-5 1/8−)	closed	
WA-169, FMNH 199726	55L	14.51±0.076 (13.3-15.85)	17.02±0.075 (15.45-18.6)	0.853±0.004 (0.776-0.917)	4 3/4− (4 1/2-5 1/8−)	closed	
WA-47a, FMNH 182405	139D	14.82±0.068 (12.7-17.3)	17.56±0.063 (15.3-19.55)	0.844±0.003 (0.762-0.971)	4 3/4 (4 3/8+-5 1/8−)	closed	
WA-47, FMNH 182300	152D	14.41±0.061 (12.85-16.95)	17.12±0.059 (15.7-19.4)	0.842±0.003 (0.776-0.935)	4 5/8+ (4 3/8+-5+)	closed	
WA-47, FMNH 182542	8D	13.90±0.025 (13.2-14.8)	17.10±0.037 (15.55-18.56)	0.810±0.009 (0.780-0.850)	4 1/2− (4 3/8-4 5/8)	closed	

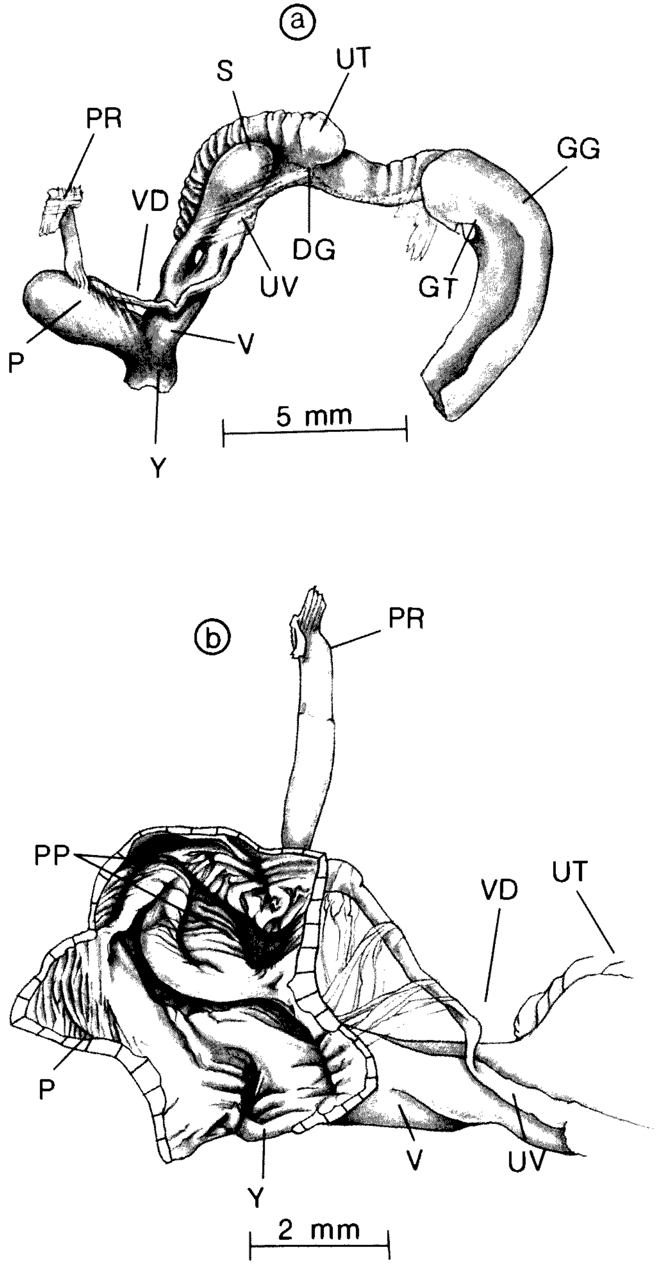


Fig. 392: Genitalia of *Plectorhagada carcharias* (Pfeiffer, 1864): WA–169, 7.3 km S of Warroora Homestead, 0.4 km S of well, near coast, N of Carnarvon, WA. 26 September 1976. FMNH 199843. (a) whole genitalia, Dissection B. (b) interior of penis, Dissection A. Scale lines as marked. Drawings by Linnea Lahlum.

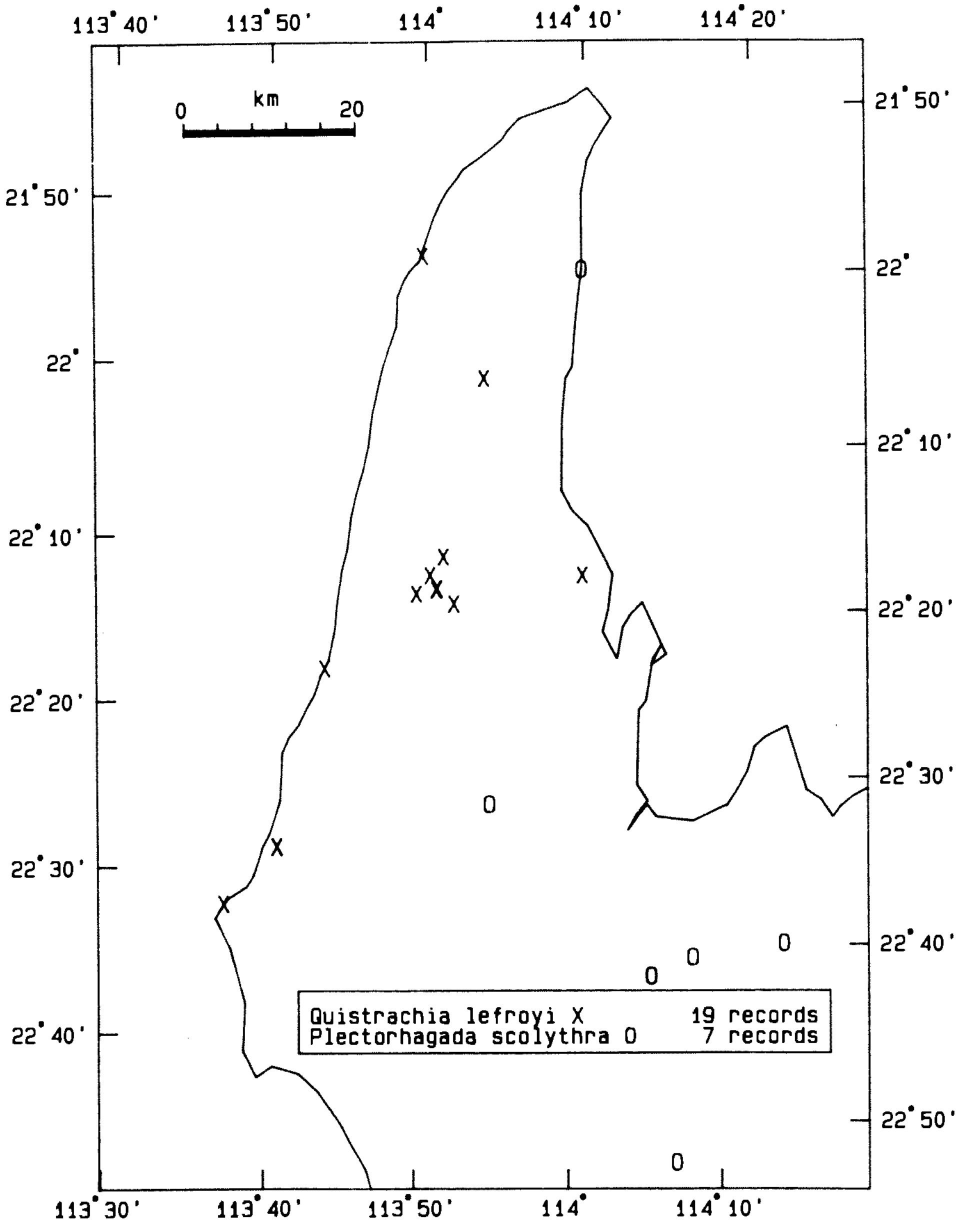
crenulated sculpture on the upper spire and their aestivation pattern of free sealing in the litter instead of sealing to another shell or rock face as do the species of *Plectorhagada*. Anatomically (**Figs 392a–b**), *P. carcharias* lacks both a penis sheath and the epiphalic caecum, the albumen gland (GG) is only moderately enlarged, the vagina (V) is very short and, in the penis chamber, the U-pilaster (PP) is drastically reduced in size and the accessory ridge area greatly enlarged. In *P. scolythra* (**Figs 393a–b**) the epiphallic caecum is a small knob, the albumen gland is smaller, there is a large but highly modified U-pilaster and there is a very prominent accessory pilaster developed. *P. plectilis* (**Figs 391a–b**) lacks the epiphallic caecum and penis sheath, has the albumen gland grossly expanded, the vagina is longer and within the penis chamber, the U-pilaster is very large and the accessory ridges reduced. Radular differences have been discussed above.

Type specimens

A single example in the Mousson Collection, Zoologisches Museum der Universität Zürich, obtained from Geale in 1874 (Zurich 510035) with the locality "W. Australien", agrees perfectly in shell sculpture with the examples grouped here as *Plectorhagada carcharias*. Height of shell 12.55 mm, diameter 16.2 mm, H/D ratio 0.775, whorls 4 3/4, umbilicus a narrow lateral crack. The only other older example is a specimen in the BMNH that McAndrew had purchased from Sowerby & Fulton in 1911. It has the locality "Shark Bay, NW Australia". Height of shell 12.6 mm, diameter 15.8 mm, H/D ratio 0.797, whorls 4 1/2+, umbilicus closed. Both shells probably are type lot examples but there is no indication that they are actual syntypes.

Material studied

WESTERN AUSTRALIA: Moogooree Station, Kennedy Range (200 yds S of Toby's Well, T. A. Darragh & G. W. Kendrick!, 12 April 1969, WAM 314.74, 6 DA, 1 DJ); Coonantha, Lyons River District (P. Evans & D. Stokes! 9 September 1970, WAM 382.74, 19 DA, 13 DJ); S of Minilya River 11.4 km W of Wandagee Station turnoff rock spurs, (WA-963, FMNH 212515, 3 DA, 2 DJ); W side of Marsh Hill, Minilya Station (T. A. Darragh & G. W. Kendrick! 9 April 1969, WAM, 3 DJ); Wandagee, Minilya River near Coolkilya Pool (G. W. Kendrick & K. J. McNamara! 5–6 September 1979, WAM 306.80, 6 DA, 2 DJ); Dirk Hartog Island (AM C.33425, 2 DA, 1 DJ); Dorre Island (top of Quoin Bluff, 19 July 1958, WAM, 6 DA) A. M. Douglas! 1959, WAM 360.74, 3 LA, 1 LJ; W. D. L. Ride! 17 July 1959, WAM, 3 DA); Quobba, N of Carnarvon (WA–167a, near lighthouse, FMNH 199769, 3 LA, 1 LJ); Ram Paddock Well, Quobba Station (WA–168, WAM 909.87, SAM D18236, AM, QM, MV, FMNH 199740, FMNH 199881, FMNH 200177, 168 LA, many LJ; WA–953, WAM 908.87, SAM D18235, AM, QM, MV, FMNH 212469–70, 99 LA, 5 DA, many LJ, 4 DJ); Cape Cuvier (M. Seymour! 20 May 1971, WAM, 2 DA); Chargoo Anticline, Gnargoo Range, E of Lake Macleod (W. Turnbull! 23 November 1976, WAM 911.87, SAM D18238, AM, MV, QM, FMNH 199065–6, 100 DA, many DJ); NE tip of Lake Macleod (E. Lundelius & W. Turnbull!, 23 November 1976, WAM 464.77, 4 DA); N side of lagoon, 6 miles S of Warroora Homestead (WA–48, FMNH 182361, FMNH 182412, 1 LA, 9 DA, 2 DJ); under salt bush 4.6 miles S of Warroora Homestead (WA–47, WAM 912.87, WAM 913.87, SAM D18239–40, AM, QM, MV, FMNH 182592, FMNH 182299–300, FMNH 182529, FMNH 182542, FMNH 182740, 88 LA, 155 DA, many LJ, many DJ); 300 yds E of WA–47 (WA–47a, FMNH 182405, FMNH 182543, 28 LA, 139 DA, 17 LJ); dunes 4.6 miles S of Warroora Homestead (WA–47b, FMNH 182533, FMNH 182414, 80 LA, 2 DA, many LJ); salt bush 4.6 miles S of Warroora Homestead (WA–47b, FMNH 182393, 12 DA, 2 DJ); 7.3 km S of Warroora Homestead



Map 32: Records of *Plectorhagada scolythra* and *Quistrachia lefroyi* on the Cape Range peninsula, WA.

(WA–169, WA–1069, WAM 910.87, SAM D18237, AM, QM, MV, FMNH 199843–4, FMNH 199661, FMNH 199726, FMNH 199875, FMNH 221717, 121 LA, 18 DA, many LJ, 2 DJ); red soil–limestone ridge 7.2 km S of Warroora Homestead (WA–954, WAM 907.87, SAM D18234, AM, MV, QM, FMNH 212471–2, 11 LA, 50 DA, 8 LJ, 8 DJ); ocean front dune 6.7 km S of Warroora Homestead (WA–955, FMNH 212476, 1 DA, 1 DJ); Boolbarli (sic) (D. Parker! August 1972, WAM, 7 DA, 1 DJ); 0.3 km S of Upper Bulbarli Well (WA–956, FMNH 212481, 2 DA, 1 DJ); sand dunes 3 miles S of Warroora Homestead (WA–46, FMNH 182359, 1 DA); Warroora access road, 1.4 miles W of Exmouth Road (WA–50, FMNH 182591, 2 LA, 4 LJ).

Range

Plectorhagada carcharias described from Shark Bay, has been collected on both Dirk Hartog and Dorre Islands, Shark Bay; inland along the Minilya River and northern part of the Kennedy Range (*ca.* 23°45'S to 24°10'S) and then coastally from Lake Macleod and Point Quobba N to just S of Warroora Homestead (*ca.* 23°30'S to 25°17'S), WA (**Maps 28–31**), a N-S distance of about 295 km. The maximum E-W range is approximately 220 km.

Diagnosis

Shell medium in size, adult diameter 12.3–20.25 mm (mean 16.93 mm), with 3 7/8+ to 5 1/2+ (mean 4 3/4–) normally coiled whorls. Apex and spire moderately and evenly elevated (**Fig. 390c**), shell height 9.9–18.3 mm (mean 14.33 mm), H/D ratio 0.665–0.986 (mean 0.846). Body whorl evenly rounded, spire whorls rather flatly rounded. Apex (**Plate 191a**) with small pustules in lines, changing to weak ridges. Upper spire (**Plate 191a–d**) with crenulated radial ridges and large micropustules, changing to fine micropustules (**Plate 191b, e**) and growth ridges on lower spire and body whorl. Umbilicus (**Fig. 390c**) normally closed, sometimes a narrow lateral crack. Body whorl descending sharply just behind lip (**Fig. 390b**). Palatal and basal lips reflected and narrowly expanded, columellar lip covering most of umbilicus. Parietal wall with moderate callus. Colour very light yellow-brown, with narrow reddish-brown spiral band and lower white zone just above periphery. Based on 1,160 measured adults.

Genitalia (**Figs 392a–b**) with large albumen gland (GG), shortened prostate (DG) and uterus (UT). Spermatheca (S) short, head lying just above base of prostate-uterus. Vagina (V) short. Vas deferens (VD) slender, entering slightly expanded head of epiphallus (E) about midway up penis. Epiphallus not circling penial retractor muscle (PR), entering penis (P) through simple pore. Penial retractor muscle inserting in arc around junction of epiphallus and penis. Penis chamber with U-pilaster reduced greatly, accessory ridge area enlarged and complex.

Central and lateral teeth of radula (**Plate 195a**) with small anterior flare, elevated cusp shaft angle, curved and bluntly pointed cusp tip, slightly shortened basal plate. Late laterals (**Fig. 195b**) with enlarged anterior flare, reduced cusp shaft angle, and sharper cusp tip. Ectocone not appearing until first marginals. Marginals typical. Jaw with greatly reduced vertical ribs.

Discussion

Plectorhagada carcharias shows considerable size variation (**Table 143**). Both large (mean diameter 18.52 mm) and small (mean 16.38 mm) sized samples are found inland along the Minilya River; the Lake Mcleod specimens are small (mean diameter 15.28 mm); Dorre Island shells are small (mean diameter 16.10 mm); the Ram Paddock, Quobba specimens are small (mean diameter 16.03–17.17 mm); and the Warroora specimens tend to be fairly large (mean diameters 16.87–18.06 mm). In two samples collected at Warroora, live specimens are slightly larger than dead specimens, but the differences are marginally significant.

No specimens clearly intermediate between the present species and *P. plectilis* were seen but the limited Dirk Hartog Island material had more prominent upper spire sculpture. No *Plectorhagada* have been reported from Bernier Island nor the Peron Peninsula.

PLECTORHAGADA MEILGANA SP. NOV.

(Plate 193a–f; Figs 389d–f; Map 28)

Comparative remarks

Plectorhagada meilgana, from Joy Helen Mine (23°15'S, 115°46'E) and near Meilga Homestead (22°46 S, 115°51'E) in the upper Henry River basin, a southern tributary of the Ashburton River, WA (**Map 28**), is relatively small (mean diameter 13.31 mm), with a moderately elevated spire (**Fig. 389d**, mean H/D ratio 0.612), narrow umbilicus (**Fig. 389f**, mean D/U ratio 10.6), relatively low whorl count (**Fig. 389d**, mean whorls 4 1/8+), angulated periphery (**Fig. 389d**), and very prominent crenulated ridging and micropustules that continue onto the shell base (**Plate 193a–f**). The two other umbilicated *Plectorhagada* species are readily differentiated. *P. rovina* Iredale, 1939 from Shark Bay has a greatly increased whorl count (**Fig. 388d**, whorls 5 7/8), very high spire (**Fig. 388d**, H/D ratio 0.869) and three red spiral colour bands. *P. gascoynensis* (E. A. Smith, 1894) from the Gascoyne District has a very low spire (**Fig. 389b**, mean H/D ratio 0.495) and rounded shell periphery plus a widely open umbilicus (**Fig. 389c**, mean D/U ratio 5.07). All other *Plectorhagada* have the umbilicus reduced to a narrow lateral crack or closed (**Table 140**). The anatomy is unknown.

Holotype

WAM 754.87, near Joy Helen Mine, Glen Florrie Station, Henry River basin (Ashburton River drainage), WA. 23°15'S, 115°46'E. Collected 1 September 1969 by A. Saar and P. J. Bridge. Height of shell 7.35 mm, diameter 10.9 mm, H/D ratio 0.674, whorls 4 1/4–, umbilical width 1.2 mm, D/U ratio 9.08.

Paratopotypes

WAM 309.74, 3 DJ from the type locality.

Paratypes

WESTERN AUSTRALIA: near old white asbestos mine, *ca.* 5 miles E of Meilga Station homestead (*ca.* 22°46'S, 115°51'E, A. Saar & P. J. Bridge! 2 September 1969, WAM 324.74, FMNH 221611, 5 DA, 1 DJ).

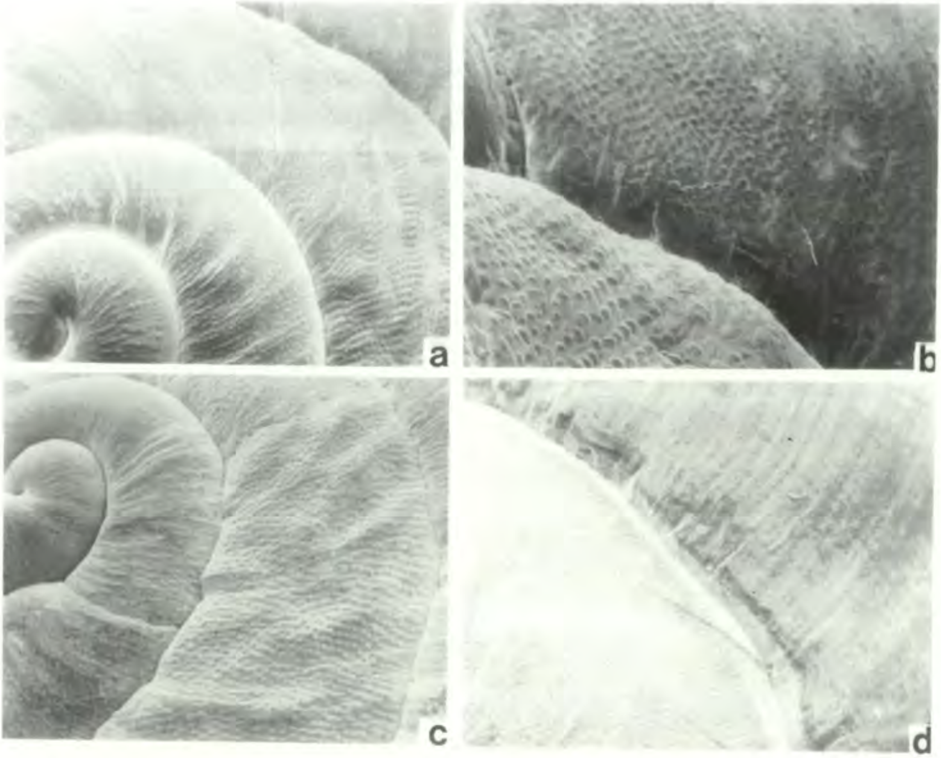


Plate 192: Shell sculpture of *Plectorhagada scolythra* sp. nov.: WA–51, Scrubby Range, E of Cardabia Homestead, WA: (a–b) FMNH 182353. a is apex and spire at 17.2X. b is mid-spire at 40X; (c–d) FMNH 182548. c is apex and spire at 18.5X. d is lower spire and body whorl at 18.5X.

Range

The two known localities for *Plectorhagada meilgana* are in the upper drainage of the Henry River, a southern tributary of the Ashburton River, WA (**Map 28**). The northern locality, near Meilga Station homestead, is about 155 km ESE from the southern-most part of Exmouth Gulf and 45 km SE of Nanutarra Roadhouse on the NW Coastal Highway; the southern locality, Joy Helen Mine, is about 53 km almost directly S of Meilga. No other land snail localities are recorded in this region, so that the total range is unknown.

Diagnosis

Shell small, adult diameter 10.9–15.0 mm (mean 13.31 mm), with 4+ to 4 1/4 (mean 4 1/8+) normally coiled whorls. Apex and spire moderately and evenly elevated (**Fig. 389e**), shell height 7.35–8.8 mm (mean 8.10 mm), H/D ratio 0.577–0.674 (mean 0.612). Body whorl distinctly angulated (**Fig. 389e**). Apex (**Plate 193a**) with relatively large, dense pustules, spire and body whorl (**Plate 193b–f**) with typical crenulated ridges and dense micropustulations, both of which extend onto the shell base with moderate size reduction. Umbilicus narrowly open (**Fig. 389f**), partly covered by

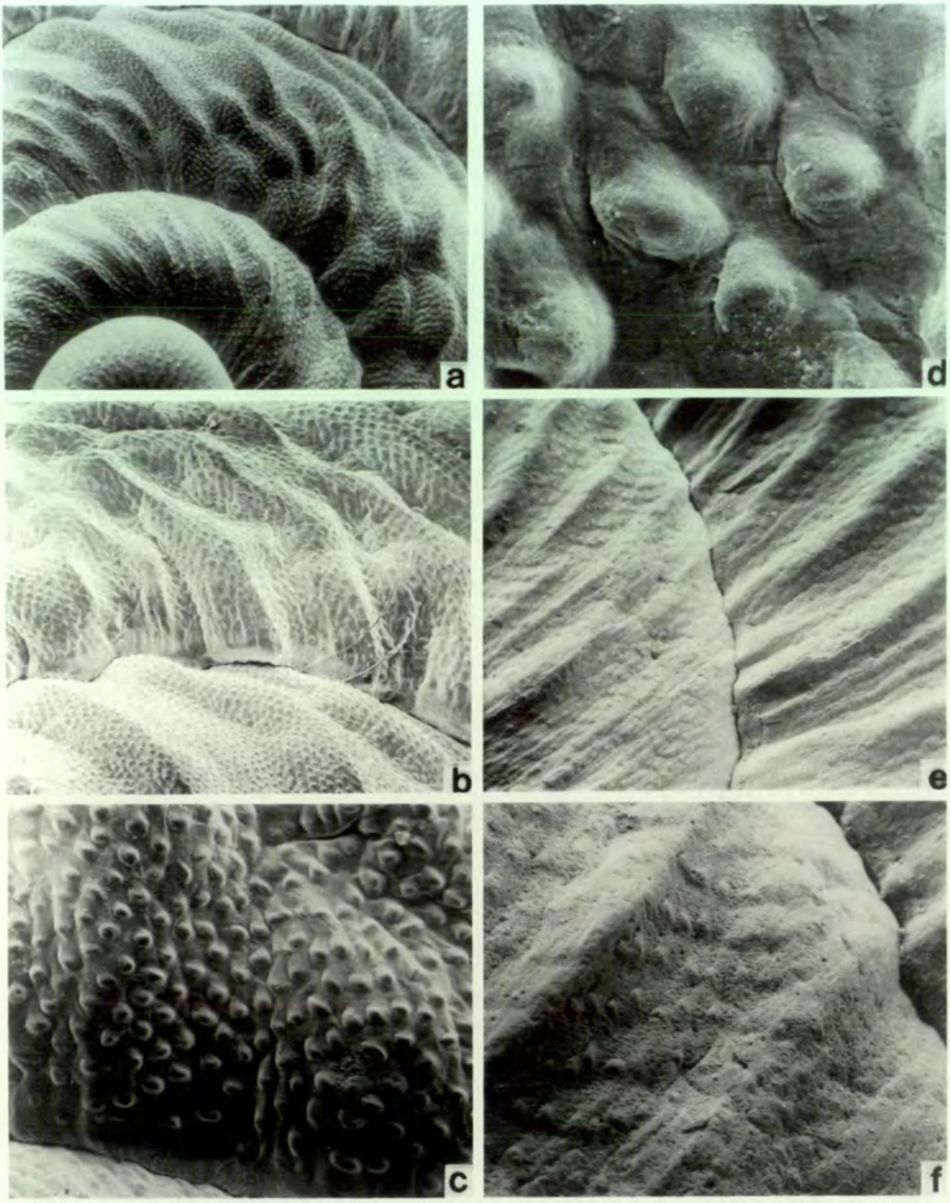


Plate 193: Shell sculpture of *Plectorhagada meilgana* sp. nov.: (a–d) near Joy Helen Mine, Glen Florrie Station, WA. Holotype. WAM 309.74. a is apex and spire at 17.6X. b is lower spire and body whorl at 24.6X. c is micro-sculpture on early spire at 84X. d is detail of micro-sculpture at 430X; (e–f) *ca* 5 miles E of Meilga Station Homestead, WA. WAM 324.74. e is lower spire and body whorl at 25.1X. f is detail on lower spire at 83X.

reflexion of columellar lip, width 1.0–1.8 mm (mean 1.30 mm), D/U ratio 7.67–14.2 (mean 10.6). Body whorl descending moderately on last portion. Palatal and basal lips moderately expanded, columellar lip more broadly expanded, parietal wall greatly thickened but with edge appressed. Colour unknown. Based on 6 measured adults.

Anatomy unknown.

Discussion

The holotype of *Plectorhagada meilgana* is a young adult (**Figs 389d–f**) with less lip expansion and parietal wall callus formation than is found in the Joy Helen Mine paratypes. It has, however, the best preserved sculpture (**Plate 193a–d**) of any available specimen, whereas the Meilga Station shells (**Plate 193e–f**) are rather badly worn. It also is much the smallest example, with the Meilga specimens ranging 12.85–15.0 mm in diameter with a lower spire. Since it is the shell sculpture that places this species, the only *Plectorhagada* with an angulated periphery, in *Plectorhagada* rather than *Pleuroxia*, the atypical example with well preserved sculpture has been selected as holotype.

The occurrence of *Plectorhagada meilgana* in the upper Henry River drainage, whereas most other species (except probably *P. gascoynensis*) are more coastal in distribution, suggests that inland survey collecting for land snails of the hill systems in this region might be fairly productive.

PLECTORHAGADA SCOLYTHRA SP. NOV.

(Plates 192a–d, 195c–f; Figs 390d–f, 393a–b; Maps 28, 30–32).

Comparative remarks

Plectorhagada scolythra sp. nov., found from the S end of the Scrubby Range N to the S end of the Rough Range, near the southern-most part of Exmouth Gulf, WA (**Maps 28, 30–32**), generally has the crenulated upper spire sculpture less prominent and the pustules much smaller (**Plate 192a, c**) than in *P. carcharias* (Pfeiffer, 1864), which ranges from Warroora Station S to Dirk Hartog Island in Shark Bay and then E along the Minilya River to the Kennedy Range (**Maps 28–31**). Both of the above species have the lower spire and body whorl with finer pustules (**Plates 191b, e, 192b, d**) than are found in *P. plectilis* (Benson, 1853) (**Plate 190a–c**), which also has the crenulated sculpture extending to just behind the lip. *P. scolythra* is slightly larger (**Table 140**) than *P. carcharias*, but this difference is no greater than the normal differences found among populations within many species. All three species have closed or nearly closed umbilici, whereas the other *Plectorhagada* species have narrow to widely open umbilici. Anatomically (**Figs 393a–b**), *P. scolythra* lacks the penis sheath, but has a very small knob of an epiphallic caecum (EC), the albumen gland (GG) is only moderately enlarged, the U-pilaster within the penis chamber is highly modified, and the accessory ridge area is greatly enlarged. *P. carcharias* (**Figs 392a–b**) lacks both the epiphallic caecum and the penis sheath, the albumen gland is proportionately larger, the U-pilaster is greatly reduced in size, and the accessory ridges are less developed. *P. plectilis* (**Figs 391a–b**) also lacks both the penis sheath and the epiphallic caecum, the albumen gland is enormous, and the U-pilaster dominates the penis chamber, with the accessory ridges very small. Differences in radular structure have been discussed above.

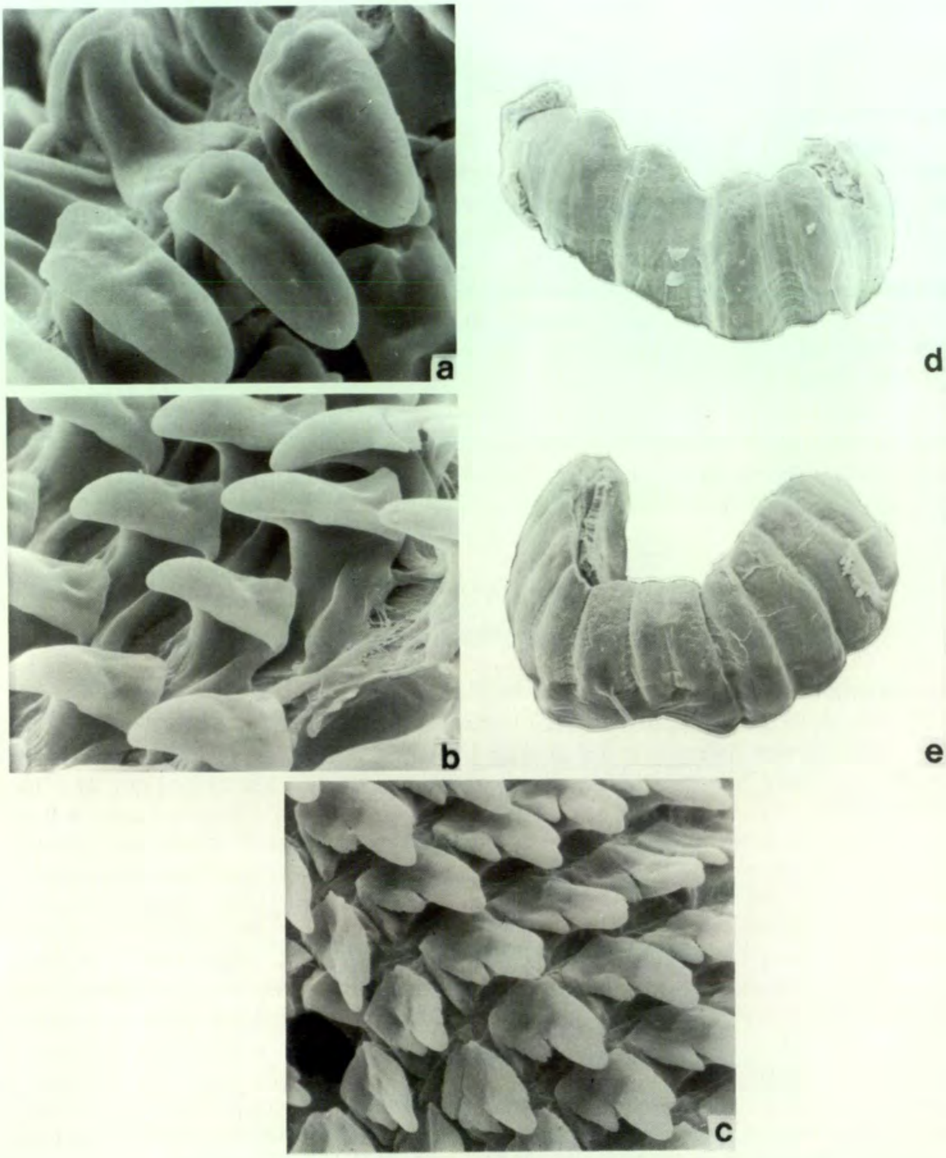


Plate 194: Radular teeth and jaws of *Plectorhagada plectilis* (Benson, 1853): Hamelin Pool, Shark Bay, WA. 17 August 1975. WAM 1362.75: (a) Dissection A, central and early laterals at 930X; (b) Dissection B, lateral teeth at 900X; (c) Dissection A, marginal teeth at 750X; (d) Dissection A, jaw at 90X; (e) Dissection B, jaw at 97X.

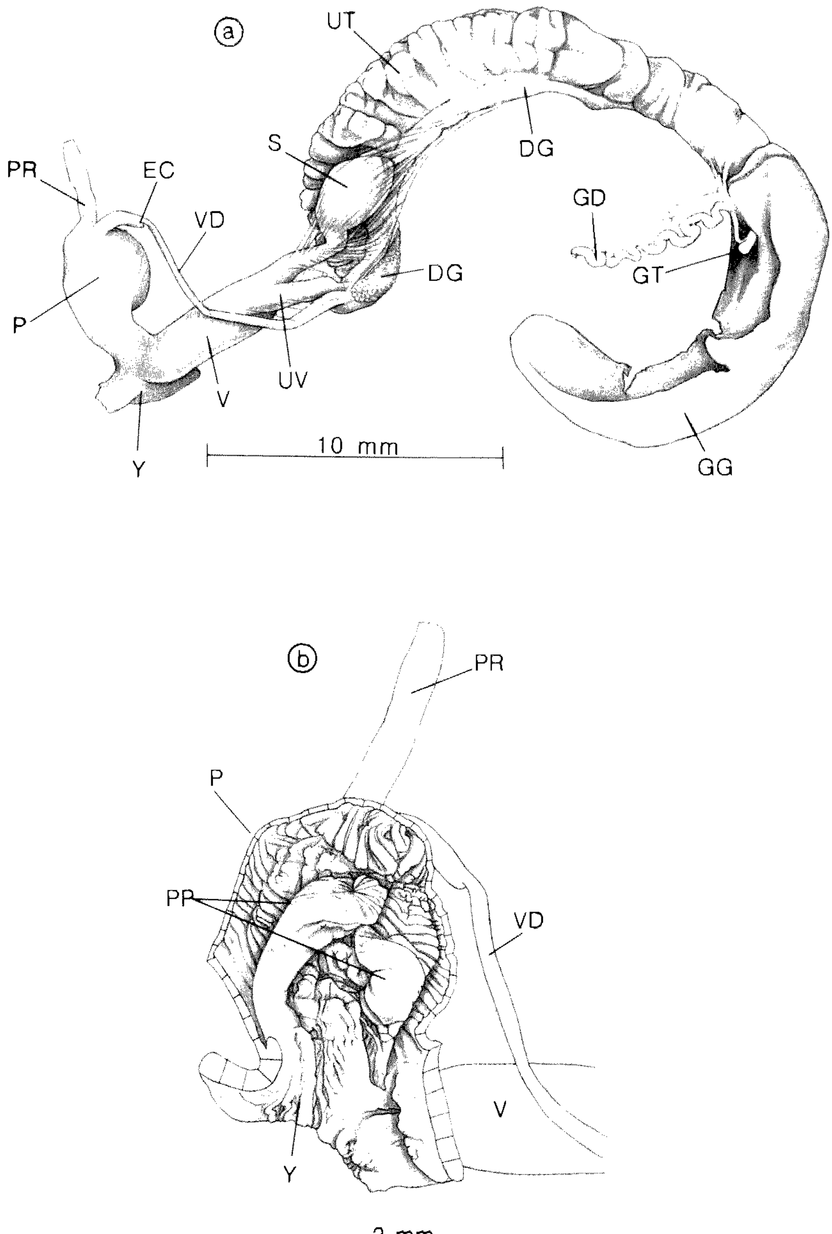


Fig. 393: Genitalia of *Plectorhagada scolythra* sp. nov.: WA 51, Scrubby Range, 12.8 miles E of Exmouth Road from Cardabia Station turnoff, WA. 5 February 1974. FMNH 182548. (a) whole genitalia, Dissection B. (b) interior of penis, Dissection C. Scale lines as marked. Drawings by Linnea Lahlum.

Table 144: Local variation in *Plectorhagada scolythra.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
WA-51, FMNH 182353	56D	14.8±0.132 (13.1-17.25)	17.76±0.119 (15.75-19.9)	0.833±0.004 (0.758-0.893)	$4\frac{5}{8}$ ($4\frac{3}{8}$+-5+)	closed	
WA-51, FMNH 182548	30L	14.93±0.139 (13.2-16.6)	17.78±0.131 (16.2-19.3)	0.839±0.005 (0.784-0.907)	$4\frac{5}{8}$ ($4\frac{3}{8}$+-$4\frac{7}{8}$−)	closed	
WA-957, FMNH 212482	31D	15.06±0.166 (13.45-17.0)	17.83±0.152 (16.7-19.4)	0.845±0.007 (0.778-0.963)	$4\frac{3}{4}$ ($4\frac{3}{8}$+-5+)	0.68±0.037 (0.3-1.05)	29±2.150 (16.5-68)
WA-170, FMNH 199735	39L	15.3±0.085 (14.3-16.85)	18.03±0.109 (16.4-19.5)	0.849±0.005 (0.772-0.902)	$4\frac{5}{8}$+ ($4\frac{3}{8}$+-$4\frac{7}{8}$−)	closed	
WA-170, FMNH 199906	29L	15.11±0.132 (13.35-16.7)	17.73±0.141 (16.7-19.5)	0.853±0.005 (0.796-0.912)	$4\frac{5}{8}$+ ($4\frac{3}{8}$+-$4\frac{3}{4}$+)	closed	
WA-957, FMNH 212484	77L	15.46±0.085 (14.2-17.25)	18.12±0.079 (16.7-20.05)	0.854±0.004 (0.779-0.934)	$4\frac{3}{4}$+ ($4\frac{1}{2}$+-5+)	0.74±0.018 (0.45-1.1)	25±0.618 (16.5-40)
E side Remarkable Hill, WAM 341.74	7L	15.19±0.303 (13.8-16.4)	18.99±0.226 (18.2-19.9)	0.800±0.012 (0.758-0.854)	$4\frac{3}{8}$ ($4\frac{1}{4}$-$4\frac{1}{2}$)	closed	
creek bed, W of Giralia Hstd, FMNH 199067	19D	15.79±0.207 (14.55-17.5)	18.6±0.156 (17.4-19.6)	0.849±0.008 (0.768-0.913)	$4\frac{3}{4}$ ($4\frac{1}{2}$+-5−)	closed	
WA-179, FMNH 199771	9L	15.61±0.214 (14.75-16.95)	17.71±0.268 (16.65-19.3)	0.882±0.008 (0.855-0.934)	$4\frac{3}{4}$− ($4\frac{5}{8}$−-$4\frac{3}{4}$+)	closed	
WA-418, FMNH 199746	8L	15.44±0.242 (14.4-16.15)	18.05±0.274 (17.0-19.1)	0.856±0.012 (0.795-0.910)	$4\frac{5}{8}$ ($4\frac{1}{2}$−-$4\frac{3}{4}$−)	closed	
WA-27, FMNH 182703	9D+4L	15.44±0.145 (14.6-16.7)	17.84±0.101 (17.25-18.45)	0.866±0.009 (0.814-0.907)	$4\frac{5}{8}$+ ($4\frac{1}{2}$+-$4\frac{3}{4}$+)	closed	

Table 144: Local variation in *Plectorhagada scolythra* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
WA-418 FMNH 199745	11D	15.98±0.298 (14.3-17.55)	18.54±0.312 (16.9-20.75)	0.862±0.010 (0.805-0.906)	$4^{5}/_{8}$+ ($4^{3}/_{8}$+-)	closed	
15 miles SE jctn Ningaloo+Exmouth Rd., AM C.87638	5D	15.03±0.757 (14.0-18.0)	18.43±0.406 (17.25-19.75)	0.814±0.025 (0.768-0.911)	$5^{7}/_{8}$− ($5^{5}/_{8}$+-6.3)	closed	
Scrubby Range, 19.7 km E of Cardabia turnoff FMNH 213484	77L	15.47±0.085 (14.2-17.25)	18.12±0.079 (16.7-20.05)	0.854±0.004 (0.779-0.934)	$4^{3}/_{4}$+ ($4^{1}/_{2}$+-5+)		
Toothawarra Creek, WAM	6D	15.80±0.593 (14.3-16.3)	17.66±0.743 (16.25-18.7)	0.861±0.006 (0.802-0.945)	$4^{5}/_{8}$ ($4^{5}/_{8}$-$4^{3}/_{4}$)		
WA-27, WA-179, 8.7 km E of Bullara Hstd, FMNH 182703	16D	15.44±0.145 (14.6-16.7)	17.84±0.101 (17.25-18.45)	0.866±0.009 (0.814-0.907)	$4^{5}/_{8}$+ ($4^{1}/_{2}$+-$4^{3}/_{4}$+)		
WA-27, WA-179, 8.7 km E of Bullara Hstd, FMNH 199771	9L	15.61±0.214 (14.75-16.95)	17.71±0.268 (16.65-19.3)	0.882±0.008 (0.855-0.934)	$4^{5}/_{8}$+ ($4^{5}/_{8}$−-$4^{3}/_{4}$+)		
11 km W of Giralia Hstd, FMNH 199067	19D	15.79±0.207 (14.55-17.5)	18.60±0.156 (17.4-19.6)	0.849±0.008 (0.768-0.913)	$4^{3}/_{4}$ ($4^{1}/_{2}$+-5−)		
WA-418, 13.8 km W of Giralia Hstd, FMNH 199746	8L	15.45±0.242 (14.4-16.15)	18.05±0.274 (17.0-19.1)	0.856±0.012 (0.795-0.910)	$4^{5}/_{8}$ ($4^{1}/_{2}$−-$4^{3}/_{4}$−)		
WA-418, 13.8 km W of Giralia Hstd, FMNH 199745	11D	15.99±0.298 (14.3-17.55)	18.54±0.312 (16.95-20.75)	0.862±0.010 (0.805-0.906)	$4^{5}/_{8}$ ($4^{3}/_{8}$+-$4^{3}/_{4}$+)		

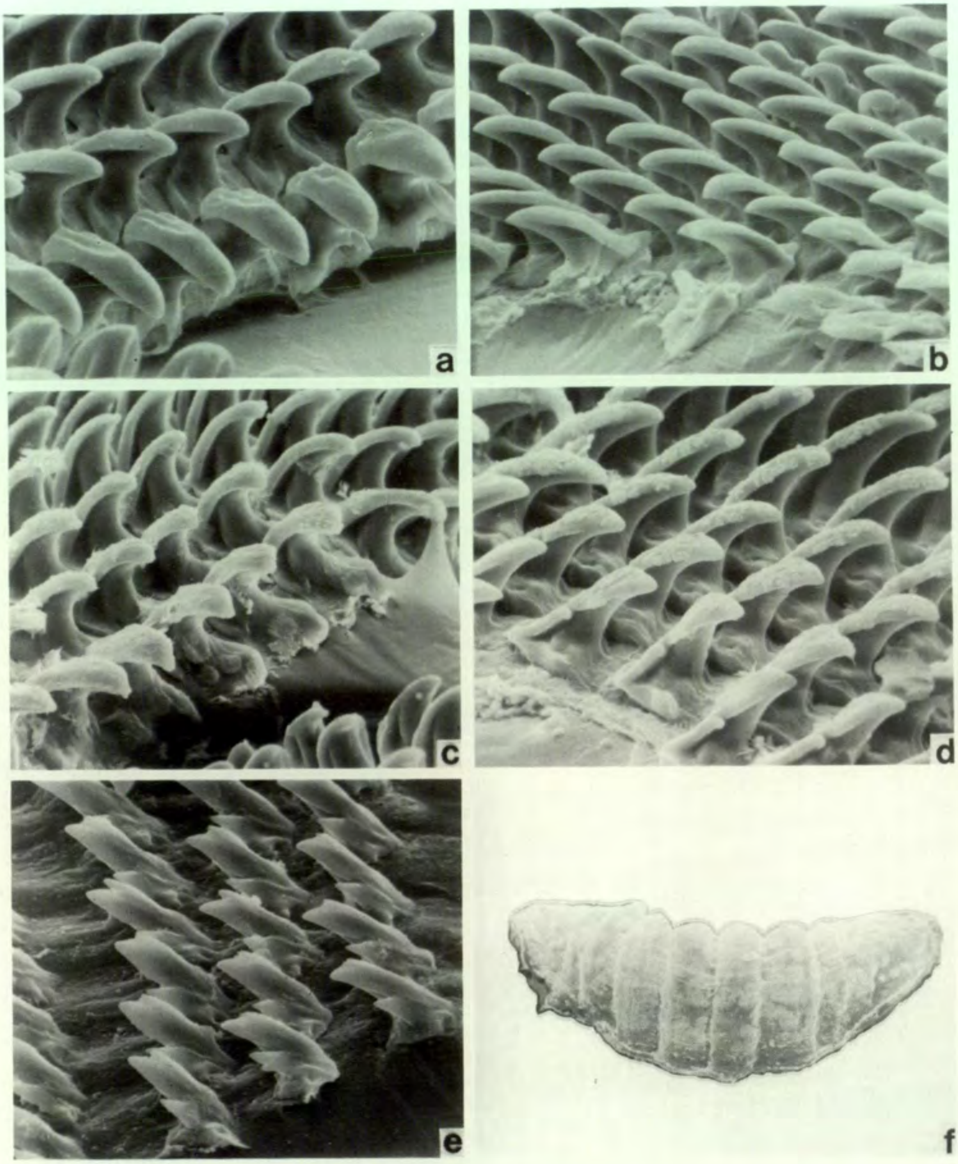


Plate 195: Radular teeth and jaws of *Plectorhagada carcharias* (Pfeiffer, 1864) and *P. scolythra* sp. nov.: (a–b) *P. carcharias*. WA–169, Warroora Station, Gascoyne District, WA. 26 September 1976. FMNH 199843. a is central and early laterals at 470X. b is latero-marginal transition at 480X; (c–f) *P. scolythra*. WA–51, Scrubby Range, S of Exmouth Gulf, WA. 5 February 1974. FMNH 182548, Dissection A. c is central and early laterals at 505X. d is late laterals at 670X. e is mid marginals at 610X. f is jaw at 54X.

Holotype

WAM 752.87, WA–51, Cardabia Station 12.8 miles E of Exmouth Road from Cardabia turnoff, Scrubby Range, Western Australia. 23°07'00"S, 114°02'57"E. Collected by A. Solem & L. Price 5 February 1974. Height of shell 14.6 mm, diameter 17.7 mm, H/D ratio 0.825, whorls 4 3/4–, umbilicus a narrow lateral crack.

Paratopotypes

WAM 883.87, WAM 884.87, AM C200,712, SAM D18217–8, MV F59500, MV F60022, QM 46372, FMNH 182353, FMNH 182548, 30 LA, 56 DA, 51 LJ, 19 DJ from the type collection; WA–170, WAM 888.87, AM C200,713, SAM D18222, MV F.59441, QM 52980, FMNH 199735, FMNH 199906, 68 LA, many LJ from the type locality; WA–957, WAM 886.87, WAM 887.87, AM C.200,714, SAM D18220–1, MV F.59451, QM 46371, FMNH 212482–4, 77 LA, 31 DA, 36 LJ, 8 DJ from the type locality.

Paratypes

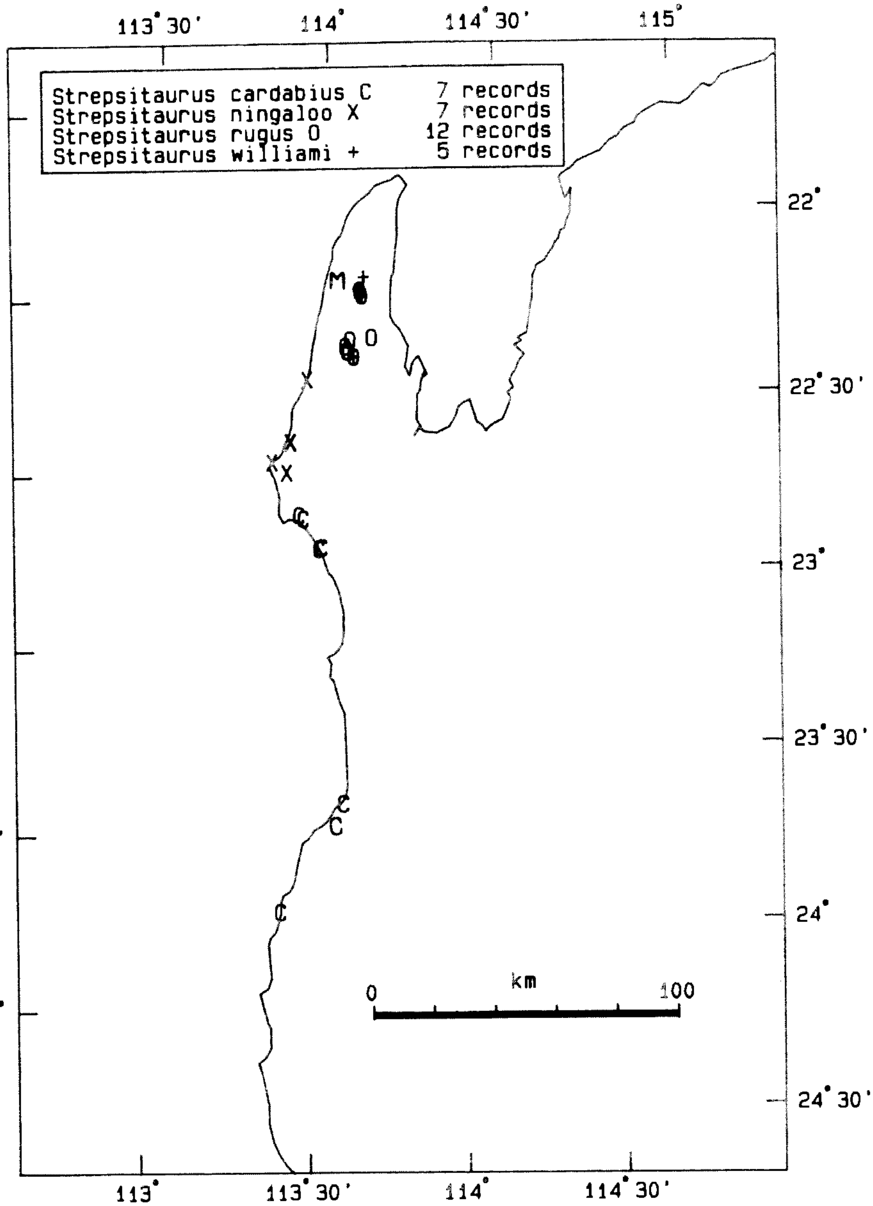
WESTERN AUSTRALIA: Remarkable Hill (114°05'E, 23°02'S), Scrubby Range (T. A. Darragh & G. W. Kendrick! 9 April 1969, WAM 341.74, 7 LA); Section Hill, Scrubby Range (G. W. Kendrick! 19 August 1975, WAM 1366.75, 1 DA); Centenary Outcamp, Cardabia Station (G. W. Kendrick! 19 August 1975, WAM 1367.75, 6 DA, 1 DJ); Toothawarra Creek (114°23'14"E, 22°49'29"S), Cardabia Station, Scrubby Range (T. A. Darragh & G. W. Kendrick! 4 April 1969, WAM 319.74, 4 DA, 1 DJ); creekbed 5.4 miles (= 8.7 km) E of Bullara Homestead, Bullara-Giralia road (WA–27, WA–179, FMNH 182703, FMNH 199771, FMNH 200172, 15 LA, 9 DA, 10 LJ); creekbed 11 km W of Giralia Station, Bullara-Giralia road (E. Lundelius & W. Turnbull! 21 November 1976, WAM 471.77, WAM 472.77, WAM 478.77, FMNH 199067, 22 DA, 20 DJ); 13.8 km E of Bullara Homestead, Bullara-Giralia road (WA–418, WAM 885.87, SAM D18219, AM C200,767, QM 52981, FMNH 199745–6, FMNH 199741, 21 LA, 2 LJ); near Giralia Homestead (W. Turnbull! 1964, FMNH 171641, 4 DA, 4 DJ); gullies in S part of Rough Range, near Exmouth Gulf (G. W. Kendrick! 25 May 1965, WAM 312.74, 3 DA, 5 DJ); Exmouth rubbish dump area (WA–19, FMNH 182453, FMNH 182664, 8 LA, 5 DA, 5 LJ, 1 DJ); Exmouth gravel reserve, 2.2 km N of Mowbowra Creek, E side Cape Range (WA–1078, FMNH 221740, 19 LA).

Range

Plectorhagada scolythra sp. nov., has a compact range just S of Exmouth Gulf (**Maps 28, 30–32**), extending from the S end of the Rough Range (*ca.* 22°30'S) to probably the S end of the Scrubby Range (*ca.* 23°10'S), a N-S distance of about 65 km. The E-W range is about 20 km, between 114°and 114°09'E. It has not yet been found in the Cape Range.

Diagnosis

Shell relatively large, adult diameter 15.75–20.75 mm (mean 18.06 mm), with 4 1/4 to 5 1/2+ (mean 4 5/8+) normally coiled whorls. Apex and spire moderately and evenly elevated (**Fig. 390e**), shell height 13.1–17.6 mm (mean 15.29 mm), H/D ratio 0.748–0.963 (mean 0.847). Body whorl evenly rounded, without trace of angulation, whorls of spire relatively flat (**Fig. 390e**). Apex (**Plate 192a, c**) with large micropustules arranged in radial rows. Upper and part of mid spire (**Plate 192a, c**) with crenulated ridges and small micropustulations, lower spire and body whorl (**Plate 192a, b, d**) with fine pustules and irregular growth ridges. Umbilicus (**Fig. 390f**) closed or with a



Map 33: Records of the various *Strepsitaurus* species in the Cape Range area, WA, including *Strepsitaurus milyeringus* (M).

narrow lateral crack. Body whorl descending sharply just behind lip (**Fig. 390e**). Palatal and basal lips reflected and narrowly expanded (**Figs 390d–f**), columellar lip covering most of umbilicus. Parietal wall with thin to medium thick callus. Colour very light yellow-brown above, lighter on shell base, usually with a narrow reddish brown spiral band above a narrow white zone, both located just above periphery. Based on 375 measured adults.

Genitalia (**Figs 393a–b**) with enlarged albumen gland (GG), shortened prostate (DG) and uterus (UT). Spermatheca (S) with head just above base of prostate-uterus. Vagina (V) short. Vas deferens (VD) very slender, entering apex of epiphallus (E) next to very small epiphallic caecum (EC) and above midpoint of penis. Epiphallus not circling penial retractor muscle (PR), entering penis (P) through a simple pore. Penial retractor muscle inserting in an arc on penis-epiphallus junction. Penis chamber with highly modified U-pilaster, accessory ridge area complex and greatly expanded.

Central and lateral teeth of radula (**Plate 195c**) with greatly reduced anterior flare, very high cusp shaft angle, strongly curved and blunt pointed cusp tip, basal plate not shortened. Late laterals (**Plate 195d**) showing abrupt shortening of basal plate and appearance of ectocone, some reduction in cusp shaft angle, and some reduction in both cusp tip curvature and degree of bluntness to the tip. Mid marginals (**Plate 195e**) retain a high cusp shaft angle, have the mesocone pointed, show a small endocone, and the ectocone is prominent, sometimes bifurcated or multicuspid. Jaw (**Plate 195f**) with a few central, broad but very low, vertical ribs, which are greatly reduced or absent on lateral margins.

Discussion

Plectorhagada scolythra sp. nov. is slightly smaller at the S end of its range (**Table 144**), but the differences are barely (significant. The Minilya River and Kennedy Range examples of *P. carcharias* are nearly the same size, but have distinctly lower spires (**Table 143**). No live material from this area is available. It is possible that dissection may result in reclassification of these populations.

Anatomical (**Figs 392a–b, 393a–b**) and radular (**Plate 195a–e**) differences between studied populations of *Plectorhagada scolythra* and *P. carcharias* are quite significant. The smaller Shark Bay examples of the latter have less globose shells than the Scrubby and Rough Range examples of the former but the Warroora and Kennedy Range specimens come close to bridging the shell shape gap. Much additional study is needed to work out the species in this complex.

The name *scolythra*, from the Greek *skolythros*, meaning low or shabby, refers to the insignificant limestone hills of the Scrubby Range inhabited by this species. The name originally was suggested to me by George W. Kendrick.

GENUS *STREPSITAURUS* GEN. NOV.

Shell small to medium in size, adult diameter 7.9 to 18.65 mm, whorls 3 3/8+ to 5 3/8+, coiling pattern normal. Spire low (*williami*, *rugus*, **Figs 394e, 395b**) to strongly elevated (*cardabius*, *ningaloo*, **Figs 394b, 395e**), H/D ratio 0.383–0.765. Apical sculpture (**Plates 196a, d, 197a, d, 237d**) of dense, often elongated micropustules, usually arranged in radial rows, sometimes coalescing and forming wavy radial ridges of varied length. Spire and body whorl (**Plates 196, 197**) with crenulated radial ridges, following growth lines (*cardabius*, **Plate 196a–b**) or strongly diagonal (*williami*, *milyeringus*, *ningaloo*, *rugus*, **Plates 196d–e, 197, 237f**), prominence variable from reduced (*williami*, **Plate 196d–e**) to very large (*ningaloo* **Plate 197a–b**), plus large micropustules and probably setae (**Plates 196–198**). Body whorl rounded (*cardabius*, **Fig. 394b**) to obtusely angulated (*rugus*, **Fig. 395e**), descending moderately to sharply behind lip. Umbilicus open (*williami*, **Fig. 394e**, *milyeringus*, **Fig. 452c**), narrow (*cardabius*, **Fig. 394c**) to closed (*ningaloo*, *rugus*, **Figs 395c, f**). Palatal and basal lips reflected and moderately to broadly expanded (**Figs 394–395**), columellar lip wider, covering part to all of umbilicus. Parietal wall with a very thick callus (*cardabius*, **Fig. 394b**) or a free lip edge (**Figs 394e, 395b, e**). Shell colour white on rib tops, reddish-brown in areas between ribs in Cape Range species, unknown in the subfossil *cardabius*. Lip white or with a slight brownish tone.

Specimens aestivate sealed to a rock face by a heavily calcified rim in the Cape Range; situation in the subfossil species *cardabius* unknown. Sometimes specimens seal to another shell but this is not common.

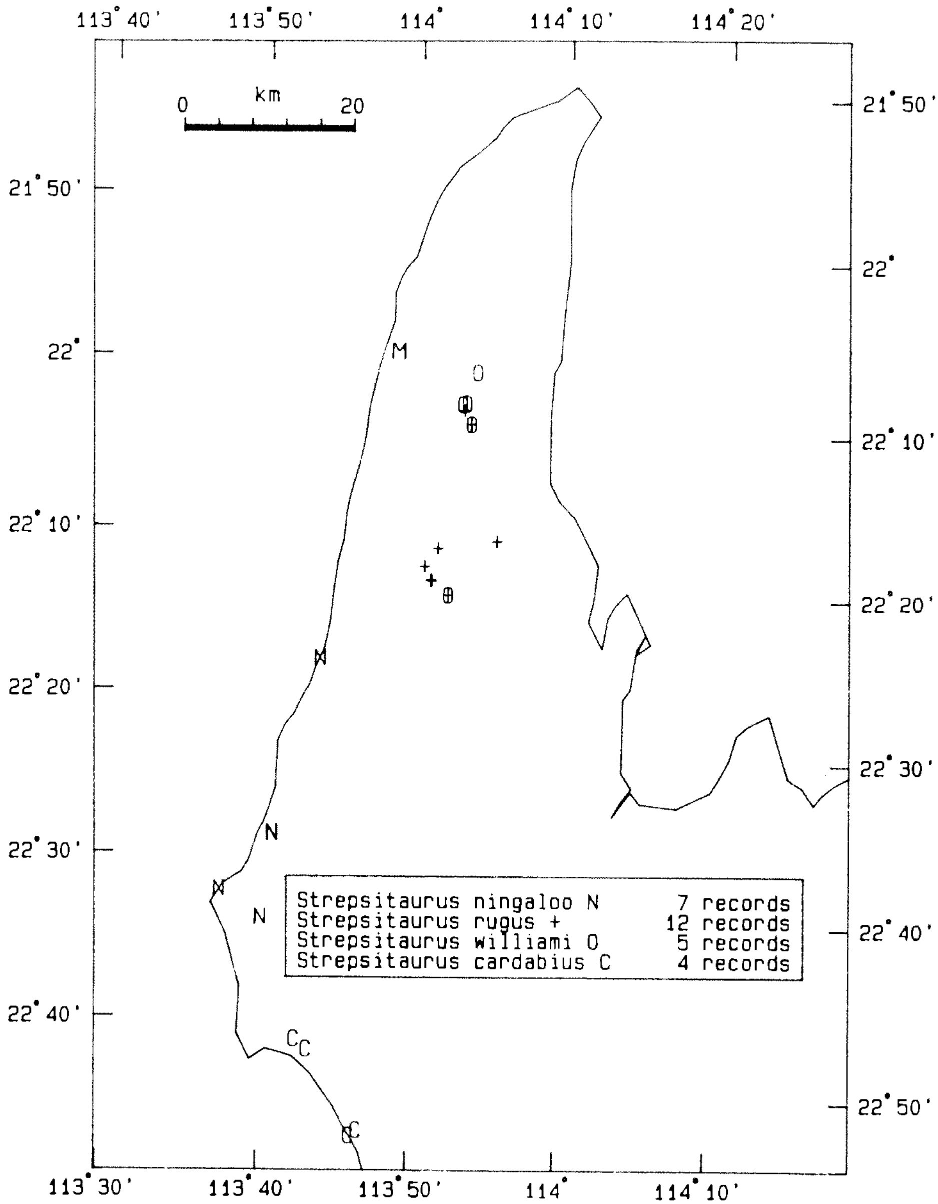
Genitalia (**Figs 396–398, 453**) with normal sized albumen gland (GG). Talon (GT) and hermaphroditic gland (GD) typical. Prostate (DG) and uterus (UT) slightly shortened. Free oviduct (UV) very short. Spermatheca (S) with short to very short shaft, expanded head at base of prostate-uterus, extending a little way upward. Vagina (V) short to medium in length, thicker than free oviduct. Vas deferens (VD) typical, entering directly into enlarged head of epiphallus (E). No epiphallic caecum. Epiphallus very thin-walled, internally with longitudinal pilasters (EPP). Penial retractor muscle (PR) variable in length, inserting in an arc on middle of epiphallus. Penis (P) short, thick-walled, internally with a massive pilaster occupying upper two-thirds of chamber. Pilaster (PP) with central groove and cross cor*ruga*tions. Lower portion of penis chamber with simple longitudinal pilasters.

Jaw (**Plates 200f, 201a–c, e, 238d**) variable, from having high vertical ribs in central region (though greatly reduced on both margins) to lacking any trace of radial ribs. Central and early lateral teeth of radula (**Plates 199a–b, 200a, 201d, f, 237a, 238a**) with greatly reduced anterior flare and generally shortened basal plate, very high cusp shaft angle, cusp tip strongly to abruptly curved and broadly rounded, ectocone absent. Late laterals (**Plates 199c, 200b–c, 237b, 238b**) with enlarged anterior flare, further shortening of basal plate, reduced cusp shaft angle and initial appearance of ectocone. Lateromarginal transition abrupt. Early marginals (**Plate 199d**) and mid-marginals (**Plate 200d, 238c**) with higher than usual cusp shaft angle, outer marginals (**Plates 199e, 200e, 237c**) typical.

Type species: *Pleuroxia ruga* Cotton, 1953 by original designation.

Comparative remarks

The usually diagonally oriented (except *cardabius*) crenulated ribs on the spire and body whorl that continue to the shell lip, the tendency of the apical pustulations to coalesce into variable radial ridgelets, massive microsculpture (**Plates 196–197, 237d–f**), low to medium elevation spire, non-inflation of the body whorl and rather broadly expanded lip are the main shell features separating *Strepsitaurus* from *Plectorhagada* Iredale, 1933. There is a clear tendency, especially in the more northern species, for species of the latter genus to have sculpture greatly reduced on the spire and body whorl, the micropustules are much smaller, the shell has a much more globose shape and the lip is less expanded. *Falspleuroxia*, from the S end of Shark Bay, has simple radial ribs, a more open umbilicus, and reduced microsculpture, although fairly close to *Strepsitaurus* in shape and general appearance.



Map 34: Records of *Strepsitaurus cardabius*, *S. ningaloo*, *S. rugus*, *S. williami* and *S. milyeringus* (M) on the Cape Range peninsula, WA.

The genitalia show many similarities to those of *Plectorhagada* – no epiphallic caecum, the epiphallus does not circle the penial retractor muscle, the short spermatheca and lack of a penis sheath. *Strepsitaurus* differs in having the penial retractor muscle insert mid-way on the epiphallus, rather than at the penis-epiphallus junction and in having the huge main pilaster within the penis chamber. A much smaller version of this pilaster is found in *Plectorhagada carcharias* (Pfeiffer, 1864) (**Fig. 392b**) and *P. scolythra* (**Fig. 393b**) and the full structure is also present in (the North West Cape *Promonturconchum superbum* (**Fig. 400b**). This structure has not been seen in any other Australian camaenid.

Previous studies

The description of *Strepsitaurus rugus* (Cotton, 1953) and citation of this in a check list by Richardson (1985: 254) are the previous references.

Distribution and comparative ecology

Maps 33–34 summarize the known records of *Strepsitaurus*. One species, *S. cardabius*, ranges from Gnaraloo N to near Ningaloo Homestead. It has been found only as a subfossil from moving or consolidated coastal or near coastal dunes. Nothing is known of its ecology. The absence of a free lip edge on the parietal wall and tendency of the crenulated radial ribs to follow the lines of growth (**Plate 196a–b**), rather than to be strongly diagonal, are its main diagnostic features. The other four species are restricted to the Rough Range and the Cape Range, North West Cape, WA. The smallest species, *S. milyeringus*, has been collected only near Milyering Well, NW Cape Range (**Maps 33–34**). It is characterised by it greatly reduced whorl count (mean 3 5/8), small diameter (mean 8.4 mm) and wide umbilicus (**Fig. 452c**, mean D/U ratio 4.44). The intermediate sized *S. williami* has been found along a 26 km section of the E side of the Cape Range, between Goat Cave near Central Hill and Shothole Canyon (**Maps 33–34**). It has a moderately open umbilicus (**Fig. 394f**), a prominent basal lip knob and the least prominent crenulated radial ribs (**Plate 196d–e**). The large *S. ningaloo* has been collected over a distance of 33 km on the W margin of the Cape Range, between Norwegian Bay and Yardie Creek (**Maps 33–34**). It is high spired, has the most prominent crenulated radial ribs (**Plate 197a–b**) and a closed umbilicus. The largest species, *S. rugus*, from the central and E portions of the Cape Range, extends from #2 Deep Well to the S part of the Rough Range, a distance of about 42 km. It has a low spire, prominent crenulated ribs (**Plate 197d–e**) and a nearly closed umbilicus.

All four Cape Range species are associated with exposed limestone surfaces. They are commonly found cemented to a vertical or near vertical face that is overhung by spinifex or other plants. They also are common on the underside of small rocks in crevices or rubble piles. Usually they seal individually, although sometimes one shell will be found sealed on top of another. The tendency seen in *Plectorhagada* of forming "chains" of five to 15 individuals linked together is not characteristic of *Strepsitaurus*.

All four species (except *S. cardabius*) have been dissected. Adult material of *S. milyeringus* and juvenile examples of *S. williami* were collected in mid-1989 after completion of the monograph. Hence illustrations are placed at the end of this review. The species differ in relative size of the terminal genital organs and the main stimulatory pilaster within the penis chamber.

The name *Strepsitaurus* is taken from the Greek *streptos* and the Latin *taurus* to honor William Turnbull, Curator Emeritus of Fossil Mammals at the Field Museum of Natural History. His collecting of North West Cape land snails in 1964, at my behest, led directly to these monographs.

KEY TO THE SPECIES OF *STREPSITAURUS*

1. Main radial crenulated ribs oblique to growth lines (**Plates 196d–e, 197a–b, d–e, 237f**); Cape Range 2

   Main radial crenulated ribs follow growth lines (**Plate 196a–b**); Ningaloo S of Gnaraloo .... *Strepsitaurus cardabius*, sp. nov. (p. 1615)

2. Umbilicus closed or a narrow lateral crack (**Figs 395c, f**); radial ribs very prominent (**Plate 197a–b, d–e**) 3

   Umbilicus widely open (**Figs 394f, 452c**) 4

3. Spire high (**Fig. 395b**); W side of Cape Range .... *Strepsitaurus ningaloo*, sp. nov. (p. 1627)

   Spire low (**Fig. 395e**); E side and central part of Cape Range .... *Strepsitaurus rugus* (Cotton, 1953) (p. 1637)

4. Whorls average 3 5/8; mean diameter 8.40 mm; ribs very prominent on lower spire and body whorl (**Plate 237f**); basal lip rarely with a prominent knob .... *Strepsitaurus milyeringus*, sp. nov. (p. 1621)

   Whorls average 4 1/2–; basal lip with a knob (**Fig. 394e**); ribs reduced in prominence (**Plate 196d–e**) .... *Strepsitaurus williami*, sp. nov. (p. 1623)

STREPSITAURUS CARDABIUS SP. NOV.
(Plate 196a–c; Figs 394a–c; Maps 33–34)

Comparative remarks

Strepsitaurus cardabius sp. nov., found as a dune fossil along the coast between Gnaraloo Station and Ningaloo Homestead, WA (**Maps 33–34**), has crenulated major sculpture (**Plate 196a–c**) on the spire and body whorl that extends across the shell base to the umbilicus, is average in size (mean diameter 14.01 mm), with a well elevated spire (**Fig. 394b**, mean H/D ratio 0.638), typical whorl count (**Fig. 394a**, mean whorls 4 1/4+), narrow umbilicus (**Fig. 394c**, mean D/U ratio 9.93) and the parietal wall has a thick callus (**Fig. 394b**), not a free lip. It's major radial sculpture more nearly follows the growth lines (**Figs 394a–c**), whereas in the four other *Strepsitaurus* species (**Figs 394–395, 452**) they are orientated diagonally across the growth lines. Other characters separating the four Cape Range *Strepsitaurus* species are the very small size (mean diameter 8.40 mm), low whorl count (mean 3 5/8), very wide umbilicus (**Fig. 452c**) and free parietal lip (**Figs 452a–c**) of *S. milyeringus*; reduced size (mean diameter 11.42 mm), low spire (**Fig. 394e**, mean H/D ratio 0.495), wide umbilicus (**Fig. 394f**, mean D/U ratio 6.08) and presence of a basal lip knob (**Fig. 394e**) in *S. williami*; the high spire (**Fig. 395b**, mean H/D ratio 0.609), closed umbilicus (**Fig. 395c**) and

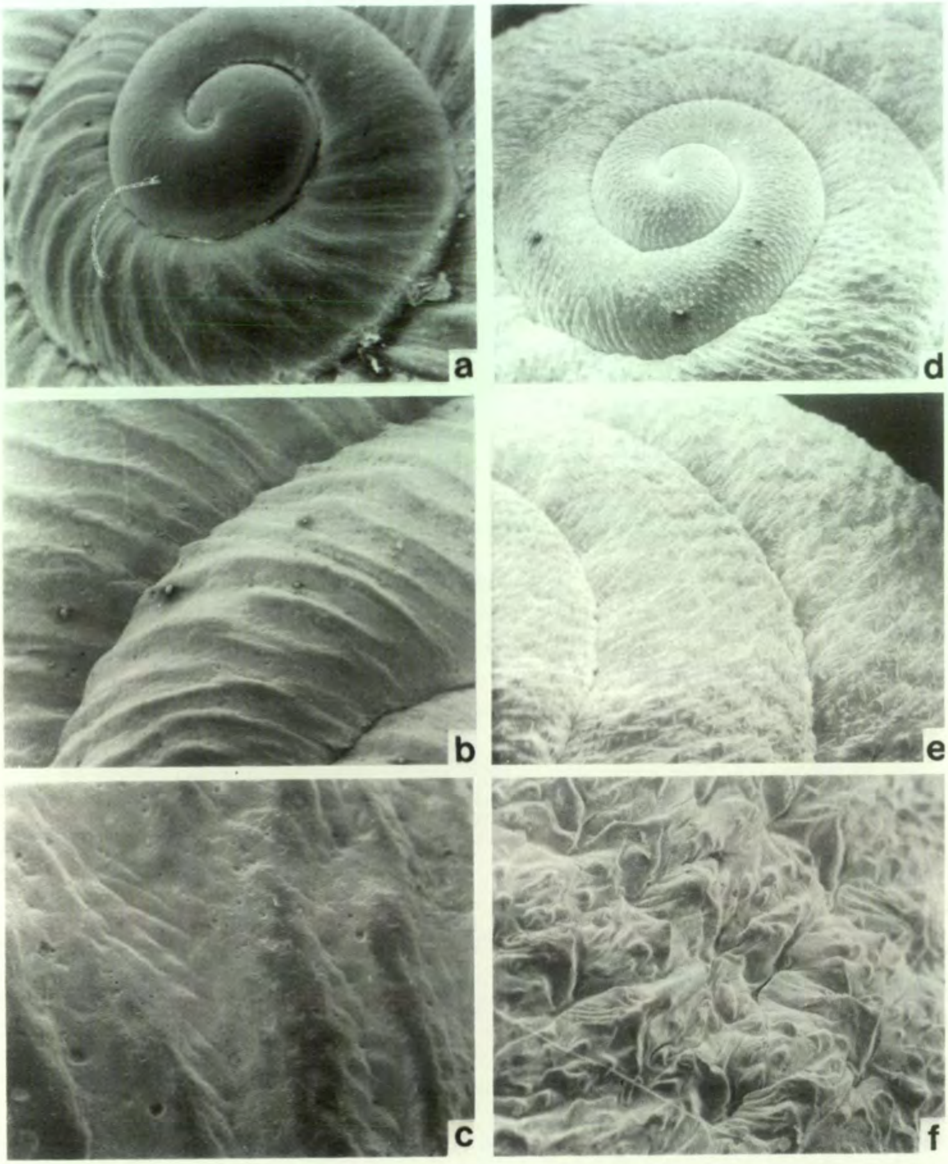


Plate 196: Shell sculpture of *Strepsitaurus cardabius* sp. nov. and *S. williami* sp. nov.: (a–c) *S. cardabius*. WA–955, dunes 6.7 km S of Warroora Homestead, N of Carnarvon, WA. FMNH 212478. a is apex and early spire at 20.4X. b is lower spire at 18.7X. c is micro-sculpture on body whorl at 490X; (d–f) *S. williami*. WA–176, along Charles Knife Road, 8.8 km W of Exmouth road, Cape Range, WA.FMNH 199427. d is apex and spire at 13.4X. e is lower spire and body whorl at 16.3X. f is micro-sculpture on lower spire at 83X. FMNH 199427.

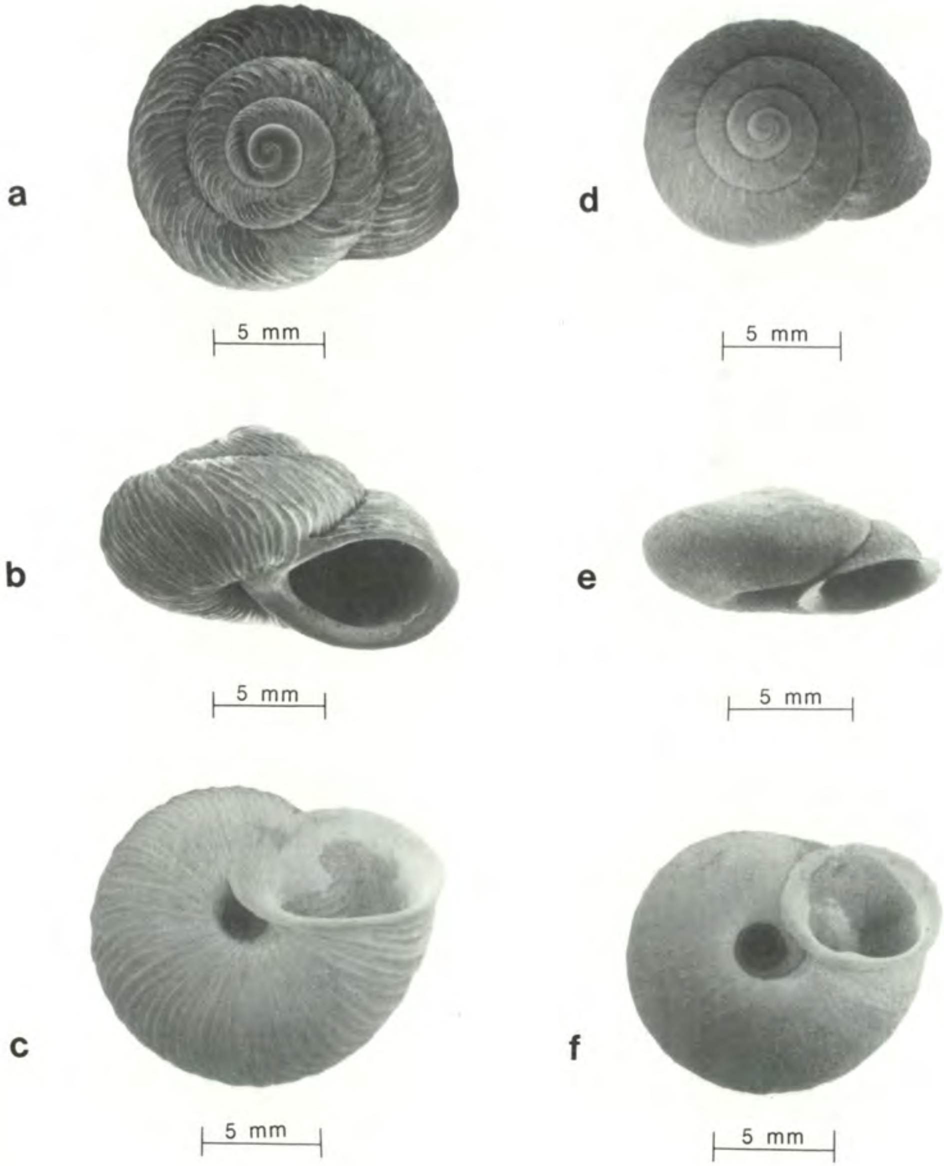


Fig. 394: Shells of *Strepsitaurus cardabius* sp. nov. and *S. williami* sp. nov.: (a–c) Holotype of *S. cardabius*. WAM 755.87. WA–955, dunes 6.7 track km S of Warroora Homestead, N of Carnarvon, WA; (d–f) Holotype of *S. williami*. WAM 756.87. Scale line as marked.

Table 145: Range of variation in Cape Range endemic genera.

Taxon	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Strepsitaurus cardabius	232	8.94 (6.9-10.6)	14.01 (11.5-16.3)	0.638 (0.552-0.759)	4¼+ (3⅞–4⅞+)	1.45 (0.9-2.2)	9.93 (6.09-16.9)
williami	146	5.63 (3.45-6.86)	11.42 (8.35-13.7)	0.495 (0.383-0.596)	4½– (3⅞–4¾+)	1.91 (1.25-2.65)	6.08 (3.72-9.33)
ningaloo	463	8.65 (6.95-11.1)	14.21 (10.95-17.3)	0.609 (0.552-0.765)	4⅜ (4⅛–4¾+)	closed or crack	
rugus	420	7.04 (4.7-9.1)	14.56 (11.3-18.65)	0.490 (0.388-0.629)	4⅜ (3¾+-5⅜+)	crack to 2.56mm	5.08-closed
milyeringus	10	4.07 (3.6-4.85)	8.40 (7.9-8.9)	0.484 (0.443-0.548)	3⅝ (3⅜-3¾+)	1.93 (1.5-2.4)	4.44 (3.49-5.53)
Promonturconchum superbum	253	22.67 (18.05-29.15)	28.93 (24.5-23.3)	0.786 (0.669-1.037)	4⅞– (4⅜-5¼+)	closed	
Caperantrum polygyrum	229	15.48 (13.2-20.7)	21.80 (19.6-29.75)	0.711 (0.461-0.891)	6¼ (5⅝-6⅞+)	closed	

strongly deflected aperture (**Fig. 395b**) of *S. ningaloo*; and the low spire (**Fig. 395e**, mean H/D ratio 0.490), angulated periphery (**Fig. 395b**), closed umbilicus (**Fig. 395c**) and sharply deflected aperture (**Fig. 395b**) of *S. rugus*. *Plectorhagada meilgana* Solem, this paper, from an inland part of the Ashburton River basin, WA (**Map 28**), is very similar in size and shape (**Table 140**) but differs in its angulated periphery (**Fig. 389e**), diagonal crenulated sculpture (**Plate 193**) and simple micropustulations. *Plectorhagada gascoynensis* (E. A. Smith, 1894), from the Gascoyne District, WA, has a rounded periphery and very low spire (**Fig. 389b**, mean H/D ratio 0.495), much wider umbilicus (**Fig. 389c**, mean D/U ratio 5.07) and diagonally crenulated sculpture (**Plate 190d–f**). The anatomy of *Strepsitaurus cardabius* is unknown.

Holotype

WAM 755.87, WA–955, ocean front dunes 6.7 track km S of Warroora Homestead, N of Carnarvon, Western Australia. 23°32'00"S, 113°45'05"E. Collected by A. Solem and B. Duckworth 9 July 1983. Height of shell 9.9 mm, diameter 15.2 mm, H/D ratio 0.651, whorls 4 1/2–, umbilical width 1.4 mm, D/U ratio 10.9.

Paratopotypes

WAM 904.87, SAM D18232, AM C.200,715, QM 46366, MV F.60067, FMNH 212478, 56 DA, 23 DJ from the type locality.

Paratypes

WESTERN AUSTRALIA: Gnaraloo, S of Gnarraloo Bay (Flemington Well, A. R. Main! 9 June 1952, WAM 320.74, 2 DA, 1 DJ); lagoon 6 miles S of Warroora Homestead (WA–48, FMNH 182363, 1 DA); 0.9 km N of Bulbarli Well (WA–1071, FMNH 221722, 1 DA); Warroora Station (D. & B. Parker! July 1977, WAM 322.80, 1 DA; under rocks near coast, N. Coleman! June 1972, MV F28294, 1 DA, 1 DJ; limestone ridge E of coastal track, 18.5 km N of homestead, 5 June 1981, WAM 1454.81, 1 DA, 2 DJ); 9 miles S of Coral Bay (coastal dune, C. Bryce! September 1978, WAM 1121.81, 1 DA); Cardabia Station (behind dunes, R. W. George! 8 April 1961, WAM 318.74, 13 DA); 11 miles S of Ningaloo (G. M. Storr! 18 October 1962, WAM 330.74, 1 DA, 1 DJ); Ningaloo-Cardabia track, 8.6 km S of 4 Mile Well (WA–173, WAM 905.87, SAM D18233, AM C.200,716, QM 46365, MV F60063, FMNH 199213, FMNH 199244, FMNH 199444, 142 DA, many DJ); 1.4 km N of 4 Mile Well, Ningaloo-Cardabia track (WA–172, WA–1073, FMNH 199895, FMNH 221728, 61 DA, 2 DJ); Brudboodjoo Point, 16 km N of Cardabia Homestead (WA–1072, FMNH 221725, 1 DA); 19 miles N of Cardabia (G. M. Storr! 18 October 1962, WAM 322.74, 5 DA); 8.7 km from Ningaloo on Exmouth road (WA–422, just W of Coral Bay turnoff, WAM 906.87, FMNH 199207, 5 DA, 5 DJ).

Range

Strepsitaurus cardabius sp. nov. has been found in coastal or near-coastal sand dunes (**Maps 33–34**) as far S as Gnaraloo (*ca.* 23°49'S), W of Lake Macleod, and as far N as the Ningaloo-Exmouth road (22°42'33"S), a distance of about 125 km. All material is subfossil, weathered out of consolidated or moving dune materials. Most records are strictly coastal, except where the dunes extend a few km inland.

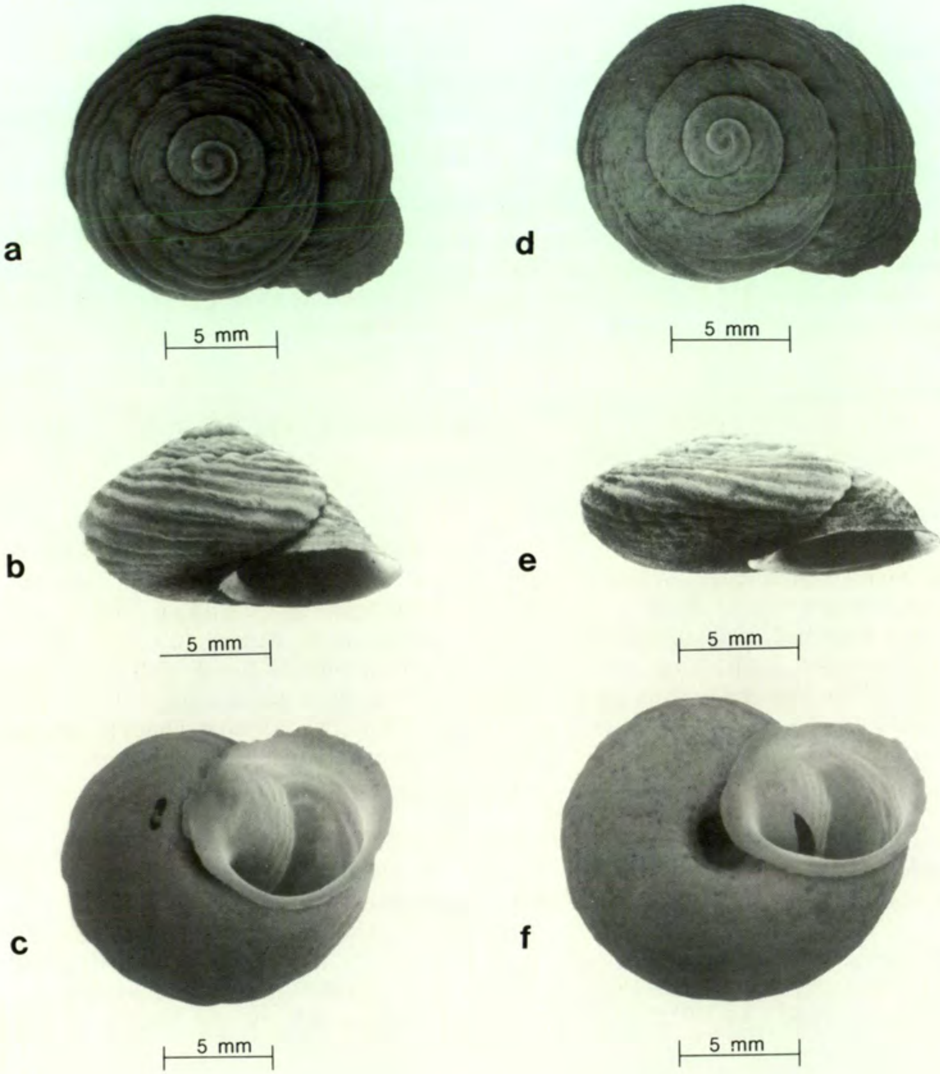


Fig. 395: Shells of *Strepsitaurus ningaloo* sp. nov. and *S. rugus* (Cotton, 1953): (a–c) Holotype of *S. ningaloo*. WAM 757.87. WA–171, Cape Range outlier 23.7 km N of Ningaloo Homestead, WA; (d–f) *S. rugus*. WA–14, near Goat Cave, Central Hill, Cape Range, WA. FMNH 182473. Scale line as marked.

Diagnosis

Shell medium in size, adult diameter 11.5–16.3 mm (mean 14.01 mm), with 3 7/8– to 4 7/8+ (mean 4 1/4+) normally coiled whorls. Apex and spire strongly and evenly elevated (**Fig. 394b**), shell height 6.9–10.6 mm (mean 8.94) mm, H/D ratio 0.552–0.759 (mean 0.638). Body whorl rounded, without trace of angulation (**Fig. 394b**). Apex (**Plate 196a**) badly worn in available material, traces of typical sculpture visible. Spire and body whorl (**Plate 196a–c**) with crenulated, anastomosing ribbing that mostly parallels lines of growth, traces of typical microsculpture occasionally seen (**Plate 196c**) lateral to major ribs. Umbilicus (**Fig. 394c**) narrow, significantly covered by reflection of columellar lip, width 0.9–2.2 mm (mean 1.45 mm), D/U ratio 6.09–16.9 (mean 9.93). Body whorl descending moderately behind lip. Palatal and basal lips reflected and moderately expanded (**Figs 394a–c**), columellar lip wider, parietal wall with thick callus. Colour unknown, as all available material weathered from dunes. Based on 232 measured adults.

Anatomy unknown.

Discussion

If live material of *Strepsitaurus cardabius* is ever found, I would not be surprised if it should prove to be generically distinct from both *Plectorhagada* and *Strepsitaurus*. Its inclusion in the latter genus is based upon the apical microsculptural remnants, its geographic location just south of the North West Cape area, its size and shape similarity (**Table 145**) to species of *Strepsitaurus* from the Cape Range rather than to the globose shells of the neighbouring *Plectorhagada carcharias* (Shark Bay to Warroora) and *Plectorhagada scolythra* (Rough Range and Scrubby Range). Most specimens are badly worn and only indications of the major sculpture can be seen.

The pattern of the major crenulated ridges following the radial growth lines (**Plate** 196a–b) and the presence of a thick parietal callus (**Fig. 394b**) instead of a free lip edge on the parietal wall are the most obvious features separating *S. cardabius* from the other *Strepsitaurus* species.

Specimens from Warroora (**Table 146**) are slightly but significantly larger than those from the more northern localities.

The name *cardabius* is taken from Cardabia Station, where much of the material representing this species has been collected.

STREPSITAURUS MILYERINGUS SP. NOV.

(Plate 237a–f; Figs 452a–c, 453a–b; Maps 33–34)

Comparative remarks

Strepsitaurus milyeringus from the W side of the Cape Range near Milyering Well, North West Cape, WA (**Maps 33–34**), is very small (mean diameter 8.40 mm), with a reduced whorl count (mean 3 5/8), low spire (mean H/D ratio 0.484), wide umbilicus (**Fig. 452c**) and the parietal lip elevated well above the parietal wall (**Figs 452b–c**). Both *Strepsitaurus rugus* and *S. ningaloo* (**Figs 395c, f**) differ in their closed or at most slightly open umbilici, much larger size (mean diameters 14.56 mm and 14.21

mm) and higher whorl counts (means for both species 4 3/8). *S. williami*, from the central part of the Cape Range, also is larger (mean diameter 11.42 mm), with a higher whorl count (mean 4 1/2–), narrower umbilicus (mean D/U ratio 6.08), the prominence of the crenulated ribs reduced and the parietal lip lying at most slightly free of the parietal wall. *S. cardabius*, from S of the North West Cape, has the radial ridges parallel to the growth lines, is much larger (mean diameter 14.01 mm), with more whorls (mean 4 1/4+), high spired (mean H/D ratio 0.638), narrowly umbilicated (mean D/U ratio 9.93) and there is a thick parietal callus (**Figs 394a–c**) rather than a free parietal lip. Anatomically (**Figs 453a–b**), *S. milyeringus* has a short vagina (V) and free oviduct (UV), proportionately enlarged epiphallus (E), no epiphallic caecum, relatively short penis (P) and a simplified main pilaster (PP). In *S. ningaloo* (**Figs 396a–b**), the penis is short and swollen with a more complex main pilaster while in *S. rugus* (**Figs 397b–c, 398**) the huge main pilaster provides immediate separation.

Holotype

WAM 848.87, WA–1084, Milyering Gorge, NW section of Cape Range, Western Australia. 22°02'13"S, 113°56'07"E. Collected by S. Osborne 27 May 1989. Height of shell 4.3 mm, diameter 8.0 mm, H/D ratio 0.538, whorls 3 5/8+, umbilical width 1.6 mm, D/U ratio 5.00.

Paratopotypes

WAM 849.87, FMNH 221762, 6 LA from the type locality.

Paratypes

WESTERN AUSTRALIA: Cape Range: S side of Milyering Gorge mouth (WA–1077, FMNH 221739, 3 DA).

Range

Strepsitaurus milyeringus has been collected in the lower reaches of Milyering Gorge and the next gorge to the S (Vince Kessner, personal communication), in the NW section of the Cape Range, WA (**Maps 33–34**). The total known range is less than 2 km.

Diagnosis

Shell very small, adult diameter 7.9–8.9 mm (mean 8.40 mm), with 3 3/8 to 3 3/4+ (mean 3 5/8) normally coiled whorls. Apex and spire slightly and evenly elevated, shell height 3.6–4.85 mm (mean 4.07 mm), H/D ratio 0.443–0.548 (mean 0.484). Body whorl rounded, without trace of angulation. Apex (**Plate 237d**) densely pustulose. Early spire (**Plate 237e**) with short, irregular ridges and very prominent pustules that are worn on top of ridges. Lower spire and body whorl (**Plate 237f**) with prominent diagonal ridges above periphery that are densely pustulose, ridges becoming zigzagged on shell base. Umbilicus wide (**Fig. 452c**), regularly decoiling, slightly narrowed by columellar lip, width 1.5–2.4 mm (mean 1.93 mm), D/U ratio 3.49–5.53 (mean 4.42). Body whorl descending sharply behind aperture. Palatal and basal lips sharply reflected and broadly expanded, columellar lip wide, parietal lip free of wall and strongly elevated. Basal lip with or without a weak knob on top of lip. Shell colour white on top of ridges, reddish-brown in interstices. Based on 10 measured adults.

Genitalia (**Figs** 453a–b) with short free oviduct (UV) and vagina (V). Spermatheca (S) with globose head appressed against prostate-uterus. Vas deferens (VD) entering directly into head of enlarged epiphallus (E). Epiphallic caecum absent. Epiphallus internally with simple elongated pilasters (EPP, **Fig. 453b**) that join upper arm of main pilaster (PP). Latter has a long slender ridge that crosses the penis apex and a much shorter vertical ridge from the other margin of the main pilaster (PP). Lower portion of main ovate mass of main pilaster and adjacent wall of penis chamber have a cluster of white inclusions that may be remnants of calcified stimulatory structures. Basal section of main pilaster a simple longitudinal ridge. Penial retractor muscle (PR) inserts in an arc on midsection of epiphallus.

Central and early lateral teeth (**Plate 237a**) with very small anterior flare, nearly vertical cusp shaft angle, strongly curved and bluntly rounded cusp tip and shortened basal plate. Late laterals (**Plate 237b**) with less curved and more broadly rounded cusp tips, latero-marginal transition marked by appearance of rapidly enlarging ectocone and weak endocone, rapid shortening of basal plate. Marginals (**Plate 237c**) typical. Jaw lost in handling.

Discussion

Strepsitaurus milyeringus, from Milyering Gorge, Cape Range, WA (**Maps 33–34**), has the lowest whorl count of any camaenid reviewed in this series of reports. The reduced size and complex shape of the main pilaster (PP, **Fig. 453b**) immediately differentiate this species.

STREPSITAURUS WILLIAMI SP. NOV.

(Plates 196d–f, 238a–d; Figs 394d–f; Maps 33–34)

Comparative remarks

Strepsitaurus williami sp. nov., from the E side of the central Cape Range, WA (**Maps 33–34**), has the diagonal crenulated radial sculpture smaller (**Plate 196e-f**) and the microsculpture more prominent, is small in size (mean diameter 11.42 mm), the spire is only slightly elevated (**Fig. 394e**, mean H/D ratio 0.495), the whorl count is normal (**Fig. 394a**, mean whorls 4 1/2–), the umbilicus is relatively widely open (**Fig. 394f**, mean D/U ratio 6.08) and the basal lip has a well developed knob (**Fig. 394e**). *S. milyeringus*, from the NW portion of the Cape Range (**Maps 33–34**), is much smaller (mean diameter 8.40 mm), with a reduced whorl count (mean 3 5/8) wider umbilicus (**Fig. 452c**, mean D/U ratio 4.44) and the basal lip has only a trace of a knob. *S. rugus* (Cotton, 1953), from the Rough and Cape Ranges, WA (**Maps 33–34**), also has a low spire (**Fig. 359e**, mean H/D ratio 0.490) but differs in its larger size (mean diamter 14.56 mm), closed or nearly closed umbilicus (**Fig. 395f**), much more prominent crenulated diagonal ridging (**Plate 197d–e**) and absence of a basal lip knob (**Fig. 394e**). *S. ningaloo*, from the W side of the Cape Range, WA (**Maps 33–34**), has very prominent diagonal crenulated ridging (**Plate 197a–b**), an elevated spire (**Fig. 395b**, mean H/D ratio 0.609), closed or nearly closed umbilicus (**Fig. 395c**) and lacks a basal lip knob (**Fig. 395b**). *S. milyeringus*, from the W side of the Cape Range, has a more widely open umbilicus (**Fig. 452c**), reduced whorl count (mean 3 5/8) and is much smaller (mean diameter 8.40 mm). *S. cardabius*, from coastal dune deposits near Ningaloo Homestead S to Gnaraloo, WA (**Maps 33–34**), has the crenulated ridging

Table 146: Local variation in *Strepsitaurus cardabius*, *S. williami* and *S. milyeringus*.

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
Strepsitaurus cardabius,							
WA-955, FMNH 212478	57D	9.22±0.070 (8.25-10.6)	14.37±0.103 (12.95-16.25)	0.642±0.005 (0.552-0.759)	$4\frac{3}{8}-$ $(4\frac{1}{8}+-4\frac{5}{8}-)$	1.57±0.034 (1.15-2.2)	9.38±0.186 (6.77-12.5)
WA-173, FMNH 199213	47D	8.72±0.108 (7.1-10.5)	13.77±0.127 (12.1-16.3)	0.633±0.004 (0.568-0.693)	$4\frac{1}{4}+$ $(4+-4\frac{5}{8}+)$	1.43±0.036 (1.05-2.1)	9.90±0.266 (6.45-13.5)
WA-173, FMNH 199244	57D	8.78±0.087 (7.25-10.1)	13.86±0.113 (11.5-15.5)	0.634±0.004 (0.588-0.714)	$4\frac{1}{4}$ $(3\frac{7}{8}--4\frac{1}{2})$	1.38±0.032 (0.9-2.0)	10.4±0.267 (6.09-16.8)
WA-173, FMNH 199444	38D	9.03±0.109 (7.75-10.5)	14.06±0.124 (12.9-15.5)	0.642±0.005 (0.582-0.720)	$4\frac{1}{4}+$ $(4\frac{1}{8}--4\frac{5}{8}-)$	1.35±0.033 (0.95-1.7)	10.6±0.267 (8.16-14.6)
Cardabia Station, WAM 318.74	12D	9.34±0.168 (8.3-10.55)	13.80±0.174 (12.95-14.8)	0.677±0.009 (0.611-0.717)	$4\frac{3}{8}-$ $(4+-4\frac{3}{8}+)$	1.53±0.076 (0.95-1.95)	9.31±0.569 (7.50-14.7)
WA-422, FMNH 199207	5D	8.60±0.464 (6.9-9.6)	13.93±0.655 (12.05-15.65)	0.617±0.14 (0.573-0.658)	$4\frac{1}{2}-$ $(4\frac{1}{4}--4\frac{7}{8}+)$	1.58±0.070 (1.35-1.75)	8.93±0.722 (7.10-11.5)
Strepsitaurus williami							
Goat Cave, FMNH 135456	10D	5.42±0.109 (4.8-5.95)	11.44±0.128 (10.75-11.95)	0.474±0.011 (0.423-0.540)	$4\frac{3}{8}$ $(4\frac{1}{4}--4\frac{5}{8}+)$	2.01±0.108 (1.6-2.55)	5.83±0.286 (4.65-7.15)
Charles Knife Road, AM C.87649	27D	6.10±0.082 (5.3-6.85)	11.14±0.081 (10.5-12.05)	0.548±0.005 (0.502-0.593)	$4\frac{1}{2}+$ $(4\frac{3}{8}--4\frac{3}{4}+)$	1.72±0.038 (1.25-2.05)	6.57±0.169 (5.61-8.80)

Table 146: Local variation in *Strepsitaurus cardabius, S. williami* and *S. milyeringus* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
Strepsitaurus williami (Cont.)							
WA-176, FMNH 199427	74D	5.52±0.056 (4.4-6.75)	11.91±0.068 (10.7-13.7)	0.464±0.004 (0.383-0.532)	4½– (4⅛+-4¾)	2.00±0.028 (1.3-2.65)	6.03±0.095 (4.52-9.33)
Shothole Canyon, GB 12632 (= WAM)	10D	5.70±0.171 (5.1-6.65)	10.64±0.214 (9.65-11.5)	0.536±0.039 (0.477-0.596)	4¼+ (4-4½)	1.72±0.087 (1.3-2.25)	6.28±0.0261 (4.73-7.62)
WA-177, FMNH 199937	5D	5.97±0.261 (5.3-6.7)	11.09±0.283 (10.25-11.95)	0.583±0.017 (0.493-0.571)	4½– (4⅜–-4½+)	2.03±0.068 (1.9-2.3)	5.51±0.304 (4.50-6.32)
Strepsitaurus milyeringus							
WA-1084 FMNH 221762	7L	3.97±0.143 (3.6-4.6)	8.29±0.130 (7.9-8.8)	0.479±0.015 (0.443-0.537)	3⅝ (3⅜+-3¾+)	1.79±0.090 (1.5-2.1)	4.68±0.209 (4.18-5.53)
WA-1077 FMNH 221739	3D	4.30±0.278 (3.95-4.85)	8.65±0.225 (8.2-8.9)	0.497±0.026 (0.461-0.548)	3½+ (3⅜-3¾+)	2.25±0.126 (2.0-2.4)	3.87±0.283 (3.49-4.43)

essentially following the growth lines (**Plate 196a–b**), the spire much more elevated (**Fig. 394b**, mean H/D ratio 0.638), the umbilicus is narrower (**Fig. 394c**, mean D/U ratio 9.93), the parietal wall has a thick callus (**Fig. 394b**) instead of a free lip edge and there is no basal lip knob (**Fig. 394b**). Of the umbilicated *Plectorhagada* species, the Gascoyne District *P. gascoynensis* (E. A. Smith, 1894) has a reduced whorl count (**Fig. 389a**, mean 3 7/8+), larger crenulated sculpture (**Plate 190d–e**) and lacks the lip knob (**Fig. 389b**), while *P. meilgana*, from inland parts of the Ashburton drainage, (**Map 28**), has an elevated spire and angulated periphery (**Fig. 389e**, mean H/D ratio 0.612), a much narrower umbilicus (**Fig. 389f**, mean D/U ratio 10.6) and lacks the lip knob. The only neighbouring species with a lip knob present, *Caperantrum polygyrum* sp. nov., from the central part of the Cape Range (**Maps 28, 35**) is very much larger (mean diameter 21.80 mm), with a greatly increased whorl count (**Fig. 399d**, mean 6 1/4) and its shell sculpture consists (**Plate 202e**) of reduced apical sculpture and a nearly smooth spire and body whorl, with no major ridging developed and only weak radial growth ridgelets. The genital anatomy of *S. williami* is unknown, as only subadult examples were collected live.

Holotype

WAM 756.87, WA–176, 8.8 km along Charles Knife Road from Exmouth road, Cape Range, Western Australia. 22°06'45"S, 114°00'09"E. Collected by Alan Solem 30 September 1976. Height of shell 5.7 mm, diameter 12.35 mm, H/D ratio 0.462, whorls 4 3/8+, umbilical width 2.4 mm, D/U ratio 5.15.

Paratopotypes

WAM 901.87, SAM D18231, AM C.200,717, QM 46379, MV F.60095, FMNH 199427, 74 DA, several DJ from the type collection.

Paratypes

WESTERN AUSTRALIA: Cape Range: Goat Cave, Central Hill (P. & W. Turnbull! June to July 1964, WAM 902.87, FMNH 135456, 10 DA, few DJ); along Charles Knife Road (W. F. Ponder! 19 January 1972, AM C.87649, 27 DA, several DJ); Thomas Carter Outlook, 10.2 km along Charles Knife Road from Exmouth road (WA–1079, FMNH 221742–3, 10 LA, 14 DA); 1 mile NE of #2 Deep Well (G. Hitchin & G. W. Kendrick! 12 May 1965, WAM 289.74, 1 DA); G. M. Storr! 19 October 1962, WAM 383.74, 2 DA; 6 miles up, G. W. Kendrick! 17 May 1965, WAM 282.74, 4 DA, 1 DJ; S side of Shothole Canyon, G. W. Kendrick! 17 May 1965, WAM 279.74, 5 DA, 1 DJ; N. Colman! 6 July 1972, MV F28291, 2 DA; WA–177, 12.5 km along Hothold Canyon road from Exmouth road, WAM 903.87, FMNH 199937, 5 DA, 1 DJ); Exmouth (S side of Nimitz Street, J. Hewitt! 2 September 1976, WAM 402.77, 7 DA, 3 DJ).

Range

Strepsitaurus williami has been collected only on the E side of the Cape Range, (**Maps 33–34**), between Goat Cave near Central Hill (22°15'S, 113°56'E) and at several places in Shothole Canyon (*ca.* 22°04'S, 114°01'E), a N-S distance of about 26 km, if the Goat Cave record is correct. They probably were sifted from dirt within Goat Cave but in several subsequent visits I have found no specimens of *S. williami* in the vicinity. If the Goat Cave record is not correct, then the total N-S range would be about

8 km. The E-W range is probably less than 5 km. The Exmouth record requires confirmation.

Diagnosis

Shell small, adult diameter 8.35–13.7 mm (mean 11.42 mm), with 3 7/8– to 4 3/4+ (mean 4 1/2–) normally coiled whorls. Apex and spire slightly and evenly elevated (**Fig. 349e**), shell height 3.45–6.85 mm (mean 5.63 mm), H/D ratio 0.383–0.596 (mean 0.495). Body whorl rounded, with at most a slight trace of obtuse angulation (**Fig. 349e**). Apex (**Plate 196d**) of prominent, usually elongated pustules, often arranged in radial rows. Spire and body whorl (**Plate 196d–f**) with low, diagonally oriented, crenulated ridges and a very prominent sculpture of micropustules. Umbilicus open (**Fig. 394f**), last whorl decoiling more rapidly, width 1.25–2.65 mm (mean 1.91 mm), D/U ratio 3.72–9.33 (mean 6.08). Body whorl descending sharply behind lip (**Fig. 394e**). Palatal and basal lips reflected and moderately expanded (**Figs 394d–f**), columeller lip wider, parietal wall with a heavy callus or raised edge that is barely free of the parietal wall. Basal lip with a low to prominent knob (**Fig. 394f**) that normally is slightly recessed or on the lip edge. Colour unknown as all available specimens collected dead. Based on 148 measured adults.

Genitalia unknown.

Central and early lateral teeth (**Plate 238a**) with very small anterior flare, near vertical cusp shaft angle, strongly curved and bluntly rounded cusp tip, basal plate relatively long. Late laterals (**Plate 238b**) with weak ectocone, large anterior flare, reduced cusp shaft angle, less rounded cusp tip, and shortened basal plate. Marginals (**Plate 238c**) typical. Jaw (**Plate 238d**) with prominent vertical ribs in central portion, lateral areas with vertical ribs greatly reduced or absent.

Discussion

Local variation in *Strepsitaurus williami* is fairly extensive (**Table 146**) and without clear geographic pattern. The Shothole Canyon sample is significantly smaller, but in view of the size and shape disparity in the two Charles Knife Road samples, no significance can be assigned to this. The Goat Cave material also is relatively depressed in shape.

Living examples of *Strepsitaurus rugus* were taken at WA–176 on Charles Knife Road in 1976. They also (**Table 146**) are small in size for that species. Live examples of both *S. williami* and *S. rugus* were taken along Charles Knife Road (WA–1079) in 1989, but only subadults of the former.

The specific name *williami*, as does the genus *Strepsitaurus*, honours the Field Museum of Natural History's Curator Emeritus of Fossil Mammals, William Turnbull, whose 1964 collecting of Cape Range land snails interested me in this fauna and led to this series of reports.

STREPSITAURUS NINGALOO SP. NOV.

(Plates 197a–c, 199a–f, 201a–b; Figs 395a–c, 396a–b; Maps 33–34)

Comparative remarks

Strepsitaurus ningaloo sp nov., from the W side of the Cape Range, WA (**Maps 33–**

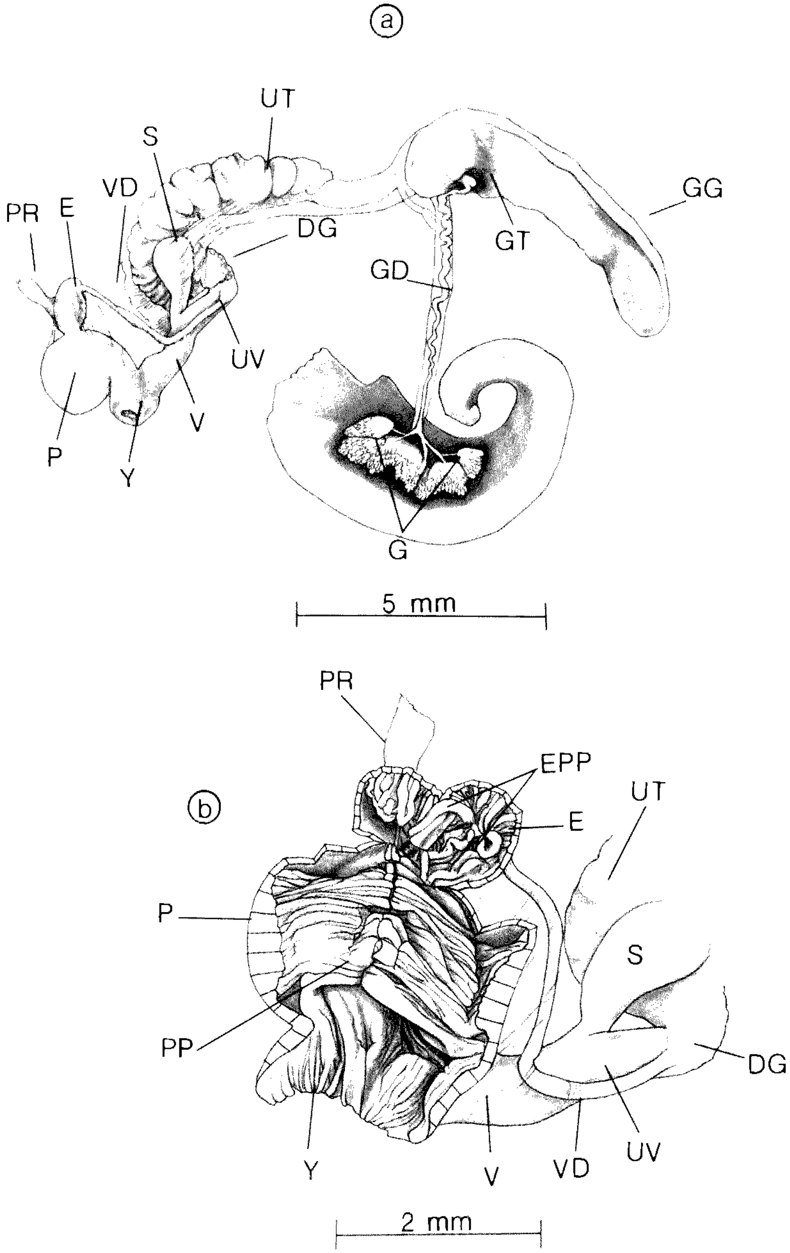


Fig. 396: Genitalia of *Strepsitaurus ningaloo* sp. nov.: WA-171, Cape Range outlier, 23.7 km N of Ningaloo Homestead, WA. 21 September 1976. FMNH 199849: (a) whole genitalia, Dissection C; (b) interior of penis complex, Dissections A and C. Scale lines as marked. Drawings by Linnea Lahlum.

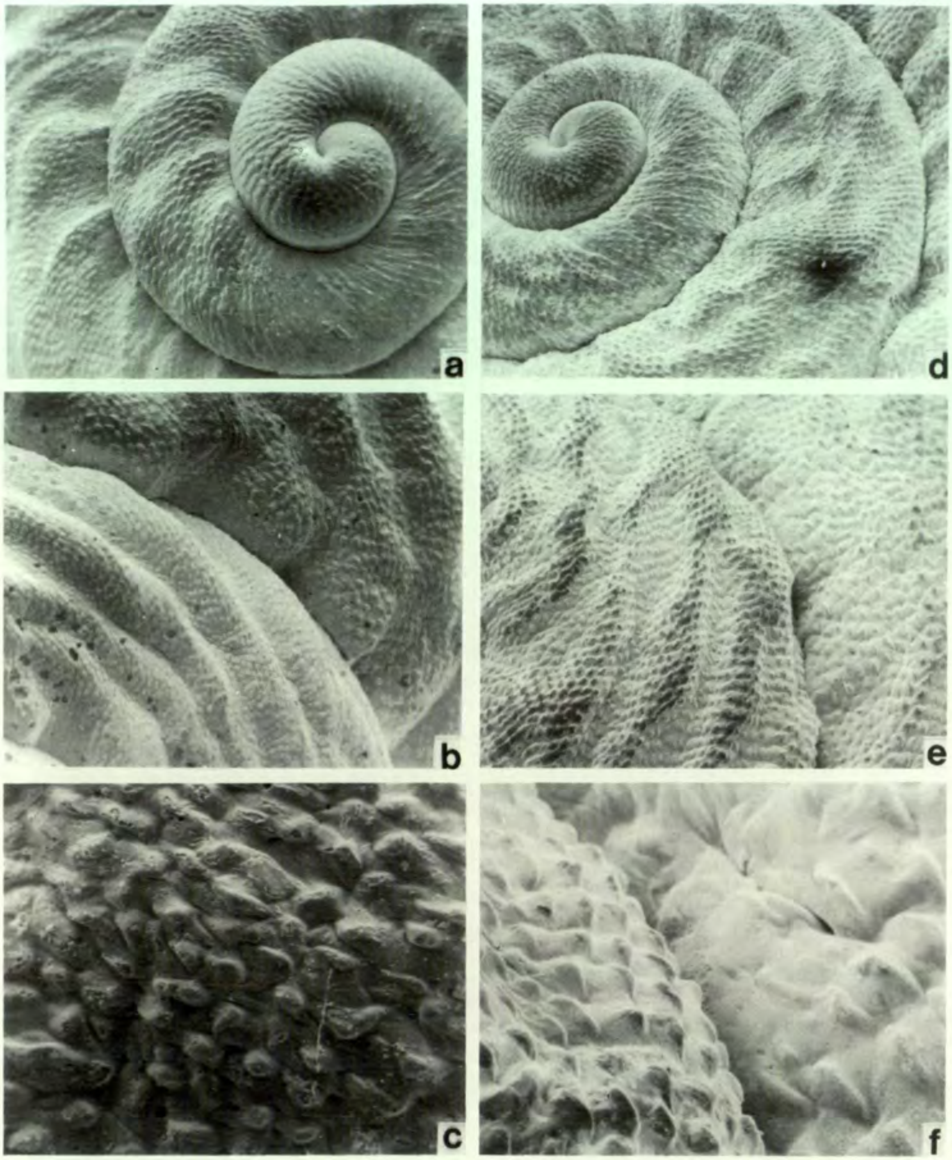


Plate 197: Shell sculpture of *Strepsitaurus ningaloo* sp. nov. and *S. rugus* (Cotton, 1953): (a–c) *S. ningaloo*. WA–23, 14.9 miles (= 23.7 km) N of Ningaloo Homestead, Cape Range, WA. FMNH 182303. a is apex and spire at 20.3X. b is lower spire and body whorl at 18X. c is mircopustules on body whorl at 93X; (d–f) *S. rugus*. WA–175, SE of Goat Cave, near Central Hill, Cape Range, WA. FMNH 199439. d is apex and spire at 18.5X. e is lower spire and body whorl at 17.8X. f is micro-sculpture along body whorl suture at 86X.

Table 147: Local variation in *Strepsitaurus ningaloo.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
2 mi. E Norwegian Bay, WAM	8D	8.91±0.233 (7.65-9.65)	14.62±0.352 (13.7-16.8)	0.611±0.019 (0.548-0.701)	$4\frac{3}{8}$ ($4\frac{1}{4}$-$4\frac{1}{2}$)
2 mi. E Norwegian Bay, WAM 491.72	4D	9.39±0.293 (8.95-10.25)	15.61±0.262 (15.0-16.2)	0.601±0.013 (0.577-0.633)	$4\frac{1}{2}$ ($4\frac{3}{8}$+-$4\frac{5}{8}$−)
WA-21, FMNH 182372	41D	8.27±0.081 (6.95-9.4)	13.18±0.134 (10.95-15.0)	0.628±0.005 (0.579-0.702)	$4\frac{3}{8}$ ($4\frac{1}{8}$+-$4\frac{5}{8}$+)
WA-22, FMNH 182697a	18L	9.10±0.125 (8.15-10.25)	14.67±0.176 (13.3-15.7)	0.621±0.007 (0.563-0.682)	$4\frac{3}{8}$ ($4\frac{1}{4}$−-$4\frac{1}{2}$+)
WA-22, FMNH 182508	13L	9.11±0.126 (8.3-9.9)	14.75±0.160 (14.15-15.9)	0.681±0.007 (0.585-0.665)	$4\frac{3}{8}$+ ($4\frac{1}{4}$+-$4\frac{1}{2}$+)
WA-22, FMNH 182382	50D	8.56±0.076 (7.15-9.8)	14.13±0.105 (12.3-15.75)	0.606±0.004 (0.543-0.662)	$4\frac{3}{8}$ ($4\frac{1}{8}$−-$4\frac{5}{8}$−)
WA-23, FMNH 182511	10L	9.29±0.271 (8.2-11.1)	15.30±0.143 (14.6-16.3)	0.607±0.016 (0.545-0.722)	$4\frac{1}{2}$− ($4\frac{1}{8}$+-$4\frac{3}{4}$+)
WA-23, FMNH 182303	19D	8.53±0.118 (7.7-9.7)	14.08±0.132 (12.85-15.3)	0.606±0.008 (0.562-0.682)	$4\frac{3}{8}$ ($4\frac{1}{8}$+-$5\frac{5}{8}$+)
WA-171, FMNH 199729	31L	8.56±0.123 (7.3-10.0)	13.85±0.124 (12.55-15.3)	0.618±0.005 (0.565-0.680)	$4\frac{3}{8}$ ($4\frac{1}{8}$+-$4\frac{1}{2}$+)

Table 147: Local variation in *Strepsitaurus ningaloo* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
WA-171, FMNH 199849	115L	8.39±0.054 (7.2-9.9)	13.94±0.081 (12.1-16.2)	0.603±0.003 (0.522-0.725)	4 3/8− (4 1/8-4 5/8−)
WA-171, FMNH 199951	25L	8.49±0.146 (7.2-10.55)	14.16±0.142 (13.0-15.9)	0.599±0.006 (0.532-0.667)	4 3/8− (4 1/8+-4 3/4−)
WA-171, FMNH 199703	56L	8.63±0.082 (7.5-10.25)	14.34±0.116 (12.6-16.55)	0.602±0.004 (0.537-0.678)	4 1/4+ (4 1/8−-4 1/2)
WA-958, FMNH 212490	10L	8.84±0.202 (7.75-9.5)	14.54±0.273 (13.35-15.55)	0.608±0.006 (0.574-0.635)	4 3/8 (4 1/8+-4 1/2)
WA-958, FMNH 212489	31D	8.88±0.114 (7.5-10.55)	14.40±0.712 (12.95-15.75)	0.617±0.007 (0.551-0.765)	4 1/2 (4 1/4−-4 5/8+)
Yardie Creek, WAM 1190.81	13D	9.41±0.165 (8.6-10.35)	15.70±0.224 (14.65-17.3)	0.600±0.009 (0.561-0.659)	4 3/8 (4 1/4-4 5/8+)

34), is characterised by its average size (mean diameter 14.21 mm), elevated spire (**Fig. 395b**, mean H/D ratio 0.609), very strong diagonal crenulated ridges (**Plate 197b**), closed umbilicus (**Fig. 395c**) and absence of a lip knob (**Fig. 395b**). *S. rugus* (Cotton, 1953), from the central and E side of the Cape Range, (**Maps 33–34**), differs in its much lower spire (**Fig. 395e**, mean H/D ratio 0.490), and slightly less prominent crenulated ridging (**Plate 197d–e**). *S. williami*, from the middle portion of the Cape Range, (**Maps 33–34**), is smaller (mean diameter 11.42 mm), has a much lower spire (**Fig. 394e**, mean H/D ratio 0.495), open umbilicus (**Fig. 394f**, mean D/U ratio 6.08), reduced diagonal ridging (**Plate 196d–e**) and presence of a knob on the basal lip. *S. milyeringus*, from the NW of Cape Range near Milyering Well, has a very widely open umbilicus (**Fig. 452c**), reduced whorl count (mean 3 5/8) and is very small in size (mean diameter 8.40 mm). *S. cardabius*, found fossil in near-coastal dunes from Ningaloo Homestead S to Gnaraloo Station, (**Maps 33–34**), is very similar in size and shape (**Table 145**) but differs most obviously in having a narrowly open umbilicus (**Fig. 394c**, mean D/U ratio 9.93), the crenulated ridges essentially follow the radial growth lines rather than being oblique to them (**Plate 196a–b**) and the parietal wall has a thick callus, not a free edge (**Fig. 394b**). All *Pleuroxia* and Fals*pleuroxia* species differ in having an open umbilicus and much finer microsculpture. Anatomically (**Figs. 396a–b**), the longer, more slender vagina (V), the much shorter main pilaster (PP) and the enlarged area of basal pilasters in the penis chamber are the most obvious differences between *S. ningaloo* and *S. rugus* (**Figs 397b, 398**). *Strepsitaurus milyeringus* (**Figs 453a–b**) has a proportionately enlarged epiphallus (E) and much smaller main pilaster in the penis chamber.

Holotype

WAM 757.87, WA–171, outlier on W side of Cape Range, 23.7 km N of Ningaloo Homestead, 0.5 km from track along seismic line, Western Australia. 22°30'00"S, 113°43'55"E. Collected by A. Solem & L. Keller 10 May 1977. Height of shell 9.05 mm, diameter 15.3 mm, H/D ratio 0.592, whorls 4 3/8+, umbilicus a very narrow lateral crack.

Paratopotyes

WAM 943.87, SAM D, AM C.200,718, QM 52991, QM 52992, MV F59446, MV F.59477, FMNH 199703–4, 56 LA, 4 DA from the type collection.

Paratypes

WESTERN AUSTRALIA: W side of Cape Range: 2 miles E of Norwegian Bay (22°35'S, 113°42'30"E) (11 September 1968, WAM 491.72, 4 DA); 11.5 miles N of Ningaloo Homestead (WA–21, alluvial fan near bore, WAM 880.87, SAM D18215, AM C.200,719, QM 46370, MV F.60054, FMNH 182372, 41 DA, several DJ); 14.9 miles N of Ningaloo Homestead (WA–22, NW-facing side of ridge, WAM 881.87, WAM 882.87, SAM D18216, AM C.200,720, QM 46369, MV F.60051, FMNH 182382, FMNH 182508, FMNH 182697, 31 LA, 54 DA, 11 DJ); WA–23, steeper gully to S of WA–22, WAM 879.87, SAM D18214, AM C.200,721, FMNH 182303, FMNH 182511, FMNH 201528, 10 LA, 20 DA, 2 DJ); 23.7 km N of Ningaloo Homestead (WA–171, 27 September 1976, WAM 876.87, SAM D18213, AM C.200,722, FMNH 199849, 115 LA; WA–171, 14 December 1976, WAM 878.87, FMNH 199951, 25 LA;

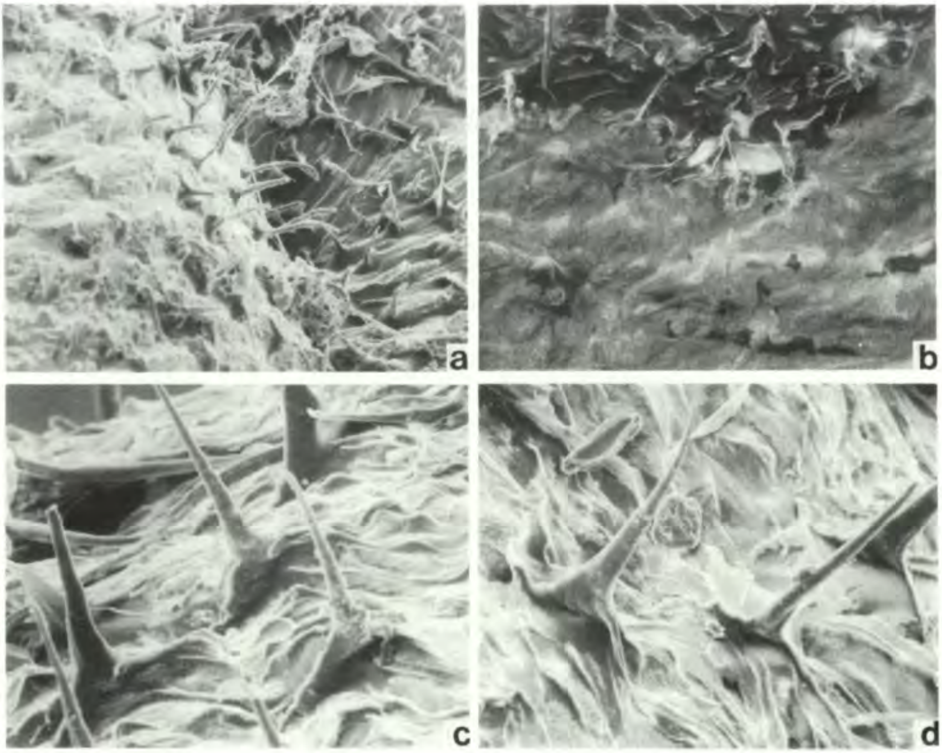


Plate 198: Periostracal setae in *Strepsitaurus rugus* (Cotton, 1953). Shothole Canyon, Cape Range, WA. WAM 279.74: (a) body whorl suture at 74X; (b) worn (lower) and intact setal areas on lower spire at 83X; (c) setae on shell base at 150X; (d) bases of setae at 160X.

WA–171, 14 April 1977, WAM 877.87, FMNH 199729, 31 LA; WA–958, 10 July 1983, FMNH 212489–90, 10 LA, 31 DA, 1 LJ, 11 DJ; WA–1074, 24 May 1989, FMNH 221729–30, FMNH 221736, 63 LA, 8 DA); mouth of Yardie Creek (P. Cawthorn! 6 April 1961, WAM 307.74, 2 DA; F. Wells! 22 June 1977, WAM 1190.81, 13 DA).

Range

Strepsitaurus ningaloo has been found on the W side of the Cape Range, WA (**Maps 33–34**), from two miles E of Norwegian Bay (22°35'S) N to the mouth of Yardie Creek (22°19'30"S), a distance of about 33 km. No collections have been made other than on the westernmost ridges of the Cape Range in this area, so that the E–W range remains unknown.

Diagnosis

Shell medium in size, adult diameter 10.95–17.3 mm (mean 14.21 mm), with 4 1/8– to 4 3/4+ (mean 4 3/8) normally coiled whorls. Apex and spire strongly and evenly elevated (**Fig. 395b**), shell height 6.95–11.1 mm (mean 8.65 mm), H/D ratio 0.552–

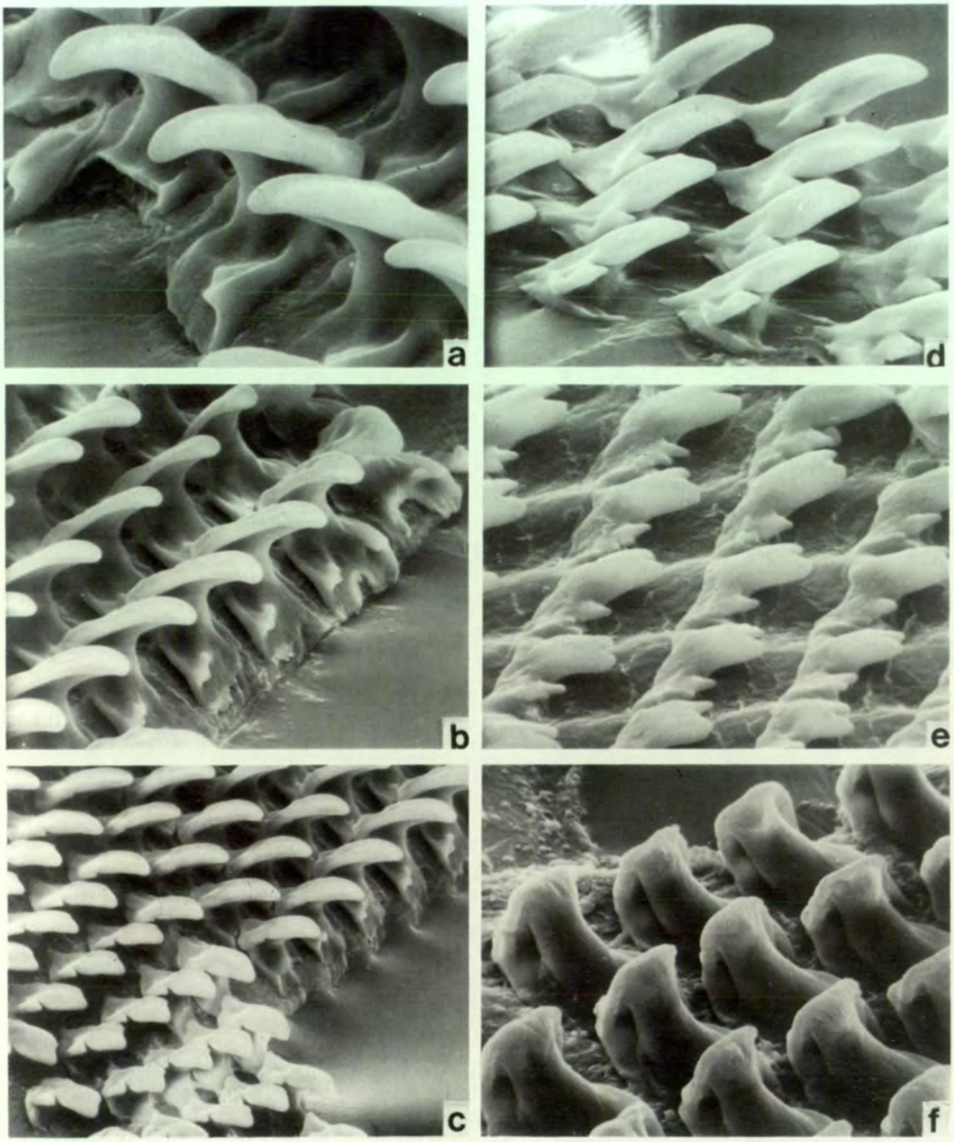


Plate 199: Radular teeth of *Strepsitaurus ningaloo* sp. nov. WA–171, 23.7 km N of Ningaloo Homestead, Cape Range, WA. 21 September 1976. FMNH 199849: (a) Dissection A, central and early lateral teeth at 1175X; (b) Dissection B, central and early laterals at 680X; (c) Dissection B, latero-marginal transition at 485X; (d) Dissection B, early marginals at 840X; (e) Dissection A, mid- to outer marginals at 1175X; (f) Dissection C, worn central and laterals, anterior tip of radula, at 930X.

0.765 (mean 0.609). Body whorl rounded to very slightly angulated (**Fig. 395b**). Apex (**Plate 197a**) with large, dense pustules generally arranged in radial order, sometimes coalesced into short, wavy ridglets. Spire and body whorl (**Plate 197a–c**) with very prominent diagonal crenulated ridges and micropustules. Umbilicus closed (**Fig. 395c**) by reflection of columellar lip. Body whorl descending very sharply behind lip. Palatal and basal lips reflected and broadly expanded, thin, columellar lip broad and usually completely covering umbilicus. Lip continuous across and barely free of parietal wall. No basal lip knob. Shell colour normally white on top of crenulated ridges, reddish-brown in low areas between ridges. Based on 463 measured adults.

Genitalia (**Figs 396a–b**) with typical apical structures. Vagina (V) of medium length, slender. Free oviduct (UV) very short, spermatheca (S) with short shaft, expanded head lying just above origin of free oviduct. Vas deferens (VD) very slender, entering directly into head of epiphallus, which is very thin-walled. No epiphallic caecum; epiphallus (E) with numerous longitudinal pilasters (**Fig. 396b**, EPP), entering penis with pilasters flowing into main pilaster (PP). Penial retractor muscle (PR) variable in length, inserting in an arc on about the middle of the epiphallus. Penis (P) elongated, thick-walled, apical half with very high corrugated main pilaster, lower portion with simple longitudinal pilasters.

Central and early lateral teeth (**Plate 199a–b**) with very small anterior flare, elevated cusp shaft angle, strongly curved and bluntly rounded cusp tip and shortened basal plate. Late laterals (**Plate 199c–d**) with initial appearance of ectocone, enlarged anterior flare, reduced cusp shaft angle and reduced tip rounding. Latero-marginal transition (**Plate 199c**) abrupt, early marginals (**Plate 199d**) with initial appearance of endoconal trace, rapid shortening of basal plate, loss of anterior flare and reduction in cusp shaft angle. Marginals (**Plate 199e**) typical. Old laterals (**Plate 199f**) showing tip erosion, not shaft breakage. Jaw (**Plate 201a–b**) with low vertical ribs of varying width, reduced on lateral margins.

Discussion

Strepsitaurus ningaloo shows minor size variation (**Table 147**). The examples from E of Norwegian Bay and Yardie Creek are slightly larger in diameter. The examples from WA–21 are significantly smaller. Specimens from WA–22, WA–23, WA–171 and WA–958 were taken from within a 10 metre stretch of exposed limestone benches. WA–22 was on a more northern slope, while WA–23 was on a south facing, steeper ravine and live adults were noticably larger in size.

While the jaw (**Plate 201a–b**) shows slight height reduction of the vertical ribs, the variation is far less than that seen in populations of *S. rugus* (**Plates 200f, 201c, e**). A view of the anterior tip of the radula (**Plate 199f**) shows nearly equal and strictly erosional loss of the upper cusp shaft, whereas normally this area shows "chipped off" loss of varying amounts. The latter is caused when the cusp, which is held at a near 45° angle, "snags" on a rock or piece of gravel and the tooth shatters. In contrast, the feeding on soil encrusting films and the strikingly curved tip, do not expose the teeth to "shattering" events.

The name *ningaloo* honours Ningaloo Station and its long-time residents, Billie, Jane and the late Edgar Lefroy, who have provided hospitality and information to so many visiting naturalists over the years.

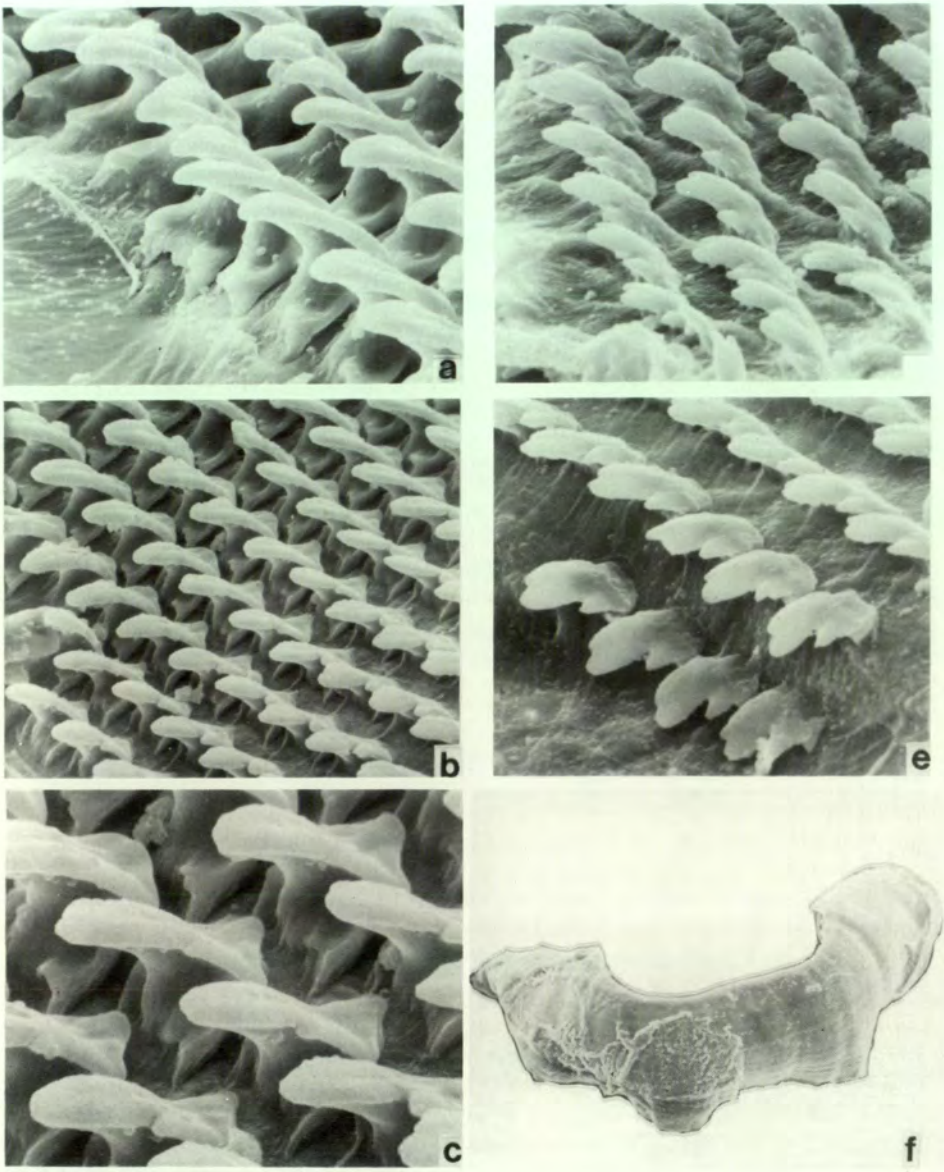


Plate 200: Radular teeth and jaw of *Strepsitaurus rugus* (Cotton, 1953). WA–16, S of Goat Cave, near Central Hill, Cape Range, WA. 17 Januray 1974. FMNH 182495, Dissection A: (a) central and early laterals at 750X; (b) latero-marginal transtion at 560X; (c) detail of latero-marginal transtion at 1325X; (d) mid-marginals at 760X; (e) outer marginals at 800X; (f) jaw at 105X.

STREPSITAURUS RUGUS (COTTON, 1953)

(Plates 197d–f, 198a–d, 200a–f, 201c–f; Figs 395d–f, 397a–c, 398; Maps 33–34)

Pleuroxia ruga Cotton, 1953, *Trans. Roy. Soc. South Austr.*, **76** (1): 26, plt. II, figs 11–12 – top of Cape Range, Exmouth Gulf, Western Australia (I. Crespin!); Richardson, 1985, *Tryonia*, 12: 254 – citation in check list.

Comparative remarks

Strepsitaurus rugus (Cotton, 1953), from the Rough Range N to the central-east portion of the Cape Range, WA (**Maps 33–34**), is of average size (mean diameter 14.56 mm), with a low spire (**Fig. 395e**, mean H/D ratio 0. 490), strong diagonal crenulated ridges (**Plate 197d–e**) and rather large microsculpture, a very narrowly open to closed umbilicus (**Fig. 395f**) and lacks a basal lip knob (**Fig. 395e**). *S. ningaloo*, from the W portion of the Cape Range (**Maps 33–34**), has a very high spire (**Fig. 395b**, mean H/D ratio 0.609), even stronger diagonal crenulated ribs (**Plate 197a–b**), a closed umbilicus (**Fig. 395f**) and lacks a basal lip knob (**Fig. 395e**). *S. williami*, from the central portion of the Cape Range (**Maps 33–34**), is smaller (mean diameter 11.42 mm), has a low spire (**Fig. 394e**, mean H/D ratio 0. 495), the crenulated diagonal ribs are much less prominent (**Plate 196d–e**) and umbilicus is widely open (**Fig. 394f**, mean D/U ratio 6.08). *S. milyeringus*, from the NW part of the Cape Range, near Milyering Well, is much smaller (mean diameter 8.40 mm), with a reduced whorl count (mean 3 5/8) and a widely open umbilicus (mean D/U ratio 4.44, **Fig. 452c**). *S. cardabius*, found in ocean-front dune deposits from Ningaloo Homestead S to Gnaraloo Station, just S of the Cape Range (**Maps 33–34**), has an angulated periphery and much higher spire (**Fig. 394b**), the crenulated radial ribs parallel the radial growth lines (**Plate 196a–b**), the umbilicus is narrowly open (**Fig. 394c**, mean D/U ratio 9.93) and the parietal lip is represented by at most a thick callus. Anatomically (**Figs 397a–c, 398**), the short vagina (V), extremely short free oviduct (UV) and spermathecal shaft (S) combine with the greatly enlarged main pilaster (PP), which occupies two–thirds of the penis chamber length, to separate *S. rugus* from *S. ningaloo* (**Figs 396a–b**) and *S. milyeringus* (**Figs 453a–b**), the only other dissected species of *Strepsitaurus*. *S. ningaloo* has the vagina and free oviduct longer, the spermathecal shaft is much longer and the main pilaster occupies only about half of the penis chamber wall.

Holotype

SAM D14452, top of Cape Range, Exmouth Gulf, Western Australia. Collected by I. Crespin. Height of shell 7.5 mm, diameter 16.5 mm, H/D ratio 0.455, whorls 4 3/8–, umbilical width 1.3 mm, D/U ratio 12.7.

Paratopotype

SAM D14452, 1 DA. Height of shell 6.9 mm, diameter 15.95 mm, H/D ratio 0.433, whorl count unknown because the shell apex is covered with glue, umbilical width 1.1 mm, D/U ratio 14.5.

Material studied

WESTERN AUSTRALIA: Rough Range (1955, WAM 111–117, 5 DA, 2 DJ;

Table 148: Local variation in *Strepsitaurus rugus.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
Rough Range, WAM 111-117	5D	7.56±0.188 (7.0-8.1)	13.97±0.585 (12.6-15.5)	0.543±0.018 (0.516-0.610)	4⅜ (4⅜−-4⅜+)	1.39±0.167 (0.85-1.85)	10.8±1.841 (8.02-18.0)
Yardie Creek, WAM 283.74	16D	7.07±0.143 (5.8-7.7)	14.85±0.211 (13.7-16.3)	0.477±0.010 (0.413-0.531)	4⅜+ (4¼-4½+)	1.57±0.081 (1.15-2.1)	9.82±0.501 (7.24-13.6)
WA-14, FMNH 182473	15D	7.04±0.147 (6.08-8.15)	15.22±0.185 (14.05-16.6)	0.463±0.010 (0.397-0.541)	4⅜+ (4⅛+-4⅝−)	1.75±0.121 (1.1-2.6)	9.27±0.610 (6.15-13.6)
WA-17, FMNH 182455	10L	7.36±0.154 (6.6-8.4)	15.73±0.216 (14.5-16.95)	0.468±0.009 (0.422-0.507)	4½ (4¼+-4¾)	1.45±0.067 (1.0-1.75)	11.0±0.541 (9.40-15.1)
WA-17, FMNH 182480	11L	7.13±0.162 (6.3-8.25)	15.18±0.280 (14.15-16.95)	0.470±0.009 (0.425-0.515)	4⅜ (4¼−-4⅝+)	1.54±0.120 (0.90-2.058)	10.6±0.916 (7.26-16.0)
WA-16, FMNH 182495	22L	7.19±0.137 (6.05-9.0)	16.54±0.196 (14.5-18.65)	0.435±0.006 (0.388-0.498)	4½+ (4⅜-4⅞−)	1.58±0.051 (1.15-2.1)	10.7±0.341 (7.87-13.9)
WA-175, FMNH 199439	16D	7.34±0.170 (6.2-8.4)	15.94±0.202 (14.3-17.4)	0.460±0.007 (0.404-0.508)	4½+ (4¼+-4⅞+)	1.68±0.088 (1.15-2.5)	9.88±0.580 (6.22-14.5)
WA-175, FMNH 199756	10L	6.61±0.156 (5.75-7.35)	15.05±0.256 (13.4-16.0)	0.440±0.008 (0.419-0.497)	4⅜− (4⅛+-4½+)	1.77±0.112 (1.15-2.35)	8.84±0.649 (6.23-12.6)
WA-178, FMNH 199404	34D	6.70±0.084 (5.75-7.6)	14.66±0.347 (13.35-16.65)	0.488±0.030 (0.404-0.511)	4⅜ (4⅛−-4⅝+)	1.67±0.057 (1.0-2.4)	9.01±0.394 (5.82-13.5)
WA-959, FMNH 212498	20D	6.84±0.108 (5.9-7.65)	14.97±0.221 (13.1-17.2)	0.457±0.005 (0.422-0.501)	4⅜+ (4¼−-4⅝+)	1.79±0.093 (1.05-2.65)	8.80±0.492 (6.33-14.3)
WA-960, FMNH 212510	7D	6.72±0.199 (6.15-7.55)	14.56±0.179 (14.1-15.2)	0.461±0.009 (0.136-0.501)	4⅜ (4⅛+-4⅝+)	1.86±0.117 (1.35-2.25)	8.08±0.652 (6.21-11.2)

Table 148: Local variation in *Strepsitaurus rugus* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
WA-18, FMNH 182554	12D	6.08±0.167 (4.9-6.9)	13.86±0.229 (12.05-15.05)	0.438±0.009 (0.399-0.492)	$4\frac{1}{2}-$ ($4\frac{1}{4}-$–$4\frac{3}{4}+$)	1.64±0.099 (1.1-2.3)	8.84±0.591 (6.51-12.8)
Treala Hill = Mt Lefroy WAM 1544.70	24D	6.75±0.095 (5.85-7.65)	15.43±0.227 (13.3-17.15)	0.439±0.006 (0.394-0.496)	$4\frac{5}{8}-$ ($4\frac{3}{8}-$–$4\frac{7}{8}+$)	1.69±0.052 (1.25-2.25)	9.27±0.258 (7.03-12.0)
Charles Knife Rd., AM C.87649	30D	7.42±0.085 (6.75-8.6)	13.17±0.132 (11.8-15.15)	0.564±0.005 (0.520-0.629)	$4\frac{1}{4}$ ($3\frac{7}{8}+$–$4\frac{1}{2}$)	1.30±0.041 (1.0-2.1)	10.4±0.317 (6.28-13.5)
WA-176a, FMNH 199935	16L	8.06±0.163 (7.0-9.1)	14.63±0.144 (13.15-15.7)	0.550±0.007 (0.495-0.601)	$4\frac{3}{8}$ ($4+$–$4\frac{3}{4}+$)	1.10±0.038 (0.85-1.45)	13.5±0.490 (10.4-17.6)
WA-176, FMNH 199423	56D	7.24±0.057 (6.35-8.5)	13.67±0.080 (12.5-15.15)	0.529±0.003 (0.477-0.601)	$4\frac{1}{4}+$ ($4\frac{1}{8}+$–$4\frac{3}{4}+$)	1.13±0.029 (0.7-1.95)	12.5±0.309 (7.19-18.0)
Shothole Canyon, WAM 383.74	13D	6.99±0.221 (5.4-8.3)	13.05±0.271 (11.5-14.5)	0.535±0.009 (0.468-0.582)	$4\frac{3}{8}$ ($4\frac{1}{4}+$–$4\frac{5}{8}-$)	1.29±0.073 (0.95-1.9)	10.5±0.590 (6.06-13.7)
C.R. #2 Deep Well WAM 303.74	30D	7.29±0.102 (6.2-8.6)	13.91±0.142 (12.65-15.25)	0.524±0.005 (0.479-0.573)	$4\frac{1}{4}+$ ($3\frac{3}{4}+$–$4\frac{1}{2}+$)	1.12±0.075 (0.0-1.85)	
near C.R. #2 Deep Well, WAM 379.74	9D	7.48±0.132 (6.75-8.15)	13.70±0.202 (12.6-14.5)	0.547±0.007 (0.508-0.568)	$4\frac{3}{8}$ ($4\frac{1}{4}-$–$4\frac{1}{2}+$)	1.36±0.093 (0.9-1.8)	10.5±0.873 (7.27-15.5)

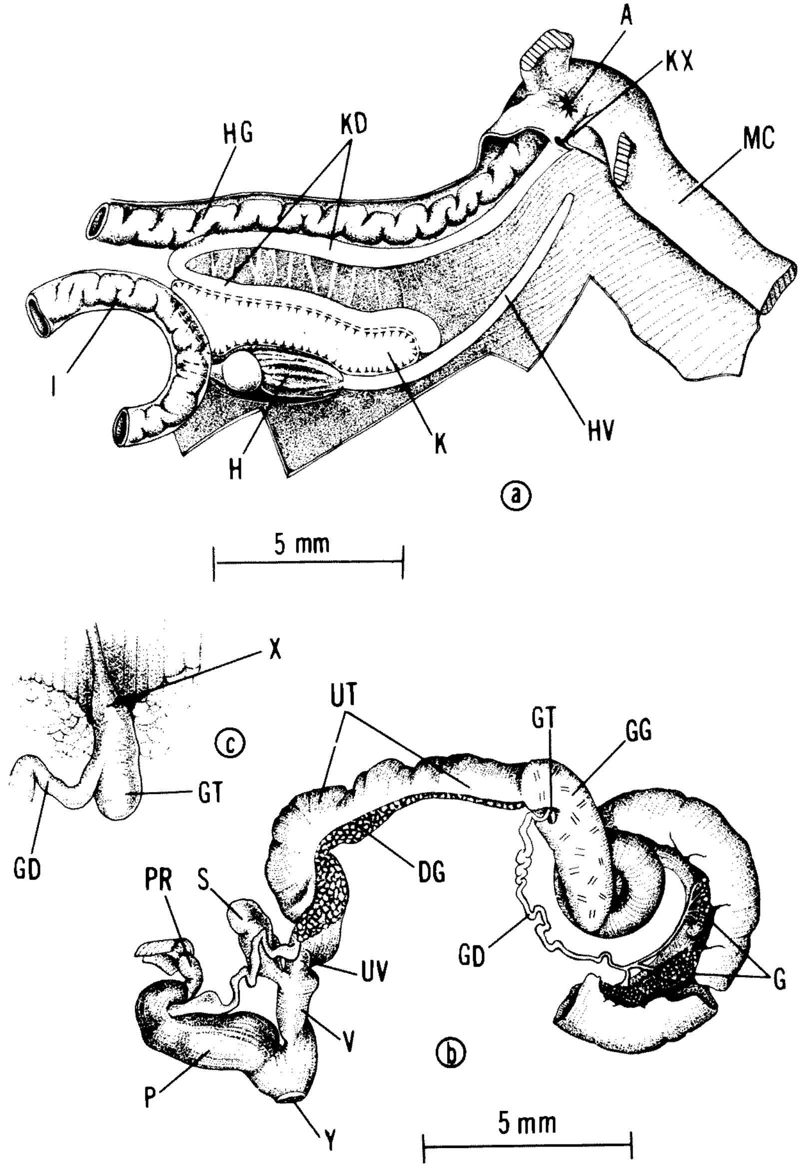


Fig. 397: Pallial region and genitalia of *Strepsitaurus rugus* (Cotton, 1953): Goat Cave, near Central Hill, Cape Range, WA. June and July 1964. FMNH 171622: (a) pallial complex; (b) whole genitalia; (c) detail of talon, greatly enlarged. Scale lines as marked. Drawings by Carole W. Christman.

southernmost part, G. W. Kendrick! 25 May 1965, WAM 281.74, 2 DA). Cape Range: along Learmonth–Cape Range track (W. Turnbull! 1964, WAM , FMNH 171638, 17 DA, several DJ); in bed of small dry watercourse (G. W. Kendrick! 10 May 1965, WAM 356.74, 7 LA); Yardie Creek, 9 miles SE of Central Hill (G. Hitchin and G. W. Kendrick! 20 May 1965, WAM 283.74, 16 DA, 7 DJ); Goat Cave, near Central Hill (P. & W. Turnbull! June to July 1964, FMNH 171621–2, 1 LA, 1 DA, 1 LJ; G. Hitchin! 15 May 1965, FMNH 171628, 1 LA; WA–14, 16 January 1974, WAM , SAM D, AM, FMNH 182473, 15 DA; WA–16, 17 January 1974, WAM 892.87, FMNH 182459, FMNH 182466, 24 LA; WA–17, 17 January 1974, FMNH 182455, FMNH 182480, FMNH 182459, FMNH 182499, FMNH 182652, FMNH 182466, 26 LA, 8 DA; WA–174, 14 December 1976, FMNH 199866, 1 LA; WA–175, 29 September 1976, WAM, FMNH 199439, 16 DA, 1 DJ; WA–175, 13 April 1977, FMNH 199756, FMNH 199903, 10 LA, 32 LJ; WA–178, 30 September 1976, WAM 889.87, AM, SAM D18223, FMNH 199404, 34 DA, 8 DJ; WA–959, 11 July 1983, WAM , AM, FMNH 212498, FMNH 212503, 2 LA, 20 DA, 2 DJ; 100 yards N of Goat Cave, G. W. Kendrick! 14–15 May 1965, WAM, 13 DA); 1.6 km N of Goat Cave (WA–960, E of track, FMNH 212510, 7 DA); 2.4 miles N of Goat Cave (WA–18, 19 January 1974, FMNH 182506, FMNH 182554, 3 LA, 12 DA, 3 DJ); Trealla Hill, along summit (G. Hitchin & G. W. Kendrick! 14 May 1965, WAM 1544.70, 24 DA, 7 DJ); along #3 Deep Well track (P. Cawthorn! 5 August 1962, WAM 287.74, 4 DA, 1 DJ); 4.2 km along Charles Knife Road (WA–1080a, FMNH 221749, 1 LA); 8.8 km along Charles Knife Road (WA–176, WAM 890.87, WAM 891.87, SAM D18224–5, AM, QM, MV, FMNH 199423, FMNH 199927, FMNH 199935, 19 LA, 56 DA, 1 LJ, 2 DJ); along Charles Knife Road, 19 January 1972, AM C.87649, 30 DA, 6 DJ); Thomas Carter Lookout, Charles Knife Road (WA–1079, FMNH 221750–1, 24 LA); rock crevices 100 yards from #2 Deep Well (G. Hitchin, P. Saar, & G. W. Kendrick! 10 May 1965, WAM 303.74, 30 DA, 4 DJ); near #2 Deep Well (G. Hitchin & G. W. Kendrick! 10 May 1965, WAM 379.74, 9 DA; G. W. Kendrick! 16 May 1965, WAM 288.74, 2 DA; G. W. Kendrick! 18 May 1965, WAM, 3 DA).

Range

Strepsitaurus rugus has been found on the North West Cape peninsula, WA (**Maps 33–34**) from the southern part of the Rough Range (*ca.* 22°28'S) N to #2 Deep Well in the Cape Range (*ca.* 22°06'S), a N-S distance of about 42 km. The Yardie Creek record requires confirmation, since otherwise the known records are from the central and E portions of the Cape Range. The probable E-W range is about 10 or 11 km.

Diagnosis

Shell medium in size, adult diameter 11.3-18.65 mm (mean 14.56 mm), with 3 3/4+ to 5 3/8+ (mean 4 3/8) normally coiled whorls. Apex and spire slightly elevated (**Fig. 395e**), shell height 4.7–9.1 mm (mean 7.08 mm), H/D ratio 0.388–0.629 (mean 0.490). Body whorl obtusely angulated (**Fig. 395e**). Apex (**Plate 197d**) with dense pustules aligned in radial rows. Spire and body whorl (**Plate 197d–e**) with strong diagonal crenulated ribs and prominent pustules. Umbilicus (**Fig. 395f**) narrowly open to closed, usually a lateral crack. Body whorl descending very sharply behind lip. Palatal and basal lips reflected and moderately expanded, columellar lip broader. Parietal wall with lip continuous, slightly free of whorl. No basal lip knob, but sometimes basal lip

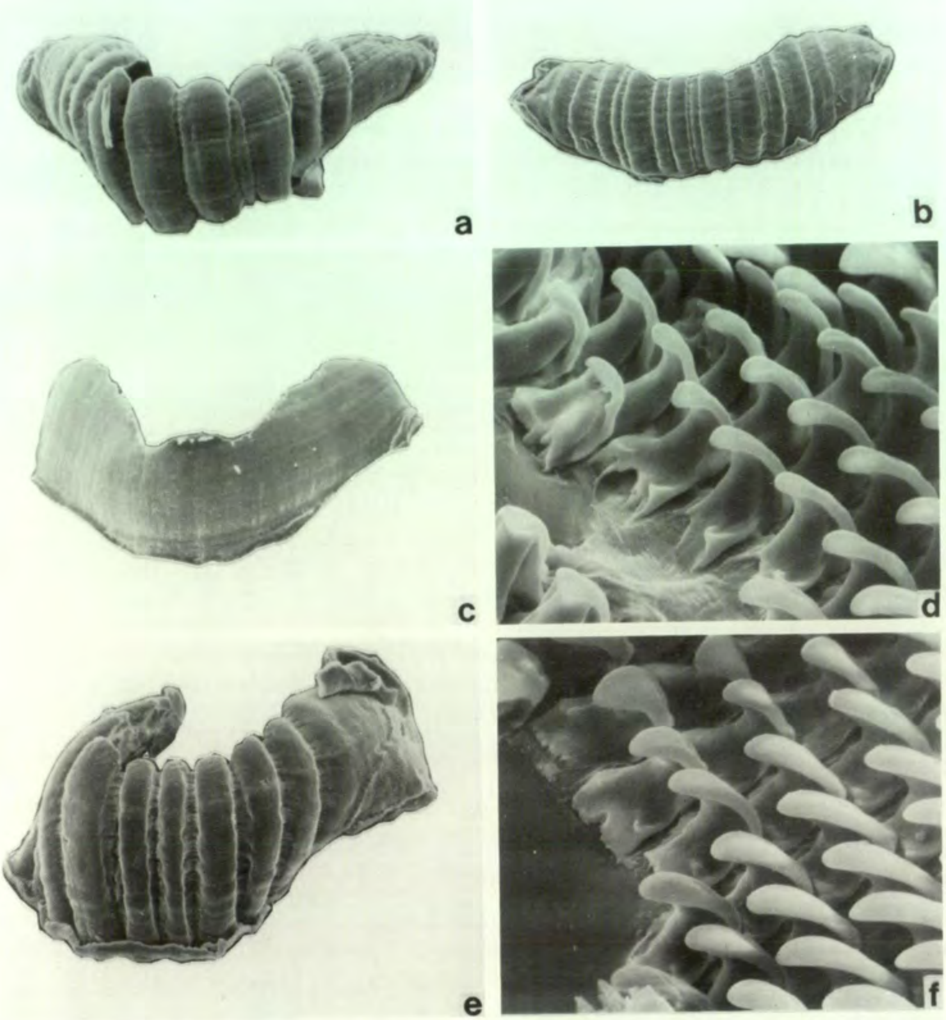


Plate 201: Jaws of *Strepsitaurus ningaloo* sp. nov. and *S. rugus* (Cotton 1953): (a–b) *S. ningaloo*. WA–171, 23.7 km N of Ningaoloo Homestead, W side Cape Range, WA. 27 September 1976. FMNH 199849. a is jaw from Dissection C at 86X. b is jaw from Dissection A at 58X; (c–d) *S. rugus*. WA–16, Goat Cave, near Central Hill, Cape Range, WA. 17 January 1974. FMNH 182495, Dissection A. c is jaw at 84X. di central and early lateral teeth at 650X; (e–f) *S. rugus*. WA–176a, Charles Knife Road, 8.8 km W of Exmouth road, E side Cape Range, WA. 30 September 1976. FMNH 199935, Dissection A. e is jaw at 10.1X. f is central and early laterals at 540X.

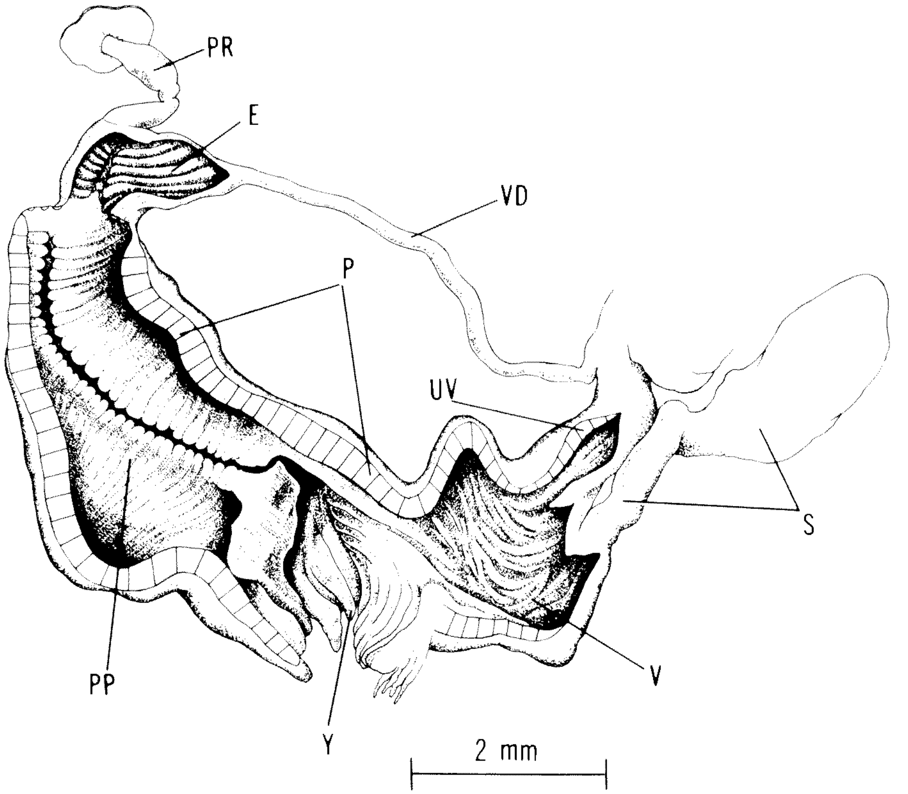


Fig. 398: Interior of terminal genitalia of *Strepsitaurus rugus* (Cotton, 1953): Goat Cave, near Central Hill, Cape Range, WA. June and July 1964. FMNH 171622. Scale line equals 2 mm. Drawing by Carole W. Christman.

thickened. Shell colour normally white on top of crenulated ridges, reddish-brown in the low areas between ridges. Based on 420 measured adults.

Genitalia (**Figs 397b–c, 398**) with very short free oviduct (UV) and vagina (V), spermatheca (S) with very short shaft. Head of spermatheca just above origin of free oviduct. Vas deferens (VD) entering directly into swollen head of epiphallus (E). No trace of epiphallic caecum. Epiphallus with simple longitudinal pilasters (EPP, **Fig. 398**), terminating at apex of huge main corrugated pilaster (PP) that extends two thirds of way down penis chamber. Penial retractor muscle (PR) inserting in an arc near middle of epiphallus. Penis (P) thick-walled, elongated, some basal pilasters present.

Central and lateral teeth of radula (**Plates 200a, 201d, f**) variable. Anterior flare small (**Plate 200a**) to absent (**Plate 201d**), basal plate length and inter-row support ridge size also varies. Cusp shaft angle from moderately elevated (**Plate 200a**) to near vertical (**Plate 201d, f**). Cusp tip curved and blunt (**Plate 200d**), to strongly curved and rounded (**Plate 201f**), to hook-shaped and shortened (**Plate 201d**). Ectocone appearing only at lateromarginal transition (**Plate 200b–c**). Late laterals (**Plate 200b–c**) with

Table 149: Local variation in *Promonturconchum superbum* and *Caperantrum polygyrum*.

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Promonturconchum superbum					
WA-23, FMNH 182304	16D	21.44±0.295 (19.55-23.9)	28.86±0.245 (27.35-30.4)	0.742±0.007 (0.669-0.786)	$4\frac{5}{8}$+ ($4\frac{1}{2}$-$4\frac{3}{4}$)
WA-14, FMNH 182471	10D	23.11±0.370 (21.5-24.55)	30.18±0.314 (28.6-31.65)	0.766±0.010 (0.706-0.805)	$4\frac{5}{8}$+ ($4\frac{1}{2}$-5)
WA-175, FMNH 199436	65D	23.15±0.131 (20.45-25.4)	29.47±0.143 (27.0-31.9)	0.786±0.005 (0.708-0.885)	$4\frac{7}{8}$ ($4\frac{5}{8}$–-$5\frac{1}{4}$–)
WA-178, FMNH 199407	14D	22.13±0.278 (19.7-23.45)	28.54±0.302 (26.35-30.5)	0.775±0.006 (0.741-0.822)	$4\frac{7}{8}$+ ($4\frac{3}{4}$–-$5\frac{1}{4}$–)
WA-175, FMNH 199749	25L	22.72±0.252 (19.0-24.45)	29.14±0.266 (26.6-31.75)	0.780±0.006 (0.716-0.857)	$4\frac{7}{8}$– ($4\frac{5}{8}$+-$5\frac{1}{4}$–)
WA-175, FMNH 199748	22L	22.57±0.239 (20.1-24.4)	28.71±0.309 (25.8-30.8)	0.787±0.006 (0.726-0.838)	$4\frac{7}{8}$ ($4\frac{5}{8}$+-$5\frac{1}{8}$–)
WA959, FMNH 212504	6L	23.01±0.378 (21.2-23.95)	29.06±0.375 (27.7-30.25)	0.792±0.017 (0.742-0.865)	5– ($4\frac{5}{8}$–-$5\frac{1}{8}$–)
WA-959, FMNH 212495	27D	22.94±0.232 (20.55-25.3)	29.12±0.255 (26.45-32.3)	0.788±0.007 (0.729-0.844)	$4\frac{7}{8}$+ ($4\frac{5}{8}$–-$5\frac{1}{8}$+)
WA-960, FMNH 212506	6L	22.27±0.218 (21.4-23.0)	28.55±0.429 (27.2-29.9)	0.781±0.012 (0.739-0.819)	$4\frac{7}{8}$– ($4\frac{3}{8}$+-$5\frac{1}{8}$+)
WA-960, FMNH 212505	8D	23.27±0.431 (21.3-24.6)	29.01±0.494 (27.0-30.7)	0.803±0.012 (0.725-0.835)	5+ ($4\frac{1}{2}$+-$5\frac{1}{4}$+)
Sta. 221, Learmonth, FMNH 171632	10D	23.29±0.402 (21.35-25.3)	29.25±0.511 (26.35-32.0)	0.789±0.009 (0.764-0.835)	$4\frac{3}{4}$ ($4\frac{1}{2}$-$4\frac{7}{8}$)
WA-176, FMNH 199428	17D	21.33±0.306 (18.05-23.45)	27.06±0.305 (24.5-29.05)	0.789±0.009 (0.729-0.874)	$4\frac{7}{8}$ ($4\frac{1}{2}$+-$5\frac{1}{4}$–)

Table 149: Local variation in *Promonturconchum superbum* and *Caperantrum polygyrum* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Caperantrum polygyrum					
Ridge opposite Goat Cave, WAM 313.74	5D	14.70±0.389 (13.7-15.5)	21.51±0.100 (21.15-21.7)	0.683±0.017 (0.636-0.724)	$6\frac{1}{8}$ ($5\frac{7}{8}$-$6\frac{1}{2}$)
WA-14, FMNH 182469	12D	15.92±0.232 (14.5-17.65)	22.93±0.374 (20.0-24.25)	0.696±0.011 (0.623-0.729)	$6\frac{1}{4}$ ($5\frac{7}{8}$-$6\frac{1}{2}$)
WA-175, FMNH 199752	8D	14.62±0.280 (13.9-16.2)	21.56±0.171 (20.9-22.3)	0.678±0.012 (0.624-0.731)	6+ ($5\frac{3}{4}$+-$6\frac{1}{4}$)
WA-175, FMNH 199437	91D	15.46±0.088 (13.4-17.5)	21.78±0.122 (19.9-29.75)	0.711±0.005 (0.461-0.813)	$6\frac{1}{4}$+ (6−-$6\frac{5}{8}$+)
WA-175, FMNH 199751	5L	14.52±0.320 (13.95-15.75)	21.57±0.202 (20.85-21.9)	0.673±0.014 (0.639-0.718)	$6\frac{1}{4}$− (6+-$6\frac{1}{4}$+)
WA-178, FMNH 199408	8D	15.01±0.159 (14.45-15.6)	21.95±0.166 (21.1-22.7)	0.684±0.005 (0.660-0.701)	$6\frac{1}{4}$+ ($6\frac{1}{8}$−-$6\frac{1}{2}$+)
WA-959, FMNH 212496	64D	15.81±0.110 (13.95-18.1)	21.75±0.113 (19.9-23.55)	0.727±0.004 (0.659-0.807)	$6\frac{1}{4}$+ ($5\frac{7}{8}$+-$6\frac{7}{8}$+)
Sta. 221, Learmonth, FMNH 171634	12D	14.51±0.214 (13.35-15.6)	21.41±0.212 (20.15-22.95)	0.677±0.010 (0.630-0.744)	6− ($5\frac{3}{4}$-$6\frac{1}{4}$)

suddenly enlarged anterior flare, which continues on earliest marginals. Endocone appears as a notch or bump on early marginals (**Plate 200b**). Both ectocone and endocone large on mid-marginals (**Plate 200d**). Marginals retain cusp shaft curvature through most of field (**Plate 200d–e**). Outer marginals (**Plate 200e**) typical. Jaw (**Plates 200f, 201c, e**) highly variable, with vertical ribs typical to completely absent, depending upon population sampled.

Discussion

The types of *Strepsitaurus rugus* are of the narrowly umbilicated form that is common in the middle and on the E side of the Cape Range. They are slightly larger than most recently collected examples but agree fully in shape and sculpture. The exact type locality is unknown.

The variation in radula and jaw structure outlined above (**Plates 200–201**) is as large as I have seen within a single species of Australian camaenid. A nearly identical variation is found in *Westraltrachia* derbyi (Cox, 1892), a species ranging from Windjana Gorge SE for about 14 km in the Napier Range, West Kimberley, WA. Cox's species has the jaw varying within the Windjana population but retaining vertical ribbing further E (Solem 1984: 454–455, plts 27–28), although the lateral teeth of the radula show only minor variation (*ibid.*, pp. 468–469, plts 38–39). This multispecies situation has arisen with the interaction *Amplirhagada* and *Westraltrachia* under sympatry that involves food specialization under conditions of microsympatry (Solem 1985a).

The Cape Range situation involves varying degrees of microsympatry. In the vicinity of Goat Cave there are five species of camaenids, *Strepsitaurus rugus*,

Table 150: Comparison of *Promonturconchum* and *Caperantrum*

Character	Genus: *Promonturconchum*	*Caperantrum*
SHELL		
Whorls	loose coiling, normal count	tight coiling, higher number
Body whorl	inflated	narrow
Shell lip	narrower, no basal knob	wider, basal knob
Parietal wall callus	thin	thick
GENITALIA		
Albumen gland	large	huge
Prostate-uterus	short	typical
Epiphallus	slender, 2/3 penis length	normal, 1/3 penis length
Epiphallic caecum	lateral knob	typical
Penis sheath	present	absent
Main pilasters	longer	shorter

Promonturconchum superbum sp. nov., *Caperantrum polygyrum* sp. nov., *Quistrachia lefroyi* sp. nov., and *Rhagada tescorum* (Benson, 1853) among all of which jaw rib reduction (**Plates 200f, 201c**) is almost complete. Along Charles Knife Road, where the jaw rib size is very large (**Plate 201e**), only *Strepsitaurus rugus* and dead examples of *S. williami* have been collected. Near Goat Cave, the radular teeth vary from specimen to specimen (**Plates 200a, 201d**), while along Charles Knife Road the teeth are *intermediate* and more uniform.

Shell sculpture of *Strepsitaurus rugus* (**Plate 197d–f**) is *intermediate* in prominence between that of *S. williami* (**Plate 196d–f**), where the major ribs are reduced, and *S. ningaloo* (**Plate 197a–c**), where it is accentuated. One population of *S. rugus*, sampled in 1965, retained periostracal setae (**Plate 198a–d**) with wide bases. These were not seen in other samples of any Cape Range *Strepsitaurus*.

Size and shape variation in *Strepsitaurus rugus* was fairly extensive (**Table 148**). The few Rough Range specimens are small, but high spired, as are those from Charles Knife Road, Shothole Canyon, and near #2 Deep Well. In contrast, samples from the central portion of the Cape Range are largest in diameter and lower in H/D ratio.

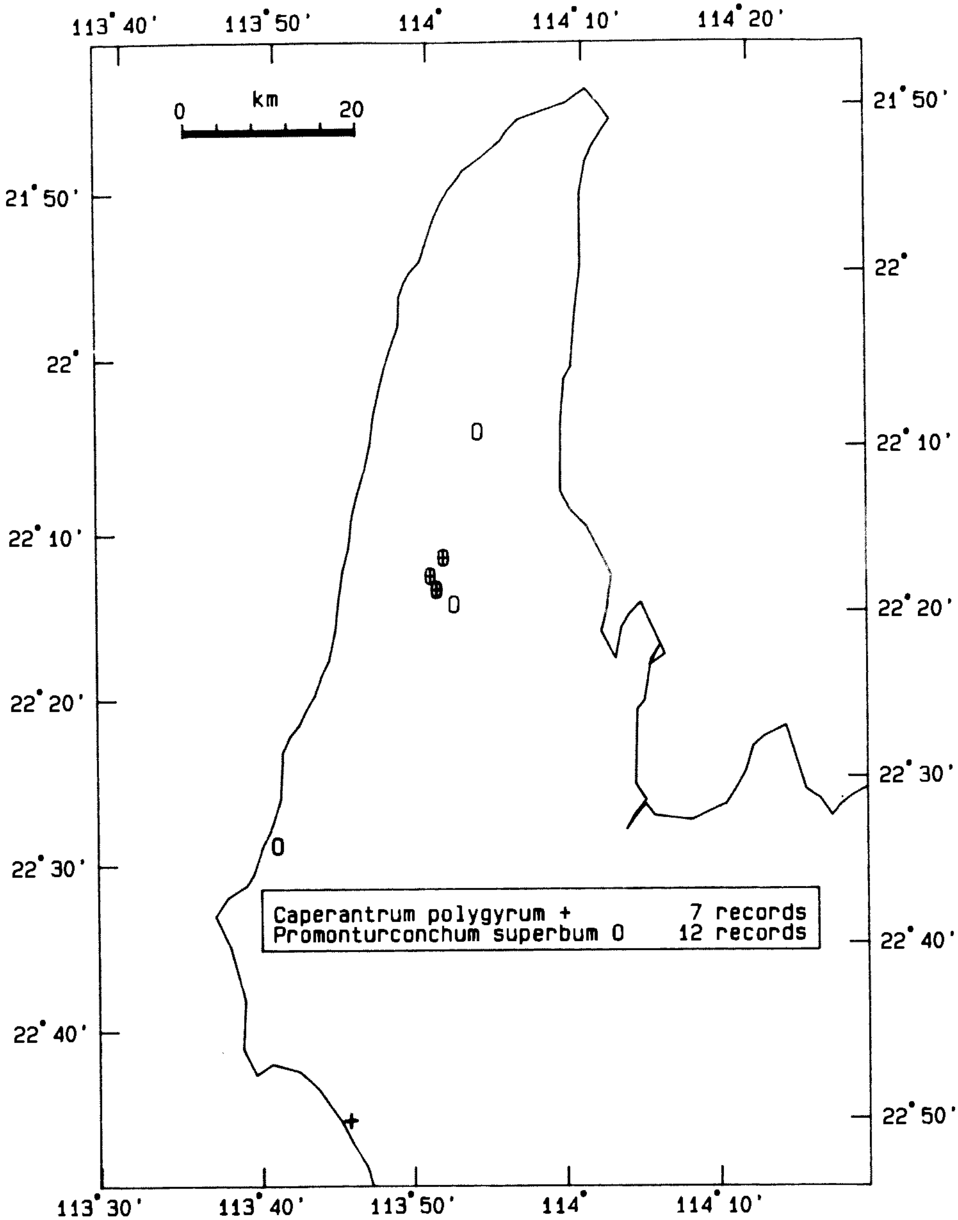
Considerably more study of this species is needed before these variations can be assessed as to their importance. It may be that additional species will have to be recognised.

GENUS *PROMONTURCONCHUM* GEN. NOV.

Shell very large, adult diameter 24.5 to 32.3 mm, whorls 4 3/8 to 5 1/4+, very loosely coiled. Apex and spire strongly and evenly elevated, not rounded above, H/D ratio 0.669–1.037. Apex (**Plate 202a**) with weak radial ridges and some pustules. Spire and body whorl (**Plate 202b**) with weak growth lines and microsculpture of incised spiral lines. Body whorl evenly rounded and strongly inflated (**Fig. 399b**), descending sharply behind lip. Umbilicus either closed (**Fig. 399c**), and covered with a heavy callus or a narrow crack visible along columellar lip. Palatal and basal lips broadly expanded, edge rolled; columellar lip wider. Parietal wall with thin callus. Colour light yellow-horn, fresh examples with broad, faint mid-palatal red spiral band. Lip white.

Specimens aestivate sealed to a rock face or another shell by a very narrow rim epiphragm that is lightly calcified.

Genitalia (**Figs 400a–b, 401 a–b**) with enlarged albumen gland (GG), both prostate (DG) and uterus (UT) shortened. Vagina (V) long and slender, equal in length to penis (P), internally with longitudinal pilasters (VS), partly corrugated into stimulatory edges. Free oviduct (UV) short, reflexed apically. Spermatheca (S) with short stalk, expanded head tightly bound to base of prostate-uterus. Vas deferens (VD) very slender, enters directly into unexpanded epiphallus (E) about one-quarter to one-third way up penis, junction marked by lateral, nodular epiphallic caecum (EC). Penis cylindrical, long, with a very thin penis sheath (PS). Epiphallus enters sheath subapically, reflexes to enter apex of penis through complex small pilasters. Penial retractor muscle (PR) inserts in an arc on penis-epiphallus junction. Penis with thick walls, chamber wall with spiral pilasters apically, three elongated corrugated pilasters in middle two-thirds, basal portion with longitudinal pilasters.



Map 35: Records of *Caperantrum polygyrum* and *Promonturconchum superbum* on the Cape Range, WA.

Jaw (**Plate 202c–d**) with a few high, usually wide vertical ribs, not reduced on margins. Central and lateral teeth of radula (**Plate 203**) with prominent anterior flare, about 45°cusp shaft angle, cusp tip slightly curved and bluntly pointed, typical basal plate length and support ridge. Late laterals (**Plate 203c**) with slightly enlarged anterior flare, reduced cusp tip curvature, no trace of ectocone. Lateromarginal transition (**Plate 203d**) and marginals (**Plate 203e–f**) typical.

Type species: *Promonturconchum superbum* sp. nov., by original designation.

Comparative remarks

Several unusual features of *Promonturconchum* are shared with *Caperantrum* gen. nov. – the incised spiral line shell microsculpture (**Plate 202b**), general pattern of penial chamber sculpture (compare **Figs 401b** and **402b**), unusual apical reflexion of the free oviduct (UV), and very elongated vagina (V). The penial chamber wall features seem to be a modification of the *Plectorhagada–Strepsitaurus* pattern but the other features are not found elsewhere in the Sinumeloninae and suggest that the Cape Range taxa may be both monophyletic and isolated from the other taxa.

There are a number of contrasts between the two genera, both in shell and anatomical features (**Table 150**). While probably closely related, they have sufficient divergences in structure to warrant generic separation. No other genera of Sinumeloninae come close in shell features. The incised spiral line microsculpture on the spire and body whorl is common in such unrelated Kimberley genera as *Amplirhagada* (see Solem 1981: 160, plt. 14f) but has not been seen in any other member of the Sinumeloninae. The shape of *Promonturconchum*, with its inflated body whorl, rapidly increasing whorl width, rolled lip edge, and high spire is only superficially similar to *Xanthomelon* or *Hadra* from northern Australia and very different from any of the Red Centre or South Australian camaenids.

Distribution and comparative ecology

The only known species of *Promonturconchum* has about a 50 km long distribution (**Maps 28, 35**) from the Rough Range N to the level of Charles Knife Road in the Cape Range. It extends both N and S of *Caperantrum polygyrum* sp. nov. (**Maps 28, 35**), which is restricted to the 20 km area between Yardie Creek and #3 Deep Well in the Cape Range. The few live examples of *Promonturconchum superbum* have been taken either crawling in the open after a rain or aestivating within fissures on cliffs or cracks between boulders in rubble, usually sealed to near-vertical rock faces with a very narrow rim epiphragm that looks much less calcified than is the seal of *Strepsitaurus* species.

Dissection of the specimens collected while active showed that the stomach was filled with small pieces of leaves or grasses. Aestivating examples had no identifiable material within the stomach. The observed food particles represent a typical dietary pattern for camaenids and correlate with the very generalised teeth of *Promonturconchum*, compared with the specialised teeth found in the sympatric *Strepsitaurus rugus* (**Plate 200a–c, 201d, f**), *Rhagada capensis* sp. nov. (**Plates 213–215**), and *Quistrachia lefroyi* sp. nov. (**Plates 230–231a–c**), which have specialised diets (see below).

The name *Promonturconchum* refers to the occurrence of specimens in the fissures of rocky limestone promontories and outcrops of the Cape Range.

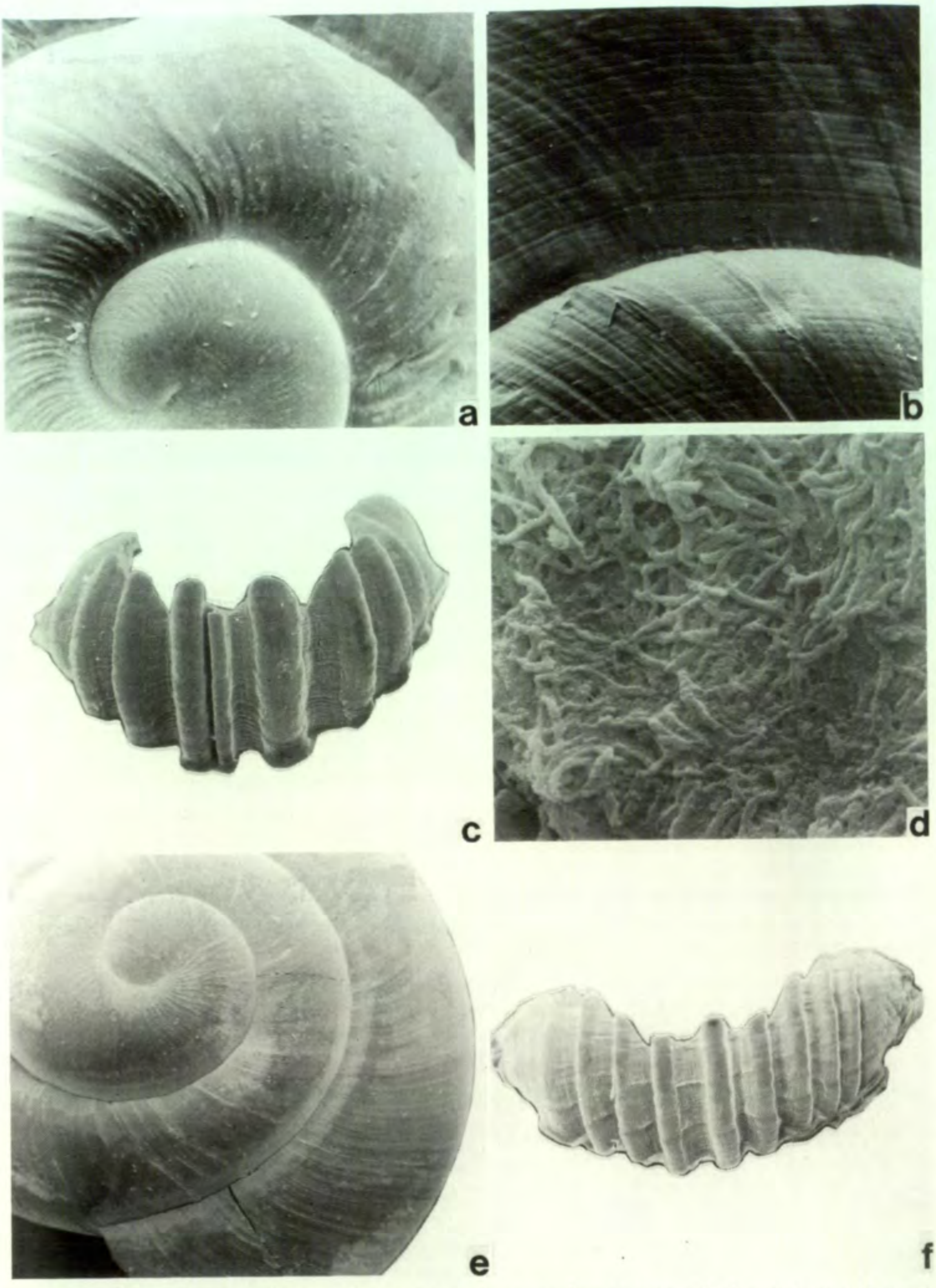


Plate 202: Shell sculpture and jaws of *Promonturconchum superbum* sp. nov. and *Caperantrum polygyrum* sp. nov.: (a–b) *P. superbum*. WA–959, near Goat Cave, Central Hill, Cape Range, WA. FMNH 212595. a is apex and early spire at 22.9X. b is spiral sculpture on lower spire at 19.8X; (c–d) *P. superbum*. WA–16, Goat Cave, Central Hill, Cape Range, WA. 16–18 January 1974. FMNH 182494, Dissection A. c is jaw at 57X. d is detail of jaw fibres at 3850X; (e) C. *polygyrum*. WA–178, Goat Cave, Central Hill, Cape Range, WA. FMNH 199408. e is apex and early spire at 16.2X; (f) C. *polygyrum*. WA–175, SE of Goat Cave, Cape Range, WA. 13 April 1977. FMNH 199752, Dissection A. f is jaw at 51.5X.

PROMONTURCONCHUM SUPERBUM SP. NOV.

(Plates 202a–d, 203a–f; Figs 399a–c, 400a–b, 401a–b; Maps 28, 35)

Comparative remarks

Promonturconchum superbum, from the Rough Range and Cape Range, WA (**Map 35**), is characterised by its very large size (mean diameter 28.93 mm), high spire (**Fig. 399b**, mean H/D ratio 0.786), rapidly increasing whorl width (**Fig. 399a**), normal whorl count (mean 4 7/8–), closed umbilicus (**Fig. 399c**), rolled lip edge (**Figs 399a–c**), inflated body whorl and microsculpture of incised spiral lines (**Plate 202b**). *Caperantrum polygyrum* sp. nov., from a small portion of the Cape Range (**Map 35**), is smaller (mean diameter 21.80 mm), less elevated (**Fig. 399e**, mean H/D ratio 0.711), with rather tightly coiled whorls (**Fig. 399d**), increased whorl count (mean 6 1/4), more broadly expanded lip (**Figs 399d–f**) with a raised ridge on the basal lip (**Fig. 399e**), closed umbilicus (**Fig. 399f**) with a heavy callus extending onto the previous whorl and the incised spiral lines are absent from the upper spire (**Plate 202e**). In the Cape Range, the widely distributed *Rhagada capensis* sp. nov. differs (**Figs 406a–c**) in its spiral red-orange colour bands, smaller size (mean diameter 20.01 mm), higher whorl count (mean 5 3/4) and less expanded lip. *Quistrachia lefroyi* sp. nov., which is common in the Cape Range, has a minutely pustulose apex (**Plate 227d**), a white peripheral zone usually bordered by narrow red bands above and below and the closed umbilicus lacks a heavy callus (**Fig. 433f**). *Plectorhagada scolythra*, from the Scrubby Range, Rough Range and E coastal plain of the Cape Range, has an area of crenulated radial ridging and large micropustules on the upper spire (**Plate 192a–c**), globose shape and lacks the incised spiral lines on the spire and body whorl. Anatomically (**Figs 400a–b, 401a–b**), *Promonturconchum superbum* has a very long and slender vagina (V), short and apically reflexed free oviduct (UV), short spermathecal shaft (S), vas deferens (VD) and epiphallus (E) equal in diameter, a small epiphallic caecum (EC) present about one-quarter way up penis complex, penis sheath (PS) present and penis chamber with large and complex main pilasters (PP). *Caperantrum polygyrum* sp. nov. (**Figs 402a–c**) has a very short spermatheca (S), lacks a penis sheath, the epiphallus (E) is larger in diameter than the vas deferens (VD), the epiphallic caecum (EC) is about one-third way down from penis apex (P) and there is very complex sculpture inside the penis chamber. *Rhagada capensis* sp. nov. (**Figs 407–409**) is easily identified by the large verge (PV) within the penis, the long epiphallus with an enlarged caecum and the much longer spermatheca. *Quistrachia lefroyi* sp. nov. (**Figs 436–439**) has the vas deferens entering at the base of the penis sheath, the penis is much longer than the sheath, the vagina is extremely elongated and the spermatheca is very short. *Plectorhagada scolythra* (**Figs 393a–b**) has very short terminal genitalia, no penis sheath, and the epiphallic caecum is reduced to a small knob.

Holotype

WAM 758.87, near Goat Cave, near Central Hill, Cape Range, North West Cape, Western Australia. *ca.* 22°15'53"S, 113°56'18"E. Collected by G. Hitchin 15 May 1965. Ex FMNH 171627, Dissection A. Height of shell 22.6 mm, diameter 28.2 mm, H/D ratio 0.801, whorls 4 3/4, umbilicus completely closed and with heavy callus.

Paratopotype

FMNH 171627, 1 LA from the type locality.

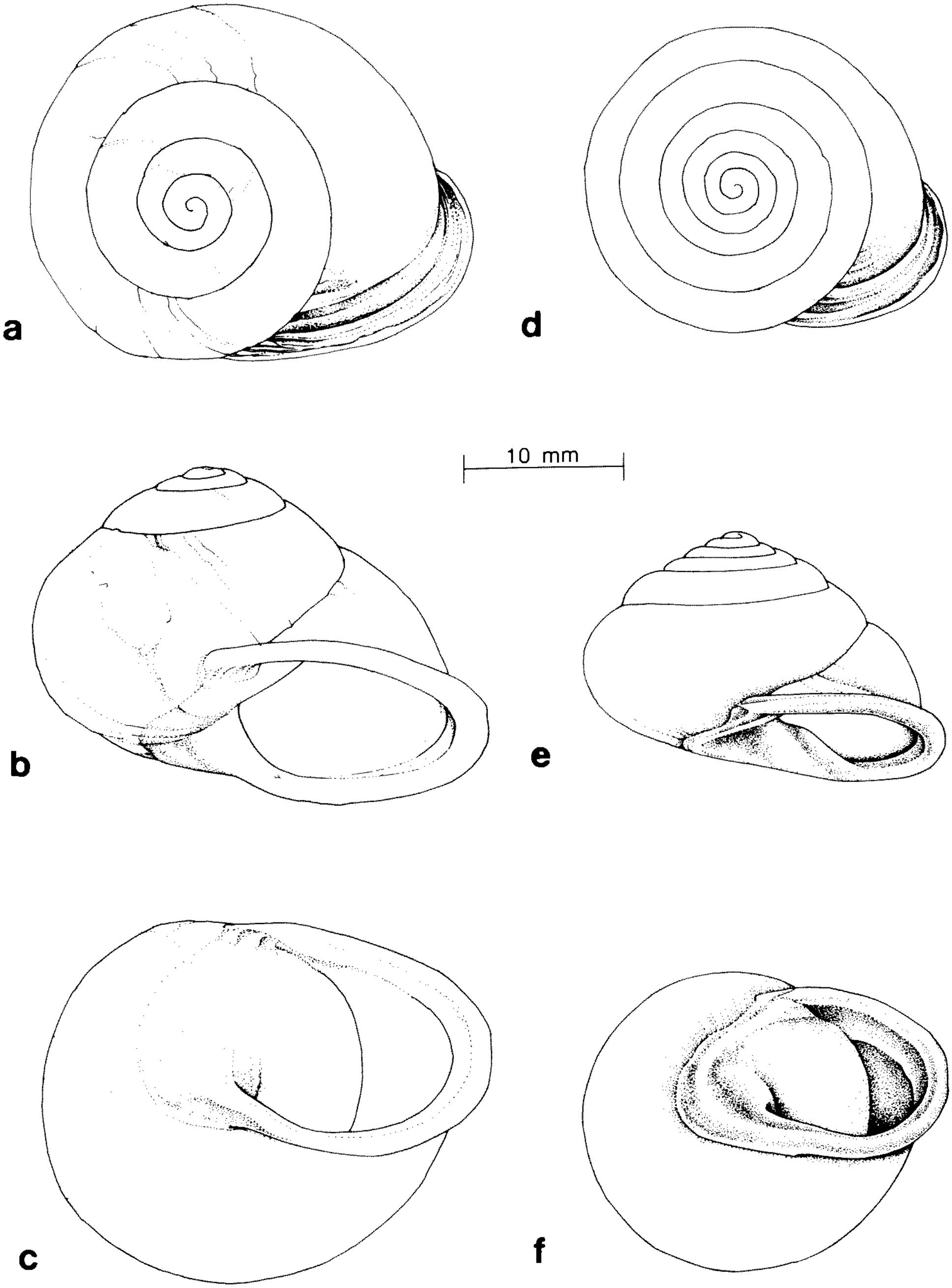


Fig. 399: Shells of *Promonturconchum superbum* sp. nov. and *Caperantrum polygyrum* sp. nov.: (a–c) Holotype of *P. superbum*. WAM 758.87, near Goat Cave, near Central Hill, Cape Range, WA; (d–f) Holotype of *C. polygyrum*. WAM 759.87, Goat Cave, near Central Hill, Cape Range, WA. Scale line equals 10 mm. Drawings by Linnea Lahlum.

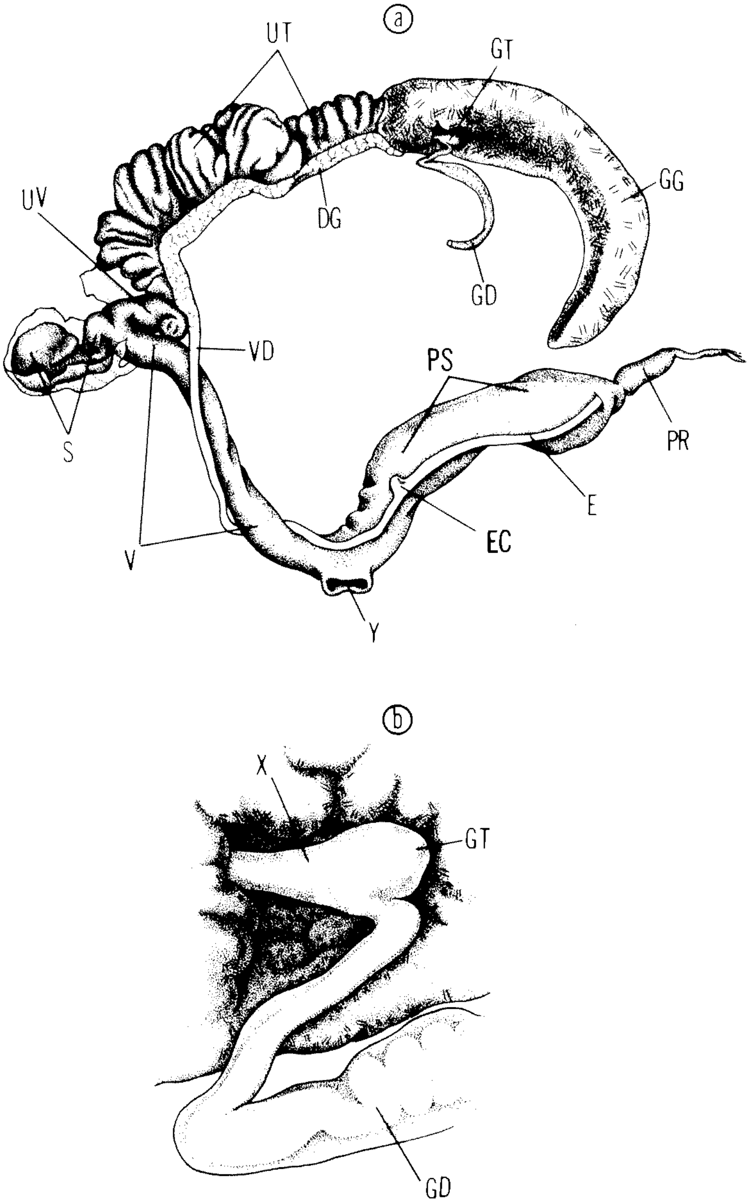


Fig. 400: Genitalia of *Promonturconchum superbum* sp. nov.: near Goat Cave, near Central Hill, Cape Range, WA. 15 May 1965. FMNH 171627, Dissection A: (a) whole genitalia; (b) detail of talon (GT) and carrefour (X). Scale line equals 5 mm. Drawings by Carole W. Christman.

Paratypes

WESTERN AUSTRALIA: Rough Range (WAM 352.74, 1 DA).

Cape Range: WAM 307.82, 5 LA; 23.7 km N of Ningaloo Homestead, W side of Cape Range (WA–23, FMNH 182304, 16 DA, 1 DJ); WA–171, FMNH 199730, 2 LA; WA–958, FMNH 212493–4, 1 DA; vicinity of Goat Cave, Central Hill (WA–16, FMNH 182493–4, FMNH 182665, 2 LA, 4 LJ; G. Hitchin & G. W. Kendrick! 15 May 1965, FMNH 182665, WAM 345.74, WAM 381.74, 7 LA, 1 LJ; WA–14, FMNH 182471, 10 DA, 2 DJ; WA–17, FMNH 182456, FMNH 182498, FMNH 182503, FMNH 182458, 4 LA, 1 DA; WA–175, 29 September 1976, WAM 897.87, SAM D18228, AM C.200,723, MV F.60056, QM 46360, FMNH 199901, FMNH 215525, 2 LA, 65 DA, 3 DJ; WA–175, 13 April 1974, WAM 896.87, SAM D18227, AM C.200724, QM 52990, MV F.59460, FMNH 199748–50, 51 LA; WA–178, FMNH 199407, 14 DA, 1 DJ; WA–959, FMNH 212494–5, FMNH 212504, 6 LA, 27 DA, 1 LJ, 1 DJ); 1.6 km N of Goat Cave (WA–960, FMNH 212505–6, 6 LA, 8 DA, 11 LJ, 1 DJ); 2.4 miles N of Goat Cave (WA–18, FMNH 182558, 5 DA); Stn. 221, S side of track from Learmonth to Cape Range (W. Turnbull! 1964, FMNH 171632, 10 DA, 4 DJ); Thomas Carter Lookout, Charles Knife Road (WA–1079, FMNH 221742–3, FMNH 221754, 12 LA, 11 DA); 8.8 km along Charles Knife Road from junction with Exmouth road (WA–176, FMNH 199428, 17 DA, 1 DJ).

Range

Promonturconchum superbum has been recorded (**Maps 28, 35**) from an unspecified locality in the Rough Range, WA and in the Cape Range from 23.7 km N of Ningaloo Homestead (22°30'S) N to Charles Knife Road (22°06'45"S). The known range is thus about 50 km long. This probably will be extended when the rest of the Cape Range is investigated for land snails.

Diagnosis

Shell very large, adult diameter 24.5–32.3 mm (mean 28.93 mm), with 4 3/8– to 5 1/4+ (mean 4 7/8–) very loosely coiled whorls. Apex and spire very strongly elevated, not rounded above (**Fig. 399b**), shell height 18.05–29.15 mm (mean 22.67 mm), H/D ratio 0.699–1.037 (mean 0.786). Body whorl evenly rounded, inflated (**Fig. 399b**). Apex (**Plate 202a**) with irregular radial ridgelets, some micropustules, spire and body whorl (**Plate 202b**) with incised spiral lines. Umbilicus closed (**Fig. 399c**) with an extended callus, or a narrow crack visible along part of columellar lip. Body whorl descending very sharply behind lip (**Fig. 399b**). Palatal and basal lips reflected, strongly expanded, with rolled edges; columellar lip broader. Parietal wall with thin callus. Shell colour yellow-brown, some live examples show a faint reddish, broad, supraperipheral spiral band. Lip white. Based on 253 measured adults.

Genitalia (**Figs 400a–b, 401a–b**) with enlarged albumen gland (GG). Talon (GT) and carrefour (X) typical. Prostate (DG) and uterus (UT) shortened. Vagina (V) very long and slender, about equal in length to penis (P). Interior of penis with a section of corrugated stimulatory pilasters (VS). Free oviduct (UV) very short, reflexed apically before uniting with spermathecal shaft. Spermatheca (S) with short shaft, globular head tightly bound to base of prostate-uterus. Vas deferens (VD) very slender, entering directly into epiphallus about one-third of way along penis. Epiphallic caecum (EC) a small lateral knob. Epiphallus (E) same diameter as vas deferens, entering penis

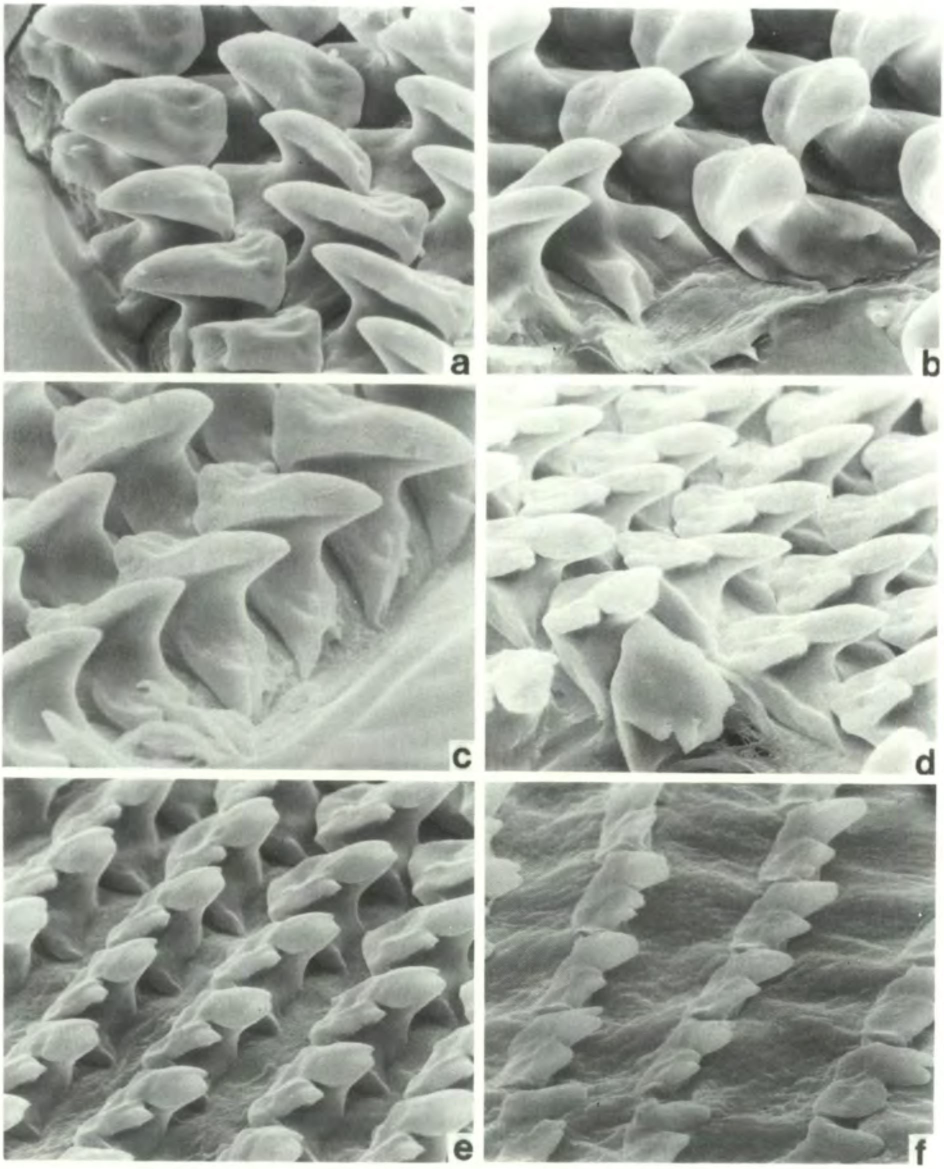


Plate 203: Radular teeth of *Promonturconchum superbum* sp. nov.: WA–16, S of Goat Cave, near Central Hill, Cape Range, WA. 17 January 1974. FMNH 182494, Dissection A: (a) central and early laterals at 610X; (b) central and early laterals at 680X; (c) late laterals at 790X; (d) latero-marginal transition at 760X; (e) early marginals at 720X; (f) outer marginals at 750X.

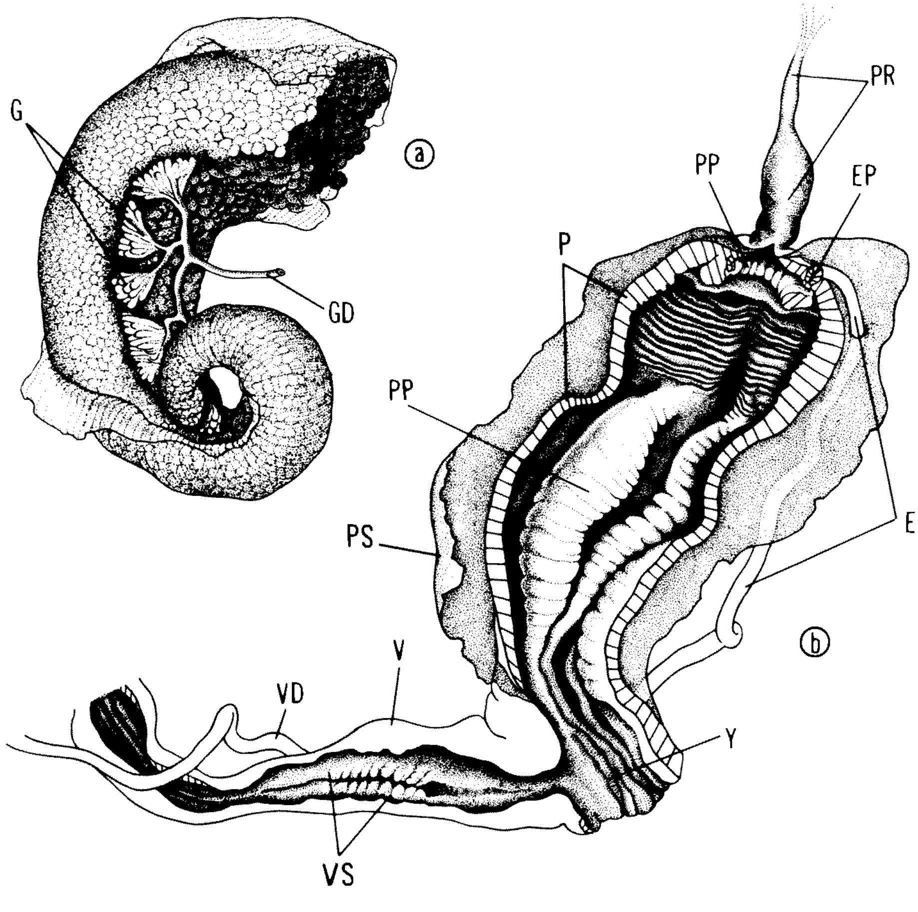


Fig. 401: Genitalia of *Promonturconchum superbum* sp. nov.: near Goat Cave, near Central Hill, Cape Range, WA. 15 May 1965. FMNH 171627, Dissection A: (a) ovotestis (G); (b) interior of penis (P) and vagina (V). Scale lines as marked. Drawings by Carole W. Christman.

sheath (PS) subapically, continuing to penis apex and then reflexing to enter apex of penis chamber through short pilasters. Penial retractor muscle inserting in an arc on epiphallus-penis junction. Penis sheath thin walled, extending from atrium (Y) to penial retractor muscle insertion. Penis thick walled, apical portion with narrow spiral pilasters adjacent to a larger spiral ridge just below entry of epiphallus. Middle portion of penis chamber with three long and corrugated pilasters (PP), basal area with simple longitudinal ridges.

Central and lateral teeth of radula (**Plate 203a–b**) with very prominent anterior flare, typical basal plate and support ridge, about 45° cusp shaft angle, cusp tip slightly curved and blunt, no ectocone present. Late laterals (**Plate 203c**) with slightly enlarged anterior flare, increased cusp shaft angle, shortened basal plate and reduced basal support ridge. Lateromarginal transition (**Plate 203d**) marked by appearance of large ectocone, loss of anterior flare and sudden shortening of basal plate, weak endoconal node on some teeth. Marginals (**Plate 203e–f**) without unusual features. Jaw (**Plate 202c–d**) with very high and usually broad vertical ribs that continue nearly to margins. Surface of ribs worn smooth, inter-rib areas showing typical fibrous composition.

Discussion

Promonturconchum superbum is smallest at the extremes of its known distribution – the Rough Range and along Charles Knife Road in the Cape Range, where mean diameter is about 27 mm. In the heart of the Cape Range (**Table 149**), it reaches 29–30 mm in mean diameter. Since all live-collected material was taken within a few metres of Goat Cave near Central Hill, no information on any possible geographic variation in genital structure can be offered.

The name *superbum* relates to the very large size and glossy colour of the shell, (which contrasts greatly with the typically dull coloured shells from this part of Western Australia), the very unusual pattern of whorl width increment and the unusual features of the genital system.

GENUS *CAPERANTRUM* GEN. N44OV.

Shell large, adult diameter 19.6 to 29.75 mm, whorls 5 5/8 to 6 7/8+, very tightly coiled. Apex and spire moderately elevated (**Fig. 399e**), rounded above, H/D ratio 0.461–0.891. Apex (**Plate 202e**) with fine, wavy radial ridgelets, upper spire with very fine radial ridglets, lower spire with radial growth lines and incised spiral lines. Body whorl evenly rounded, descending very sharply just behind lip. Umbilicus closed (**Fig. 399f**), usually with extended heavy callus. Palatal and basal lips strongly expanded, edge rolled, a long elevated knob on basal lip. Columellar lip wider, parietal wall with thick callus. Shell colour yellow-brown, fine reddish peripheral and subsutural spiral bands. Lip often with reddish-purple or pink tinge.

Specimens aestivate sealed to near-vertical surfaces in fissures or large rock rubble piles. Epiphragm a thin, lightly calcified rim.

Genitalia (**Figs 402a–b**) with huge albumen gland (GG). Talon (GT), hermaphroditic duct (GD), prostate (DG) and uterus (UT) normal. Vagina (V) equal in length to penis (P), slender, without internal corrugated pilasters. Free oviduct (UV) short, reflexed apically. Spermatheca (S) with short shaft, expanded head tightly bound to base of prostate-uterus. Vas deferens (VD) very slender, entering expanded epiphallus at a slight angle. Epiphallic caecum (EC) small. Epiphallus (E) about one-third length of penis, entering penis apically through simple pilasters. Penial retractor muscle (PR) inserts in an arc on penis-epiphallus junction. Epiphallus and vas deferens bound to penis by a sheet of connective tissue but no penis sheath present. Penis with thick walls. Upper penis chamber walls with short section of spiral pilasters, middle part with longitudinal corrugated ridges, basal section with simple pilasters.

Jaw (**Plate 202f**) with high, narrow vertical ribs that continue nearly to lateral margins. Central and lateral teeth (**Plate 204a**) with prominent anterior flare, rather high cusp shaft angle, only slight cusp tip curvature, no ectocone and blunt cusp tip. Late laterals (**Plate 204b**) with increased anterior flare, faint ectoconal trace and reduced cusp shaft angle. Lateromarginal transition (**Plate 204c**) abrupt and typical. Mid and outer marginals (**Plate 204d**) typical.

Type species: *Caperantrum polygyrum* sp. nov., by original designation.

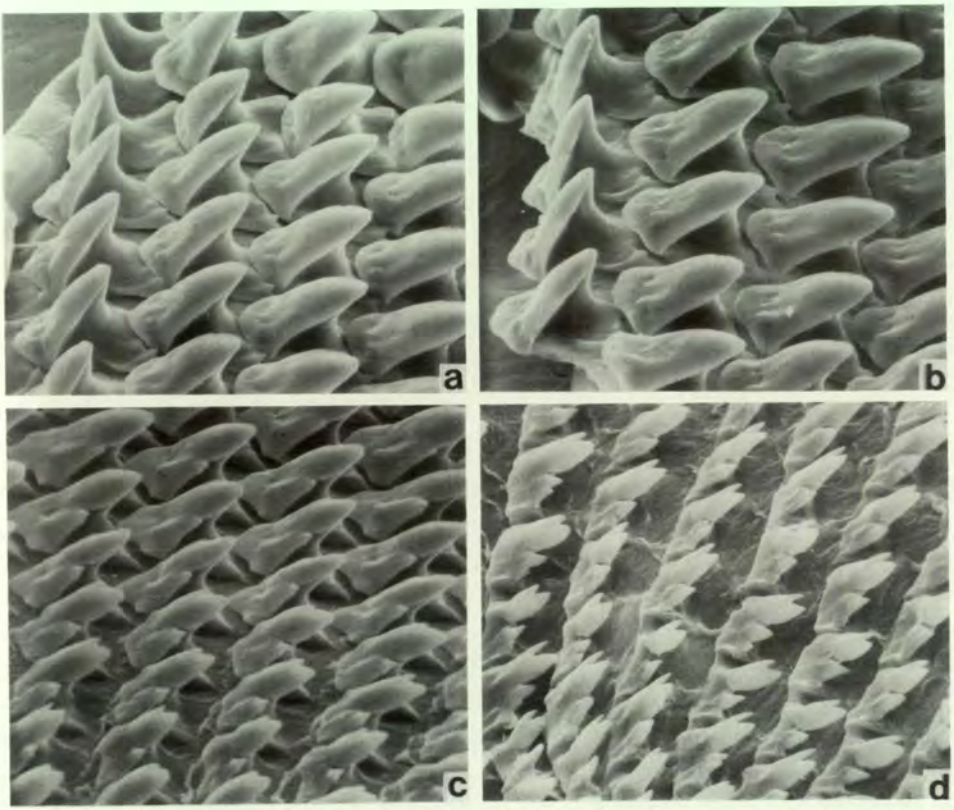


Plate 204: Radular teeth of *Caperantrum polygyrum* sp. nov.: WA–175, SE of Goat Cave, near Central Hill, Cape Range, WA. 13 April 1977. FMNH 199752, Dissection A: (a) central and early laterals at 510X; (b) late laterals at 590X; (c) latero-mrginal transition at 550X; (d) outer marginals at 600X.

Comparative remarks

Caperantrum polygyrum sp. nov. shares the unusual (for Sinumeloninae) incised spiral shell microsculpture (**Plate 202b**), apically reflexed free oviduct (UV), general pattern of penis chamber sculpture and elongated vagina (V) with *Promonturconchum superbum* (compare **Figs 400–402**), also restricted to the Cape Range. They contrast in a number of features (**Table 150**) and are ranked as genera because of these cumulative differences. The shell shape of *Caperantrum* resembles some of the Kimberley dome-shaped *Amplirhagada* (see Solem 1981a: 254, figs 55a–f), which also may have a weak basal lip knob. The shell lip structures are completely different and the genital anatomical characters of the two genera have no significant similarities.

Distribution and comparative ecology

Caperantrum polygyrum has been collected only in the Cape Range (**Maps 28, 35**), between Yardie Creek and the track to #3 Deep Well, a distance of about 20 km. This lies completely within the known range of *Promonturconchum superbum* (**Maps 28, 35**). The few live specimens have been found aestivating, sealed by a thin calcified rim epiphragm to rock faces or other shells, usually mixed in with specimens of *Promonturconchum superbum*. Large fissures may be "graveyards" for generations of these species, with a few live examples amidst hundreds of "shell bones".

No data on feeding habits are available. The radular structure is generalised (**Plate 204a–d**). All examples mounted had the lateral teeth with the higher cusp shaft angle, seen in **Plate 204a**, than is found in *Promonturconchum superbum* (**Plate 203a–b**). This difference may indicate dietary specialization by the two taxa but more material must be dissected and opportunistic feeding observations undertaken.

The name *caperantrum* is a literal translation of Goat Cave into Latin and recognises the very unusual nature of camaenid land snails found in the Cape Range.

CAPERANTRUM POLYGYRUM SP. NOV.

(Plates 202e–f, 204a–d; Figs 399d–f, 402a–c; Maps 28, 35)

Comparative remarks

Caperantrum polygyrum from a small section of the central Cape Range, WA (**Maps 28, 35**), is large (mean diameter 21.80 mm), with a moderately elevated, rounded spire (**Fig. 399e**, mean H/D ratio 0.711), tightly coiled whorls (**Fig. 399d**), increased whorl count (mean whorls 6 1/4), microsculpture of incised spiral lines, a long knob on the basal lip (**Fig. 399e**) and the lips very broadly expanded and with rolled edge. The even larger (mean diameter 28.93 mm) *Promonturconchum superbum*, also from the Cape Range (**Maps 28, 35**), has a higher spire (**Fig. 399b**, mean H/D ratio 0.786), fewer (mean 4 7/8–) and much more loosely-coiled whorls (**Fig. 399a**), the lips narrower and without a lip knob (**Figs 399a–c**). Of the other Cape Range camaenids, *Plectorhagada scolythra* has the early spire with crenulated radial ribs (**Plate 192a, c**) and the lower spire with dense micropustulations; *Quistrachia lefroyi* is smaller (**Table 160**), globose in shape, with fewer whorls, a peripheral white colour zone and pustulose microsculpture. Anatomically (**Figs 402a–c**), *Caperantrum polygyrum* is characterised by the lack of a penis sheath, apical reflexion of the free oviduct (UV), short epiphallus (E) that is larger in diameter than the vas deferens (VD) and complex wall sculpture

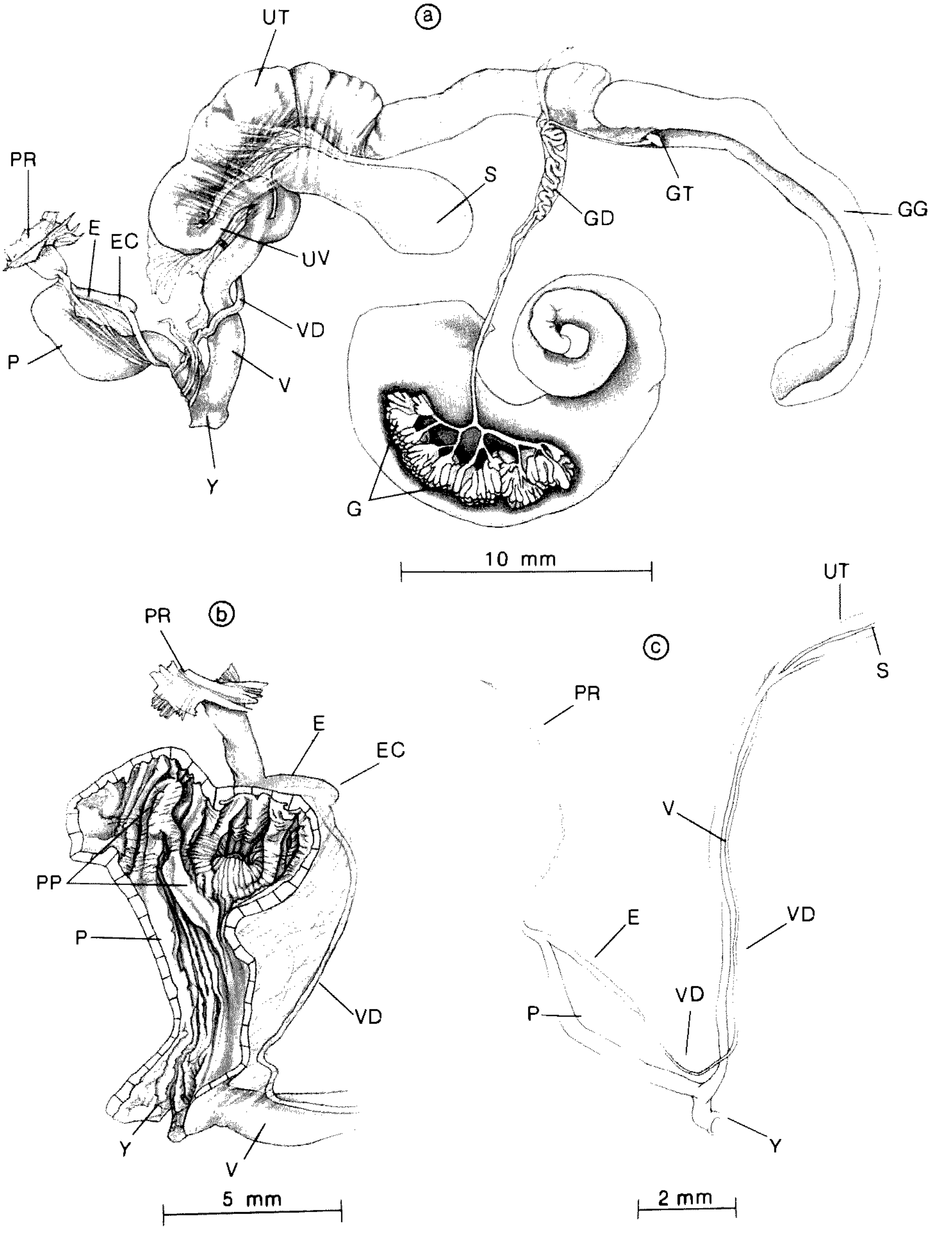


Fig. 402: Genitalia of *Caperantrum polygyrum* sp. nov.: (a–b) WA–175, Goat Cave, near Central Hill, Cape Range, North West Cape, WA. FMNH 199751, Dissections A and B. a is whole genitalia. b is interior of penis and vagina; (c) juvenile genitalia. WA–16, gully S of Goat Cave, near Central Hill, Cape Range, WA. 17 January 1974. FMNH 182494, Dissection B. Scale lines as marked. Drawings by Linnea Lahlum (a–b) and Elizabeth A. Liebman (c).

within the penis chamber. *Promonturconchum superbum* (**Figs 400–401**) is most similar but differs in having a penis sheath (PS), the longer epiphallus (E) is the same diameter as the vas deferens (VD) and the central portion of the penis chamber wall sculpture is longer and more complex. *Rhagada capensis* sp. nov. (**Figs 407–409**) has the epiphallus (E) greatly enlarged and with a long caecum (EC), an apical verge (PV) within the nearly smooth-walled penis chamber, and a much longer spermatheca (S). *Quistrachia lefroyi* sp. nov. (**Figs 436–439**) has the vas deferens (VD) entering at the base of the penis sheath (PS), the penis much longer than the sheath, and quite different penis chamber wall sculpture. *Plectorhagada scolythra* (**Figs 393a–b**) has very short terminal genitalia, no penis sheath and the penis chamber has much finer wall sculpture.

Holotype

WAM 759.87, WA–175, Goat Cave, near Central Hill, Cape Range, Western Australia; *ca.* 22°15'53"S, 113°56'18"E. Collected by Alan Solem 29 September 1976. Ex FMNH 199437. Height of shell 15.6 mm, diameter 23.2 mm, H/D ratio 0.672, whorls 6 1/4+, umbilicus completely closed by lip reflection and heavy callus.

Paratopotypes

WAM 898.87, WAM 899.87, SAM D18229, AM C.200,725, MV F.60026, QM 46367, FMNH 199437, FMNH 199747, FMNH 199751–2, FMNH 199905, 7 LA, 98 DA, 3 LJ from the type locality.

Paratypes

WESTERN AUSTRALIA: Cape Range: Yardie Creek (G. Hitchin & G. W. Kendrick! 20 May 1965, WAM 321.74, 2 DA; F. Wells! 22 June 1977, WAM 1119.81, 2 DA); Goat Cave, near Central Hill (WAM 313.74, 5 DA); WA–14, FMNH 182469, 12 DA, 1 DJ; WA–17, FMNH 182651, 1 DA; WA–18, FMNH 182556, 3 DA; WA–174, FMNH 199867, 2 DA; WA–178, FMNH 199408, 8 DA, 3 DJ; WA–959, WAM 900.87, SAM D18230, AM C.200,726, MV F.60017, QM 46368, FMNH 212496, FMNH 212502, 1 LA, 64 DA, 1LJ, 16 DJ); Stn 221, S side of track from Learmonth to Cape Range, W. Turnbull! 1964, FMNH 171634, 12 DA, 3 DJ); along track to #3 Deep Well (P. Cawthorne! 5 August 1962, WAM 316.74, 3 DA).

Range

Caperantrum polygyrum has been found in the Cape Range, WA (**Maps 28, 35**) between Yardie Creek and the track to #3 Deep Well, a distance of perhaps 20 km. It is rarer than *Promonturconchum superbum*, which occurs at the same localities but has an extended range both N and S.

Diagnosis

Shell large, adult diameter 19.6–29.75 mm (mean 21.80 mm), with 5 5/8 to 6 7/8+ (mean 6 1/4) very tightly coiled whorls (**Fig. 399d**). Apex and spire moderately elevated (**Fig. 399e**), somewhat rounded above, shell height 13.2–20.7 mm (mean 15.48 mm), H/D ratio 0.461–0.891 (mean 0.711). Body whorl evenly rounded, not inflated (**Fig. 399e**). Apex (**Plate 202e**) with very fine irregular radial riblets. Upper spire with fine radial growth ridgelets, lower spire and body whorl with irregular growth ridglets and incised spiral lines. Umbilicus closed (**Fig. 399f**), with an extended columellar callus. Body whorl descending very sharply just behind lip (**Fig. 399e**). Palatal and basal lips reflected, very broadly expanded, edge rolled. Columellar lip wider, parietal wall with heavy callus. Shell colour yellow-brown, fresh examples with narrow red, mid-palatal and subsutural spiral bands. Lip often with purple-red to pinkish colour tinge. Based on 229 measured adults.

Genitalia (**Figs 402a–c**) with huge albumen gland (GG), vagina (V) slender, equal in length to penis (P), internally with simple longitudinal ridges. Free oviduct (UV) short, reflexed apically. Spermatheca (S) with short shaft, expanded head tightly bound to base of prostate-uterus, which is normal in length. Vas deferens (VD) slender, entering expanded head of epiphallus (E) at an angle, epiphallic caecum (EC) small. Penis (P) long, club-shaped. Epiphallus about one-third length of penis, entering latter apically through a cluster of short pilasters. Penial retractor muscle (PR) inserting in arc on epiphallus-penis junction. No penis sheath present but epiphallus and vas deferens loosely connected to penis by a sheet of connective tissue. Penis chamber wall with short apical area of spiral pilasters, middle portion with longitudinal corrugated pilasters, basal section with simple longitudinal pilasters.

Central and lateral teeth of radula (**Plate 204a**) with large anterior flare, very high cusp shaft angle, bluntly pointed and only slightly curved cusp tip, no trace of ectocone. Late laterals (**Plate 204b**) with increased anterior flare, reduced cusp shaft angle and shortened basal plate. Lateromarginal (**Plate 204c**) and marginal (**Plate 204d**) teeth typical. Jaw (**Plate 202f**) with high, narrow vertical ribs that extend nearly to lateral margins.

Discussion

Caperantrum polygyrum shows only minor size and shape variation (**Table 149**), which is not surprising considering that essentially all of the larger samples were taken in the vicinity of Goat Cave near Central Hill, Cape Range.

The name *polygyrum* refers to the increased whorl count of this species, which is very unusual for any member of the subfamily Sinumeloninae.

SUBFAMILY PLEURODONTINAE VON IHERING, 1912

The presently confirmed Australian distribution (**Map 62**) of this subfamily is:

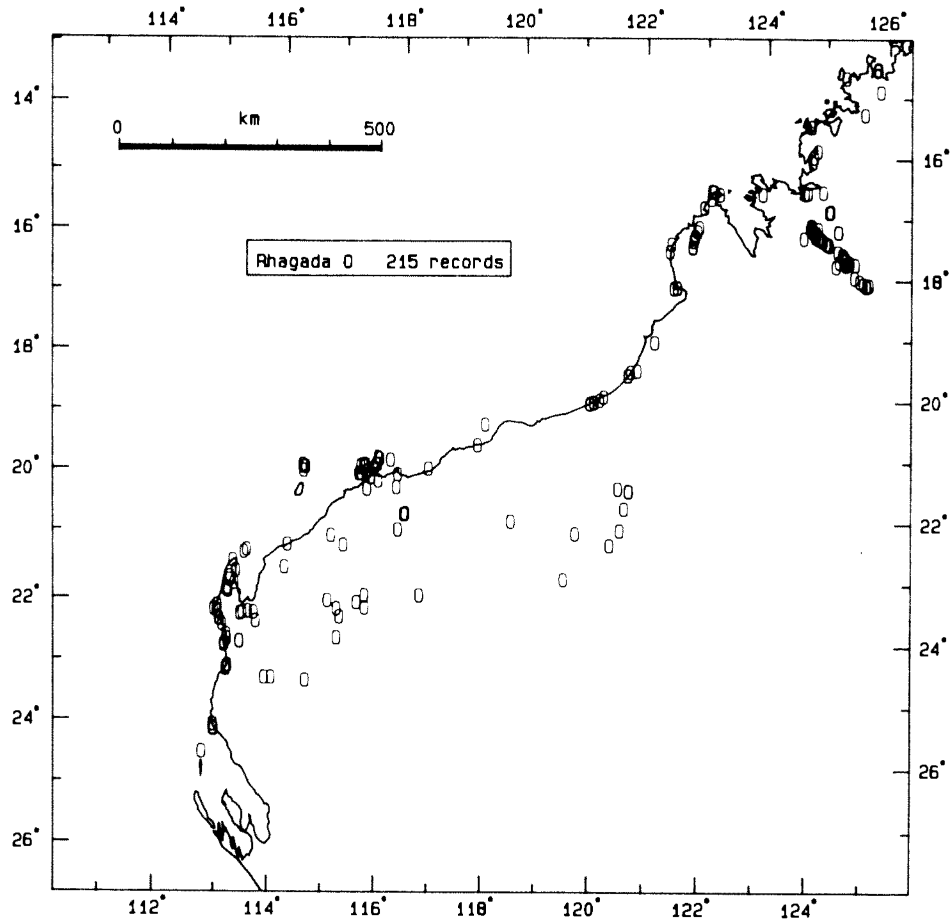
1) the Red Centre (see Part VI), where there are two highly modified monotypic genera, *Vidumelon* Iredale, 1937 and *Divellomelon* Iredale, 1937; a modified genus, *Dirutrachia* Iredale, 1937, with three scattered species with short ranges; and one widely distributed genus, *Semotrachia* Iredale, 1933 (+ *Catellotrachia* Iredale, 1933 and *Spernachloritis* Iredale, 1933), with 25 known species and probably another 25 still be be discovered and described;

2) the Mitchell Plateau to Shark Bay range of *Rhagada* Albers, 1860 that is delineated below.

The differences between these genera will be discussed, in part, below relative to gross climatic shifts and elsewhere, as more extralimital taxa can be assigned here.

GENUS *RHAGADA* ALBERS, 1860

Rhagada Albers, 1860, *Die Heliceen nach natürlicher Verwantschaft, Zweite Ausgabe (Eduard von Martens)*. Leipzig: Engelmann. pp. 108–109 – type species *Helix reinga* 'Gray' Pfeiffer, 1846 by original designation; Pilsbry, 1890, *Man. Conch.*, (2) **6:** 185–191 – review of species; Pilsbry, 1894, *Man. Conch.*, (2) **9:** 135–136 – as subgenus of *Thersites* Pfeiffer, 1855; Hedley, 1916, *Jour. Roy. Soc. Western Aust.*, **1:** 69–70 – check list of species, including many now referred to other genera; Iredale, 1938, *Aust. Zool.*, **9** (2): 112–113 – check list of species; Iredale, 1939, *Jour. Roy. Soc. Western Aust.*, **25:** 58–63 – monograph of WA species; Zilch, 1960, *Handbuch der Paläozoologie, Gastropoda, Euthyneura*, **6**, 2 (2): 616 – as a subgenus of *Thersites* Pfeiffer, 1865; Solem, 1985, *Rec. Western Aust. Mus.*,



Map 36: Records of *Rhagada* in WA.

Table 151: Range of variation in *Rhagada*.

Taxon	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Rhagada torulus	347	11.77 (8.45-14.65)	14.29 (12.0-17.2)	0.823 (0.679-0.966)	$5\frac{1}{4}$ ($4\frac{3}{8}$-$5\frac{5}{8}$+)
R. globosa	269	10.01 (8.02-12.1)	12.36 (10.1-14.5)	0.810 (0.692-0.960)	$4\frac{3}{4}$+ (4-$5\frac{5}{4}$)
R. capensis	488	15.10 (12.55-20.7)	20.01 (16.95-24.25)	0.775 (0.623-0.991)	$5\frac{3}{4}$ ($4\frac{5}{8}$-$6\frac{3}{4}$+)
R. convicta	721	15.29 (12.9-18.65)	20.15 (16.55-23.95)	0.759 (0.671-0.906)	$5\frac{1}{2}$ (5–-$6\frac{5}{8}$–)
R. pilbarana	55	17.30 (15.8-19.15)	22.97 (21.05-25.35)	0.753 (0.691-0.846)	6 ($5\frac{3}{4}$+-$6\frac{3}{8}$–)
R. perprima	18	14.90 (9.25-18.0)	19.84 (15.8-22.3)	0.746 (0.585-0.821)	$5\frac{5}{8}$+ (5+-$6\frac{1}{4}$–)
R. richardsoni	278	13.35 (9.05-17.05)	17.79 (14.4-22.9)	0.749 (0.585-0.833)	$5\frac{1}{4}$ ($4\frac{1}{4}$-6+)
R. radleyi	127	11.58 (8.5-14.8)	16.64 (13.6-19.7)	0.693 (0.573-0.853)	$5\frac{1}{8}$ ($4\frac{1}{2}$-$5\frac{3}{4}$–)
R. plicata	70	7.85 (6.6-9.55)	10.35 (9.0-12.05)	0.758 (0.673-0.839)	$4\frac{5}{8}$+ ($4\frac{1}{4}$–-$4\frac{7}{8}$+)
R. minima	65	8.37 (6.55-10.2)	11.81 (10.15-13.65)	0.702 (0.585-0.842)	$4\frac{3}{4}$+ ($4\frac{1}{4}$-$5\frac{5}{8}$)
R. intermedia	104	8.75 (7.5-10.5)	11.69 (9.95-14.85)	0.749 (0.669-0.849)	$4\frac{5}{8}$– ($4\frac{1}{8}$+-$5\frac{1}{8}$)

Table 151: Range of variation in *Rhagada* (continued)

Taxon	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
R. aff. elachystoma	28	11.10 (9.3-13.3)	15.23 (13.9-17.55)	0.735 (0.644-0.848)	5 (4 5/8-5 3/8+)
R. elachystoma	77	10.09 (8.7-12.05)	14.04 (11.85-17.55)	0.740 (0.640-0.848)	4 7/8– (4 1/2-5 3/8+)
R. angulata	48	7.77 (6.0-10.95)	13.61 (11.85-17.1)	0.742 (0.640-0.822)	4 3/4 (4 1/2-5 1/4)
R. dampierana	109	7.80 (6.1-10.15)	18.08 (15.8-22.45)	0.416 (0.349-0.571)	4 7/8– (4 1/4-5 1/2–)
R. dringi	218	8.26 (6.85-10.95)	12.31 (10.65-14.9)	0.671 (0.591-0.794)	4 5/8+ (4 1/4–-5 3/8+)
R. reinga	64	9.08 (7.95-10.75)	12.48 (10.95-13.9)	0.728 (0.665-0.815)	5 1/8 (4 3/4+-5 3/8+)
R. bulgana	398	10.91 (7.95-14.9)	14.35 (11.15-18.3)	0.760 (0.657-0.889)	5 1/2 (4 3/4-6 3/8+)
R. cygna	153	8.95 (7.55-11.0)	11.75 (10.1-14.0)	0.762 (0.657-0.886)	5 1/8 (4 5/8+-5 5/8–)

Suppl. **20:** 875–919, figs 222–235, plates 89–92, tables 89–91 – monograph of Kimberley species; Richardson, 1985, *Tryonia*, **12:** 264–268 – check list.

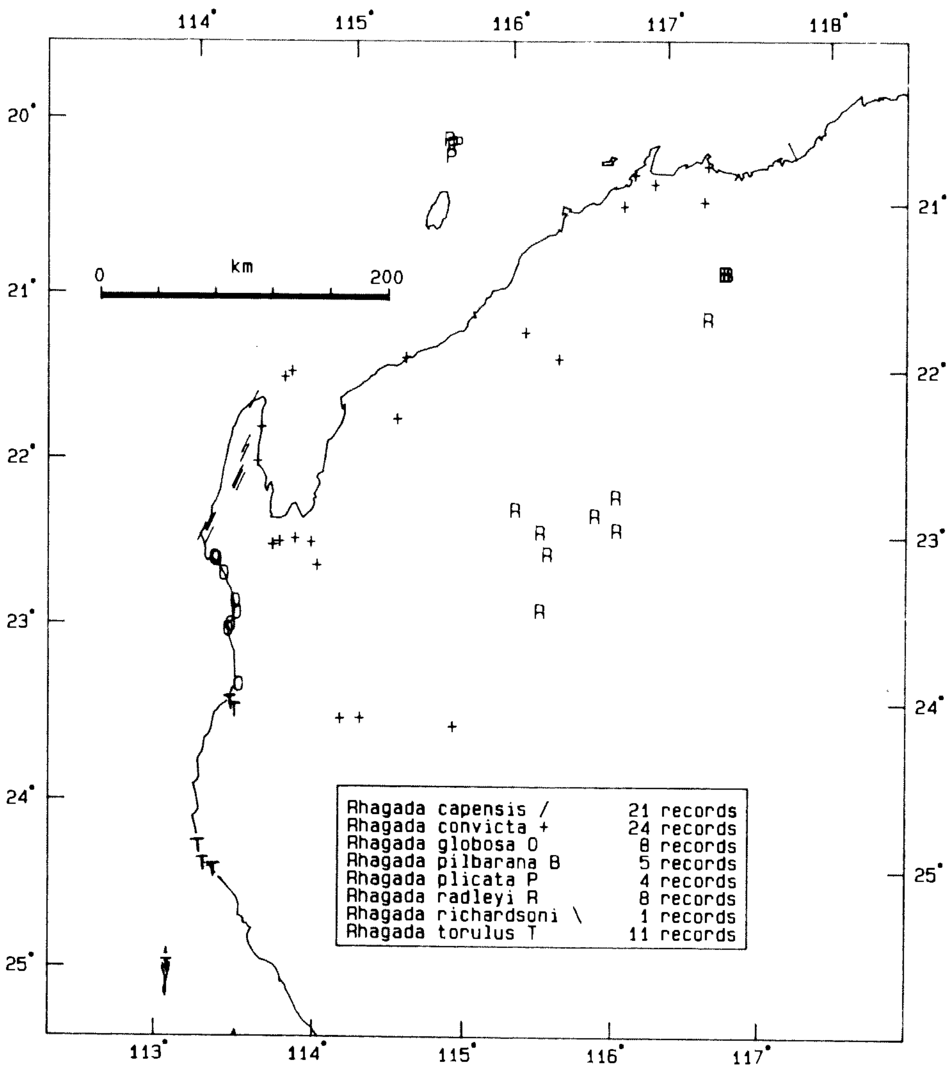
Bellrhagada Iredale, 1938, *Aust. Zool.* **9** (2): 114–115 – type species *Rhagada plicata* Preston, 1914 by original designation; Iredale, 1939, *Jour. Roy. Soc. Western Aust.*, **25:** 71–72 – review of species; Richardson, 1985, *Tryonia*, **12:** 65 – check list citation.

Tumegada Iredale, 1939, *Jour. Roy. Soc. Western Aust.*, **25**: 62 – a new subgenus, *Helix convicta* Cox, 1876 type species by original designation.

Shell small to large in size, quite variable, adult diameter 9.0–25.65 mm, whorls 4 to 6 3/4, coiling pattern depends upon spire elevation, from nearly flat in *dampierana* sp. nov. (**Fig. 422e**) to globose in the more southern species (*torulus*, **Fig. 403e**, *globosa* sp. nov., **Fig. 403g**), most with moderately to strongly elevated spires, some rounded above, H/D ratios 0.349–0.991. Apical sculpture (**Plates 205–210**) absent or very weak, spire and body whorl with either radial ridgelets (**Plates 205e–f, 206a–b, d–f**, etc) or prominent radial ribs (**Plates 207–209**) that may continue onto the shell base (**Plate 208c**). Microsculpture of all species consists of short to medium length, irregular periostracal ridgelets (**Plates 206c, 207c, 209c–d, 210b–c**) that overlie vague calcareous undulations that are much wider (**Plate 209d**). Body whorl evenly rounded in most species, sometimes weakly angulated in *minima* sp. nov. and *intermedia* sp. nov., obtusely angulated in *angulata* sp. nov. (**Fig. 422b**), and with a protruded keel in *dampierana* sp. nov. (**Plate 208c, Fig. 422e**). Body whorl descending slightly (**Figs 429b, e**) to rather strongly (**Figs 406b, 411b**) behind aperture, which may be somewhat narrowed by a combination of descent and thickening (**Figs 403e, 416b**). Umbilicus normally closed, with a greatly expanded columellar callus, some species with a columellar lip ridge, others with a narrow lateral crack, a few with distinctly open umbilicus (**Fig. 422c**, Solem, 1985: 879, fig. 223f; 881, fig. 225c). Degree of lip reflection and expansion highly variable among species. Weak basal lip knob occasionally present in more northern taxa from Dampier Land and the Kimberley. Shell colour basically white, with two prominent red spiral bands, supraperipheral and subsutural, that may be joined by narrower accessory bands of red to orange in many species (**Figs 406b, 414b, 416f**). Occasionally these secondary bands may be widened. A few taxa have a reddish suffusion on the apex that may extend to cover the entire spire (**Figs 427, 429e**). Lip white.

Specimens aestivate burrowing into sandy soil, in litter under spinifex or bushes, less frequently in rock rubble. Live specimens have been collected from lawns, by the shaded sides of termite mounds and under isolated trees (in the 80 Mile Beach area). A calcified epiphragm is secreted across the shell aperture. Multiple epiphragms have not been observed.

Genitalia basically conservative (Solem, 1985: figs 227–235) (**Figs 404, 405, 407–410, 412–413, 415, 417, 419, 421, 423–424, 426, 428, 430–431**). Major variations correlate with shifts in moisture patterns from the monsoonal Kimberley to desert-like Shark Bay region. Ovotestis (G) shows no seasonal size variation, number of alveolar clusters highly variable. Albumen gland (GG) small in Kimberley and Dampier Land, massive in North West Cape to Shark Bay area. Prostate (DG) and uterus (UT) greatly shortened in areas where albumen gland is enlarged. Spermatheca (S) short to long, simple to tightly kinked in different species. Free oviduct (UV) normally short, often curved. Vagina (V) short to medium in length. Epiphallic caecum (EC) highly variable in length. Epiphallus (E) long, coiled. Penial retractor muscle (PR) inserts on epiphallus a short to moderate distance beyond penis apex. Penis (P) short to long, often expanded apically. Penis sheath absent, but often a sheet of fibres connects epiphallus and penis. Verge (PV) massive and smooth-surfaced with prominent sperm groove in Kimberley and Dampier Land taxa, reduced in *dringi* from 80 Mile Beach, greatly reduced in more southerly species, varying from dome-shaped (*intermedia* sp.



Map 37: Records of *Rhagada capensis*, *R. convicta*, *R. globosa*, *R. pilbarana*, *R. plicata*, *R. radleyi*, *R. richardsonii* and *R. torulus* from Cape Keraudren S to the Shark Bay area, WA.

nov., **Fig. 421b**) to conical (*angulata* sp. nov., **Fig. 423b**) to cylindrical (*capensis* sp. nov., **Fig. 408a**), rarely secondarily elongated (*pilbarana* sp. nov., **Fig. 412b**), surface smooth to corrugated (**Fig. 410b**), sperm groove generally short and inconspicuous. Head wart permanently exposed, absent in juveniles, first appearing in subadults, small to large, mostly circular to ovate, occasionally elongated (Solem, 1985: 914, fig. 233c). Pustules of wart usually grey, slightly to much darker in tone than surrounding skin areas, except in *capensis* sp. nov. where the body colour may be black. Body colour yellow-white in all other Dampier Land to Shark Bay and Kimberley species.

Jaws vary geographically. Kimberley species (Solem, 1985: 892, plate 89) mostly have broad vertical ribs over much of the jaw, showing rib size and number reduction only in *harti*. Most Dampier Land taxa (**Plates 224d, 225b, f**), except for *cygna* sp. nov. (**Plate 226f**), retain relatively standard ribbing but rib numbers and width are slightly (*dringi*, **Plate 223d**) to drastically reduced in more southern species. Only a few narrow ribs, located in the middle portion of the jaw, remain (**Plates 211f, 212c, 213f, 215a–f, 218c, f219b, d, f, 220d**). Reduction of jaw ribbing is carried furthest in *capensis* sp. nov. (**Plate 215a–c**), which has specialised radular teeth. Central and lateral teeth of radula vary in prominence of anterior flare and ectocone, cusp shaft angle, degree of cusp curvature, sharpness of cusp tip, and basal plate length (**Plates 211–214, 216–226**), with the greatest alteration seen in *capensis* (**Plates 213a–d, 214a–f, 231d–f**).

Type species: *Helix reinga* 'Gray' Pfeiffer, 1846 by original designation.

Comparative remarks

The unusual periostracal microsculpture (**Plate 210b–c**), smooth or nearly smooth shell apex (**Plates 205–210**), lack of micropustules on the shell surface and simple radial ribs (when present) are the few conchological features that distinguish *Rhagada* from *Quistrachia* or any of the west coast Sinumeloninae. Species of *Rhagada* with many accessory spiral colour bands are easily recognised but species in which the colour banding is reduced to the supraperipheral and possibly only a slight subsutural band can be (and are) confused easily with such species as *Quistrachia warroorana* sp. nov. (**Figs 433a–c**), *Q. leptogramma* (Pfeiffer, 1846) (**Figs 447a–c**), *Plectorhagada rovina* (Iredale, 1939) (**Figs 388a–c**) or *P. scolythra* (**Figs 390d–f**).

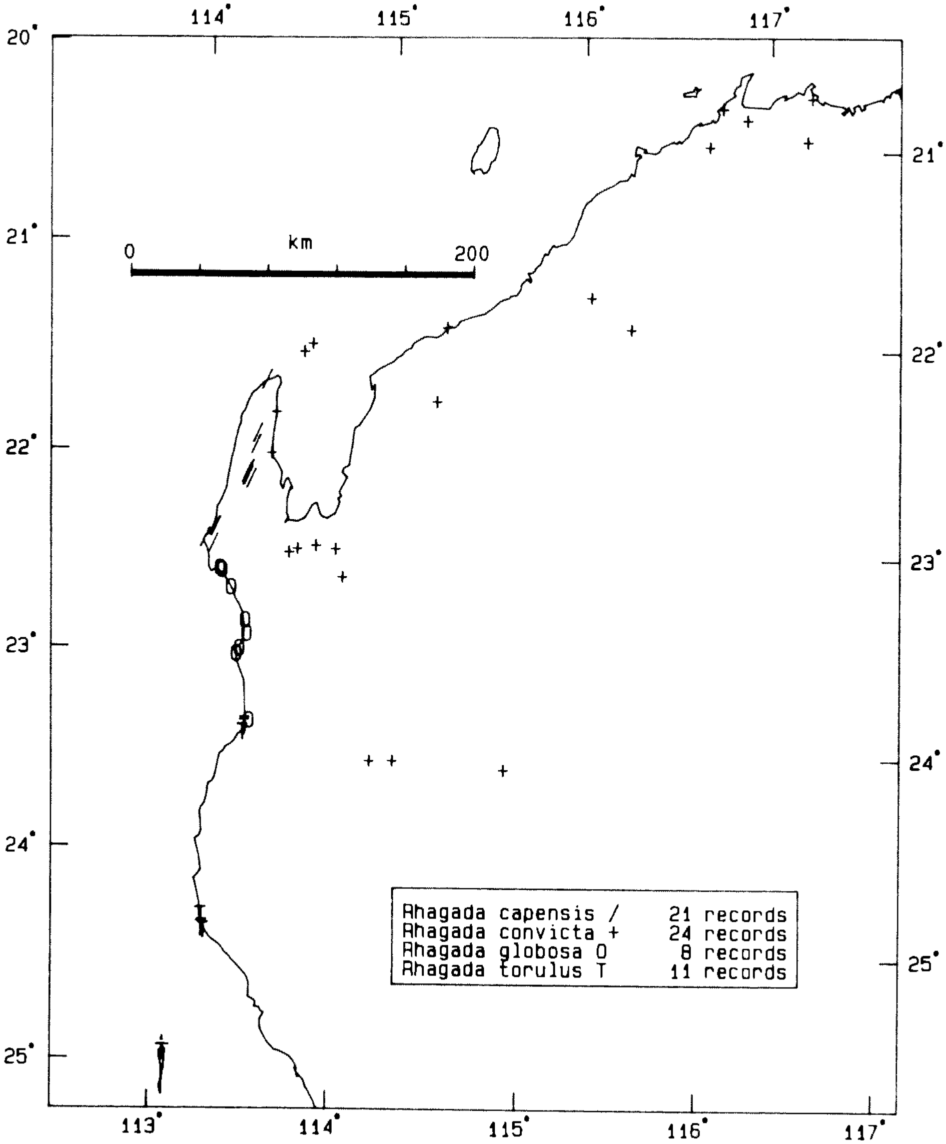
Quistrachia (**Plates 227–228**) has mostly pustulose apical sculpture and several types of distinctive post-apical sculpture. It is readily separated by the genital features – absence of a verge, epiphallus and epiphallic caecum; presence of a well developed penis sheath; entry of the vas deferens into the base of the penis sheath and insertion of the penial retractor muscle on the vas deferens-penis junction.

The various sinumelonine genera substitute stimulatory pilasters for vergic structure, have a generally short epiphallus and minute epiphallic caecum, the penial retractor muscle insert on the penis apex and a short, simple spermatheca.

The other Australian Pleurodontinine genera are restricted to the Red Centre (**Map 62**) and have recently been monographed in Part VI (Solem, 1993). They have a generally long spermatheca that reaches to the base of the albumen gland, except in *Vidumelon wattii* (Tate, 1894), in which extraordinary whorl number increase has elongated the prostate-uterus more than the albumen gland (Solem, 1993: fig. 365a), resulting in a separation between the albumen gland base and spermathecal head. The shells of the Red Centre genera differ in shape, size, sculpture and colour but the basic pattern of the genitalia agrees with that of *Rhagada*.

Previous studies and nomenclature

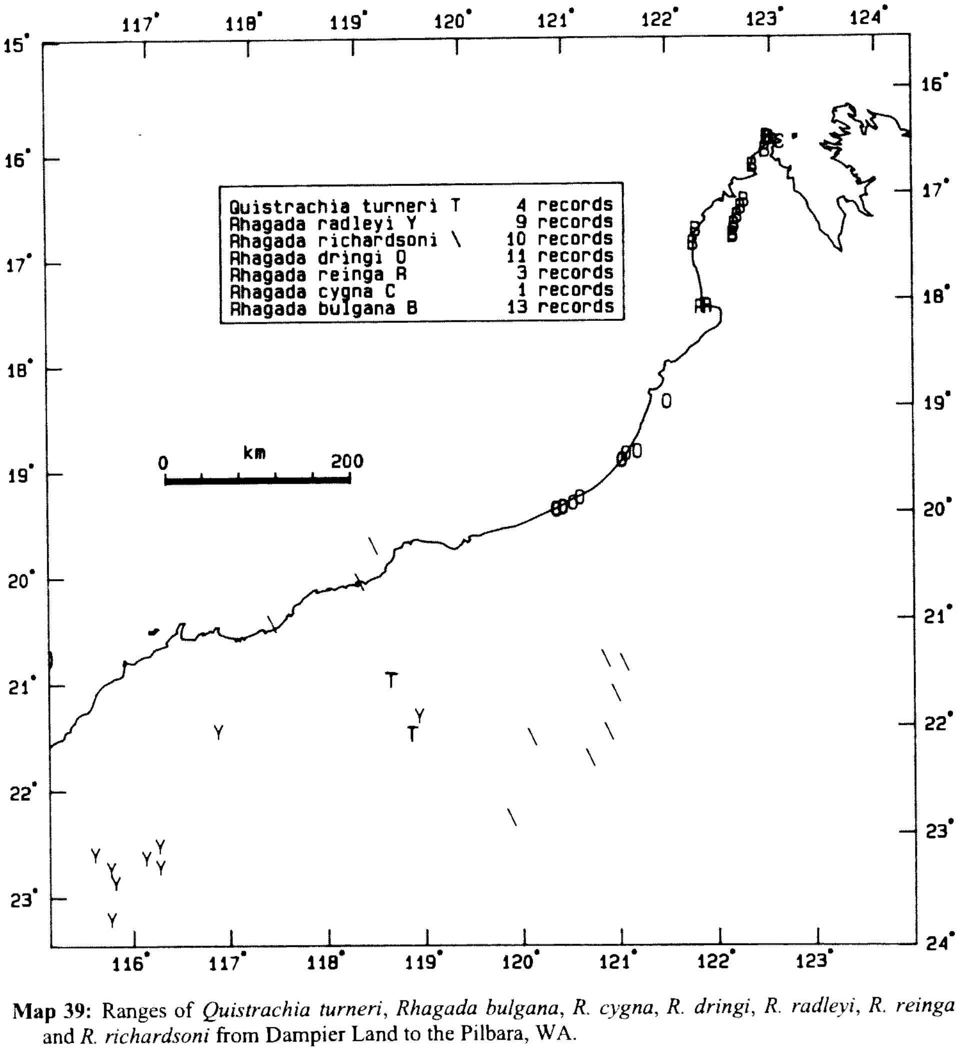
The early review by Pilsbry (1890: 185–191) was not updated until the conchological



Map 38: Records of *Rhagada capensis*, *R. convicta*, *R. globosa* and *R. torulus* from Cossack to the Shark Bay area, WA.

monograph by Iredale (1939: 58–63). In the intervening years, scattered descriptions of Australian species by Preston (1908, 1914) and several Indonesian species (that probably are convergent) added some data. Iredale (1938: 114–115) proposed the generic name *Bellrhagada* for those species with radial ribs on the spire and, a year later, the uncharacterised subgeneric name *Tumegada* Iredale (1939: 62) for *R. convicta* (Cox, 1876). Solem (1985: 875–919) reviewed the Kimberley *Rhagada*, describing three new species and noting the presence of another probable new species in the Prince Regent River Reserve.

There is little to add to the data given in Solem (1985: 875–876) regarding previous publications, reassignment of misclassified species and the questionable affinities of Indonesian taxa. SEM photos of *Rhagada supracostulata* Schepman, 1892 (**Plate**



Map 39: Ranges of *Quistrachia turneri, Rhagada bulgana, R. cygna, R. dringi, R. radleyi, R. reinga* and *R. richardsoni* from Dampier Land to the Pilbara, WA.

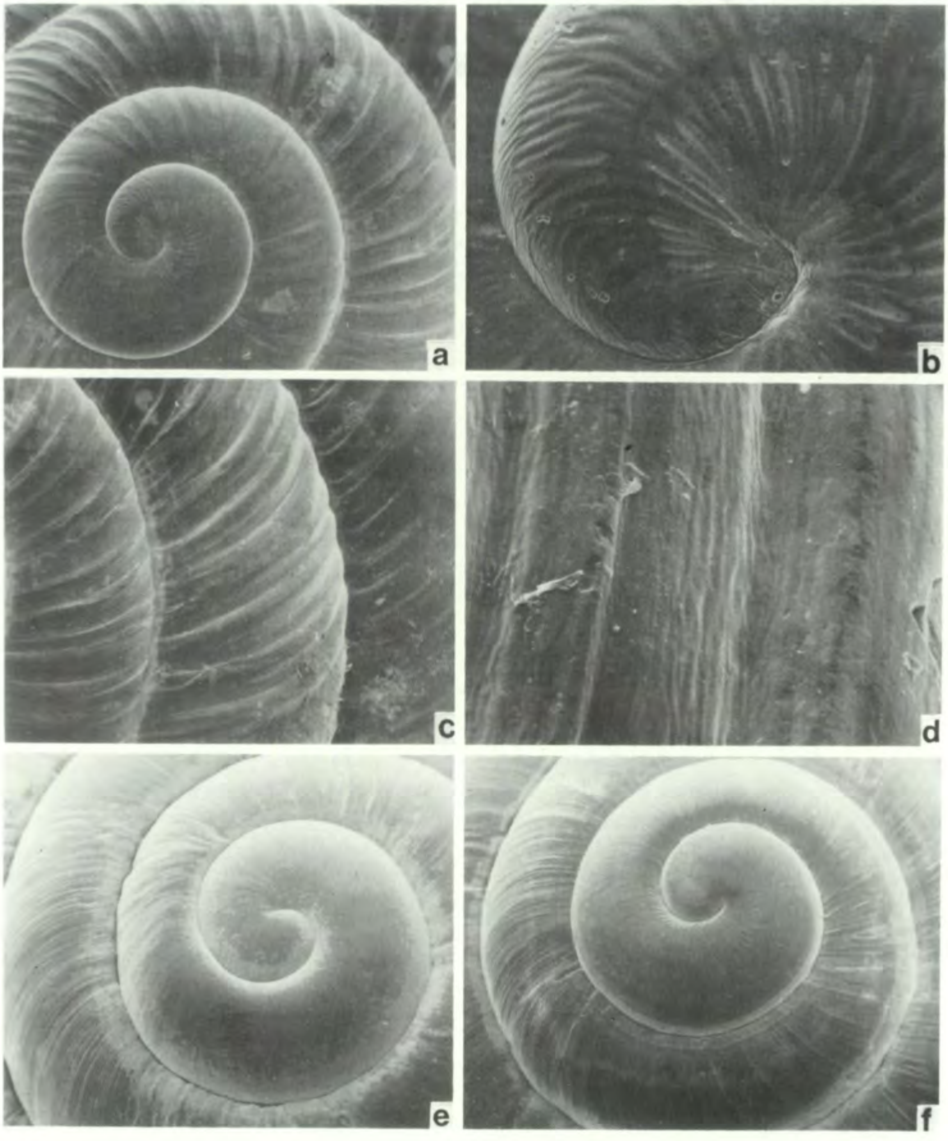


Plate 205: Shell sculpture in "*Rhagada*" *supracostulata* Schepman, 1892, *Rhagada torulus* (Férussac, 1819) and *R. globosa* sp. nov.: (a–d) "*R*". *supracostulata*. Sumba, Indonesia. FMNH 41308 ex W. F. Webb. a is apex and spire at 17.4X. b is detail of apical sculpture at 86X. c is spire sculpture at 16.3X. d is micro-sculpture on body whorl at 160X; (e) *R. torulus*. WA–52, Point Quobba, N of Carnarvon, WA. FMNH 182590, Dissection A. e is apex and spire at 19.1X; (f) *R. globosa*. Bill Bay, Cardabia Station, S of North West Cape, WA. WAM 385.74, Dissection C. f is apex and spire at 17.3X.

205a–d) show far stronger apical sculpture, less clearly defined and wider spaced radial ribbing and a lack of the periostracal microsculpture that characterises (**Plate 207c**) the Australian species of *Rhagada*. This is the most "*Rhagada*"– like of the Indonesian taxa, yet the above features, form of the shell lip and pattern of umbilical opening are not typical of *Rhagada*. Despite the lack of any anatomical data, I now am even more inclined to consider that they are convergent taxa.

Two older names do present some problems. *Rhagada reinga* (Pfeiffer, 1846) is here associated with populations from Broome, although with some hesitation. It is the type species but no original specimens could be located. *Helix tescorum* Benson, 1853 (see Iredale, 1939: 62 for previous references) was described from Shark Bay. No remotely similar shell has been found there subsequently. Both description and early illustrations suggest that it could be a badly weathered subfossil example of the *convicta–capensis* group. Sand dune examples of these taxa show the same canaliculated suture as the result of probable wind-blown sand erosion. Indeed, I have left a trail of temporary labels in museums around the globe suggesting this very synonymy. But in the absence of its type and the failure to locate this morph in the Shark Bay area, it seems best not to assign it to any set of populations.

Distribution and basic ecology

Rhagada is thus considered to be an Australian endemic. The total of 29 species reviewed from the Kimberley (Solem, 1985b, 1991) and in this monograph, combine to make *Rhagada* the second most diverse camaenid genus in WA, second only to the Kimberley endemic *Amplirhagada*.

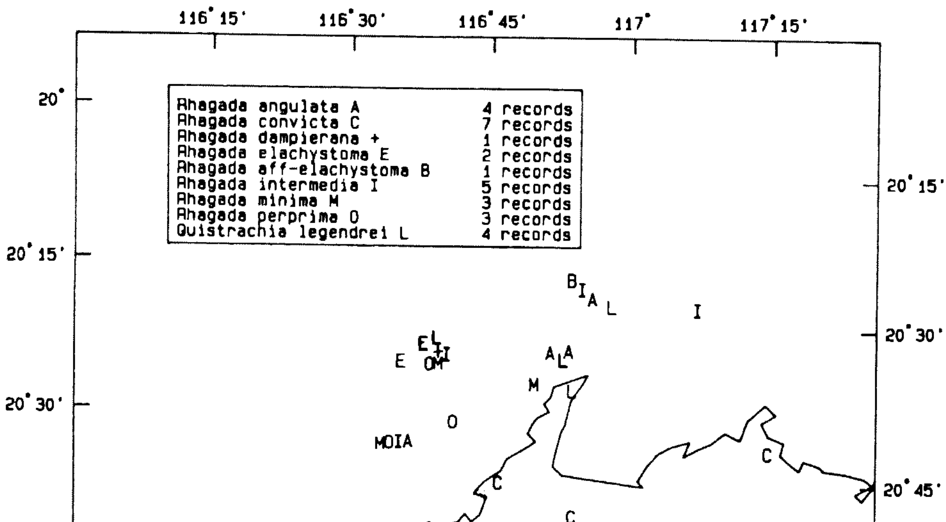
From the 1880's at least through the 1910's, species of *Rhagada* were very common along the Napier and Oscar Ranges in the southern Kimberley (**Map 42**). Their decline in numbers since then results from destruction of vegetation by unwarranted deliberate burning (=pyromania) (Solem, 1985b: 876–877).

Scattered records (**Map 41**) exist for the West Kimberley but nowhere are colonies abundant. *Rhagada crystalla* Solem (1985: 915–919, figs 226a–c, 234a–b, 235a–b) from the Mitchell Plateau is the northernmost known form. There are undescribed morphs from the Prince Regent River Reserve (Solem, 1985: 919) and similar shells from near Bigge Island (RFS 05–2) and Augustus Island (RFS 26–1), a large smooth-surfaced shell from the W coast of George Water (RFS 22–3) and a form similar to *R. dringi* in shape and sculpture that was moderately common from George Water to S of Walcott Inlet (RFS 21–3, RFS 23–1, RFS 23–4a, RFS 30–1, RFS 30–2). Three long dead examples from Wilson Spring (16°59'S, 123°46'E), Kimbolton (WAM 8.87, W. H. Butler! 1 September 1975) may belong to the same group. The above material will be reviewed elsewhere.

The material reviewed below ranges from the N tip of Dampier Land through Bernier Island, Shark Bay. **Maps 37–41** summarise the ranges of the 18 recognised species. Others undoubtedly exist. Records of a ribbed species from Barrow Island (WAM 237.74, D. L. Serventy! 19 September 1958, 1 DA; WAM 232.74, L. Smith! August 1973, 1 DA; WAM 284.82, N coast between Surf Point and Cape Dupuy, G. W. Kendrick! 26 September 1981, 3 DA) are sparse, but believable by their number. A set (WAM 295.74, G. W. Kendrick! 28 May 1965) from 4 miles WNW of Mt Turner, Pilbara, contains small, smooth surfaced, umbilicated shells with broad colour bands that do not match any other Pilbara species. Two "bones" from along the Tom Price rail line were collected between the 155–160 mile pegs on Hamersley Station by I. Crawford in January 1966 (WAM 1133.81) and cannot be associated with any named species.

Except for the Dampier Archipelago (**Map 40**), distributions are allopatric. Since collecting on the Dampier Archipelago has been sporadic and opportunistic, many islands have no records at all and exact localities are not available for most records, it is only desirable to report that five species are reported from Rosemary Island (*R. dampierana* sp. nov., *R. intermedia* sp. nov., *R. minima* sp. nov., *R. elachystoma* (von Martens, 1878) and *R. perprima* Iredale, 1939) and four from Enderby Island (*R. angulata* sp. nov., *R. intermedia* sp. nov., *R. minima* sp. nov., and *R. perprima* Iredale, 1939). Clearly there is a remarkable radiation in the Dampier Archipelago but much additional field work is needed in this region before its dimensions will be known.

As in the Kimberley, all observed aestivation records involve sandy soil or litter under low vegetation. *Rhagada* is a "free sealer", secreting calcified epiphragms that can be shed very quickly once an aestivating snail is exposed to moisture.



Map 40: Dampier Archipelago records of *Quistrachia legendrei*, *Rhagada angulata*, *R. convicta*, *R. dampierana*, *R. elachystoma*, *R.* aff. *elachystoma*, *R. intermedia*, *R. minima* and *R. perprima* with island borders omitted.

Table 152: Local variation in *Rhagada torulus* and *R. globosa*.

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Rhagada torulus					
Bernier Island, WAM 305.74	25D	10.33±0.137 (8.45-11.45)	13.59±0.107 (12.4-14.7)	0.760±0.007 (0.835-0.679)	$5\frac{1}{8}$ ($4\frac{3}{4}$−-$5\frac{3}{8}$+)
WA-52, FMNH 182380	14D	11.91±0.128 (11.1-13.0)	12.12±0.185 (14.2-16.4)	0.787±0.009 (0.740-0.840)	$5\frac{1}{4}$− ($4\frac{7}{8}$-$5\frac{3}{8}$)
WA-167, FMNH 199893	18D	11.94±0.140 (11.0-12.95)	14.68±0.120 (13.8-15.35)	0.814±0.007 (0.756-0.864)	$5\frac{1}{4}$− (5+-$5\frac{1}{2}$+)
WA-167a, FMNH 199916	12L	11.37±0.209 (10.1-12.4)	14.21±0.213 (13.1-15.35)	0.799±0.007 (0.770-0.834)	$5\frac{1}{8}$ ($4\frac{7}{8}$−-$5\frac{3}{8}$+)
WA-167a, FMNH 199768	24L	11.38±0.095 (10.55-12.75)	14.02±0.122 (12.55-15.35)	0.813±0.008 (0.739-0.894)	$5\frac{1}{8}$ (5+-$5\frac{3}{8}$−)
WA-168, FMNH 199739	24L	11.17±0.119 (10.05-12.15)	13.90±0112 (12.55-14.65)	0.803±0.007 (0.739-0.894)	5+ ($4\frac{3}{4}$−-$5\frac{1}{4}$−)
WA-168, FMNH 199883	16L	11.55±0.227 (10.15-13.55)	14.49±0.233 (13.1-16.1)	0.798±0.011 (0.709-0.913)	5 ($4\frac{7}{8}$−-$5\frac{3}{8}$−)
WA-953, FMNH 212468	15L	11.59±0.163 (10.8-12.9)	14.36±0.224 (12.75-15.75)	0.809±0.013 (0.744-0.893)	$5\frac{1}{4}$+ ($5\frac{1}{8}$−-$5\frac{5}{8}$+)
WA-46, FMNH 182360	17D	12.89±0.244 (10.6-14.4)	15.47±0.255 (12.8-17.2)	0.834±0.008 (0.770-0.880)	$5\frac{1}{8}$− ($4\frac{3}{8}$-$5\frac{1}{2}$)
WA-955, FMNH 212475	56D	11.75±0.119 (9.8-14.2)	14.20±0.126 (12.5-16.95)	0.827±0.005 (0.742-0.916)	$5\frac{3}{8}$+ ($5\frac{1}{8}$−-$5\frac{5}{8}$+)

Table 152: Local variation in *Rhagada torulus* and *R. globosa* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Rhagada torulus (continued)					
WA-956, FMNH 212480	26L	12.05±0.192 (10.35-13.65)	13.82±0.161 (12.15-15.0)	0.871±0.007 (0.811-0.944)	$5\frac{1}{4}+$ $(4\frac{7}{8}+-5\frac{5}{8}-)$
WA-956, FMNH 212479	67D	12.56±0.107 (9.85-14.65)	14.49±0.096 (12.0-16.85)	0.867±0.005 (0.690-0.966)	$5\frac{3}{8}-$ $(4\frac{7}{8}+-5\frac{5}{8}+)$
Rhagada globosa					
Warroora Station, WAM 1455.81	24D	9.94±0.115 (8.55-10.95)	12.15±0.115 (11.0-13.1)	0.819±0.007 (0.732-0.901)	$4\frac{3}{4}+$ $(4\frac{1}{2}--5\frac{1}{8}+)$
Bill Bay, Cardabia Stn, WAm 385.74	13L	10.34±0.192 (9.1-11.45)	12.38±0.165 (11.35-13.3)	0.836±0.015 (0.765-0.93)	$4\frac{7}{8}+$ $(4\frac{3}{4}-5\frac{1}{4})$
WA-25, FMNH 182396	85D	10.48±0.080 (9.0-12.1)	13.05±0.060 (12.0-14.2)	0.803±0.003 (0.692-0.875)	$4\frac{3}{4}$ $(4\frac{1}{2}-5\frac{3}{8})$
WA-24, FMNH 182398	74D	9.56±0.059 (8.2-10.9)	11.61±0.059 (10.1-12.6)	0.824±0.004 (0.748-0.909)	5 $(4\frac{1}{4}-5\frac{7}{8}+)$
WA-26, FMNH 182384	41D	10.25±0.108 (9.0-11.8)	12.76±0.100 (11.1-14.5)	0.803±0.008 (0.730-0.960)	$4\frac{7}{8}$ $(4\frac{1}{8}-5\frac{3}{4})$
WA-173, FMNH 199243	6D	9.61±0.217 (8.9-10.2)	11.63±0.126 (11.25-11.9)	0.827±0.019 (0.780-0.908)	$4\frac{7}{8}+$ $(4\frac{1}{4}--5+)$
WA-172, FMNH 199896	13D	9.00±0.111 (8.5-9.7)	11.58±0.165 (10.7-12.5)	0.777±0.010 (0.698-0.826)	$4\frac{5}{8}$ $(4\frac{1}{2}--4\frac{7}{8}-)$

Patterns of shell variation

The most obvious variable is the colour pattern. When it is reduced to just the two primary spiral bands, there can be striking similarity. If shape and size also coincide, then confusion will result, witness the many pre-1939 literature records. The Shark Bay *R. torulus* (Férussac, 1819) (**Figs 403a–e**), Dampier Land *R. bulgana* sp. nov. (**Figs 429a–c**), and Prince Regent River *R.* sp. (Solem, 1985: 882, figs 226d–f) are such "look alikes". The much larger *R. pilbarana* sp. nov. (**Figs 411a–b**) and *R. perprima* (**Figs 411c–d**) have the same colour, but obviously differ in other shell features. The opposite trend, in which there are many spiral bands and an apical or spire colour suffusion, is seen in *R. globosa* sp. nov. (**Figs 403f–h**) from just S of the North West Cape, *R. reinga* (Pfeiffer, 1846) from near Broome, *R. cygna* sp. nov. (**Figs 429d–f**) from the N tip of Dampier Land and *R. harti* Solem (1985: 881, figs 225d–f) from the King Leopold Ranges. Most other species are intermediate in colour patterns. The occurrence of the extremes clearly is mosaic, not geographically co-ordinated, strongly suggesting that there is colour pattern convergence.

The presence of prominent radial ribbing on at least the spire, in contrast, does show some geographic unity. This character state is found in most of the Dampier Archipelago species, *R. dringi* (Pfeiffer, 1846) from 80 Mile Beach (**Plate 209a–b**), *R. plicata* Preston, 1914 from the Montebello Islands (**Plate 207a**) and in some of the still undescribed W Kimberley taxa. The Dampier Land, Oscar and Napier Range taxa in the West Kimberley, and mainland species living S of the Dampier-Cossack region do not have this ribbing. Only two of the Dampier Archipelago species, *R. angulata* sp. nov. and *R. perprima*, lack prominent radial ribbing.

Peripheral angulation is restricted to some Dampier Archipelago species (*R. minima* sp. nov., *R. intermedia* sp. nov., *R. angulata* sp. nov., **Figs 418d, 420b, d, 422b**) and development of a peripheral keel is known only in *R. dampierana* sp. nov. (**Fig. 422e**) from Rosemary Island, Dampier Archipelago.

Degree of lip expansion is highly variable, without any clear pattern. Slight to moderate aperture narrowing is confined to taxa from the S end of the range (some *globosa* sp. nov. and *R. torulus*) or inland (*R. radleyi*). Presence of a weak lip knob is found in a few, mainly northern or Kimberley species. The degree of umbilical opening depends upon the combination of columellar lip expansion and spire elevation – low spired taxa with narrow lip expansion tend to have a wider umbilical crack than do high spired species with a broadly expanded lip. Again, there is no simple geographic pattern.

Patterns of anatomical variation

There are clear geographic patterns of change in jaw and genital features, extending from the Kimberley itself S to the Shark Bay *R. torulus*. These changes correlate with the N-S gradation in climate. The S and W Kimberley experience a monsoonal climate, with a defined summer wet season of 600–800 mm rainfall. Towards the south, there is (**Table 166**) a progressive reduction in median annual rainfall, decrease in the number of rain events, less seasonality and finally, at Geraldton, which lies on the N fringes of the winter rain belt, there is a reversal in all features.

The jaws of all Kimberley species (Solem 1985: 892, plate 89) retain very prominent vertical ribs. In the Dampier Land and Broome taxa (**Plates 224d, 225b, f, 226f**) the ribs are narrower but still prominent, and tend to concentrate toward the middle of the jaw. *R. dringi*, from 80 Mile Beach (**Plate 223d, f**) has a variable jaw. More southern species have only a very few and usually narrow ribs (**Plates 211–222**). The greatest degree of rib reduction is found in the Cape Range endemic in Cape, Rough and Scrubby Ranges *R. capensis* sp. nov. (**Plate 215a–c**) which, when microsympatric with other camaenids, is a feeding specialist on new green shoots of plants.

Radular tooth variation, in contrast, correlates more with animal size and there are two examples of apparent feeding specialization. The central and early lateral radular teeth of Kimberley species (Solem 1985: plates 90–92) have a moderate anterior flare, normal cusp shaft angle, a slightly curved cusp tip and often a weak ectoconal notch or small ectocone. The smaller Dampier Land to 80 Mile Beach area species (**Plates 223–226**) have a larger ectocone and less cusp tip curvature. The larger size Dampier Archipelago species (**Plates 221–222**) show a reduced ectocone and increased cusp curvature. The inland species *R. radleyi* (**Plate 220a–c**) has a greatly enlarged anterior flare, increased cusp shaft elevation, at most a weak ectoconal notch and almost no cusp tip curvature. I suspect that it has a feeding specialisation, but have not seen it alive and active. Between Cossack and the Minilya River there are several large species (**Plates 216–219**) with reduced or lost ectocones, little cusp tip curvature and an often elevated cusp shaft angle. In the Cape Range Rough and Scrubby Range, *R. capensis* (**Plate 213–214**) shows a variety of structures, with elevated cusp shaft angle and altered inter-row basal support ridge. It has an observed preference for new green shoots or leaves instead of dead vegetation – hence the altered jaw and radula. The comparatively small *R. torulus* (**Plate 211a, e**) and *R. globosa* sp. nov. (**Plate 212a, d**) have prominent ectocones, cusp tip curvature and thus closely resemble the Kimberley pattern.

In summary, unless there are local feeding specializations, larger species lack ectocones and usually have reduced cusp shaft angle, while small species have curved cusp tips and better developed ectocones.

Genital changes are more dramatic and nearly linear. Kimberley species of *Rhagada* (Solem 1985: 890–917, figs 227–235) have normally sized albumen glands (GG), the spermatheca (S) is variable in length, is normally tightly kinked and its head often does not extend past the mid-point of the prostate-uterus. There is considerable interspecific variation in length of the free oviduct (UV), vagina (V) and epiphallic caecum (EC). The penis (P) is of medium length and has a large verge (PV) that fills most of the penis chamber. This verge is smooth surfaced, with a very prominent and long sperm groove and varies greatly among species in diameter, shape and length. *R. basedowana* Iredale, 1939 (Solem 1985: 911, fig. 232c) is unusual in that the verge is slender and spathulate in shape, resembling closely the typical vergic structure seen in the Red Centre genus *Semotrachia* (see Part VI). The Dampier Land species (**Figs 428, 430–432**) retain the same vergic and spermathecal structures but show some enlargement of the albumen gland. *R. dringi* (**Figs 426a–d**), from the 80 Mile Beach area, has a smaller, distinctly shortened verge that is still massive, a short penis, a shortened spermatheca and noticably enlarged albumen gland.

In most Dampier Archipelago and Montebello Islands taxa (**Figs 413, 419, 421, 423–424**), the verge is very short, either conical or dome-shaped, with a rugose or corrugated surface. The epiphallic caecum varies from medium length to very long, the penis varies from short to long and the albumen gland is very large. The spermatheca is kinked, at least apically, except in *R. dampierana* sp. nov. (**Fig. 424a**), which probably is secondarily enlarged in size. The large sized *R. perprima* (**Figs 413a–b**) differs in having a long penis with a tapering verge of medium length and only the upper portion of the spermatheca kinked, reflecting its larger size and probable affinity with the *convicta–pilbarana–capensis* series of species. The *R. richardsoni* and *R. radleyi* pair differ in penis and verge (**Figs 415, 417**), while *R. pilbarana* sp. nov. (**Figs 412a–b**) has a greatly elongated verge. The spermatheca is kinked and the albumen gland is greatly enlarged. *R. convicta* (**Figs 410a–c**) is the southernmost species and features a corrugated surface verge, which presumably is capable of great expansion in size through hydraulic pressure.

The remaining three species, *R. capensis* sp. nov. from the Cape, Rough and Scrubby Ranges (**Figs 407–409**), *R. globosa* from coastal dunes slightly to the south (**Figs 405a–b**), and *R. torulus* from Warroora S to Shark Bay (**Figs 404a–e**), have simple cylindrical verges with little surface sculpture, huge albumen glands, strongly kinked spermathecae, and shortened prostate-uterus regions.

At the level of Port Hedland, where there is the major break in seasonal concentration of rainfall and reduction in annual amount (**Table 166**), the pattern of great enlargement of the albumen gland, shortening of the prostate-uterus, kinking of the spermatheca and great size reduction or simplification of the verge becomes obvious, with continuing alteration through the more southern taxa.

Unfortunately, much of the available material had been in formalin at some time, with resultant changes in glandular areas of the genitalia. It will be necessary to collect and study new material before attempting a detailed analysis of the genital changes for phylogenetic studies. The major geographic trends are obvious but the details of vergic and penis chamber structures remain to be determined.

The following artificial key is based only on easily observable shell features of fully adult, fresh shells. In order for the key to be usable by non-specialists and to be of manageable size, geographic criteria have been used because of the extensive local size and shape variation noted within species. Use of genital and radular features would have produced a much shorter and more satisfactory key but observation of these features requires skilled dissection and tedious radular preparation for SEM examination. Worn or juvenile examples will not key out. Reference to **Maps 37–41** will suggest geographically possible taxa and then use of the text should permit successful identification.

KEY TO THE SPECIES OF *RHAGADA*

1. Spire without prominent radial ribs (**Plates 205e–f, 206a–b, d–f**) 7
   Spire with prominent radial ribs (**Plates 205a–b, 207a–b, d–f, 208b–c, 209a–b**) 2

2. Shell periphery evenly rounded (**Figs 418b, d, 420b, d, 425b**) 3
   Shell periphery with a protruded keel (**Plate 208c, Figs 422d–f**) ....
   .... *Rhagada dampierana* sp. nov. (p. 1760)

3. Dampier Archipelago 4
   Montebello Islands or 80 Mile Beach area 6

4. Shell smaller, mean diameter about 12 mm 5
Shell larger, mean diameter about 14 mm ....
.... *Rhagada elachystoma* (von Martens, 1878) (p. 1746)

5. Mean H/D ratio about 0.700; radial ribs stop at shell periphery ....
.... *Rhagada intermedia* sp. nov. (p. 1743)
Mean H/D ratio about 0.750; radial ribs continue partway onto shell base ....
.... *Rhagada minima* sp. nov. (p. 1741)

6. Mean diameter *ca.* 10.4 mm; spire higher (**Fig. 418b**), mean H/D ratio 0.760; Montebello Islands .... *Rhagada plicata* Preston, 1914 (p. 1737)
Mean diameter *ca.* 12.3 mm; spire lower (**Fig. 425b**), mean H/D ratio 0.670; 80 Mile Beach area .... *Rhagada dringi* (Pfeiffer, 1846) (p. 1764)

7. Body whorl evenly rounded 8
Body whorl with angulated periphery (**Fig. 422b**) ....
.... *Rhagada angulata* sp. nov. (p. 1754)

8. Mean diameter less than 15 mm; or aperture distinctly narrowed by descension (**Fig. 403f**) 9
Mean diameter over 16.5 mm; or aperture not narrowed by descension 13

9. Colour on shell of only two red spiral bands (**Figs 403b, 429b**); shell larger, mean diameter about 14.3 mm 10
Colour on shell consists of many red to orange spiral lines, plus normally a reddish spire suffusion (**Figs 427b, 429e**); shell smaller, mean diameters 11.5–12.5 mm 11

10. Dampier Land; lip broadly expanded (**Fig. 429c**) ....
.... *Rhagada bulgana* sp. nov. (p. 1780)
Shark Bay N to Warroora Homestead; lip not expanded (**Fig. 403e**) ....
.... *Rhagada torulus* (Férussac, 1819) (p. 1680)

11. Dampier Land or Broome 12
Just S of North West Cape; mean whorl count 4 3/4; mean H/D ratio 0.870 ....
.... *Rhagada globosa* sp. nov. (p. 1685)

12. Broome area; mean diameter near 12.5 mm ....
.... *Rhagada reinga* (Pfeiffer, 1846) (p. 1773)
N tip of Dampier Land; mean diameter 11.75 mm ....
.... *Rhagada cygna* sp. nov. (p. 1785)

13. Coastal plains and Cape, Rough and Scrubby Ranges, Minilya River N to Dampier Archipelago-Cossack area 14
Coastal plains from Depuch Island to Cape Keraudren, thence inland to Oakover and upper Ashburton River basins 17

14. Shell with many narrow spiral colour bands (**Fig. 406b**); body of animal dark grey in colour; Cape Range and Scrubby Range (**Map 38**) .... *Rhagada capensis* sp. nov. (p. 1689)

Shell with 0–2 spiral bands; body of animal yellow-white in colour 15

15. Lip well expanded; supraperipheral and subsutural colour bands bright in tone (**Figs 411b, d**) 16

Lip narrow; colour bands faint or reduced to translucent zones (**Fig. 406e**); Minilya River to Cossack .... *Rhagada convicta* (Cox, 1870) (p. 1699)

16. Larger, mean diameter 23 mm; Python Pool and Mt Herbert, Chichester Range ... . *Rhagada pilbarana* sp. nov. (p. 1707)

Smaller, mean diameter 16–21 mm; Dampier Archipelago .... *Rhagada perprima* Iredale, 1939 (p. 1712)

17. Inland on Fortescue and Ashburton River drainages (**Maps 37, 39**); mean H/D ratio 0.700; umbilicus normally with lateral crack .... *Rhagada radleyi* Preston, 1908 (p. 1729)

Coastal from Depuch Island to Cape Keraudren, inland to Roy Hill and Oakover River basin (**Map 37**); mean H/D ratio 0.750; umbilicus usually closed .... *Rhagada richardsonii* (E. A. Smith, 1874) (p. 1718)

RHAGADA TORULUS (FÉRUSSAC, 1819)

(Plates 205e, 211a–f; Figs 403a–e, 404a–e; Maps 29–31, 37–38)

Helix torulus Férussac, 1819, *Hist. Moll.*, liv. **6:** plt. 28, figs 3–4 – Nouvelle Hollande (= Shark Bay, WA (Iredale 1938)); Férussac, 1821, *Syst. Tab. Hist. Moll.*, p. 34; Pfeiffer, 1841, in: Martini & Chemnitz, *Syst. Conch. Cab.*, I, (12), **2:** 43, plt. 72, figs 4–5; Pfeiffer, 1848, *Monog. Helic. viv.*, **1:** 238; Cox, 1868, *Monog. Aust. Land Shells*, p. 42, plt. XI, fig. 5 (copy of Férussac); Tryon, 1887, *Man. Conch.*, (2) **3:** 215; E. A. Smith, 1894, *Proc. Malac. Soc. London*, **1:** 89.

Helix (*Rhagada*) *torulus* (Férussac), Pilsbry, 1890, *Man. Conch.*, (2) **6:** 189.

Thersites (*Rhagada*) *torulus* (Férussac), Pilsbry, 1894, *Man. Conch.*, (2) **9:** 136.

Rhagada torulus (Férussac), Hedley, 1916, *Jour. Roy. Soc. Western Aust.*, **1:** 70 – check list citation; Iredale, 1938, *Aust. Zool.*, **9** (2): 112 – check list citation; Iredale, 1939, also published as *Jour. Roy. Soc. Western Aust.*, **25:** 58–59, plt. IV, fig. 1 – discusses identity and restricts type locality to Shark Bay, Western Australia; Zilch, 1960, *Hand. Paläo.*, **6** (2): 617 (copy of Férussac's figure); Richardson, 1985, *Tryonia*, 12: 267 – check list citation.

Comparative remarks

Rhagada torulus, which ranges coastally from Bernier Island, Shark Bay to near Warroora Homestead, N of Carnarvon (**Map 30**), is medium sized (mean diameter 14.29 mm), thick-shelled, globose (**Figs 403b, e**, mean H/D ratio 0.823), with the

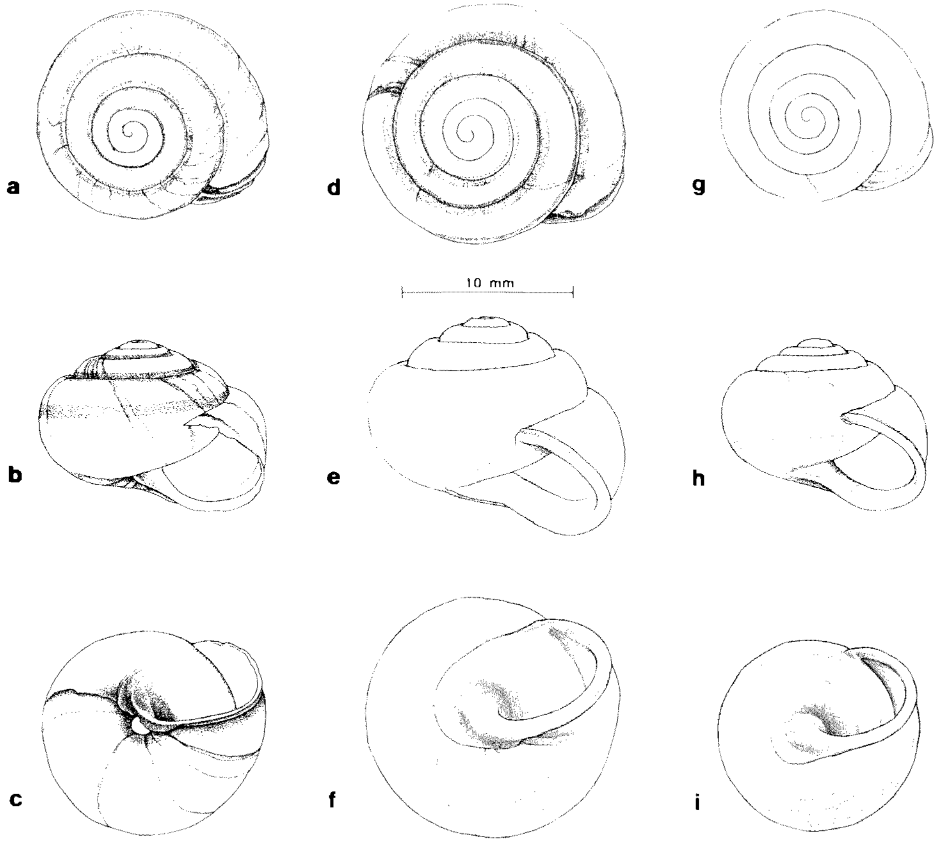


Fig. 403: Shells of *Rhagada torulus* (Férussac, 1819) and *R. globosa* sp. nov.: (a–c) *R. torulus*, Bernier Island, Shark Bay, WA. Topotype. WAM 369.74; (d–f) *R. torulus*, WA–956, Upper Bulbarli Well, Warroora Station, WA. FMNH 212479; (g–i) *R. globosa*, WA–172, 1.4 km N of 4 Mile Well, Ningaloo–Cardabia track, S of Cape Range, WA. Holotype. WAM 760.87. Scale line equals 10 mm. Drawings by Linnea Lahlum.

aperture narrowed, lip internally thickened and the umbilicus completely closed by a broad callus (**Fig. 403c**). Shell colour variable: a red spiral peripheral to slightly supraperipheral band always present (**Figs 403b, e**) and usually joined by a very narrow subsutural band; occasionally narrow accessory spiral bands on base and spire; rarely a broad reddish brown suffusion on spire. Its shell apex is smooth and the spire has, at most, radial growth ridgelets (**Plate 205e**).

The nearest species, *R. globosa* sp. nov., from just N of Warroora along the coast to near Ningaloo Homestead (**Map 37**), is smaller (mean diameter 12.36 mm), has a reduced whorl count (mean 4 3/4+), the aperture is not constricted (**Fig. 403g**), the lip is slightly expanded and the colouration differs in that there usually are accessory spiral bands, an apical colour suffusion and the main spiral bands are narrower (**Figs 403f–h**). *R. globosa* sp. nov. agrees in shell sculpture (**Plate 205f**), except that weak traces of apical sculpture are retained.

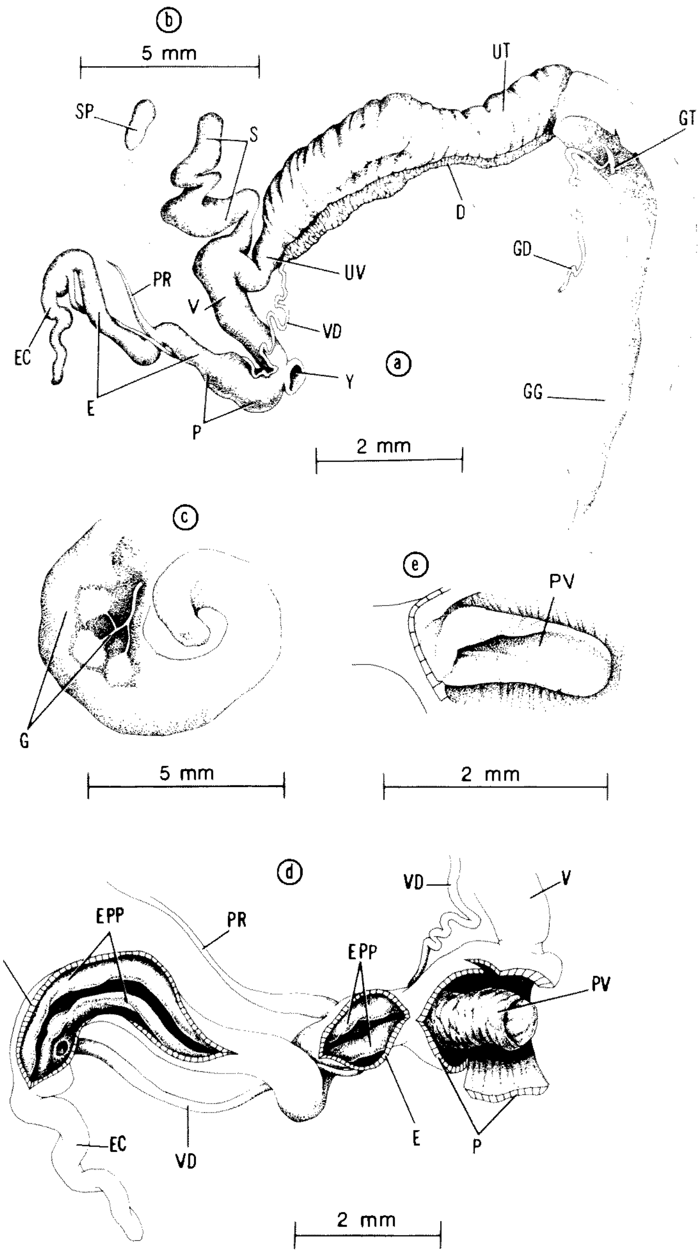


Fig. 404: Genitalia of *Rhagada torulus* (Férussac, 1819): Bernier Island, Shark Bay, WA. 20 May 1963. WAM 369.74, Dissection A: (a) whole genitalia; (b) spermatophore; (c) position of ovotestis clumps; (d) interior of penis and epiphallus; (e) other side of verge (PV). Scale lines as marked. Drawings by Elizabeth A. Liebman (a–d) and Linnea Lahlum (e).

The Dampier Archipelago radiation differs in the non-globose shapes and expanded lips (**Figs 418, 420, 422**) and the general presence of radial ribbing (**Plates 207–208**) above the periphery. Of the northern species, *R. bulgana* from Dampier Land (**Map 41**) is the most similar in size (mean diameter 12.48 mm), whorl count (mean 5 1/8), spire sculpture (**Plate 210d**) and colour (**Figs 429a–c**) but differs obviously in its flared lip, much lower spire (mean H/D ratio 0.760) and lack of apertural narrowing.

The most similar species, *Quistrachia warroorana* sp. nov., from just S of Warroora Homestead and the Scrubby Range, (**Map 46**), is slightly larger in size (mean diameter 14.94 mm), equally globose (**Fig. 433b**, mean H/D ratio 0.821) but with a much lower whorl count (mean 4 3/8+), the lip only slightly expanded, umbilicus with either a narrow lateral crack (**Fig. 433c**) or closed and without a broadly expanded callus. The shell has a narrow peripheral red spiral colour band extending to the aperture, sometimes bordered below by a white zone, never with a subsutural red spiral colour band or accessory spiral bands and the shell apex (**Plate 227a–b**) is densely pustulose.

Anatomically (**Figs 404a–e**), *R. torulus* has an enormous albumen gland (GG), multi-kinked spermatheca (S), very short penis (P) with nearly cylindrical verge (PV) and quite long epiphallic caecum (EC). *R. globosa* sp. nov. (**Figs 405a–b**) has the spermatheca (S) less kinked, the vagina (V) is much longer and more slender, the penis (P) is longer and the verge (PV) longer. *R. bulgana* sp. nov. (**Figs 430a–e**) has the albumen gland (GG) normal in size, the spermatheca (S) is almost unkinked, the vagina (V) is very short, penis (P) long, verge (PV) smooth-surfaced with a complex lateral groove and the epiphallic caecum (EC) is extremely large.

Type specimens

No possible type lot specimens were seen during this project. The type locality restriction to Bernier Island, Shark Bay, WA by Iredale (1939: 58–59) permits using Bernier Island specimens to establish this species concept.

Material studied

WESTERN AUSTRALIA: Bernier Island (W. D. L. Ride! 21 July 1959, WAM 305.74, 25 DA, 12 DJ; B. K. Bowen! 21–25 July 1959, WAM 350.74, 1 LA; G. M. Storr! 20 May 1963, WAM 369.74, 1 LA; J. L. Bannister! 16 April 1969, WAM, 2 DA); Dorre Island (Disaster Bay and northwards, S. M. Slack-Smith! 5 March 1980, WAM, 4 DA; W. D. L. Ride! 17 July 1959, WAM, 32 DA, 9 DJ); Monkey Mia, Shark Bay (S. M. Slack-Smith! October 1970, WAM 1227.81, 4 DA, 2 DJ); Point Quobba, N of Carnarvon (WA-52, WAM 779.87, SAM D18138, AM, FMNH 182380, FMNH 182590, 4 LA, 13 DA, 6 LJ, 4 DJ; lighthouse, R. Prince! 12 October 1975, WAM, 11 DA; WA–167, dunes, FMNH 199893–4, 1 LA, 18 DA, 2 LJ, 5 DJ; WA–167a, near lighthouse, FMNH 199768, FMNH 199915–6, 36 LA, 7 DA, many LJ, 1 DJ; SE of the Blow Holes, C. Dortch! 31 July 1976, WAM, 1 DA; Blow Holes, N. Coleman! 22 June 1973, MV, 3 LA, 1 DA, 3 LJ); Ram Paddock Well, N of Quobba (WA–168, WAM 777.87, SAM D18136, AM, QM, MV, FMNH 199739, FMNH 199882–3, FMNH 200175–6, 44 LA, 13 DA, 1 LJ, 2 DJ; WA–953, WAM , FMNH 212468, 15 LA, 1 LJ); Cape Cuvier (M. Seymour! 20 May 1971, WAM, 1 DA); N of Cape Cuvier (S. M. Slack-Smith! September 1970, WAM, 4 DA, 3 DJ); Warroora Station (WA–46, 3 miles S of homestead, WAM 780.87, SAM D18139, AM, QM, FMNH 182360, 17 DA, 3 DJ; WA–47, 4.6 miles S of homestead, FMNH 182593, 1 LJ; WA–955, 6.7 km S of homestead, subfossil in sand dunes, WAM 776.87, SAM D18135, FMNH 212475, 56 DA, 66 DJ; WA–956, 0.3 km S of Upper Bulbarli Well, Warroora Station, WAM 774.87, WAM 775.87, SAM D18134–5, AM, MV, QM, FMNH 212479–80, 26 LA, 67 DA, 2 LJ, 8 DJ); Upper Bulbarli Well,, Warroora Station (WA–1070, FMNH 221719, 1 LA); 0.9 km N of Upper Bulbarli Well Warroora Station (WA–1071, FMNH 221721, 4 DA).

Range

Rhagada torulus is the southernmost species of *Rhagada*. It has been recorded (**Map 30**) from Bernier Island, Shark Bay (25°S) to Bulbarli Well on Warroora Station (23°32'S). From the S tip of Bernier Island to Bulbarli Well is about 170 km. All known records are coastal but, since no inland collecting has been attempted in this region, the actual E-W range remains to be determined. There is a 25 km gap between the northernmost record of *R. torulus* near Upper Bulbarli Well and the southernmost record for *R. globosa* sp. nov. (**Map 30**).

Diagnosis

Shell medium in size, adult diameter 12.0–17.2 mm (mean 14.29 mm), with 4 3/8 to 5 5/8+ (mean 5 1/4) rather tightly coiled whorls (**Fig. 403a**). Apex and spire strongly and, in general, evenly elevated (**Figs 403b, e**), rarely rounded above, shell height 8.45–14.65 mm (mean 11.77 mm), H/D ratio 0.679–0.966 (mean 0.823). Body whorl evenly rounded. Shell apex with, at most, faint trace of sculpture (**Plate 205e**), spire and body whorl with microscopic growth ridgelets. Umbilicus (**Fig. 403c**) completely closed by a broadly expanded columellar callus. Body whorl sometimes descending slightly behind lip, aperture noticeably narrowed, lip somewhat thickened internally. A prominent peripheral and a very narrow subsutural red spiral colour band present in all specimens, occasionally narrower accessory spiral bands on spire and shell base, rarely with a reddish brown spire suffusion. Based on 347 measured adults.

Genitalia (**Figs 404a–e**) with greatly enlarged albumen gland (GG), short free oviduct (UV), kinked spermatheca (S), medium length vagina (V). Epiphallus (E) long, coiled, with large caecum (EC) and prominent longitudinal pilasters (EPP). Penis (P) very short, internally with smooth walls. Verge (PV) cylindrical, with slightly wrinkled surface and near-medial lateral slit (**Fig. 404e**). Spermatophore (SP, **Fig. 404b**) present in apex of spermatheca, with slender tube extending into free oviduct channel. Head wart a large circular patch of pustules, only slightly darker in colour than head area.

Central and early lateral teeth of radula (**Plate 211a**) with slight anterior flare, typical cusp shaft angle and the pointed cusp tip with only slight curvature. Ectocone appears on 2nd lateral, endocone (**Plate 211e**) on late laterals. Late laterals with slightly increased anterior flare (**Plate 211b, e**), early marginals (**Plate 211b–e**) without unusual features. Jaw (**Plate 211f**) with very few and widely separated narrow vertical ribs, sides without ribbing.

Discussion

Rhagada torulus is the southernmost species of the genus, and the enlargement of its albumen gland (**Fig. 404a**, GG) is carried further than in any *Rhagada* species.

The same aridity probably accounts for the size difference between live and dead specimens at WA–956 (**Table 152**). The dead examples from a nearby sand dune deposit (WA–955) also are relatively large. Local geographic variation of this disjunctly distributed species (**Map 29**) is moderate, and summarised as:

	Bernier Island (27 adults)	Warroora (181 adults)
Height in mm	10.31 (8.45–11.45)	12.19 (9.8–14.65)
Diameter in mm	13.57 (12.4–14.7)	14.39 (12.0–17.2)
H/D ratio	0.760 (0.679–0.835)	0.847 (0.690–0.966)
Whorls	5 1/8 (4 3/4– – 5 3/8+)	5 1/3 (4 3/8 – 5 5/8+)

	Quobba Blow Holes (82 adults)	Ram Paddock Well (57 adults)
Height in mm	11.64 (11.2–13.3)	11.30 (9.9–13.55)
Diameter in mm	14.43 (12.55–15.6)	14.13 (12.55–16.1)
H/D ratio	0.808 (0.739–0.894)	0.800 (0.709–0.912)
Whorls	5 1/8+ (4 7/8– – 5 1/2+)	5 1/8– (4 3/4– – 5 3/8+)

The Bernier Island specimens are smaller and less elevated than those from further N. This may reflect the fact that *R. torulus* is the only camaenid reported from Bernier Island, whereas at the other known localities it occurs with *Plectorhagada* or *Quistrachia*.

Specimens were dissected from Bernier Island (**Figs 404a–e**), Point Quobba (WA–52), Ram Paddock Well (WA–953) and Warroora (WA–956). The Bernier Island example was considerably retracted and **Figs 404a**, d show the penis (P) shorter than in the relaxed condition and the verge (PV) in a state of partial contraction. Dissected individuals from the other stations were fully or almost fully expanded and thus both the penis and verge appeared noticeably longer. The presence of a spermatophore (SP, **Figs 404b**) in the Bernier Island specimen, collected 20 May 1963, does not necessarily indicate natural reproduction timing. A note on the original label states "under sheets of iron at Hospital" and thus suggests a "watered area" or at least "spray zone" from a watered site.

RHAGADA GLOBOSA SP. NOV.

(Plates 205f, 212a–f; Figs 403f–h, 405a–c; Maps 30–31, 37–38)

Comparative remarks

Rhagada globosa from N of Warroora Homestead to near Ningaloo Homestead, WA (**Map 30**), is small in size (mean diameter 12.36 mm), with reduced whorl count (mean 4 3/4+), nearly globose in shape (**Fig. 403g**, mean H/D ratio 0.810) and has a relatively thick shell. Aperture slightly deflected, lip a little expanded, umbilicus usually covered by a broad expansion of the columellar callus, sometimes with a narrow lateral crack remaining. Shell colour with a faint apical reddish suffusion, narrow major red bands, and normally accessory bands on spire and shell base (**Figs 403f–h**). Shell apex (**Plate 205f**) with weak radial elements, spire with growth micro-ridgelets. *R. torulus*, from Bernier Island, Shark Bay to just S of Warroora Homestead

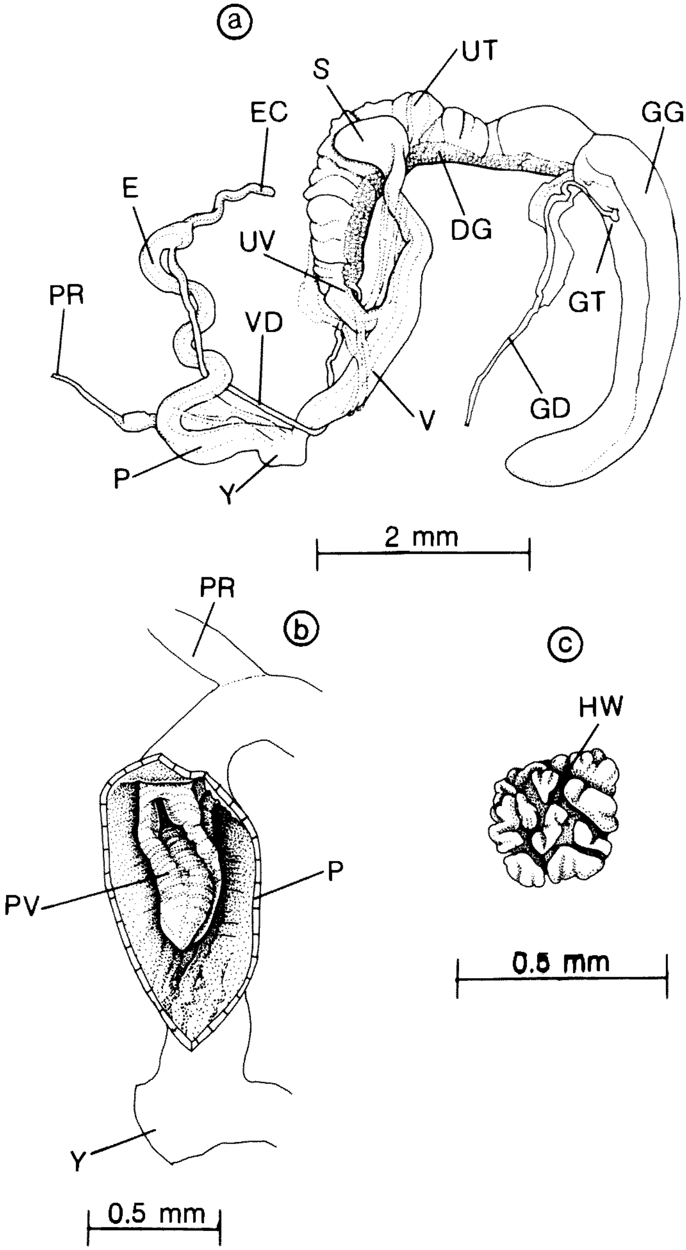


Fig. 405: Genitalia of *Rhagada globosa* sp. nov.: coastal sand dunes, Bill Bay, 2 miles S of Pt Maud, Cardabia Station, WA. July 1966. WAM 385.74, Dissection B: (a) whole genitalia; (b) verge; (c) head wart. Scale lines as marked. Drawings by Linnea Lahlum.

(**Map 30**), is much larger (mean diameter 14.29 mm), with more whorls (mean 5 1/4), a thicker shell, more constricted aperture (**Figs 403b, e**) and generally only the two basic spiral red colour bands. Species of similar size from the Montebello Islands (*R. plicata* Preston, 1914), Dampier Archipelago (*R. minima* sp. nov., *R. intermedia* sp. nov.), and 80 Mile Beach (*R. dringi*) differ most obviously in their strong radial sculpture (see **Plates 207a–d, 209a–b**) above the periphery. The Broome area *R. reinga* (Pfeiffer, 1846) and the northern tip of Dampier Land *R. cygna* sp. nov. have lower spires (**Figs 427a–c, 429d–f,** mean H/D ratios 0.728 and 0.762 respectively), much stronger banding, a very narrow lateral umbilical crack and often a weak basal lip knob. The very large species (mean diameters 19.59–20.15 mm) *R. capensis* sp. nov., *R. convicta* (Cox, 1870), *R. perprima* Iredale, 1939, are lower spired. Anatomically (**Figs 405a–b**), *R. globosa* has a very large albumen gland (GG), the epiphallic caecum (EC) is very long and slender, spermatheca (S) less kinked than in *R. torulus* (**Fig. 404a**), vagina (V) slender and relatively long, the penis (P) long, verge (PV) cylindical, smooth, with simple longitudinal groove. *R. torulus* (**Figs 404a–d**) has the spermatheca (S) strongly kinked, the penis (P) shorter and an even larger albumen gland (GG). *R. capensis* sp. nov. from the Scrubby and Cape Ranges (**Maps 37, 38**) differs in the much shorter epiphallic caecum (EC, **Fig. 407b**), nearly unkinked spermatheca (S), reduced size of the albumen gland (GG) and short vagina (V). *R. convicta*, from lowlands between the Minilya River and Cossack (**Maps 37, 38, 40**), has a near-triangular verge (PV) with corrugated surface (**Fig. 410b–c**), short and thick vagina (V) and nearly unkinked spermatheca (S).

Holotype

WAM 760.87, WA–172, 1.4 km N of 4 Mile Well, Ningaloo-Cardabia road, Western Australia. 22°43'14"S, 113°44'30"E. Collected 27 September 1976 by A. Solem. Height of shell 9.8 mm, diameter 12.25 mm, H/D ratio 0.800, whorls 4 7/8, umbilicus completely closed by a broad callus.

Paratopotypes

WAM 783.87, WAM 784.87, SAM D18142, AM C.200,727, FMNH 199896–7, 4 LA, 13 DA, 10 DJ from the type collection.

Paratypes

WESTERN AUSTRALIA: 18.5 km N of Warroora Homestead (E side coastal track, G. W. Kendrick! 5 June 1981, WAM 1455.81, FMNH 208778, 27 DA, 5 DJ); 9 miles S of Coral Bay on coastal dunes (C. Bryce! September 1978, WAM 1192.81, 1 DA, 4 DJ); *ca.* 2 miles S of Coral Bay Hotel (H. Henderson! 14 June 1971, WAM 126.94, 4 DA); Maud's Landing (D. Parker! 13 October 1975, WAM 124.94, 1 DA); Bill Bay, 2 miles S of Pt Maud (B. R. Wilson! July 1966, WAM 385.74, WAM 1542.70, WAM 127.94, 13 LA, 27 DA, 4 DJ); Pt. Maud (WA–25, WAM 781.87, SAM D18140, AM C.200,728, MV F.60069, QM 45029, FMNH 182396, FMNH 182504, FMNH 182746, 2 LA, 88 DA, 3 LJ, 18 DJ); Cardabia Station (R. W. George! 8 April 1961, WAM 123.94, 5 DA, 4 DJ); 3 miles SE of Cardabia Station (G. M. Storr! 18 October 1962, WAM 121.94, 10 DA); 4.5 miles N of Cardabia Homestead (WA–24, coastal dunes, WAM 187.79, WAM 786.87, SAM D18144, AM c.200,729, MV F.60050, QM 45028, FMNH 182398, FMNH 182730, 108 DA, 53 DJ); Bruloodjoo Point, 16 km N of

Cardabia Homestead (WA–1072, FMNH 221723, 17 DA); 10 miles N of Cardabia Homestead (WA–26, coastal dunes, WAM 785.87, SAM D18143, AM C.200,720, QM 45027, MV F.60052, FMNH 182384, 41 DA, 8 DJ); 8.6 km S of 4 Mile Well (WA–173, consolidated coastal dunes, WAM 782.87, SAM D18141, FMNH 199214, FMNH 199243, FMNH 199445, 12 DA, 15 DJ); 1.4 km N of 4 Mile Well (WA–1073, FMNH 221726–7, 17 LA, 78 DA); 8.7 km from Ningaloo on Exmouth road (WA–422, FMNH 199206, 1 DA, 1 DJ); Norwegian Bay, N of Point Cloates (1 September 1968, WAM 122.94, 2 DA).

Range

Rhagada globosa ranges along the coast from 18.5 km N of Warroora Homestead (23°19'S, 113°48'E) nearly to Ningaloo Homestead (WA–422, 22°42'S, 113°44'E), a distance of about 69 km (**Maps 30–31**); all records are coastal. Hence no E–W range can be estimated. *R. globosa* seems limited to sandy soils.

Diagnosis

Shell small, adult diameter 10.1–14.5 mm (mean 12.36 mm), with 4 3/8 to 5 5/8+ (mean 4 3/4+) rather tightly coiled whorls (**Fig. 403f**). Apex and spire strongly and almost evenly elevated (**Fig. 403g**), sometimes rounded above, shell height 8.2–12.1 mm (mean 10.01 mm), H/D ratio 0.692–0.960 (mean 0.810). Body whorl evenly rounded. Shell apex (**Plate 205f**) with weak radial sculpture, spire and body whorl with microscopic growth ridgelets. Umbilicus (**Fig. 403h**) usually completely closed by expansion of columellar lip, sometimes with a very narrow lateral crack remaining. Body whorl descending slightly behind lip (**Fig. 403g**), which is a little thickened and expanded. Supraperipheral and subsutural red spiral colour bands narrow, usually with narrower accessory bands on shell base and spire. Apex usually with a light reddish colour suffusion. Based on 269 measured adults.

Genitalia (**Figs 405a–b**) with very large albumen gland (GG), short free oviduct (UV), kinked spermatheca (S), long and slender vagina (V). Epiphallus (E) long, coiled, with slender caecum (EC). Penis (P) of medium length, expanded apically, internally with some basal pilaster sculpture. Verge (PV) cylindrical, with simple lateral groove and nearly smooth surface. Head wart (**Fig. 405c**) large, circular, only slightly darker than head.

Central and lateral teeth of radula (**Plate 212a, d**) with small anterior flare, typical cusp shaft angle, cusp tip, and tip curvature. Ectocone appears on 2nd lateral, endocone not until late laterals. Only slight increase in anterior flare on late laterals (**Plate 212b, e, f**). Lateromarginal transition and marginals (**Plate 212b, e, f**) without unusual features. Jaw (**Plate 212c**) with very few, widely spaced, narrow vertical ribs in central half, margins without ribs.

Discussion

Rhagada globosa is represented in collections mainly by long-dead examples weathered (or blown) out of coastal dunes. The type collection (WA–172) was excavated from sand on the south margin of a large termite mound, with living examples taken at a depth of 10–20 cm. None was found on the N side of the mound, which was exposed to direct sunlight. All live specimens had calcified epiphragms across the aperture, most were found with the shell aperture up. Two live adults were taken under spinifex at Point Maud (WA–25) and a good series was taken by Barry Wilson at Bill Bay in July 1966, "crawling among spinifex grass and bushes after night showers". Apparently they aestivate buried in the sand in shaded areas but whether otherwise generally dispersed is unknown.

Size variation is moderate (**Table 152**) and without geographic direction.

The name *globosa* refers to the shape of the shell.

RHAGADA CAPENSIS SP. NOV.

(Plates 206a, 213a–f, 214a–f, 215a–c, 231d–f; Figs 406a–c, 407a–b, 408a–c, 409a–b; Maps 37–38)

Comparative remarks

Rhagada capensis which ranges from the N tip of the Cape Range to 23°07'S in the Scrubby Range (**Maps 37–38**), is one of the larger species of the genus (mean diameter 20.01 mm), with increased whorl count (mean 5 3/4), high but generally rounded spire (**Fig. 406b**, mean H/D ratio 0.775), aperture moderately to sharply deflected behind lip, not narrowed, lip well expanded, umbilicus nearly always closed by broad expansion of columellar lip (**Fig. 406c**). Shell white, with numerous narrow spiral red or orange bands, supraperipheral and subsutural spiral bands normally more prominent. Some examples with accessory bands reduced or lost. Shell apex smooth (**Plate 206a**), spire with widely spaced irregular growth ridgelets. *R. convicta* (Cox, 1870), which lives in the plains areas E and S of the Cape and Scrubby Ranges, and extends N past Onslow to Dampier and Cossack (**Maps 37–38**), is very similar in shell features, differing primarily in having the shell lip not as expanded (**Fig. 406d–f**) but more heavily thickened internally, the colour markings almost always consisting just of narrow supraperipheral and subsutural bands, which may be reduced to translucent zones rather than red bands; some specimens have a light brown spire suffusion and a light supraperipheral zone. *R. pilbarana* sp. nov. from the Pilbara (**Map 37**) is larger (mean diameter 22.97 mm, mean whorl count 6), has reduced colouration (**Figs 411a–b**) and the shell lip is more expanded. *R. perprima* Iredale, 1939 from the Dampier Archipelago (**Map 40**), is very similar in size and shape but the colour (**Figs 411c–d**) is reduced to only the two basic bands and the shell lip is widely expanded.

Body colour in *R. capensis* is unusual in that the head, tentacles, neck and upper portion of the tail are dark grey to black, fading to lighter grey in preservative. In contrast, specimens of *R. convicta*, *R. pilbarana* sp. nov., and *R. perprima* have the entire body white to yellow-white, with at most a light grey tone to the head wart. Anatomically (**Figs 407b, 408a–b, 409a–b**), *R. capensis* has an enlarged albumen gland (GG), partly kinked spermatheca (S), variable length penis (P), vagina (V) and epiphallic caecum (EC); smooth surfaced cylindrical verge with small posterior groove. *R. convicta* (**Figs 410a–c**) has a less-kinked spermatheca, much thicker vagina (V), short penis (P), the verge (PV) has a corrugated surface, sometimes triangular in shape and the sperm groove is relatively short (**Fig. 410c**). *R. pilbarana* sp. nov. (**Figs 412a–b**) has a very large verge that is greatly elongated. *R. perprima* (**Figs 413a–b**) has a very large epiphallic caecum (EC) and the corrugated verge (PV) gradually tapers. Radular teeth are variable (**Plates 213–214, 231d–f**) and the jaws (**Plate 215a–c**) consistently have weaker vertical ribs than in *R. convicta* (**Plate 215d–f**).

Table 153: Local variation in *Rhagada capensis.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Scrubby Range					
WA-51, FMNH 182549	16L	15.38±0.125 (14.75-16.55)	19.40±0.189 (18.5-21.4)	0.794±0.007 (0.759-0.877)	5½ (5¼+-5¾+)
WA-170, FMNH 199734	10L	15.16±0.260 (13.5-16.8)	18.96±0.360 (16.6-20.15)	0.800±0.011 (0.743-0.861)	5⅜ (4⅝+-5¾−)
WA-957, FMNH 212485	13L	15.22±0.185 (14.2-16.15)	19.61±0.125 (19.0-20.5)	0.776±0.008 (0.725-0.820)	5⅜+ (5¼−-5⅝+)
Cape Range W side, N of Ningaloo					
WA-22, FMNH 182383	19D	14.68±0.189 (13.0-16.05)	19.50±0.169 (18.05-20.7)	0.753±0.008 (0.703-0.830)	5¾ (5½+-6⅛+)
WA-22, FMNH 182695	12L&D	14.89±0.157 (14.05-15.9)	19.81±0.185 (18.85-20.9)	0.752±0.007 (0.718-0.798)	5¾ (5½−-6−)
WA-22, FMNH 182507	18L	15.03±0.228 (13.5-16.7)	19.98±0.218 (18.8-22.1)	0.752±0.008 (0.712-0.831)	5¾+ (5½−-6⅛+)
WA-23, FMNH 182302	15D	14.59±0.171 (13.05-15.7)	19.50±0.218 (18.05-20.95)	0.749±0.009 (0.689-0.812)	5¾ (5⅜+-6−)
WA-23, FMNH 182492	7L	15.30±0.381 (14.1-16.55)	20.30±0.462 (18.5-21.9)	0.754±0.012 (0.718-0.810)	5¾+ (5⅝−-6⅛−)
WA-23, FMNH 182510	21L	15.04±0.206 (13.45-17.05)	20.37±0.187 (18.7-21.6)	0.739±0.009 (0.657-0.806)	5⅞ (5½−-6⅛+)
WA-171, FMNH 199728	26L	15.03±0.147 (13.8-16.95)	19.65±0.123 (18.35-20.85)	0.766±0.008 (0.705-0.869)	5¾ (5−-6½)

Table 153: Local variation in *Rhagada capensis* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
WA-171, FMNH 199701	69L	14.83±0.099 (13.25-17.05)	19.93±0.089 (18.55-21.7)	0.745±0.005 (0.663-0.887)	$5\frac{3}{4}$ ($5\frac{3}{8}$–-$6\frac{1}{8}$–)
WA-171, FMNH 199848	23L	15.45±0.296 (12.7-20.4)	20.24±0.183 (18.75-21.5)	0.764±0.015 (0.671-1.032)	$5\frac{3}{4}$ ($5\frac{1}{4}$+-$6\frac{1}{4}$–)
WA-958, FMNH 212487	19D	14.27±0.153 (13.3-15.5)	19.50±0.153 (17.85-20.55)	0.732±0.007 (0.679-0.784)	$5\frac{3}{4}$ ($5\frac{1}{2}$–-$6\frac{1}{8}$–)
WA-958, FMNH 212488	67L	14.56±0.084 (13.1-16.6)	19.57±0.088 (17.5-21.35)	0.744±0.004 (0.692-0.844)	$5\frac{7}{8}$– ($5\frac{1}{2}$–-$6\frac{3}{8}$–)
WA-21, FMNH 182373	7D	13.98±0.307 (12.85-15.15)	18.69±0.290 (18.05-20.1)	0.748±0.009 (0.702-0.771)	$5\frac{3}{4}$ ($5\frac{5}{8}$–-$6\frac{1}{8}$–)
Goat Cave					
WA-17, FMNH 182497	7L	16.72±0.286 (15.45-18.0)	22.21±0.212 (21.3-22.75)	0.753±0.011 (0.712-0.791)	$5\frac{7}{8}$ ($5\frac{1}{2}$+-6+)
WA-17, FMNH 182512	4L	17.33±0.432 (16.5-18.35)	21.87±0.320 (21.45-22.8)	0.793±0.021 (0.763-0.855)	$6\frac{1}{8}$ (6+-$6\frac{1}{4}$–)
WA-17, FMNH 182465	6L	17.47±0.268 (16.6-18.3)	22.52±0.285 (21.5-23.4)	0.776±0.011 (0.745-0.823)	6 ($5\frac{7}{8}$-$6\frac{1}{8}$)
WA-17, FMNH 182653	4L	16.72±0.390 (15.9-17.75)	22.17±0.298 (21.7-23.05)	0.754±0.012 (0.719-0.770)	6 ($5\frac{7}{8}$–-$6\frac{1}{4}$–)
Charles Knife Road					
WA-176, FMNH 199424	8D	13.64±0.308 (12.8-14.9)	19.31±0.282 (18.4-20.55)	0.707±0.016 (0.625-0.773)	$5\frac{3}{4}$+ ($5\frac{1}{2}$+-$6\frac{1}{4}$–)

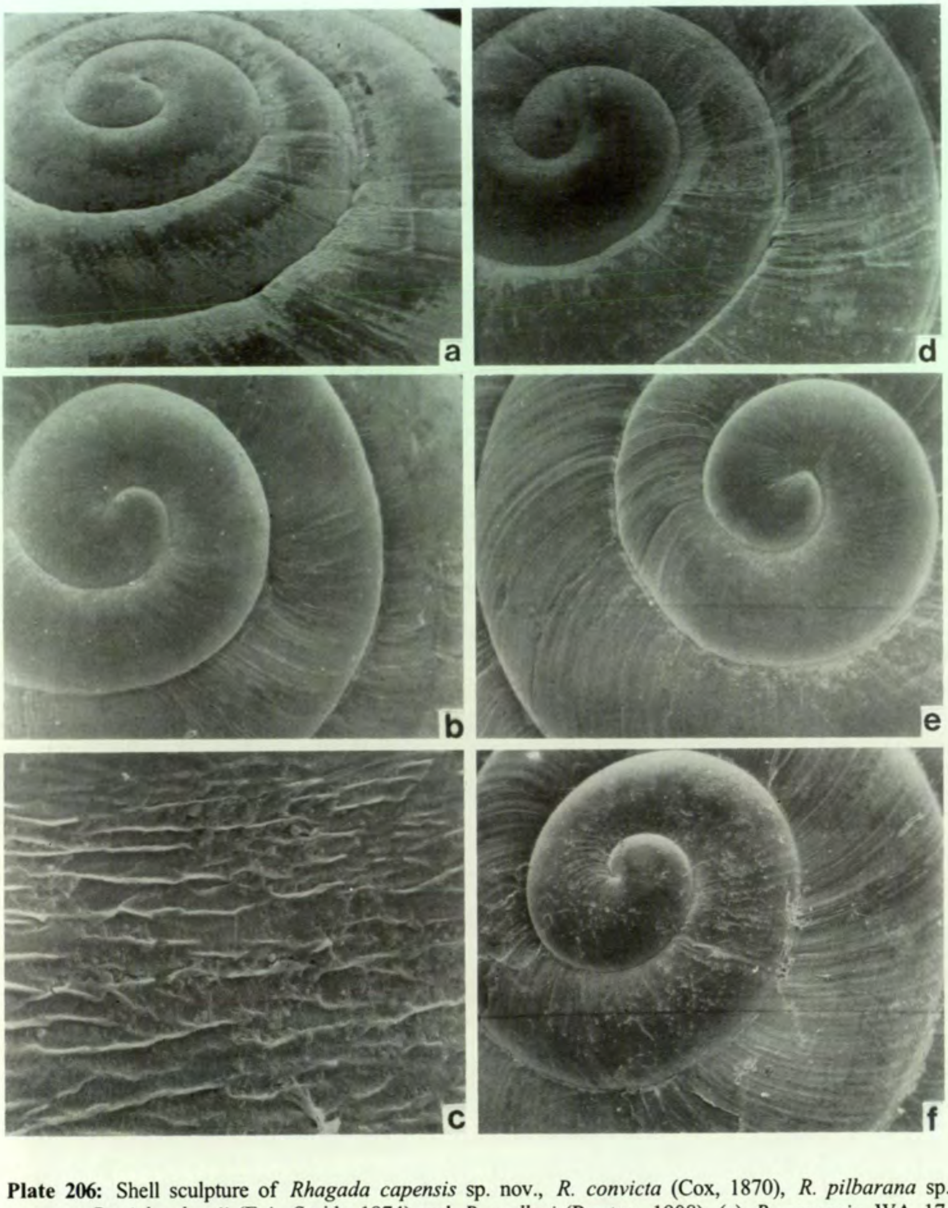


Plate 206: Shell sculpture of *Rhagada capensis* sp. nov., *R. convicta* (Cox, 1870), *R. pilbarana* sp. nov., *R. richardsonii* (E.A. Smith, 1874) and *R. radleyi* (Preston, 1908): (a) *R. capensis*. WA–17, Goat Cave, near Central Hill, Cape Range, WA. FMNH 182642. a is apex and spire at 15.5X; (b–c) *R. convicta*. WA–180, Intercourse Island road, Dampier, WA. FMNH 200274. b is apex and spire at 17.2X. c is microsculpture at 425X; (d) *R. pilbarana*. WA–182, Mt Herbert, Chichester Range, WA. FMNH 199785. d is apex and spire at 16X; (e) *R. richardsoni*. WA–1,058, Cape Keraudren, E of Port Hedland, WA. FMNH 211983. e is apex and spire at 17.4X; (f) *R. radleyi*. WA–417, Glen Florrie Station, Pilbara, WA. FMNH 199306. f is apex and spire at 17.5X.

Holotype

WAM 761.87, WA–174, Goat Cave near Central Hill, Cape Range, Western Australia. 22°15'33"S, 113°56'18"E. Collected 28–29 September 1976 by A. Solem. Height of shell 16.75 mm, diameter 22.45 mm, H/D ratio 0.746, whorls 6+, umbilicus completely closed by a broad callus.

Paratopotypes

FMNH 199732, 1 LA from the type locality.

Paratypes

WESTERN AUSTRALIA: Scrubby Range, (WA–51, 20.2 km E of Exmouth road, opposite Cardabia turnoff, WAM 826.87, SAM D18178, AM C.200,731, QM 52995, MV F.59465, FMNH 182349, FMNH 182549, 16 LA, 10 DA, 13 LJ, 8 DJ; WA–170, WAM 825.87, SAM D18177, AM C.200,732, FMNH 199734, FMNH 199907, 15 LA, 5 LJ; WA–957, FMNH 212485–6, 13 LA, 4 DA, 2 LJ); 10 miles from Ningaloo on Ningaloo-Exmouth road, WAM 331.74, 8 LA, 8 LJ; 2 miles E of Norwegian Bay (22 August 1968, WAM 388.74, 4 LA); Stn 221, Learmonth-Cape Range crest road (W. Turnbull!, FMNH 171633, FMNH 171635, 12 DA, 11 DJ); vicinity of Goat Hill, near Central Hill (WA–14, FMNH 182472, FMNH 182668, 3 LA, 2 DA; WA–15, FMNH 182488, 5 LA; WA–17, FMNH 182465, FMNH 182479, FMNH 182497, FMNH 182512, FMNH 182642, FMNH 182653, FMNH 182702, 33 LA; WA–175, FMNH 199440, FMNH 199755, FMNH 199902, 2 LA, 3 DA, 1 LJ; WA–178, FMNH 199403, FMNH 199406, 8 DA; WA–959, FMNH 212497, 3 LA; G. Hitchin! 15 May 1965, FMNH 171626, 3 LA; W. Turnbull! 6 July 1964, FMNH 171623, 2 DA, 3 DJ); 1.8 km N of Goat Cave on crest road (WA–960, FMNH 212507–8, 2 DA, 1 LJ, 1 DJ); 2.4 miles N of Goat Cave on crest road (WA–18, FMNH 182557, 3 DA, 1 DJ); 18.55 km N of Ningaloo Homestead on Yardie Creek track (WA–21, FMNH 182373, 7 DA, 10 DJ); 23.7 km N of Ningaloo Homestead on Yardie Creek track, W side Cape Range (WA–22, WAM 828.87, SAM D18180, FMNH 182383, FMNH 182507, FMNH 182695, 30 LA, 24 DA, 2 LJ, 4 DJ; WA–23, WAM 827.87, SAM D18179, AM C.200,733, FMNH 182302, FMNH 182492, FMNH 182510, 28 LA, 15 DA, 5 LJ, 1 DJ; WA–171, WAM 824.87, SAM D18176, AM C.200,734, QM, MV, FMNH 199701, FMNH 199705, FMNH 199728, FMNH 199848, FMNH 199950; WA–958, WAM 822.87, WAM 823.87, SAM D18174–5, AM C.200,735, QM 52996, MV F.59449, FMNH 212487–8, 67 LA, 19 DA, 2 LJ, 3 DJ; WA–1074–5, 24 May 1989, FMNH 221731–2, FMNH 221734–5, 27 LA, 19 DA); Charles Knife Road 8.8 km W of turnoff from Exmouth road (WA–176, FMNH 199424, 8 DA, 2 DJ); Thomas Carter Lookout, Charles Knife Road (WA–1079, FMNH 221761, FMNH 221755, 3 LA); Shothole Canyon (G. M. Storr! 19 October 1962, WAM 304.74, 5 DA, 6 DJ; G. W. Kendrick! 21 August 1975, WAM 1375.75, 1 DJ); Vlaming Head (WAM 1361.75, 4 LA).

Range

Rhagada capensis sp. nov. has been collected from 23°07'S in the Scrubby Range to Vlaming Head (21°48'S, 114°06'E), near the N tip of the North West Cape, a distance of 145 km (**Maps 37–38**). This is not a continuous distribution, the plains areas between the Scrubby and Rough Ranges, and between the Rough and Cape Ranges, being occupied by populations of *Rhagada convicta* (Cox, 1876) (**Maps 37–38**). *R. capensis* is found most commonly under large spinifex tussocks near limestone exposures, less frequently in rocky rubble of the limestone hillsides.

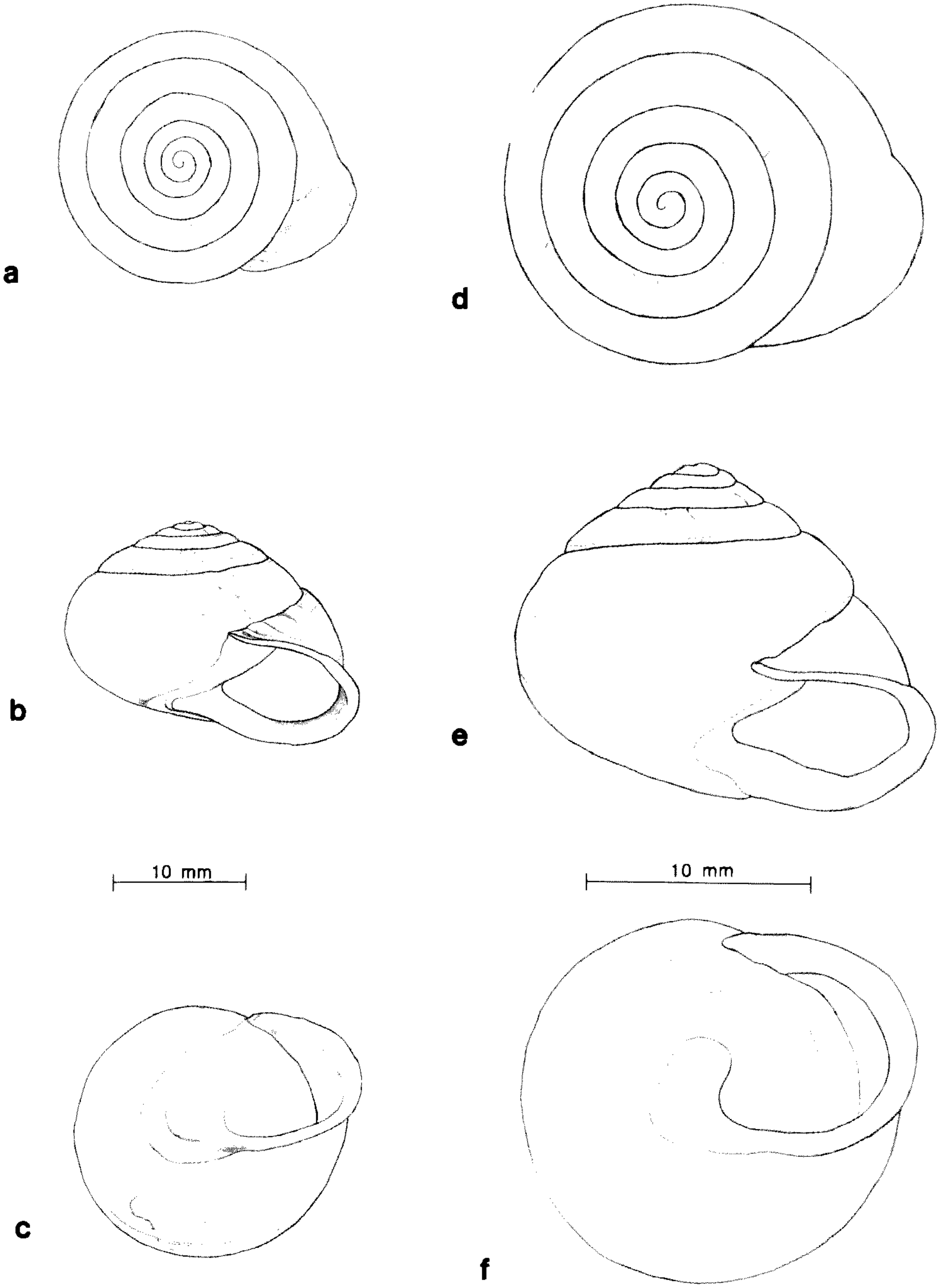


Fig. 406: Shells of *Rhagada capensis* sp. nov. and *R. convicta* (Cox, 1870): (a–c) Holotype of *R. capensis*. WAM 761.87. WA–174, Goat Cave, near Central Hill, Cape Range, WA; (d–f) *R. convicta*. FMNH 41601 ex W. F. Webb, J. Ritchie, Jr. Probable type lot example. Scale line equals 10 mm. Drawings by Linnea Lahlum (a–c) and Margaret Baker (d–f).

Diagnosis

Shell very large, adult diameter 16.96–24.25 mm (mean 20.01 mm), with 4 5/8 to 6 3/4+ (mean 5 3/4) rather tightly coiled whorls (**Fig. 406a**). Apex and spire strongly elevated, usually somewhat rounded above (**Fig. 406b**), shell height 12.55–20.7 mm (mean 15.10 mm), H/D ratio 0.623–0.991 (mean 0.775). Body whorl evenly rounded. Shell apex (**Plate 206a**) nearly smooth, spire and body whorl with irregularly spaced, radial growth ridgelets. Umbilicus (**Fig. 406c**) completely closed by an expanded columellar callus. Body whorl descending slightly to moderately behind lip, which is thin and moderately expanded. Numerous red to orange spiral colour bands normally present, with the supraperipheral usually darker and more prominent. Based on 488 measured adults.

Genitalia (**Figs 407b, 408a–c, 409a–b**) with enlarged albumen gland (GG), very short free oviduct (UV), slightly to moderately kinked spermatheca (S), medium to long vagina (V) and medium length epiphallic caecum (EC). Penis (P) medium length to long, slender, verge (PV) cylindrical, with nearly smooth surface and long posterior sperm groove. Head wart (**Fig. 408c**) elongate-ovate, large, dark grey in colour, about same tone as head.

Central and early lateral teeth of radula highly variable. In central Cape Range examples (**Plate 213a–b**), the anterior flare is greatly reduced, there is a very high cusp shaft angle and pointed cusp tip, no cusp tip curvature and the inter-row basal plate support ridge is specialised; in animals from the Scrubby Range (**Plate 214a**) and near Norwegian Bay (**Plate 214e**), the cusp shaft angle is reduced and the cusp tip is much blunter; and at Vlaming Head (**Plate 231d**), the laterals have even lower cusp shaft angle, blunter cusp tip and still reduced anterior flare. Late lateral teeth in central Cape Range specimens (**Plate 213c–d**) with greatly enlarged anterior flare, rapidly increasing ectocone, lowered cusp shaft angle and slight endocone; less enlarged anterior flare in material from Scrubby Range (**Plate 214b**) and only slight anterior flare size increase (**Plate 214f**) in specimens from near Norwegian Bay. Specimens from N of Ningaloo (**Plate 214d**) have modest anterior flare enlargement, while those from Vlaming Head (**Plate 231e–f**) have lowered cusp angle but the anterior flare is greatly enlarged as in the central Cape Range examples. Marginal teeth (**Plates 213e, 214b, d, f, 231e–f**) without unusual features. Jaws (**Plates 213f, 215a–c**) from all areas with reduced vertical ribbing showing individually variable spacing.

Discussion

Size and shape variation in *Rhagada capensis* is considerable (**Table 153**), both between and within areas. The live-dead data are inadequate, since mainly live examples were collected. At WA–23 (N of Ningaloo), live examples taken in January 1974 from a basically NW facing outcrop are noticeably larger, but nearly ten years later (WA–958, 10 July 1983), live and dead specimens from a more westerly portion of the same promontory are essentially identical in size and shape with the dead examples from 1974. Whether this is allochronic or sun exposure induced variation is unknown.

The variation within geographic area remains to be studied, since my collecting was focused on repetitive samples from the same populations to study changes, if any, in the reproductive system over the course of a year. The few differences shown among samples may represent time shifts in size distribution or different facies along a 10–20 metre zone. Because *Rhagada capensis* is less rock-associated than some of the other

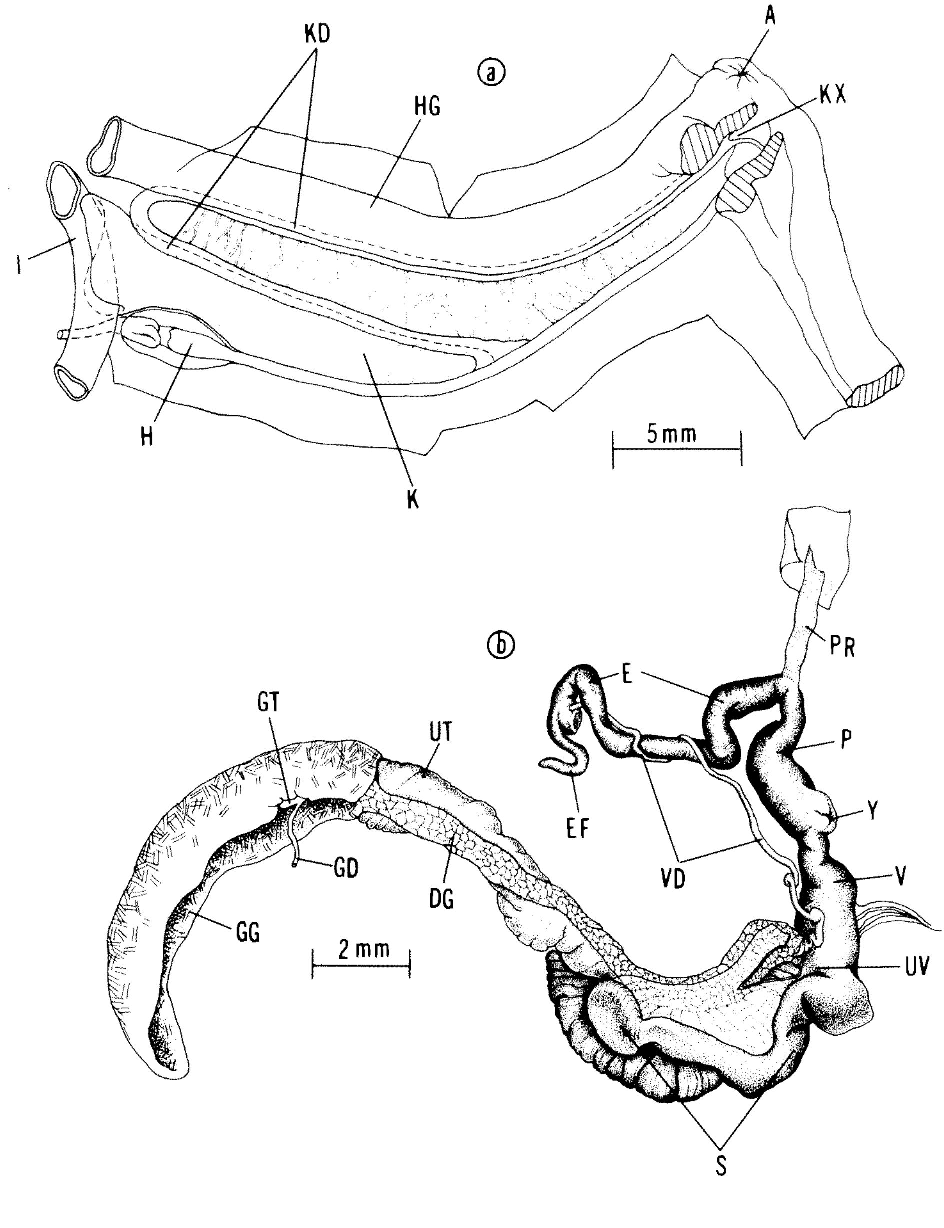


Fig. 407: Pallial region and whole genitalia of *Rhagada capensis* sp. nov.: Goat Cave, near Central Hill, Cape Range, WA. June–July 1964. FMNH 171623, Dissection A: (a) pallial region; (b) whole genitalia. Scale lines as marked. Drawings by Carole W. Christman.

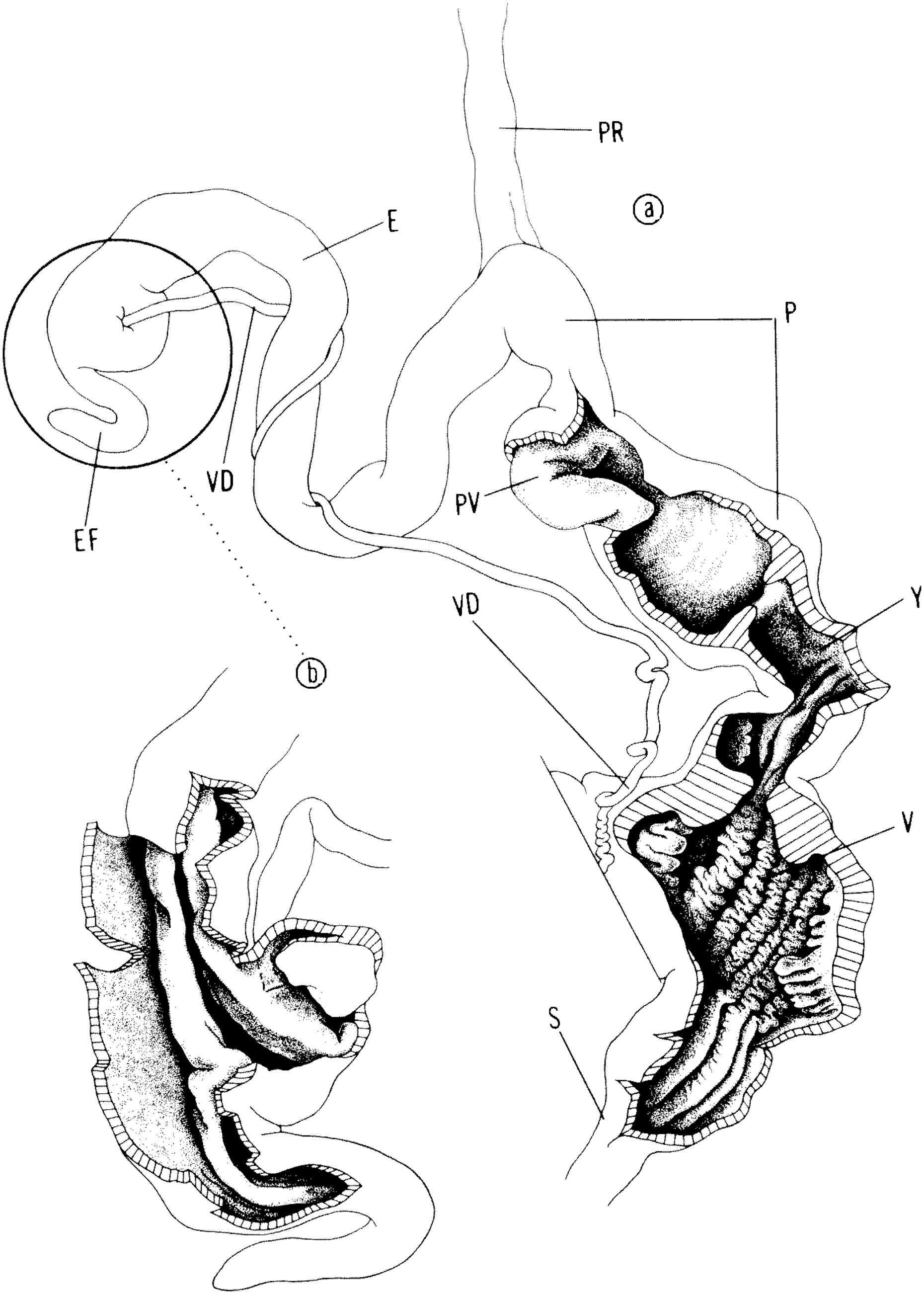


Fig. 408: Interior of penis, epiphallus and vagina of *Rhagada capensis* sp. nov. Goat Cave, near Central Hill, Cape Range, WA. June–July 1964. FMNH 171623, Dissection A: (a) interior of penis and vagina; (b) interior of epiphallus; (c) head wart. Scale lines as marked. Drawings by Carole W. Christman (a–b) and Linnea Lahlum (c).

Cape Range camaenids, samples were taken from a somewhat larger area, introducing the possibility of micro-variation.

A summation of size variation from four local areas follows:

	Goat Cave (53 specimens)	N of Ningaloo (329 specimens)
Height	16.71 (14.9–17.25)	14.78 (12.65–20.4)
Diameter	22.13 (20.25–24.25)	19.75 (16.95–22.8)
H/D ratio	0.759 (0.736–0.855)	0.714 (0.563–0.869)
Whorls	6– (4 7/8+ – 6 3/8–)	5 3/4 (4 7/8+ – 6 1/2)
	Scrubby Range (69 specimens)	Shothole Canyon (4 specimens)
Height	15.29 (12.55–16.8)	13.51 (12.6–14.7)
Diameter	19.46 (16.6–21.4)	20.09 (19.15–21.3)
H/D ratio	0.786 (0.674–0.877)	0.673 (0.623–0.719)
Whorls	5 1/2– (4 5/8+ – 6 1/8+)	5 1/2+ (5 3/8 – 5 5/8)

The central Cape Range examples are significantly larger and with a higher whorl count; the Scrubby Range specimens are smaller but with a higher spire; and the few

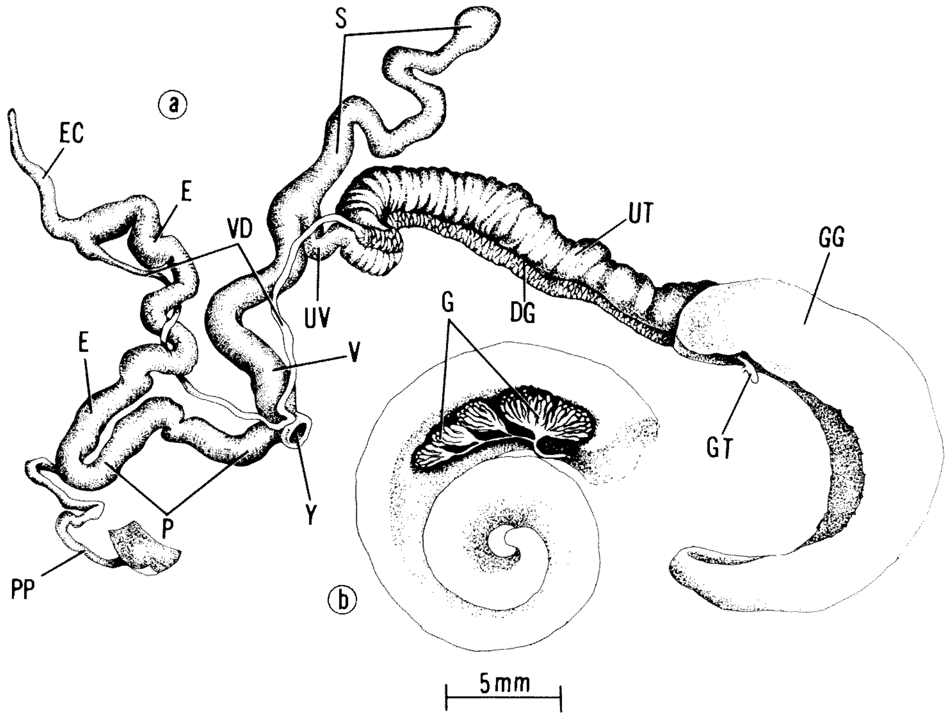


Fig. 409: Genitalia of *Rhagada capensis* sp. nov.: Vlaming Head, N tip of Cape Range peninsula, WA. October 1975. WAM 1361.75, Dissection B: (a) whole genitalia; (b) ovotestis. Scale lines as marked. Drawings by Elizabeth A. Liebman.

Shothole Canyon shells are noticeably lower spired. Much more collecting and study are needed.

The radular and jaw variation (**Plates 213–215a–c, 231d–f**) is spectacular, geographical and correlates at least partly with patterns of microsympatry. This is discussed further below. In the central Cape Range, where the lateral teeth are most altered, *Rhagada capensis* in January 1974 was observed feeding on the new green leaves of herbaceous plants that sprouted in the three days following a probable 25+ mm rainfall.

The name *capensis* honours the Cape Range, primary habitat of this species.

RHAGADA CONVICTA (COX, 1870)

(Plates 206b–c, 215d–f, 216a–f, 217a–f; Figs 406d–f, 410a–c; Maps 37–38, 40)

Helix convicta Cox, 1870, *Proc. Zool. Soc. London,* **1870:** 171, plt. XVI, fig. 6 – Nichol (= Nickol) Bay, West Australia; Pfeiffer 1876, *Monog. Helic. viv.*, **7:** 323; Brazier 1880, *Jour. Conchyl.*, **28:** 308.

Helix (*Rhagada*) *convicta* Cox, Pilsbry 1890, *Man. Conch.*, (2) **6:** 187–188 (in part), plt. 14, fig. 65, plt. 35, figs 8–10; E. A. Smith 1894, *Proc. Malac. Soc. London,* **1:** 89 – Cossack and Bezout Island, Western Australia (J. J. Walker).

Thersites (*Rhagada*) *convicta* (Cox), Pilsbry 1894, *Man. Conch.*, (2) **9:** 136.

Rhagada convicta (Cox), Hedley 1916, *Jour. Roy. Soc. Western Austr.,* **1:** 69 – check list citation; Iredale, 1938, *Aust. Zool.,* **9** (2): 112 – check list citation; Iredale 1939, also published as *Jour. Roy. Soc. Western Aust.,* **25:** 61–62 (in part), plt. IV, fig. 10; Richardson 1985, *Tryonia*, 12: 265.

Comparative remarks

Rhagada convicta, which ranges in plains areas from the Minilya River NE to Dampier and Cossack (**Maps 37–38**), is a large species (mean diameter 20.15 mm), with slightly increased whorl count (mean 5 1/2), strongly elevated spire (**Fig. 406e**, mean H/D ratio 0.759), aperture slightly deflected behind lip, not narrowed, lip expanded, umbilicus closed by broad expansion of columellar lip (**Fig. 406f**). Shell white or with a light brownish suffusion, a narrow supraperipheral and/or subsutural red or brownish spiral color band often present, frequently reduced in tone to faintly coloured or even a translucent zone. Rarely, examples from wetter areas show a few traces of accessory spiral bands. Shell apex (**Plate 206b**) with faint traces of sculpture, spire and body whorl with irregular very fine growth ridgelets. *R. capensis*, which inhabits the Scrubby and Cape Ranges (**Maps 37–38**), is very similar in shell features, differing most obviously in the more expanded lip (**Figs 406a–c**) and normal presence of accessory colour bands. *R. pilbarana* sp. nov., from Python Pool and Mt. Herbert, in the Chichester Range (**Map 37**), is much larger (mean diameter 22.97 mm), with a higher whorl count (mean 6), has a much more expanded shell lip (**Figs 411a–b**), and the two spiral colour bands are bright red. The Dampier Archipelago (**Map 40**) species, *R. perprima* Iredale, 1939, is the same size and shape as *R. convicta*, but has the bright colour bands and expanded lip (**Figs 411c–d**). None of the other smooth-surfaced

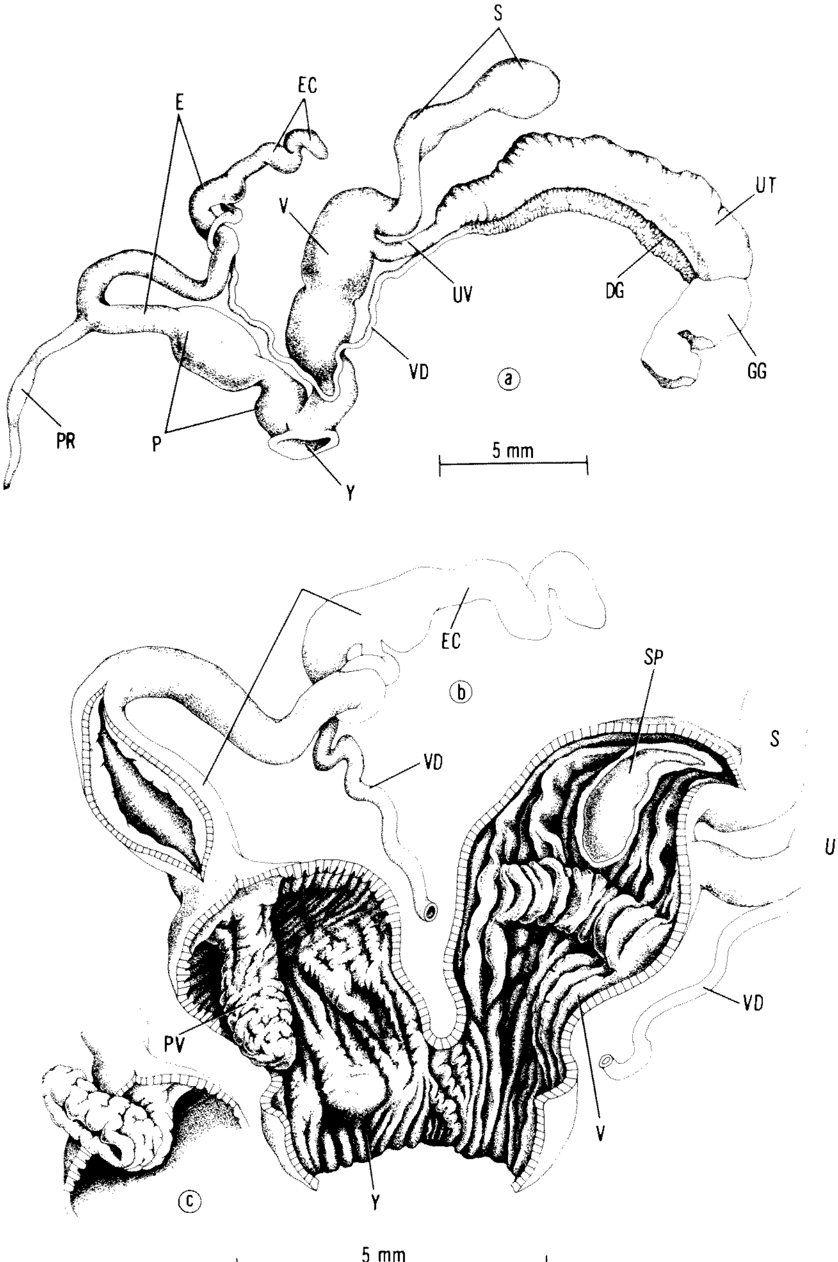


Fig. 410: Genitalia of *Rhagada convicta* (Cox, 1870): WA–27, sides of dry creek 8.7 km E of Bullara Homestead, Bullara-Giralia road, N of Scrubby Range, WA. 23 January 1974. FMNH 182705, Dissection A: (a) whole genitalia; (b) interior of penis and vagina, note presence of spermatophore; (c) detail of verge. Scale lines as marked. Drawings by Elizabeth A. Liebman.

Rhagada is at all similar in size and shape. Body colour of *R. convicta* is yellow-white, with a grey tone to the head wart. Anatomically (**Figs 410a–c**), *R. convicta* generally has only a generally only slightly kinked spermatheca (S), large albumen gland (GG), long epiphallic caecum (EC), short to medium length penis (P), verge (PV) tapering, with corrugated surface and short posterior groove. *R. capensis* differs most obviously (**Figs 407b, 408a–b, 409**) in its long, cylindical verge (PV), short epiphallic caecum (EC), generally more strongly kinked spermatheca (S) and in having the body with grey to black colouration on the head, neck and tail. *R. pilbarana* sp. nov. (**Figs 412a–b**) has a greatly elongated verge (PV), while *R. perprima* (**Figs 413a–b**) has a very large epiphallic caecum (EC). The jaw (**Plate 215d–f**) consistently has more prominent vertical ribs than in *R. capensis* (**Plate 215a–c**).

Holotype

AM C.33433, Nichol (= Nickol) Bay, Western Australia. Height of shell 17.25 mm, diameter 23.1 mm, H/D ratio 0.802, whorls 5 7/8, umbilicus completely closed.

Paratopotypes

AM C.33433, AM C.64905, FMNH 41601, 9 DA from the type collection.

Material studied

WESTERN AUSTRALIA: Wandagee Station, Minilya River (WA–962, WAM 834.87, FMNH 212513, 2 DA; WA–963, 11.4 km W of Wandagee, FMNH 212514, 1 DA); Williambury Station (J. L. White! 3 October 1976, WAM 470.77, 3 DA); Toothawarra Creek, Scrubby Range (T. A. Darragh and G. W. Kendrick! 4 April 1969, WAM 374.74, 6 LA); creek crossing *ca.* 3 miles E of Bullara Homestead (R. W. George! 9 April 1961, WAM, 6 DA); 6 miles E of Bullara (G. M. Storr! 19 October 1962, WAM, 7 DA); Bullara Station, within 200 yards of Cyclone Bore (T. A. Darragh & G. W. Kendrick! 4 April 1969, WAM, 1 DA); creek beds 11 km W of Giralia Hstd (E. Lundelius and W. Turnbull! 21 October 1976, WAM 461.77, 2 DA); 7 miles W of Giralia Homestead, near creek (G. Hitchin & G. W. Kendrick! 25 May 1965, WAM, 10 DA); creek beds along Bullara-Giralia road, Scrubby Range (WA–27, WAM 830.87, SAM D18182, AM, QM, MV, FMNH 182756, FMNH 182705, 60 LA, 16 DA, 1 DJ; WA–179, WAM 833.87, SAM D18185, AM, QM, MV, FMNH 199647, FMNH 199772, FMNH 200171, FMNH 199889, 119 LA, many LJ; #64, FMNH 199062, 20 DA, 10 DJ; WA–418, FMNH 199742–4, 42 LA, several LJ); near Giralia Homestead (#227, FMNH 171640, 36 DA, 4 DJ); plains E of Cape Range (banks of Exmouth Gulf, S of Charles Knife Road, WAM 1363.75, 2 DA; Exmouth Gravel Reserve (WA–1078, FMNH 221741, 4 LA); WA–19, Exmouth rubbish dump, WAM 829.87, SAM D18181, AM, FMNH 182452, FMNH 182648, 57 LA, 25 DA, many LJ, 31 DJ); Exmouth (WAM 1363.75, 2 DA); Muiron Islands (W. K. Youngson! 11 June 1970, 1 DA); South Muiron Island (B. Hutchins! 4 June 1977, WAM 1113.81, 4 DA, 1 DJ; W. K. Youngson! 11 June 1970, 5 DA, 6 DJ); North Muiron Island (T. Prince and W. K. Youngson! 12 July 1970, WAM 344.74, 1 LA); Onslow road, 5.8 miles NNW of Roebourne road (WA–45, WAM 835.87, SAM D18186, AM, QM, MV, FMNH 182335, FMNH 182271, FMNH 182541, 8 LA, 68 DA, 8 LJ, many DJ); Challyan Pool, Onslow District (I. Crawford! 5 January 1966, WAM, 2 DA); 1 mile W of Onslow (WA–44, FMNH 182340, 3 DA, 1 DJ); 13 km S of Cane River crossing (C. Bryce! 13 November 1976, WAM, 2 DA); Yarraloola, off Pannawonica road (WA–29, FMNH 182595, 6 DA, 3 DJ); Yarraloola Homestead, N bank Robe River (WA–28, FMNH 182641, 6 DA); Cooyapooya road, 5.2–7.9 miles E of Roebourne (WA–38, FMNH 182364, 12 DA, 1 DJ); S of Bob Well on Miller Creek, Cooyapooya Station (B. J. Wright! 1 January 1968, WAM, 2 DA); Maitland River crossing (WA–30, FMNH 182411, 2 LA; B. G. Muir! 12 August 1972, WAM, 2 DA); Karratha (WA–33, WAM 832.87, SAM D18184, AM, QM, MV, FMNH 182647, FMNH 182641, 31 LA, 4 DA, several LJ); 1.5 miles ESE of Karratha Homestead (P. Roberts! 25 July 1976, WAM 10 DA, 1 DJ); Cossack (WA–35, NW of courthouse, FMNH 182550, 14 LA, 3 DA, 7 LJ); Intercourse Island road, S of Dampier (WA–32, FMNH 182739, 2 DA; WA–32a, WAM 831.87, SAM D18183, AM, QM, MV, FMNH 182597–8, 29 LA, many LJ; WA–180, FMNH 199738, FMNH 199876, FMNH 199644, FMNH 200274–5, 116 LA, 3 DA, many LJ, 11 DJ; WA–723, FMNH 205367, 12 LA, 4LJ; WA–1081, FMNH 221756, 1 DA); Dampier (B. R. Wilson! 21 May 1973, WAM, 15 DA, 7 DJ).

Range

Rhagada convicta has the largest range of any *Rhagada* species, with a mainly coastal plains distribution (**Map 38**) extending from the Minilya River, between at least Wandagee and Williambury Stations (23°52'S), thence N to Exmouth, both Muiron Islands, Onslow and the Dampier-Karratha-Cossack area. This covers a N-S range of about 430 km in a direct line and perhaps 475 km along the coastal arc. The E-W range probably does not exceed 120 km, since *R. convicta* is a species of the low plains. It is replaced in the Scrubby and Cape Ranges by *R. capensis* (**Map 37**). The inland *R. radleyi* Preston, 1908 extends in the hills from Millstream (21°37'S, 117°05'E), Fortescue River S to Joy Helen Mine (23°14'S, 115°48'E) on the Henry River, a tributary of the Ashburton River. There is about a 90–100 km gap between the Dampier and Cossack records of *R. convicta* and the nearest records of *R. radleyi* and 150 km between the Meilga record of *R. radleyi* and the Giralia records of *R. convicta* (**Map** 37).

Diagnosis

Shell very large, adult diameter 16.55–23.95 mm (mean 20.15 mm), with 5– to 6 5/8– (mean 5 1/2) rather tightly coiled whorls (**Fig. 406d**). Apex and spire strongly and mostly evenly elevated (**Fig. 406e**), shell height 12.9–18.65 mm (mean 15.29 mm), H/D ratio 0.671–0.906 (mean 0.759). Body whorl evenly rounded. Apex with traces of sculpture, spire and body whorl (**Plate 206b**) with irregularly spaced radial micro-ridgelets and typical anastomosing irregular periostracal ridgelets (**Plate 206c**). Umbilicus (**Fig. 406f**) completely closed by broad expansion of columellar lip. Body whorl usually descending behind lip, which is modestly expanded and often thickened internally, aperture not narrowed. Colour white, usually with typical supraperipheral and subsutural red spiral bands, which may be reduced to faint brownish traces or even a narrow translucent zone. Some examples with a brownish spire suffusion. Based on 721 measured adults.

Genitalia (**Figs 410a–c**) with enlarged albumen gland (GG), shortened prostate-uterus, spermatheca (S) only slightly kinked, short free oviduct (UV), vagina (V) variable in length and diameter. Epiphallic caecum (EC) long and slender. Penis (P) short to medium long, verge (PV) triangular to tapering, with corrugated surface, short lateral sperm groove. Head wart small, circular, slightly darker in tone than neck region.

Central and lateral teeth of radula (**Plates 216a, c–d, f, 217a, b, e**) with modest (**Plates 216f, 217a–b**) to prominent (**Plates 216a, c, 217e**) anterior flare, normal to somewhat elevated (60°) cusp shaft angle, bluntly pointed and slightly curved cusp tip; ectocone usually not appearing until late laterals. Late laterals (**Plates 216b, e, 217c, d**) with greatly enlarged anterior flare, prominent ectocone and small endodone; lateromarginal transition and marginals (**Plates 216b, e, 217d, f**) typical. Jaws (**Plate 215d–f**) with a few relatively prominent vertical ribs, highly variable in width, number and position.

Discussion

Whereas *R. capensis* is hill system associated and shows considerable area variation (see above), *R. convicta* has been taken primarily in open situations or along creek and river beds and is much less variable. The reduced shell and body colouration of *R. convicta* and the genital differences of shorter epiphallic caecum (EC) and smooth cylindrical verge (PV) in *R. capensis* (**Figs 407b, 408a, 409**) contrast with the very long epiphallic caecum and tapering verge with corrugated surface found in *R. convicta* (**Figs 410a–c**).

Detailed studies may demonstrate that *R. convicta*, as delineated here, is a complex of species but available data are not sufficient to subdivide the populations into systematic entities.

There is some local variation in size (**Table 154**). The largest individuals were collected near Cossack (WA–35), Karratha (WA–33) and dunes near the Exmouth dump (WA–19). Specimens from the Muiron Islands and the types from Nickol Bay (AM C.33433, AM C.33464) also are large. Those from the Dampier area (WA–32a, WA–180, WA–723) are somewhat smaller, while those from Onslow and the Bullara-Giralia area SE of the Cape Range are the smallest. There is considerable within-population variation (**Table 154**), and a summary of size variation within the Dampier-Cossack and Bullara-Giralia areas is instructive:

	Dampier-Cossack (280 specimens)	Bullara-Giralia (257 specimens)
Height	15.51 (12.95–18.3)	15.05 (12.9–17.2)
Diameter	20.46 (17.6–23.95)	19.99 (16.55–22.6)
H/D ratio	0.759 (0.671–0.906)	0.754 (0.679–0.864)
Whorls	5 1/2+ (5 1/8– – 6+)	5 3/8+ (5– – 5 3/4+)

While the means are different, the ranges are very similar. It seems probable that local moisture factors are responsible for the size and shape variation. The comparatively minor radular variation observed (**Plates 216–217**) probably reflects the fact that rarely is *R. convicta* found sympatrically with other camaenids. In the Bullara-Giralia area and at the Exmouth rubbish dump it occurs with *Plectorhagada scolythra* (WA–19, WA–27, WA–179, WA–418) but elsewhere it is the only camaenid present and thus not subject to snail competition for food.

Table 154: Local variation in *Rhagada convicta.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Minilya River Williamburg, Stn, WAM 470.77	2D	14.07 (13.45-14.7)	18.56 (18.15-18.95)	0.757 (0.741-0.774)	$5\frac{3}{8}$ ($5\frac{3}{8}$−-$5\frac{3}{8}$+)
S of Exmouth Gulf					
Toothawarra Creek, WAM 374.74	6L	15.76±0.220 (14.85-16.3)	20.90±0.224 (20.05-21.6)	0.755±0.014 (0.722-0.812)	$5\frac{1}{2}$− ($5\frac{1}{4}$-$5\frac{5}{8}$)
WA-27, FMNH 182705	76L&D	15.15±0.082 (13.35-17.2)	20.05±0.083 (17.85-21.6)	0.756±0.003 (0.679-0.826)	$5\frac{1}{2}$− ($5\frac{1}{8}$-$5\frac{3}{4}$+)
WA-179, FMNH 199647	70L	14.93±0.94 (13.45-16.65)	19.93±0.118 (16.55-22.6)	0.750±0.005 (0.687-0.864)	$5\frac{1}{2}$− (5+-$5\frac{5}{8}$+)
WA-179, FMNH 200171	18L	15.33±0.227 (13.6-17.05)	20.37±0.184 (19.25-22.55)	0.753±0.009 (0.687-0.834)	$5\frac{3}{8}$+ ($5\frac{1}{8}$+-$5\frac{3}{4}$+)
WA-179, FMNH 199772	19L	15.16±0.180 (13.8-17.05)	20.03±0.203 (18.85-22.2)	0.747±0.008 (0.703-0.831)	$5\frac{1}{2}$− ($5\frac{1}{8}$+-$5\frac{5}{8}$−)
WA-179, FMNH 199889	12L	15.15±0.213 (13.85-16.15)	20.24±0.177 (19.3-21.15)	0.749±0.009 (0.704-0.812)	$5\frac{3}{8}$+ (5−-$5\frac{5}{8}$+)
WA-418, FMNH 199743	8L	14.60±0.334 (13.1-16.25)	19.72±0.391 (18.15-21.8)	0.741±0.010 (0.699-0.779)	$5\frac{3}{8}$+ ($5\frac{3}{8}$−-$5\frac{1}{2}$−)
WA-418, FMNH 199744	11L	14.48±0.228 (13.5-15.8)	19.27±0.272 (17.85-20.8)	0.751±0.006 (0.715-0.780)	$5\frac{1}{4}$+ ($5\frac{1}{8}$+-$5\frac{1}{2}$+)
WA-418, FMNH 199742	23L	15.00±0.177 (12.9-16.25)	19.84±0.165 (18.0-21.2)	0.756±0.006 (0.687-0.808)	$5\frac{1}{2}$− ($5\frac{1}{8}$−-$5\frac{5}{8}$+)

Table 154: Local variation in *Rhagada convicta* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Exmouth					
WA-19, FMNH 182452	75L&D	15.94±0.942 (13.8-17.85)	21.46±0.105 (19.5-23.95)	0.743±0.004 (0.675-0.820)	5¼+ (5¼−-6−)
WA-19, FMNH 182648	17D	17.28±0.189 (15.15-18.45)	21.74±0.191 (20.3-23.1)	0.795±0.007 (0.737-0.847)	5⅞− (5½−-6⅝−)
Onslow area					
WA-45, FMNH 182541	8L	14.25±0.180 (13.45-14.9)	18.59±0.161 (17.95-19.25)	0.767±0.007 (0.736-0.797)	5⅜− (5¼−-5½−)
WA-45, FMNH 182335	68D	14.51±0.077 (13.0-16.4)	18.88±0.078 (17.3-20.4)	0.769±0.003 (0.707-0.841)	5⅜ (5+-5¾+)
WA-44, FMNH 182340	7D	15.70±0.361 (14.15-16.8)	19.87±0.446 (18.0-21.65)	0.790±0.011 (0.761-0.842)	5½ (5⅛+-5¾−)
Robe River area					
WA-28, FMNH 182641	21L&D	15.75±0.154 (14.3-17.1)	20.67±0.165 (18.5-22.25)	0.763±0.006 (0.725-0.814)	5½+ (5¼+-6+)
WA-29, FMNH 182595	6D	16.56±0.308 (15.8-17.4)	20.89±0.324 (19.95-22.0)	0.793±0.015 (0.727-0.831)	5⅝+ (5½+-5⅞+)

Table 154: Local variation in *Rhagada convicta* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Dampier					
WA-32a FMNH 182597	29L	15.21±0.165 (13.05-16.8)	19.65±0.182 (17.7-21.55)	0.775±0.007 (0.723-0.907)	5⅝ (5¼+-5⅞+)
WA-180, FMNH 199876	13L	14.51±0.187 (13.5-15.7)	19.39±0.257 (17.85-21.1)	0.749±0.008 (0.681-0.805)	5½− (5⅛−-5¾+)
WA-180, FMNH 200275	42L	15.28±0.137 (13.1-17.0)	20.05±0.116 (17.9-22.2)	0.762±0.005 (0.680-0.832)	5½ (5+-5⅞−)
WA-180, FMNH 199644	30L	14.90±0.190 (13.0-17.1)	19.67±0.151 (17.9-21.2)	0.758±0.009 (0.671-0.895)	5½+ (5⅜−-5−)
WA-180, FMNH 199738	21L	14.85±0.213 (12.95-16.6)	19.21±0.214 (17.6-21.3)	0.774±0.010 (0.699-0.859)	5½− (5¼+-5⅞+)
WA-723, FMNH 205367	12L	15.23±0.128 (14.4-15.9)	20.04±0.179 (19.25-21.25)	0.760±0.007 (0.807-0.720)	5½+ (5⅜−-5¾+)
Karratha					
WA-33, FMNH 182647	14L	17.12±0.247 (14.65-18.3)	21.54±0.223 (20.15-22.85)	0.795±0.010 (0.728-0.867)	5¾− (5⅜+-5⅞−)
Cossack					
WA-35, FMNH 182550	17L&D	15.98±0.199 (14.1-17.15)	21.29±0.177 (19.95-22.95)	0.751±0.008 (0.677-0.799)	5½ (5⅜−-5⅝+)

RHAGADA PILBARANA SP. NOV.

(Plates 206d, 218a–c; Figs 411a–b, 412a–b; Map 37)

Comparative remarks

Rhagada pilbarana sp. nov., reported only from Python Pool and Mt Herbert, Chichester Range, Pilbara (**Map 37**), is the largest known species of the genus (mean diameter 22.97 mm), with high whorl count (mean 6), high but rounded spire (**Fig. 411b**, mean H/D ratio 0.753), aperture descending noticeably behind lip, not narrowed; lip well expanded, slightly thickened; umbilicus closed by expansion of columellar lip. Shell white with narrow, slightly supraperipheral red spiral colour band, often trace of subsutural band, rarely a few accessory colour bands. Shell apex (**Plate 206d**) with weak radial sculpture, spire and body whorl with radial growth ridgelets. *R. convicta,* from Cossack W to both sides of Exmouth Gulf and thence S to the Minilya River (**Map 38**), is smaller (mean diameter 20.15 mm) with a lower whorl count (mean 5 1/2), the spiral banding is less prominent and the shell lip is much less expanded (**Figs 406d–f**). *R. perprima* Iredale, 1939, from the Dampier Archipelago (**Map 40**), is quite similar in shell features (**Figs 411c–d**) but is much smaller (mean diameter 19.59 mm) and shows obvious anatomical changes. The inland *R. radleyi* Preston, 1908, from Millstream on the Fortescue River SW to Joy Helen Mine on the Henry River in the upper Ashburton River drainage (**Map 37**), is quite small in comparison (mean diameter 16.66 mm), with lower whorl count (mean 5 1/8), low spire (**Fig. 416b, e**, mean H/D ratio 0.696), slightly angulated periphery and often a slight umbilical crack. *R. richardsonii* (E. A. Smith, 1874), which ranges coastally from Depuch Island to Cape Keraudren, thence inland to Roy Hill on the Fortescue River and NE to the Oakover and Davies Rivers (**Map 37**), also is much smaller (mean diameter 17.79 mm), with lower whorl count (mean 5 1/4), usually many spiral colour bands and often a narrow umbilical crack. Anatomically, *R. pilbarana* (**Figs 412a–b**) has the albumen gland (GG) moderately enlarged, only slightly kinked spermatheca (S), medium length epiphallic caecum (EC), long penis (P) and verge (PV) very long and tapering, surface wrinkled. *R. convicta* (**Figs 410a–c**) has the epiphallic caecum much longer and the verge is very much smaller and with corrugated surface. *R. perprima* (**Figs 413a–b**) has a very long epiphallic caecum, penis and vagina, while the verge is shorter and more tapered. The radular teeth (**Plate 218a–b**) have an elevated cusp shaft angle.

Holotype

WAM 762.87, WA–40, SW side of Mt Herbert, Chichester Range, Western Australia. 21°19'S, 117°13'E. Collected 29 January 1974 by A. Solem & L. Price. Height of shell 18.1 mm, diameter 22.7 mm, H/D ratio 0.797, whorls 6 1/8+, umbilicus completely closed by a broad callus having a raised outer edge.

Paratopotypes

WAM 815.87, SAM D18167, AM C.200,736, QM 45021, MV F60012, FMNH 182336, FMNH 182535, 3 LA, 19 DA, 1 LJ, 12 DJ from the type locality.

Paratypes

WESTERN AUSTRALIA: Pilbara: Mt Herbert (WA–182, WAM 813.87, WAM 814.87, SAM D18166, AM C.200,737, QM 52985, MV F59469, FMNH 199219,

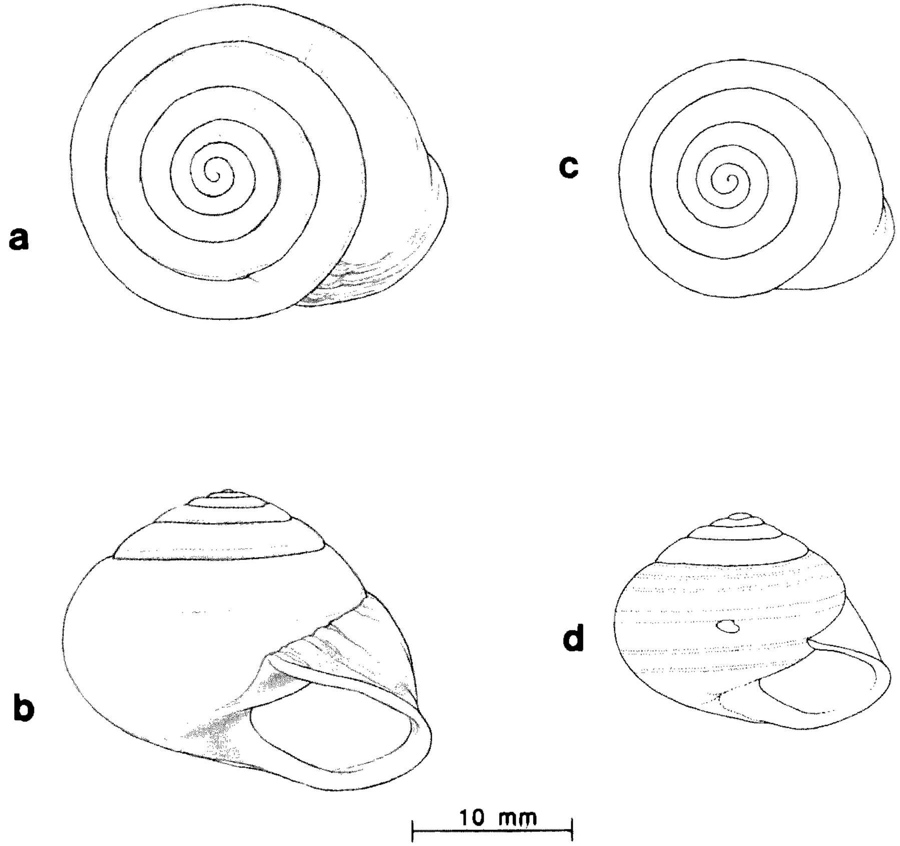


Fig. 411: Shells of *Rhagada pilbarana* sp. nov. and *R. perprima* Iredale, 1939: (a–b) Holotype of *R. pilbarana*. WAM 762.87. WA–40, gully SW of Mt Herbert, Chichester Range, WA; (c–d) Holotype of *Rhagada convicta perprima* Iredale, 1939. Rosemary Island, Dampier Archipelago, WA. AM C.64864. Scale lines equal 10 mm. Drawings by Linnea Lahlum (a–b) and Elizabeth A. Liebman (c–d).

FMNH 199785, FMNH 199909–10, 15 LA, 7 DA, 2 DJ; WA–722, WAM 812.87, AM C.200, 738, FMNH 205365–6, 1 LA, 4 DA; WA–1082, FMNH 212758, 4 DA); Python Pool (WA–39, slopes above, WAM 816.87, SAM D18168, AM C.200,739, QM 52984, FMNH 182357, FMNH 182538, 3 LA, 6 DA, 3 LJ; WA–181, FMNH 199384, 2 DJ).

Range

R. pilbarana has been collected only at Python Pool and the nearby slopes of Mt Herbert, about 5 km apart, Chichester Range (**Map 37**). This is only about 32 km away from Millstream, Fortescue River, the nearest locality for *R. radleyi* (Preston, 1908) and about 60 km S of the Roebourne–Cossack records of *R. convicta*.

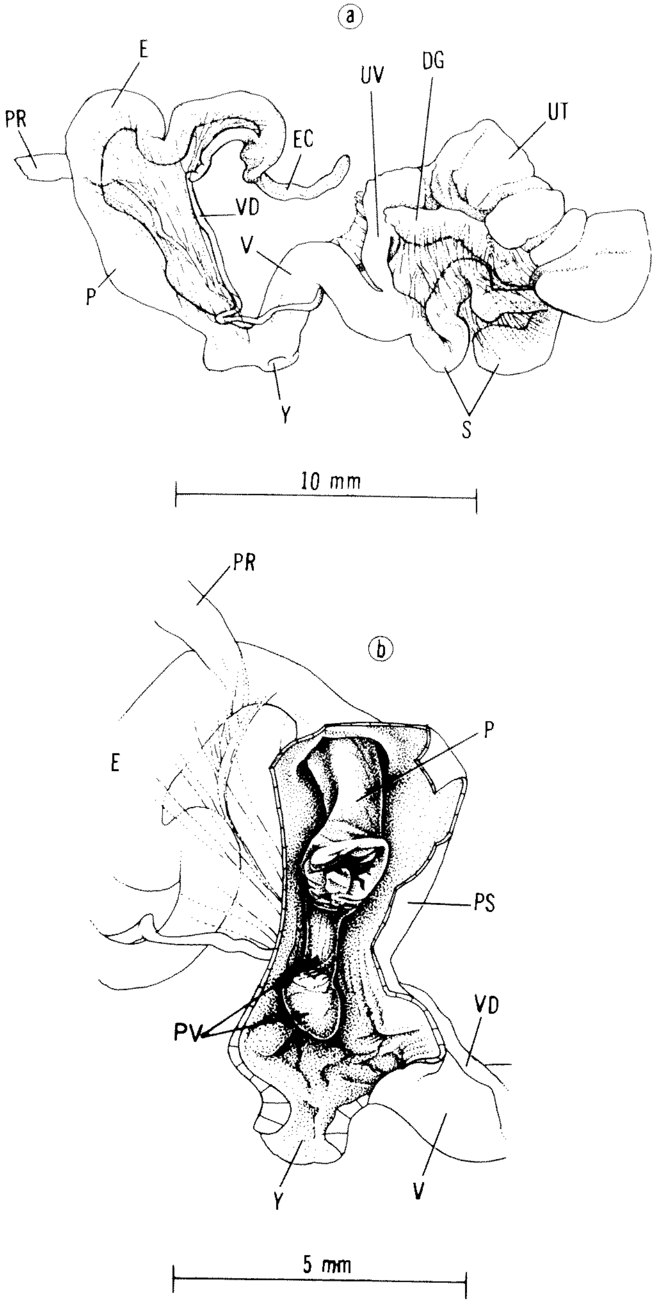


Fig. 412: Genitalia of *Rhagada pilbarana* sp. nov.: WA–182, SE corner of Mt Herbert, Chichester Range, WA. (a) 2 October 1976. FMNH 199910, Dissection A: whole genitalia; (b) 10 April 1977. FMNH 199785, Dissection A, penis interior. Scale lines as marked. Drawings by Linnea Lahlum.

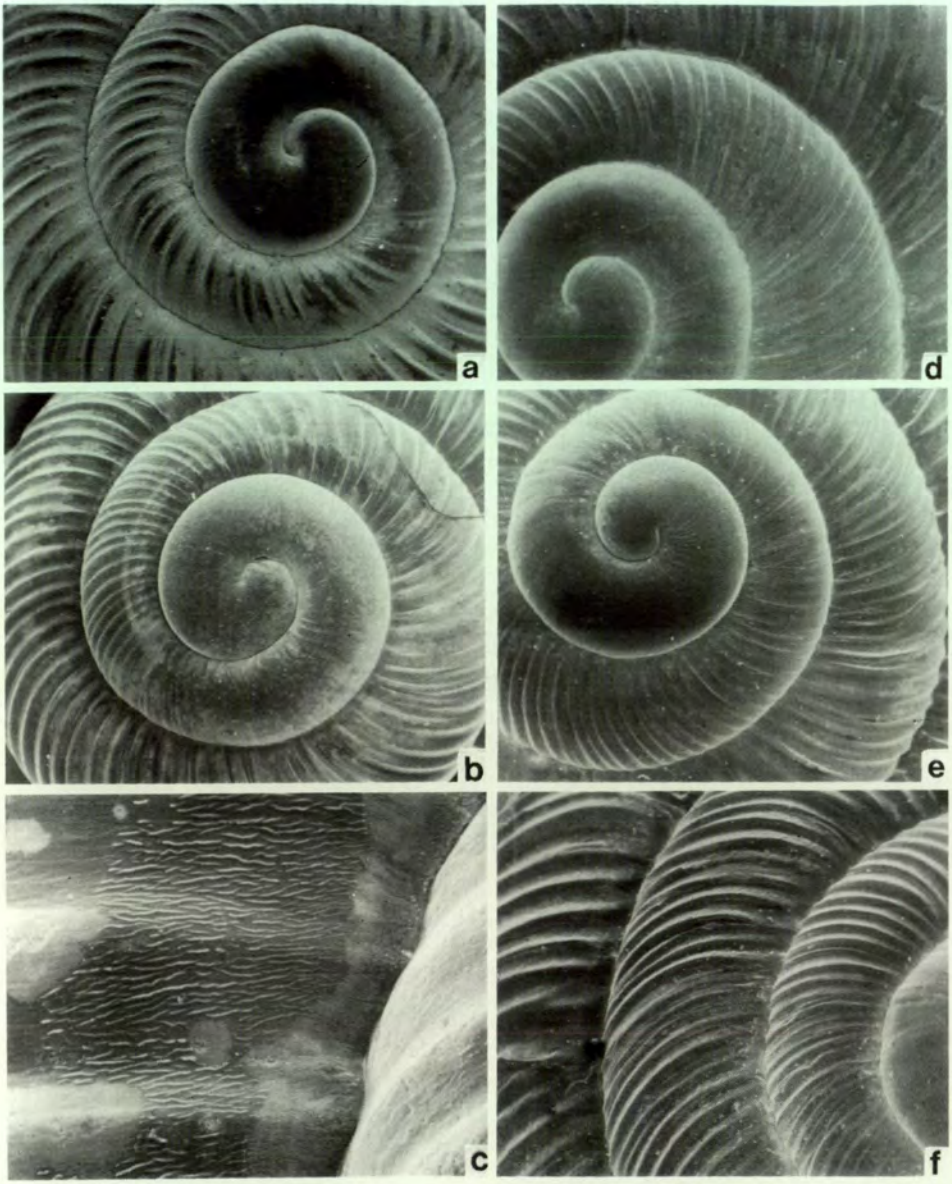


Plate 207: Shell sculpture of *Rhagada plicata* Preston, 1944, *R. minima* sp. nov., *R. intermedia* sp. nov. and *R. elachystoma* (von Martens, 1878): (a) *R. plicata*. Trimouille Island, Montebello Islands, WA. WAM 32.87. a is apex and spire at 15.6X; (b–c) *R. minima*. Rosemary Island, Dampier Archipelago, WA. WAM 248.74. b is apex and spire at 15.8X. c is micro-sculpture on lower spire at 145X; (d) *R. intermedia*. Delambre Island, Dampier Archipelago, WA. WAM 1131.81. d is apex and spire at 30.5X; (e–f) *R. elachystoma*. Kendrew Island, Dampier Archipelago, WA. WAM 241.74. e is apex and spire at 31X. f is lower spire and body whorl at 30.5X.

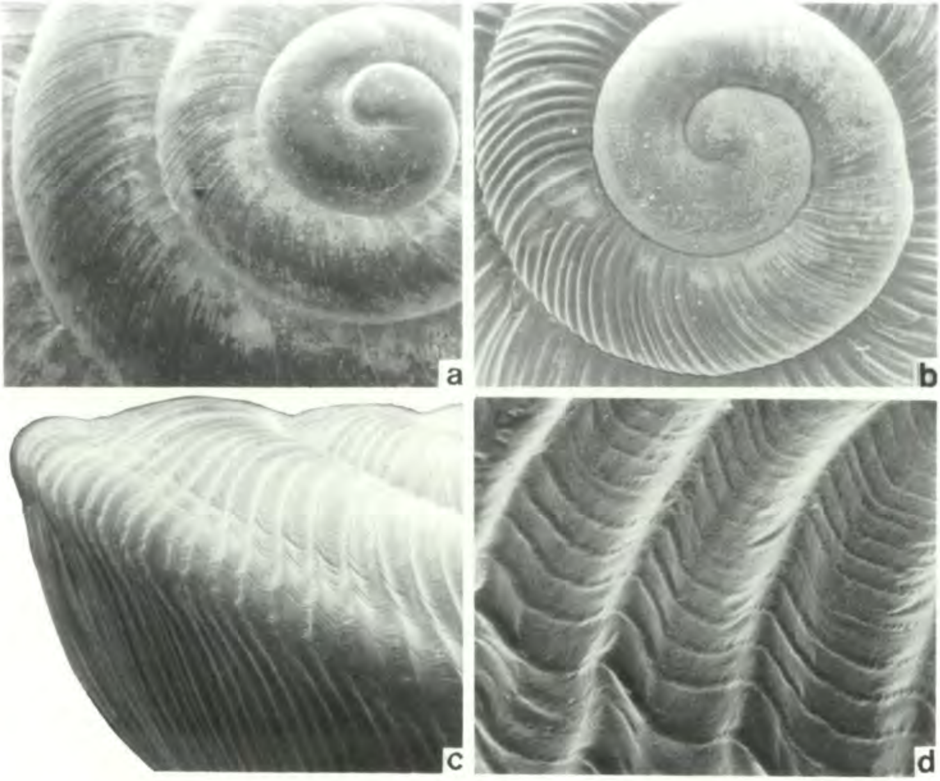


Plate 208: Shell sculpture of *Rhagada angulata* sp. nov. and *R. dampierana* sp. nov.: (a) *R. angulata*. Legendre Island, Dampier Archipelago, WA. WAM 229.70. a is apex and spire at 16X; (b–d) *R. dampierana*. Rosemary Island, Dampier Archipelago, WA. WAM 219.74. b is apex and spire at 16X. c is view of peripheral keel and basal sculpture at 17.3X. d is detail of supraperipheral spiral micro-ridging at 83X.

Diagnosis

Shell very large, adult diameter 21.05–25.35 mm (mean 22.97 mm), with 5 3/4+ to 6 3/8– (mean 6) rather tightly coiled whorls (**Fig. 411a**). Apex and spire strongly elevated, usually rounded above (**Fig. 411b**), shell height 15.8–19.15 mm (mean 17.30 mm), H/D ratio 0.691–0.846 (mean 0.753). Body whorl evenly rounded. Shell apex (**Plate 206d**) with traces of radial sculpture, spire and body whorl with irregular radial ridgelets. Umbilicus closed by expanded columellar callus. Body whorl descending noticeably behind lip (**Fig. 411b**), which is broadly expanded. Narrow red spiral supraperipheral and sometimes subsutural colour bands present, rarely a trace of accessory bands on spire and shell base. Based on 55 measured adults.

Genitalia (**Figs 412a–b**) with large albumen gland (GG), short free oviduct (UV), spermatheca (S) kinked on upper portion, vagina (V) medium length with large diameter, epiphallic caecum (EC) very long, penis (P) long. Verge (PV) greatly elongated, at times club-shaped, surface rugose, long posterior sperm groove. Head wart ovate to circular, light grey in colour whereas neck and foot are yellow-white, sometimes with a lighter grey tone.

Central and early lateral teeth of radula (**Plate 218a**) with moderate anterior flare, high cusp shaft angle and blunt tip with slight curvature. Late laterals (**Plate 218b**) with greatly enlarged anterior flare, small ectocone, high cusp shaft angle and more pointed tip. Jaw (**Plate 218c**) with a few very widely spaced, rather high vertical ribs on middle section.

Discussion

Rhagada pilbarana probably has a number of additional colonies than the two that have been sampled to date but the combination of rock talus for shelter and sufficient vegetation to provide leaves for food is not common in this region. Such colonies will be scattered. Of the known material, five examples are from Python Pool and 50 are from Mt Herbert. This reflects the greater attention given the latter locality as the result of finding material there of *Quistrachia herberti* sp. nov. (see below). The Python Pool examples do not differ significantly in size and shape (**Table 155**) from the Mt Herbert population.

The name *pilbarana* honours the fascinating iron country of the Pilbara.

RHAGADA PERPRIMA IREDALE, 1939
(Plate 218d–f; Figs 411c–d, 413a–b; Map 40)

Helix convicta von Martens, 1888 (not Cox, 1870), *Monatsber. K. Akad. Wiss. Berlin,* **1877**: 272–273, plt. I, figs 6–7 – Mermaid Strait, Dampier Archipelago, Western Australia.

Helix (*Rhagada*) *convicta* (Cox), Pilsbry 1890, *Man. Conch.*, (2) **6:** 187–188 (in part), plt. 30, figs 7, 11 (copied from von Martens).

Rhagada convicta perprima Iredale, 1939, *Jour. Roy. Soc. Western Aust.,* **25:** 62, plt. IV, fig. 13 – Rosemary Island, Western Australia.

Comparative remarks

Rhagada perprima, from Rosemary, Enderby and West Lewis Islands, Dampier Archipelago, (**Map 40**), is a large species (mean diameter 19.59 mm), with increased whorl count (mean 5 5/8+), high and slightly rounded spire (**Fig. 411c**, mean H/D ratio 0.770), aperture descending just behind lip which is well expanded and slightly thickened; umbilicus closed by expansion of columellar lip. Shell white, supraperipheral and subsutural red spiral bands often reduced to translucent zones, some West Lewis Island specimens with partial accessory bands. Apex and spire badly worn in available material, sculpture not observed. *R. convicta*, which ranges from Cossack SW to Exmouth Gulf and thence S to the Minilya River (**Map 37**), is very similar in shell features but lacks the broadly expanded shell lip and, in the Dampier area, the shell often has a brownish colour suffusion that is lacking in *R. perprima*. The Cape Range species, *R. capensis* (**Maps 37–38**), is very similar in size and shape,

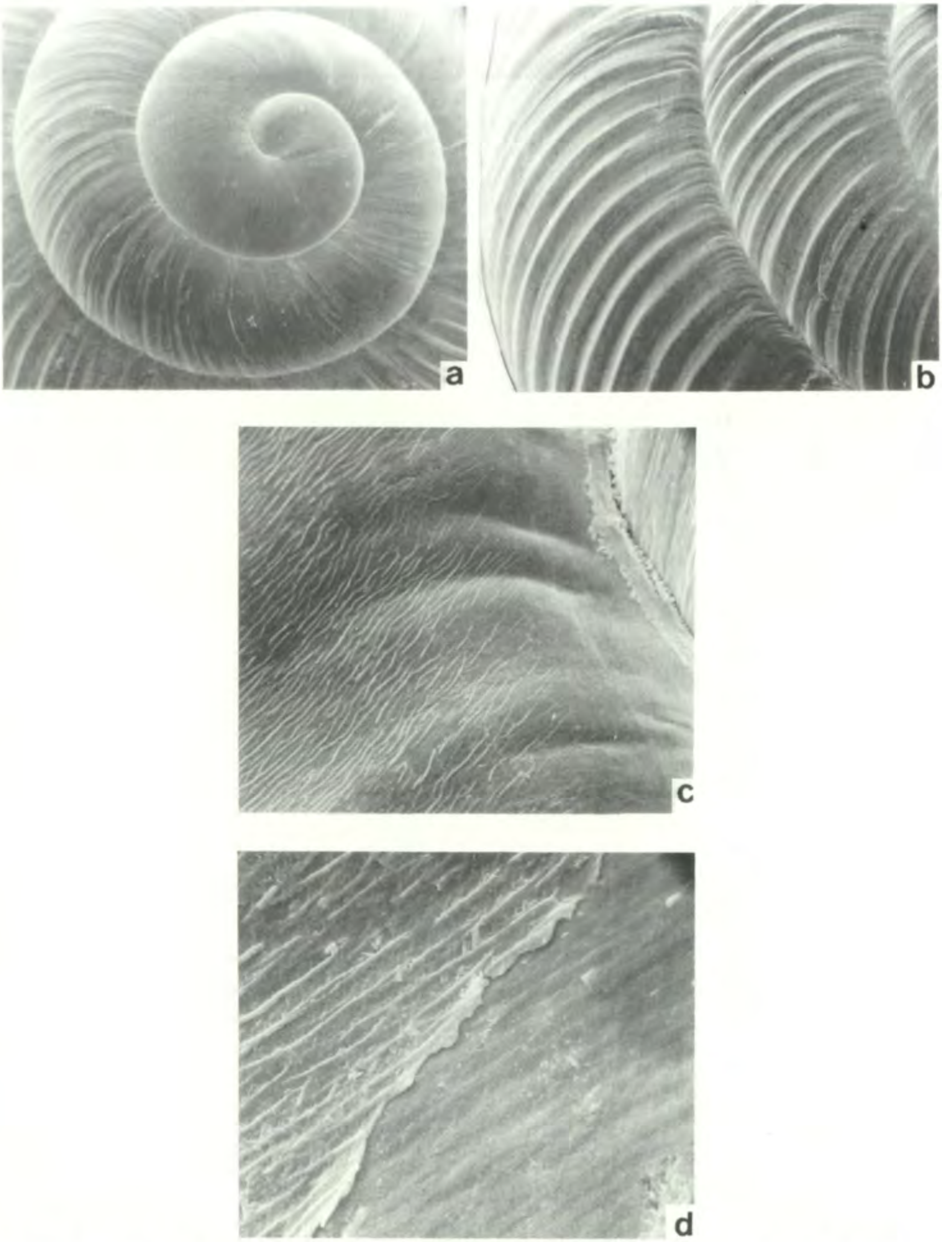


Plate 209: Shell sculpture of *Rhagada dringi* (Pfeiffer, 1846). WA–409, 3.4 km SW of Anna Plains Homestead, 80 Mile Beach, WA. FMNH 199368: (a) apex and spire at 19.1X; (b) lower spire and body whorl at 18.8X; (c) micro-sculpture on body whorl at 190X; (d) shift from periostracum (upper left) with micro-ridges and outer calcified layer (lower right) with vague ridgelets at 860X.

but differs in having many spiral colour bands and the umbilical closure is by a broader expansion of the shell lip. *R. pilbarana*, from Python Pool and Mt Herbert (**Map 37**), is larger (mean diameter 22.97 mm) and differs in anatomical details. *R. richardsonii* (E. A. Smith, 1874), from between Depuch Island and Cape Keraudren to the E and inland to the Oakover River area (**Map 37**), is much smaller (mean diameter 17.79 mm), with many colour bands and often a narrow umbilical crack. Anatomically, *R. perprima* (**Figs 413a–b**) has a large albumen gland (GG), short free oviduct (UV), spermatheca (S) and base of the prostate-uterus kinked, very long epiphallic caecum (EC), long vagina (V), medium length penis (P) and rather short tapering verge (PV) with corrugated surface. *R. pilbarana* (**Figs 412a–b**) has a much elongated verge and shorter epiphallic caecum. *R. convicta* (**Figs 410a–c**) has both penis and vagina shortened, with the verge more elongated and less evenly tapering. *R. capensis* (**Figs 407b, 408a–b, 409**) has the epiphallic caecum very short, the verge cylindrical and with a smooth surface. The jaw (**Plate 218f**) has the rib prominence greatly reduced.

Holotype

AM C.64864, Rosemary Island, [Dampier Archipelago], Western Australia. Shell height 14.7 mm, diameter 17.9 mm, H/D ratio 0.821, whorls 5 1/2, umbilicus completely closed by a broad callus.

Paratopotypes

AM C.64867, 2 DA from the type locality.

Material studied

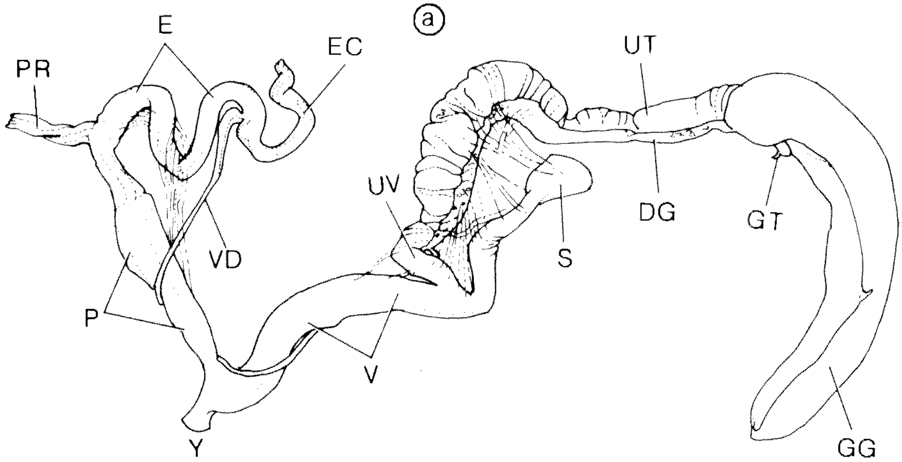
WESTERN AUSTRALIA: Dampier Archipelago: West Lewis Island (D. Hutchison! 20 June 1971, WAM 797.71, 2 LA; D. Hutchison! 20 June 1971, WAM 18.87, FMNH 208763, 4 DA, 3 DJ; W. D. L. Ride! 12 June 1962, WAM 17.87, 6 DA, 1 DJ); Enderby Island (G. W. Kendrick! 22 August 1961, WAM 220.74, 3 DA, 1 DJ).

Range

Rhagada perprima has been collected from Rosemary, Enderby and West Lewis Islands. The known range for this species covers about 15 x 23 km. The mainland Dampier area species *R. convicta* (**Map 37**) is common between Cossack and Dampier and ranges SW to Exmouth Gulf and S to the Minilya River. *R. richardsonii* (E. A. Smith, 1874) is found E and ENE from Depuch Island to Cape Keraudren (**Map 37**) and then inland to the Oakover River and Roy Hill in the upper Fortescue River basin.

Diagnosis

Shell large, adult diameter 15.8–22.3 mm (mean 19.84 mm), with 5+ to 6 1/4– (mean 5 5/8+) rather tightly coiled whorls (**Fig. 411c**). Apex and spire strongly elevated, often rounded above (**Fig. 411d**), shell height 9.25–18.0 mm (mean 14.90 mm), H/D ratio 0.585–0.821 (mean 0.746). Body whorl evenly rounded. Shell apex worn in available material, spire and body whorl with irregular radial growth ridgelets. Umbilicus completely closed by expansion of columellar lip. Body whorl descending just behind lip, which is broadly expanded (**Figs 411c–d**). Shell white, a red supraperipheral and narrow subsutural band present, occasionally traces of accessory bands. Based on 18 measured adults.



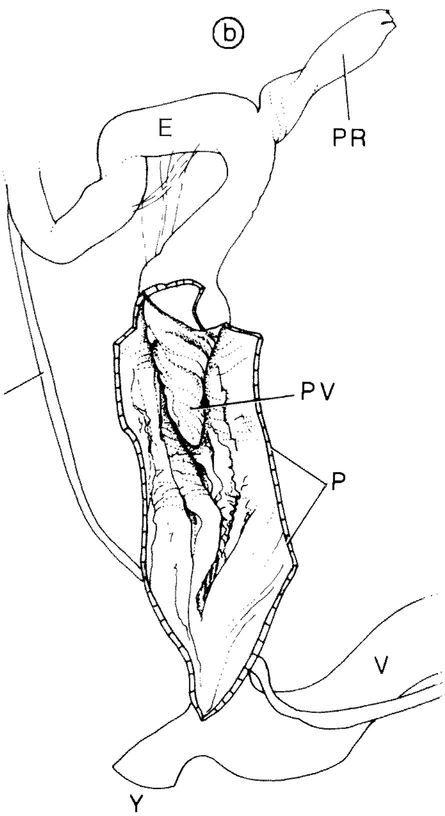


Fig. 413: Genitalia of *Rhagada perprima* Iredale, 1939: West Lewis Island, Dampier Archipelago, WA. 20 June 1971. WAM 797.71, Dissection B: (a) whole genitalia; (b) verge. Scale lines as marked. Drawings by Linnea Lahlum.

Table 155: Local variation in *Rhagada richardsoni*, *R. radleyi* and *R. pilbarana*.

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Rhagada richardsoni					
Depuch Island WAM 306.74	11D	10.10±0.271 (9.05-11.65)	15.79±0.155 (14.8-16.35)	0.639±0.012 (0.585-0.712)	4¾+ (4¼-5⅛)
WA-1058, FMNH 211984	41L	11.70±0.103 (10.3-14.0)	15.67±0.106 (14.5-17.35)	0.747±0.004 (0.705-0.808)	5 (4¾-5⅜−)
WA-1058, FMNH 211985	35L	11.71±0.084 (10.8-12.8)	15.85±0.077 (15.0-17.05)	0.739±0.004 (0.689-0.812)	5− (4¾-5¼−)
WA-1058, FMNH 211983	46D	11.65±0.088 (10.4-13.15)	15.78±0.082 (14.65-16.75)	0.739±0.004 (0.688-0.832)	4⅞+ (4⅝+-5⅛+)
Roy Hill, WAM 340.74	12L	14.83±0.266 (13.9-17.0)	19.88±0.251 (18.5-20.9)	0.746±0.013 (0.681-0.823)	5½ (5¼+-5¾)
#42, FMNH 182358	10D	14.89±0.141 (14.05-15.5)	18.68±0.246 (17.5-20.1)	0.798±0.008 (0.759-0.833)	5½+ (5⅜−-5¾+)
Davies River, WAM 253.74	8D	15.52±0.236 (14.6-16.35)	20.93±0.407 (19.2-22.9)	0.742±0.009 (0.712-0.794)	5½+ (5⅜-5¾)
Skull Springs, 30-XII-1970, WAM 258.74	9D	15.50±0.213 (14.95-16.65)	20.20±0.307 (18.85-21.5)	0.768±0.009 (0.735-0.807)	5½− (5⅜-5¾)
#22, Nullagine, FMNH 199061	53D	15.56±0.099 (13.85-17.05)	20.24±0.105 (18.3-22.05)	0.769±0.004 (0.721-0.832)	5½+ (5¼+-6+)
#33, Oakover R., FMNH 199061	8D	14.61±0.306 (13.4-16.25)	19.32±0.381 (18.0-21.05)	0.756±0.005 (0.736-0.775)	5½− (5⅜+-5⅝−)
#46, Braeside, FMNH 199063	8D	15.15±0.269 (14.0-15.95)	20.17±0.123 (19.7-20.85)	0.751±0.010 (0.711-0.779)	5¾ (5⅜+-5¾)
#56, Burromine, FMNH 199060	15D	14.78±0.236 (13.8-16.6)	19.50±0.288 (17.0-21.75)	0.758±0.007 (0.717-0.814)	5½ (5¼−-5¾+)

Table 155: Local variation in *Rhagada richardsoni, R. radleyi* and *R. pilbarana* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Rhagada radleyi					
Millstream, WAM 299.74	12D	10.60±0.199 (9.6-11.8)	15.20±0.167 (14.4-16.3)	0.691±0.008 (0.634-0.747)	5 $(4\frac{1}{2}-5\frac{3}{8})$
Millstream, WAM 1369.75	9D	11.27±0.288 (10.25-12.35)	15.69±0.139 (15.05-16.25)	0.718±0.016 (0.653-0.789)	$5\frac{1}{4}-$ $(4\frac{7}{8}--5\frac{1}{2}-)$
Joy Helen Mine, WAM 298.74	10D	11.32±0.256 (10.1-12.85)	16.45±0.349 (15.2-18.5)	0.685±0.011 (0.625-0.744)	$4\frac{7}{8}$ $(4\frac{5}{8}-5)$
WA-417, FMNH 199774	11L	13.03±0.307 (11.55-14.8)	18.42±0.279 (17.15-19.95)	0.706±0.010 (0.657-0.761)	$5\frac{1}{4}$ $(5+-5\frac{1}{4}-)$
WA-417, FMNH 199306	40D	12.88±0.098 (11.8-14.15)	18.10±0.120 (16.75-19.7)	0.711±0.004 (0.655-0.775)	$5\frac{1}{4}-$ $(5+-5\frac{1}{2}+)$
Meilga Homestead, WAM 300.74	5D	9.85±0.239 (9.1-10.45)	15.56±0.178 (15.05-16.05)	0.633±0.012 (0.590-0.659)	$4\frac{7}{8}+$ $(4\frac{7}{8}-5\frac{3}{8})$
Rhagada pilbarana					
WA-39, FMNH 182357	3D	17.22 (17.05-17.35)	23.37 (22.2-24.0)	0.737 (0.718-0.768)	6+ $(6--6\frac{1}{8}+)$
WA-40, FMNH 182336	19D	17.25±0.225 (15.8-19.15)	22.81±0.163 (21.2-23.65)	0.756±0.011 (0.691-0.846)	6− $(5\frac{3}{4}+-6\frac{1}{4}-)$
WA-182, FMNH 199785	13L	17.39±0.181 (16.6-18.7)	23.04±0.290 (21.05-24.4)	0.755±0.008 (0.718-0.819)	$6\frac{1}{8}-$ $(6--6\frac{1}{4}-)$

Genitalia (**Figs 413a–c**) with enlarged albumen gland (GG), short free oviduct (UV), spermatheca (S) that is kinked apically, partly kinked prostate-uterus, long vagina (V), very long epiphallic caecum (EC), long penis (P), verge (PV) medium in length, tapering, with corrugated surface. Head wart ovate, small, reddish-grey in colour, much darker than head and neck.

Central and early lateral teeth of radula (**Plate 218d**) with slightly elevated cusp shaft angle and blunt tip, modest anterior flare, no trace of ectocone. Late laterals (**Plate 218e**) with greatly enlarged anterior flare, ectocone appearing at lateromarginal transition. Jaw (**Plate 218f**) with a few low vertical ribs at irregular intervals.

Discussion

Rhagada perprima is known from very limited material. The types from Rosemary Island agree in shell form and colour with those from West Lewis Island but are much smaller in size. The Enderby Island material is even smaller, has a much less elevated spire and is represented by long-dead examples only. The island size and shape variation summarises as follows:

	West Lewis (12 specimens)	Rosemary (3 specimens)	Enderby (3 specimens)
Height	16.43 (15.0–18.0)	13.63 (12.8–14.7)	10.01 (9.25–10.4)
Diameter	21.24 (20.9–22.3)	17.90 (17.4–18.4)	16.17 (15.8–16.6)
H/D ratio	0.774 (0.714–0.814)	0.762 (0.728–0.821)	0.619 (0.585–0.646)
Whorls	5 7/8– (5 1/2 – 6 1/4)	5 3/8+ (5+ – 5 5/8)	5 3/8– (5– – 5 1/2-)

It is quite possible that the Enderby population represents yet another species but the material is inadequate for description.

One new adult and one full adult from West Lewis Island (WAM 797.71) were dissected. The full adult is illustrated (**Figs 413a–b**). At some point, these had been preserved in formalin, so that dissection was difficult and details of the penis and vergic surfaces obscured. My interpretation will have to be checked by study of new material.

It is not known from which point on Mermaid Strait members of the Gazelle Expedition collected both this species and *Rhagada elachystoma* (von Martens, 1878: 272–274). They were collected together *"im Grasland* [= spinifex?] *etwa 2 Stunden landeinwärts"*.

RHAGADA RICHARDSONII (E. A. SMITH, 1874)
(Plates 206e, 219a–g; Figs 414a–f, 415a–c; Maps 37, 39)

Helix richardsonii E. A. Smith, 1874, *Zoology of the Voyage of H. M. S. Erebus & Terror,* **2:** Mollusca, p. 2, plt. 4, figs 14 (two views) – Dupuch's (=Depuch) Island, West Coast of Australia; Pilsbry 1889, *Man. Conch.,* (2) **4:** plt. 36, figs 35–36.

Helix (*Rhagada*) *richardsonii* E. A. Smith, E. A. Smith 1894, *Proc. Malac. Soc. London*, **1:** 89 – cites *Helix elachystoma* von Martens, 1878 as a probable synonym; Pilsbry 1890, *Man. Conch.*, (2) **6:** 185–186.

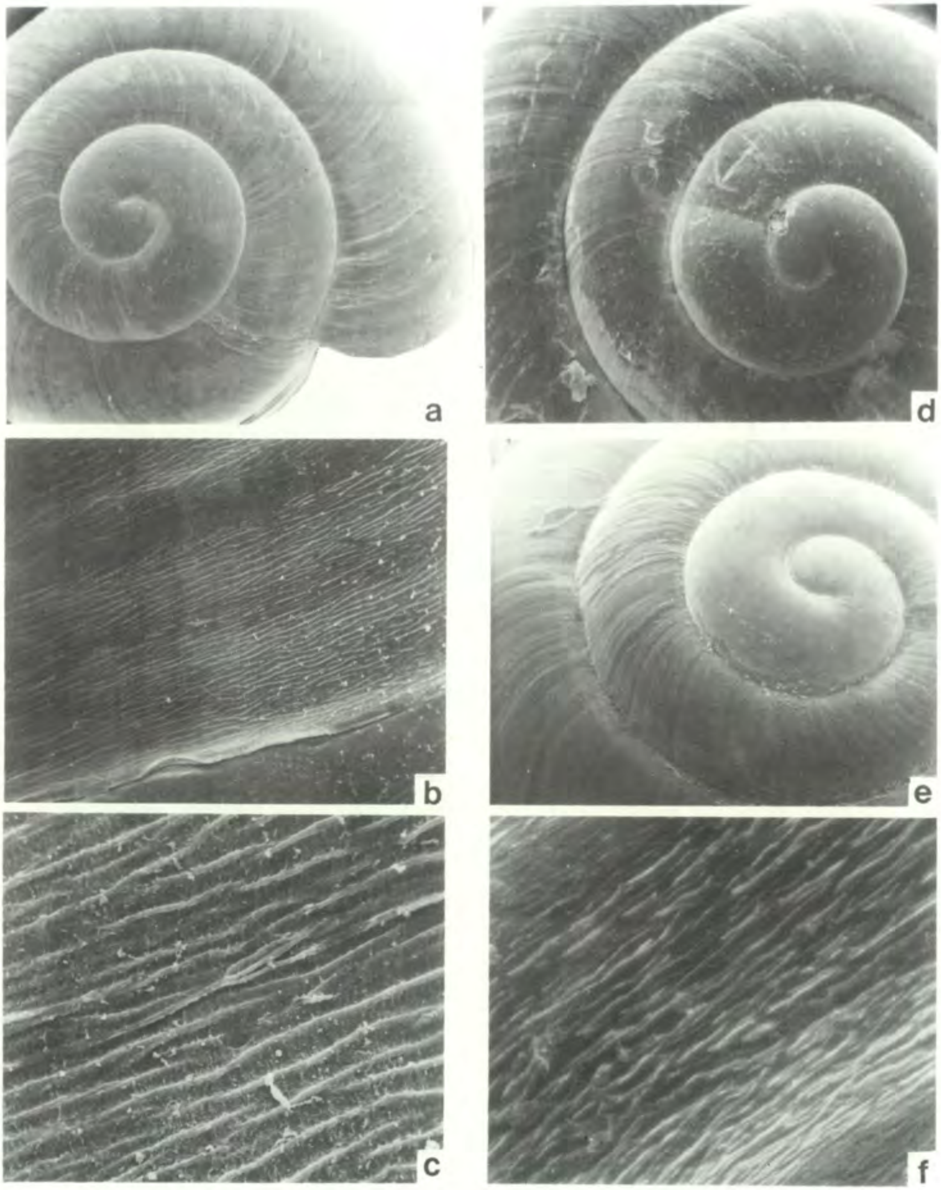


Plate 210: Shell sculpture of *Rhagada reinga* (Pfeiffer, 1846), *R. bulgana* sp. nov. and *R. cygna* sp. nov.: (a–c) *R. reinga*. WA–406, Roebuck Bay Caravan Park, Broome, WA. FMNH 199361. a is apex and spire at 14.8X. b is lower spire micro-sculpture at 145X. c is detail of periostracal micro-sculpture at 700X; (d) *R. bulgana*. WA–186, Bulgan Creek, Cape Leveque, Dampier Land, WA. FMNH 199777, Dissection B. d is apex and spire at 17.9X; (e–f) *R. cygna*. WA–184, One Arm Point, Cygnet Bay, Dampier Land, WA. FMNH 200271. e is apex and spire at 16.5X. f is microsculpture on body whorl at 415X.

Thersites (*Rhagada*) *richardsonii* (E. A. Smith), Pilsbry 1894, *Man. Conch.*, (2) **9:** 136.

Rhagada richardsonii (E. A. Smith), Hedley 1916, *Jour. Roy. Soc. Western Aust.*, **1:** 70 – check list citation; Iredale 1938, *Aust. Zool.*, **9** (2): 112 – check list citation; Iredale 1939, *Rec. West. Aust. Mus.* **2**(1): 59–60, plt. IV, fig. 7.

Rhagada richardsoni (*sic*) (E. A. Smith), Richardson 1985, *Tryonia* 12: 266 – check list citation.

Rhagada convicta strella Iredale, 1939, *Rec. West. Aust. Mus.* **2**(1): 62, plt. IV, fig. 11 – Strelly (=Strelley) River, Western Australia (J. R. Cleland).

Rhagada convicta tambra Iredale, 1939, *Rec. West. Aust. Mus.* **2**(1): 62 plt. 4, fig. 12 – Tambrey Station, Fortescue River, Western Australia.

Comparative remarks

Rhagada richardsonii, which ranges coastally from Depuch Island ENE to Cape Keraudren and thence inland to the Oakover and upper Fortescue Rivers (**Map 37**), is

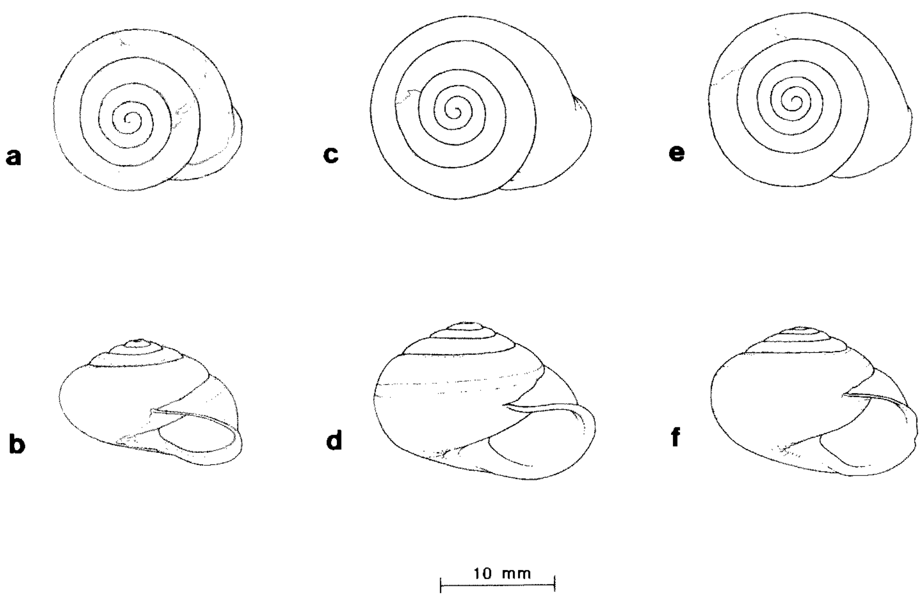


Fig. 414: Shells of *Rhagada richardsonii* (E. A. Smith, 1874): (a–b) Depuch Island, E of Dampier, WA. Topotype. WAM 372.74; (c–d) Holotype of *Rhagada convicta strella* Iredale, 1939. Strelley River, De Grey River tributary, WA. AM C.30451; (e–f) Holotype of *Rhagada convicta tambra* Iredale, 1939. Tambrey Station, Fortescue River, WA. AM C.64848. Scale lines equal 10 mm. Drawings by Linnea Lahlum (a–b) and Elizabeth A. Liebman (c–f).

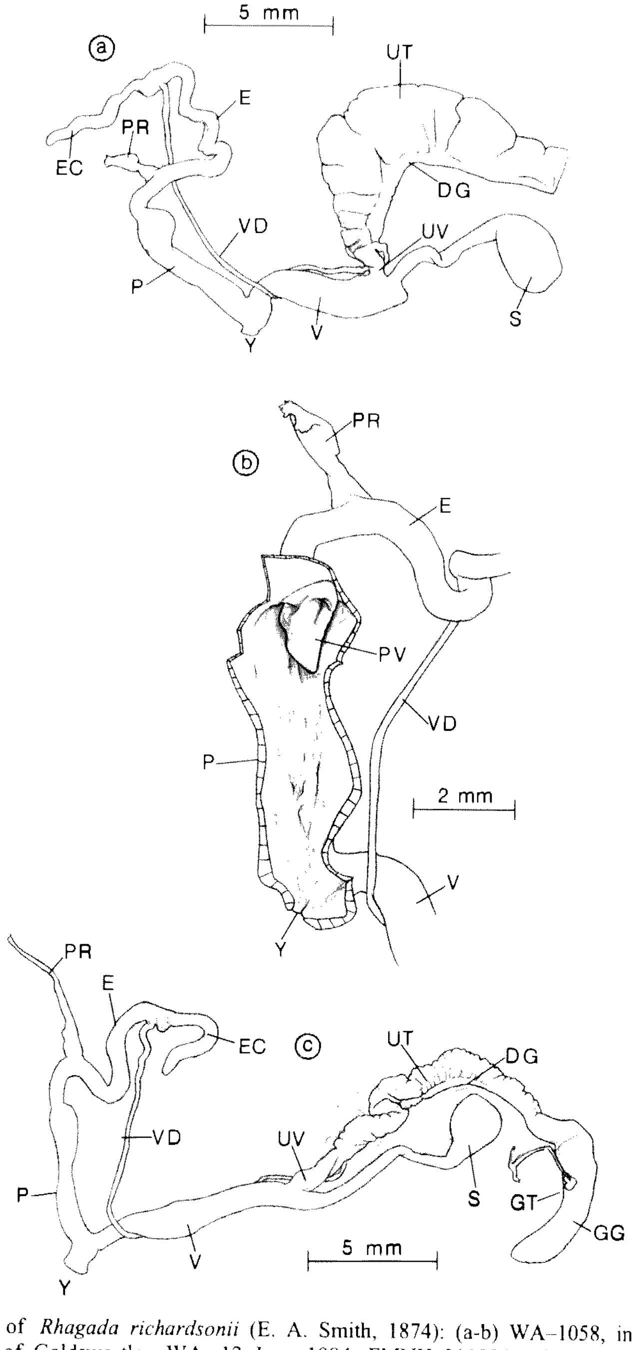


Fig. 415: Genitalia of *Rhagada richardsonii* (E. A. Smith, 1874): (a-b) WA–1058, inland of Cape Keraudren, NE of Goldsworthy, WA. 12 June 1984. FMNH 211984, Dissection A: (a) whole genitalia; (b) verge; (c) Roy Hill, Fortescue River, WA. 3 May 1970. WAM 340.74, Dissection A. Whole genitalia. Scale lines as marked. Drawings by Linnea Lahlum.

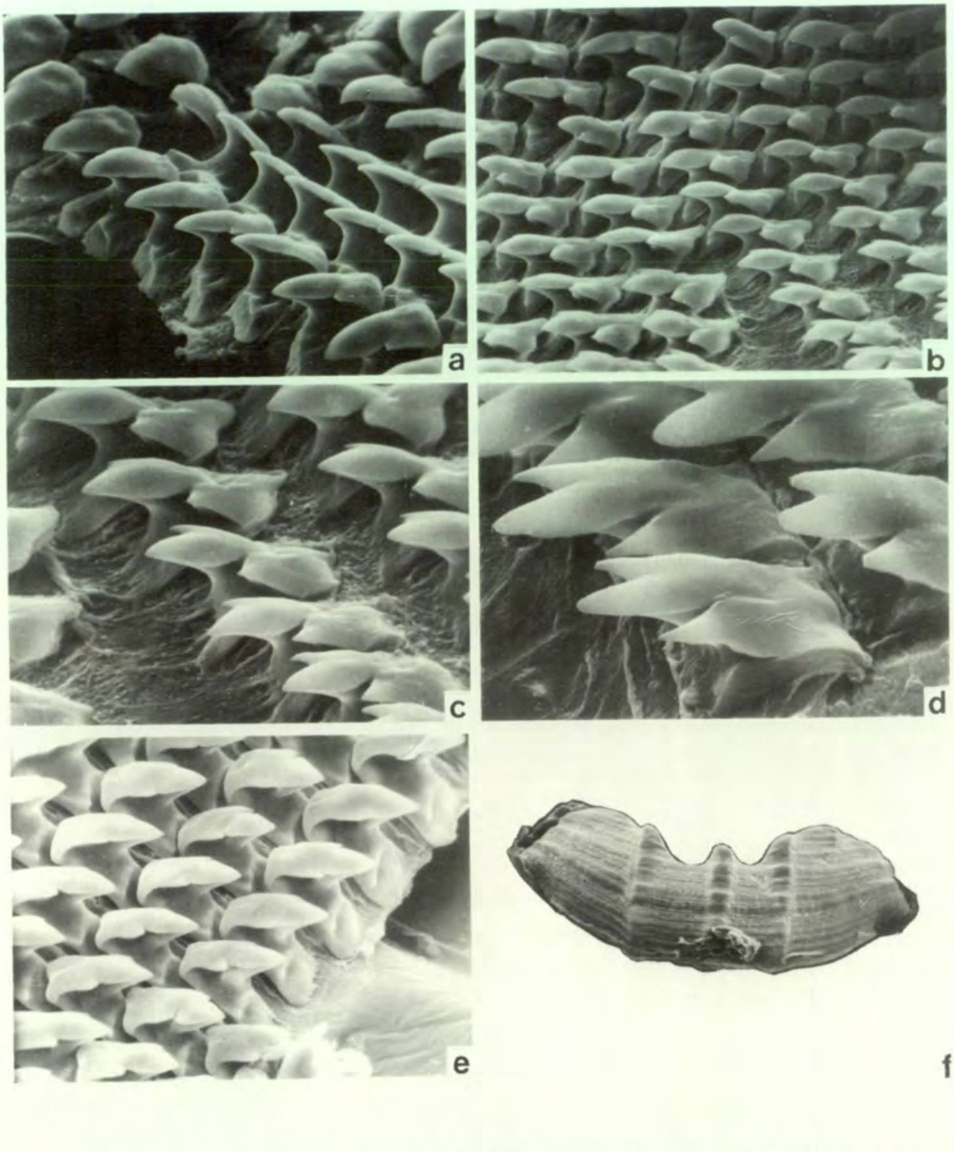


Plate 211: Radular teeth and jaw of *Rhagada torulus* (Férussac, 1819): (a–d) WA–953, Ram Paddock Well, N of Quobba Homestead, N of Carnarvon, WA. 8 July 1983. FMNH 212468, Dissection A. a is central and early laterals at 490X. b is latero-marginal transition at 420X. c is detail of early marginals at 875X. d is structure of mid-marginals at 1450X; (e–f) WA–956, S of Warroora Homestead, N of Carnarvon, WA. 9 July 1983. FMNH 212480, Dissection A. e is central and early laterals at 455X. f is jaw at 53X.

a medium-sized species (mean diameter 17.79 mm), with typical whorl count (mean 5 1/4), medium to strongly elevated spire (**Figs 414a, c, e**, mean H/D ratio 0.749), aperture usually sharply deflected behind lip, slightly narrowed, lip only slightly expanded, umbilicus sometimes with a narrow lateral crack remaining open. Shell white, normally with many narrow spiral colour bands on at least part of the shell, some examples with a wider upper palatal band, or with a light spire colour suffusion. Shell apex (**Plate 206e**) with weak radial ridging, spire and body whorl with prominent growth ridgelets.

R. radleyi Preston, 1908, from the Fortescue to Ashburton River drainages (**Map 37**), is slightly smaller (mean diameter 16.64 mm), generally less elevated (mean H/D ratio 0.693) and usually has a lateral umbilical crack. The larger species (mean diameters 19.84–22.97 mm) from Cossack through the North West Cape to the Minilya River (*R. convicta*, *R. perprima*, *R. pilbarana*) lack the accessory spiral bands (except *R. capensis* from the North West Cape), have an almost always closed umbilicus, the aperture is not narrowed and the lip is more broadly expanded. Anatomically (**Figs 415a–c**), *R. richardsonii* has a slightly enlarged albumen gland (GG), the spermatheca (S) is only slightly kinked, vagina (V) long and slender, epiphallic caecum (EC) very long, penis (P) elongated, verge (PV) narrowing abruptly from base to mid-point, beyond which is a short cylindrical section, surface weakly corrugated. The neighbouring *R. radleyi* (**Figs 417a–c**) has the spermatheca strongly kinked, the vagina short and with increased diameter, the penis shortened and the verge short, moderately tapered, with corrugated surface. *R. convicta* (**Figs 410a–c**) has the spermatheca kinked, a much shorter epiphallic caecum and even shorter penis. The very large verge of *R. pilbarana* (**Fig. 412b**) and the combination of kinked spermatheca and shortened penis with simpler verge (**Figs 413a–b**) in *R. perprima* separate those species. The smooth cylindrical verge (**Fig. 408a**) of *R. capensis* is the most obvious distinguishing character of that species. Radula and jaws (**Plate 219a–g**) are variable among populations.

Type material of *Helix richardsonii* E. A. Smith, 1874

No specimens that could be considered types of *Helix richardsonii* E. A. Smith, 1874 were located during this study. The original description cited the whorl count as 4 1/2 to 5, diameter as 19 mm and shell height as 12 mm, giving an H/D ratio of approximately 0.632. These figures agree with topotypes from Depuch Island (see below).

Holotype of *Rhagada convicta strella* Iredale, 1939

AM C.30451, Strelley River, [De Grey River] Western Australia. Height of shell 14.45 mm, diameter 19.4 mm, H/D ratio 0.745, whorls 5 1/4+, umbilicus closed.

Holotype of *Rhagada convicta tambra* Iredale, 1939

AM C.64848, Tambrey Station, Fortescue River, Western Australia. Height of shell 13.5 mm, diameter 18.2 mm, H/D ratio 0.742, whorls 5 5/8-, umbilicus closed.

Material studied

WESTERN AUSTRALIA: Pilbara: Roy Hill, Fortescue River (A. M. Douglas and L. Koch! 3 May 1970, WAM 340.74, 11 LA, 2 LJ; WAM, 5 DA); Davies River, upper De

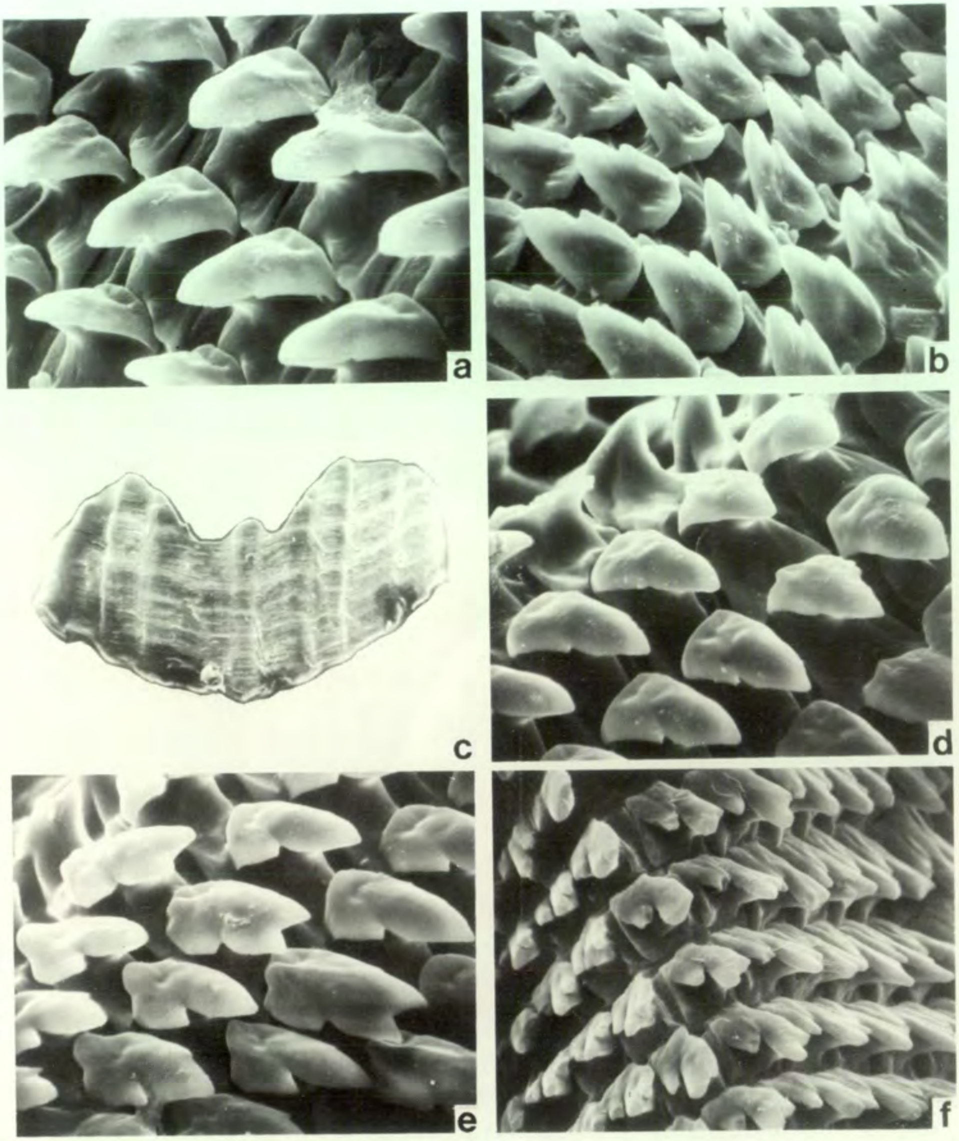


Plate 212: Radular teeth and jaw of *Rhagada globosa* sp. nov.: (a–c) WA–25, Pt Maud, Cardabia Station, S of North West Cape, WA. 23 January 1974. FMNH 182505. a is central and early laterals at 978X. b is latero-marginal transition from mid-radular view at 725X. c is jaw at 57.3X; (d–f) Bill Bay, 2 miles S of Point Maud, Cardabia Station, WA. July 1966. WAM 385.74. d is central and early laterals at 716X. e is latero-marginal transition at 728X. f is mid marginals at 717X.

Grey River (near Shag Pool, John Abbott! 17 May 1972, WAM 253.74, 7 DA, 2 DJ); Skull Springs, E of Nullagine (J. Wombey!, 30 December 1970, WAM 334.74, 1 LA; J. Wombey! 30 December 1970, WAM 258.74, 9 DA; #22, 10 km E of, W. Turnbull! 24 October 1976, WAM 473.77, WAM 821.87, SAM D18173, AM, QM, MV, FMNH 199061, 55 DA, 17 DJ); #33, Upper Carawine Gorge, Oakover River (W. Turnbull! 3 October 1976, FMNH 199064, WAM 466.77, 10 DA, 2 DJ); #56, Burromine Station, 10 km S of Oakover River crossing (W. Turnbull! 16 November 1976, WAM 479.77, FMNH 199060, 17 DA, 6 DJ); #46, Braeside Station, Oakover River (W. Turnbull! November 1976, WAM 480.77, FMNH 199063, 10 DA, 3 DJ); Depuch Island (W. D. L. Ride! 30 May 1962, WAM 372.74, 1 LA, 1 LJ; W. D. L. Ride! June 1962, WAM 306.74, FMNH 208782, 11 DA, 2 DJ); Port Hedland (WA–42, 1 mile S of, FMNH 182358, 10 DA, 2 DJ); Cape Keraudren (WA–1058, 2 km inland, WAM 819.87, WAM 820.87, SAM D18171–2, AM, QM, MV, FMNH 211983–5, 76 LA, 46 DA, 17 LJ, 17 DJ; WA–1083, FMNH 221759–60, 65 LA).

Range

Rhagada richardsonii ranges (**Maps 37, 39**) coastally from Depuch Island (117°43'E) ENE to Cape Keraudren (119°46'E). Inland it has been taken as far S as Roy Hill in the upper Fortescue River basin and has an extensive range from Skull Springs near Nullagine (121°00'E) and Burromine along much of the Oakover and Davies Rivers, upper tributaries of the De Grey River. The E–W range from Burromine to Depuch Island is about 355 km and the N–S range from Cape Keraudren to Roy Hill is about 295 km, giving *R. richardsonii* the second largest range of any *Rhagada* species. This is exceeded only by the range of the coastal plains *R. convicta*, which also is the nearest species, ranging (**Map 37**) from Cossack and Dampier SW to the North West Cape and Minilya River. *R. radleyi* Preston, 1908 has an inland hills range to the S, extending from the Fortescue through Ashburton drainages (**Map 37**). *R. dringi* (Pfeiffer, 1846) extends N along 80 Mile Beach (**Map 39**).

Diagnosis

Shell medium in size, adult diameter 14.4–22.9 mm (mean 17.79 mm), with 4 1/4 to 6+ (mean 5 5/8+) normally coiled whorls. Apex and spire strongly elevated (**Figs 414b, d, f**), usually rounded above, shell height 9.05–17.05 mm (mean 13.35 mm), H/D ratio 0.585–0.833 (mean 0.749). Body whorl evenly rounded or with a very slight peripheral angulation. Shell apex (**Plate 206e**) with weak radial sculpture, spire and body whorl with prominent growth ridgelets. Umbilicus closed by expansion of columellar lip or with a very narrow lateral crack, this condition varying among populations. Body whorl descending slightly to moderately behind aperture, which may be slightly narrowed, lip moderately expanded, slightly thickened internally. Shell with numerous spiral red to orange colour bands, usually very narrow, often absent from short and irregular portions of body whorl, sometimes an upper palatal band wider and darker in colour. Based on 278 measured adults.

Genitalia (**Figs 415a–c**) with only slightly enlarged albumen gland (GG), at most slightly kinked spermatheca (S), very short free oviduct (UV), vagina (V) long and enlarged basally with small pilasters, epiphallic caecum (EC) very long. Penis (P) long and slender, verge (PV) elongated, tapering rapidly initially, beyond which is a shorter cylindrical section, surface corrugated. Head wart small, ovate, much darker in colour than neck and foot.

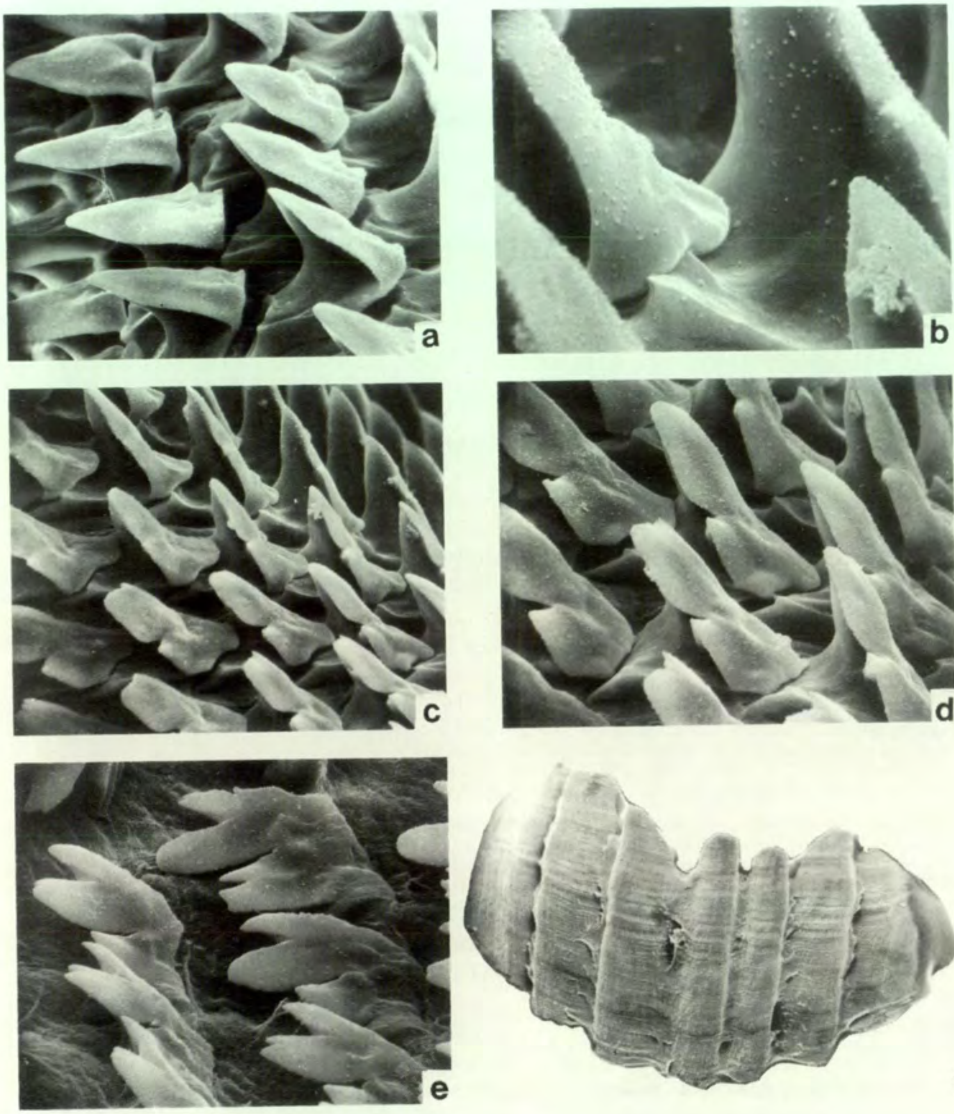


Plate 213: Radular teeth and jaw of *Rhagada capensis* sp. nov. Goat Cave, near Central Hill, Cape Range, WA. June and July 1964. FMNH 171623, Dissection A: (a) central and early laterals at 560X; (b) detail of lateral tooth basal plate interlock system at 2175X; (c) late laterals at 560X; (d) latero-marginal transition at 820X; (e) late marginals at 1000X; (f) jaw at 56X.

Central and lateral teeth of radula (**Plate 219a, c, e**) variable among populations in anterior flare and cusp shaft angle, tip sharp and slightly or not curved. Late laterals (**Plate 219g**) typical in enlargement of anterior flare, rapid size increment in ectocone, appearance of endocone. Lateromarginal transition and early marginals (**Plate 219g**) typical. Jaws (**Plate 219b, d, f**) variable in rib number, spacing and prominence.

Discussion

Rhagada richardsonii ranges (**Map 37**) from the coast E through the Oakover River area and has the second largest range of any *Rhagada*. There is considerable size and shape variation, suggesting that this may be another complex of species. Anatomical material was available only from Cape Keraudren (**Figs 415a–b**) at the N end of the coastal range, a single live adult from Skull Springs, E of Nullagine (WAM 334.74) and from Roy Hill on the upper Fortescue River (**Fig. 415c**) at the SE edge of the outlined range. Since these three populations agree in genital structures and basic shell features, they are grouped under the same name, pending availability and study of additional material.

Shell size and shape differences within the Nullagine–Oakover River area are minor (**Table 155**). Unfortunately, this is the only area from which we have good samples representing several populations. Grouping material into general area situations produces the following results:

	Depuch Island (12 specimens)	Cape Keraudren (132 specimens)
Height	10.14 (9.05–11.65)	11.74 (10.3–14.0)
Diameter	15.77 (14.8–16.35)	15.80 (14.4–17.6)
H/D ratio	0.643 (0.585–0.712)	0.743 (0.688–0.832)
Whorls	4 3/4+ (4 1/4 – 5 1/8)	5– (4 1/4 – 5 1/2)

	Oakover River–Nullagine (120 specimens)	Roy Hill (12 specimens)
Height	15.29 (13.4–17.05)	14.83 (13.9–17.0)
Diameter	19.95 (17.0–22.9)	19.88 (18.5–20.9)
H/D ratio	0.767 (0.711–0.833)	0.746 (0.681–0.823)
Whorls	5 1/2+ (5 1/4– – 6+)	5 1/2 (5 1/4+ – 5 3/4)

While the Depuch Island and Cape Keraudren specimens agree in size, the former have a much more depressed shape. The Cape Keraudren, Oakover River–Nullagine and Roy Hill populations agree in shape but the inland shells are much larger in size and with a considerable increment in whorl count. Size and shape of the inland shells agree well with *R. convicta* (Cox, 1870) (see above) but the columellar closure of the umbilicus usually leaves an elevated ridge in *R. richardsonii* that is absent in examples of *R. convicta*. The very long penis, long vagina, and unkinked elongated spermatheca of the inland populations also link them to to *R. richardsonii* rather than *R. convicta*.

Although *R. richardsonii* is the only camaenid present at Roy Hill, Skull Springs and Cape Keraudren, the places for which we have radular information (**Plate 219**), both the latter populations show some to marked elevation of the cusp shafts but without the increase in cusp tip curvature that usually accompanies such a change. While the increased cusp shaft angle suggests that a dietary specialization may be involved, the nature of any such specialization remains to be discovered.

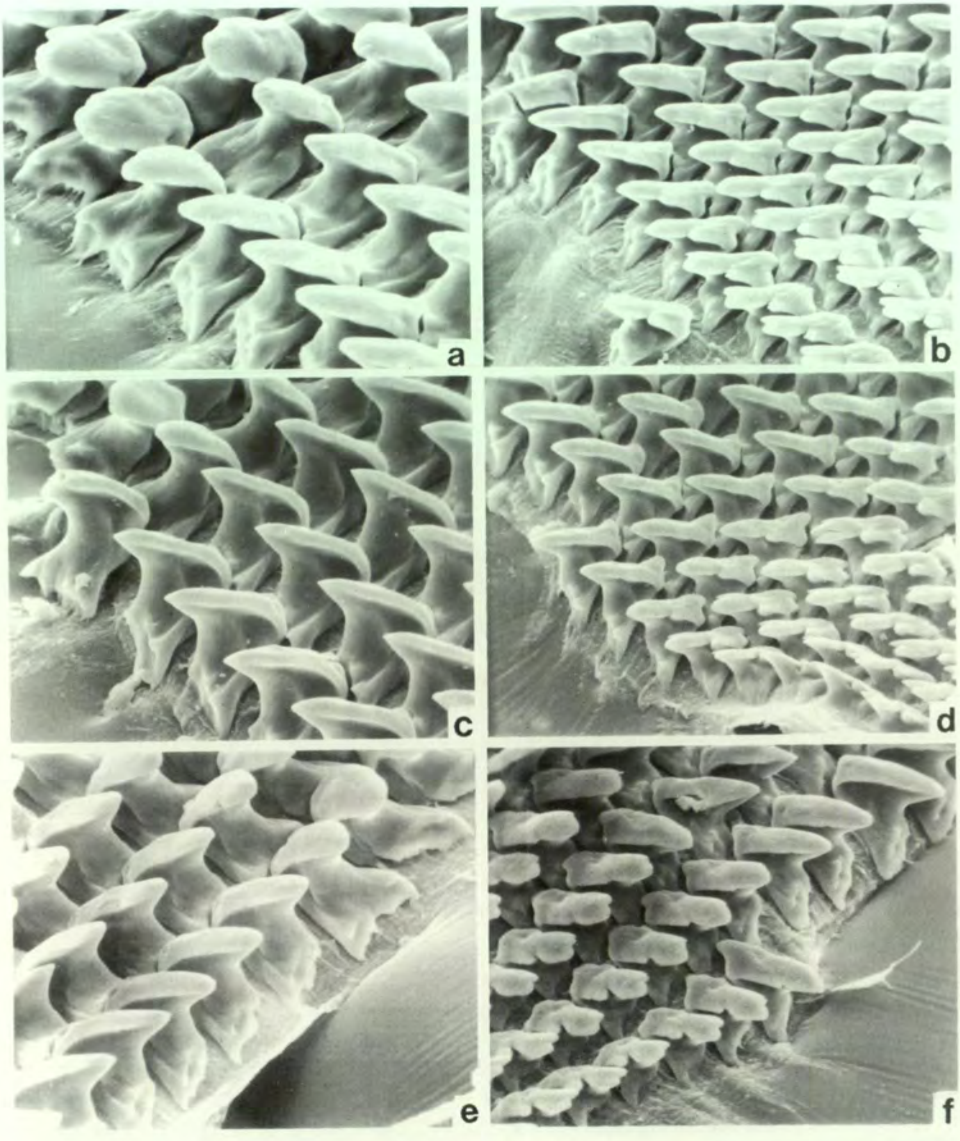


Plate 214: Radular teeth of *Rhagada capensis* sp. nov.: (a–b) WA–957, Scrubby Range, S of Exmouth Gulf, WA. 9 July 1983. FMNH 212485, Dissection A. a is central and early laterals at 500X. b is latero-marginal transition at 355X; (c–d) WA–23, W side of Cape Range, 14.9 miles N of Ningaloo Homestead, WA. FMNH 182492, Dissection A. c is central and early laterals at 495X. d is latero-marginal transition at 375X; (e–f) ca 2 miles E of Norwegian Bay, Ningaloo Station, S of North West Cape, WA. 22 July 1968. WAM 388.74, Dissection A. e is central and early laterals at 405X. f is latero-marginal transition at 330X.

RHAGADA RADLEYI PRESTON, 1908

(Plates 206f, 220a–d; Figs 416a–f, 417a–c; Maps 37, 39)

Rhagada radleyi Preston, 1908, *Proc. Malac. Soc. London,* **8:** 120, 2 figs – Western Australia; Hedley 1916, *Jour. Roy. Soc. Western Aust.,* **1:** 70 – check list citation; Iredale 1938, *Aust. Zool.*, **9** (2): 112 – check list citation; Iredale 1939, *Jour. Roy. Soc. Western Aust.,* **25:** 60, plt. 4, fig. 8 – copy of original description; Richardson 1985, *Tryonia*, **12:** 166 – check list citation.

Comparative remarks

Rhagada radleyi Preston, 1908, found from Millstream on the Fortescue River SSW to the upper Ashburton River drainage (**Map 37**), is medium in size (mean diameter 16.64 mm), with near average whorl count (mean 5 1/8), moderately elevated and rounded spire (**Fig. 406b**, mean H/D ratio 0.693), aperture moderately deflected behind lip, slightly narrowed, lip narrowly expanded, umbilicus usually (**Figs 416c, f**) with a very narrow lateral crack despite the columellar lip expansion. Shell white, with a few to many spiral red to orange colour bands, supraperipheral and subsutural ones often wider and darker, sometimes a light colour suffusion present. Shell apex (**Plate 206f**) with some radial sculpture, spire and body whorl with prominent radial growth ridgelets. The slightly larger (mean diameter 17.79 mm) and higher spired (mean H/D ratio 0.749) *R. richardsonii*, which ranges (**Maps 37, 39**) from the coast between Depuch Island and Cape Keraudren, thence E through the Oakover River basin, tends to have more examples with a closed umbilicus but differs mainly in anatomy. *R. convicta*, from Cossack and Dampier SW to the North West Cape and Minilya River (**Map 37**), is larger (mean diameter 20.15 mm), with a higher spire (**Fig. 406e**, mean H/D ratio 0.759), closed umbilicus (**Fig. 406f**) and generally has only two or no spiral colour bands. The only other large species with multiple colour bands is *R. capensis* from the North West Cape (**Map 37**). It averages 5 3/4 tightly coiled whorls (**Fig. 406a**), has a completely closed umbilicus (**Fig. 406c**) and a mean diameter of 20.15 mm. Anatomically (**Figs 417a–c**), *R. radleyi* has a large albumen gland (GG), kinked spermatheca (S), short vagina (V), long epiphallic caecum (EC), relatively long penis (P) and short tapered verge (PV) with corrugated surface. *R. richardsonii* (**Figs 415a–c**) has a normally-sized albumen gland, the spermatheca is, at most, very slightly kinked, vagina is much longer and the verge is much longer. *R. convicta* (**Figs 410a–c**) has spermatheca, vagina and penis shortened but a longer verge. *R. capensis* (**Figs 408–409**) has a much shorter epiphallic caecum and a cylindrical, smooth-surfaced verge. The central and early lateral teeth of *R. radleyi* (**Plate 220a**) have a prominent anterior flare and elevated cusp shaft angle, with both conditions accentuated in the late laterals (**Plate 220b**).

Paratypes

FMNH 41591 ex Webb, Gude, Preston, Western Australia. Height of shell 9.7 mm, diameter 14.95 mm, H/D ratio 0.649, whorls 5 1/8, umbilical width 0.85 mm, D/U ratio 17.6, nearly closed by columellar lip.

Material studied

WESTERN AUSTRALIA: near Joy Helen Mine, Glen Florrie Station (A. Saar and

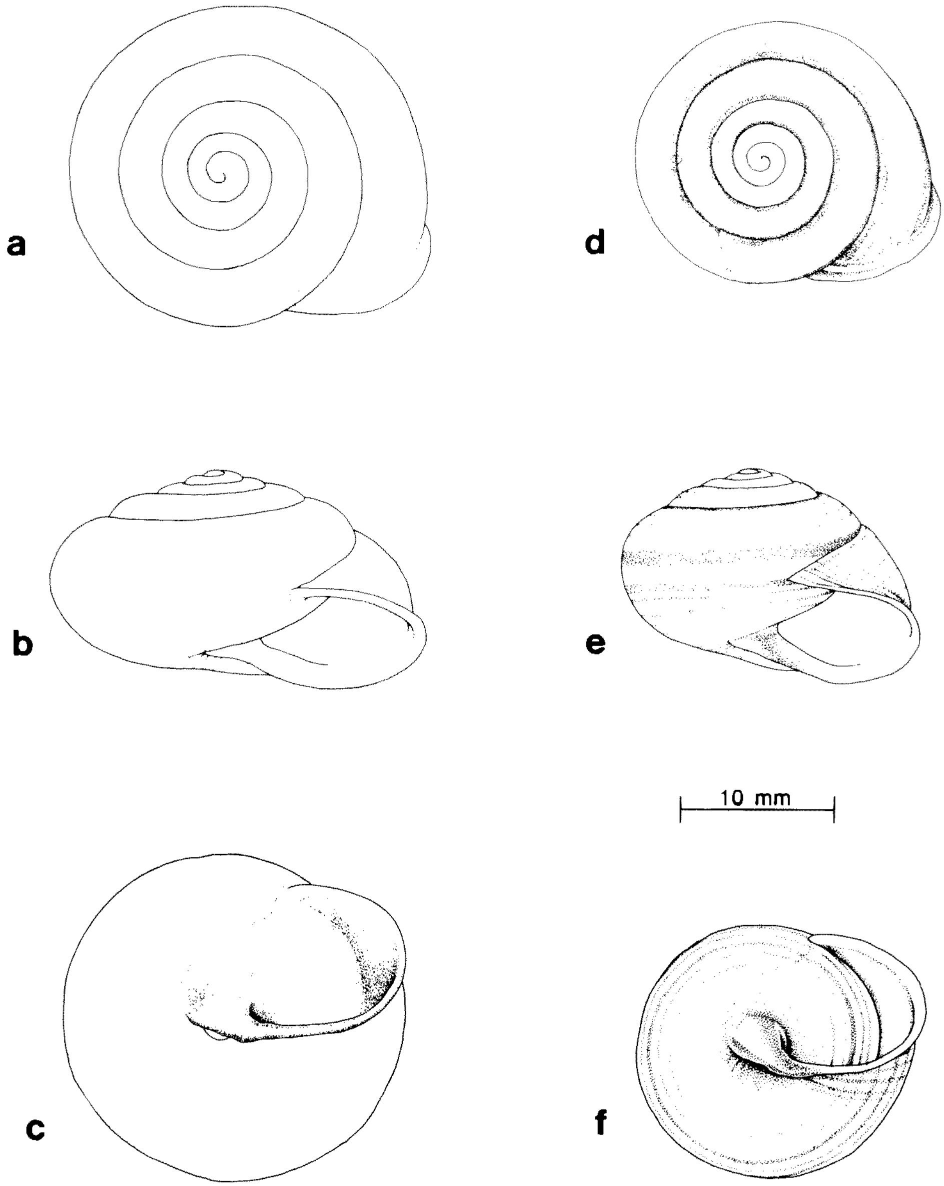


Fig. 416: Shells of *Rhagada radleyi* Preston, 1908: (a–c) Paratype. Western Australia. BMNH 1908.7.2.3; (d–f) WA–417, Glen Florrie Station, WA. FMNH 199306. Scale lines equal 10 mm. Drawings by Linnea Lahlum.

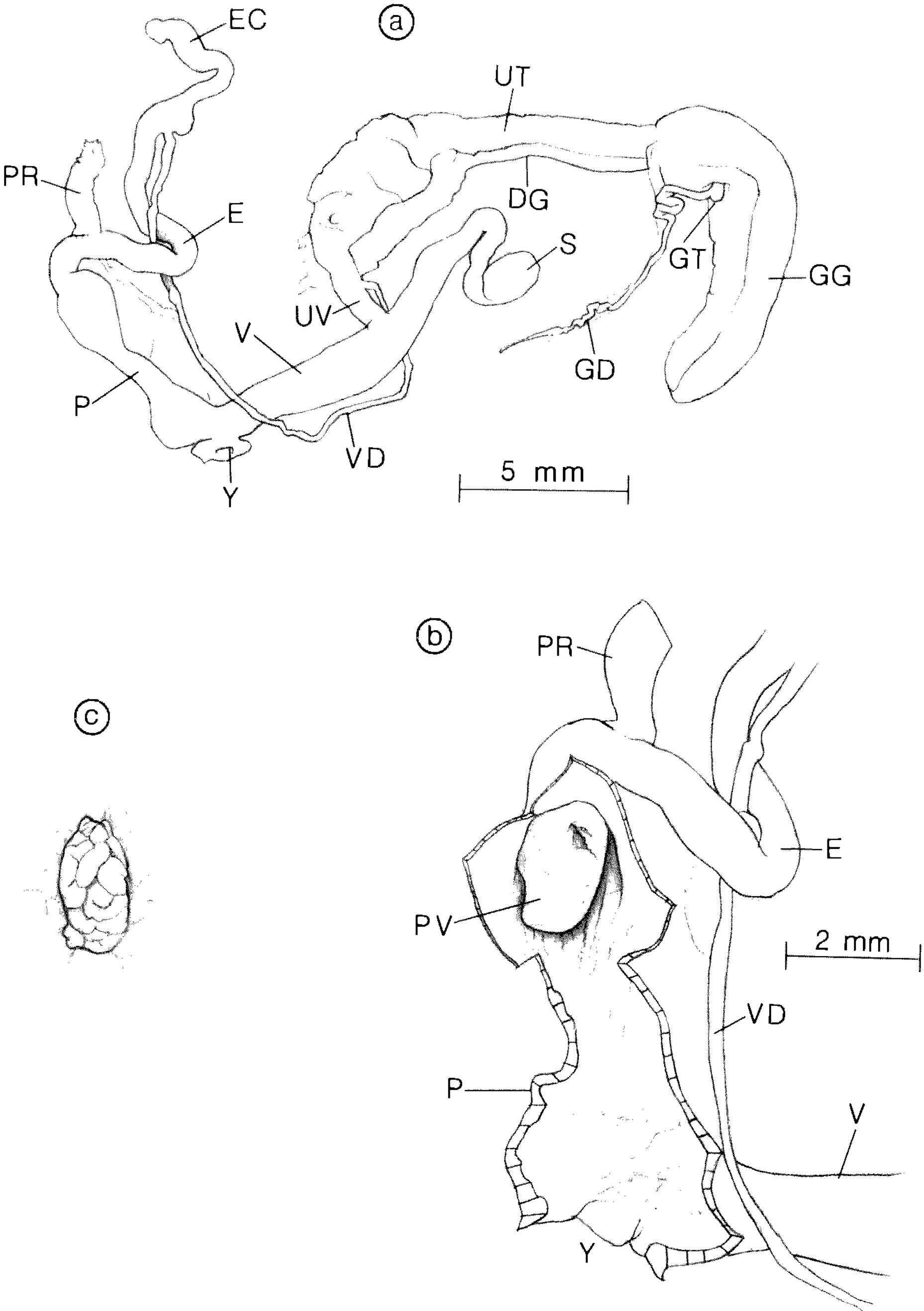


Fig. 417: Genitalia of *Rhagada radleyi* Preston, 1908: WA–417, Glen Florrie Station, WA. 11 April 1977. FMNH 199774, Dissection A: (a) whole genitalia; (b) verge; (c) head wart. Scale lines as marked. Drawings by Linnea Lahlum.

P. J. Bridge! 1 September 1969, WAM 298.74, FMNH 208780, 17 DA, 4 DJ); Glen Florrie Station (WA–417, WAM 817.87, SAM D18169–70, AM, QM, MV, FMNH 199306, FMNH 199774, 11 LA, 40 DA, several LJ, 19 DJ); asbestos mine 5 miles E of Meilga Station (A. Saar and P. J. Bridge! 2 September 1969, WAM 300.74, 5 DA, 2 DJ); Amethyst Mine, 17 km SE of Wyloo Homestead (P. E. Evans!, WAM 1132.81, 1 DA, 3 DJ); Wyloo Station (A. Saar and P. J. Bridge! 29 August 1969, WAM 302.74,

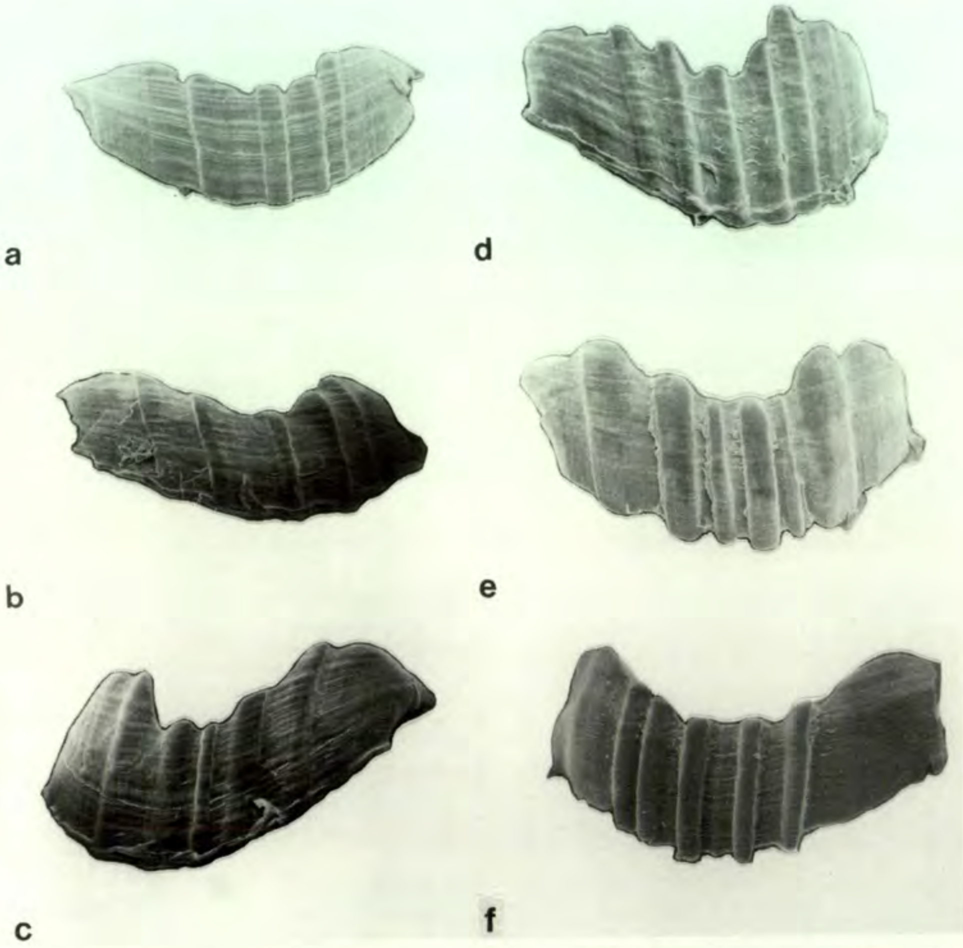


Plate 215: Jaws of *Rhagada capensis* sp. nov. and *R. convicta* (Cox, 1870): (a) *R. capensis*. WA–23, W side of Cape Range, 23.7 km N of Ningaloo Homestead, WA. 22 January 1974. FMNH 182492, Dissection A. jaw; (b) *R. capensis*. 2 miles E of Norwegian Bay, Ningaloo Station, S of North West Cape, WA. 22 July 1968. WAM 388.74, Dissection A. jaw; (c) *R. capensis*. WA–957, Scrubby Range, S of Exmouth Gulf, WA. 9 July 1983. FMNH 212485, Dissection A. c is jaw at 43.5X; (d) *R. convicta*. North Muiron Island, off North West Cape, WA. 12 July 1970. WAM 344.71, Dissection A. d is jaw at 39.5X; (e) WA–45, SE of Onslow, WA. 3 February 1974. FMNH 182541, Dissection A. e is jaw at 39X; (f) *R. convicta*. WA–33, Karratha, Pilbara, WA. 25 January 1974. FMNH 182647, Dissection A. f is jaw at 44X.

FMNH 208779, 12 DA, 5 DJ; 15 miles NE, J. Abbott! August 1970, WAM 293.74, 4 DA, 2 DJ; Log Hut, A. Saar and P. J. Bridge!, WAM 357.74, 2 LJ); Brown's Well, Oakover River district (John Abbott! May 1972, WAM, 2 DA); Mt Price, Parry Range (J. Abbott! WAM 7.87, 3 DA, 1 DJ); Millstream, Fortescue River (WA–41, FMNH 182537, 1 DA; July 1975, WAM 1368.75, 1 LA; 21 July 1958, WAM, 1 DA; 22 July 1958, WAM 278.74, 4 DA; 18 January 1958, WAM 286.74, 1 DA; W. D. L. Ride!, WAM 299.74, FMNH 208781, 13 DA; T. Start! 18 June 1978, WAM 1112.81, 2 DA; Palm Pool, J. Clark! November 1974, WAM 1369.75, 9 DA, 1 DJ; Crystal Pool, R. Roe! 6 September 1983, WAM 27.87, WAM 34.87, 9 DA, 3 DJ; Deep Reach Pool, D. Roberts and J. Stoddard! 22 November 1978, WAM 314.80, 3 DA; Crossing Pool, R. Roe! 6 September 1983, WAM 11.87, 2 DA).

Range

Rhagada radleyi has been found between Millstream on the Fortescue River (21°37'S, 117°05'E) SSW to Joy Helen Mine (23°14'S, 115°48'E) on the Henry River in the upper Ashburton drainage (**Maps 37, 39**), a distance of about 225 km. The known E–W range would be covered by a diagonal zone about 50 km wide but may be significantly extended when areas to the E are investigated for land snails. The nearest records of the coastal plains species *Rhagada convicta* (**Map 37**) are 90–100 km away at Cossack or 155 km away along the Bullara–Giralia road just S of Exmouth Gulf. The more northern *Rhagada richardsonii* extends from Depuch Island to Cape Keraudren and thence inland to the Oakover River and S to Roy Hill on the upper Fortescue (**Map 37**).

Diagnosis

Shell medium in size, adult diameter 13.6–19.7 mm (mean 16.64 mm), with 4 1/2 to 5 3/4– (mean 5 1/8) normally coiled whorls. Apex and spire moderately elevated, rounded above (**Figs 416b, e**), shell height 8.5–14.8 mm (mean 11.58 mm), H/D ratio 0.573–0.853 (mean 0.693). Body whorl evenly rounded. Shell apex (**Plate 206f**) with radial sculpture, spire and body whorl with prominent radial growth ridgelets. Umbilicus (**Figs 416c, f**) usually with a slight lateral crack present. Body whorl descending variably behind aperture, which is slightly narrowed. Lip thin, narrowly expanded. Shell white or with a faint, very light brownish tone, normally with many spiral red or orange colour bands that are quite variable in width. Some specimens with fewer and wider bands present. Based on 127 measured adults.

Genitalia (**Figs 417a–c**) with enlarged albumen gland (GG), spermatheca complexly and tightly kinked, free oviduct (UV) short and curved, vagina (V) relatively short and thick. Epiphallic caecum (EC) very long. Penis (P) quite long, enlarged basally where longitudinal pilasters are prominent, very slender medially, enlarged apically. Verge (PV) short, tapering rapidly, with corrugated surface. Head wart (**Fig. 417c**) small, elongate–ovate, slightly darker in colour than head area.

Central and lateral teeth of radula (**Plate 220a**) with small anterior flare, elevated cusp shaft angle, cusp tip pointed and barely curved, ectocone absent, basal plate slightly elongated. Late laterals (**Plate 220b**) retain the high cusp angle, show greatly enlarged anterior flare, and very slight ectoconal trace. Lateromarginal transition (**Plate 220c**) and early marginals typical. Jaw (**Plate 220d**) with a few prominent vertical ribs at irregular intervals on medial portion.

Table 156: Local variation in *Rhagada plicata* and Dampier Archipelago species.

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Rhagada plicata					
Hermite Island, WAM 371.74	6L	7.39±0.154 (6.85-7.75)	10.09±0.182 (9.5-10.5)	0.732±0.004 (0.722-0.743)	$4\frac{1}{2}$ ($4\frac{3}{8}$-$4\frac{5}{8}$−)
Hermite Island, WAM 31.87	13D	7.38±0.096 (6.95-8.05)	9.64±0.077 (9.25-10.1)	0.765±0.009 (0.724-0.826)	$4\frac{1}{2}$+ ($4\frac{3}{8}$+-$4\frac{3}{4}$−)
Hermite Island, WAM 267.74	8D	8.15±0.205 (7.2-9.0)	10.51±0.266 (9.3-11.55)	0.776±0.003 (0.763-0.792)	$4\frac{1}{2}$+ ($4\frac{3}{8}$+-$4\frac{1}{2}$−)
Hermite Island, WAM 261.74	6D	7.94±0.351 (6.65-9.05)	10.67±0.267 (9.9-11.45)	0.743±0.017 (0.673-0.788)	$5\frac{7}{8}$ ($4\frac{1}{4}$-$4\frac{5}{8}$)
Hermite Island, WAM 1122.81	7D	8.05±0.332 (6.8-8.95)	10.34±0.309 (9.1-11.3)	0.778±0.019 (0.699-0.839)	$4\frac{5}{8}$+ ($4\frac{3}{8}$-$4\frac{7}{8}$)
Hermite Island, WAM 1111.81	6D	8.36±0.180 (7.75-9.0)	11.13±0.304 (10.25-12.05)	0.752±0.010 (0.723-0.799)	$4\frac{5}{8}$− ($4\frac{1}{2}$+-$4\frac{5}{8}$+)
Alpha Island, WAM 30.87	8D	7.28±0.133 (6.6-7.75)	9.85±0.194 (9.0-10.7)	0.732±0.010 (0.702-0.792)	$4\frac{1}{2}$+ ($4\frac{1}{2}$−-$4\frac{5}{8}$+)
Trimouille Island, WAM 32.87	7D	8.15±0.314 (7.2-9.45)	10.73±0.289 (9.75-11.75)	0.758±0.013 (0.702-0.803)	$4\frac{1}{2}$ ($4\frac{3}{8}$+-$4\frac{3}{4}$−)
Rhagada minima					
Rosemary Island, WAM 20.87	23D	9.22±0.111 (8.35-10.05)	12.09±0.097 (10.9-13.05)	0.763±0.008 (0.693-0.842)	$4\frac{3}{4}$ ($4\frac{1}{2}$−-$5\frac{1}{8}$+)
Rosemary Island, WAM 248.74	13D	7.82±0.094 (7.1-8.25)	11.62±0.123 (11.15-12.7)	0.673±0.007 (0.632-0.714)	$4\frac{5}{8}$+ ($4\frac{3}{8}$+-5+)

Table 156: Local variation in *Rhagada plicata* and Dampier Archipelago species.

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Rhagada minima (continued)					
Rosemary Island, WAM 252.74	16D	7.56±0.221 (6.55-9.65)	11.51±0.231 (10.15-13.3)	0.656±0.010 (0.585-0.730)	$4\frac{1}{2}$ ($4\frac{1}{4}$-$4\frac{3}{4}$)
Enderby Island, WAM 234.74	3D	8.13 (8.0-8.3)	13.52 (13.4-13.6)	0.603 (0.586-0.620)	$5\frac{1}{4}$− ($4\frac{7}{8}$-$5\frac{5}{8}$)
Rhagada intermedia					
Delambre Island, WAM 358.74	25L	8.76±0.111 (7.9-9.75)	11.80±0.125 (10.5-13.15)	0.743±0.007 (0.669-0.793)	$4\frac{1}{2}$+ ($4\frac{1}{4}$−-$4\frac{7}{8}$−)
Delambre Island, WAM 139.68	25D	8.72±0.110 (7.65-9.95)	11.59±0.105 (10.5-12.45)	0.752±0.007 (0.693-0.826)	$4\frac{1}{2}$+ ($4\frac{1}{4}$+-5−)
Delambre Island, WAM 1131.81	19D	8.17±0.119 (7.5-9.3)	11.03±0.125 (9.95-12.25)	0.741±0.009 (0.684-0.824)	$4\frac{1}{2}$− ($4\frac{1}{8}$+-$4\frac{5}{8}$+)
Legendre Island, WAM 225.74	17D	8.65±0.140 (7.85-9.6)	11.31±0.136 (10.55-12.55)	0.765±0.010 (0.681-0.842)	$4\frac{1}{2}$ ($4\frac{3}{8}$-$4\frac{7}{8}$)
Enderby Island, WAM 16.87	9D	9.52±0.195 (8.2-10.35)	13.44±0.250 (12.25-14.85)	0.708±0.010 (.669-.780)	$4\frac{3}{4}$ ($4\frac{3}{8}$-$5\frac{1}{8}$)

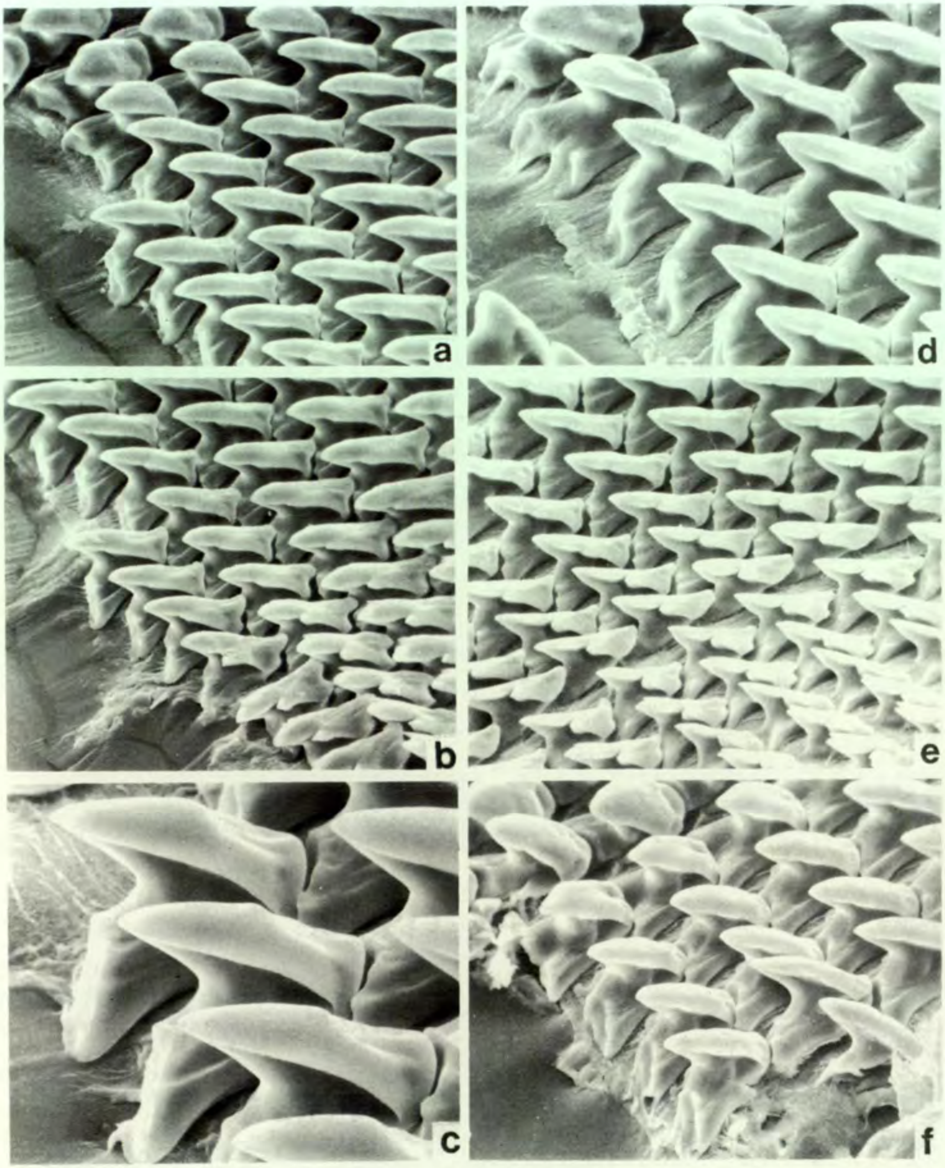


Plate 216: Radular teeth of *Rhagada convicta* (Cox, 1870): (a–b) North Muiron Island, off North West Cape, WA. 12 July 1970. WAM 344.74, Dissection A. a is central and laterals at 340X. b is late laterals and latero-marginal transition at 340X; (c) Toothawarra Creek, Cardabia Station, S of Exmouth Gulf, WA. 4 April 1969. WAM 374.74, Dissection A. c is 1st and 2nd laterals at 850X; (d–e) WA–45, SE of Onslow, WA. 3 February 1974, Dissection A. d is central and early laterals at 530X. e is latero-marginal transition at 395X; (f) WA–32a, Intercourse Island road, Dampier, Pilbara, WA. 25 January 1974. FMNH 182597, Dissection A. f is central and early laterals at 370X.

Discussion

Rhagada radleyi is represented in collections mainly by scattered records of a few individuals. Only the Glen Florrie (WA–417) sample is large and contains adequate material for dissection. The live-collected Millstream example (WAM 1368.75) was so deeply retracted that the specimen would have been destroyed in any dissection attempt. Variation in the essentially single records from Joy Helen Mine, Meilga Station and Glen Florrie Station is summarised in **Table 155**. A summary of the scattered samples from Millstream and Wyloo Station follows:

	Millstream Crossing (42 specimens)	Wyloo Station (15 specimens)
Height	11.04 (9.5–14.1)	10.20 (8.4–12.3)
Diameter	15.63 (14.1–18.65)	15.43 (14.05–16.9)
H/D ratio	0.703 (0.634–0.796)	0.655 (0.575–0.702)
Whorls	5 1/8– (4 1/2 – 5 5/8–)	5+ (4 3/4 – 5 1/2)

There is substantial difference in diameter, with the Glen Florrie shells much bigger than the Joy Helen and Meilga specimens from the same general region. The Joy Helen and Millstream examples have higher spires, while the Wyloo shells are low spired.

R. radleyi was described without a precise locality and was based on very worn material. None of the sampled localities can be cited as a possible type source since the measured type examples do not agree with average features of any population.

RHAGADA PLICATA PRESTON, 1914

(Plates 207a, 221a–d; Figs 418a–b, 419a–c; Map 37)

Rhagada plicata Preston, 1914, *Proc. Malac. Soc. London,* **11** (1): 13–14, fig. – Montebello Islands, Western Australia; Hedley 1916, *Jour. Roy. Soc. Western Aust.,* **1**: 70.

Bellrhagada plicata (Preston), Iredale 1938, *Aust. Zool.,* **9** (2): 114 – Check list citation; Iredale 1939, *Jour. Roy. Soc. Western Aust.,* **25:** 71, plt. V, fig. 16; Richardson 1985, *Tryonia*, **12:** 65 – Check list citation.

Comparative remarks

Rhagada plicata Preston, 1914, recorded from several of the Montebello Islands, WA (**Map 37**), is the smallest species of *Rhagada* (mean diameter 10.35 mm), with a reduced whorl count (mean 4 5/8+), strongly and evenly elevated spire (**Fig. 418b**, mean H/D ratio 0.758), aperture slightly to moderately deflected behind lip, not narrowed, lip narrowly expanded and thin, umbilicus usually closed by broad expansion of columellar lip. Shell white, with a prominent supraperipheral and with narrow subsutural red spiral colour bands, sometimes reduced to translucent zones. Most examples with a few accessory spiral bands. Shell apex smooth (**Plate 207a**), spire and body whorl with prominent, regularly spaced, rather crowded radial ribs that are essentially absent from shell base. *R. minima* sp. nov., from Rosemary, Conzinc and Enderby Islands, Dampier Archipelgo (**Map 40**), is larger (mean diameter 11.91 mm), with a lower spire (**Fig. 418d**), a narrow to moderate umbilical crack (**Fig. 418e**) and radial sculpture that often extends onto shell base. *R. intermedia*, from several of the Dampier Archipelago Islands (**Map 40**), is larger (mean diameter 11.69 mm), essentially identical in shape (**Fig. 420b**, mean H/D ratio 0.749), has a usually-closed or nearly-closed umbilicus and less prominent radial ribbing (**Plate 207d**) that is greatly reduced to absent on shell base. *R. dringi* (Pfeiffer, 1846), from the 80 Mile Beach area (**Map 39**), is larger (mean diameter 12.31 mm) at the same whorl count, has a much lower spire (**Fig. 425b**), an often narrow umbilical crack and very prominent radial ribbing (**Plate 209a–b**) that is greatly reduced on shell base.

Anatomically (**Figs 419a–c**), *R. plicata* has a large albumen gland (GG), long spermatheca (S) that is kinked only at the head, very short free oviduct (UV), short vagina (V) with large diameter and very long epiphallic caecum (EC). Penis (P) short, verge (PV) short and conical with corrugated surface. *R. intermedia* sp. nov. (**Figs 421a–c**) has a short spermatheca that is folded into a "U" shape, medium length vagina, medium length penis and short, dome-shaped verge. *R. dringi* (**Figs 426a–d**) has a very large albumen gland, short and kinked spermatheca, very short vagina and penis and medium length epiphallic caecum. The verge tapers gradually, has a nearly smooth surface and short posterior sperm groove.

Paratype

Montebello Islands. FMNH 41617 ex Webb, Gude, Preston, 1 DA. Height of shell 7.4 mm, diameter 9.6 mm, H/D ratio 0.771, whorls 4 3/4, umbilicus nearly closed, a slight lateral crack remaining.

Material studied

WESTERN AUSTRALIA: Montebello Islands (G. P. Whitley, 18 September 1945, AM, 8 DA): North West Island (T. Start! 10 June 1981, WAM 28.87, 6 DA, 3 DJ); Trimouille Island (T. Start! 10 June 1981, WAM 32.87, 7 DA, 5 DJ); Alpha Island (T. Start! 10 June 1981, WAM 30.87, 8 DA, 5 DJ); Hermite Island (T. Start! 11 June 1981, WAM 31.87, FMNH 208776, 13 DA, 12 DJ; E side, P. Kailada! 13 December 1979, WAM 1111.81, 6 DA, 2 DJ; Big Lagoon on E shore, S. Slack-Smith! 11 December 1979, WAM 1122.81, 7 DA, 3 DJ; S end, R. W. George! 23 September 1958, WAM 261.74, 6 DA; R. W. George! 22 September 1958, WAM 267.74, 8 DA, 5 DJ; W. H. Butler! 28 December 1966, WAM 371.74, 6 LA, 7 LJ).

Range

Rhagada plicata has been collected on four of the Montebello Islands, (**Map 37**) – Hermite, Alpha, Trimouille and North West. The N–S range (Hermite through North West Island) is 16 km; the E–W range (including Trimouille Island) is only 8 km. A few specimens of a species of *Rhagada* have been collected on Barrow Island to the S, but they cannot be referred to a known species and the specimens are not adequate for description.

Diagnosis

Shell small, adult diameter 9.0–12.05 mm (mean 10.35 mm), with 4 1/4– to 4 7/8 (mean 4 5/8+) normally coiled whorls. Apex and spire strongly and usually evenly elevated (**Fig. 418b**), shell height 6.6–9.55 mm (mean 7.85 mm), H/D ratio 0.673–0.839 (mean 0.758). Body whorl evenly rounded. Shell apex (**Plate 207a**) smooth, spire and body whorl with prominent, rather widely spaced radial ribs that are almost completely absent from shell base. Umbilicus usually completely covered by columellar

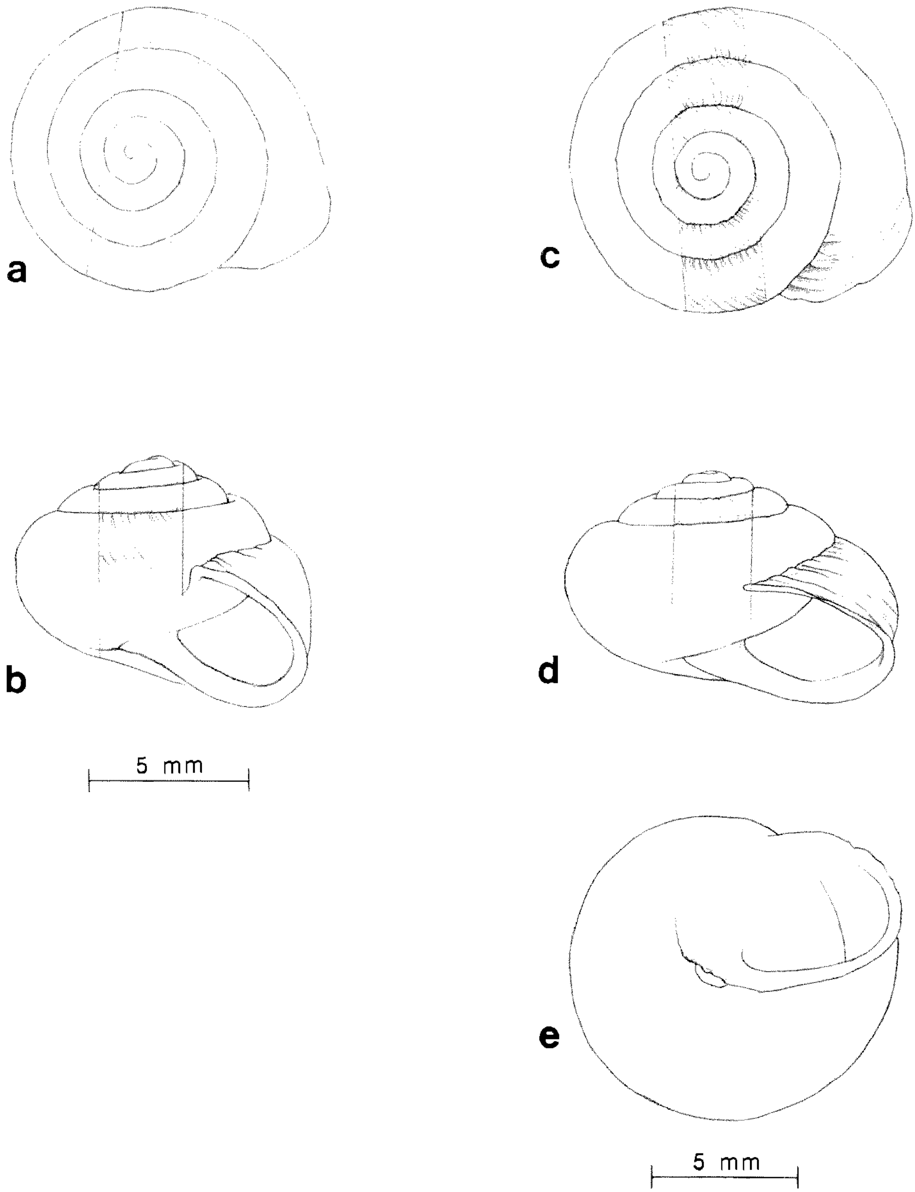


Fig. 418: Shells of *Rhagada plicata* Preston, 1914 and *R. minima* sp. nov.: (a–b) *R. plicata*. Hermite Island, Montebello Islands, WA. WAM 262.74; (c–e) Holotype of *R. minima*. WAM 763.87. Rosemary Island, Dampier Archipelago, WA.

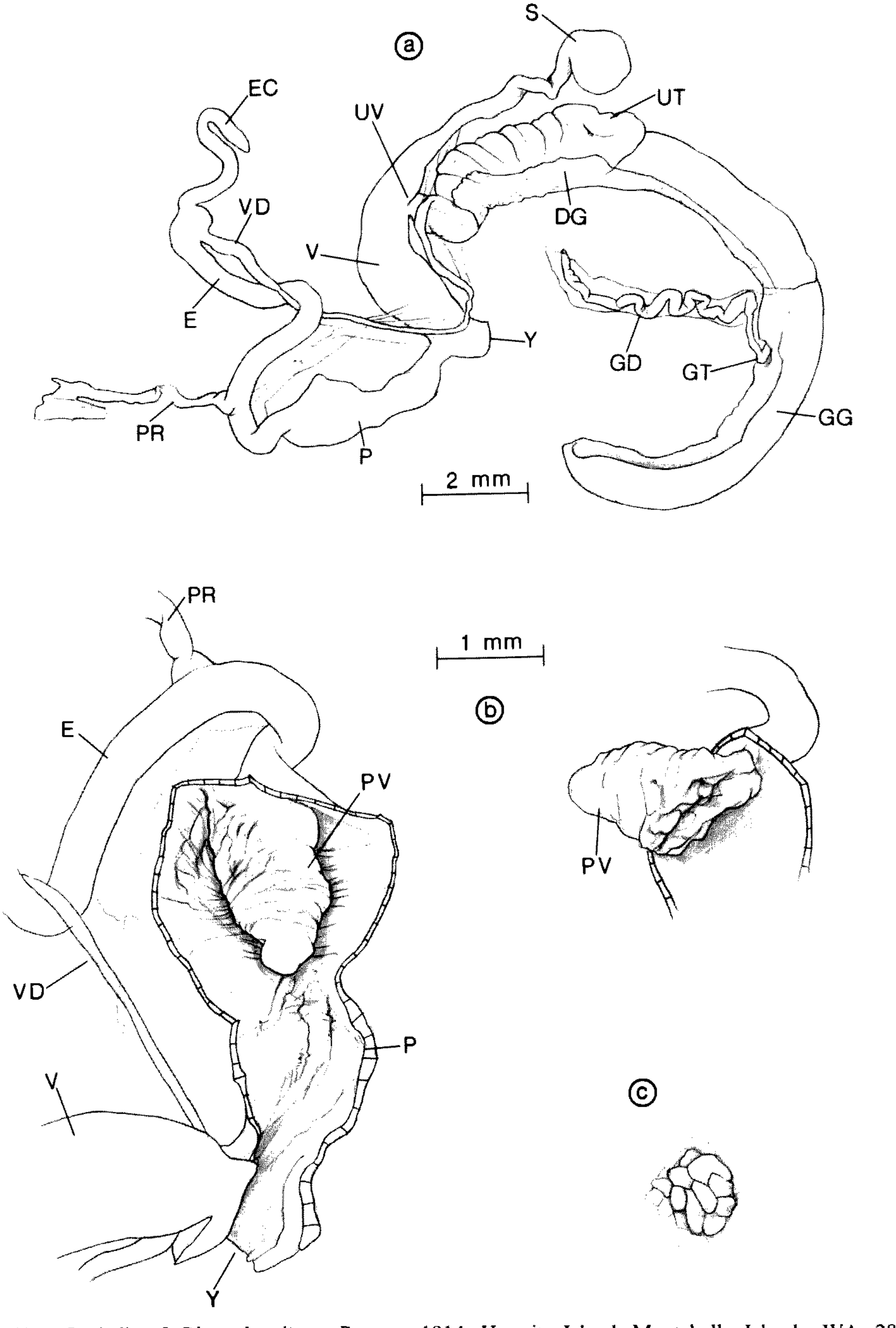


Fig. 419: Genitalia of *Rhagada plicata* Preston, 1914: Hermite Island, Montebello Islands, WA. 28 December 1966. WAM 371.74, Dissection B: (a) whole genitalia; (b) verge; Dissection D: (c) head wart. Scale lines as marked. Drawings by Linnea Lahlum.

callus expansion, often a raised ridge visible, rarely a very narrow lateral crack. Body whorl descending slightly behind lip, which is narrowly expanded and thin. Numerous spiral colour bands, supraperipheral and subsutural most prominent. Based on 70 measured adults.

Genitalia (**Figs 419a–c**) with large albumen gland (GG), long spermatheca (S) that is kinked only at apex, very short free oviduct (UV), vagina (V) short and wide and epiphallic caecum (EC) very long. Penis (P) short, verge (PV) conical, tapering rapidly, with corrugated surface. Head wart (**Fig. 419c**) large, oval, grey in colour, much darker than neck and foot.

Central and early lateral teeth (**Plate 221a**) with small anterior flare, slight ectoconal cusp, pointed cusp tip with slight curvature and normal cusp shaft angle. Lateromarginal transition (**Plate 221b**) and marginals typical (**Plate 221c–d**). Jaw with few prominent vertical ridges in middle section.

Discussion

Most available material of *Rhagada plicata* is from Hermite Island, Montebello Islands (**Table 156**). The single significant samples from the other islands suggest that there is considerable local variation in shell parameters. A listing of the respective mean dimensions follows:

	Alpha	Hermite	North West	Trimouille
Specimens	8	46	5	7
Height	7.28	7.82	8.83	8.15
Diameter	9.95	10.29	11.14	10.73
H/D ratio	0.732	0.760	0.792	0.758
Whorls	4 1/2+	4 3/4-	4 5/8	4 1/2

These specimens were collected over a number of years, hence the possibility of allochronic variation cannot be excluded. Since the collecting records do not indicate the ecological conditions under which they were found, the possibility exists that exposure differences might be reflected in the size differences among the Hermite Island populations (**Table 156**). It is thus premature to suggest that the size variations among islands might correlate with island size or other easily measurable factors. The fact of the size variation does suggest that additional field work could be expected to yield interesting results concerning both local and island variation.

RHAGADA MINIMA SP. NOV.

(Plate 207b–c; Figs 418c–e; Map 40)

Comparative remarks

Rhagada minima sp. nov., recorded from Rosemary, Conzinc and Enderby Islands in the Dampier Archipelago (**Map 40**), is a small species (mean diameter 11.91 mm), with reduced whorl count (mean 4 5/8+), moderately elevated and rounded spire (**Fig. 418d**, mean H/D ratio 0.702), aperture slightly descending behind lip which is narrowly expanded, umbilicus often with a narrow lateral crack (**Fig. 418d**). Body whorl often weakly angulated. Shell white, with numerous narrow spiral reddish colour bands, supraperipheral and subsutural bands usually wider and darker. Shell apex smooth (**Plate 207b**), spire and body whorl with prominent radial ribs that extend partly onto shell base. *R. plicata*, from the Montebello Islands, (**Map 37**), is smaller (mean diameter 10.35 mm) and higher spired (**Fig. 418b**, mean H/D ratio 0.758) at the same whorl count and its radial ribbing does not extend onto the shell base. *R. intermedia* sp. nov., also from the Dampier Archipelago (**Map 40**), also is higher spired (**Fig. 420b**, mean H/D ratio 0.749) but usually has a closed umbilicus and less prominent radial ribbing. *R. dringi* (Pfeiffer, 1846), from the 80 Mile Beach area (**Map 39**), differs most obviously in its very prominent and crowded radial ribbing (**Plate 209a–b**) that does not continue onto the shell base and the usual presence of an umbilical crack. Anatomy of *R. minima* is unknown.

Holotype

WAM 763.87, in leaf litter and rock crevices, Rosemary Island, Dampier Archipelago, Western Australia, Australia. Collected 19 August 1961 by G. W. Kendrick. Height of shell 7.9 mm, diameter 11.6 mm, H/D ratio 0.681, whorls 5, umbilicus very narrow, width 0.75 mm, columellar lip extension broken.

Paratopotypes

WAM 248.74, FMNH 208772, 14 DA, 13 DJ from the type collection.

Paratypes

WESTERN AUSTRALIA: Rosemary Island (ex WAM 327.74, 1 DA; G. M. Storr! 15 June 1962, WAM 252.74, 19 DA, 17 DJ; D. L. Serventy! 1952, WAM 20.87, FMNH 208773, 25 DA, 5 DJ; G. W. Kendrick! 24 August 1961, WAM 14.87, 3 DA, 1 DJ; G. W. Kendrick! 19 August 1961, WAM 22.87, 2 DA, 4 DJ; N end of central ridge, G. W. Kendrick! 19 August 1961, WAM 15.87, 4 DA, 3 DJ); Conzinc Island (G. Connell! 2 September 1983, WAM 36.87, 1 DA); Enderby Island (H. Williams and M. McDonald! 16 June 1962, WAM 234.74, 2 DA, 3 DJ).

Range

Rhagada minima has been collected on three islands in the Dampier Archipelago – Rosemary, Conzinc and Enderby (**Map 40**). The distance from Rosemary through Enderby is about 22 km, from Enderby through Conzinc is 33 km and the Rosemary to Conzinc distance is 23 km. The known range thus approximates to an equilateral triangle.

Diagnosis

Shell small, adult diameter 10.15–13.65 mm (mean 11.91 mm), with 4 1/4 to 5 5/8 (mean 4 5/8+) normally coiled whorls (**Fig. 416c**). Apex and spire moderately elevated, rounded above (**Fig. 416d**), shell height 6.55–10.2 mm (mean 8.37 mm), H/D ratio 0.585–0.842 (mean 0.702). Body whorl often weakly angulated. Shell apex smooth (**Plate 207b**), spire and body whorl with very prominent radial ribs that partly extend onto shell base. Umbilicus (**Fig. 418e**) often with a narrow lateral crack. Body whorl descending slightly behind lip, which is narrowly expanded and thin. Many narrow spiral color bands present, the supraperipheral and subsutural usually wider. Based upon 65 measured adults.

Anatomy unknown.

Discussion

The name *minima* refers to the fact that this is the smallest species in the Dampier Archipelago radiation of *Rhagada*. Variation among populations on Rosemary Island is fairly large (**Table 156**). The limited material from Enderby Island (3 specimens) and Conzinc Island (1 specimen) fall outside the limits of Rosemary variation. This suggests that more field work in needed before the exact status of these populations can be determined.

RHAGADA INTERMEDIA SP. NOV.

(Plates 207d, 221e–f; Figs 420a–b, 421a–c; Map 40)

Comparative remarks

Rhagada intermedia sp. nov., recorded from Delambre, Enderby, Legendre and Rosemary Islands, Dampier Archipelago, WA (**Map 40**), is a small species (mean diameter 11.69 mm), with reduced whorl count (mean 4 5/8–), high and somewhat rounded spire (**Fig. 420b**, mean H/D ratio 0.749), aperture somewhat descending behind lip, which is thin and narrowly expanded, umbilicus closed by expansion of columellar lip. Body whorl sometimes slightly angulated. Shell white, with several narrow spiral red or reddish-orange bands, the supraperipheral and subsutural often wider and darker in colour. Shell apex smooth (**Plate 207d**), spire and body whorl with prominent radial ribs, rather widely spaced, that are greatly reduced or absent on shell base. *R. minima*, also from the Dampier Archipelago (**Map 40**), differs in its lower spire (**Fig. 418d**, mean H/D ratio 0.702), umbilicus generally with an open lateral crack and more prominent radial ribbing (**Plate 207b**). The somewhat larger (mean diameter 12.31 mm) *R. dringi* (Pfeiffer, 1846), from 80 Mile Beach (**Map 39**), has a much lower spire (**Fig. 425b**, mean H/D ratio 0.671) at the same whorl count, and much more prominent, crowded radial sculpture that does not continue onto the shell base. *R. plicata*, from the Montebello Islands (**Map 37**), is nearly identical in shape (**Fig. 418b**, mean H/D ratio 0.758) but is smaller (mean diameter 10.35 mm) at the same whorl count and often has an umbilical ridge present instead of a smooth callus closure.

Anatomically (**Figs 421a–c**), *R. intermedia* has a large albumen gland (GG), the spermatheca (S) is short, folded into a "U" but not kinked, free oviduct (UV) very short, vagina (V) medium in length, epiphallic caecum (EC) long, penis medium in length, swollen apically, verge (PV) short, dome-shaped, with rugose surface. Head wart (**Fig. 421c**) large, oval, dark grey in colour, much darker than head and neck tissue. *R. plicata* (**Figs 419a–c**) has a longer spermatheca that is only kinked at the top, a short vagina and penis, very long epiphallic caecum and the verge is conical with corrugated surface. *R. dringi* (**Figs 426a–d**) has a very large albumen gland, kinked spermatheca, short vagina and penis, medium length epiphallic caecum and the verge is elongated, weakly corrugated and with a long sperm groove.

Holotype

WAM 764.87, in leaf litter and soil, Delambre Island, Dampier Archipelago, Western Australia, Australia. Collected 29 August 1961 by G. W. Kendrick. Height of shell 9.25 mm, diameter 11.85 mm, H/D ratio 0.781, whorls 4 3/4+, umbilicus completely closed by a broad callus.

Paratopotypes

WAM 358.74, FMNH 208770, 25 LA, 12 LJ from the type locality.

Paratypes

WESTERN AUSTRALIA: Dampier Archipelago: Legendre Island (R. D. Royce! 10 June 1962, WAM 225.74, FMNH 208771, 17 DA, 4 DJ); Delambre Island (8 November 1974, WAM 1131.81, 19 DA, 25 DJ; G. W. Kendrick! 29 August 1961, WAM 139.68, 9 DA, 8 DJ); Enderby Island (G. M. Storr! 15 June 1962, WAM 16.87, 9 DA, 8 DJ); Elphick Knob off Rosemary Island (G. Connell! 20 August 1983, WAM 24.87, 8 DA, 2 DJ); Rosemary Island, Lady Nora Flats, NE side (B. R. Wilson! 30 October 1971, WAM 8.87, 1 DA).

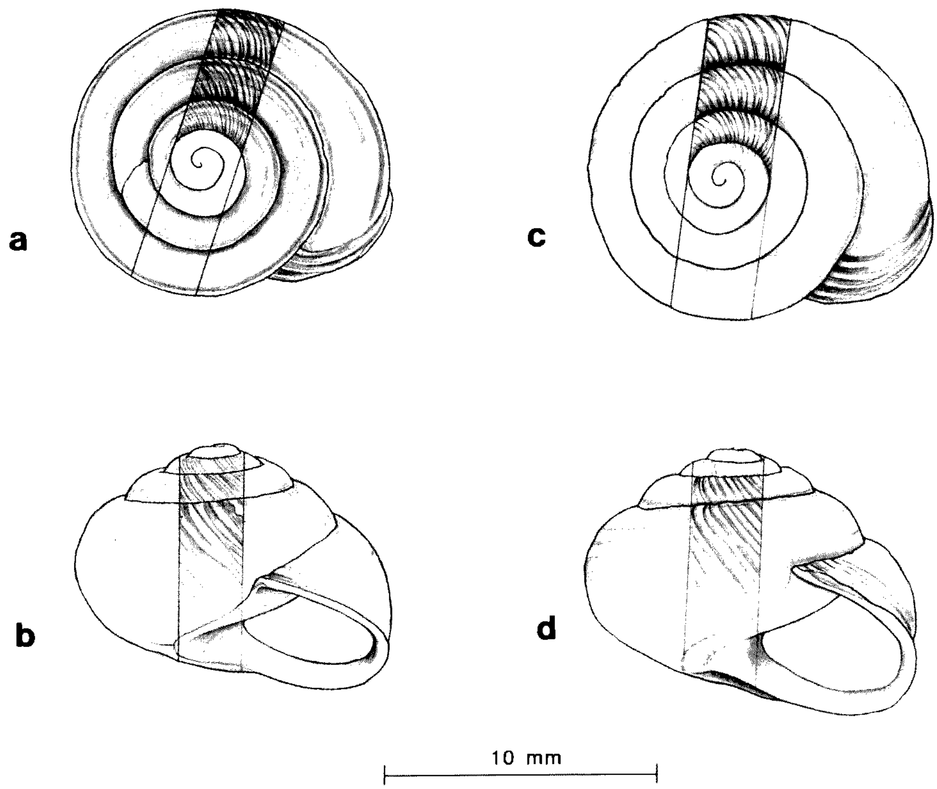


Fig. 420: Shells of *Rhagada intermedia* Solem, herein and *R. elachystoma* (von Martens, 1878): (a–b) Holotype of *R. intermedia*. WAM 764.87. Delambre Island, Dampier Archipelago, WA; (c–d) *R. elachystoma*. Kendrew Island, Dampier Archipelago, WA. WAM 241.74. Scale line equals 10 mm. Drawings by Linnea Lahlum.

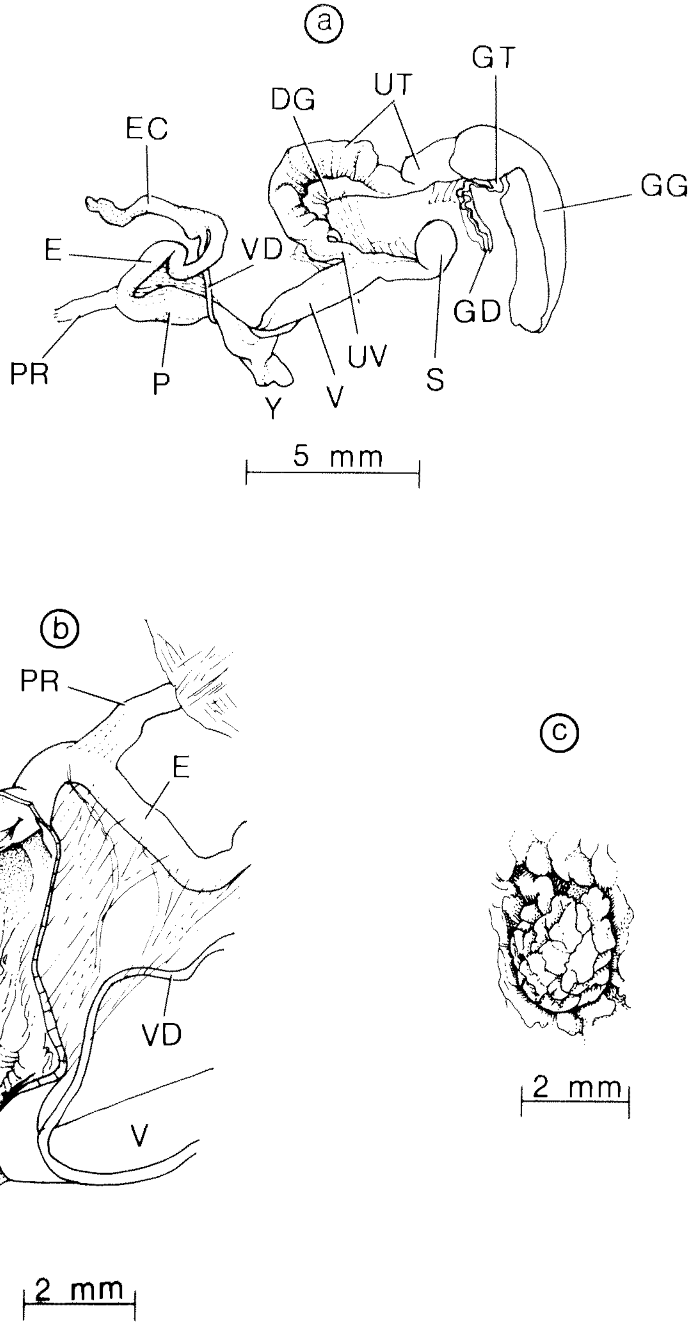


Fig. 421: Genitalia of *Rhagada intermedia* sp. nov.: Delambre Island, Dampier Archipelago, WA. 29 August 1961. WAM 358.74, Dissection A: (a) whole genitalia; Dissection B: (b) verge; (c) head wart. Scale lines as marked. Drawings by Linnea Lahlum.

Range

Rhagada intermedia has been collected from four islands (**Map 40**) in the Dampier Archipelago, WA – Delambre, Enderby, Legendre and Rosemary with its offshore islet, Elphick Knob. The maximum linear range distance is 67 km.

Diagnosis

Shell small, adult diameter 9.95–14.85 mm (mean 11.69 mm), with 4 1/8+ to 5 1/8 (mean 4 5/8–) normally coiled whorls (**Fig. 420a**). Apex and spire moderately elevated (**Fig. 420b**), shell height 7.5–10.5 mm (mean 8.75 mm), H/D ratio 0.669–0.849 (mean 0.749). Body whorl sometimes weakly angulated. Shell apex smooth (**Plate 207d**), spire and body whorl with prominent, rather widely spaced radial ribs that are greatly reduced on shell base. Umbilicus completely closed by expansion of columellar callus. Body whorl descending slightly behind lip, which is thin and narrowly expanded. Colour white, with numerous red to orange, narrow, spiral colour bands, the supraperipheral and subsutural usually wider and darker in tone. Based on 104 measured adults.

Genitalia (**Figs 421a–c**) with large albumen gland (GG), spermatheca (S) short, folded into a "U", not kinked; free oviduct (UV) short, vagina (V) medium in length, epiphallic caecum (EC) long, penis (P) medium in length, swollen apically, verge (PV) short, dome-shaped, with rugose surface. Head wart (**Fig. 421c**) large, oval, dark grey in colour.

Central and early lateral teeth of radula (**Plate 221e**) with moderate anterior flare, slightly elevated cusp shaft angle, curved and bluntly pointed cusp tip, ectoconal notch appearing on 4th or 5th lateral. Jaw (**Plate 221f**) with a few weak to prominent vertical ribs on middle section.

Discussion

Rhagada intermedia is generally distributed in the Dampier Archipelago (**Map 40**), with records from Delambre, Enderby, Rosemary Island and its outlier – Elphick Knob and Legendre Islands. Shell variation is summarised in **Table 156**. The Enderby examples are larger, low spired and with increased whorl count. The single Rosemary and few Elphick Knob examples are intermediate in size, with the latter high-spired. The Legendre and Delambre specimens appear to be the same in size and shape.

Unfortunately, only the one sample from Delambre Island could be dissected.

The name *intermedia* indicates that this species is intermediate in shell shape between *Rhagada elachystoma* (von Martens, 1878) and *R. angulata* sp. nov.

RHAGADA ELACHYSTOMA (VON MARTENS, 1878)
(Plate 207e–f; Figs 420c–d; Map 40)

Helix elachystoma von Martens, 1878, *Monatsber. K. Akad. Wiss. Berlin,* **1877:** 273–274, plt. I, figs 8–9 – Mermaid Strait, Dampier Archipelago, Western Australia; von Martens 1879, *Novit. Conch*., **5**: 35, plt. 144, figs 1–4; E. A. Smith 1894, *Proc. Malac. Soc. London,* **1:** 89 – cited as a synonym of *Rhagada richardsonii* (E. A. Smith, 1874); Iredale 1939, *Jour. Roy. Soc. Western Aust.,* **25:** 59–60 – listed as a synonym of *Rhagada richardsonii* (E. A. Smith, 1894).

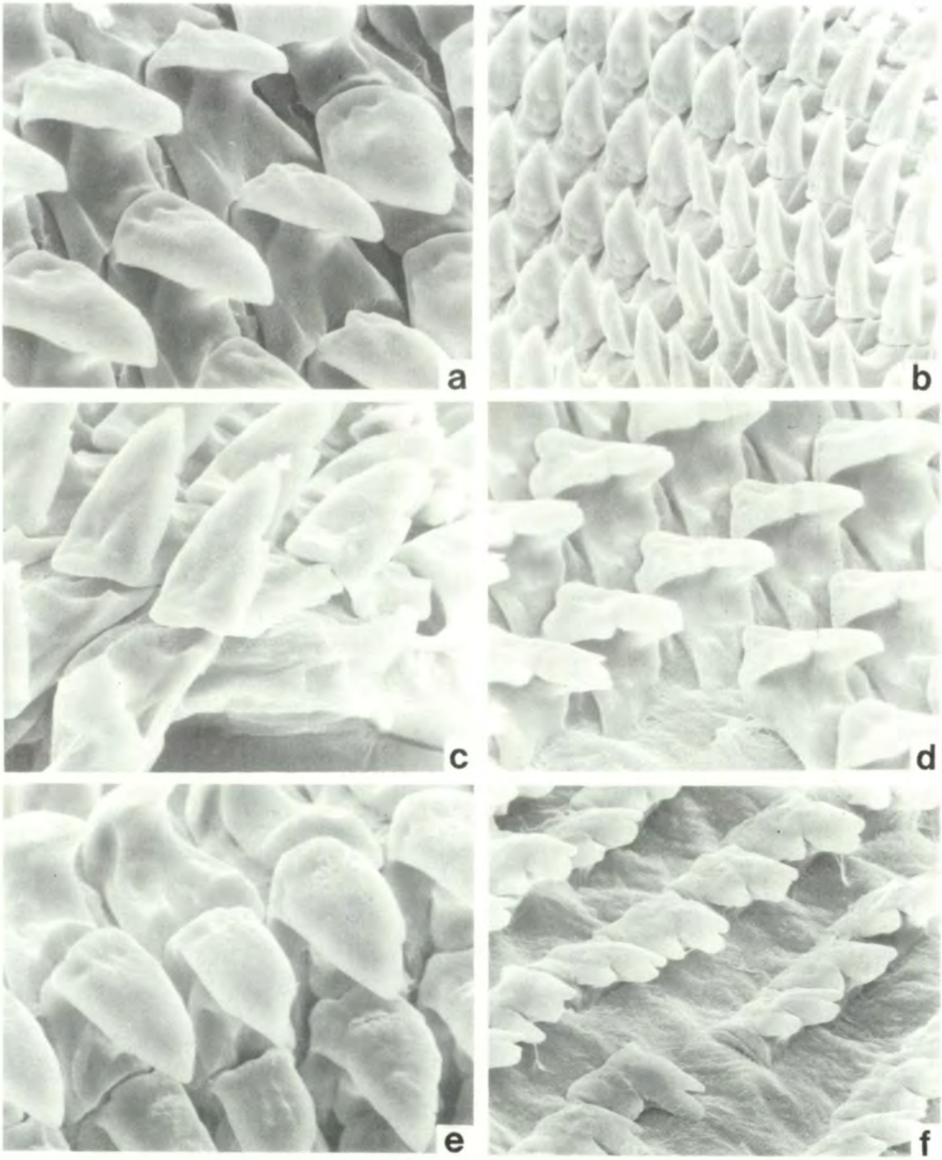


Plate 217: Radular teeth of *Rhagada convicta* (Cox, 1870). WA–27, creek crossing on Bullara-Giralia road, 8.7 km E of Bullara Homestead, S of Exmouth Gulf, WA. 23 January 1974. FMNH 182705: (a–d) Dissection D. a is central and early laterals at 650X. b is central and early laterals in high angle view at 310X. c is late laterals at 650X. d is early marginals at 640X; (e–f) Dissection C. e is central and early laterals at 630X. f is late marginals at 610X.

Table 157: Local variation in *Rhagada elachystoma, R. angulata* and *R. dampierana.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Rhagada elachystoma					
Kendrew Island, WAM 241.74	62D	10.05±0.076 (8.95-11.5)	13.53±0.077 (12.35-14.6)	0.743±0.004 (0.659-0.822)	$4\frac{3}{4}-$ ($4\frac{1}{2}$-$5\frac{1}{8}$)
Rosemary Island, WAM 327.74	6D	10.56±0.223 (9.75-11.1)	14.69±0.238 (13.85-15.45)	0.719±0.009 (0.701-0.760)	$4\frac{7}{8}+$ ($4\frac{7}{8}$-$5\frac{1}{8}$)
Rhagada aff. *elachystoma*					
Legendre Island, WAM 224.74	22D	11.33±0.202 (9.7-13.3)	15.41±0.195 (13.9-17.55)	0.742±0.011 (0.665-0.848)	5 ($4\frac{5}{8}$-$5\frac{3}{8}$)
Legendre Island, WAM 21.87	6D	10.29±0.281 (9.3-11.0)	14.78±0.273 (13.9-15.05)	0.703±0.015 (0.644-0.746)	5− ($4\frac{5}{8}$-$5\frac{1}{4}-$)
Rhagada angulata					
Dolphin Island, WAM 342.74	14L	8.28±0.146 (7.55-9.4)	14.44±0.174 (13.2-15.35)	0.574±0.009 (0.504-0.641)	$5\frac{1}{8}+$ ($4\frac{3}{4}+$-$5\frac{3}{8}+$)
Dolphin Island, WAM 1129.74	9D	7.57±0.166 (6.75-8.5)	13.44±0.121 (12.85-13.9)	0.563±0.009 (0.525-0.622)	$5\frac{1}{8}-$ ($4\frac{7}{8}-$-$5\frac{3}{8}+$)
Legendre Island, WAM 229.70	11D	6.55±0.125 (6.0-7.55)	12.19±0.145 (11.55-13.1)	0.538±0.006 (0.500-0.577)	$4\frac{3}{4}-$ ($4\frac{1}{2}$-$4\frac{7}{8}$)

Table 157: Local variation in *Rhagada elachystoma, R. angulata* and *R. dampierana* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Rhagada dampierana					
Rosemary Island, WAM 219.74	11D	8.50±0.242 (7.15-9.7)	19.49±0.493 (17.1-22.45)	0.437±0.013 (0.385-0.513)	5- (4⅞--5⅛+)
Rosemary Island, WAM 373.74	29L	8.17±0.130 (6.7-10.15)	18.53±0.180 (16.75-21.25)	0.442±0.008 (0.571-0.360)	5- (4½-5½-)
Rosemary Island, WAM 221.74	14D	7.01±0.140 (6.25-7.8)	17.11±0.273 (15.8-18.7)	0.411±0.008 (0.349-0.462)	4⅝+ (4¼-5+)
Rosemary Island, WAM 10.87	20D	8.43±0.536 (7.05-18.1)	18.37±0.267 (16.35-20.6)	0.459±0.026 (0.377-0.910)	4⅞ (4⅝-5⅛)
Rosemary Island, WAM 12.87	6D	8.89±0.309 (8.2-10.1)	17.72±0.305 (16.75-18.6)	0.504±0.009 (0.478-0.543)	5⅛+ (5--5½-)
Rosemary Island, WAM 1549.70	29D	6.89±0.100 (6.1-8.25)	17.83±0.144 (16.6-19.25)	0.386±0.004 (0.353-0.440)	4⅝+ (5¼-5)

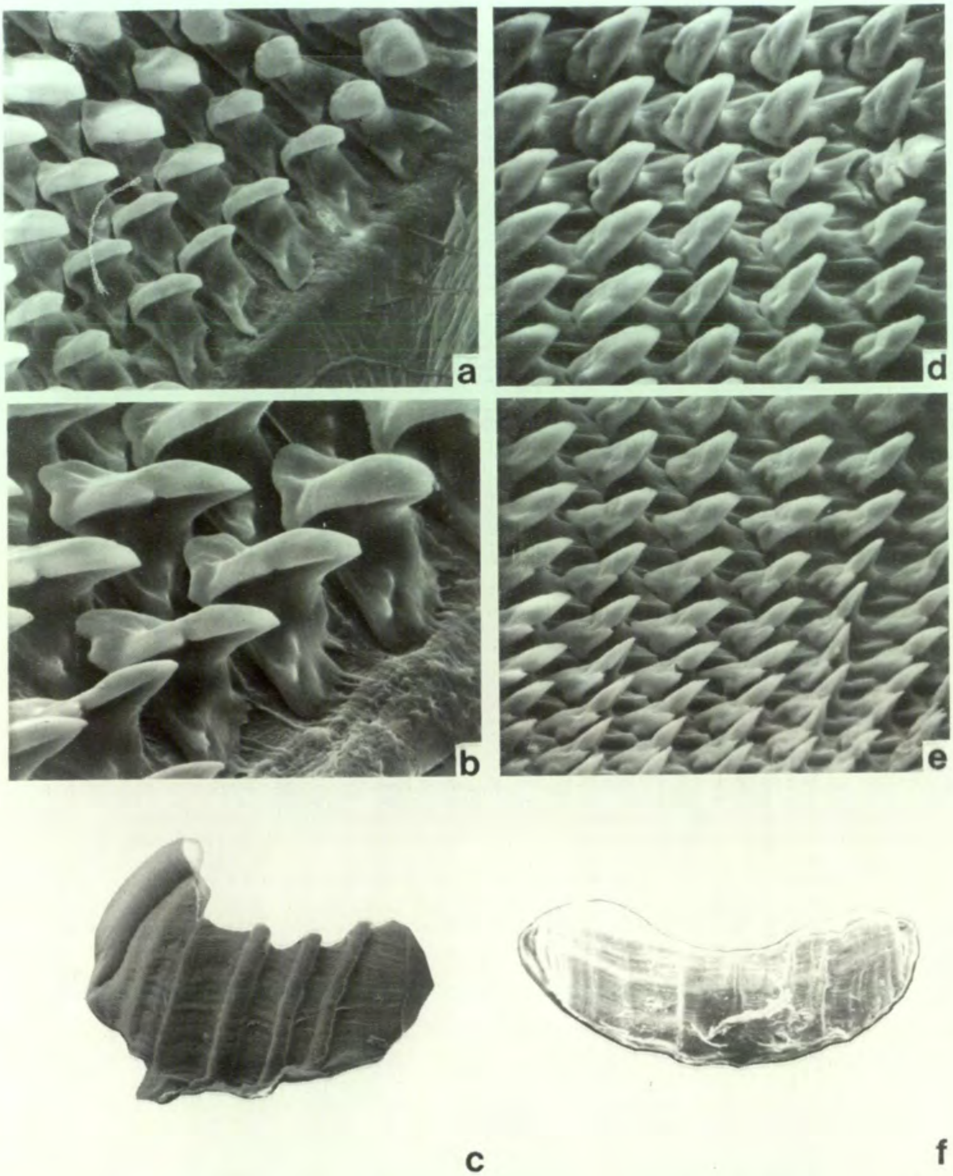


Plate 218: Radular teeth and jaws of *Rhagada pilbarana* sp. nov. and *R. perprima* (Iredale, 1939): (a–c) *R. pilbarana*. WA–182, Mt Herbert, Chichester Range, WA. 10 April 1977. FMNH 199785, Dissection A. a is central and early laterals at 370X. b is late laterals at 750X. c is jaw at 39.5X; (d–f) *R. perprima*. West Lewis Island, Dampier Archipelago, WA. 20 June 1971. WAM 797.71, Dissection B. d is central and early laterals from high anterior angle at 380X. e is latero-marginal transition at 380X. f is jaw at 39X.

Helix (*Rhagada*) *elachystoma* (von Martens), Pilsbry 1890, *Man. Conch.*, (2) **6:** 187, plt. 11, figs 41–43 (copied from von Martens).

Thersites (*Rhagada*) *elachystoma* (von Martens), Pilsbry 1894, *Man. Conch.*, (2) **9:** 136 – check list citation.

Rhagada elachystoma (von Martens), Iredale 1938, *Aust. Zool.*, **9** (2): 112 – check list citation; Richardson 1985, *Tryonia*, **12:** 266 – check list citation as a synonym of *Rhagada richardsonii* (E. A. Smith, 1874).

Comparative remarks

Rhagada elachystoma (von Martens, 1878), from Kendrew and Rosemary Islands, Dampier Archipelago (**Map 40**), is smaller than average (mean diameter 14.04 mm) with a slightly reduced whorl count (mean 4 7/8-), usually strongly elevated spire that may be rounded above (**Fig. 420d**, mean H/D ratio 0.740), aperture descending slightly to moderately behind lip, which is thin and narrowly expanded, umbilicus closed with a narrowly expanded callus or with a slight lateral crack remaining. Shell white, with numerous spiral red or orange bands of varying width. Accessory bands occasionally wide, in other examples reduced or lost with main supraperipheral and subsutural bands still prominent. Shell apex nearly smooth (**Plate 207e–f**), spire and body whorl with very prominent radial ribs that may continue onto shell base with no reduction; may become partly reduced above and below periphery, or prominent above and nearly absent from shell base. Of the larger Dampier Archipelago taxa, *R. angulata* sp. nov. (**Figs 422a–c**) is closest in size and shape (**Table 151**) but differs most obviously in its angulated periphery, lack (**Plate 208a**) of radial ribs on the shell, much more widely expanded lip and generally narrowly open umbilicus. *R. dampierana* sp. nov. (**Plate 208b–d**, **Figs 422d–f**) is much larger, nearly flat-spired (mean H/D ratio 0.416) and has prominent ribbing crossing a protruded peripheral keel. The other Dampier species are either much smaller (*minima*, *intermedia*) or greatly enlarged and lack radial ribs (*perprima*). Of the ribbed extralimital species, *R. plicata* from the Montebello Islands is very small (mean diameter 10.35 mm) and with much more tightly coiled whorls (**Figs 418a, 420c**); *R. dringi* (Pfeiffer, 1846) from 80 Mile Beach is smaller (mean diameter 12.31 mm) and with very crowded radial ribs that are absent from shell base.

Anatomy unknown.

Material studied

WESTERN AUSTRALIA: Dampier Archipelgo: Kendrew Island (6 May 1974, WAM 241.74, FMNH 208768, 62 DA, many DJ; G. Connell! 15 February 1983, WAM 26.87, 4 DA, 1 DJ; MV, 4 DA); Rosemary Island (2 May 1973, WAM 327.74, FMNH 208767, DA, 26 DJ; 2 May 1973, WAM 329.74, 2 DA, 2 DJ).

Possibly related populations

WESTERN AUSTRALIA: Dampier Archipelago: Legendre Island (W. D. L. Ride! 9 June 1962, WAM 224.74, FMNH 208769, 21 DA, 6 DJ; W. D. L. Ride! 8 June 1962, WAM 21.87, 5 DA, 1 DJ; W. D. L. Ride! 9 June 1962, WAM 23.87, 2 DA, 4 DJ).

Range

Rhagada elachystoma is found on Rosemary Island and its tiny satellite, Kendrew

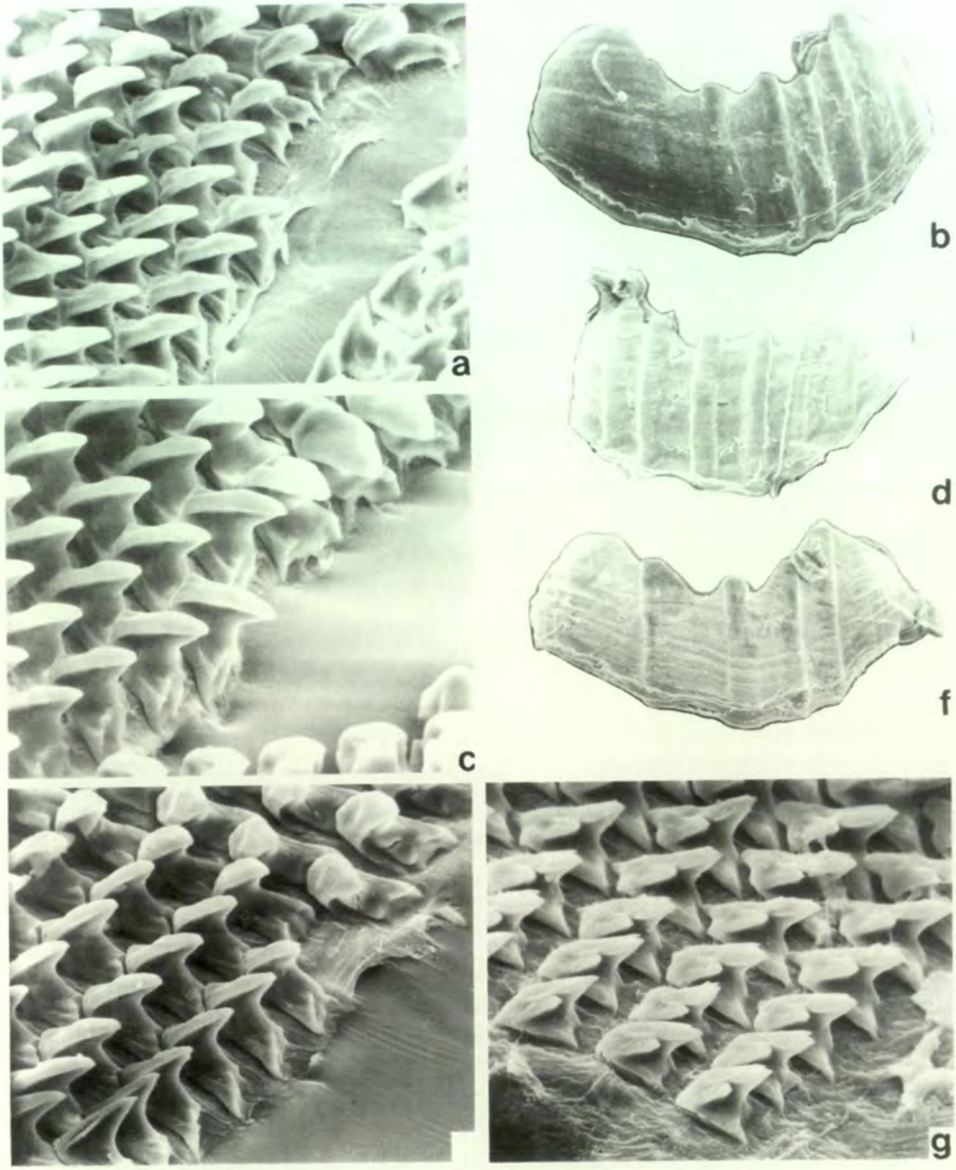


Plate 219: Radular teeth and jaws of *Rhagada richardsonii* (E. A. Smith, 1874): (a–b) Roy Hill, Fortescue River, Pilbara, WA. 3 May 1970. WAM 340.74, Dissection A. a is central and laterals at 360X. b is jaw at 48X; (c–d) Skull Springs, E of Nullagine, Pilbara, WA. 30 December 1970. WAM 334.74, Dissection A. c is central and laterals at 410X. d is jaw at 38X; (e–g) WA–1,058, Cape Keraudren, E of Port Hedland, Pilbara, WA. 12 June 1984. e is FMNH 211984, Dissection A, central and early laterals at 370X. f is FMNH 211985, Dissection A, jaw at 48X. g is FMNH 211984, Dissection A, lateromarginal transition at 375X.

Island, Dampier Archipelago (**Map 40**). A possibly related form, for which there is only poor material available, has been recorded from the barrier island, Legendre. The maximum range for Kendrew and Rosemary Islands is 5 x 10 km. Legendre Island is 13 km long and with a maximum width of 1.5 km.

Diagnosis

Shell smaller than average, adult diameter 11.85–17.55 mm (mean 14.04 mm), with 4 1/2 to 5 3/8+ (mean 4 7/8-) normally coiled whorls. Apex and spire moderately to strongly elevated (**Fig. 420d**), often rounded above, shell height 8.7–12.05 mm (mean 10.09 mm), H/D ratio 0.640–0.848 (mean 0.740). Body whorl evenly rounded. Shell apex (**Plate 207e**) smooth; spire and body whorl (**Plate 207e–f**) with very prominent, crowded radial ribs that may continue onto shell base; lower ribs that may be somewhat reduced on shell base; or very reduced ribs that are absent from shell base. Umbilicus often distinctly open, sometimes reduced to a narrow crack, sometimes barely closed. Body whorl descending slightly to moderately behind lip, which is thin and slightly expanded. Numerous red to orange narrow spiral bands normally present, reduced to typically two major bands or with some accessory bands widened in other individuals. Based on 77 measured adults.

Anatomy unknown.

Discussion

Rhagada elachystoma was collected in the vicinity of Mermaid Strait during the Gazelle Expedition together with *Rhagada perprima* "*im Grasland etwa 2 Stunden landeinwärts*" (von Martens, 1878: 272–274). Both species have been recorded subsequently from Rosemary Island, but until a thorough field survey of the Dampier Archipelago is completed, it is premature to assign a type locality.

Samples from both Kendrew and Rosemary Islands show the great variability in shell ridging mentioned above, which is not found in any of the other *Rhagada* with prominent radial ridges. Only two samples were large enough for statistical analysis (**Table 157**). A summary of the size data of all adult material from the two islands shows that the Rosemary Island specimens are distinctly larger, lower spired, and with increased whorl count:

	Kendrew (69 specimens)	Rosemary (8 specimens)
Height	10.03 (8.7–11.5)	10.58 (9.25–12.05)
Diameter	13.45 (11.85–14.6)	14.96 (13.85–17.1)
H/D ratio	0.746 (0.659–0.822)	0.708 (0.640–0.760)
Whorls	4 3/4– (4 1/2 – 5 1/8)	5– (4 3/4 – 5 1/4)

The limited material from Legendre Island is worn and without trace of shell colour. The lower sculpture on these shells may be the result of wear or may represent an actual sculptural size difference. The specimens also differ slightly in size and shape (**Table 157**), agreeing more with the Rosemary than the Kendrew Island specimens.

Although no type material was located, the original description and illustrations of *Rhagada elachystoma* closely match the recently collected material.

RHAGADA ANGULATA SP. NOV.

(Plates 208a, 222a–b; Figs 422a–c, 423a–b; Map 40)

Comparative remarks

Rhagada angulata sp. nov., from several islands in the Dampier Archipelago (**Map 40**), is medium sized (mean diameter 13.61 mm), with reduced whorl count (mean 4 3/4), relatively low, rounded spire (**Fig. 422b**, mean H/D ratio 0.742), aperture usually slightly descending behind lip which is thin and broadly expanded, umbilicus varying from a narrow crack (**Fig. 422c**) to moderately open. Body whorl obtusely angulated. Shell white, with many narrow, red to orange spiral colour bands, normally the supraperipheral and subsutural bands wider and darker in colour, sometimes accessory bands reduced in number. Shell apex smooth (**Plate 208a**), spire and body whorl with prominent radial growth ridgelets, no major radial ribs. The other small to medium sized Dampier Archipelago species (*R. minima*, *R. intermedia*, *R. elachystoma*) and the Montebello Islands *R. plicata* differ most obviously in having very prominent radial ridges at least above the periphery (**Plates 207a–f**), which are lacking in *R. angulata* (**Plate 208a**). The larger (mean diameter 18.08 mm) *Rhagada dampierana* sp. nov. has both very prominent radial ribs (**Plate 208b–d**, **Figs 422d–f**) and a protruded peripheral keel that immediately identifies it. The mainland species *R. richardsonii*, from Depuch Island to Cape Keraudren (**Map 37**, **Figs 414a–f**), and the inland *R. radleyi* from Millstream on the Fortescue River S to the upper Ashburton drainage (**Map 37**, **Figs 416a–f**) are much larger (**Table 151**) in diameter, higher in whorl count and have the shell lip much less expanded.

Anatomically (**Figs 423a–b**), *R. angulata* has a large albumen gland (GG), the medium length spermatheca (S) is strongly kinked, both vagina (V) and epiphallic caecum (EC) are of medium length. Penis (P) long with conical verge having a corrugated surface. *R. intermedia* (**Figs 421a–b**) has a short spermatheca that is not kinked, the epiphallic caecum is long, the verge very short and dome-shaped. *R. dampierana* sp. nov. (**Figs 424a–b**) has the spermatheca not kinked, the epiphallic caecum very long, the penis longer than the vagina, and the verge is proportionately very small and triangular in shape. The genital structures of both *R. minima* and *R. elachystoma* are unknown.

Holotype

WAM 765.87, Dolphin Island, Dampier Archipelago, Western Australia, Australia. Collected 3 June 1962 by G. M. Storr. Height of shell 8.4 mm, diameter 14.3 mm, H/D ratio 0.587, whorls 5 3/8, umbilicus a narrow lateral opening, nearly closed.

Paratopotypes

WAM 342.74, FMNH 208764, 14 LA, 10 LJ from the type locality.

Paratypes

WESTERN AUSTRALIA: Dampier Archipelago: Dolphin Island (W. D. L. Ride! 7 June 1962, WAM 1127.81, 3 DA, 3 DJ; A. Burbidge! 6 August 1974, WAM 1129.81, 9 DA, 5 DJ; G. M. Storr! 3 June 1962, WAM 1126.81, 3 DA, 5 DJ; K. Youngson! 19 June 1970, WAM 1128.81, 2 DA, 3 DJ); Enderby Island (G. W. Kendrick! 22 August 1961, WAM 227.74, FMNH 208765, 4 DA); Angel Island (K. Youngson! 18 June

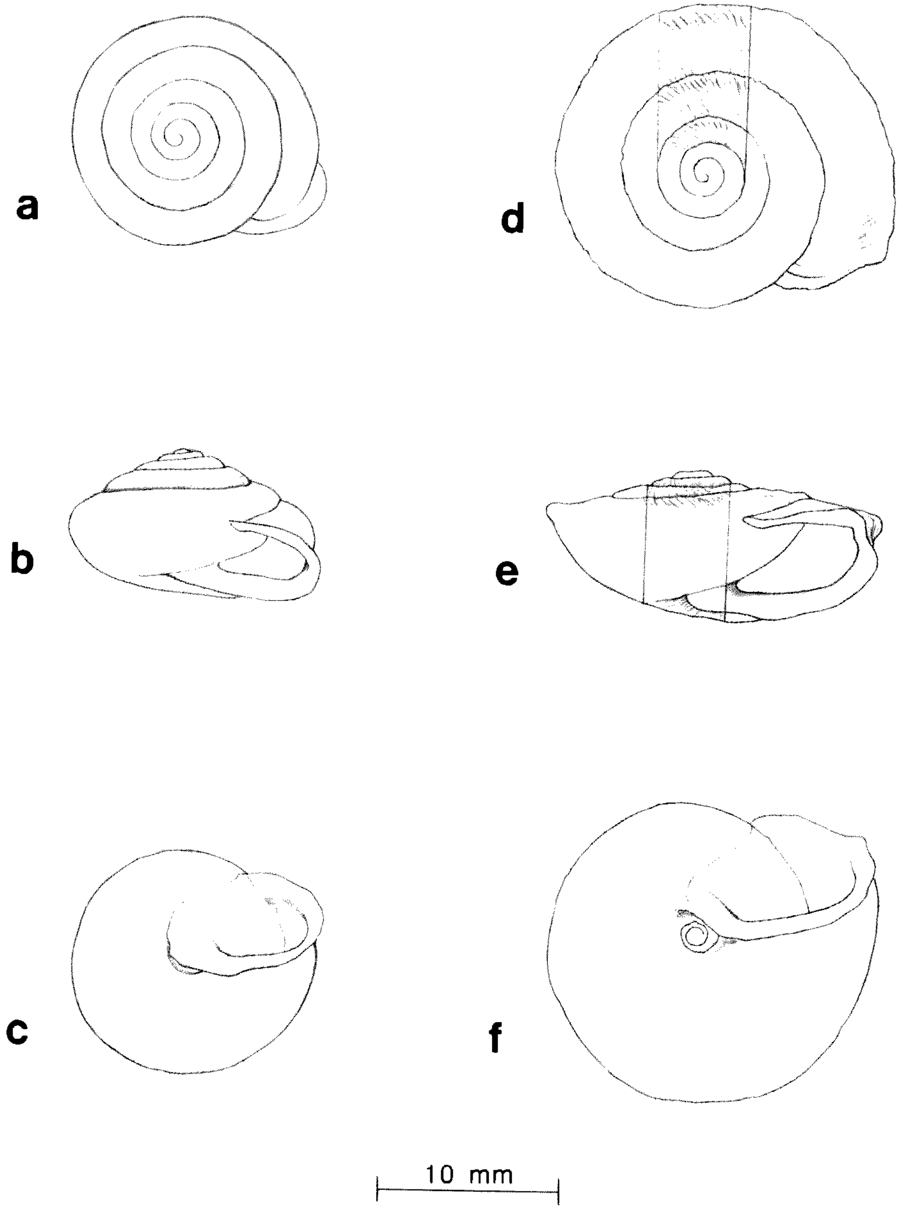


Fig. 422: Shells of *Rhagada angulata* sp. nov. and *R. dampierana* sp. nov.: (a–c) Holotype of *R. angulata*. WAM 765.87, Dolphin Island, Dampier Archipelago, WA; (d–f) Holotype of *R. dampierana*. WAM 766.87, Rosemary Island, Dampier Archipelago, WA. Scale line equals 10 mm. Drawings by Linnea Lahlum.

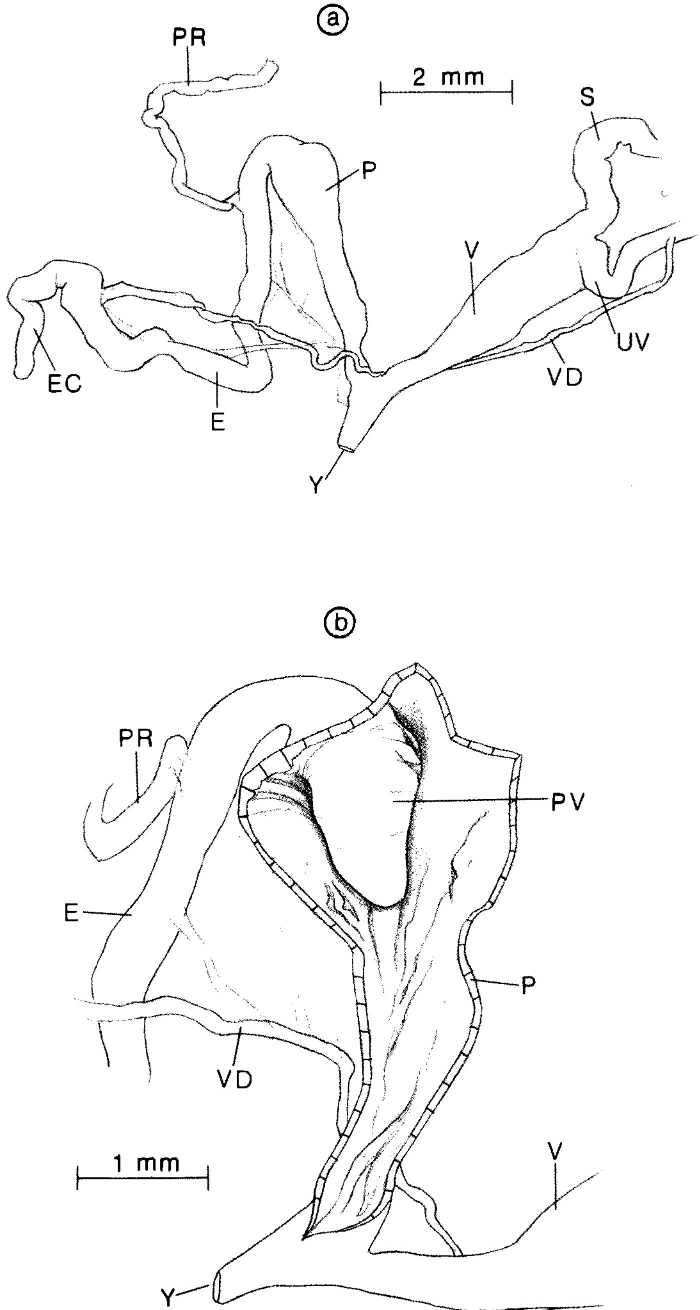


Fig. 423: Genitalia of *Rhagada angulata* sp. nov.: Dolphin Island, Dampier Archipelago, WA. 3 June 1962. WAM 342.74, Dissection B: (a) terminal genitalia; (b) verge. Scale lines as marked. Drawings by Linnea Lahlum.

1970, WAM 230.74, 1 DA; K. Youngson! 18 June 1970, WAM 1130.81, 2 DA, 1 DJ); Legendre Island (K. Youngson! 19 June 1970, WAM 229.70, FMNH 208766, 15 DA, 4 DJ).

Range

Rhagada angulata has been collected from four islands in the Dampier Archipelago (**Map 40**). Legendre, Angel and Dolphin Islands are tightly grouped into an area about 13 x 17 km. Enderby Island is isolated about 22 km to the WSW. It is about four by 13 km in size.

Diagnosis

Shell medium in size, adult diameter 11.85–17.1 mm (mean 13.61 mm), with 4 1/2 to 5 1/4 (mean 4 3/4) normally coiled whorls (**Fig. 422a**). Apex and spire moderately elevated, rounded above (**Fig. 422b**), shell height 6.0–10.95 mm (mean 7.77 mm), H/D ratio 0.640–0.822 (mean 0.742). Body whorl obtusely angulated (**Fig. 422b**). Shell apex (**Plate 208a**) smooth, spire and body whorl with prominent radial growth ridgelets and growth pause ridges but no well defined radial ribs. Umbilicus (**Fig. 422c**) varying from a narrow crack to moderately open with degree of closure determined by flare of columellar lip. Body whorl descending slightly behind lip, which is thin and broadly expanded. Many red to orange narrow spiral colour bands present, the supraperipheral and subsutural often darker and wider. Based on 48 measured adults.

Genitalia (**Figs 423a–b**) with long albumen gland (GG), spermatheca (S) short and kinked, vagina (V) medium in length, epiphallic caecum (EC) medium in length. Penis (P) long, verge (PV) short and triangular, with corrugated surface. Head wart not observed because of deep retraction of available material and shrinkage incurred apprently during formalin fixation.

Central and lateral teeth of radula (**Plate 222a**) with average anterior flare, weak ectocone, typical cusp shaft angle, cusp tip noticeably curved and bluntly pointed. Lateromarginal transition and marginal teeth typical. Jaw (**Plate 222b**) with an increased number of prominent, relatively wide vertical ribs, that are absent from side margins.

Discussion

Rhagada angulata, with its combination of an obtusely angulated periphery, flared lip and no radial ribs, is easily separated from the other Dampier Archipelago species of similar size. The very large (mean diameter 19.84 mm), multiwhorled (mean 5 5/8+) *R. perprima* also has the expanded lip (**Figs 411c–d**) and no radial ribs but lacks the multiple colour banding.

Almost no data are available concerning local variation in size and shape (**Table 157**) because of small sample size. A summary of island variation follows:

	Angel Island (2 specimens)	Dolphin Island (31 specimens)
Height	7.2–7.3	7.97 (6.75–9.4)
Diameter	12.35–13.95	14.07 (12.65–15.6)
H/D ratio	0.572–0.583	0.567 (0.504–0.641)
Whorls	4 7/8+ – 5	5 1/8 (4 5/8 – 5 3/8+)

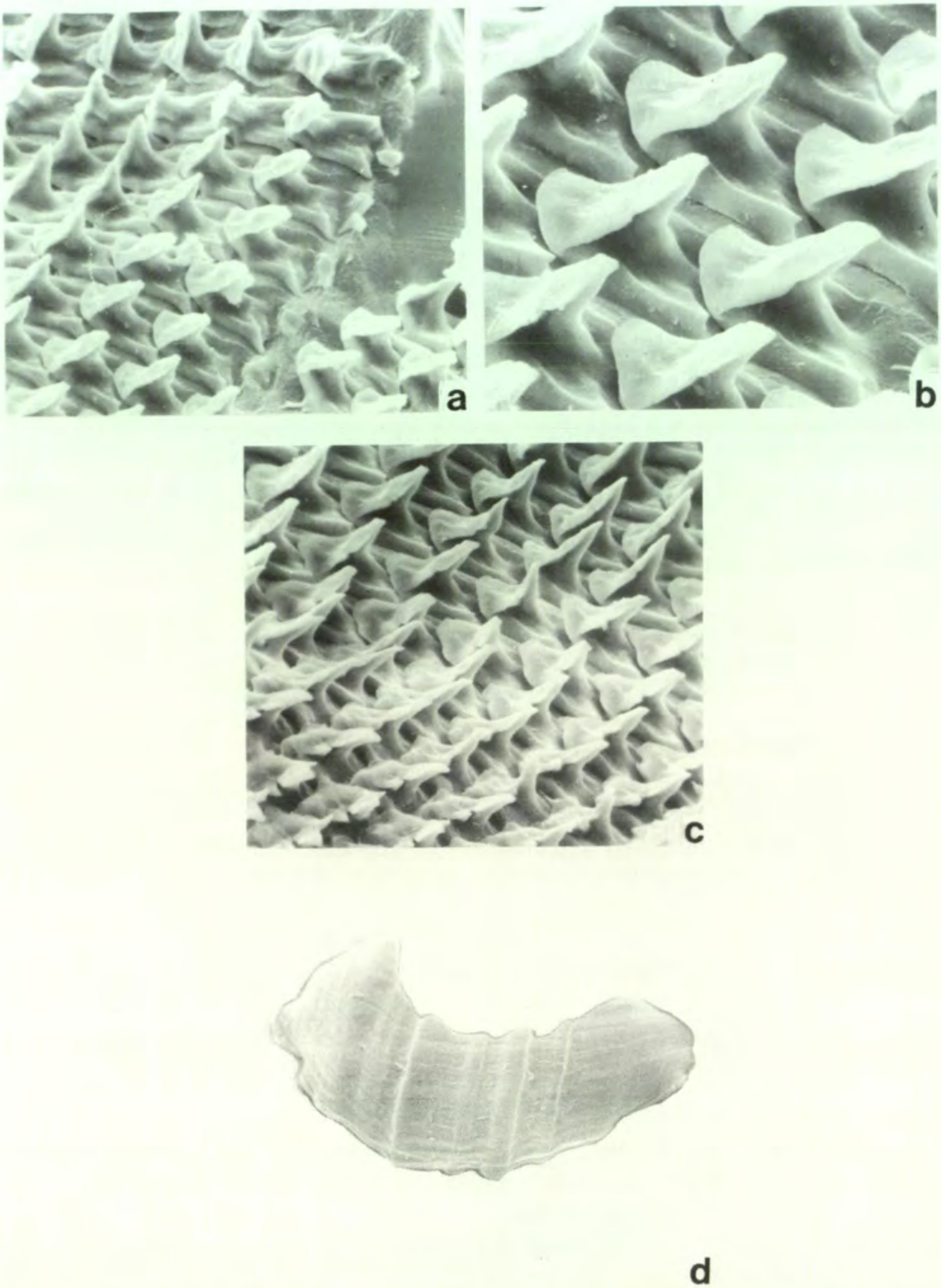


Plate 220: Radular teeth and jaw of *Rhagada radleyi* Preston, 1908: WA–417, Glen Florrie Station, Pilbara, WA. 11 April 1977. FMNH 199774, Dissection A: (a) central and early laterals at 360X; (b) late laterals at 850X; (c) latero-marginal transition at 420X; (d) jaw at 52X.

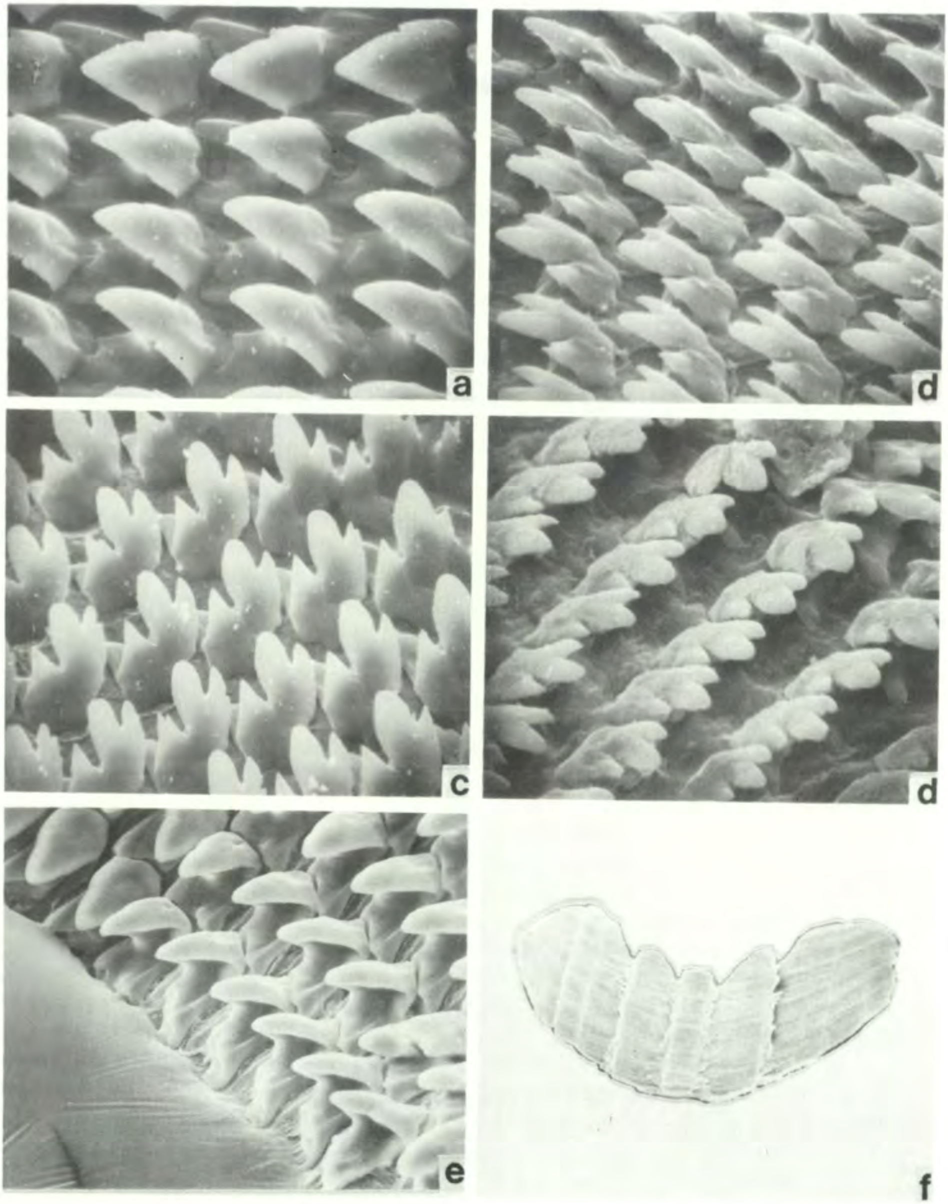


Plate 221: Radular teeth and jaws of *Rhagada plicata* Preston, 1914 and *R. intermedia* sp. nov.: (a–d) *R. plicata*. Hermite Island, Montebello Islands, WA. 21 December 1966. WAM 371.74, Dissection A. a is central and early laterals from top viewing angle at 750X. b is latero-marginal transition at 730X. c is high angle view of early marginals at 760X. d is low angle view of early marginals at 750X; (e–f) *R. intermedia*. Delambre Island, Dampier Archipelago, WA. 29 July 1961. WAM 358.74, Dissection A. e is central and early laterals at 435X. f is jaw at 57X.

	Enderby Island (4 specimens)	Legendre Island (11 specimens)
Height	9.86 (8.1–10.95)	6.54 (6.0–7.55)
Diameter	15.92 (15.0–16.7)	12.19 (11.55–13.1)
H/D ratio	0.619 (0.541–0.690)	0.538 (0.500–0.577)
Whorls	5 1/4 (5 – 5 3/8)	4 3/4– (4 1/2 – 4 7/8)

The differences in size and shape are substantial but all samples share the lip, umbilical and sculptural features mentioned above. The size and whorl count differences between Enderby and Legendre examples are larger than the differences between many species but in the absence of anatomical material from the several islands and, in view of the unusual and uniform lip, umbilical and shell sculpture, it seems prudent to cluster these populations as a single variable species while calling attention to the variation.

Unfortunately the only available preserved material of *R. angulata* had all of the specimens retracted into the shell and had at one time been placed in formalin. It was not possible to observe the head wart at all and details of the verge structure require study of new material.

The name *angulata* refers to the distinctly angulated shell periphery of this species. Of the remaining *Rhagada*, the keeled *R. dampierana* (**Figs 422d–f**) is the only species with a significant peripheral angulation, although there is obtuse peripheral angulation in some examples of *R. intermedia*.

RHAGADA DAMPIERANA SP. NOV.

(Plates 208b–d, 222c–f; Figs 422d–f, 424a–c; Map 40)

Comparative remarks

Rhagada dampierana, sp. nov., from Rosemary Island, Dampier Archipelago (**Map 40**), is immediately identifiable by its protruded peripheral keel (**Plate 208c–d, Figs 422d–f**) that is crossed by prominent and crowded radial ribs. It is one of the larger Dampier Archipelago species (mean diameter 18.08 mm) and also is distinguished by its flat or very low spire (**Fig. 422e**, mean H/D ratio 0.416). *R. angulata*, also from the Dampier Archipelago (**Map 40**), lacks radial ribbing and has an obtuse peripheral angulation. No other WA species come close in shell shape or sculpture. Anatomically (**Figs 424a–c**), *R. dampierana* has a large albumen gland (GG), spermatheca (S) not kinked, free oviduct (UV) folded into the side of uterus (UT), vagina (V) medium in length and epiphallic caecum (EC) very long. Penis (P) longer than vagina, verge (PV) small and triangular. Jaw (**Plate 222f**) with prominent vertical ribs of varying width over most of jaw surface. Other Dampier Archipelago species have the spermatheca shorter and usually kinked, a shorter epiphallic caecum and differences in verge size and shape.

Holotype

WAM 766.87, rocky hill slope, N side of southern valley, SW part of Rosemary Island, Dampier Archipelago, Western Australia, Australia. Collected 22 May 1973 by B. R. Wilson. Height of shell 8.1 mm, diameter 19.0 mm, H/D ratio 0.426, whorls 5+,

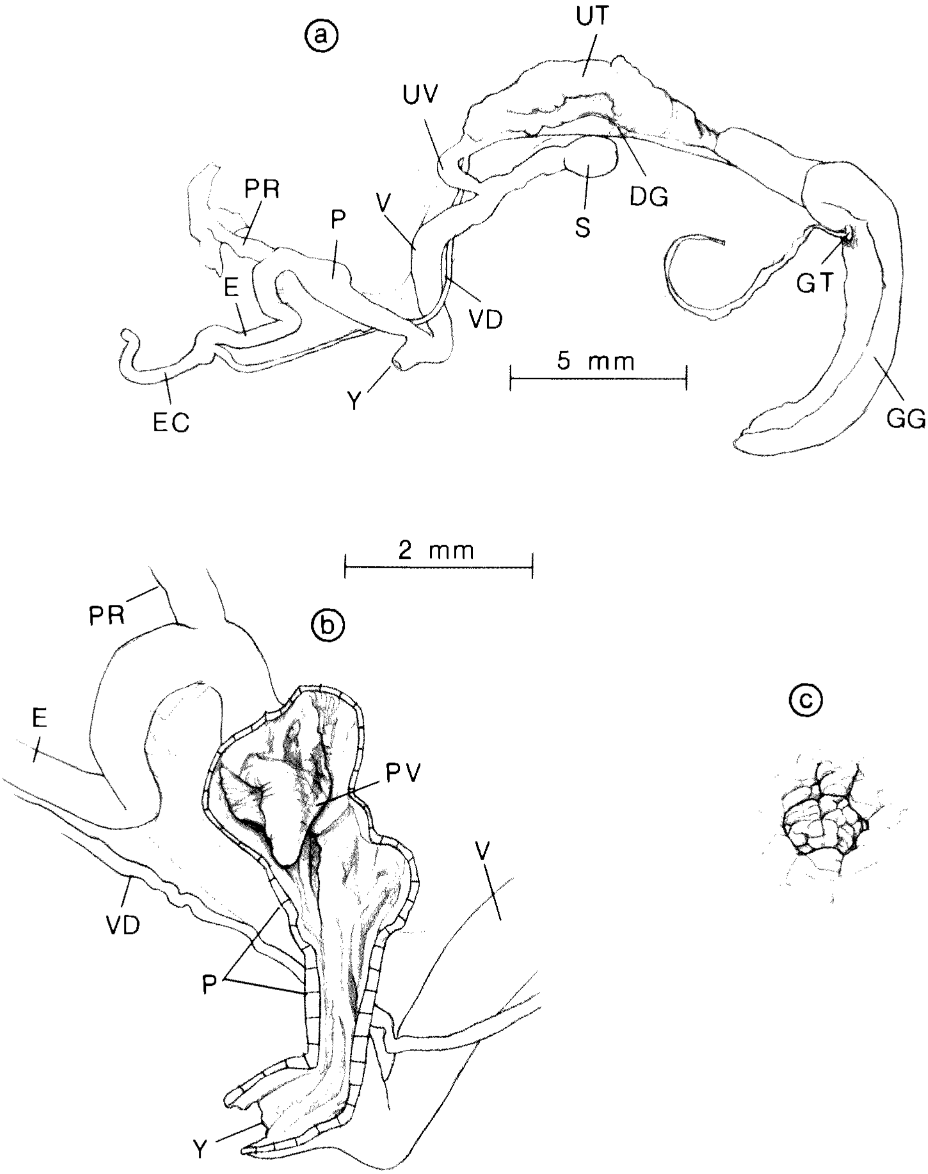


Fig. 424: Genitalia of *Rhagada dampierana* sp. nov.: Rosemary Island, Dampier Archipelago, WA. 22 May 1973. WAM 373.74, Dissection D: (a) whole genitalia; (b) verge; (c) head wart. Scale lines as marked. Drawings by Linnea Lahlum.

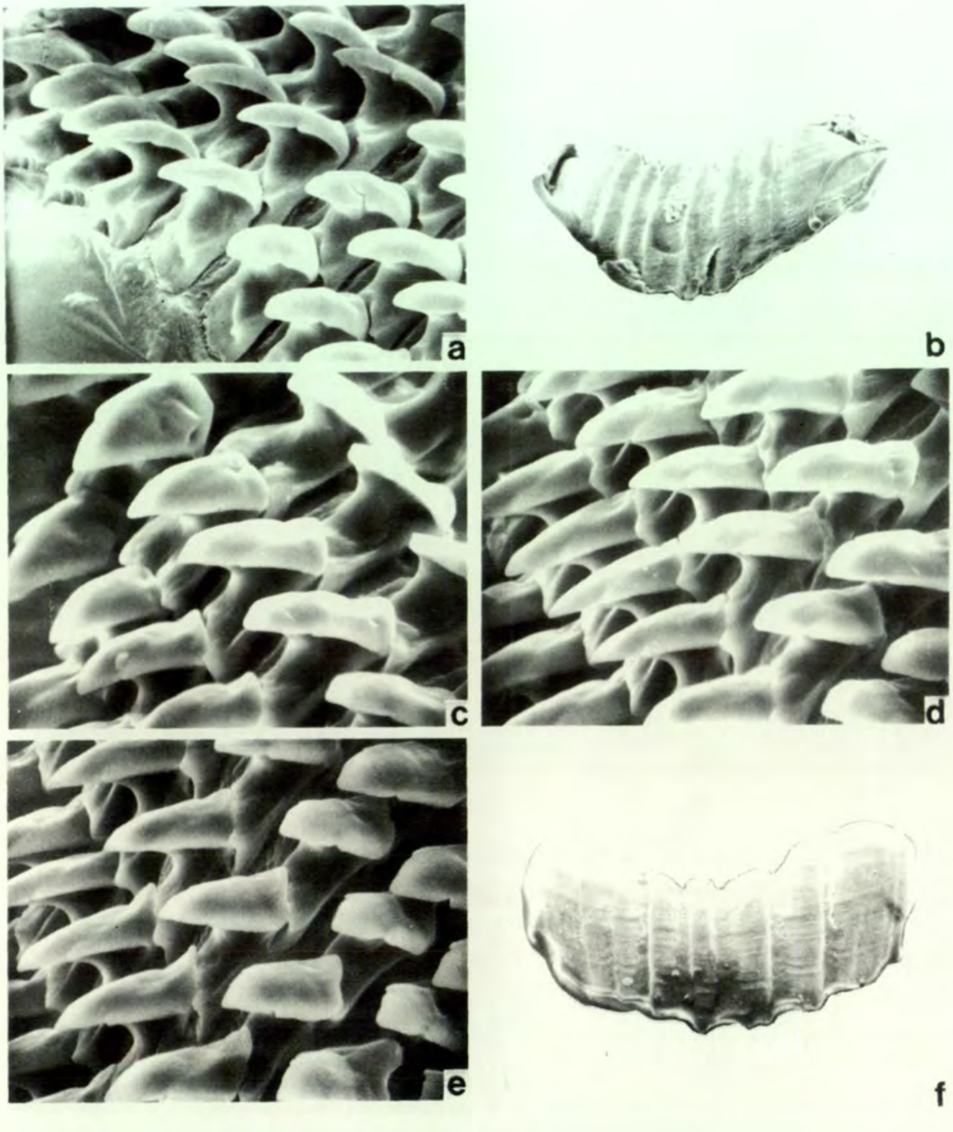


Plate 222: Radular teeth and jaws of *Rhagada angulata* sp. nov. and *R. dampierana* sp. nov.: (a–b) *R. angulata*. Dolphin Island, Dampier Archipelago, WA. 3 June 1962. WAM 342.74, Dissection C. a is central and early laterals at 670X. b is jaw at 71X; (c–f) *R. dampierana*. Rosemary Island, Dampier Archipelago, WA. 22 May 1973. WAM 373.74, Dissection C. c is central and early laterals at 670X. d is early laterals at 630X. e is late laterals at 670X. f is jaw at 54X.

umbilical width 1.75 mm, D/U ratio 10.9, umbilicus about one-third covered by columellar lip reflection, umbilical margin shouldered.

Paratopotypes

WAM 219.74, WAM 373.74, FMNH 208761–2, 29 LA, 11 DA, many LJ, 12 DJ from the type locality.

Paratypes

WESTERN AUSTRALIA: Dampier Archipelago: Rosemary Island ("Boulder Hill", G. W. Kendrick! 21 August 1961, WAM 221.74, 13 DA, 2 DJ; B. R. Wilson! 22 May 1973, WAM 10.87, 20 DA, 8 DJ; middle of central ridge, G. W. Kendrick! 24 August 1961, WAM 12.87, 5 DA, 2 DJ; W. D. L. Ride! 15 June 1962, WAM 1549.70, 19 DA, 8 DJ).

Range

Rhagada dampierana has been collected only on Rosemary Island (**Map 40**), which is about 4 by 7 km in size.

Diagnosis

Shell relatively large, adult diameter 15.8–22.45 mm (mean 18.08 mm), with 4 1/4 to 5 1/2– (mean 4 7/8-) normally coiled whorls (**Fig. 422a**). Apex and spire flat to modestly elevated (**Fig. 422b**), sides of spire may be slightly concave, whorls on spire strongly flattened. Shell height 6.1–10.15 mm (mean 7.80 mm), H/D ratio 0.349–0.571 (mean 0.416). Body whorl with a protruding thread-like peripheral keel (**Plate 208c–d**, **Figs 422d–f**). Shell apex (**Plate 208b**) nearly smooth, spire and body whorl with very prominent radial ribs that cross the protruded keel (**Plate 208c**) to the shell base where they are reduced in prominence, and with a crowded spiral microsculpture (**Plate 208d**). Umbilicus (**Fig. 422f**) usually narrowly open, closed in about one-third of observed specimens, maximum observed width 2.3 mm. Body whorl, at most, descending slightly behind lip, which is broadly expanded and rolled; columellar lip reflected and broadened to cover most to all of umbilicus. Spiral colour bands narrow, reduced in number and width, apex with a slight colour suffusion. Based on 109 measured adults.

Genitalia (**Figs 424a–c**) with large albumen gland (GG), long spermatheca (S) that is not kinked, medium length free oviduct (UV) that is folded into the side of uterus (UT), vagina (V) medium length and epiphallic caecum (EC) very long. Penis (P) longer than vagina, verge (PV) small and conical, diameter equal to height. Head wart (**Fig. 424c**) small, dark grey, elongate–ovate across neck.

Central and early lateral teeth of radula (**Plate 222c**) with prominent anterior flare, normal cusp shaft angle, weak ectoconal notch, strongly curved and bluntly rounded cusp tip. Late laterals (**Plate 222d**) with increased anterior flare, more pointed and less curved cusp tip, lateromarginal transition (**Plate 222e**) typical. Jaw (**Plate 222f**) with narrow vertical ribs over most of surface.

Discussion

Specimens of *Rhagada dampierana* collected in 1961–2 are noticeably smaller than those collected in 1973. This could be either allochronic variation or reflect local ecological conditions. Live specimens were taken in May 1973 the morning after "overnight showers" and dead examples from the same place are the largest examples observed to date. Presumably the snail aestivates buried in sandy soil.

One sample of live-collected snails from "rocky hill slope on N side of S valley in SW part of [Rosemary] Island", collected 22 May 1973 by Barry R. Wilson provides possible evidence of hybridization between *Rhagada dampierana* and *R. elachystoma*. They have been left catalogued as WAM 248.73 to facilitate detailed study and have not been included in the variation analyses of the two species. Two of the shells have the sculpture and keel of *dampierana* and three have the sculpture and umbilicus of *elachystoma*. Measurements of the five examples follow:

	Height	Diameter	H/D ratio	Whorls	
dampierana	9.55	16.2	0.590	5 1/4-	crack
"	10.1	15.05	0.671	5 1/8+	1.6
elachystoma	9.35	14.7	0.636	5+	crack
"	9.6	14.85	0.646	4 3/4+	crack
"	10.7	15.1	0.709	5	closed

These specimens of *dampierana* have a strongly elevated spire, more widely spaced ribbing and greatly increased H/D ratio compared with other specimens of this species. The last example of *elachystoma* agrees well in size and shape with the other Rosemary Island examples of that species (see above in Discussion of *elachystoma*) but the other two specimens have a reduced shell height and thus a lower H/D ratio. This situation, in which the "*dampierana*" type shells have a spire elevation and rib spacing more like *elachystoma* and the "*elachystoma*" type shells have a lowered spire and thus approach *dampierana*, obviously is suggestive of hybridization. The material is too limited for any firm conclusions to be reached but the situation obviously deserves further study.

Dissection of a fourth "*elachystoma*" specimen was carried out many years ago. The genitalia differed obviously from those of *dampierana* in having a very short and tightly kinked spermatheca and a long epiphallic caecum. Since no typical *R. elachystoma* have been dissected, the significance of these changes are uncertain. The two specimens of "*dampierana*" were so far retracted into their shells that destruction of the latter would have been required for dissection. Study of this problem is thus left to others.

The name *dampierana* for this magnificent species recognises the surprising radiation of *Rhagada* in the Dampier Archipelago.

RHAGADA DRINGI (PFEIFFER, 1846)

(Plates 209a–d, 223a–f; Figs 425a–c, 426a–d; Maps 39, 41)

Helix dringi Pfeiffer, 1846, *Symbolae Helic.*, **3:** 73 – "Austral. oriental."; Pfeiffer 1848, *Monog. Helic. viv.*, **1:** 289 – "Australia oriental, prope Torres Strait (Dring in Mus. Cuming); Reeve 1852, *Conch. Icon,* **7:** plt. 128, fig. 769; Cox 1864, *Cat. Aust. Land Shells*, p. 13; Cox 1868, *Monog. Austr. Land Shells*, p. 64, plt. XI, fig. 9; Hedley 1888, *Proc. Roy. Soc. Queensland,* **5:** 63; Pilsbry 1889, *Man. Conch.*, (2) **4:** plt. 36, fig. 40; Pilsbry 1890, *Man. Conch.*, (2) **6:** 186–187; Pilsbry 1894, *Man.*

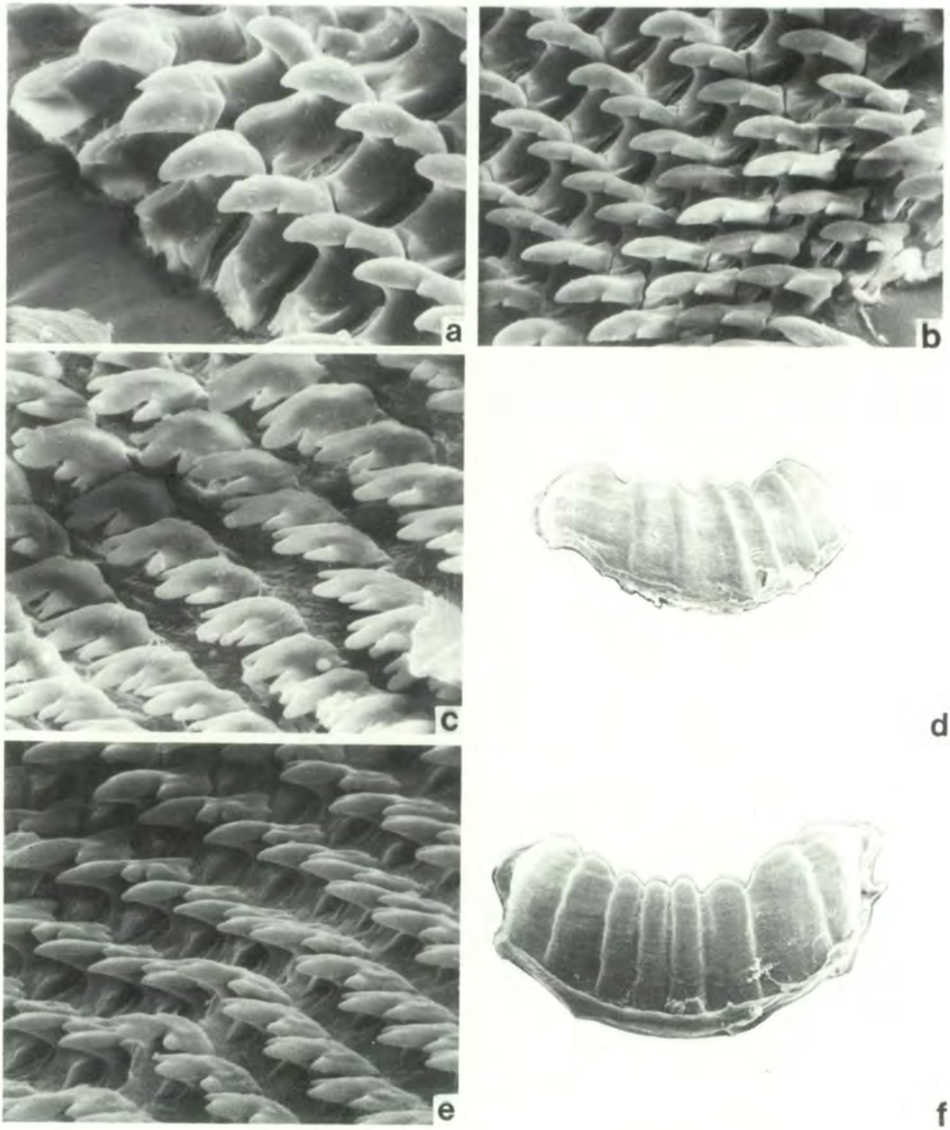


Plate 223: Radular teeth and jaws of *Rhagada dringi*. WA–409, 3.4 km SW of Anna Plains Homestead, 80 Mile Beach, WA. 27 March 1977. FMNH 199763: (a–d) Dissection A. a is central and early laterals at 680X. b is mid- and late laterals at 490X. c is outer marginals at 680X. d is jaw at 120X; (e–f) Dissection B. e is latero-marginal transition at 680X. f is jaw at 71X.

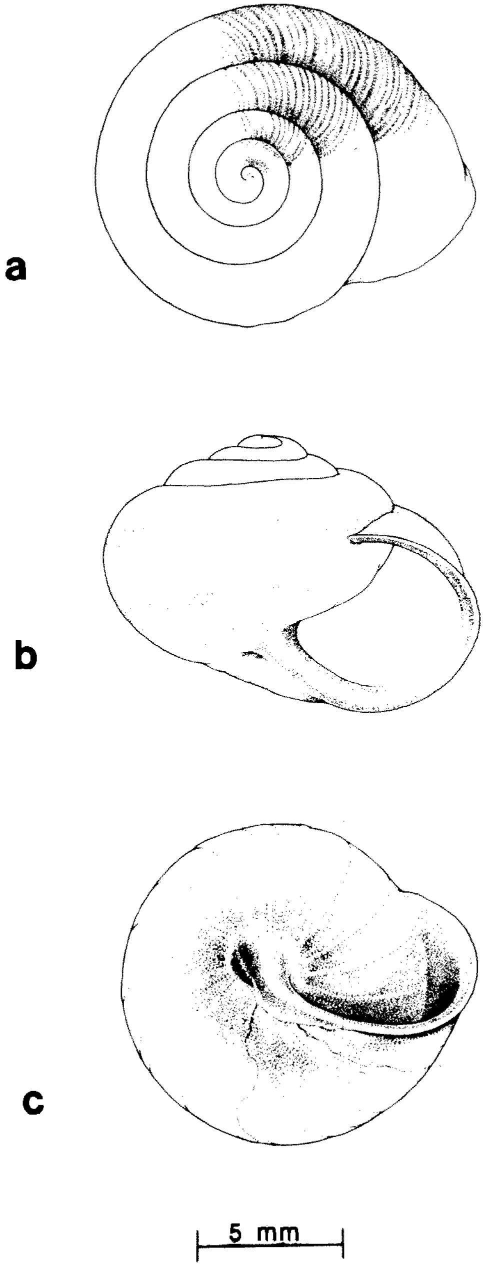


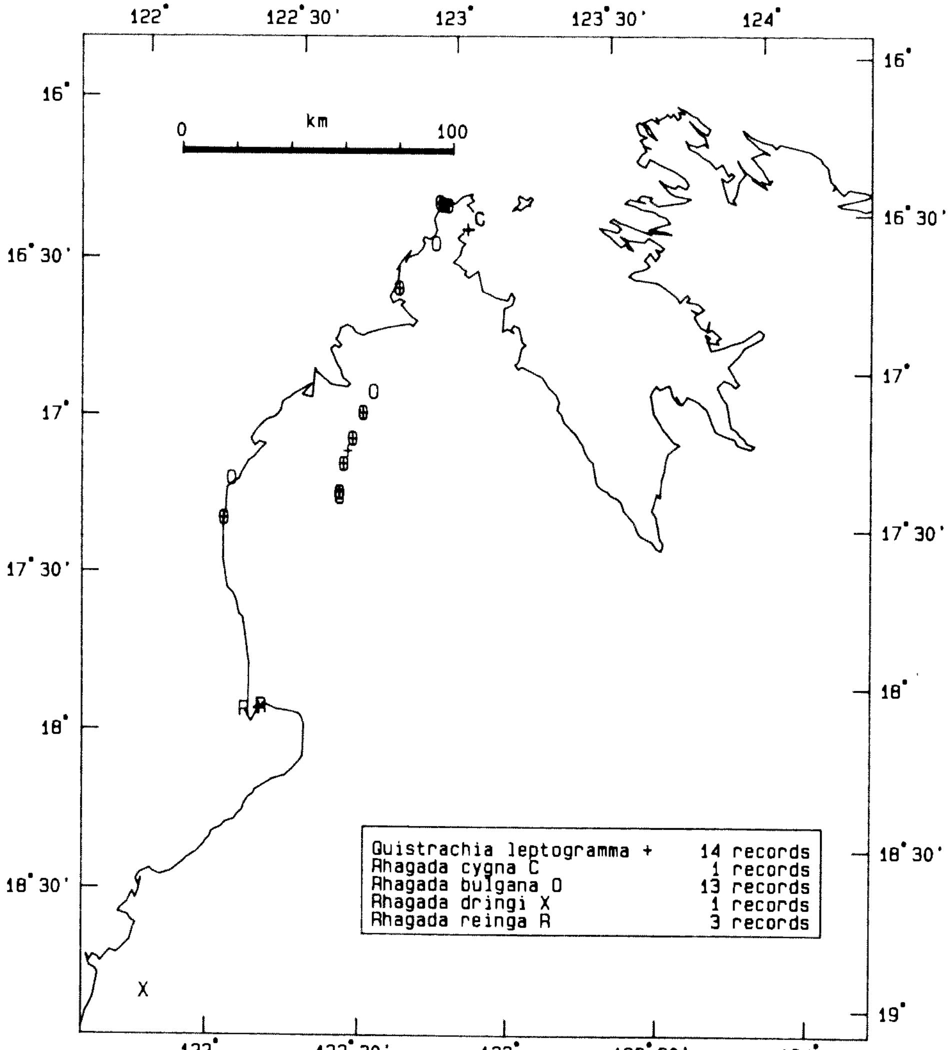
Fig. 425: Shell of *Rhagada dringi* (Pfeiffer, 1846): Lectotype of *Helix dringi* Pfeiffer, 1846. BMNH 197785. Scale line equals 10 mm. Drawings by Elizabeth A. Liebman.

Conch., (2) **9**: 136; Iredale 1938, *Aust. Zool.*, **9** (2): 114 – cited as a possible *Bellrhagada*; Iredale 1939, *Jour. Roy. Soc. Western Aust.*, **25**: 71–72.

Bellrhagada dringi (Pfeiffer), Richardson 1985, *Tryonia*, **12:** 65 – check list citation.

Comparative remarks

Rhagada dringi (Pfeiffer, 1846), which ranges along the 80 Mile Beach area from 12 km SW of Wallal Downs turnoff to 39 km N of Nita Downs turnoff along National



Map 41: Dampier Land records of *Quistrachia leptogramma*, *Rhagada bulgana*, *R. cygna*, *R. dringi* and *R. reinga*.

Highway 1 (**Map 39**), is a relatively small species (mean diameter 12.31 mm), with reduced whorl count (mean 4 5/8+), moderately to strongly elevated spire (**Fig. 425b**, mean H/D ratio 0.671), aperture descending slightly behind lip, which is thin and moderately expanded; umbilicus (**Fig. 425c**) sometimes with a narrow lateral crack, usually closed by broad expansion of columellar callus. Shell white, several narrow to wide red spiral colour bands. Shell apex (**Plate 209a**) with weak radial elements, spire and body whorl with strong radial ribs (**Plate 209b**) that become greatly reduced to absent on shell base. Similar sized species from the Dampier Archipelago either lack radial ribbing (*R. angulata*, **Plate 208a**), have a much expanded lip (*R. elachystoma*, **Figs 420c–d**), or are noticeably higher spired (**Figs 418d**, **420b**). The near-northern species *R. reinga* (Pfeiffer, 1846) from Broome (**Map 41**), *R. bulgana* sp. nov. from the northern half of Dampier Land (**Map 41**) and *R. cygna* sp. nov. from the N tip of Dampier Land (**Map 41**), all lack prominent radial ribbing (**Plate 210**).

Anatomically (**Figs 426a–d**), *R. dringi* has a very large albumen gland (GG), short and kinked spermatheca (S), short vagina (V), medium length epiphallic caecum (EC) and short penis (P). Verge (PV) medium sized, tapering, with long sperm groove. Dampier Archipelago species of *Rhagada* differ in having the verge reduced to a low conical (**Figs 423b, 424b**), elongated and tapering (**Fig. 413b**) or dome-shaped (*intermedia*, **Fig. 423b**) organ. The Broome–Dampier Land species (**Figs 428, 430–432**) have proportionately much smaller albumen glands, larger verges, and simpler spermathecae.

Holotype

BMNH 197785, Australis oriental (error), ex Hugh Cuming. Shell height 9.55 mm, diameter 12.55 mm, H/D ratio 0.761, whorls 4 5/8-, umbilicus closed.

Paratopotype

BMNH 197785, 1 DA from the type collection. Shell height 8.75 mm, diameter 11.5 mm, H/D ratio 0.761, whorls 4 1/2, umbilicus closed.

Material studied

WESTERN AUSTRALIA: 80 Mile Beach area: Wallal Downs (WA–411, 14.5 km SW of Mandora Homestead, WAM 790.87, FMNH 199362, FMNH 199766, 6 LA, 9 DA, 2 LJ, 11 DJ; WA–412, 100 m SW from Wallal Downs turnoff, WAM 788.87, SAM D18146, AM, FMNH 199779–80, 1 LA, 8 DA, 6 LJ, 10 DJ; Wallal Downs turnoff, K. G. Buller & G. W. Kendrick! 28 June 1967, WAM 277.74, 5 DA, 3 DJ); Mandora (WA–410, 3.9 km SW of homestead on road to coast, WAM 789.87, SAM D18147, FMNH 199764, FMNH 199369, 5 LA, 6 DA, 3 LJ, 3 DJ; Mandora Road, 1 mile from shore, I. Crawford! 26 August 1966, WAM 301.74, 4 DA, 2 DJ; 6 miles N of Mandora Homestead, A. M. Douglas & G. W. Kendrick! 2 June 1966, WAM 280.74, 3 DA); Anna Plains (5 miles SW of, Consett Davis! 2 June 1943, AM C.95064, 4 DA, 2 DJ; WA–409, 3.4 km SW of Anna Plains Homestead, WAM 791.87, SAM D18148, AM, QM, FMNH 199368, FMNH 199763, 4 LA, 26 DA, 5 LJ, 4 DJ; WA–407, Noreen Bore, WAM 793.87, WAM 794.87, SAM D18150, AM, QM, MV, FMNH 199360, FMNH 199788, 76 LA, 22 DA, many LJ, 9 DJ; Noreen Well, Consett Davis! 2 June 1943, AM C.95255, 1 DA; WA–408, 8.2 km NE of Noreen Bore, WAM 792.87, SAM D18149, FMNH 199736–7, 11 LA, 5 DA, 10 LJ, 1 DJ); 39 km N of Nita

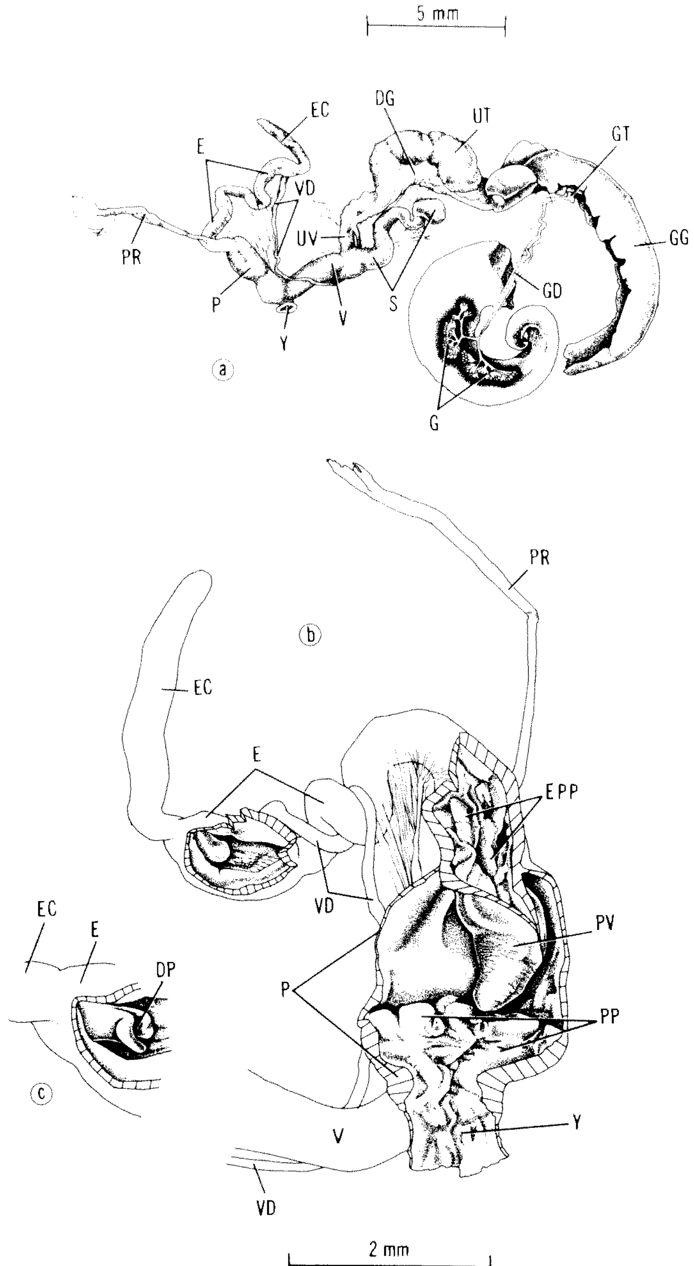


Fig. 426: Genitalia of *Rhagada dringi* (Pfeiffer, 1846): WA-409, Anna Plains Station, 80 Mile Beach, WA. 27 March 1977. FMNH 199763: (a) whole genitalia, Dissection A; (b) interior of penis and epiphallus, Dissection B; (c) epiphallic pore, Dissection B; (d) head wart. Scale lines as marked. Drawings by Linnea Lahlum.

Table 158: Local variation in *Rhagada dringi.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
WA-411, FMNH 199766	6L	8.08±.155 (7.65-8.65)	12.34±.254 (11.55-13.2)	.655±.013 (0.621-0.714)	4 5/8− (4 3/8+-4 7/8+)	0.58±0.33 (0.5-0.75)	21.5±.978 (18.1-24.5)
WA-411, FMNH 199362	9D	8.53±0.203 (7.65-9.65)	12.90±0.280 (11.6-14.2)	0.661±0.006 (0.636-0.690)	4 3/4− (4 3/8+-5+)		
WA-412, FMNH 199780	8D	7.84±0.128 (7.2-8.3)	11.64±0.183 (10.85-12.55)	0.674±0.006 (0.659-0.702)	4 1/2+ (4 3/8−-4 3/4−)		
Wallal turnoff, WAM 277.74	4D	8.74±0.231 (8.3-9.4)	12.50±0.540 (11.9-14.1)	0.701±0.013 (0.666-0.724)	4 3/4+ (4 5/8+-4 7/8−)		
WA-410, FMNH 199764	5L	7.72±0.241 (6.9-8.2)	12.24±0.278 (11.5-13.0)	0.630±0.008 (0.600-0.643)	4 1/2+ (4 3/8+-4 5/8+)		
WA-410, FMNH 199369	6D	8.37±0.330 (7.4-9.4)	12.96±0.526 (11.35-14.8)	0.646±0.004 (0.634-0.661)	4 3/4− (4 1/2−-5)		
WA-409, FMNH 199368	26D	7.94±0.103 (7.1-8.85)	11.98±0.107 (11.1-12.85)	0.662±0.005 (0.607-0.718)	4 5/8 (4 3/8−-5−)		
WA-409, FMNH 199763	4L	7.93±0.221 (7.65-8.6)	11.86±0.12 (11.65-12.2)	0.669±0.013 (0.643-0.705)	4 5/8 (4 1/2-4 3/4−)		

Table 158: Local variation in *Rhagada dringi* (continued)

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
WA-407, FMNH 199788	76L	7.99±0.73 (6.85-9.45)	11.96±0.085 (10.65-14.15)	0.668±0.004 (0.591-0.757)	$4\frac{5}{8}$ ($4\frac{1}{4}$–-5+)	0.67±0.019 (0.4-1.1)	19.0±0.571 (10.5-30)
WA-407, FMNH 199360	22D	8.19±0.141 (6.95-9.25)	12.37±0.192 (11.0-14.1)	0.662±0.005 (0.623-0.713)	$4\frac{1}{2}$– ($4\frac{3}{8}$–-5–)	0.71±0.036 (0.45-1.0)	18.4±1.012 (11.65-29)
WA-408, FMNH 199737	5D	8.69±0.361 (7.75-9.65)	13.04±0.433 (12.05-14.25)	0.666±0.012 (0.638-0.704)	$4\frac{7}{8}$– ($4\frac{5}{8}$–-$5\frac{1}{8}$+)		
WA-408, FMNH 199736	11L	7.89±0.101 (7.4-8.45)	11.65±0.147 (10.9-12.5)	0.677±0.006 (0.653-0.712)	$4\frac{1}{2}$+ ($4\frac{3}{8}$+-$4\frac{5}{8}$+)		
WA-720, FMNH 205359	8L	9.58±0.205 (8.6-10.55)	13.77±0.170 (13.05-14.25)	0.696±0.013 (0.637-0.741)	5+ ($4\frac{7}{8}$–-$5\frac{1}{4}$)		
WA-720, FMNH 205360	7D	9.89±0.212 (9.1-10.95)	13.69±0.296 (12.55-14.9)	0.724±0.018 (0.657-0.794)	5+ ($4\frac{3}{4}$+-$5\frac{3}{8}$+)		

Downs turnoff (WA–720, WAM 787.87, SAM D18145, AM, QM, MV, FMNH 205359–60, 18 LA, 7 DA, 1 DJ).

Range

The known range of *Rhagada dringi* extends along the 80 Mile Beach area from 12 km SW of the Wallal Downs turnoff (WA–411, 19°54'S, 120°34'E), NE to 39 km N of Nita Downs turnoff (WA–720, 18°47'S, 121°50'E, near Frazier Downs turnoff), a distance of about 185 km along the arc of the shore and National Highway 1 (**Map 39**). No collecting has been attempted either in the relatively barren plains from WA–720 to Broome (about 100 km), where *Rhagada reinga* (Pfeiffer, 1846) lives (**Map 41**), or in the 85 km gap from near Wallal Downs (WA–411) to Cape Keraudren (19°57'S, 119°44'E), the most northeasterly record for *Rhagada richardsonii* (**Map 37**).

Diagnosis

Shell smaller than average, adult diameter 10.65–14.9 mm (mean 12.31 mm), with 4 1/4– to 5 3/8+ (mean 4 5/8+) normally coiled whorls (**Fig. 425a**). Apex and spire moderately elevated (**Fig. 425b**), shell height 6.85–10.95 mm (mean 8.26 mm), H/D ratio 0.591–0.794 (mean 0.671). Body whorl evenly rounded. Shell apex (**Plate 209a**) with weak radial sculpture, spire and body whorl with prominent radial ribs (**Plate 209b**) that are greatly reduced in prominence on or absent from shell base. Umbilicus (**Fig. 425c**) with a faint lateral crack or closed by columellar callus. Body whorl descending slightly behind lip, which is narrowly expanded, usually thickened internally. Several narrow to wide, red, spiral colour bands usually present, apex with a slight colour suffusion. Based on 218 measured adults.

Genitalia (**Figs 426a–d**) with enlarged albumen gland (GG), short free oviduct (UV), short kinked spermatheca (S), short vagina (V), medium length epiphallic caecum (EC). Penis (P) short, verge (PV) large, tapering, more than half length of chamber, with long sperm groove. Head wart (**Fig. 426d**) small, oval, slightly darker in colour than head and tail.

Central and early lateral teeth of radula (**Plate 223a**) with moderate anterior flare, prominent ectocone, normal cusp shaft angle, strongly curved blunt cusp tip. Late laterals (**Plate 223b**) with enlarged anterior flare. Lateromarginal transition (**Plate 223e**) and outer marginals (**Plate 223c**) typical. Jaws (**Plate 223d, f**) quite variable in both rib numbers and width.

Discussion

Rhagada dringi probably is distributed generally along the coastal dunes and sandy soils in the 80 Mile Beach area. Specimens were abundant in the litter under trees and shrub patches along the highway and near the beach. No attempt has been made to collect E of the Highway and thus the width of the distribution is unknown.

Local variation in the larger samples is summarised in **Table 158**. At every station, the diameter of dead adults was marginally to significantly larger than for live adults. This presumably reflects the fact that Broome, Wallal Downs and Port Hedland all had modestly to drastically below-average rainfall in the 1969 through 1975 period (abstracted from Bureau of Meteorology records), during which the 80 Mile Beach living adult *R. dringi* would have reached adult size.

Geographical variation in shell size, based on live examples, shows a mixed pattern from N to S. The means are: Nita Downs (WA–720, 13.77 mm); Noreen Bore (WA–408, 11.65 mm; WA–407, 11.96 mm); Anna Plains (WA–409, 11.86 mm); Mandora (WA–410, 12.24 mm); and Wallal Downs (WA–411, 12.34 mm). At both extremes of the known range, shells are slightly to moderately larger in size.

RHAGADA REINGA (PFEIFFER, 1846)

(Plates 210a–c, 224a–d; Figs 427a–c, 428a–c; Maps 39, 41)

Helix reinga Pfeiffer, 1846, *Symbolae Hel*, **3:** 31, 50, 73 – New Zealand (error); Pfeiffer 1848, *Monog. Helic. viv.*, **1:** 289; Pfeiffer 1851, In: *Martini & Chemnitz, Syst. Conch. Cab.*, I (12) **2:** 52, plt. 73, figs 8–9; Reeve 1852, *Conch. Icon.*, **7:** plt. 128, figs 772a–b; Hutton 1883, *Trans. Proc. New Zealand Inst.*, **16:** 194; Pilsbry 1889, *Man. Conch.*, (2) 4: pl. 36, fig. 39; Hedley 1894, *Proc. Malac. Soc. London,* **1:** 260 – Kings Sound, Western Australia (error); Hedley 1916, *Jour. Roy. Soc. Western Aust.*, **1:** 70 – as synonym of *Rhagada torulus* (Férussac, 1819); Iredale 1933, *Rec. Aust. Mus.*, **19** (1): 52; Iredale 1938, *Aust. Zool.*, **9** (2): 112 – as synonym of *Rhagada torulus* (Férussac, 1819).

Helix (*Rhagada*) *reinga* (Pfeiffer), Pilsbry 1890, *Man. Conch.*, (2) **6:** 185; E. A. Smith 1894, *Proc. Malac. Soc. London,* **1:** 89 – Port Essington (error) and Dampier Archipelago (error) (Brit. Mus.), Roebuck Bay (J. J. Walker!), Burner (= Napier) Ranges (error), Western Australia.

Thersites (*Rhagada*) *reinga* (Pfeiffer), Pilsbry 1894, *Man. Conch.*, (2) **9:** 135–136; Pilsbry 1895, *Man. Conch.*, (2) **9:** 343.

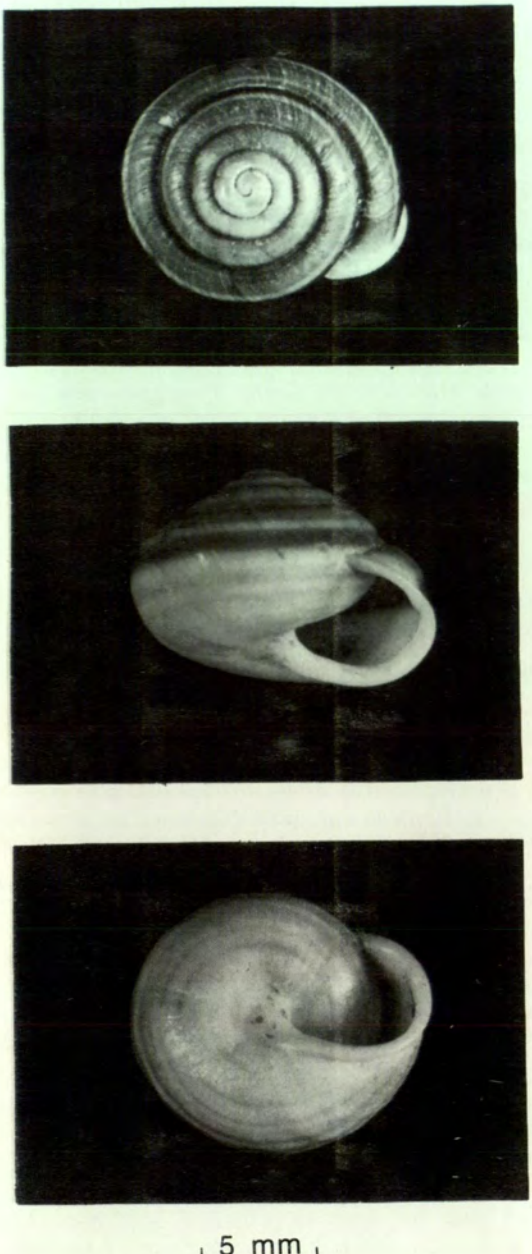
Rhagada reinga (Pfeiffer), Ancey 1898, *Proc. Linn. Soc. New South Wales*, **22:** 776 – Oscar Range, Western Australia (probably based on *R. gatta* Iredale, 1939); Iredale 1939, *Jour. Roy. Soc. Western Aust.*, **25:** 59, plt. IV, fig. 2 – Broome, WA; Richardson 1985, *Tryonia*, **12:** 267–268 – check list citation as synonym of *Rhagada torulus* (Férussac, 1819).

Comparative remarks

Rhagada reinga (Pfeiffer, 1846), recorded only from the vicinity of Broome (**Map 41**), is a relatively small species (mean diameter 12.48 mm) with near-average whorl count (mean 5 1/8), high rounded spire (**Fig. 427b**, mean H/D ratio 0.728), aperture slightly deflected behind lip which is narrowly expanded and slightly thickened inside, umbilicus (**Fig. 427c**) either closed or with a very narrow lateral crack. Lip sometimes with a weak basal knob. Shell white, with many narrow red to orange spiral bands, sometimes reduced to the two standard wider bands and usually a spire suffusion of light brownish red extending down to periphery. Shell apex (**Plate 210a**) smooth, spire and body whorl with prominent radial growth ridgelets and irregular growth pauses. *R. cygna* sp. nov., from the NE tip of Dampier Land (**Map 41**) is a little smaller (mean diameter 11.75 mm) at the same whorl count (mean 5 1/8), higher spired (mean H/D ratio 0.762) and has a more broadly expanded lip (**Figs 429d–f**), but agrees in colour and lack of radial ribs. *R. bulgana* sp. nov., from the N half of Dampier Land (**Map** a

b

c



5 mm

Fig. 427: Shell of *Rhagada reinga* (Pfeiffer, 1846): Broome, WA. AM C.64851. Scale line equals 10 mm.

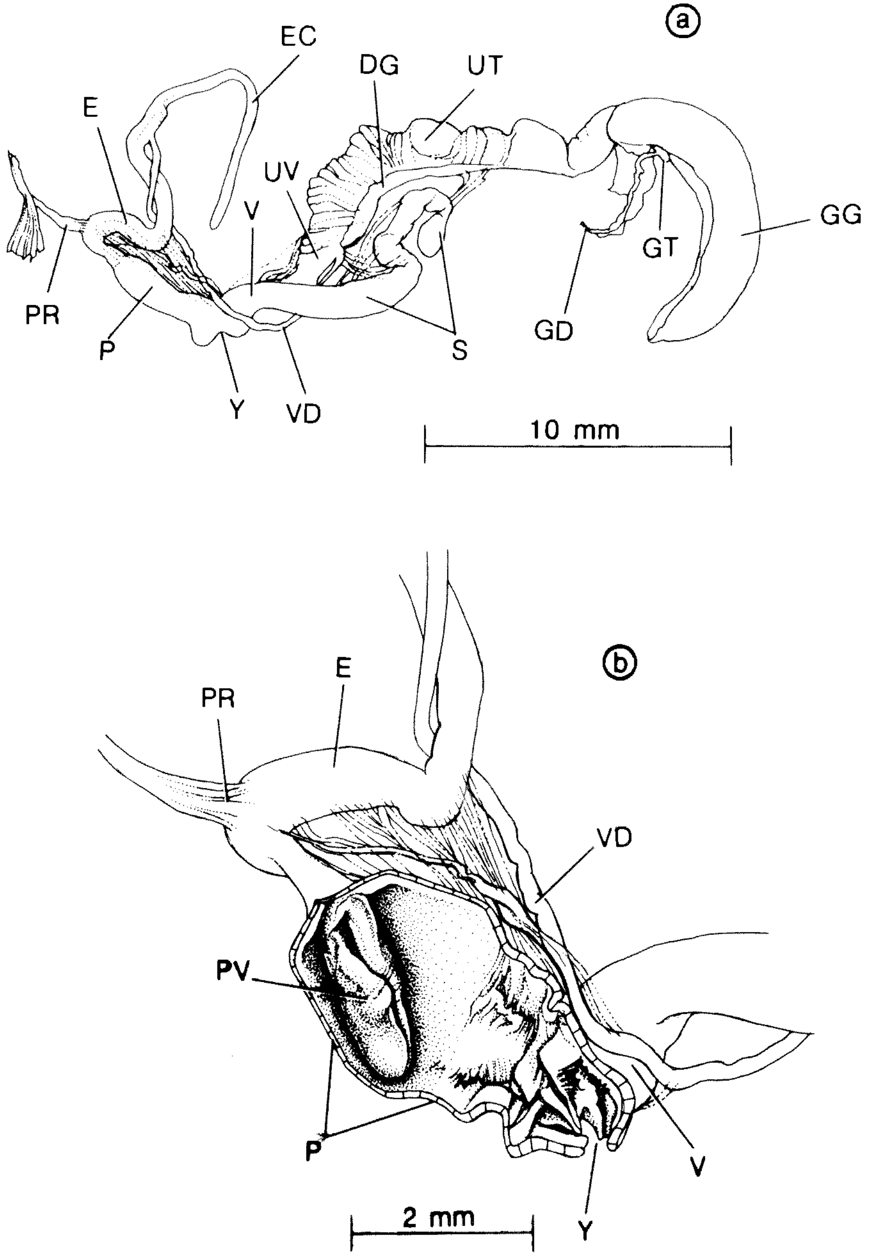


Fig. 428: Genitalia of *Rhagada reinga* (Pfeiffer, 1846): WA–718, Roebuck Bay Caravan Park, Broome, WA. 23 June 1980. FMNH 205356, Dissection B: (a) whole genitalia; (b) verge; (c) head wart. Scale lines as marked. Drawings by Linnea Lahlum.

41), is much larger (mean diameter 14.35 mm), has a higher whorl count (mean 5 1/2) and has the red banding reduced to the standard supraperipheral and subsutural bands. It lacks any spire suffusion. *R. dringi* and most of the Dampier Archipelago taxa differ in having prominent radial ribbing at least above shell periphery. Anatomically (**Figs 428a–c**), *R. reinga* has a large albumen gland (GG), tightly kinked spermatheca (S), short vagina (V) and extremely long epiphallic caecum (EC). Penis (P) short and slender, verge (PV) long, tapering gradually over distal half, sperm groove long.

Type lot material

Zurich 510030, Western Australia, ex Mousson, Sowerby (in 1874), 2 DA.

Material studied

WESTERN AUSTRALIA: Broome (G. W. Kendrick! 13 September 1984, WAM, 37 DA, 16 DJ; MV 28293, 1 DA, 1 DJ; G. P. Whitley! 4 October 1945, AM C.64851, 1 DA; WA–406, Roebuck Bay Caravan Park, WAM 796.87, SAM D18153, FMNH 199361, FMNH 199776, 7 LA, 4 DA, 4 LJ, 8 DJ; WA–718, Roebuck Bay Caravan Park, WAM 795.87, SAM D18152, AM, FMNH 205356, 13 LA, 2 LJ; WA–421, near Bali Hai Caravan Park, WAM 797.87, SAM D18154, AM, MV, QM, FMNH 199321, FMNH 200200, 1 LA, 35 DA, 2 DJ); Roebuck Bay (J. J. Walker! 1891, BMNH 91.11.21.167–169, 3 DA; AM C.33897, ex C. Hedley, 1 DA).

Range

Material referred here to *Rhagada reinga* (Pfeiffer, 1846) has been found only in the immediate vicinity of Broome (**Map 41**), implying a range of only a very few km. No collections have been made in the area between Broome and Coulomb Point (southern record of *Rhagada bulgana* sp. nov.), a distance of about 67 km, or between Broome and the northernmost record of *R. dringi* (**Map 41**), a distance of about 100 km.

Diagnosis

Shell smaller than average, adult diameter 10.95–13.9 mm (mean 12.48 mm), with 4 3/4+ to 5 3/8+ (mean 5 1/8) normally coiled whorls (**Fig. 427a**). Apex and spire strongly elevated (**Fig. 427b**), shell height 7.95–10.75 mm (mean 9.08 mm), H/D ratio 0.665–0.815 (mean 0.728). Body whorl evenly rounded. Shell apex (**Plate 210a**) smooth, spire and body whorl with radial growth irregularities and prominent radial micro-ridgelets. Umbilicus (**Fig. 427c**) closed or with a very narrow lateral crack. Body whorl descending slightly behind lip, which is thin, moderately expanded and sometimes with a low basal lip knob. Spire with a dark reddish-brown spire suffusion and usually several red to orange spiral colour bands. Based on 64 measured adults.

Genitalia (**Figs 428a–c**) with large albumen gland (GG), tightly kinked spermatheca (S), short free oviduct (UV), short vagina (V) and very long epiphallic caecum (EC). Penis (P) short, slender. Verge (PV) long, tapering gradually, with long sperm groove, surface smooth. Head wart (**Fig. 428c**) very small, oval, barely darker than head and neck.

Central and early lateral teeth of radula (**Plate 224a, c**) with prominent anterior flare, normal or slightly elevated cusp shaft angle, slightly curved and sharp pointed cusp tip, well developed ectocone on laterals. Late laterals with enlarged anterior flare,

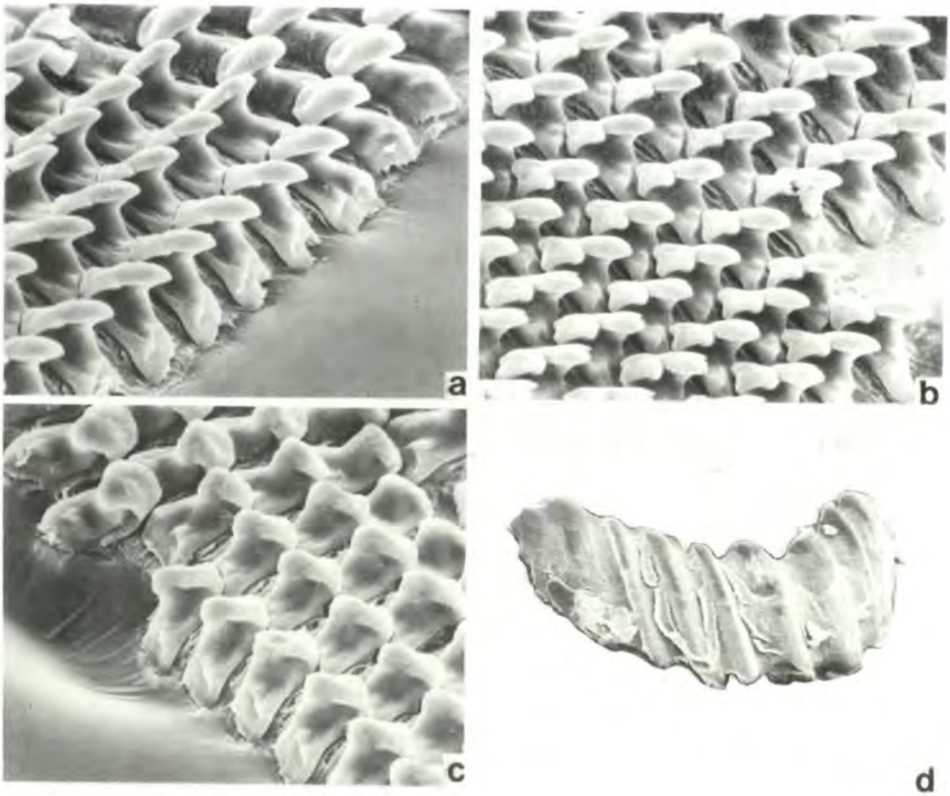


Plate 224: Radular teeth and jaw of *Rhagada reinga* (Pfeiffer, 1846). WA–718, behind Roebuck Bay Caravan Park, Broome, WA. 23 June 1980. FMNH 205356, Dissection B: (a) central and early laterals at 540X; (b) latero-marginal transition at 530X; (c) worn central and laterals at 530X; (d) jaw at 68X.

lateromarginal transition (**Plate 224b**) typical. Jaw (**Plate 224d**) with prominent, rather widely spaced vertical ribs over most of surface.

Discussion

No specimens actually labelled as types of *Rhagada reinga* were located. The initial illustration was cited as being inaccurate in the accompanying text, with the lip knob essentially omitted. The colour suffusion on the spire shown in all the illustrations and present in the Zurich examples is matched by the Broome examples but the lip knob in the Zurich shells is far more prominent than in any of the recently-collected material. I cheerfully admit that *reinga* may be based on an as yet not rediscovered taxon. It comes closest to these Broome populations and they are used to establish the structures of the type species in *Rhagada*. The alternative would be to propose a new species name for the Broome shells and then list *reinga* as an unknown species.

Since all samples were taken from areas within Broome itself, which would be subject to at least occasional garden hose or sprinkler waterings throughout the year, the lack of interpopulational variation (**Table 159**) is not surprising.

Table 159: Local variation in Dampier Land *Rhagada* species.

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
Rhagada reinga					
WA-406, FMNH 199776	7L	8.95±0.203 (8.3-9.9)	12.34±0.134 (12.0-12.95)	0.725±0.011 (0.692-0.783)	5 (4⅞−-5¼+)
WA-421, FMNH 199321	35D	8.92±0.106 (7.95-10.75)	12.24±0.112 (10.95-13.7)	0.729±0.006 (0.665-0.815)	5⅛+ (4⅞−-5⅜−)
WA-718, FMNH 205356	13L	9.13±0.155 (8.2-9.95)	12.70±0.162 (11.65-13.9)	0.719±0.008 (0.666-0.779)	5 (4¾+-5¼+)
Rhagada bulgana					
WA-403, FMNH 199348	6D	11.42±0.342 (10.35-12.5)	15.47±0.435 (14.25-17.0)	0.739±0.013 (0.688-0.775)	5¾− (5½−-6−)
WA-404, FMNH 199790	67L	11.88±0.080 (10.5-13.15)	15.48±0.099 (13.5-17.5)	0.768±0.004 (0.661-0.850)	5⅝+ (5¼−-6⅞−)
WA-404, FMNH 199333	100D	11.82±0.078 (10.35-14.15)	15.70±0.096 (13.85-18.3)	0.754±0.005 (0.657-0.889)	5⅝+ (4⅞+-6⅜−)
WA-187, FMNH 199918	9D	10.89±0.218 (10.05-12.15)	14.67±0.236 (13.4-15.6)	0.742±0.006 (0.725-0.781)	5½ (5⅛+-5⅝+)
WA-189, FMNH 199379	9D	12.64±0.331 (11.65-14.9)	16.20±0.210 (15.5-17.75)	0.779±0.012 (0.733-0.839)	6− (5⅝−-6⅜+)
WA-405, FMNH 199775	25L	11.36±0.114 (10.0-12.46)	14.46±0.143 (13.15-16.05)	0.786±0.006 (0.728-0.589)	5½ (5⅛−-5¾−)

Table 159: Local variation in Dampier Land *Rhagada* species (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
WA-186, FMNH 199926	56L	9.46±0.093 (7.95-11.15)	12.52±0.085 (11.4-14.5)	0.755±0.005 (0.683-0.855)	$5\frac{1}{4}$ ($4\frac{3}{4}$+-$5\frac{3}{4}$−)
WA-186, FMNH 199777	37L	9.85±0.107 (8.4-11.35)	12.94±0.126 (11.55-14.9)	0.761±0.006 (0.702-0.850)	$5\frac{1}{4}$+ ($4\frac{7}{8}$+-$5\frac{3}{4}$−)
WA-186, FMNH 199925	37D	9.57±0.104 (8.55-11.5)	12.69±0.099 (11.4-14.1)	0.754±0.007 (0.691-0.854)	$5\frac{1}{4}$− ($4\frac{3}{4}$-$5\frac{5}{8}$+)
WA-185, FMNH 199938	19D	9.98±0.227 (8.35-12.1)	13.15±0.237 (11.15-14.8)	0.759±0.007 (0.702-0.820)	$5\frac{3}{8}$ ($5\frac{1}{8}$−-6−)
Rhagada cygna					
WA-184, FMNH 199781	11L	9.01±0.231 (7.9-10.0)	11.80±0.199 (10.8-12.95)	0.763±0.010 (0.711-0.821)	$5\frac{1}{4}$ ($4\frac{7}{8}$+-$5\frac{1}{2}$+)
WA-184, FMNH 200273	56L	8.75±0.087 (7.55-10.4)	11.48±0.090 (10.1-13.8)	0.763±0.005 (0.703-0.851)	$5\frac{1}{8}$ ($4\frac{3}{4}$+-$5\frac{5}{8}$−)
WA-184, FMNH 200271	72D	9.07±0.086 (7.6-11.0)	11.87±0.082 (10.4-14.0)	0.763±0.005 (0.657-0.886)	$5\frac{1}{8}$+ ($4\frac{5}{8}$+-$5\frac{1}{2}$+)

RHAGADA BULGANA SP. NOV.

(Plates 210d, 225a–f; Figs 429a–c, 430a–f; Maps 39, 41)

Comparative remarks

Rhagada bulgana sp. nov., which is found in the northern half of the Dampier Peninsula (**Map 41**), is average in size (mean diameter 14.35 mm), with increased whorl count (mean 5 1/2), high spire that is sometimes rounded (**Fig. 429b**, mean H/D ratio 0.760), aperture slightly descending behind lip which is moderately expanded, umbilicus (**Fig. 406c**) almost always closed by broad expansion of columellar lip. Shell white, with narrow red spiral supraperipheral and subsutural colour bands, apex and very early spire sometimes with light colour suffusion. No specimens show accessory colour bands. Shell apex (**Plate 210d**) smooth, spire and body whorl with relatively prominent radial growth ridgelets. Both *R. cygna* sp. nov. from the N tip of Dampier Land (**Map 41**) and *R. reinga* from the vicinity of Broome (**Map 41**) differ obviously in their smaller size (mean diameters 11.75 mm and 12.48 mm respectively), lower whorl counts (means of both 5 1/8) and colour pattern of many spiral bands. *R. dringi* from the 80 Mile Beach area (**Map 39**), and most of the Dampier Archipelago species have prominent radial ribs at least above the shell periphery (see **Plates 207–209, Figs 418, 420, 422, 425**). The most similar species, *R. torulus* from Shark Bay N to near Warroora Homestead (**Map 38**), is the same size and basic colour pattern but is slightly more elevated (mean H/D ratio 0.823), has the aperture narrowed and without lip expansion and shows many anatomical differences.

Anatomically (**Figs 430a–f**), *R. bulgana* has a normal sized albumen gland (GG), medium length unkinked spermatheca (S), medium length free oviduct (UV), short vagina (V) and very long epiphallic caecum (EC). Penis (P) medium in length, verge (PV) cylindical, smooth surfaced, with long sperm groove. *R. cygna* sp. nov. (**Figs 431a–b, 432a–c**) agrees in most features but the penis is shorter and the verge larger in diameter. *R. reinga* (**Figs 428a–c**) has the albumen gland greatly enlarged, verge reduced in size and an extremely long epiphallic caecum. *R. dringi* (**Figs 426a–d**) has a much larger albumen gland, the spermatheca shortened and kinked and has the verge greatly reduced in size. *R. torulus* (**Figs 404a–e**) has an enormous albumen gland, short and tightly kinked spermatheca, shorter epiphallic caecum and the verge is short and cylindrical with a corrugated surface.

Holotype

WAM 767.87, WA–186, 1.5 km along Bulgan Creek road, near Cape Leveque, N tip of Dampier Land, Western Australia. 16°24'12"S, 122°55'31"E. Collected 6 October 1976 by A. Solem. Height of shell 9.75 mm, diameter 12.95 mm, H/D ratio 0.753, whorls 5 3/8, umbilicus completely closed by broad expansion of columellar lip.

Paratopotypes

WAM 801.87, WAM 809.87, SAM D18157, SAM D18163, AM C.200,740, QM 52986, MV F59478, FMNH 199925–6, 56 LA, 36 DA, many LJ, 22 DJ from the type locality.

Paratypes

WESTERN AUSTRALIA: Dampier Land: Coulomb Point (W. H. Butler! July 1971,

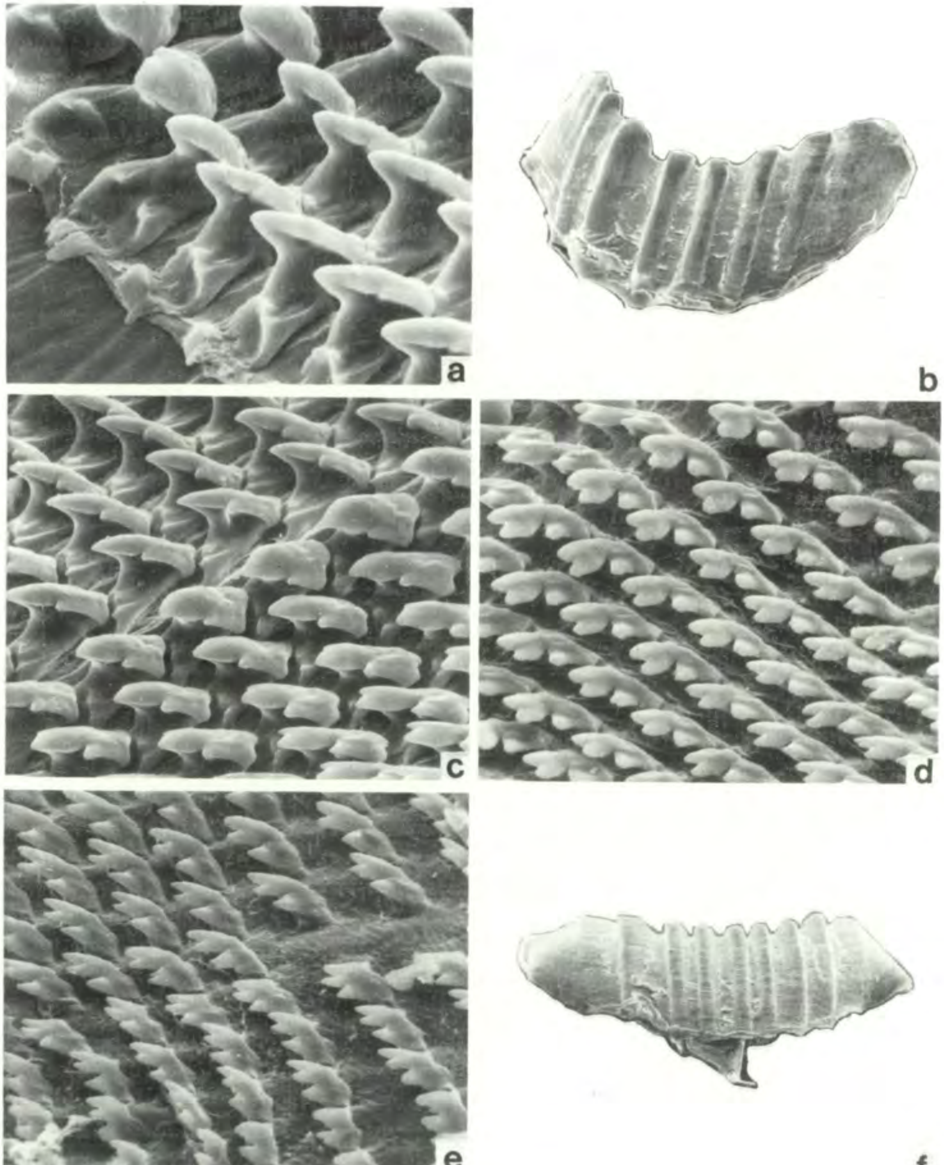


Plate 225: Radular teeth and jaws of *Rhagada bulgana* sp. nov.: WA–186, Bulgan Creek, Cape Leveque, Dampier Land, WA. 24 March 1977. FMNH 199777: (a–b) Dissection B. a is central and early laterals at 780X. b is jaw at 63X; (c–f) Dissection A. c is latero-marginal transition at 570X. d is early and mid marginals at 590X. e is outer marginals at 590X. f is jaw at 51X.

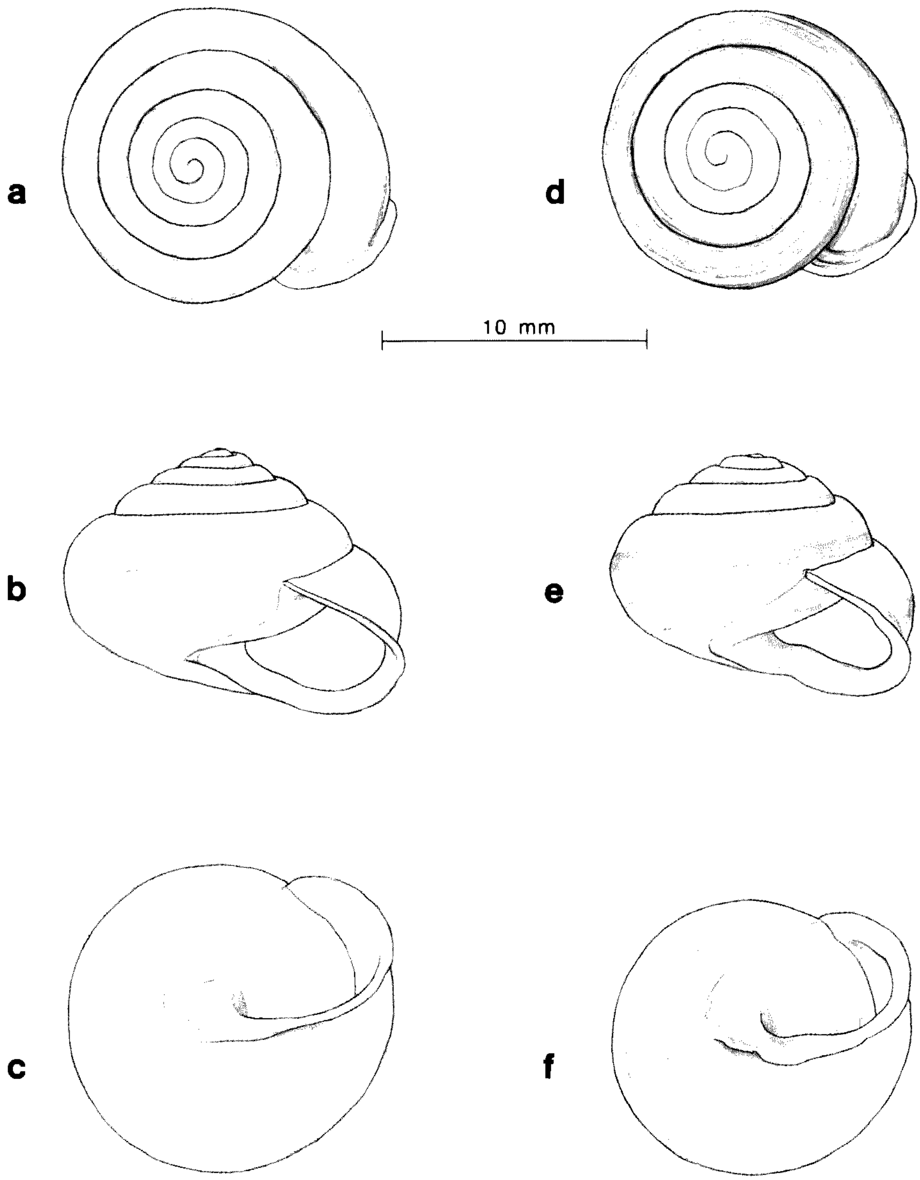


Fig. 429: Shells of *Rhagada bulgana* sp. nov. and *R. cygna* sp. nov.: (a–c) Holotype of *R. bulgana*. WAM 767.87. WA–186, Bulgan Creek, Cape Leveque, Dampier Land, WA; (d–f) Holotype of *R. cygna*. WAM 768.87. WA–184, vine thicket behind Cygnet Bay Pearl Fisheries, One Arm Point, Dampier Land, WA. Scale line equals 10 mm. Drawings by Linnea Lahlum.

WAM 296.74, 1 DA, 1 DJ); Cape Bertholot (E of, B. R. Wilson & S. Slack-Smith! 5 September 1975, WAM 407–77, 4 DA, 7 DJ); Broome–Cape Leveque road (WA–403, 80 km in, WAM 803.87, FMNH 199348, 6 DA; WA–404, 90.3 km in, WAM 805.87, SAM D18158–9, AM C.200,741, QM 45025, MV F60023, FMNH 199333, FMNH 199790, 67 LA, 100 DA, many LJ, many DJ;109 km in, S. Slack-Smith! 6 September 1975, WAM 428.77, 1 DA, 2 DJ); Beagle Bay area (WA–187, 47.5 km S of turnoff, WAM 802.87, FMNH 199917–8, 9 DA, 1 LJ, 1 DJ; WA–188, 26.2 km S of turnoff, WAM 808.87, SAM D18162, AM C.200,742, FMNH 199932, FMNH 199934, 1 LA, 6 DA, 5 DJ; WA–189, 16.1 km S of turnoff, WAM 807.87, SAM D18161, AM C.200,743, FMNH 199379, 9 DA, 9 DJ); Alligator Creek, 2 1/2 miles SW of mouth, D. Hembree! 28 September 1975, WAM 425.77, 3 DA); Lombadina road junction (WA–405, 2.7 km S of, WAM 806.87, SAM D18160, AM C.200,744, FMNH 199775, 25 LA, 11 LJ); Cape Leveque (WA–185, WAM 811.87, SAM D18165, AM C.200,745, FMNH 199938–9, 2 LA, 19 DA, 5 DJ; WA–186, WAM 810.87, SAM D18164, AM C.200,746, FMNH 199777, 37 LA, many LJ; near Cygnet Bay, WAM 429.77, 2 DA).

Range

Rhagada bulgana has been collected in the northern half of the Dampier Peninsula, between Coulomb Point and Cape Leveque, a distance of about 135 km (**Map 41**). No collections have been made between Coulomb Point and Broome, a distance of about 67 km. At the N tip, near One Arm Point, it is replaced by *Rhagada cygna* (**Map 41**). At Broome (**Map 41**) it is replaced by *Rhagada reinga*.

Diagnosis

Shell medium in size, adult diameter 11.15–18.3 mm (mean 14.35 mm), with 4 3/4 to 6 3/8+ (mean 5 1/2) normally coiled whorls. Apex and spire strongly elevated (**Fig. 429b**), rarely rounded above, shell height 7.95–14.9 mm (mean 10.91 mm), H/D ratio 0.657–0.889 (mean 0.760). Body whorl evenly rounded. Shell apex (**Plate 210d**) smooth, spire and body whorl with prominent radial ridgelets. Umbilicus (**Fig. 429c**) completely closed by expansion of columellar callus. Body whorl usually descending slightly behind lip, which is thin and narrowly expanded. Shell white, narrow red supraperipheral and subsutural colour bands present but no examples with accessory bands seen. Based on 398 measured adults.

Genitalia (**Figs 430a–f**) with normal sized albumen gland (GG), prostate (DG) and uterus (UT) long, spermatheca (S) medium length and not kinked, free oviduct (UV) normal length, vagina (V) short and epiphallic caecum (EC) very long. Penis (P) short verge (PV) cylindrical, smooth surfaced, with long sperm groove. Head wart (**Fig. 430f**) small, oval, slightly darker than surrounding tissue.

Central and early lateral teeth of radula (**Plate 225a**) with small anterior flare, elevated cusp shaft angle, prominent ectocone on laterals, cusp tip bluntly pointed with little curvature. Late laterals (**Plate 225c**) with slightly larger anterior flare and cusp tip curvature, reduced cusp shaft angle, large ectocone and more sharply pointed cusp tip. Lateromarginal transition (**Plate 225c**) and marginals (**Plate 225d–e**) typical. Jaws (**Plate 225b, f**) with several very large radial ribs spread along middle two-thirds of jaw, absent from side margins.

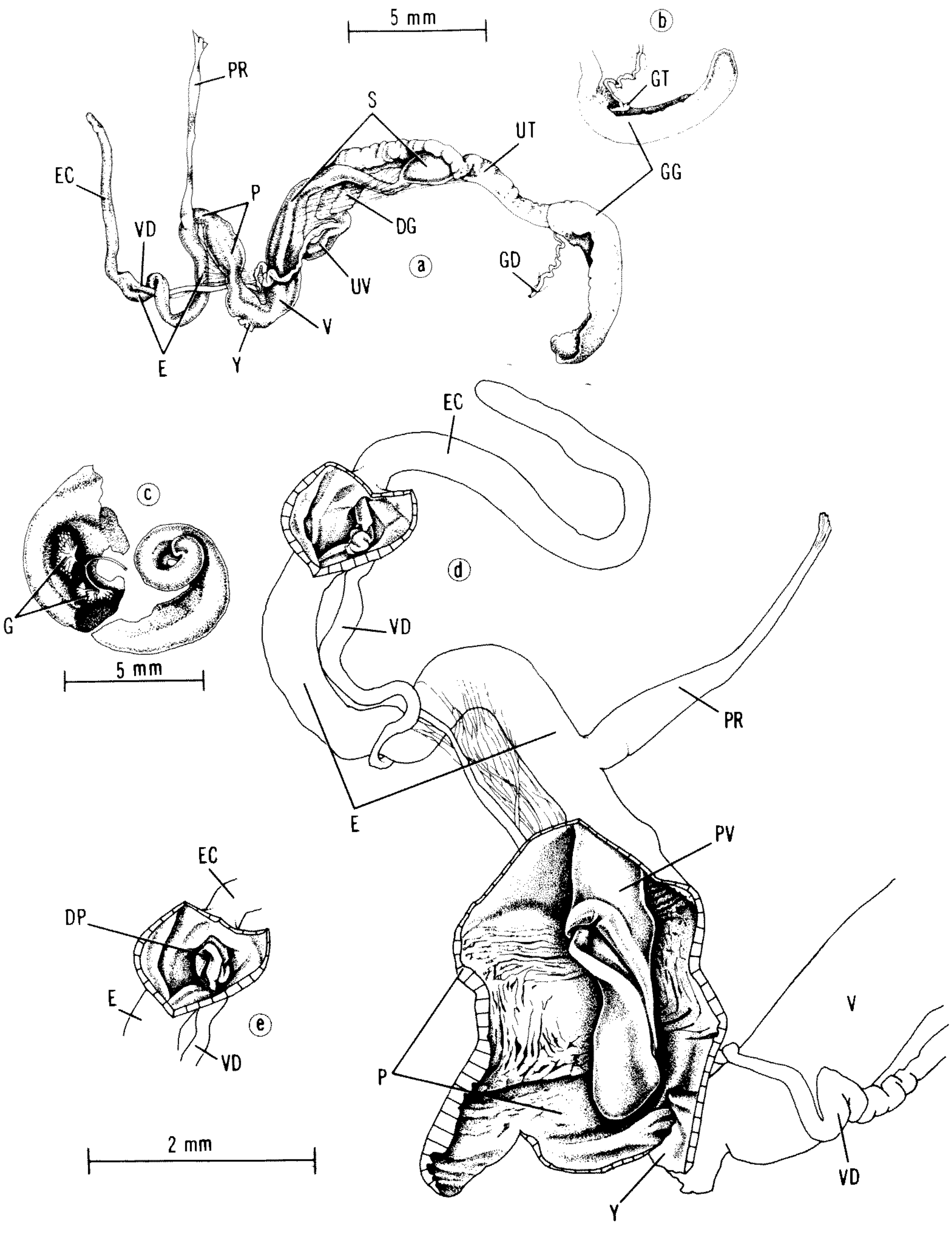


Fig. 430: Genitalia of *Rhagada bulgana* sp. nov.: WA–186, Bulgan Creek road, Cape Leveque, Dampier Land, WA. 6 October 1976. FMNH 199926: (a) whole genitalia, Dissection A; (b) detail of talon, Dissection A; (c) ovotestis, Dissection A; (d) interior of penis and epiphallus, Dissection B; (e) epiphallic pore, Dissection B; (f) head wart, undissected specimen. Scale lines as marked. Drawings by Linnea Lahlum.

Discussion

Rhagada bulgana shows a patchy distribution, either being extremely common or absent. Specimens have been found in sandy soil under fallen trees, or sealed to leaves or small branches a few feet above the ground. This is the only Western Australian camaenid that I have seen on plants above ground, except during feeding activity.

In June 1987, the Rain Forest Survey team from the Western Australian Wildlife Research Centre found this species to be common 4.5 km ENE of Cape Borda (RFS 29–2, 128 specimens) and 2 km SE of Cape Leveque (RFS 29–3, 126 specimens). Both localities fall within the range outlined above. They agree in size and structure with other material but are not included in the variation data and have not been designated as paratypes.

Shape variation (**Table 159**) among populations is insignificant. Mean diameter ranges from 12.52 mm to 16.20 mm, with no clear geographic or allochronic patterns detected.

The name *bulgana* is taken from the type locality, Bulgan Creek.

RHAGADA CYGNA SP. NOV.

(Plates 210e–f, 226a–f; Figs 429d–f, 431a–b, 432a–c; Maps 39, 41)

Comparative remarks

Rhagada cygna sp. nov., from One Arm Point, N tip of Dampier Land (**Map 41**), is a small species (mean diameter 11.75 mm), with reduced whorl count (mean 5 1/8), high spire (**Fig. 429e**, mean H/D ratio 0.762), aperture slightly to moderately descending behind lip, which is moderately expanded and somewhat thickened, occasionally with a weak basal lip knob present; umbilicus (**Fig. 429f**) may be closed by the broad expansion of the columellar callus or open with a very narrow lateral crack remaining. Shell white, with many red to orange spiral colour bands of varying width, and a strong spire suffusion. Shell apex (**Plate 210e**) nearly smooth, spire and body whorl with prominent, irregular radial ridgelets. The most similar species, *R. reinga* from the vicinity of Broome (**Map 41**), agrees in colour pattern but is larger (mean diameter 12.48 mm) at the same whorl count (mean 5 1/8) and less elevated (**Fig. 427b**, mean H/D ratio 0.728). *R. dringi* from the 80 Mile Beach area (**Map 39**) and nearly all the small Dampier Archipelago species (**Plates 207–209**) have prominent radial ribs at least above the shell periphery. The one exception, *R. angulata*, lacks the radial ribs (**Plate 208a**), has an obtusely angulated periphery (**Fig. 422b**), often moderately open umbilicus and a very broadly expanded lip (**Figs 422a–c**). None of the more southern species show striking similarities.

Anatomically (**Figs 432a–c**), *R. cygna* has a normal sized albumen gland (GG), short free oviduct (UV), medium length spermatheca (S) that is kinked apically, medium length vagina (V) and long epiphallic caecum (EC). Penis (P) short, verge (PV) large, wide, smooth surfaced, with very prominent sperm groove extending nearly to its tip. *R. bulgana* (**Figs 430a–f**) has the verge slender and cylindrical, with the sperm groove stopping well short of the tip, a longer spermatheca and longer free oviduct. *R. dringi* (**Figs 426a–d**) has a greatly enlarged albumen gland, kinked and shortened spermatheca, much smaller verge and shorter epiphallic caecum. More

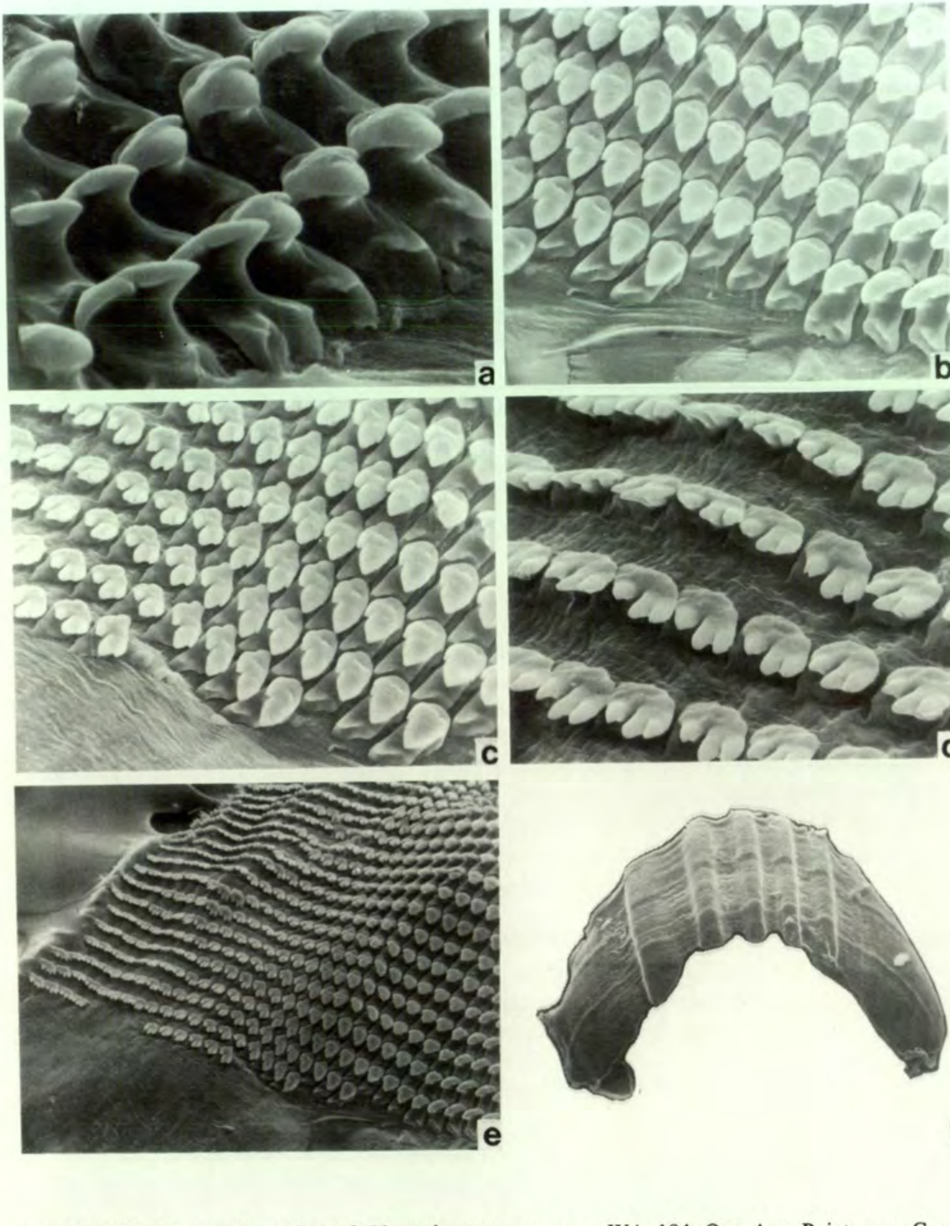


Plate 226: Radular teeth and jaw of *Rhagada cygna* sp. nov.: WA–184, One Arm Point, near Cape Leveque, Dampier Land, WA. 6 October 1976. FMNH 200273: (a) Dissection B. a is central and early laterals at 19.6X; (b–f) Dissection A. b is central and early laterals in top view at 355X. c is latero-marginal transition from top viewing angle at 59X. d is outer marginals at 670X. e is part row at 140X. f is jaw at 60X.

southern species all have the greatly enlarged albumen glands, much smaller verges and shortened prostate-uterus areas.

Holotype

WAM 768.87, WA–184, liana patch behind Cygnet Bay Pearl Fisheries, One Arm Point, N tip of Dampier Land, Western Australia. 16°27'13"S, 123°02'40"E. Collected 6 October 1976 by A. Solem. Height of shell 9.1 mm, diameter 11.7 mm, H/D ratio 0.778, whorls 5 1/8–, umbilicus with a very narrow lateral crack remaining.

Paratopotypes

WAM 798.87, SAM D18155–6, AM C.200,747, QM 45026, MV F60003, MV F60092, FMNH 200271, FMNH 200273, 56 LA, 71 DA, many LJ, many DJ.

Paratypes

WESTERN AUSTRALIA: Dampier Land: One Arm Point area (WA–184, 24 March

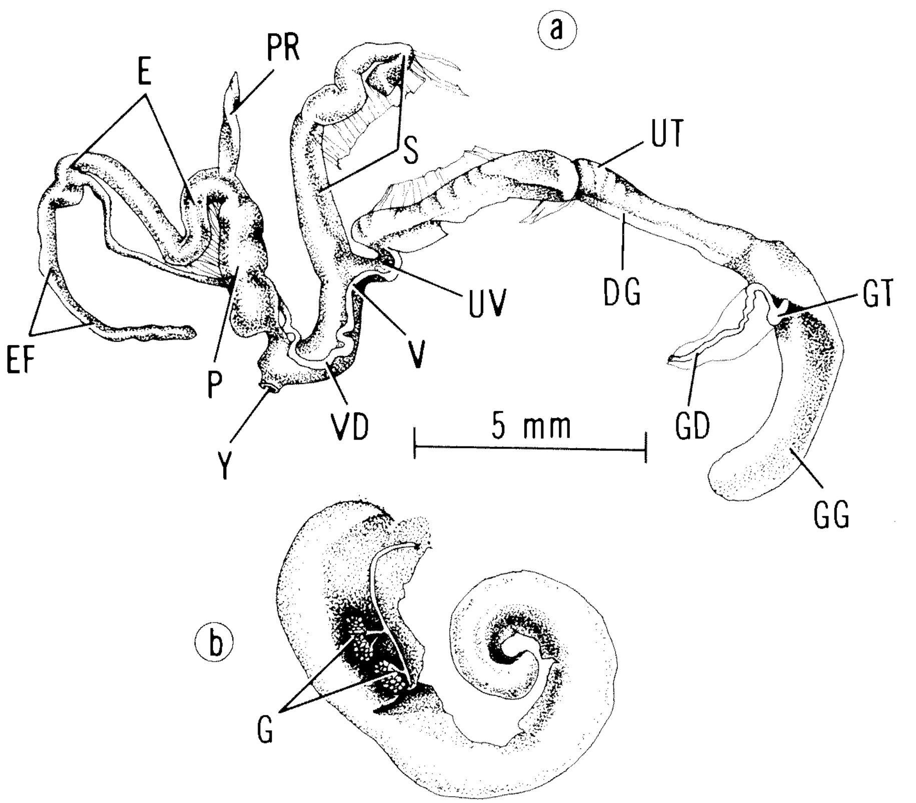


Fig. 431: Genitalia of *Rhagada cygna* sp. nov.: WA–184, liana patch behind Cygnet Bay Pearl Fisheries, One Arm Point, Dampier Land, WA. 6 October 1976. FMNH 200273, Dissection A: (a) whole genitalia; (b) ovotestis. Scale lines as marked. Drawings by Linnea Lahlum.

1977, WAM 800.87, FMNH 199781–2, 11 LA, 2 DA, 2 LJ); One Arm Point, N. Coleman! 5 November 1972, MV F75302, 12 DA).

Range

Rhagada cygna, sp. nov., has been found only in the vicinity of One Arm Point, N tip of Dampier Land (**Map 41**). Its total range probably is about 10 km radius before being replaced by *Rhagada bulgana* (**Map 41**).

Diagnosis

Shell small, adult diameter 10.1–14.0 mm (mean 11.75 mm), with 4 5/8+ to 5 5/8– (mean 5 1/8) normally coiled whorls. Apex and spire strongly elevated (**Fig. 429e**), rarely rounded above, shell height 7.55–11.0 mm (mean 8.95 mm), H/D ratio 0.657–0.886 (mean 0.762). Body whorl evenly rounded. Shell apex (**Plate 210e**) nearly

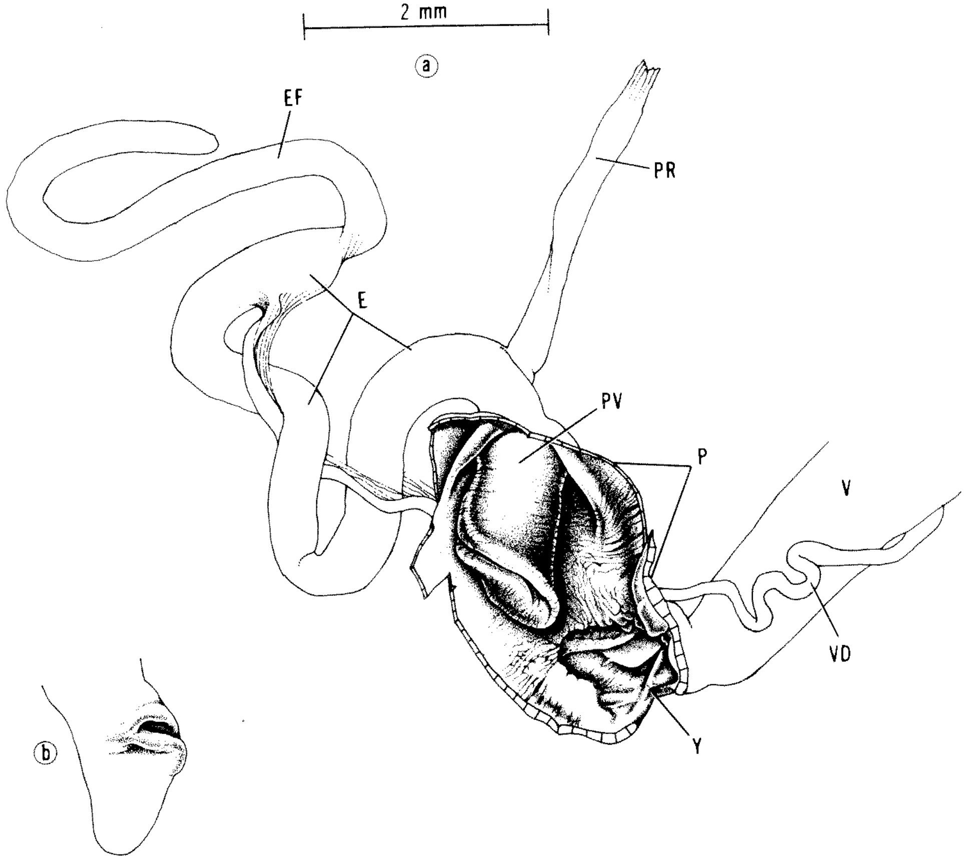


Fig. 432: Genitalia of *Rhagada cygna* sp. nov.: WA–184, liana patch behind Cygnet Bay Pearl Fisheries, One Arm Point, Dampier Land, WA. 6 October 1976. FMNH 200273, Dissection B: (a) penis chamber; (b) detail of verge; (c) head wart. Scale lines as marked. Drawings by Linnea Lahlum.

smooth, spire and body whorl with growth pauses and prominent radial ridgelets. Umbilicus (**Fig. 429f**) closed by broad expansion of columellar callus. Body whorl descending slightly behind lip, which is thin and moderately expanded. Shell white, with a strong spire suffusion of reddish brown, numerous narrow to wide, red to orange, spiral bands present. Based on 153 measured adults.

Genitalia (**Figs 431a–b, 432a–c**) with normal sized albumen gland (GG) and prostate-uterus, spermatheca (S) medium long and kinked apically, free oviduct (UV) short, vagina (V) typical and epiphallic caecum (EC) long. Penis (P) short, verge (PV) very large, two-thirds length of penis, smooth surfaced, prominent sperm groove extending nearly to tip. Head wart (**Fig. 432c**) very small, circular, same colour as neck tissue.

Central and lateral teeth of radula (**Plate 226a–b**) with typical anterior flare, normal cusp shaft angle, pointed and curved cusp tip, prominent ectocone and large basal plate support ridge. Lateromarginal transition and marginals (**Plate 226c–d**) typical. Jaw (**Plate 226f**) with a few prominent vertical ribs in middle portion, sides without ribs.

Discussion

The few samples of *Rhagada cygna* differ slightly in mean shell diameter (**Table 159**) but not in proportions.

The name *cygna* is taken from the nearby Cygnet Bay.

SUBFAMILY POSITION UNCERTAIN

The genus *Quistrachia* cannot be referred to the Camaeninae, Pleurodontinae or Sinumeloninae, the three presently defined Australian subfamilies (Solem 1992, 1993). While some individual features agree with one or another subfamily, *Quistrachia* not only lacks the diagnostic features, but shows an unusual pattern of reproductive structures that probably can be used to define a separate unit. In all probability, relatives will be found in the China-Solomon Island arc or Queensland. Currently we know too little about camaenids in these areas to delineate additional subfamilies.

Among the diagnostic features of *Quistrachia* in relation to other west coast taxa are the basal entry of the vas deferens into a well defined penis sheath and the lack of vas attachment to the sheath wall; the lack of a clearly defined epiphallus, much less an epiphallic caecum; absence of any vergic structure; very unusual main pilaster with its near-continuous variation between fused and bifurcated conditions; generally long vagina; variety of penis chamber wall sculpture and absence of any head wart.

There are resemblances to some of the drier zone Kimberley genera: most species of the genus *Cristilabrum* (Solem, 1981b) share the basal entry of the vas deferens into the penis sheath and the absence of a clearly defined epiphallus but they have a very different structural pattern inside the penis. The genus *Kimboraga* Iredale, 1933 (see Solem 1985: 818–845) has more similarity in penial structures but has different main pilasters, a mid-sheath entry of the vas deferens and very different shell features. It is not possible, at this time, to say whether these similarities are convergent or indicative of monophyly.

Rather than introduce a possibly redundant subfamily name, I choose to leave *Quistrachia* as unplaced.

Table 160: Range of variation in *Quistrachia* species.

Taxon	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
Quistrachia							
Q. warroorana	357	12.26 (9.2-15.8)	14.94 (11.9-18.8)	0.821 (0.720-0.977)	4⅜+ (3⅞-4⅞+)		
Q. lefroyi	591	15.86 (11.7-20.2)	18.69 (13.4-21.9)	0.849 (0.642-1.010)	4⅞ (4⅜-5⅝+)		
Q. species	7	12.80 (12.25-13.5)	17.13 (15.95-18.0)	0.749 (0.711-0.849)	5¼+ (5⅛–-5½+)		
Q. barrowensis	105	14.07 (10.9-20.6)	16.60 (13.75-22.75)	0.844 (0.750-0.980)	4⅞– (4⅜-5⅝+)		
Q. montebelloensis	84	12.31 (10.3-14.3)	15.13 (13.35-17.8)	0.813 (0.738-0.889)	4⅝ (4⅜–-4⅞–)	1.03 (0.8-1.4)	14.9 (11.5-20)
Q. legendrei	23	15.57 (11.95-18.5)	21.33 (18.0-24.25)	0.729 (0.665-0.784)	4⅜+ (4¼-4⅝)		
Q. herberti	46	10.73 (9.0-12.55)	16.84 (15.25-19.7)	0.637 (0.518-0.695)	4¾ (4⅛+-5⅛–)	2.06 (1.45-2.9)	8.36 (6.52-11.5)
Q. turneri	165	13.66 (10.0-15.65)	17.23 (13.25-18.95)	0.792 (0.716-0.870)	4⅜ (4⅛–-4⅝–)		
Q. leptogramma	54	15.09 (11.5-18.3)	17.50 (13.75-21.4)	0.862 (0.817-0.946)	4⅝+ (4¼–-5+)	1.30 (0.9-1.9)	14.0 (9.87-19.6)
Q. monogramma	662	10.21 (7.75-12.8)	17.03 (14.1-20.65)	0.599 (0.509-0.753)	4⅜ (3⅞–-4⅞–)	2.68 (1.65-3.9)	6.45 (4.39-10.4)

GENUS *QUISTRACHIA* IREDALE, 1939

Quistrachia Iredale, 1939, *Jour. Roy. Soc. Western Aust.*, **25:** 51–52 – type species *Trachia monogramma* Ancey, 1898 by original designation; Richardson 1985, *Tryonia*, **12:** 264 – check list citation; Solem 1985, *Rec. Western Aust. Mus., Suppl*, **20:** 846–857, plt. 84a–d, figs 213a–c, 214a–d, 215d–f, tables 83, 87 – review of *Quistrachia monogramma* (Ancey, 1898).

Shell small to large in size, variable within species, adult diameter 11.9–24.75 mm, whorls 3 7/8 to 5 5/8, coiling pattern looser in *Q. legendrei* sp. nov. and *Q. leptogramma*. Spire moderately (*Q. monogramma*) to very strongly (*Q. turneri* sp. nov.) elevated, most species globose, H/D ratios 0.509–1.010. Body whorl inflated in *lefroyi* (**Fig. 433e**) and *leptogramma* (**Fig. 447b**). Apical sculpture (**Plates 227–228**) of dense micropustules that may coalesce into radial ridgelets, spire and body whorl with pustules or ridgelets, some taxa with periostracal micro-ridgelets. Body whorl evenly rounded, except obstusely angulated in *Q. legendrei* sp. nov. (**Figs 442b, e**). Body whorl descending slightly in lower spired taxa, markedly in more globose species. Umbilicus a narrow lateral crack to moderately open (*Q. herberti* sp. nov., **Fig. 444f**, and *monogramma*; see Solem, 1985: 848, fig. 213c). Lip expansion moderate in most species, reduced in *Q. warroorana* sp. nov. Shell colour usually yellow-white, some species with a peripheral white zone bordered above by a light to medium red spiral band (*Q. warroorana* sp. nov., *Q. lefroyi* sp. nov., *Q. barrowensis* sp. nov., *Q. montebelloensis* sp. nov.), others with a yellow-brown spire suffusion that may extend onto the shell base (*Q. herberti* sp. nov., *Q. turneri* sp. nov.) or stop abruptly near the periphery (*Q. legendrei* sp. nov.), have a brown suffusion and weak peripheral red band (*Q. monogramma*), or have several red spiral bands of varying width (*Q. leptogramma*). Lip white, except for a pinkish tinge in some examples of *Q. turneri* sp. nov.

Specimens aestivate loose in litter (*Q. warroorana* sp. nov., *Q. lefroyi* sp. nov., *Q. herberti* sp. nov., *Q. leptogramma*, *Q. monogramma*) with a thin calcified epiphragm across the aperture, or seal to rocks or other shells with a mucoid ring (*Q. turneri* sp. nov.) or partially calcified ring (*Q. legendrei* sp. nov.). Situation unknown in *Q. barrowensis* sp. nov., *Q. montebelloensis*, and *Q.* species.

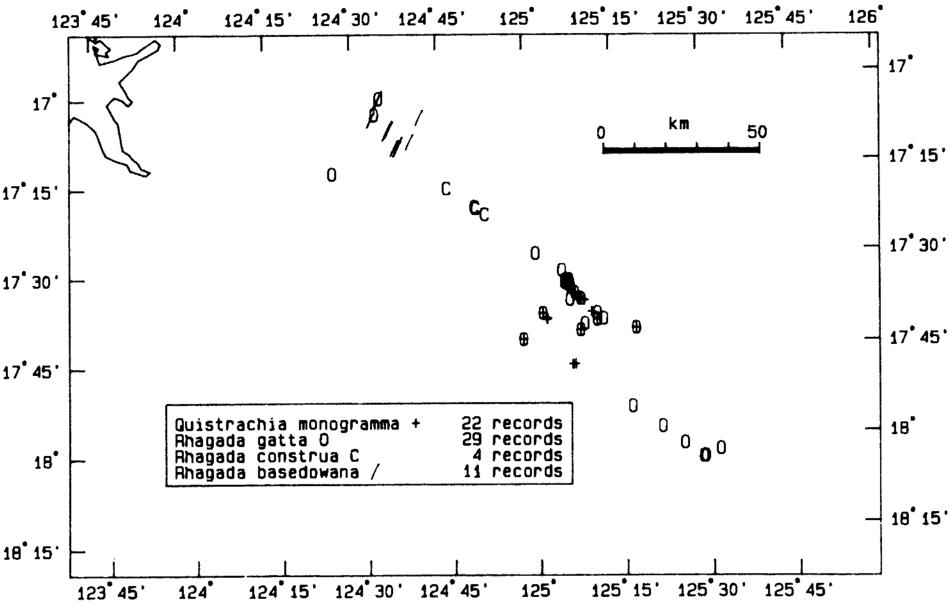
Genitalia (**Figs 434–439, 441, 443, 445–446, 448–450**) variable on a conservative pattern. Ovotestis (GG) not variable seasonally in southern taxa. Albumen gland (GG) enlarged in most Pilbara taxa. Prostate (DG) and uterus (UT) shortened in many species when albumen gland enlarged. Spermatheca (S) short to very short, head often expanded. Free oviduct (UV) short to medium and curved. Vagina (V) from short (*Q. herberti* sp. nov., **Fig. 445a**) to extremely long (some *Q. lefroyi* sp. nov., **Fig. 436a**). Vas deferens (VD) entering base of penis sheath at peni-oviducal angle, ascending free of wall to apex of penis sheath, where it reflexes, receives partial insertion of penial retractor muscle and enters expanded male channel through a pilaster or pore. Some species show an apical area of longitudinal pilasters that may serve an epiphallic function, others have the vas entering at the start of pustulose wall sculpture, presumably penis surfaces. Penis sheath (PS) thin-walled in most species, basal wall area thick in *Q. leptogramma* (**Figs 449a, 450**) and *Q. monogramma* (Solem 1985: 852, fig. 214b). Penis (P) varying from equal to (*Q. monogramma*) to four times (*Q. lefroyi* sp. nov., **Fig. 438b**) length of sheath. No verge or vergic papilla present. Main pilaster (PT) always present, but highly variable in length, degree of bifurcation or fusion, where fusion occurs. Penis chamber wall mainly densely pustulose, with a variety of pustule types. Basal portion of penis chamber with simple (*Q. lefroyi* sp. nov., **Fig. 438b**, *Q. legendrei* sp. nov., **Fig. 443b**, *Q. turneri* sp. nov., **Fig. 446b**) or corrugated (*Q. herberti* sp. nov., **Fig. 445b**) longitudinal pilasters usually present. Body colour yellow-white, except much darker in *Q. lefroyi* sp. nov.

Jaws (**Plates 229e, 230e–f, 233d, 234f, 236d**) with prominent vertical ribs, the number variable, usually reduced on outer margins. Central and early lateral teeth of radula (**Plates 229–236**) tend to have enlarged anterior flares and elevated cusp shaft angles (especially *Q. lefroyi* sp. nov., **Plate 230**, and *Q. barrowensis* sp. nov., **Plate 232a–b**) but otherwise the radular teeth are generalised in structure.

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

Comparative remarks

The pustulose shell apex and continuation of pustules on the spire (**Plates 227–228**), absence of any strong post-apical shell sculpture and open umbilicus or narrow lateral crack are the main shell features separating *Quistrachia* from species of *Rhagada*. Just south of Warroora Homestead south of the North West Cape, specimens of *Rhagada torulus* (**Figs 403a–e**) and *Quistrachia warroorana* sp. nov. (**Figs 433a–c**), for example, are essentially identical in appearance and were long confused in the field. While anatomically they are very different, I have not been able to devise a key couplet that would separate even slightly worn adult examples. *Plectorhagada scolythra* (**Figs 390d–f**) also is very similar.

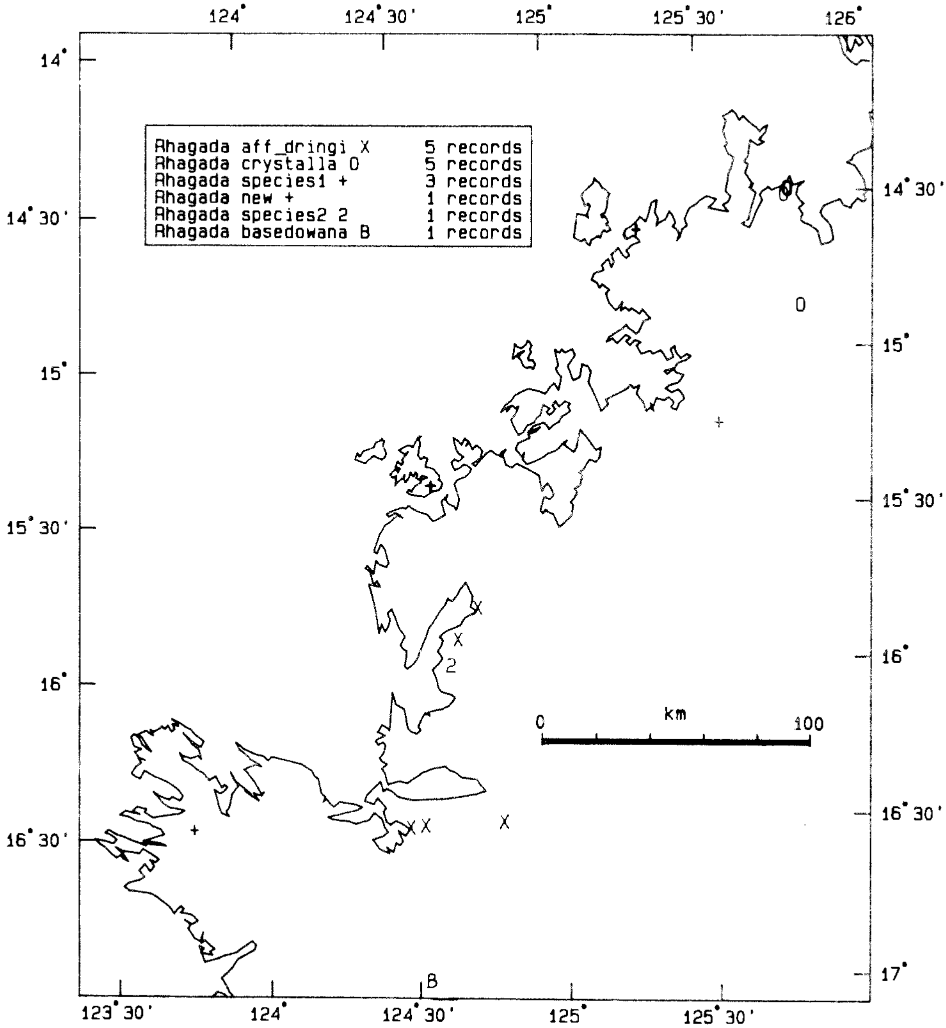


Map 42: Napier Range, S Kimberley records of *Quistrachia monogramma*, *Rhagada basedowana*, *R. construa* and *R. gatta*.

The male genital system of *Quistrachia* differs in many features from that of *Rhagada* and the west coast Sinumeloninae. The entry of the vas deferens into the penis sheath at the peni–oviducal angle, rather than apically; the complete absence of a verge or vergic papilla; the absence of even a trace of an epiphallic caecum and no clearly differentiated epiphallus; the unusual main pilaster that can be bifurcated or fused and the pustulose penis chamber wall sculpture are features limited to *Quistrachia* within the area of study.

Previous studies and nomenclature

Quistrachia leptogramma (Pfeiffer, 1846) had consistently been referred to *Rhagada* (see below) because of its spiral colour bands until Iredale (1939: 72–74) placed it,

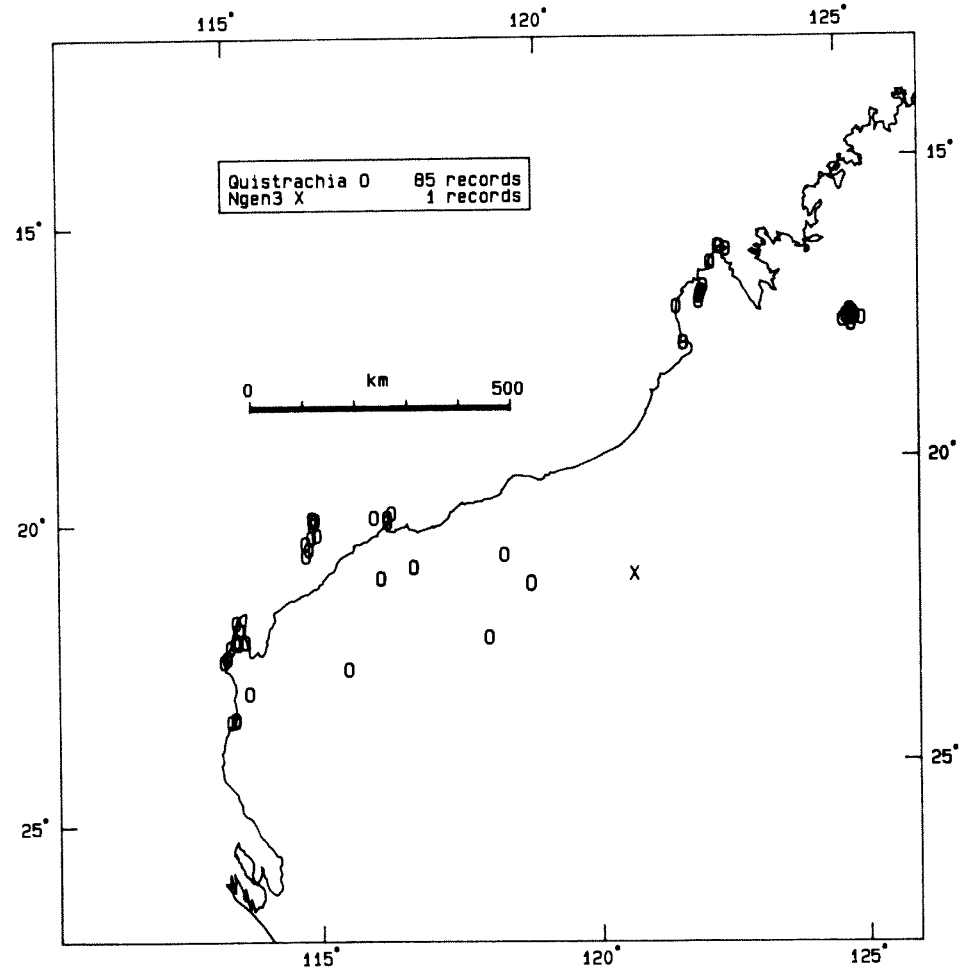


Map 43: Records of species belonging to *Rhagada* from the W Kimberley, WA.

with *Xanthomelon prudhoensis* (E. A. Smith, 1894), *X. obliquirugosa* (E. A. Smith, 1894) and *Quistrachia montebelloensis* (Preston, 1914), into the genus *Globorhagada* Iredale, 1933, which was based, essentially, on the somewhat inflated body whorls. The other previously-described species, *Quistrachia monogramma* (Ancey, 1898), had been placed in the Indonesian genus *Planispira* Beck, 1837 by Hedley (1915: 69), then into the new monotypic genus *Quistrachia* by Iredale (1939: 51–52). Richardson (1985: 264) gave a check list citation. Solem (1985: 846–857) reviewed the anatomy and shell variation in *Q. monogramma*.

Distribution and basic ecology

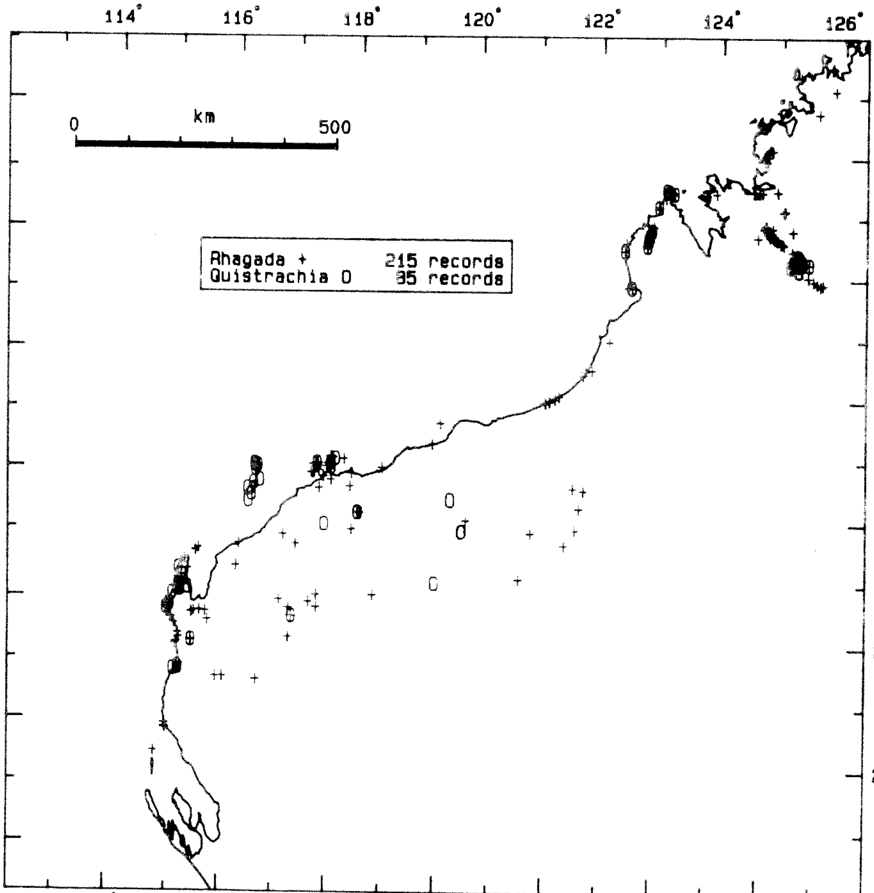
Quistrachia is currently known to occur between the Oscar Range W to Dampier Land and then S through the Pilbara and coastal areas to near Warroora Homestead south of North West Cape (**Maps 44, 46**).



Map 44: Records of new genus 3 and *Quistrachia* species in WA.

The pattern of distribution in WA is of isolated records for both populations and species, with many local disjunctions and few continuous ranges. If species records for *Rhagada* are compared with those for *Quistrachia* in the same region (**Map 45**), the former are more extensive and the gaps between species are much smaller. The pattern is equivalent to that seen for *Sinumelon* and *Pleuroxia* in other parts of Australia, where species of the latter genus have small ranges that are widely separated, whereas *Sinumelon* has a nearly continuous distribution.

None of the WA *Quistrachia* species overlaps geographically and, where disjunct records are available (*Q. warroorana* sp. nov., *Q. legendrei* sp. nov., *Q. herberti* sp. nov., *Q. turneri* sp. nov., **Map 46**), the separated populations do show significant shell differences. A sample from Glen Florrie Station (WA–417, **Figs 444a–c**, **Map 46**) undoubtedly represents a new species but is not named because of inadequate material. W. H. Butler, 24 April 1976, collected a dead example (WAM 6.87) at Marandoo



Map 45: Comparative ranges of *Rhagada* and *Quistrachia* in WA.

minesite, Mt Bruce, Hamersley Range National Park, Pilbara (22°35'S, 118°27'E) that appears to be a giant relative of *Q. turneri* sp. nov. This very worn shell has a height 17.5 mm, diameter 23.0 mm, H/D ratio 0.761, whorls 4 3/4+, umbilicus open narrowly but the lip is broken and measurement is not possible. It is the largest *Quistrachia* seen to date. Probably many additional colonies and species remain to be discovered.

Of the known species, only *Q. legendrei* sp. nov. and *Q. turneri* sp. nov. are found sealed to rocks or other shells. The remaining taxa are free sealers with thin calcified epiphragms.Patterns of shell variation

Patterns of shell variation

Size variation (**Table 160**) is considerably less than in *Rhagada* (**Table 151**) from the same regions. The reason for this is unknown. Shape variation appears sporadic, rather than linear. The inflated body whorls of *Q. leptogramma* and *Q. lefroyi* sp. nov., looser whorl coiling in *Q. legendrei* sp. nov. and *Q. leptogramma*, various experiments in spiral banding and changes in shell sculpture do not show clear geographic trends. Lip expansion is less in the species of the Cape Range area but highly variable in the Pilbara taxa.

Patterns of anatomical variation

Limited data on *Quistrachia warroorana* sp. nov. (**Fig. 435b**) and *Q. leptogramma* (**Fig. 448c**) suggest that maturation follows the pattern found in Kimberley genera by Solem & Christensen (1984), with the male organs reaching functional size before the female organs. The S Kimberley *Q. monogramma* shows the seasonal pattern associated with a predictable wet season (see Solem, 1985: 854, 857). Dissection of taxa from the Pilbara and Cape Range area detected no seasonality of genital organ size consistent with the lack of a dependable wet season situation.

Although occupying the same geographic zone as *Rhagada* (**Maps 36, 44–45**), *Quistrachia* does not show the same linear pattern of genital organ change found in the former genus. The *Rhagada* pattern of a consistent albumen gland (GG) increase and a size reduction in verge (PV) and penis complex from the Kimberley to Carnarvon is not matched in *Quistrachia*. The largest penes and vaginas are found in the more southern taxa – *Q. warroorana* sp. nov. (**Figs 434b, 435a**) from south of the Cape Range, *Q. lefroyi* sp. nov. (**Figs 436a, 437a–b, 438b**) from the Cape Range area, and *Q. barrowensis* sp. nov. (**Figs 441a–c**) from Barrow Island, with the Dampier to Kimberley taxa, living in areas with greater rainfall having smaller terminal genitalia. The reasons for this are unknown.

Although there is essential linearity of species from N to S, there is no consistent pattern of main pilaster (PT) or penis chamber wall sculpture. The shortest bifurcated main pilaster is found in *Q. herberti* sp. nov. (**Fig. 445b**) from the inland Pilbara, and the longest in *Q. warroorana* sp. nov. (**Fig. 434b**) from the Scrubby Range; the shortest fused main pilaster in *Q. turneri* sp. nov. (**Fig. 446b**) from the inland Pilbara, and the longest in *Q. lefroyi* sp. nov. (**Fig. 438b**) from the Cape Range area.

The albumen gland (GG) is very large in *Q. barrowensis* sp. nov. (**Fig. 441a**) but not in *Q. legendrei* sp. nov. (**Fig. 443a**) and is of *intermedia*te size in the more southern species.

It seems probable that *Quistrachia* is better adapted than *Rhagada* to life under limited and irregular moisture conditions, since the morphological changes are much less dramatic and extensive.

The following highly artificial key will work for even small samples of recently-dead adults. Worn examples and juveniles cannot be keyed out. The extensive size differences among colonies and colour variations noted in the species accounts also may result in errors. When in doubt, refer to geographical location, as none of the species are sympatric. Do not be surprised if you have found a new species!

KEY TO THE WESTERN AUSTRALIAN SPECIES OF *QUISTRACHIA*

1. Umbilicus open, measurable (**Figs 440f, 444f, 447c**) 2
   Umbilicus a narrow lateral slit or not measurable in most examples 5

2. Lip thin and moderately expanded (**Figs 444d–f**) 3
   Lip conspicuously thickened (**Figs 440d–f**); Montebello Islands .... *Quistrachia montebelloensis* (Preston, 1914) (p. 1827)

3. One or more red spiral colour bands; shell surface smooth; Dampier Land or S Kimberley 4
   No spiral colour band; spire with radial ridgelets; Pilbara .... *Quistrachia herberti* sp. nov. (p. 1835)

4. Shell light brown; one spiral colour band; body whorl not inflated; S Kimberley .... *Quistrachia monogramma* (Ancey, 1898)
   Shell yellow-white; several red spiral colour bands; body whorl inflated (**Figs 447a–c**) .... *Quistrachia leptogramma* (Pfeiffer, 1846) (p. 1844)

5. Shell colour brown, lighter on base; no spiral colour bands or zones 6
   Shell with peripheral colour zone or zones 7

6. Dampier area; body whorl obtusely angulated (**Figs 442b, e**) .... *Quistrachia legendrei* sp. nov. (p. 1829)
   Vicinity of Turner & Yule Rivers, Pilbara; body whorl evenly rounded (**Fig. 444h**) .... *Quistrachia turneri* sp. nov. (p. 1840)

7. Body whorl not inflated (**Figs 433b, 440b, 444b**) 8
   Body whorl inflated (**Fig. 443e**; Cape Range area .... *Quistrachia lefroyi* sp. nov. (p. 1807)

8. Lip well expanded (**Figs 440a–c, 444a–c**) 9
   Lip narrow; spiral colour band bright red; shell white; Warroora to Scrubby Range .... *Quistrachia warroorana* sp. nov. (p. 1799)

9. Shape globose (**Fig. 440b**); colour bands faint; Barrow Island .... *Quistrachia barrowensis* sp. nov. (p. 1821)
   Spire less elevated (**Fig. 444b**); Glen Florrie Station, Pilbara .... *Quistrachia* species (p. 1820)

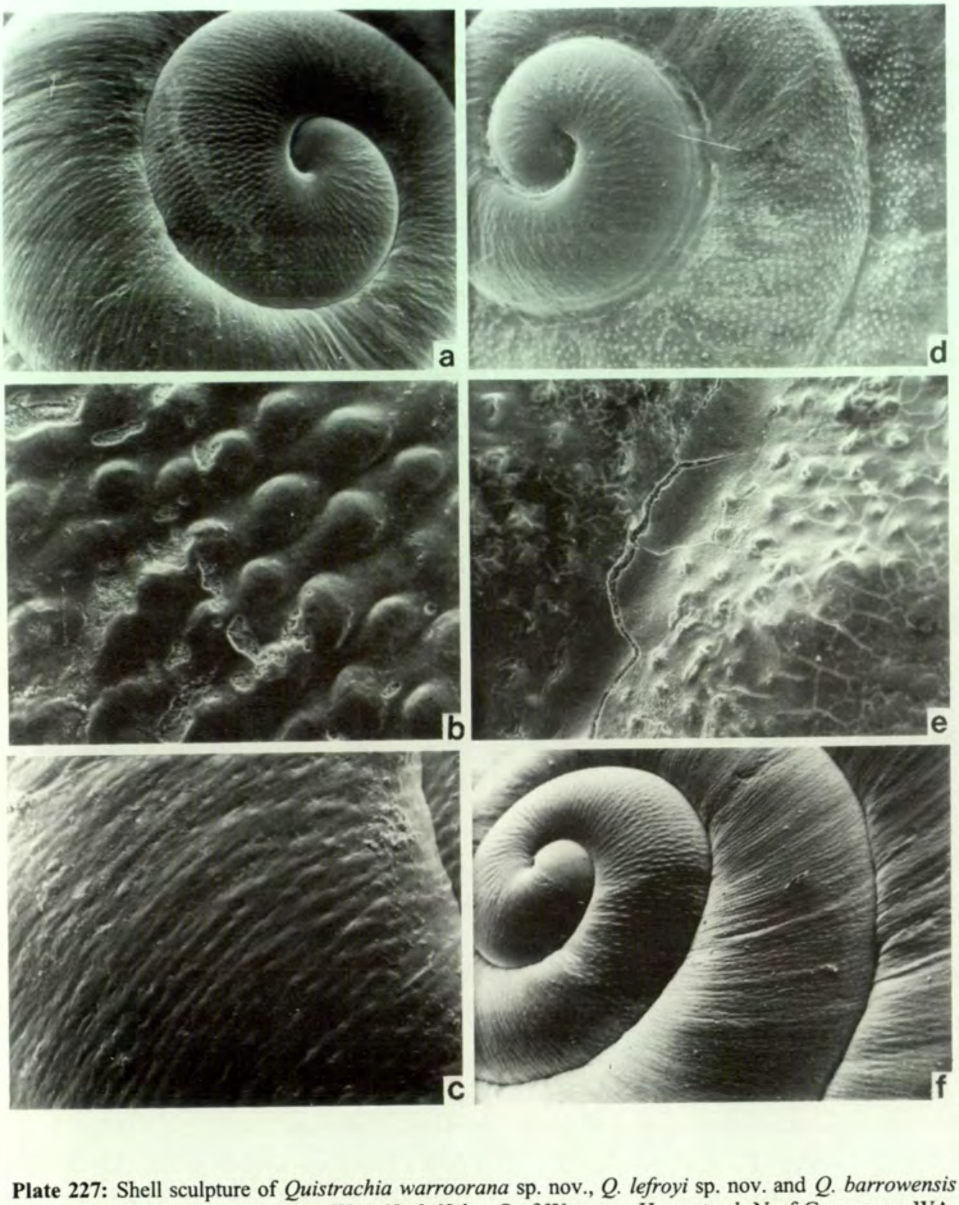


Plate 227: Shell sculpture of *Quistrachia warroorana* sp. nov., *Q. lefroyi* sp. nov. and *Q. barrowensis* sp. nov.: (a–c) *Q. warroorana*. WA–48, 9.68 km S of Warroora Homestead, N of Carnarvon, WA. FMNH 182362. a is apex and spire at 19.5X. b is detail of apical sculpture at 190X. c is microsculpture on early spire at 48X; (d–e) *Q. lefroyi*. near Goat Cave, near Central Hill, Cape Range, WA. WAM 1541.70. d is apex and spire at 18.3X; e is microsculpture on lower spire at 85X; (f) *Q. barrowensis*. South claypan, Barrow Island, WA. WAM 364.75. f is apex and spire at 18.9X.

QUISTRACHIA WARROORANA SP. NOV.

(Plates 227a–c, 229a–e; Figs 433a–c, 434a–b, 435a–b; Maps 30–31, 46)

Comparative remarks

Quistrachia warroorana sp. nov., from just S of Warroora Homestead and the Scrubby Range, S of the Cape Range (**Map 46**), is small in size (mean diameter 14.94 mm), globose (**Fig. 433b**, mean H/D ratio 0.821), with a low whorl count (mean 4 3/8+), the lip only slightly expanded and umbilicus with either a narrow lateral crack (**Fig. 433c**) or closed but not with a broadly expanded callus. Body whorl evenly rounded. Shell with a narrow peripheral red spiral colour band extending to shell aperture, sometimes bordered below by a white zone, never with a subsutural red spiral colour band or accessory spiral bands. Shell apex (**Plate 227a–b**) densely pustulose, spire and body whorl (**Plate 227c**) with elongated pustulations. The most similar species is *Rhagada torulus*, which ranges from Shark Bay N to Bulbarli Well, Warroora (**Map 30**). It is a little smaller in size (mean diameter 14.29 mm), identical in shape (**Fig. 403b**, mean H/D ratio 0.823) but has an increased whorl count (mean 5 1/4). Fresh examples of *R. torulus* can be recognised easily by the essentially smooth shell apex (**Plate 205e**), presence of a subsutural (**Figs 403a–e**) red spiral colour band and/or accessory spiral bands, closure of the umbilicus by a broad callus (**Fig. 403c**) and sometimes narrowing of the aperture. *Plectorhagada scolythra*, from the Scrubby and Rough Ranges (**Map 30**), has crenulated ridging on the upper spire and the colouration of the next species. *Quistrachia lefroyi* sp. nov., from the Cape Range and surrounding plains (**Map 32**), normally is much larger (mean diameter 18.69 mm), with increased whorl count (mean 4 7/8), has a peripheral white zone flanked above and below by reddish bands of varying width (**Figs 433d–f**), an inflated body whorl (**Fig. 433e**) and denser micro-pustules (**Plate 227d–e**).

Anatomically (**Figs 434a–b, 435a–b**), *Q. warroorana* has the vagina (V) about 1.5 times the length of the penis sheath (PS), the penis (P) is twice the length of the penis sheath, the main pilaster (PT) extends bifurcated the entire length of the penis and the penis chamber wall has spirally oriented, elongated fine pustules. *Q. lefroyi* sp. nov. (**Figs 436–439**) is immediately separable by the usual extreme elongation of both the vagina (V) and penis (P), fusion of the main pilaster (PT), penis chamber wall sculpture of simple rounded pustules and elongation of the basal section of the penis with simple to corrugated pilasters. No other known *Quistrachia* has the main pilaster so elongated and bifurcated for its entire length.

Holotype

WAM 769.87, WA–49, slope at bore, 3.4 miles S of Warroora Homestead, N of Carnarvon, Western Australia. 23°31'S, 113°45'E. Collected 4 February 1974 by A. Solem and L. Price. Height of shell 12.2 mm, diameter 14.7 mm, H/D ratio 0.830, whorls 4 1/2–, umbilicus a barely visible lateral crack.

Paratopotypes

WAM 839.87, WAM 840.87, SAM D18189–90, AM C.200,748, MV F60065, QM 49967, FMNH 182352, FMNH 182589, 27 LA, 22 DA, 12 LJ, 4 DJ.

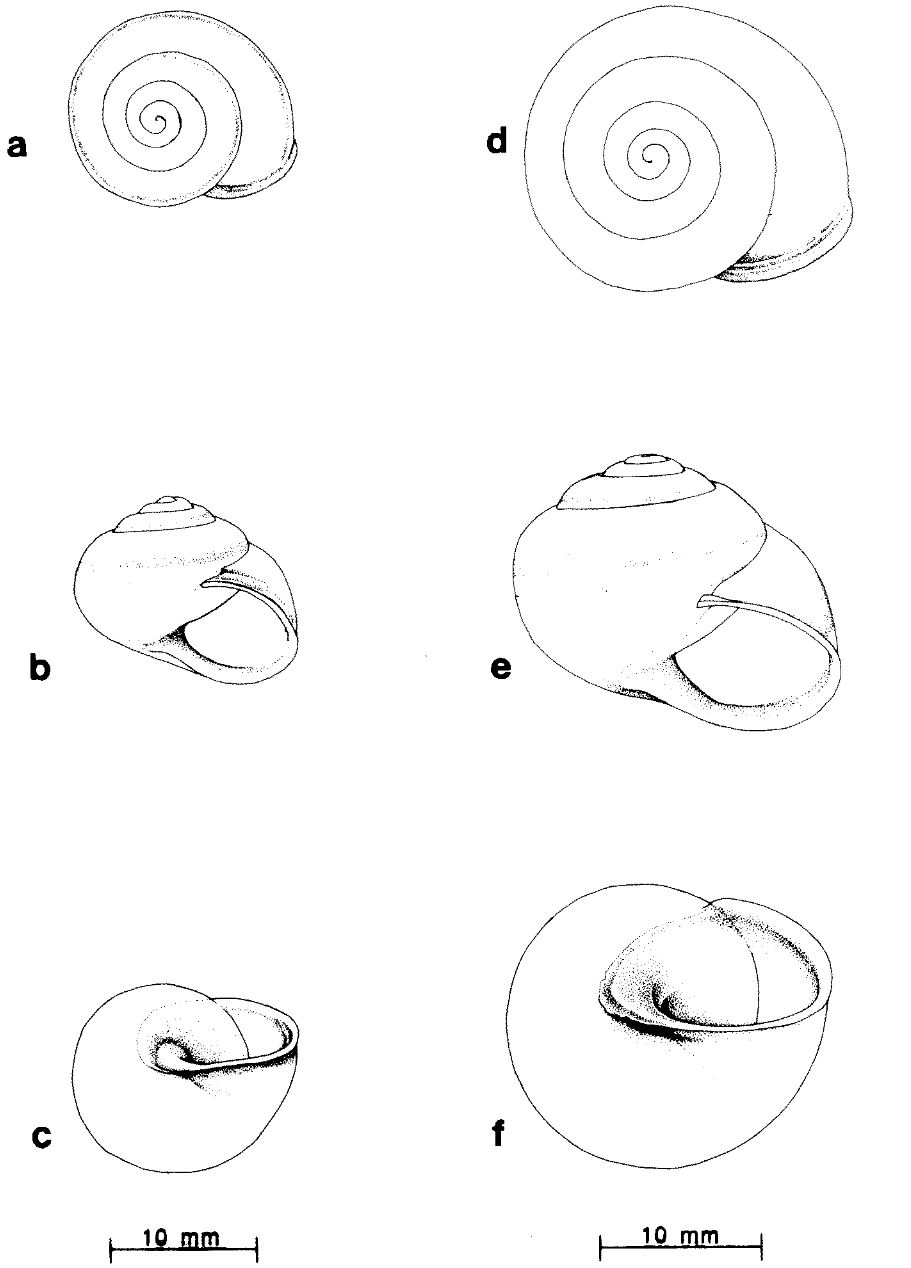


Fig. 433: Shells of *Quistrachia warroorana* sp. nov. and *Q. lefroyi* sp. nov.: (a–c) Holotype of *Q. warroorana*. WAM 769.87. WA–49, 3.4 miles S of Warroora Homestead, slope near coast at bore, N of Carnarvon, WA; (d–f) Holotype of *Q. lefroyi*. WAM 772.87. Near Goat Cave, near Central Hill, Cape Range, WA. Scale line equals 10 mm. Drawings by Linnea Lahlum.

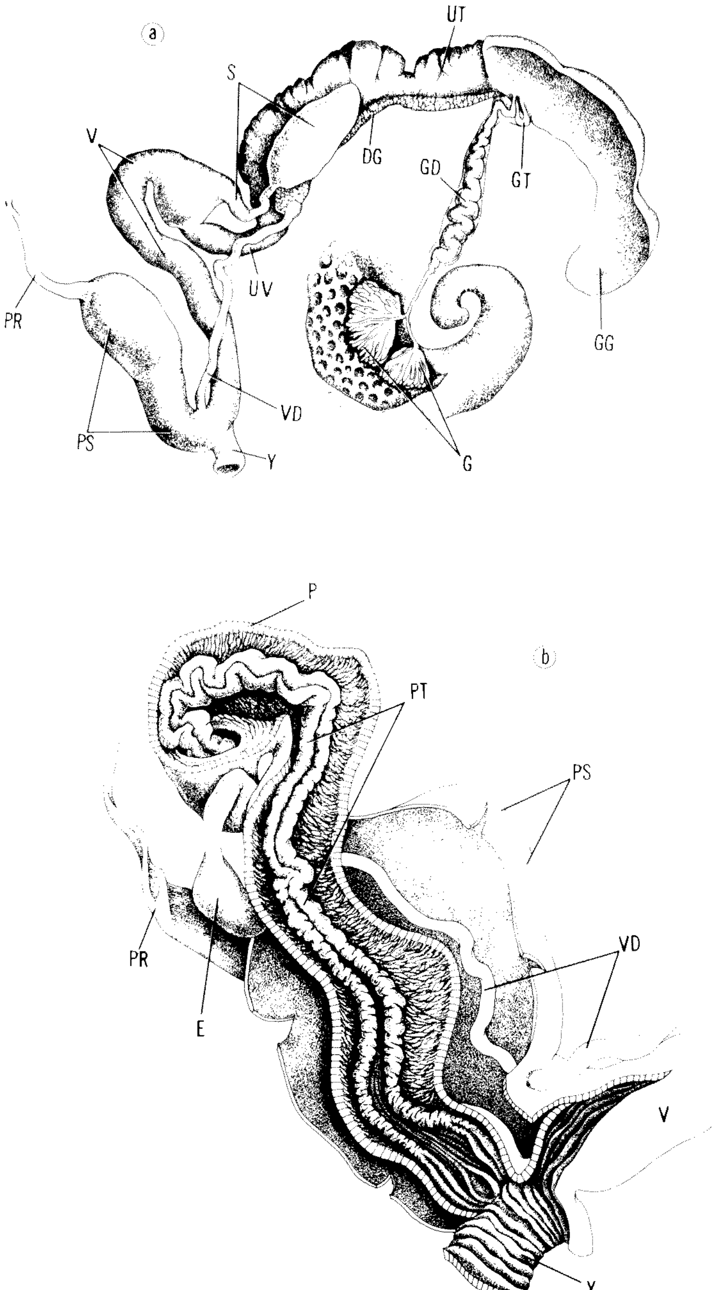


Fig. 434: Genitalia of *Quistrachia warroorana* sp. nov.: WA–51, Scrubby Range, E of Cardabia Homestead, S of Exmouth Gulf, WA. 5 February 1974. FMNH 182547, Dissection C: (a) whole genitalia; (b) interior of penis. Scale lines as marked. Drawings by Elizabeth A. Liebman.

Paratypes

WESTERN AUSTRALIA: Warroora Station (WA–47, 4.6 miles S of homestead, in litter under bushes near coast, WAM 846.87, WAM 947.87, SAM D18193, AM C.200,749, QM 46931, MV F60060, FMNH 182385–6, FMNH 182530, FMNH 182544, 9 LA, 34 DA, 9 LJ, 6 DJ; WA–47a, 4.6 miles S of homestead, slightly inland, WAM 845.87, SAM D18192, AM C.200,750, QM 52982, MV F.60005, FMNH 182404, FMNH 182531, 21 LA, 8 DA, 13 LJ; WA–47b, salt bush by track and dune crest 4.6 miles S of Homestead, WAM 843.87, WAM 844.87, SAM D18191, AM C.200,751, QM 46930, MV F59499, FMNH 182387, FMNH 182415, FMNH 182532, 11 LA, 46 DA, 3 LJ, 25 DJ); WA–48, under bushes 6 miles S of Homestead, WAM 841.87, WAM 842.87, SAM D18190, AM C.200,752, FMNH 182362, FMNH 182413, FMNH 182588, 10 LA, 23 DA, 4 LJ, 6 DJ; WA–169, coastal area 7.3 km S of Homestead, WAM 837.87, WAM 838.87, WAM 863.87, SAM D18188, SAM D18202, AM C.200,753, MV F59444, QM52983, FMNH 199845–6, FMNH 199662, FMNH 199727, FMNH 199874, 75 LA, 8 DA, many LJ, 2 DJ; 0.6 km S of Bulbarli Well (WA–1069, FMNH 221718, 12 LA); WA–954, red soil-limestone ridges near coast, 7.2 km S of homestead, WAM 864.87, SAM D18203, AM, FMNH 212473–4, 19 LA, 24 DA, 11 LJ, 3 DJ; 0.9 km N of Bulbarli Well (WA–1071, FMNH 221720, 11 LA); Scrubby Range, SE of Cape Range. (WA–51, 12.8 miles E of Cardabia Homestead turnoff on Exmouth road, WAM 836.87, SAM D18187, AM C.700,755, QM, MV, FMNH 182348, FMNH 182547, 16 LA, 3 DA, many LJ, 5 DJ).

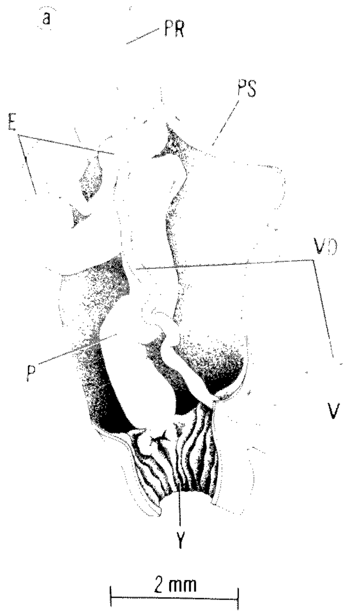
Range

Quistrachia warroorana sp. nov. has a disjunct range (**Map 30**) S of Cape Range. It has been taken once in the Scrubby Range (WA–51, 23°07'S, 114°03'E) and then at a few coastal scrub localities from 3.4 to 6 miles S of Warroora Homestead (WA–47, WA–48, WA–49, WA–169, WA–954, 23°31–33'S, 113°45'E), about 55 km SSW from the Scrubby Range. Numerous collections of *Strepsitaurus cardabius*, *Rhagada globosa*, *R. convicta* and *R. capensis* have been made in intervening localities, so that this distributional gap probably is real and not an artifact caused by lack of collecting.

Diagnosis

Shell small, adult diameter 11.9–18.8 mm (mean 14.94 mm), with 3 7/8 to 4 7/8+ (mean 4 3/8+) normally coiled whorls. Apex and spire strongly and evenly elevated (**Fig. 227b**), shell height 9.2–15.8 mm (mean 12.26 mm), H/D ratio 0.720–0.977 (mean 0.821). Body whorl evenly rounded. Shell apex (**Plate 227a–c**) densely pustulose, with pustules continuing onto spire and body whorl. Umbilicus (**Fig. 433c**) either a very narrow lateral crack or closed by lip reflection, never with a broadly reflected callus. Body whorl descending slightly behind lip, which is narrowly expanded and thin. A red peripheral colour band usually bordered below by a narrow white zone, accessory bands never present. Based on 357 measured adults.

Genitalia (**Figs. 434a–b, 435a–b**) with albumen gland (GG) of adult equalling length of prostate-uterus, spermatheca (S) short, base expanded. Free oviduct (UV) long, vagina (V) much longer than penis sheath (PS). Penis (P) about twice length of sheath. Main pilaster (PT) extends entire length of penis, bifurcated, blending basally into short section of longitudinal pilasters. Wall of penis chamber with spirally oriented, elongated pustules.



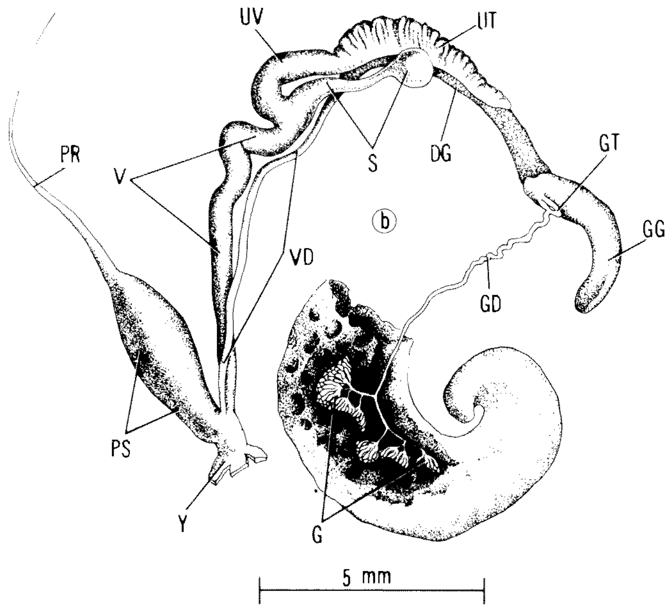


Fig. 435: Genitalia of *Quistrachia warroorana* sp. nov.: WA–51, Scrubby Range, E of Cardabia Homestead, S of Exmouth Gulf, WA. 5 February 1974. FMNH 182547: (a) open penis sheath, Dissection C; (b) whole genitalia of subadult, Dissection E. Scale lines as marked. Drawings by Elizabeth A. Liebman.

Table 161: Local variation in *Quistrachia warroorana.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
WA-47, FMNH 182386	34D	12.19±0.087 (10.8-13.2)	15.35±0.108 (14.1-16.6)	0.794±0.004 (0.720-0.850)	$4\frac{3}{8}$ ($3\frac{7}{8}$-$4\frac{1}{2}$)
WA-47, FMNH 182530	8L	12.56±0.207 (11.9-13.75)	14.71±0.155 (14.15-15.2)	0.853±0.009 (0.828-0.905)	$4\frac{1}{2}$– ($4\frac{7}{8}$–-$4\frac{5}{8}$+)
WA-47a, FMNH 182531	21L	12.72±0.127 (11.7-13.85)	15.05±0.190 (13.65-17.0)	0.847±0.010 (0.776-0.977)	$4\frac{1}{2}$+ ($4\frac{3}{8}$+-$4\frac{3}{4}$+)
WA-47a, FMNH 182404	8D	12.96±0.256 (12.2-14.0)	15.80±0.297 (14.5-17.3)	0.821±0.010 (0.790-0.880)	$4\frac{1}{2}$ ($4\frac{3}{8}$-$4\frac{1}{2}$)
WA-47b, FMNH 182415	42D	11.85±0.085 (10.8-13.0)	14.96±0.097 (14.1-16.2)	0.793±0.005 (0.750-0.890)	$4\frac{3}{8}$ ($4\frac{1}{4}$-$4\frac{1}{2}$)
WA-47b, FMNH 182532	11D	11.27±0.190 (10.2-12.3)	14.15±0.200 (12.9-15.0)	0.797±0.010 (0.760-0.854)	$4\frac{1}{4}$+ ($4\frac{1}{8}$-$4\frac{1}{2}$)
WA-48, FMNH 182362	23D	12.18±0.156 (11.0-13.7)	14.96±0.133 (14.0-16.4)	0.814±0.007 (0.740-0.860)	$4\frac{3}{8}$ ($4\frac{1}{8}$-$4\frac{1}{2}$)
WA-48 FMNH 182588	9L	11.79±0.298 (10.9-13.2)	14.68±0.292 (13.7-16.6)	0.803±0.010 (0.770-0.850)	$4\frac{1}{4}$+ ($4\frac{1}{8}$-$4\frac{1}{2}$)
WA-169, FMNH 199874	15L	12.31±0.112 (11.65-13.05)	14.86±0.180 (13.7-16.1)	0.829±0.008 (0.770-0.883)	$4\frac{3}{8}$+ ($4\frac{1}{8}$+-$4\frac{1}{2}$+)

Table 161: Local variation in *Quistrachia warroorana* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
WA-169, FMNH 199727	28L	11.06±0.118 (9.2-12.3)	13.23±0.100 (11.9-14.35)	0.836±0.007 (0.773-0.903)	$4\frac{3}{8}$ ($4\frac{1}{8}$+-$4\frac{5}{8}$+)
WA-169, FMNH 199845	8D	12.75±0.194 (11.7-13.55)	15.29±0.171 (14.7-16.05)	0.834±0.009 (0.795-0.859)	$4\frac{1}{2}$− ($4\frac{1}{4}$+-$4\frac{5}{8}$−)
WA-169, FMNH 199846	14L	12.49±0.128 (11.8-13.35)	15.06±0.103 (14.5-15.55)	0.829±0.008 (0.781-0.896)	$4\frac{3}{8}$ ($4\frac{3}{8}$−-$4\frac{1}{2}$+)
WA-954, FMNH 212474	24D	13.06±0.162 (11.4-14.8)	15.70±0.134 (14.85-17.15)	0.831±0.008 (0.761-0.920)	$4\frac{1}{2}$+ ($4\frac{1}{4}$+-$4\frac{7}{8}$+)
WA-954, FMNH 212473	19L	12.41±0.110 (11.65-13.15)	14.98±0.120 (14.1-15.85)	0.829±0.003 (0.907-0.853)	$4\frac{1}{2}$− ($4\frac{3}{8}$−-$4\frac{5}{8}$+)
WA-51, FMNH 182547	16L	13.85±0.156 (13.1-15.3)	15.69±0.158 (14.4-16.75)	0.883±0.008 (0.818-0.952)	$4\frac{1}{2}$ ($4\frac{1}{4}$-$4\frac{3}{4}$−)

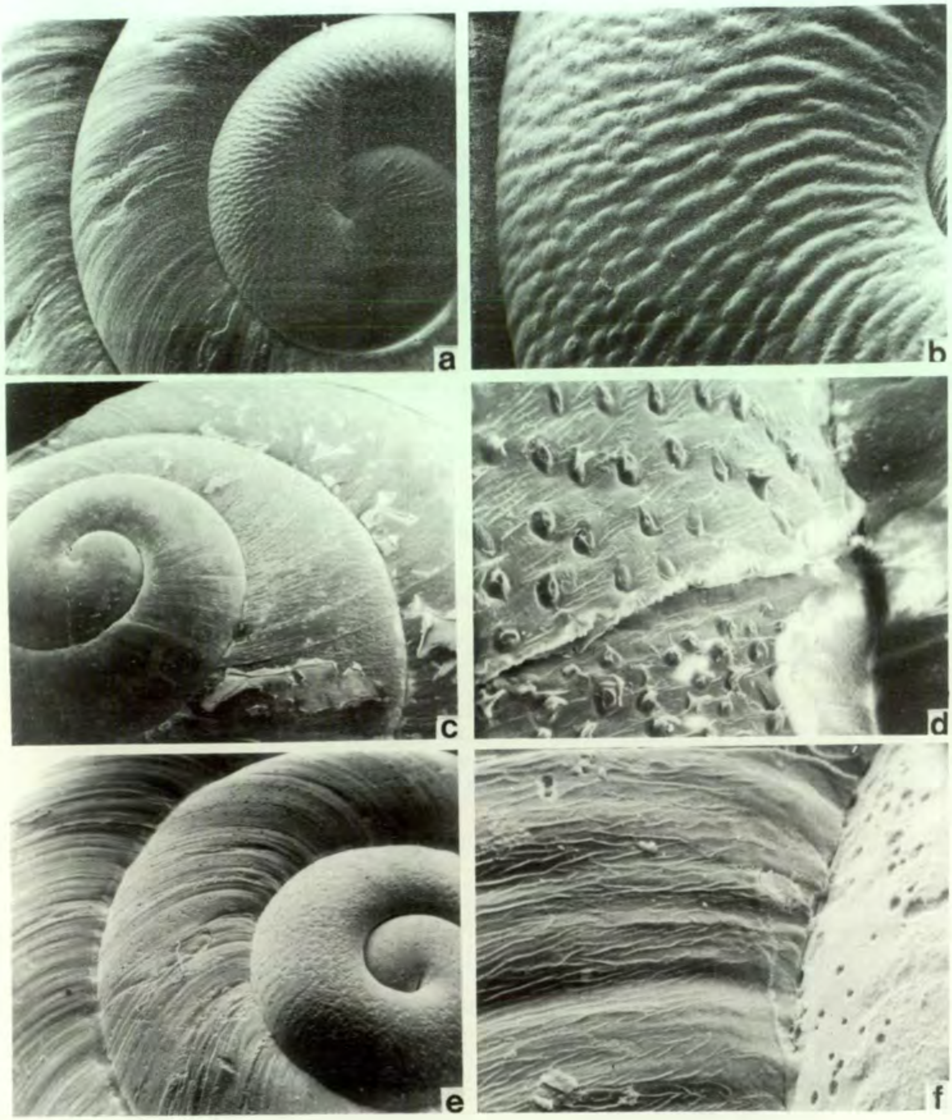


Plate 228: Shell sculpture of *Quistrachia montebelloensis* (Preston, 1914), *Q. legendrei* sp. nov. and *Q. herberti* sp. nov.: (a–b) *Q. montebelloensis*. Trimouille Island, Montebello Islands, WA. WAM 266.74. a is apex and spire at 19.9X. b is detail of apex at 49X; (c–d) *Q. legendrei*. Legendre Island, Dampier Archipelago, WA. WAM 338.74. c is apex and spire at 14.2X. d is micro-sculpture on mid-spire at a repaired break at 145X; (e–f) *Q. herberti*. WA–182, SW corner of Mt Herbert, Chichester Range, WA. FMNH 199908. e is apex and spire at 17.1X. f is micro-sculpture on early spire at 175X.

Central and early lateral teeth of radula (**Plate 229a, c**) with prominent anterior flare and ectocone, normal cusp shaft angle, bluntly rounded and slightly curved cusp tip. Lateromarginal transition (**Plate 229b**) and outer marginals (**Plate 229d**) typical. Jaw (**Plate 229e**) with narrow, prominent vertical ribs over most of surface.

Discussion

The Scrubby Range examples of *Quistrachia warroorana* are slightly larger and distinctly higher-spired (**Table 161**) than are the populations from Warroora Station. The latter samples were taken from a variety of habitats but showed only minor size and shape variation. Material weathered from a coastal dune (WA–47b, FMNH 182415) did have a slightly lower spire but did not differ significantly in diameter or whorl count.

No anatomical differences were found between the Warroora and Scrubby Range populations.

In general, specimens of *Quistrachia warroorana* are found associated with red soil and limestone, while those of *Rhagada torulus* live in sandy soil areas. The shells are extremely similar in features visible to the naked eye and were continually confused in the field. Worn examples would be essentially impossible to separate.

The name *warroorana* is in token appreciation for access and hospitality extended by residents of Warroora Station during my several collecting stops.

QUISTRACHIA LEFROYI SP. NOV.

(Plates 227d–e, 230a–f, 231a–c; Figs 433d–f, 436a–b, 437a–b, 438a–b, 439a–c; Maps 32, 46)

Comparative remarks

Quistrachia lefroyi sp. nov., which ranges from Norwegian Bay to the N tip of the Cape Range (**Map 32**), has a medium-sized to large shell (mean diameter 18.69 mm), is globose in shape (**Fig.** 433e, mean H/D ratio 0.849), with an increased whorl count (mean 4 7/8), very narrowly expanded and thin lip and umbilicus (**Fig. 433f**) normally a narrow lateral crack, never with a broadly expanded callus. Body whorl evenly rounded. Shell with a narrow peripheral white spiral zone, generally with a narrow red band above and below, sometimes with lower band reduced or missing, never with accessory spiral bands. Shell apex and early spire densely pustulose (**Plate 227d–e**). The most similar species is *Plectorhagada scolythra*, from the Rough Range and the Scrubby Range (**Map 30**), which is nearly identical in size and shape (mean diameter 18.06 mm, **Fig. 390e**, mean H/D ratio 0.847, mean whorl count 4 5/8+) and has the same colour pattern but it differs obviously in the presence of crenulated ridging on at least the upper spire (**Plate 192a, c**) and in its anatomy (**Figs 393a–b**). *Q. warroorana*, from S of Warroora Homestead to the Scrubby Range (**Map 30**), is smaller (mean diameter 14.94 mm), has a less inflated body whorl (**Fig. 433b**), reduced whorl count (mean 4 3/8+) and only a single red spiral band. *Q. barrowensis* sp. nov., from Barrow Island (**Map 46**) and *Q. montebelloensis* (Preston, 1914) from the Montebello Islands (**Map 46**) have less inflated body whorls, reduced colouration, a usually more open umbilical crack (**Figs 440a–f**) and many anatomical differences. Anatomically (**Figs**

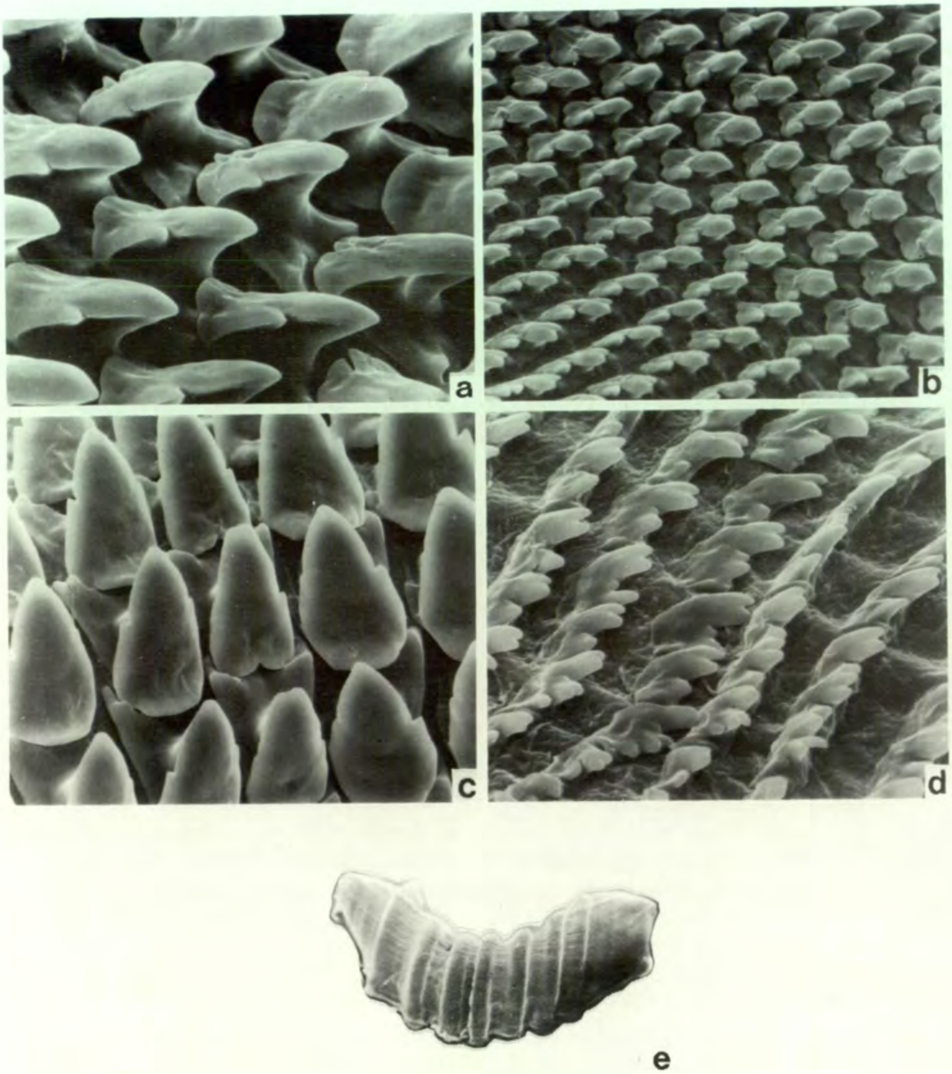


Plate 229: Radular teeth and jaw of *Quistrachia warroorana* sp. nov.: (a–d) WA–51, Scrubby Range, 12.8 miles E of Exmouth road from Cardabia Station turnoff, WA. 5 February 1974. FMNH 182547, Dissection E. a is central and laterals at 730X. b is latero-marginal transition at 730X. c is top view of central and laterals at 650X. d is outer marginals at 730X; (e) WA–49, slope at bore, 5.48 km S of Warroora Homestead, N of Carnarvon, WA. 4 February 1974. FMNH 182589, Dissection A. e is jaw at 37X.

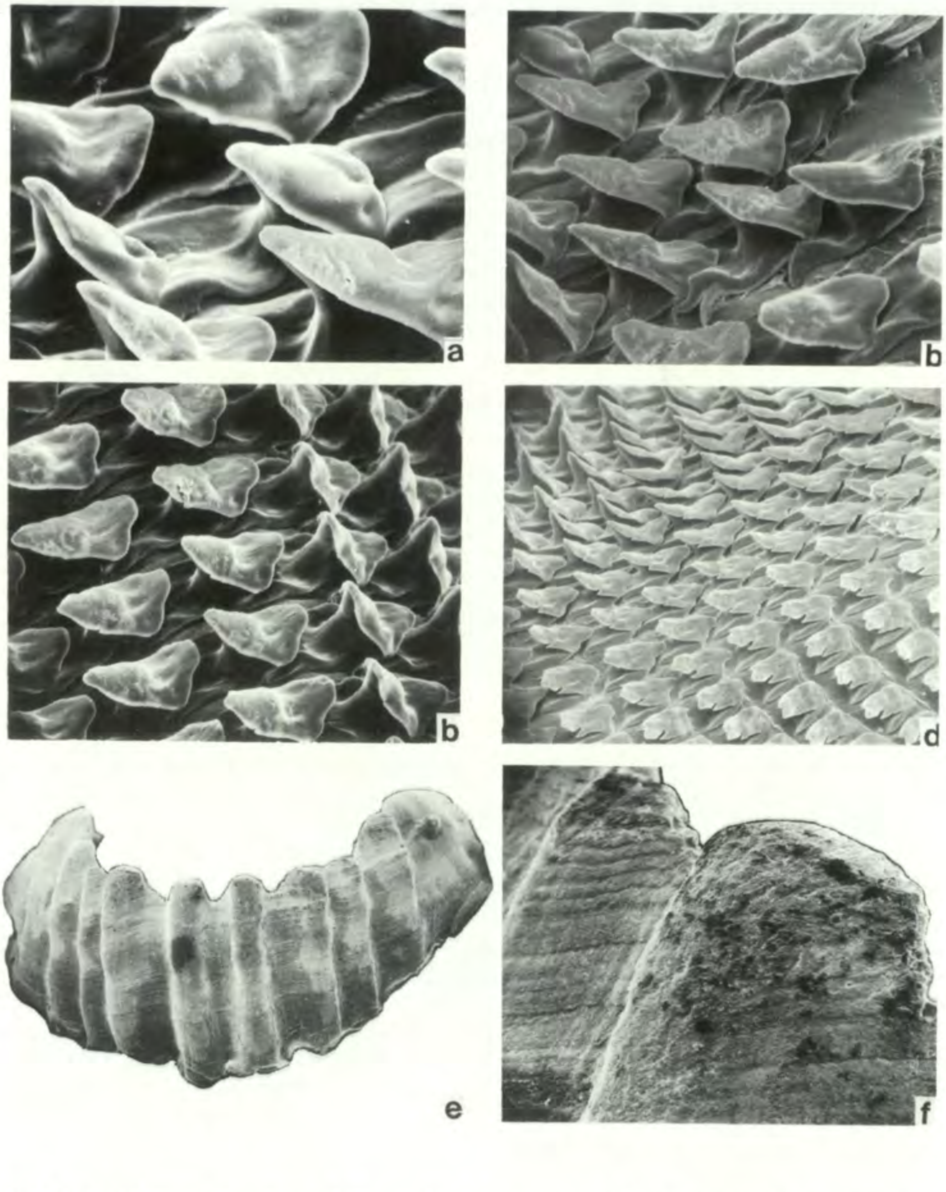


Plate 230: Radular teeth and jaw of *Quistrachia lefroyi* sp. nov.: Goat Cave, near Central Hill, Cape Range, North West Cape, WA. June and July 1964. FMNH 171624, Dissection A: (a) central and first laterals at 1000X; (b) early laterals at 610X; (c) mid-laterals at 470X; (d) lateromarginal transition at 305X; (e) jaw at 53X; (f) worn spot on jaw rib top at 365X.

436–439), *Q. lefroyi* is quite variable in organ lengths, with vagina (V) and penis (P) ranging from equal to four times length of penis sheath (PS) but populations agree in total fusion of the main pilaster (PT) that extends the entire penis length, the pustulose upper penis chamber wall and elongated simple to corrugated pilasters on basal chamber wall. *Q. warroorana* (**Figs 434–435**) differs most obviously in having the main pilaster bifurcated for its entire length and the penis chamber wall with spirally oriented, minute elongated pustules. *Q. barrowensis* (**Figs 441a–c**) has the basal part of the main pilaster bifurcated, a very long penis and vagina and the chamber wall has longitudinal pustules and secondary pilasters.

Holotype

WAM 772.87, near Goat Cave, Central Hill, Cape Range, Western Australia. *ca.* 22°15'50"S, 113°56'20"E. Collected July and August 1964 by Priscilla and William Turnbull. Height of shell 18.0 mm, diameter 20.6 mm, H/D ratio 0.874, whorls 4 7/8+, umbilicus with a very narrow lateral crack.

Paratopotypes

WAM 847.87, AM C.200,756, FMNH 171624, 3 LA, 1 DA, 4 LJ from the type collection.

Paratypes

WESTERN AUSTRALIA: Cape Range: W side, 2 miles E of Norwegian Bay (*ca.* 22°36'S, 113°43'E, WAM 386.74, 2 LA); W side, N of Ningaloo (WA–21, 18.55 km N on alluvial fan at bore, WAM 858.87, SAM D18199, AM C.200,757, QM 46934, MV F60062, FMNH 182401, 28 DA, 17 DJ; WA–22, 14.9 miles N on outcrop, WAM 857.87, FMNH 182356, 11 DA, 4 DJ; WA–23, 14.9 miles N, WAM 849.87, WAM 856.87, SAM D18198, AM C.200,758, QM 46932, MV F.60021, FMNH 182301, FMNH 182509, 12 LA, 28 DA, 12 DJ; WA–171, 23.7 km N on same outcrop as WA–23, FMNH 199702, FMNH 199731, FMNH 199850, FMNH 199949, 6 LA, 1 DA, 6 LJ; WA–958, 23.7 km N, WAM 850.87, WAM 851.87, SAM D18194–5, AM c.200,759, QM 46933, MV F60053, FMNH 212491–2, 15 LA, 24 DA, 5 LJ, 7 DJ; WA–1074–5, FMNH 221733, FMNH 221737, 25 DA); 10.5 km S of Yardie Creek (WA–1076, FMNH 221738, 3 LA); Tantabiddi Well, Yardie Creek (W. H. Butler! 23 July 1963, WAM 359.74, 8 LJ); 2.8 miles S of Goat Cave (WA–13, FMNH 182682, 2 LJ, 2 DJ); immediate vicinity of Goat Cave, near Central Hill; G. Hitchin! 15 May 1965, FMNH 171625, 2 LA, 1 LJ; WA–14, WAM 861.87, FMNH 182470, FMNH 182667, 7 LA, 8 DA, 5 LJ, 24 DJ; WA–15, FMNH 182489, 1 LA, 3 LJ; WA–17, WAM 859.87, WAM 860.87, SAM D18200–1, AM C.200,760, MV F59458, QM 52988, FMNH 182454, FMNH 182457, FMNH 182464, FMNH 182496, FMNH 182513, FMNH 182654–5, FMNH 182704, 244 LA, 2 DA; WA–174, WAM 854.87, WAM 855.87, SAM D18197–8, AM C.200,761, QM52989, MV F59468, FMNH 199733, FMNH 199868, FMNH 199880, 35 LA, many LJ; WA–175, FMNH 199753–4, FMNH 199904, 7 LA, 1 LJ; WA–959, WAM 852.87, WAM 853.87, SAM D18196, AM, FMNH 212499–501, 7 LA, 9 DA, 3 LJ, 5 DJ; WA–1080, FMNH 221748, 7 LA); 1.6 km N of Goat Cave (WA–960, FMNH 212509, 1 DA); 2.4 miles N of Goat Cave along ridge track (WA–18, FMNH 182555, 1 DA); within 100 yds of Cape Range # 2 Deep Well (G. Hitchin, A. Saar, G. W. Kendrick! 10 May 1965, WAM 128.94, 20 DA,

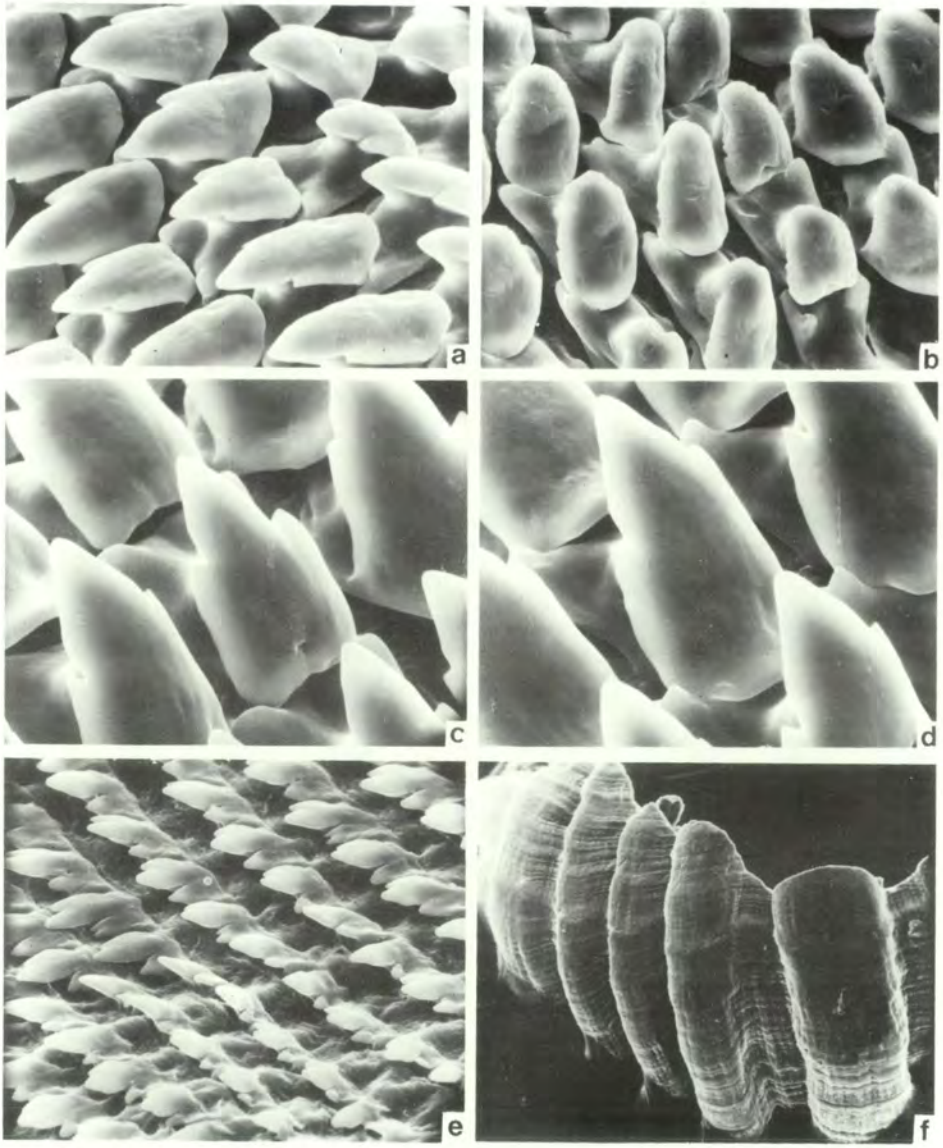


Plate 231: Radular teeth of sympatric *Quistrachia lefroyi* sp. nov. and *Rhagada capensis* sp. nov. from N tip of Cape Range. Vlaming Head near North West Cape, WA. October 1975. WAM 1361.75: (a–c) Dissection B. *Quistrachia lefroyi*. a is central and early laterals at 4475X. b is latero-marginal transition at 730X. c is top angle view of latero-marginal transition at 380X; (d–f) Dissection A. *Rhagada capensis*. d is central and early laterals at 790X. e is latero-marginal transition at 3825X. f is detail of latero-marginal transition at 530X.

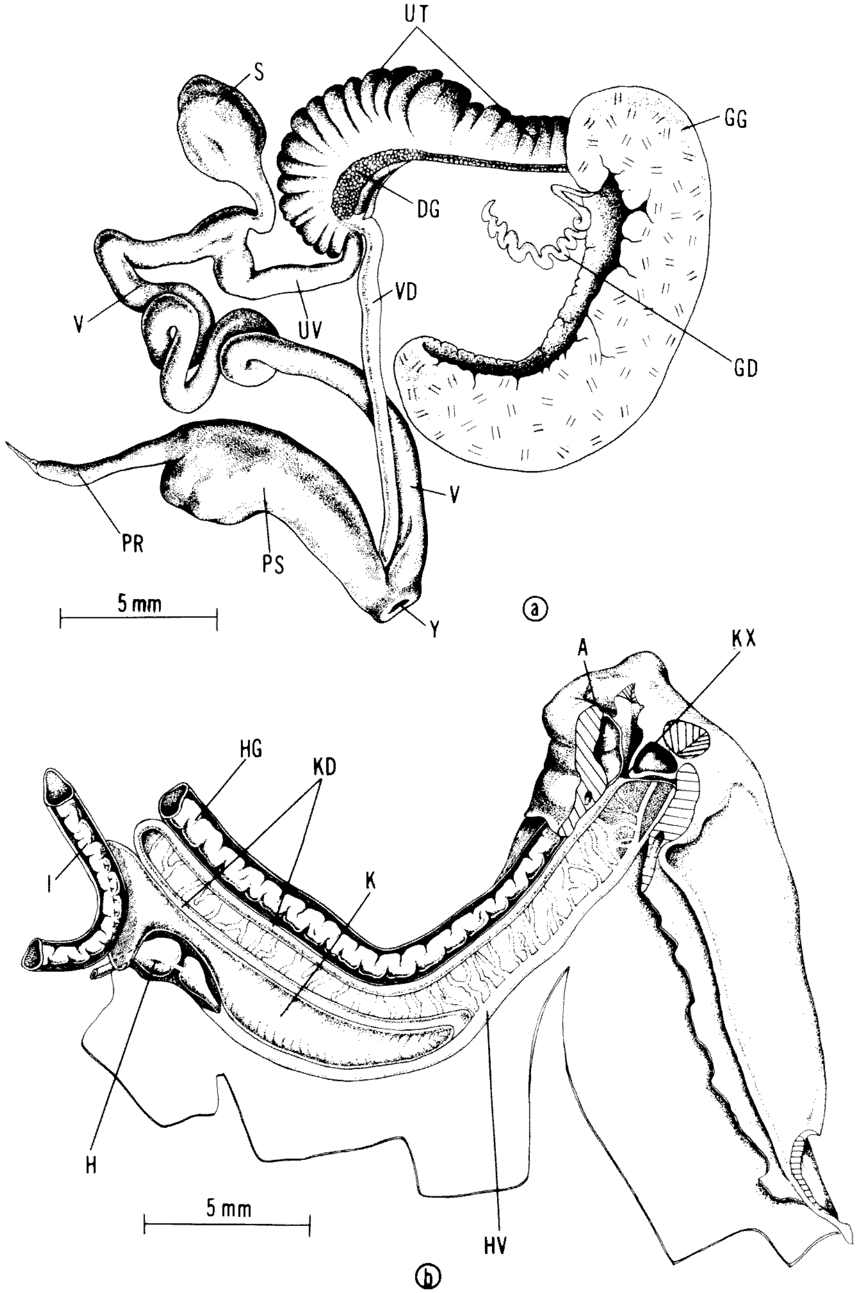


Fig. 436: Whole genitalia and pallial region of *Quistrachia lefroyi* sp. nov.: Goat Cave, near Central Hill, Cape Range, WA. June and July 1964. FMNH 171624, Dissection A: (a) whole genitalia; (b) pallial complex. Scale lines equal 5 mm. Drawings by Carole W. Christman.

32 DJ; Exmouth road, 1 km S of Learmonth (WA–961, WAM 848.87, FMNH 212511–2, 2 LA, 5 DA, 3 DJ); Stn 221, Learmonth to crest track (FMNH 171639, 1 DA, 4 DJ); Thomas Carter Lookout, Charles Knife Road (WA–1079, FMNH 221752–3, 25 LA); Shothole Canyon (WA–177, FMNH 199398, 3 DA; Vlaming Head, tip of North West Cape (October 1975, ex WAM 1361.75, 1 LA).

Range

Quistrachia lefroyi lives in the Cape Range and neighbouring plains from the level of Norwegian Bay (22°36'S) to Vlaming Head (21°46'S) at its N tip, a linear range of about 89 km (**Map 32**). It generally has been found under spinifex near limestone rubble or in the rubble itself. S of Learmonth (WA–961) is the only place where it has been found alive on open plains. It has not been taken in the Rough or Scrubby Ranges, nor in the Bullara-Giralia plains area. *Q. lefroyi* is a free-sealer that aestivates in litter, often side by side with *Rhagada capensis*. The nearest species to the S is *Q. warroorana* (**Maps 30, 46**) from both the Scrubby Range and Warroora Station on the coast (**Map 31**). *Q. barrowensis* sp. nov. from Barrow Island and *Q. montebelloensis* sp. nov. from the Montebello Islands (**Map 46**) occur to the NE.

Diagnosis

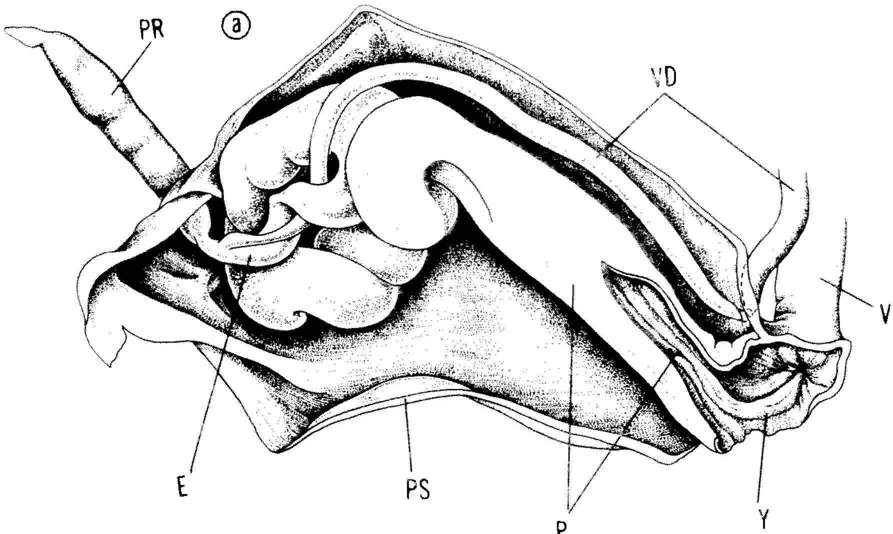
Shell medium to large, adult diameter 13.4–21.9 mm (mean 18.69 mm), with 4 3/8 to 5 5/8+ (mean 4 7/8) normally coiled whorls (**Fig. 433d**). Apex and spire strongly and evenly elevated (**Fig. 433e**), shell height 11.7–20.2 mm (mean 15.86 mm), H/D ratio 0.642–1.010 (mean 0.849). Body whorl noticeably inflated (**Fig. 433e**), evenly rounded. Shell apex (**Plate 227d–e**) densely pustulose with pustules continuing onto spire and body whorl. Umbilicus (**Fig. 433f**) a narrow lateral crack or closed, never with a broad callus. Body whorl usually descending gradually behind lip which is thin and, at most, narrowly expanded. A white peripheral colour band bordered above by a narrow red to brownish spiral band and usually a slightly narrower or fainter reddish band below the white zone. Shell usually with a light brownish suffusion above periphery. Based on 591 measured adults.

Genitalia (**Figs 436a, 437a–b, 438a–b, 439a–c**) with albumen gland (GG) longer than prostate-uterus, spermatheca (S) very short, with well expanded head next to prostate-uterus base. Free oviduct (UV) medium in length, curved. Vagina (V) varying in length from nearly equal (**Fig. 439a**) to penis sheath (PS) to four times as long (**Fig. 436a**); penis (P) varying to same extent in length. Main pilaster (PT) always fused for entire length and equalling penis length. Wall of upper penis chamber pustulose, lower portion with simple longitudinal (**Fig. 438b**) to corrugated pilasters.

Central and early lateral teeth of radula (**Plates 230a, 231a**) variable, with huge to moderate anterior flare, elevated to normal cusp shaft angle, cusp pointed or blunt, straight or slightly curved. Late laterals (**Plates 230b–d, 231b**) equally variable. Marginals (**Plate 230d, 231c**) typical. Jaw (**Plate 230e–f**) with prominent vertical ribs over most of surface.

Discussion

The few dead adults (4) taken in Shothole Canyon are clearly dwarfed – diameters only 14.1–16.8 mm (mean 15.65 mm), H/D ratios 0.821–0.837 (mean 0.829), whorls 4 3/4– to 5 1/8– (mean 4 7/8+) compared with specimens from other parts of the Cape



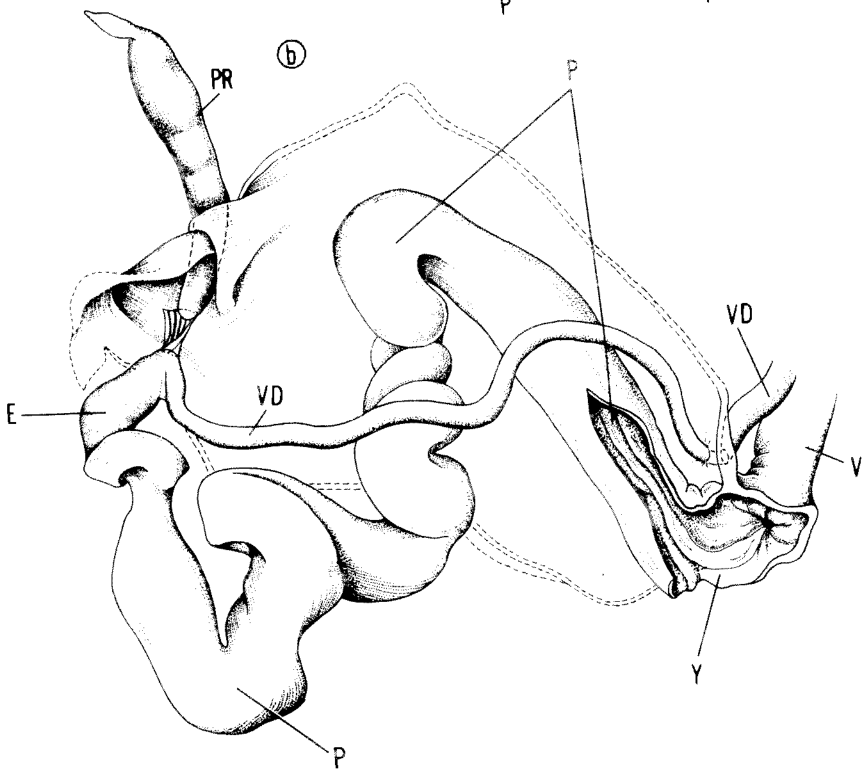


Fig. 437: Opened penis sheath of *Quistrachia lefroyi* sp. nov.: Goat Cave, near Central Hill, Cape Range, WA. June and July 1964. FMNH 171624, Dissection A: (a) penis coiled within open sheath; (b) penis partly uncoiled. Scale line equals 5 mm. Drawings by Carole W. Christman.

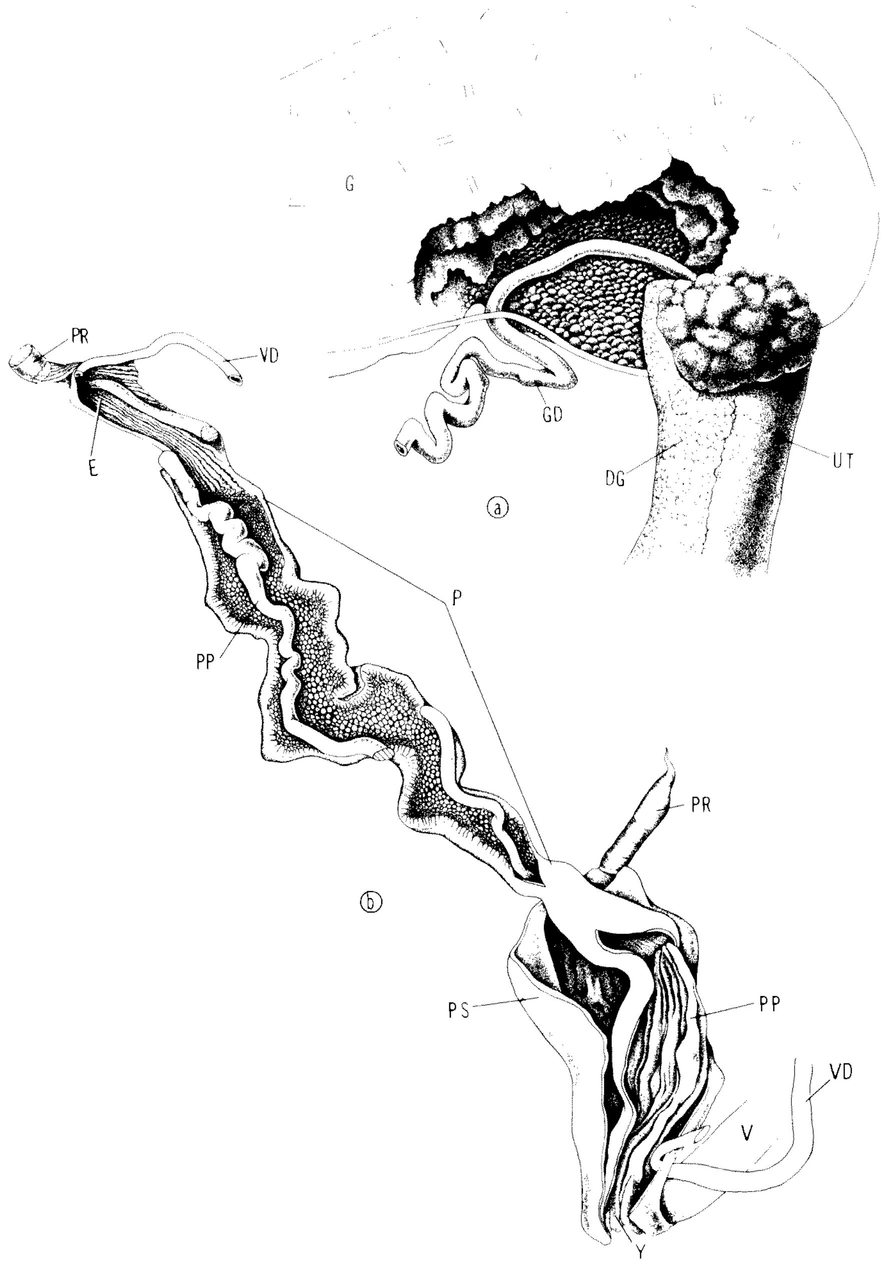


Fig. 438: Detail of apical genitalia and penis interior of *Quistrachia lefroyi* sp. nov.: Goat Cave, near Central Hill, Cape Range, WA. June and July 1964. FMNH 171624, Dissection A: (a) apical genital detail; (b) interior of penis (P). Scale lines as marked. Drawings by Carole W. Christman.

Table 162: Local variation in *Quistrachia lefroyi.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
N of Ningaloo					
WA-21, FMNH 182401	28D	13.59±0.182 (12.1-15.6)	16.49±0.141 (15.3-18.1)	0.823±0.009 (0.754-0.915)	$4\frac{3}{4}-$ ($4\frac{1}{2}$-5)
WA-22, FMNH 182356	11D	13.95±0.256 (12.6-15.6)	17.20±0.182 (16.3-18.2)	0.811±0.011 (0.754-0.864)	$4\frac{3}{4}-$ ($4\frac{1}{2}$-5)
WA-23, FMNH 182509	12L	14.01±0.238 (13.05-15.9)	16.66±0.210 (15.75-18.55)	0.841±0.009 (0.796-0.893)	$4\frac{7}{8}$ ($4\frac{5}{8}+$-$5\frac{1}{8}+$)
WA-23, FMNH 182301	28D	13.76±0.121 (12.5-14.6)	16.92±0.127 (15.7-18.3)	0.814±0.005 (0.763-0.872)	$4\frac{5}{8}+$ ($4\frac{1}{2}$-$4\frac{7}{8}$)
WA-958, FMNH 212492	15L	14.14±0.177 (13.1-15.15)	16.37±0.225 (15.4-17.95)	0.865±0.010 (0.812-0.937)	5 ($4\frac{3}{4}+$-$5\frac{1}{8}+$)
WA-958, FMNH 212491	24D	13.83±0.125 (12.9-15.05)	16.33±0.146 (14.8-17.7)	0.847±0.006 (0.814-0.905)	5– ($4\frac{5}{8}-$-$5\frac{1}{8}+$)
Norwegian Bay, WAM	12D	14.74±0.244 (13.5-15.6)	16.23±0.172 (15.5-17.5)	0.909±0.013 (0.857-1.010)	$4\frac{7}{8}-$ ($4\frac{1}{2}$-$5\frac{1}{8}$)
Goat Cave					
WA-14, FMNH 182667	7L	17.70±0.434 (16.3-19.6)	20.14±0.287 (19.1-21.0)	0.879±0.022 (0.805-0.975)	5– ($4\frac{3}{4}$-$5\frac{1}{2}$)
WA-14, FMNH 182470	8D	16.55±0.204 (15.7-17.3)	19.69±0.106 (19.2-20.1)	0.841±0.012 (0.785-0.876)	$4\frac{7}{8}-$ ($4\frac{1}{2}$-5)
WA-17, FMNH 182704	44L	17.11±0.094 (15.1-18.1)	19.94±0.104 (18.6-21.6)	0.859±0.004 (0.791-0.911)	$4\frac{7}{8}$ ($4\frac{5}{8}$-$5\frac{1}{4}$)

Table 162: Local variation in *Quistrachia lefroyi* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls
Western Australia					
WA-17, FMNH 182655	79L	16.67±0.099 (14.6-18.7)	19.82±0.083 (18.2-21.2)	0.841±0.004 (0.752-0.926)	$4\frac{7}{8}$- ($4\frac{1}{2}$-5)
WA-17, FMNH 182454	25L	16.65±0.224 (15.0-18.8)	19.78±0.178 (18.3-21.4)	0.842±0.008 (0.758-0.964)	$4\frac{3}{8}$ ($4\frac{5}{8}$-$5\frac{1}{4}$)
WA-17, FMNH 182654	80L	16.83±0.099 (14.65-20.0)	19.24±0.085 (17.65-21.35)	0.875±0.004 (0.783-0.956)	$5\frac{1}{8}$ ($4\frac{5}{8}$+-6+)
WA-174, FMNH 199733	20L	16.37±0.149 (15.3-17.65)	18.88±0.121 (18.0-19.8)	0.868±0.007 (0.791-0.914)	$4\frac{7}{8}$ ($4\frac{3}{4}$+-$5\frac{1}{8}$)
WA-174, FMNH 199868	15L	17.12±0.219 (15.65-18.3)	19.28±0.204 (18.0-20.5)	0.889±0.010 (0.770-0.937)	5 ($4\frac{3}{4}$--$5\frac{1}{4}$+)
WA-959, FMNH 212499	9D	16.66±0.326 (15.3-18.15)	18.94±0.375 (19.5-21.2)	0.879±0.010 (0.851-0.940)	$5\frac{1}{8}$- (5--$5\frac{1}{4}$+)
Cape Range within 100 yds, of Cr No. 2 Deep Well, WAM	20D	14.42±0.154 (13.35-16.1)	17.23±0.135 (16.1-18.8)	0.837±0.007 (0.794-0.920)	$4\frac{7}{8}$- ($4\frac{3}{4}$-$5\frac{1}{8}$)
Exmouth dump					
WA-961, FMNH 212511	7D	16.12±0.425 (15.05-17.9)	18.98±0.425 (19.4-20.55)	0.850±0.021 (0.771-0.928)	$5\frac{1}{8}$ ($4\frac{7}{8}$+-$5\frac{3}{8}$+)

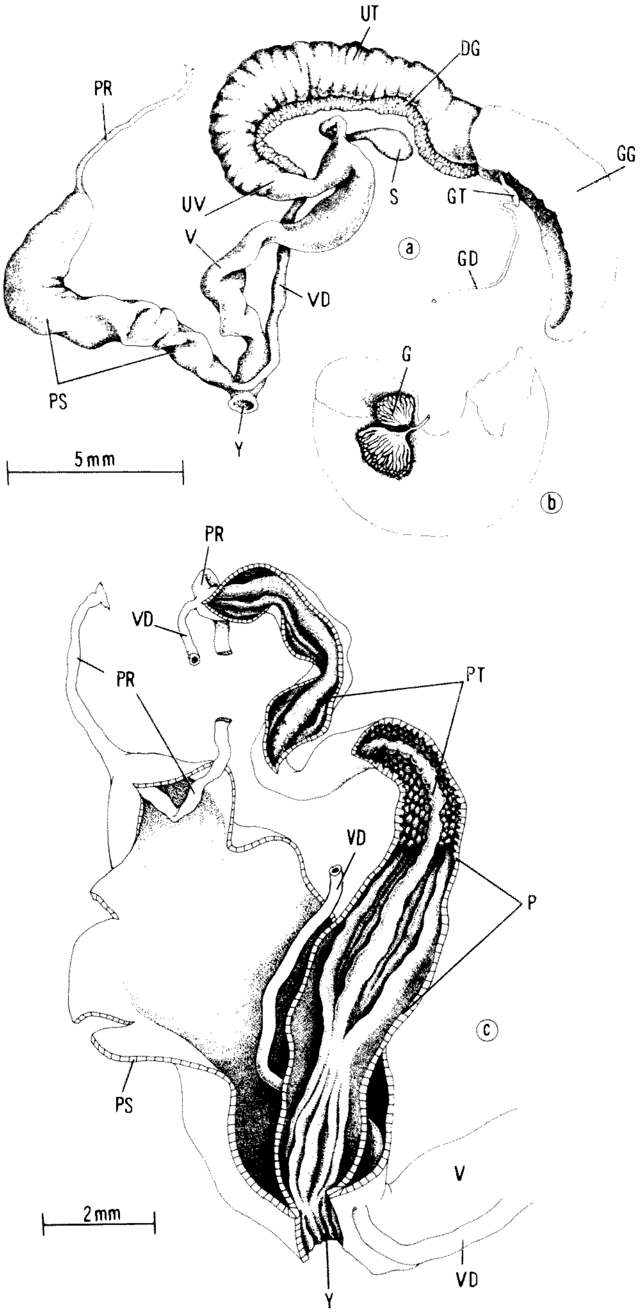
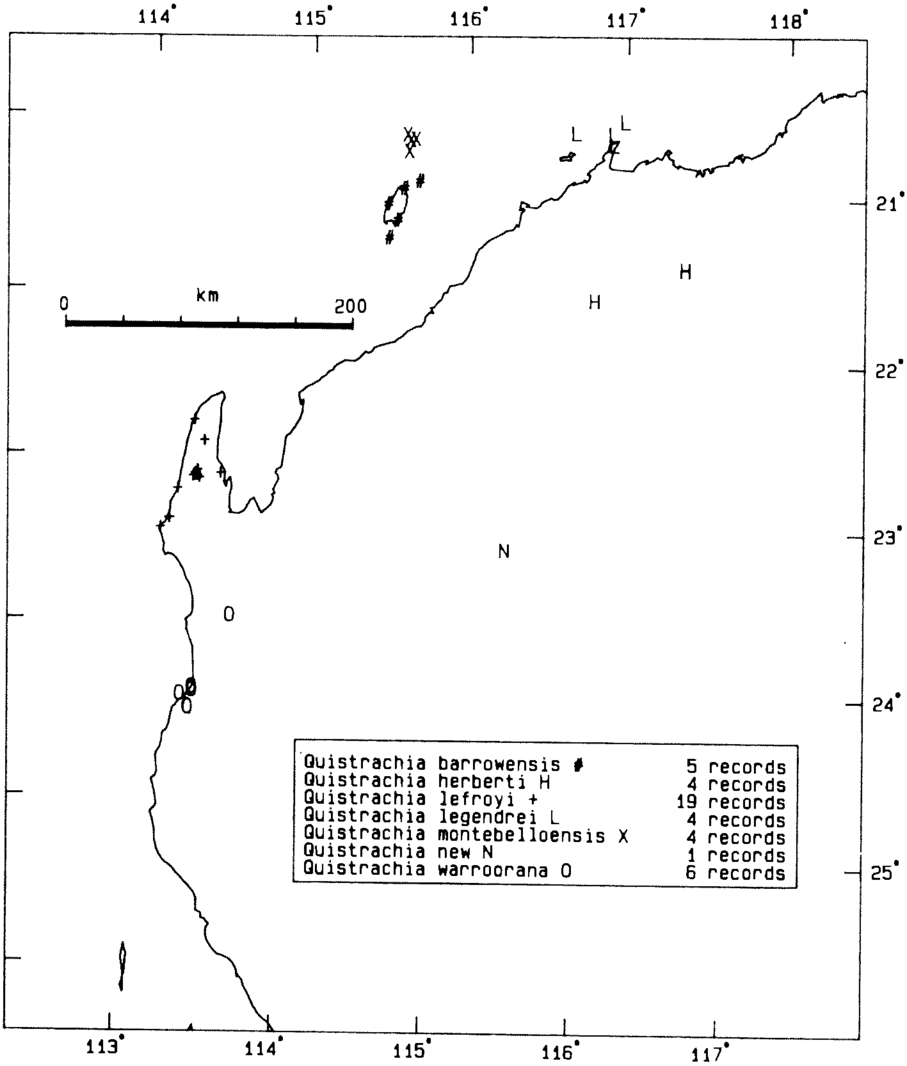


Fig. 439: Genitalia of *Quistrachia lefroyi* sp. nov.: Vlaming Head, tip of Cape Range peninsula, WA. October 1985. WAM 1361.75, Dissection A: (a) whole genitalia; (b) location of ovotestis; (c) penis interior. Scale lines as marked. Drawings by Elizabeth A. Liebman.

Range (**Table 162**). The single live adult from Vlaming Head (WAM 1361.75) and those from 23.7 km N of *Ningaloo* on the W side of the Range (WA–22, WA–23, WA–171, WA–958) are noticeably smaller in diameter and with slightly lower whorl count than are those from the Goat Cave area near Central Hill (**Table 162**). Dissection of the speciemsn from N of *Ningaloo* and the Learmonth plains showed genital structures that agree basically with those found at both Vlaming Head (**Figs 439a–c**) and Goat Cave (**Figs 436a, 437a–b, 438a–b**).



Map 46: Records of *Quistrachia barrowensis*, *Q. herberti*, *Q. lefroyi*, *Q. legendrei*, *Q. montebelloensis*, *Q.* new species and *Q. warroorana* from Dampier Archipelago to the Shark Bay area, WA.

Quistrachia lefroyi shows more genital variation than any Australian camaenid that I have studied previously. In the central portion of the Cape Range, where it is sympatric with several other camaenids, and on the coastal plain 1 km S of Learmonth (WA–961), the vagina (V) and penis (P) are greatly elongated, reaching several times the length of the penis sheath (PS, **Figs 436a, 437a–b, 438b**). At Vlaming Head (**Figs 439a, c**) both organs are much shorter, while, on the W side of the Cape Range, they are only slightly longer than the penis sheath (WA–23, WA–958). All these populations agree in having the main pilaster fused and extending the length of the penis itself and the upper portion of the penis chamber wall is pustulose. The longer free oviduct (UV) and very short spermatheca (S) also are shared. The basal portion of the penis chamber wall varies from simple to corrugated longitudinal ridges. Since the shell features of these populations are the same, although size differs (**Table 162**), they are kept as a single species pending study of material from additional populations.

Unlike the situation in *Strepsitaurus*, one species of *Quistrachia* occupies both sides of the Cape Range, whereas *Strepsitaurus ningaloo* inhabits the W portion N to Yardie Creek, *S. rugus* extends from the Rough Range to just past Charles Knife Road in the Cape Range, *S. milyeringus* inhabits the NW section and *S. williami* is found on the E side from probably Goat Cave N to Shothole Canyon, Cape Range.

Radular variation (**Plates 230, 231a–c**) probably correlates with dietary specialization. At Goat Cave, where *Rhagada capensis*, *Promonturconchum superbum*, *Caperantrum polygyrum* and *Strepsitaurus rugus* also occur, activated specimens of *Quistrachia lefroyi* were observed just after a rain storm, scraping the bark off twigs of low herbaceous plants. The enlarged anterior flare undoubtedly correlates with the greater stress encountered by these teeth when feeding. In contrast, at Vlaming Head, where only *Rhagada capensis* is also found, the size of the anterior flare is greatly reduced (**Plate 231a**).

The name *lefroyi* honours Billie Lefroy, Jane Lefroy and the late Edgar Lefroy of Ningaloo Station, who have given so much help to visiting naturalists. It is a small token of appreciation for their help.

QUISTRACHIA SPECIES

(Figs 444a–c; Map 46)

Comparative remarks

Quistrachia species, from Glen Florrie Station, Pilbara (**Map 46**), is medium-sized, diameter 15.95–18.0 mm (mean 17.13 mm), elevated whorl count of 5 1/8– to 5 1/2+ (mean 5 1/4+), with a moderately elevated spire that is rounded above (**Fig. 444b**), shell height 12.25–13.5 mm (mean 12.80 mm), H/D ratio 0.711–0.849 (mean 0.749). Body whorl evenly rounded, descending behind aperture. Lip well-expanded, thin. Umbilicus a narrow lateral crack or closed. Shell with single peripheral spiral red colour band. Shell sculpture unknown. The greatly elevated whorl count, compared with those of *Q. herberti* sp. nov. and *Q. turneri* sp. nov. (**Table 160**), rounded spire and essentially closed umbilicus separate the present *Q.* species from the other Pilbara taxa, while the expanded lip differentiates it from the North West Cape to Warroora species, *Q. warroorana* and *Q. lefroyi*. Anatomy unknown.

Material studied

WESTERN AUSTRALIA: Pilbara: Glen Florrie Station (WA–417, 41.1 km from Uaroo Station boundary on track to homestead, SW side of rocky hill, 23°S, 116°E, WAM 862.87, FMNH 199307, 7 DA).

Range

Quistrachia species has been found in limited numbers on Glen Florrie Station, (**Map 46**). Little collecting has been done in this region, and additional colonies probably exist.

Discussion

All seven examples of *Quistrachia* species are too worn to show any trace of microsculpture on the shell. One example does retain a peripheral colour band. The narrow lateral crack retained by the umbilicus is characteristic of *Quistrachia* and makes it highly unlikely that this species is a *Rhagada*. In size (**Tables 160, 164**) and shape, *Q.* species shows similarities to both *Q. turneri* sp. nov. and *Q. herberti* sp. nov. (**Figs 444a–i**). Without fresh material which shows the shell sculpture and anatomical data, description is unwarranted.

Specimens of *Rhagada radleyi* Preston, 1914 (**Figs 416d–f**) were very common at this locality. They differ obviously in shape, markings and umbilical features. No examples were taken with the Meilga or Joy Helen Mine collections of *Plectorhagada meilgana* (see above), the nearest positive collecting stations.

QUISTRACHIA BARROWENSIS SP. NOV.
(Plates 227f, 232a–e, Figs 440a–c, 441a–c, Map 46)

Comparative remarks

Quistrachia barrowensis sp. nov. from Barrow Island and its associated islets (**Map 46**), is medium-sized (mean diameter 16.60 mm), globose (**Fig. 440b**, mean H/D ratio 0. 844), with 4 3/8 to 5 5/8+ (mean 4 7/8–) normally coiled whorls (**Fig. 440a**), the lip well expanded and umbilicus usually very narrowly open, rarely closed. Body whorl evenly rounded. Shell with a faint brownish spiral band just above peripheral white zone, spire sometimes with a light brownish suffusion. Shell apex (**Plate 227f**) with elongated dense pustules, spire and body whorl with crowded elongated pustules and ridgelets. *Q. lefroyi*, from the Cape Range (**Map 32**), has an inflated body whorl (**Fig. 433e**), darker colour, is much larger (mean diameter 18.69 mm) and has simple apical pustules (**Plate 227d**). *Q. warroorana*, from just S of the Cape Range (**Maps 30, 46**), is much smaller (mean diameter 14.94 mm); with a reduced whorl count (mean 4 3/8+), no lip expansion and brighter colouration. The Montebello Islands (**Map 46**) *Q. montebelloensis* (Preston, 1914) is very similar in shell sculpture (**Plate 228a–b**), colour and shape (**Fig. 440e**), but is smaller (mean diameter 15.13 mm) and has the lip significantly thickened.

Anatomically (**Figs 441a–c**), *Q. barrowensis* has the vagina (V) slightly longer than the penis sheath (PS), the penis (P) three times the length of the penis sheath, the main pilaster (PT) bifurcated on its lower quarter, then fused to apex. Penis chamber wall

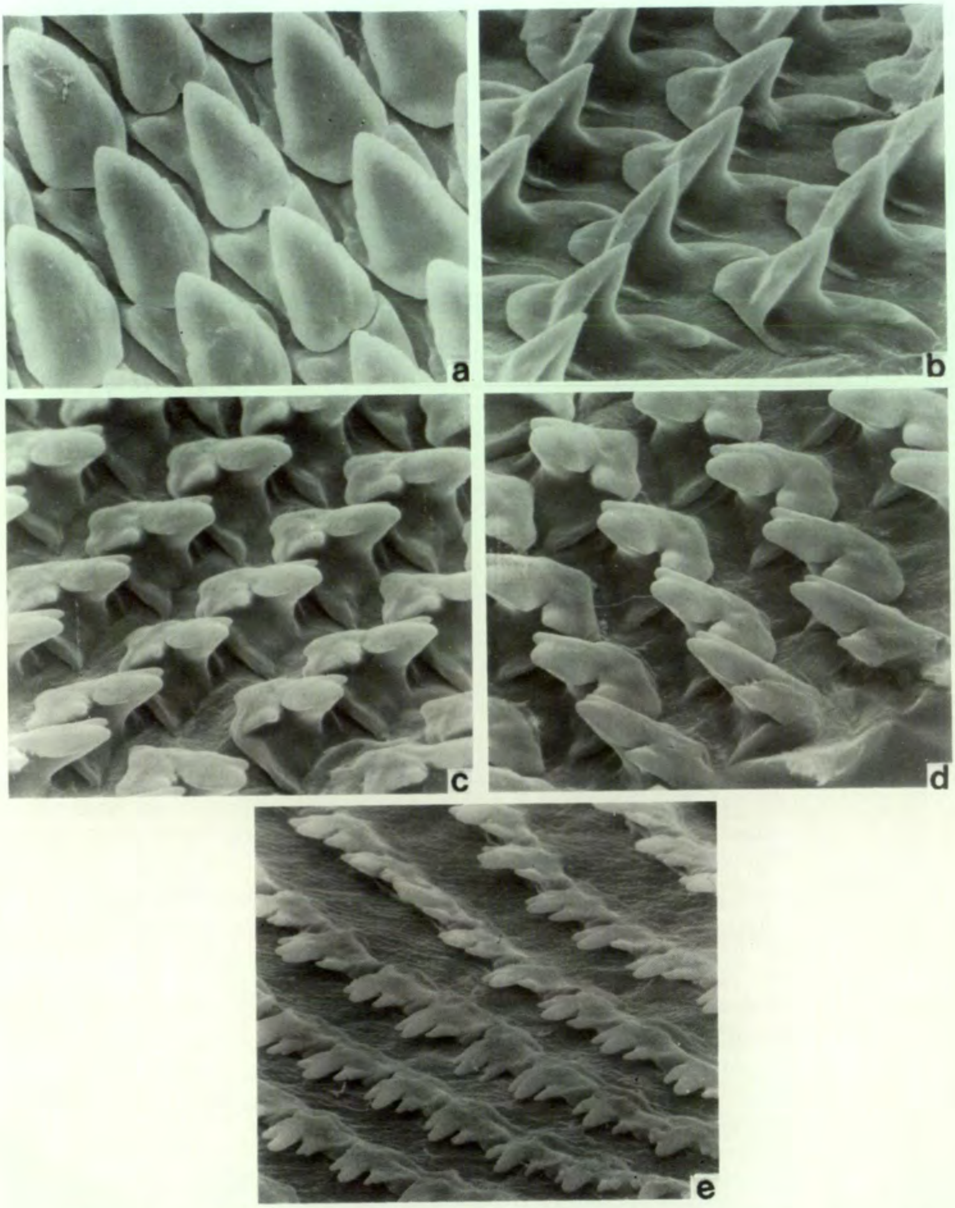


Plate 232: Radular teeth of *Quistrachia barrowensis* sp. nov.: South claypan, Barrow Island, WA. 2 April 1971. WAM 364.74, Dissection B: (a) top view of central and early laterals at 680X; (b) mid-laterals at 630X; (c) latero-marginal transition at 720X; (d) early marginals at 740X; (e) outer marginals at 740X.

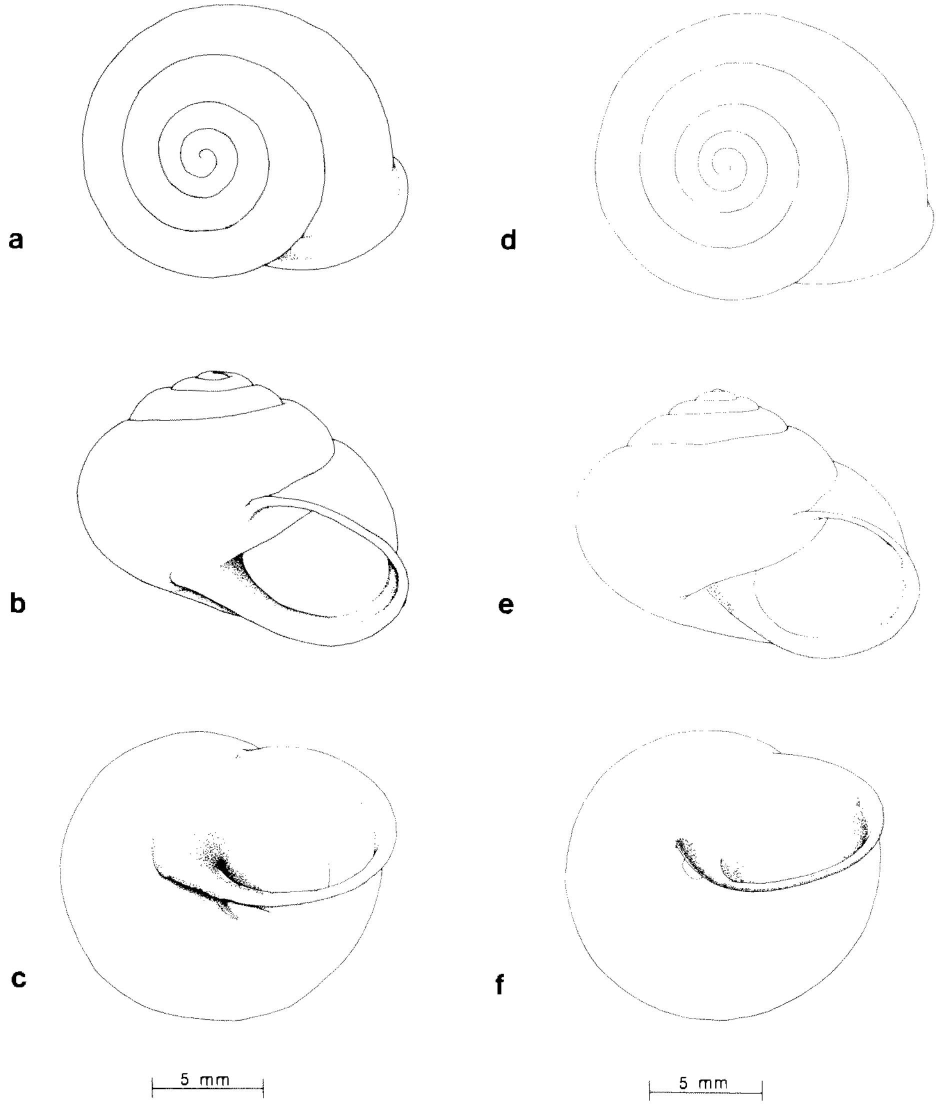


Fig. 440: Shells of *Quistrachia barrowensis* sp. nov. and *Q. montebelloensis* (Preston, 1914): (a–c) Holotype of *Q. barrowensis*. WAM 364.74. South claypan, Barrow Island, WA; (d–f) Paratype of *Rhagada montebelloensis* Preston, 1914. BMNH 1905.8.19.57. Montebello Islands, WA. Scale lines equal 10 mm. Drawings by Linnea Lahlum (a–c) and Elizabeth A. Liebman (d–f).

with short to long, sometimes corrugated, longitudinal ridges. *Q. lefroyi* (**Figs 436–439**) differs in having the main pilaster fused for its entire length and in having the penis chamber wall with at least one portion pustulose and usually the vagina very long. *Q. legendrei* sp. nov. (**Figs 443a–b**) has a short thick vagina, the penis slightly longer than the penis sheath, the main pilaster bifurcated for its entire length and the penis chamber wall sculpture is pustulose above and consists of longitudinal pilasters basally. The more northern species have relatively short main pilasters, penes and vaginae.

Holotype

WAM 364.74, South Claypan, Barrow Island, WA. *ca.* 20°52'S, 115°24'E. Collected 2 April 1971 by A. A. Burbidge and W. H. Butler. Height of shell 12.55 mm, diameter 15.05 mm, H/D ratio 0.834, whorls 4 1/2, umbilicus a very narrow lateral crack.

Paratopotypes

WAM 773.87, 2 LA from the type collection.

Paratypes

WESTERN AUSTRALIA: Barrow Island (W. H. Butler! 27 May 1964, WAM 366.74, 12 LA, 5 LJ; R. Perry! 2 April 1971, WAM 255.74, 1 DJ; D. L. Serventy! 19 September 1958, WAM 315.74, 6 DA; Mohan Yadav! 23 September 1966, WAM 119.94, 2 DA; near SW corner, L. A. Smith & W. H. Butler! 23 August 1973, WAM 354.74, 5 LA, 3 LJ; Stn 7, S end Flacourt Bay, September 1966, WAM 3594.67, WAM 3598.67, FMNH 208787, 28 DA, 13 DJ; sand hills near Flacourt Bay, 100 yards inland, G. W. Kendrick! 29 September 1981, WAM 278.82, 2 DA; near #5 Separator Station, December 1974, WAM 325.81, 1 DA; near well S27, L. A. Smith! 20 August 1973, WAM 368.74, 3 LJ; N side Bandicoot Bay, G. W. Kendrick! 27 September 1981, WAM 280.82, WAM 281.82, 3 DA; N coast between Surf Point and Cape Dupuy, G. W. Kendrick! September 1981, WAM 282.82, WAM 283.82, FMNH 208788, 13 DA, 7 DJ); South Pasco Island (Stn 9, 6 September 1966, WAM 3618.67, FMNH 208783, 15 DA, 3 DJ); South Double Island (R. W. George! 19 September 1988, WAM 242.74, FMNH 208785, 11 DA, 2 DJ); islets W of Double Island (18 September 1958, WAM 236.74, 2 DA); Lowendal Islands (W. H. Butler! 17 March 1985, WAM 442.88, FMNH 208784, 13 LA, 3 LJ).

Range

Quistrachia barrowensis has been collected at a number of localities on Barrow Island itself and from several of the offshore satellite islands – South Pasco, South Double, islets W of Double and Lowendal Island (**Map 46**). It is replaced on the Montebello Islands by *Q. montebelloensis* (Preston, 1914). The other neighbouring species are *Q. lefroyi* from the Cape Range to the SW (**Maps 32, 46**) and the Dampier Archipelago species *Q. legendrei* to the E (**Maps 40, 46**).

Diagnosis

Shell small to large, adult diameter 13.75–22.75 (mean 16.60 mm), with 4 3/8 to 5 5/8+ (mean 4 7/8–) normally coiled whorls (**Fig. 440a**). Apex and spire strongly elevated, often slightly rounded above (**Fig. 440b**), shell height 10.9–20.6 mm (mean

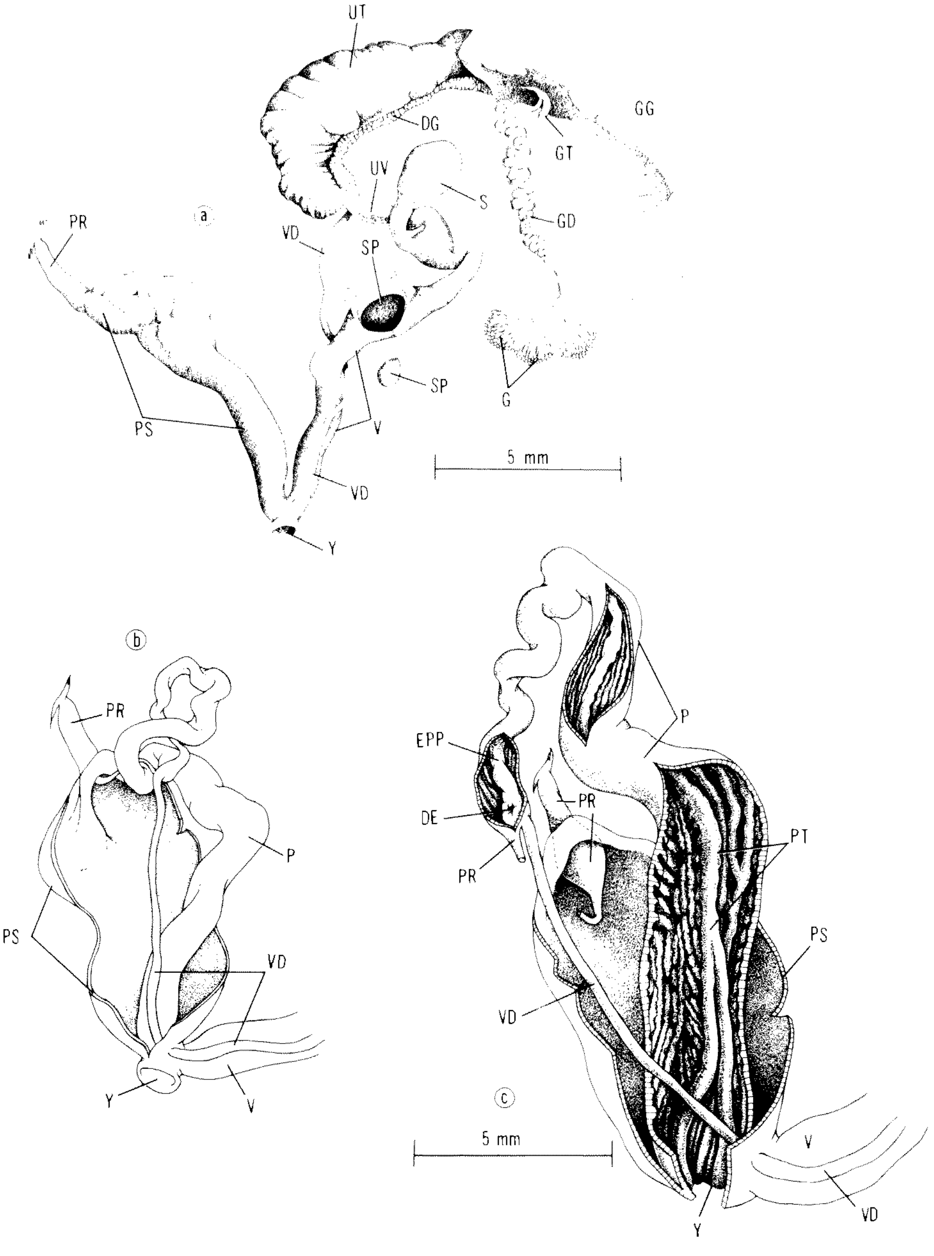


Fig. 441: Genitalia of *Quistrachia barrowensis* sp. nov.: South clay pan, Barrow Island, WA. 2 April 1971. WAM 364.74, Dissection A: (a) whole genitalia; (b) penis sheath opened; (c) interior of penis. Scale lines as marked. Drawings by Elizabeth A. Liebman.

Table 163: Local variation in *Quistrachia barrowensis* and *Q. montebelloensis.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
Quistrachia barrowensis							
S Pasco Island, WAM 3618.67	15D	14.82±0.205 (13.2-15.95)	16.83±0.262 (15.05-18.2)	0.881±0.008 (0.829-0.944)	$5\frac{1}{2}-$ $(4\frac{7}{8}-5\frac{5}{8})$	0.94± (0.6-1.45)	18.7±1.065 (10.6-28.4)
Barrow Island, WAM 366.74	12L	12.90±0.235 (11.8-14.0)	15.55±0.209 (14.5-16.65)	0.829±0.009 (0.784-0.873)	$4\frac{3}{4}+$ $(4\frac{1}{2}--5+)$	0.964±0.034 (0.75-1.15)	16.4±0.635 (13.2-20.4)
Barrow Island, WAM 282.82	12D	12.74±0.209 (11.65-14.25)	15.35±0.205 (14.3-16.9)	0.833±0.006 (0.800-0.869)	$4\frac{5}{8}+$ $(4\frac{1}{5}+-4\frac{7}{8}-)$	0.704±0.033 (0.5-0.85)	22.4±1.158 (17.0-30)
Flacourt Bay, WAM 3598.67	28D	12.20±0.141 (10.9-14.0)	15.18±0.127 (13.75-16.65)	0.804±0.005 (0.755-0.874)	$4\frac{1}{2}+$ $(4\frac{3}{8}-4\frac{3}{4})$	0.66± (0.3-1.0)	24.7±1.661 (15.3-50.0)
S Double Island, WAM 242.74	11D	17.93±0.451 (16.2-20.6)	20.51±0.368 (19.25-22.75)	0.871±0.011 (0.812-0.938)	$5\frac{1}{8}-$ $(4\frac{1}{2}-5\frac{3}{8})$	0.452± (0.15-0.75)	58±11.645 (27-162)
Lowendal Islands WAM 442.88	13L	16.39±0.228 (15.24-17.75)	18.33±0.195 (17.15-19.6)	0.894±0.006 (0.854-0.931)	$4\frac{7}{8}$ $(4\frac{3}{4}-5\frac{1}{4}-)$		
Quistrachia montebelloensis							
Alpha Island, WAM 30.87	7D	11.90±0.302 (10.3-12.9)	14.37±0.189 (13.35-14.8)	0.828±0.013 (0.771-0.884)	$4\frac{5}{8}-$ $(4\frac{3}{8}+-4\frac{5}{8}+)$	1.08±0.044 (0.95-1.25)	13.4±0.601 (11.5-15.3)
Montebello Islands, WAM 28.87	11D	12.99±0.246 (11.4-14.3)	15.98±0.283 (14.95-17.8)	0.813±0.008 (0.760-0.842)	$4\frac{5}{8}-$ $(4\frac{3}{8}--4\frac{3}{4}-)$	1.06±0.046 (0.8-1.25)	15.4±0.761 (12.0-20.1)
Hermite Island, WAM 257.74	4D	12.13±0.683 (10.75-13.95)	14.78±0.484 (13.65-15.9)	0.818±0.020 (0.787-0.876)	$4\frac{5}{8}-$ $(4\frac{1}{2}--4\frac{3}{4}+)$	1.00±0.071 (0.85-1.2)	15.0±1.107 (12.8-17.2)

14.07 mm), H/D ratio 0.750–0.980 (mean 0.844). Body whorl evenly rounded. Shell apex (**Plate 227f**) with dense elongated pustules, spire and body whorl with elongated, crowded radial ridgelets. Umbilicus (**Fig. 440c**) normally narrowly open, rarely closed. Body whorl descending slightly to moderately behind lip, which is reflected and expanded, remaining thin. Periphery with a faint white zone, often with a very light reddish brown spiral zone just above, spire often with a weak brownish suffusion. Based on 105 measured adults.

Genitalia (**Figs 441a–c**) with albumen gland (GG) much longer than prostate-uterus, spermatheca (S) short with expanded head at base of prostate-uterus. Free oviduct (UV) long, curved. Vagina (V) slightly longer than penis sheath (PS). Penis (P) three times length of sheath, internal wall sculpture with elongated longitudinal ridgelets basally, becoming longitudinal pilasters apically. Main pilaster (PT) bifurcated basally, then fusing and extending to apex of penis with epiphallic pore (DE) entering through pilaster apex.

Central and early lateral teeth of radula (**Plate 232a**) with prominent anterior flare, weak ectoconal notch, high cusp shaft angle, bluntly pointed and barely curved cusp tip. Mid-lateral teeth (**Plate 232b**) with greatly enlarged anterior flare, very high cusp shaft angle, bare trace of ectoconal cusp. Lateromarginal transition and marginals (**Plate 232c–e**) typical. Jaw without unusual features.

Discussion

It was possible to dissect only Barrow Island specimens of *Quistrachia barrowensis*, as the live-collected examples from the Lowendal Islands were deeply retracted and had dried out at some point.

One of the interesting aspects to this species is that the specimens from the N part of Barrow Island (Cape Dupuy and Bandicoot Bay) and the offshore islands are distinctly larger than those from the rest of Barrow Island (**Table 163**). Such size increment on small islands is known in regard to other land snails, although small island dwarfing is common in most other groups of organisms. It is quite possible that a complex of taxonomic units is united under this name but without live-collected material for study, it is best to lump these populations.

The apparently altered radular teeth of *Q. barrowensis* agree with those of *Q. lefroyi* from the main Cape Range (**Plate 230a–c**), where that species feeds on bark.

A comparative ecological study on land snails from Barrow Island and the Montebello Islands might yield interesting data. On Barrow Island, *Quistrachia* is widely distributed and variable but there are limited records of *Rhagada*. On the Montebello Islands, *Rhagada* is common but *Quistrachia* seems less abundant.

The name *barrowensis* is from Barrow Island.

QUISTRACHIA MONTEBELLOENSIS (PRESTON, 1914)

(Plate 228a–b; Figs 440d–f; Map 46)

Rhagada montebelloensis Preston, 1914, *Proc. Malac. Soc. London,* **11** (1): 13 – Montebello Islands, Western Australia; Richardson 1985, *Tryonia*, **12:** 265 – Check list citation.

Globorhagada montebelloensis (Preston), Iredale 1938, *Aust. Zool.*, **9** (2): 114 – check list citation; Iredale 1939, *Jour. Roy. Soc. Western Aust.*, **25:** 73, plt. V, fig. 20.

Comparative remarks

Quistrachia montebelloensis (Preston, 1914), which lives on many of the Montebello Islands (**Map 46**), is relatively small (mean diameter 15.13 mm), globose (**Fig. 440e**, mean H/D ratio 0.813), with an average number (mean 4 5/8) of normally coiled whorls (**Fig. 440d**), the lip well expanded and thickened and umbilicus (**Fig. 440f**) narrowly open (mean D/U ratio 14.9). Body whorl evenly rounded. Shell with a faint peripheral white zone, sometimes a faint trace of a colour band above it. Shell apex (**Plate 228a–b**) with prominent elongated pustules that partly coalesce; spire and body whorl with irregular radial ridgelets. *Q. barrowensis*, from Barrow Island (**Map 46**), does not have the lip thickened and is larger (mean diameter 16.60 mm) in size. The Cape Range species (**Map 32**), *Q. lefroyi*, normally is much larger (mean diameter 18.69 mm), has an inflated body whorl (**Fig. 433e**), a less expanded lip that is not thickened (**Figs 433d–f**) and much brighter colouration. *Q. legendrei*, from the Dampier Archipelago (**Map 46**), is much larger (mean diameter 21.33 mm), less elevated (mean H/D ratio 0.729), has a brownish spire and the thin lip is broadly expanded. Anatomy unknown.

Paratypes

Montebello Islands, Western Australia. BMNH 1905.8.19.57, FMNH 41624, ex Webb, Gude, Preston, 2 DA, 1 DJ. Shell heights 12.0 and 13.2 mm, diameters 15.3 and 15.9 mm, H/D ratios 0.784 and 0.830, whorls 4 3/8+ and 4 3/4+, umbilici with a narrow lateral crack.

Material studied

WESTERN AUSTRALIA: Montebello Islands (AM C.64885, 1 DA, figured by Iredale 1939: plt. V, fig. 20; AM C.34281, ex C. Hedley, 1 DA, 1 DJ; G. P. Whitley! 18 September 1945, AM, 8 DA; AM C.49687, ex Iredale, 1 DA; AM C.64922, 1 DA); Hermite Island (R. W. George! 23 September 1958, WAM 257.74, 3 DA, 2 DJ; A. Start! 11 June 1981, ex WAM 31.87, 3 DA, 1 DJ; Big Lagoon on E side, S. M. Slack-Smith! 11 December 1979, ex WAM 1122.81, 3 DA); Alpha Island (A. Start! 10 June 1981, ex WAM 30.87, FMNH 208775, 8 DA); Trimouille Island (A. Start! 10 June 1981, ex WAM 32.87, 2 DA; R. E. Johnstone! 30 June 1970, WAM 266.74, 2 DA); North West Island (A. Start! 10 June 1981, ex WAM 28.87, FMNH 208774, 11 DA, 1 DJ).

Range

Quistrachia montebelloensis has been collected on four of the Montebello Islands – Hermite, Alpha, Trimouille and North West. They cover a N-S distance of 16 km. On Barrow Island to the S, it is replaced by *Q. barrowensis*, on the Cape Range to the SW by *Q. lefroyi* and in the Dampier Archipelago by *Q. legendrei* sp. nov. (**Maps 40, 46**).

Diagnosis

Shell small, adult diameter 13.35–17.8 mm (mean 15.13 mm), with 4 3/8– to 4 7/

8– (mean 4 5/8) normally coiled whorls (**Fig. 440d**). Apex and spire strongly elevated, sometimes rounded above (**Fig. 440e**), shell height 10.3–14.3 mm (mean 12.31 mm), H/D ratio 0.738–0.889 (mean 0.813). Body whorl evenly rounded. Shell apex (**Plate 228a–b**) with dense elongated pustules that may coalesce; spire and body whorl with irregular radial ridgelets. Umbilicus (**Fig. 440f**) narrowly open, width 0.8–1.4 mm (mean 1.03 mm), D/U ratio 11.5–20 (mean 14.9). Body whorl, at most, descending slightly behind lip, which is moderately expanded and thickened (**Figs 440d–f**). Periphery with a faint white zone and sometimes a narrow very light brownish spiral band above, spire with a weak light brownish suffusion. Based on 84 measured adults.

Anatomy unknown.

Discussion

Very few available lots of *Quistrachia montebelloensis* contained enough adult specimens to analyze variation (**Table 163**), and they give no indication of any size difference between island populations. The more abundant material of *Rhagada plicata* from Hermite Island (**Table 156**) suggests that "on island" size variation in that species may be larger than "between island" variation. Possibly *Q. montebelloensis* will show the same variation.

No live-collected material was located and thus the genital structures of *Q. montebelloensis* remain unknown.

QUISTRACHIA LEGENDREI SP. NOV.

(Plates 228c–d, 233a–c; Figs 442a–f, 443a–b; Maps 40, 46)

Comparative remarks

Quistrachia legendrei, from the vicinity of the mainland town of Dampier and from several islands in the Dampier Archipelago (**Map 46**), is large (mean diameter 21.33 mm), with an elevated spire (**Fig. 442b, e**, mean H/D ratio 0.729), comparatively few (mean 4 3/8+) rather loosely coiled whorls (**Figs 442a, d**), a broadly expanded thin lip and very narrow to closed umbilicus (**Figs 442c, f**). Body whorl obtusely angulated. Spire with yellow-brown suffusion, sometimes darker just at periphery, shell base much lighter, often nearly white. Shell apex (**Plate 228c–d**) finely pustulose, spire and body whorl with scattered large pustules and periostracal micro-ridgelets. *Q. herberti* sp. nov. (**Plate 228e–f**) and *Q. turneri* sp. nov. both lack the scattered pustules, although sharing the periostracal micro-ridgelets. The former has a rather wide umbilicus (**Fig. 444f**), is low spired (mean H/D ratio 0.637, **Fig. 444e**), has an evenly rounded periphery and the shell base is brownish. *Q. turneri* sp. nov. has a much narrower lip, closed umbilicus (**Fig. 444i**), higher spire (mean H/D ratio 0.792, **Fig. 444h**) and the shell base is dark brownish-yellow.

Anatomically (**Figs 443a–b**), *Q. legendrei* has the vagina (V) slightly shorter than the penis sheath (PS), the penis (P) length less than 1.5 times that of the penis sheath, the main pilaster (PT) bifurcated and equal in length to the penis. Penis chamber wall with simple longitudinal pilasters on lower half, densely pustulose above. In *Q. leptogramma* (**Figs 449a, 450**) the main pilaster is fused basally; in *Q. turneri* sp. nov. (**Fig. 446b**) it is fused apically; in *Q. herberti* sp. nov. (**Fig. 445b**) it is very much

Table 164: Local variation in *Quistrachia legendrei, Q.* sp, *Q. herberti, Q. turneri* and *Q. leptgramma.*

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
Quistrachia legendrei							
Dolphin Island, WAM 349.74	11D	17.49±0.185 (16.25-18.5)	23.31±0.220 (22.2-24.25)	0.753±0.007 (0.726-0.782)	4 1/2- (4 3/8-4 5/8)		
Rosemary Island, WAM 328.74	5D	13.43±0.321 (12.85-14.7)	19.40±0.117 (19.1-19.75)	0.693±0.020 (0.665-0.769)	4 3/8 (4 1/4-4 3/8)	0.50±0.034 (0.4-0.55)	39 (34-47)
Quistrachia sp.							
WA-417, Glen Florrie Station, FMNH 199307	7D	12.80±0.169 (12.25-13.5)	17.13±0.250 (15.95-18.0)	0.749±0.018 (0.711-0.849)	5 1/4+ (5+-5 1/2+)		
Quistrachia herberti							
WA-40, FMNH 182379	15D	10.42±0.180 (9.0-11.65)	16.96±0.281 (15.7-19.7)	0.615±0.009 (0.518-0.660)	4 5/8+ (4 1/8+-4 3/4+)	2.18±0.084 (1.75-2.9)	7.93±0.288 (6.76-9.64)
WA-182, FMNH 199220	18D	10.74±0.118 (9.8-11.65)	16.59±0.142 (15.35-17.55)	0.648±0.004 (0.613-0.695)	4 7/8- (4 5/8+-5+)	2.02±0.074 (1.45-2.65)	8.38±0.308 (6.52-11.5)
WA-722, FMNH 205364	6D	10.81±0.200 (10.25-11.6)	16.90±0.170 (16.2-17.4)	0.640±0.013 (0.600-0.674)	4 3/4 (4 1/2+-5-)	1.91±0.085 (1.65-2.25)	8.93±0.327 (7.53-9.88)
Quistrachia turneri							
Woodstock WAM 448.88	5L	11.62±0.418 (10.0-12.4)	15.22±0.497 (13.25-16.0)	0.763±0.007 (0.746-0.790)	4 3/8- (4 1/4--4 3/8+)		
Woodstock WAM 449.88	14D	11.78±0.140 (10.85-12.65)	15.08±0.175 (14.05-16.35)	0.782±0.008 (0.716-0.825)	4 3/8- (4 1/8+-4 3/8+)		
Kunagunarrina							
WA-43, FMNH 182551	51L	14.34±0.070 (13.35-15.3)	17.75±0.068 (16.15-18.7)	0.807±0.003 (0.751-0.862)	4 3/8 (4 1/4--4 1/2+)		

Table 164: Local variation in *Quistrachia legendrei, Q.* sp, *Q. herberti, Q. turneri* and *Q. leptgramma* (continued).

Station	Number of Adults Measured	Mean, SEM and Range of: Shell Height	Shell Diameter	H/D Ratio	Whorls	Umbilical Width	D/U Ratio
Western Australia							
Quistrachia turneri (continued)							
Kunagunarrina							
WA-43, FMNH 182377	13D	13.99±0.155 (13.35-15.35)	17.81±0.171 (16.45-18.95)	0.786±0.008 (0.752-0.831)	$4\frac{1}{2}-$ ($4\frac{3}{8}-$-$4\frac{5}{8}-$)		
WA-183, FMNH 199227	26D	13.53±0.096 (12.75-14.6)	17.34±0.103 (16.4-18.6)	0.780±0.004 (0.737-0.817)	$4\frac{3}{8}$ ($4\frac{1}{4}-$-$4\frac{1}{2}+$)		
WA-183, FMNH 199784	24L	14.32±0.118 (13.15-15.65)	17.88±0.108 (16.85-18.85)	0.801±0.006 (0.743-0.870)	$4\frac{3}{8}$ ($4\frac{1}{4}-$-$4\frac{5}{8}-$)		
WA-183, FMNH 199899	6D	13.96±0.293 (12.95-14.8)	17.67±0.115 (17.2-18.0)	0.790±0.015 (0.724-0.822)	$4\frac{3}{8}$ ($4\frac{1}{4}+$-$4\frac{1}{2}+$)		
WA-721, FMNH 205361	12L	12.88±0.115 (12.3-13.5)	16.32±0.124 (15.85-17.1)	0.790±0.006 (0.756-0.824)	$4\frac{3}{8}$ ($4\frac{1}{4}-$-$4\frac{1}{2}$)		
WA-721, FMNH 205362	5D	14.12±0.145 (13.75-146)	17.95±0.175 (17.5-18.55)	0.787±0.007 (0.761-0.802)	$4\frac{3}{8}$ ($4\frac{1}{4}+$-$4\frac{1}{2}$)		
Quistrachia leptogramma							
WA-404, FMNH 199334	22D	16.75±0.188 (15.2-18.1)	19.20±0.244 (17.3-21.4)	0.873±0.006 (0.817-0.946)	$4\frac{3}{4}+$ ($4\frac{1}{2}+$-$5+$)	1.44±0.039 (1.1-1.85)	13.5±0.376 (10.8-16.9)
WA-415, FMNH 199370	6D	12.63±0.329 (11.5-14.0)	14.73±0.397 (13.75-16.5)	0.857±0.007 (0.837-0.882)	$4\frac{3}{8}$ ($4\frac{1}{4}-$-$4\frac{1}{2}+$)	0.92±0.083 (0.75-1.25)	16.6±1.312 (11.1-19.6)
WA-186, FMNH 200110	8D	14.12±0.156 (13.7-15.15)	16.82±0.269 (18.95-18.4)	0.840±0.005 (0.822-0.860)	$4\frac{5}{8}$ ($4\frac{1}{2}-$-$4\frac{7}{8}-$)	1.32±0.034 (1.2-1.45)	12.81±0.336 (11.7-14.3)

shortened and the basal wall chamber has longitudinal corrugated pilasters. Both *Q. barrowensis* (**Figs 441b–c**) and *Q. lefroyi* (**Figs 438b, 439c**) have extremely elongated penes and main pilasters that are fused for at least most of their length.

Holotype

WAM 228.74, Legendre Island, Dampier Archipelago, Western Australia. 20°23'S, 116°53'E. Collected 9 June 1962 by W. D. L. Ride. Height of shell 13.4 mm, diameter 19.1 mm, H/D ratio 0.702, whorls 4 1/4, umbilicus a very narrow lateral crack.

Paratypes

WESTERN AUSTRALIA: Dampier Archipelago: Legendre Island (W. D. L. Ride! 8 June 1962, WAM 338.74, 2 LA; W. D. L. Ride & H. Williams!, WAM 231.74, 1 DA; R. D. Royce! 10 June 1962, WAM 1134.81, 1 DA); Dolphin Island (G. M. Storr! 3 June 1962, WAM 349.74, FMNH 208777, 11 LA, 1 LJ); Rosemary Island (on ridge

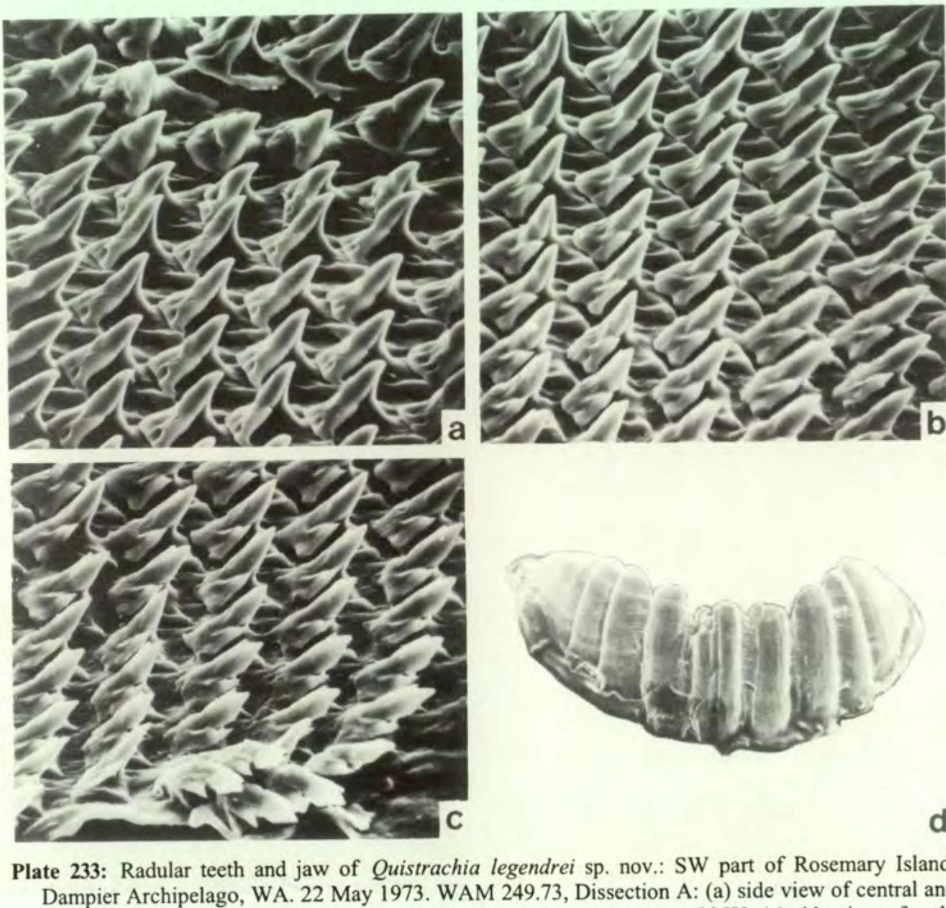


Plate 233: Radular teeth and jaw of *Quistrachia legendrei* sp. nov.: SW part of Rosemary Island, Dampier Archipelago, WA. 22 May 1973. WAM 249.73, Dissection A: (a) side view of central and laterals at 380X; (b) late laterals and early latero-marginal transition at 395X; (c) side view of early marginals at 385X; (d) jaw at 42.5X.

under stones, 22 May 1973, WAM 249.73, WAM 328.74, 1 LA, 5 DA); mainland near Dampier (King Bay, Burrup Peninsula, W. H. Butler! 12 May 1980, WAM 309.82, 1 LA, 4 LJ; Back Beach, Dampier, 18 October 1974, WAM 13.87, 1 DA).

Range

Quistrachia legendrei has been collected on the mainland from Back Beach, Dampier and the Burrup Peninsula and then from Legendre, Dolphin and Rosemary Islands in the Dampier Archipelago (**Maps 40, 46**). These records form a rough triangle, with the distances as follows: Dampier through Legendre (37 km), Burrup Peninsula through Rosemary (30 km) and Rosemary through Legendre (40 km). The nearest congeneric species are *Q. barrowensis* from Barrow Island and *Q. montebelloensis* from the Montebello Islands to the W and *Q. turneri* sp. nov. from an inland area to the S (**Maps 39, 46**).

Diagnosis

Shell large, adult diameter 18.0–24.25 mm (mean 21.33 mm), with 4 1/4 to 4 5/8 (mean 4 3/8+) rather loosely coiled whorls (**Figs 442a, d**). Apex and spire moderately

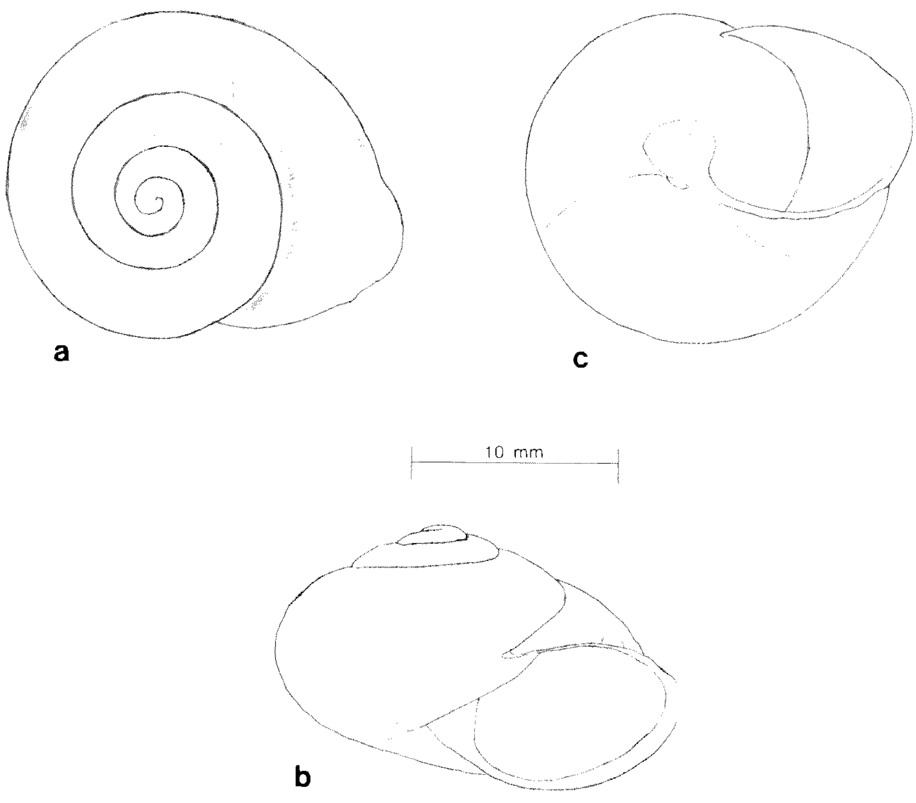


Fig. 442: Shells of *Quistrachia legendrei* sp. nov.: (a–c) Holotype. WAM 228.74. Legendre Island, Dampier Archipelago, WA. Scale line equals 10 mm. Drawings by Margaret Baker.

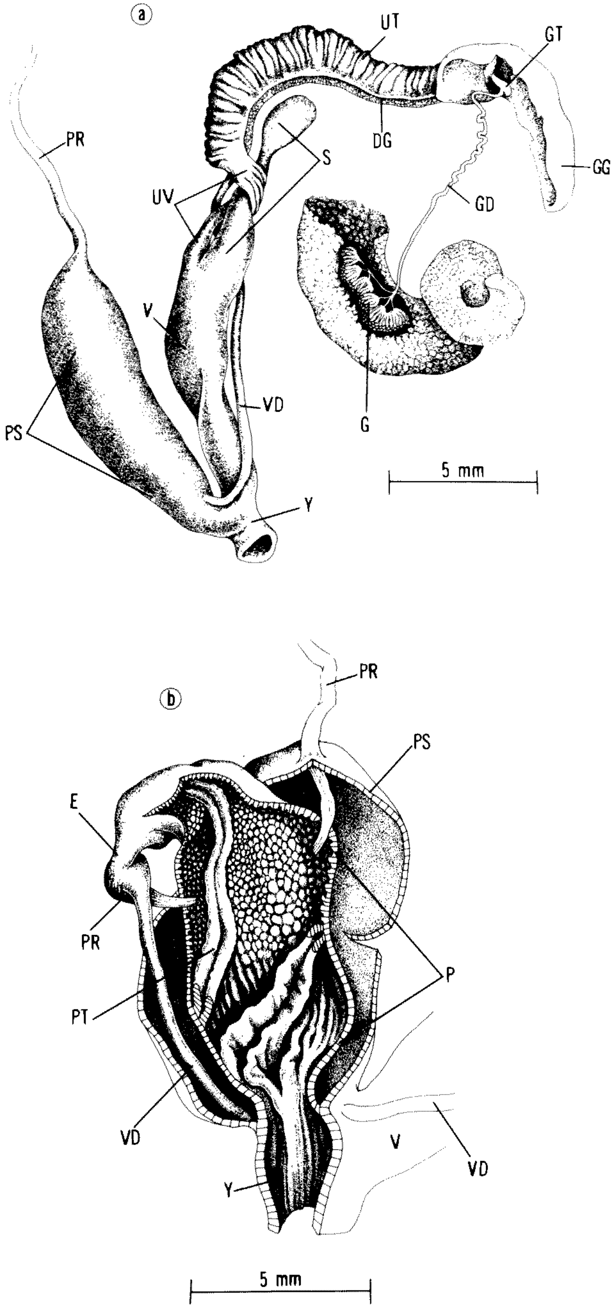


Fig. 443: Genitalia of *Quistrachia legendrei* sp. nov.: Rosemary Island, Dampier Archipelago, WA. 22 May 1973. WAM 249.73, Dissection A: (a) whole genitalia; (b) penis interior. Scale lines as marked. Drawings by Elizabeth A. Liebman.

elevated, often rounded above (**Figs 442b, e**), shell height 11.95–18.5 mm (mean 15.57 mm), H/D ratio 0.665–0.784 (mean 0.729). Body whorl obtusely angulated (**Figs 442b, e**). Shell apex (**Plate 228c–d**) minutely pustulose, spire and body whorl with large, scattered, pointed pustulations and periostracal micro-ridgelets. Umbilicus (**Figs 442c, f**) closed or a narrow slit. Body whorl moderately to strongly descending behind lip, which is thin and broadly expanded. Spire and body whorl above periphery yellow-brown, often darkest at periphery, tone changing frequently after growth pauses, base of shell yellow-white or white. Based on 23 measured adults.

Genitalia (**Figs 443a–b**) with albumen gland (GG) shorter than prostate-uterus, spermatheca (S) long, with enlarged base, head reaching partway up prostate-uterus. Free oviduct (UV) medium in length, not curved. Vagina (V) slightly shorter than penis sheath (PS), relatively large in diameter. Penis (P) about 1.5 times length of sheath. Main pilaster (PT) bifurcated, wider basally, equal in length to penis. Lower third of penis wall chamber with simple longitudinal pilasters, upper two-thirds densely pustulose.

Central and early lateral teeth of radula (**Plate 233a**) with very prominent anterior flare, elevated cusp shaft angle, small ectoconal notch, bluntly pointed and slightly rounded cusp tip. Late laterals (**Plate 233b**) with prominent ectocone, enlarged anterior flare and even higher cusp shaft angle. Lateromarginal transition and early marginal teeth (**Plate 233b–c**) typical. Jaw (**Plate 233d**) with prominent vertical ribs, reduced in prominence on lateral margins.

Discussion

The limited material of *Quistrachia legendrei* shows considerable size variation. The Dolphin Island sample (**Table 164**) and King Bay individual (diameter 22.3 mm, H/D ratio 0.784, whorl count 4 1/2+) are larger in size compared with the Rosemary Island population (**Table 164**) and scattered individuals from Legendre Island (mean of five adults is: height 12.81 mm, diameter 18.56 mm, H/D ratio 0.690, whorls 4 3/8–). There was no significant difference noted in terminal genital structure from Dolphin Island and Rosemary Island dissected specimens.

The name *legendrei* comes from the type locality, Legendre Island.

QUISTRACHIA HERBERTI SP. NOV.

(Plates 228e–f, 234a–f; Figs 444d–f, 445a–b; Map 46)

Comparative remarks

Quistrachia herberti sp. nov., from the Lower Fortescue River at Warla Pool and from Mt Herbert, Chichester Range (**Map 46**), is medium sized (mean diameter 16.84 mm), comparatively low spired (**Fig. 444e**, mean H/D ratio 0.637), with an average number (mean 4 3/4) of normally coiled whorls (**Fig. 444d**), well expanded lip and widely open umbilicus (**Fig. 444f**, mean D/U ratio 8.36). Body whorl evenly rounded. Shell apex (**Plate 228e**) pustulose, spire and body whorl with radial ridgelets and anatomosing periostracal micro-ridgelets (**Plate 228f**). *Q.* species, from Glen Florrie Station (**Map 46**), is more elevated (**Fig. 444b**), has a closed or nearly closed umbilicus (**Fig. 444c**) and a red spiral colour band. The Napier-Oscar Range species (**Map 42**),

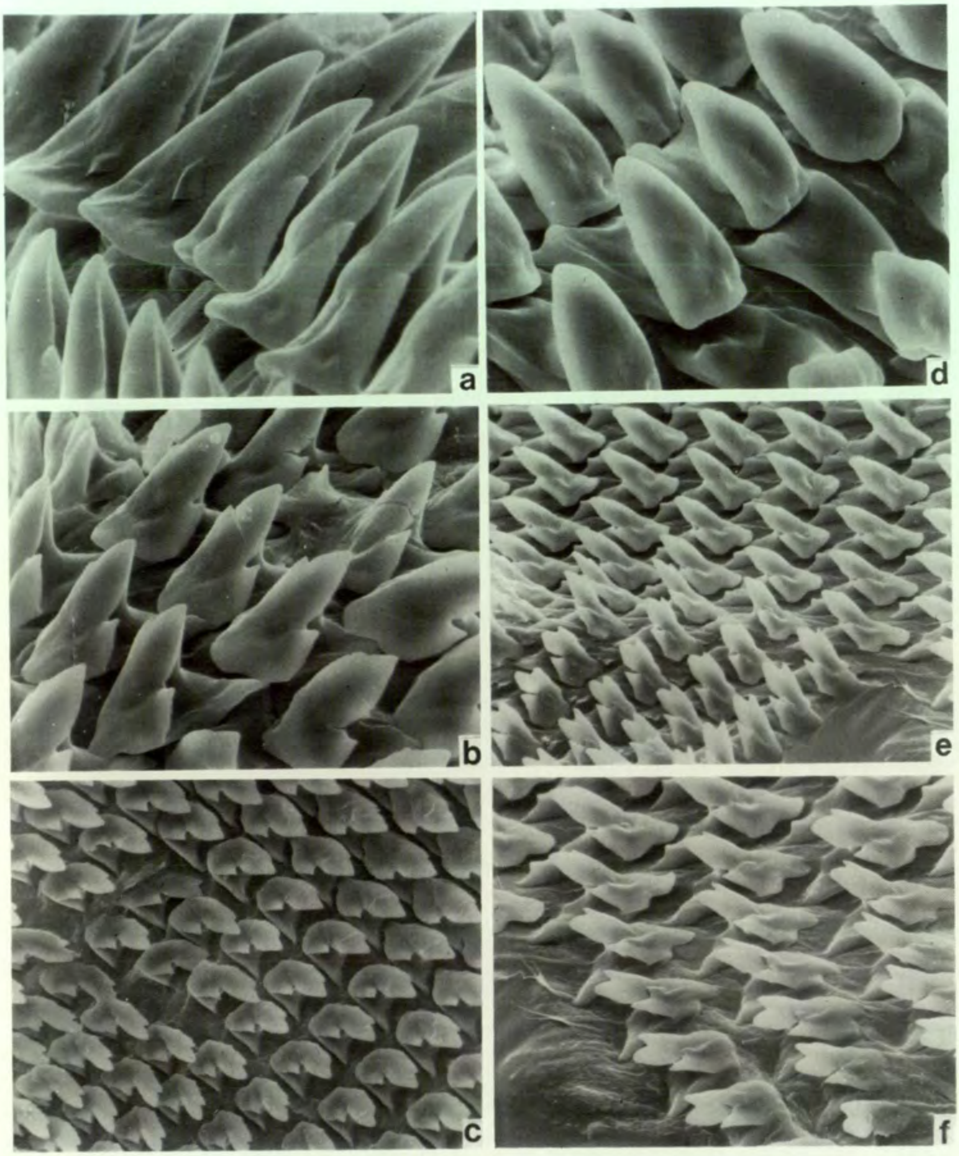


Plate 234: Radular teeth and jaw of *Quistrachia herberti* sp. nov.: WA–40, SE corner Mt Herbert, Chichester Range, WA. 29 January 1974. FMNH 182536, Dissection A: (a) central and early laterals at 630X; (b) worn central and early laterals at 630X; (c) detail of central and first lateral at 1,185X; (d) mid-laterals at 1225X; (e) late marginals at 590X; (f) part of jaw at 120X.

Q. monogramma (Ancey, 1896), has an even wider umbilicus (**Table 160**), red peripheral colour band, and smooth shell surface. *Q. turneri* sp. nov., from the Yule and Turner River basins (**Map 46**), has a nearly closed umbilicus (**Fig. 444i**), much higher spire (**Fig. 444h**, mean H/D ratio 0.792) and narrower shell lip.

Anatomically (**Figs 445a–b**), *Q. herberti* has the vagina (V) much shorter than the penis sheath, the penis (P) barely longer than the sheath, the bifurcated main pilaster (PT) less than one-quarter as long as the penis, the lower part of the penis chamber

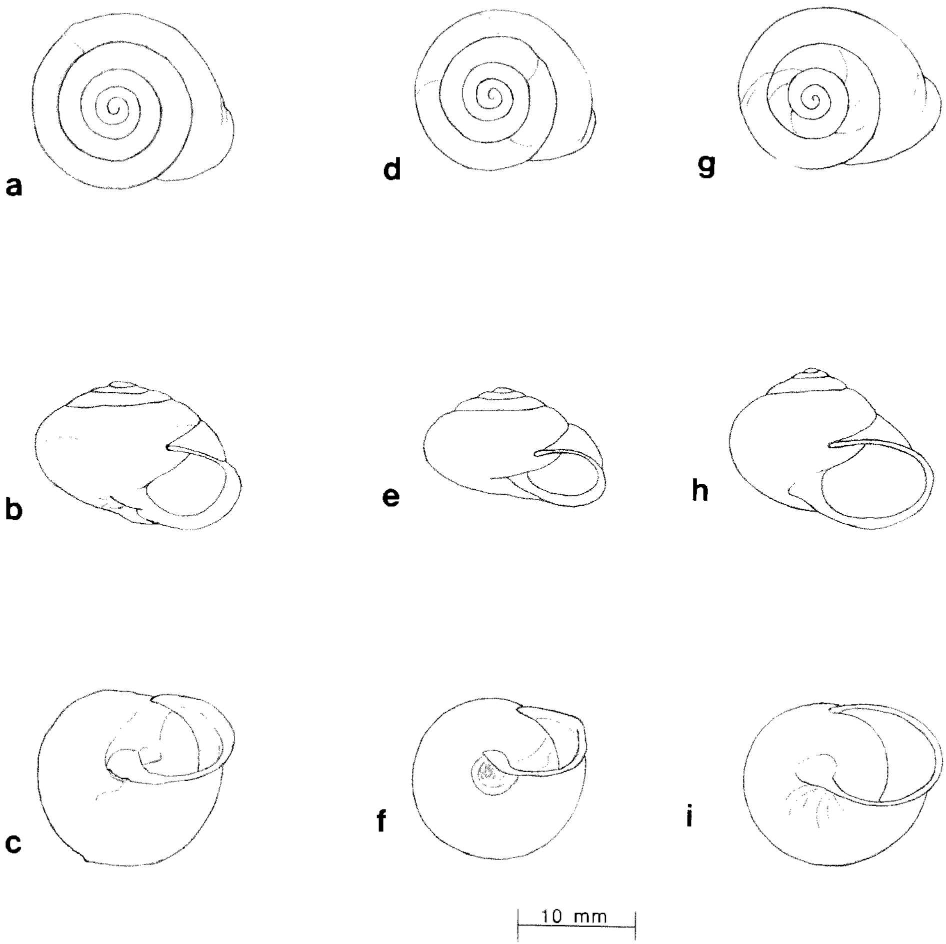


Fig. 444: Shells of *Quistrachia* sp., *Q. herberti* sp. nov. and *Q. turneri* sp. nov.: (a–c) *Q.* sp. WA–417, Glen Florrie Station, 41.1 km from Uaroo boundary along track to Homestead. FMNH 199307; (d–f) Holotype of *Quistrachia herberti*. WAM 771.87. WA–40, SW corner of Mt Herbert, Chichester Range, WA; (g–i) Holotype of *Quistrachia turneri*. WAM 770.87. WA–43, rock cliff on W bank of Kunagunarrina Pool, Turner River, Pilbara, WA. Scale line equals 10 mm. Drawings by Linnea Lahlum.

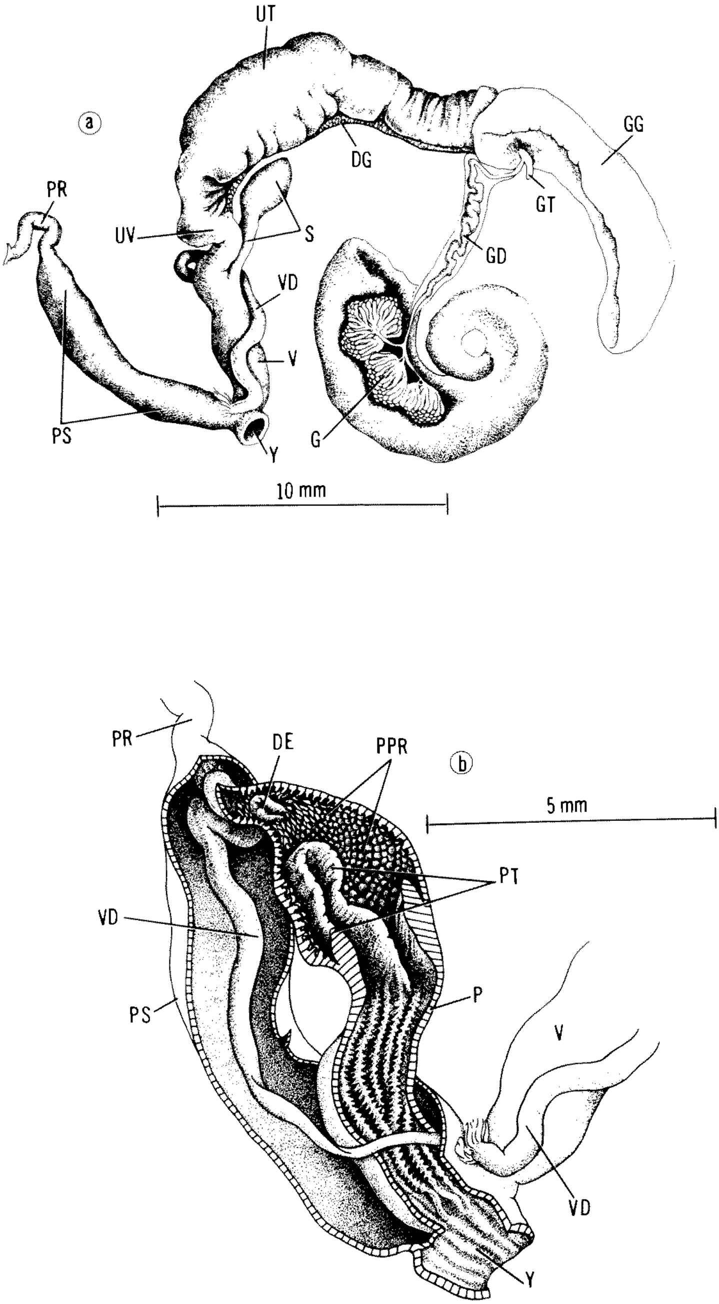


Fig. 445: Genitalia of *Quistrachia herberti* sp. nov.: WA–40, SW corner of Mt Herbert, E of Roebourne, Chichester Range, WA. 29 January 1974. FMNH 182536: (a) whole genitalia, Dissection A; (b) penis interior, Dissection B. Scale lines as marked. Drawings by Elizabeth A. Liebman.

wall with corrugated pilasters, the upper portion with dense pustules. *Q. turneri* sp. nov. (**Figs 446a–b**) has the main pilaster much longer, fused apically and reaching the atrium (Y). The penis chamber wall has pustulose sculpture on upper three-quarters and the vagina is nearly equal in length to the penis. *Q. leptogramma* (Pfeiffer, 1846) (**Figs 448–450**) has the lower half of the main pilaster fused, the lower walls of the penis sheath thickened and the penis wall chamber with all-pustulose sculpture. *Q. monogramma* (Ancey, 1898) (Solem, 1985: 852, figs 214a–c), from the Oscar and Napier Ranges, is most similar, but lacks the corrugated basal pilasters in the penis chamber and has a proportionately longer penis.

Holotype

WAM 771.87, WA–40, SW corner of Mt Herbert, Chichester Range, Western Australia. 21°19'42"S, 117°12'45"E. Collected 29 January 1974 by A. Solem and L. Price. Height of shell 10.9 mm, diameter 16.45 mm, H/D ratio 0.663, whorls 4 3/4, umbilical width 2.2 mm, D/U ratio 7.48.

Paratopotypes

WAM 868.87, WAM 869.87, SAM D18206, AM C.200,763, MV F.60085, QM 46927, FMNH 182379, FMNH 182536, FMNH 182716, 3 LA, 15 DA, 3 LJ, 14 DJ from the type collection.

Paratypes

WESTERN AUSTRALIA: Pilbara: Mt Herbert (WA–182, SW corner of Mt Herbert, WAM 869.87, SAM D18207, AM C.200,764, MV F.60094, QM 46926, FMNH 199220, FMNH 199786, FMNH 199908, 20 DA, 2 LJ, 1 DJ; WA–722, SW corner of Mt Herbert, WAM 870.87, FMNH 205363–4, 6 DA, 1 LJ, 6 DJ); Warla Pool (21°28'S, 116°37'E), Fortescue River (I. Crawford! 1 January 1966, WAM 274.74, 1 DA).

Range

The two known localities for *Quistrachia herberti* (**Map 46**) are in the lower Fortescue River basin (Warla Pool) and on essentially the divide between the westward-draining Fortescue River and Narrina Creek (Mt Herbert), one of several small streams draining northward toward Roebourne. Warla Pool is about 65 km WSW of Mt Herbert. *Q. legendrei* from the Dampier Archipelago (**Maps 40, 46**) is the nearest congeneric species to the W and *Q. turneri* from the Yule and Turner Rivers is the nearest to the NE (**Map 39**).

Diagnosis

Shell medium in size, adult diameter 15.25–19.7 mm (mean 16.84 mm), with 4 1/8+ to 5 1/8– (mean 4 3/4) normally coiled whorls (**Fig. 444d**). Apex and spire moderately elevated, often rounded above (**Fig. 444e**), shell height 9.0–12.55 mm (mean 10.73 mm), H/D ratio 0.518–0.695 (mean 0. 637). Body whorl evenly rounded. Shell apex (**Plate 228e**) minutely pustulose, spire and body whorl (**Plate 228e–f**) with irregular radial ridgelets and periostracal micro-ridgelets. Umbilicus (**Fig. 444f**) open, regularly decoiling, width 1.45–2.9 mm (mean 2.06 mm), D/U ratio 6.52–11.5 (mean 8.36). Body whorl descending moderately behind lip, which is thin and expanded. Shell yellow-brown, lighter below periphery. Based on 46 measured adults.

Genitalia (**Figs 445a–b**) with albumen gland (GG) shorter than prostate-uterus, spermatheca (S) short, with expanded head. Free oviduct (UV) short, curved. Vagina (V) much shorter than slender penis complex. Penis (P) slightly longer than penis sheath (PS). Lower half of penis chamber wall with corrugated pilasters, upper half with dense pustules. Main pilaster (PT) short, bifurcated, occupying middle third of penis chamber. Epiphallic pore (DP) entering through small pilaster.

Central and early lateral teeth of radula (**Plate 234a–c**) with prominent anterior flare, large ectocone, small endocone, high cusp shaft angle, bluntly pointed and only slightly curved cusp tip. Mid-laterals (**Plate 234d**) with enlarged anterior flare. Marginals (**Plate 234e**) and jaw (**Plate 234f**) typical.

Discussion

The Warla Pool example of *Quistrachia herberti* is well worn and falls at the low end (see **Table 160**) of the variation range (diameter 15.25 mm). It could have been collected from streamside drift after a flood and thus may have originated a considerable distance upstream.

The Mt Herbert locality consists of almost barren scree slopes of irregularly shaped red rocks. The few living specimens were found by the author at the base of a cave mouth marked by a withered, scrawny tree. Diligent searches by Laurie Price in other areas failed to locate any material, making this one of the few snails known to have defeated his collecting efforts.

The name *herberti* honours Mt Herbert.

QUISTRACHIA TURNERI SP. NOV.

(Plate 235a–f; Figs 444g–i, 446a–b; Map 39)

Comparative remarks

Quistrachia turneri sp. nov., from the Yule and Turner River basins, Pilbara (**Map 39**), is of medium size (mean diameter 17.23 mm), high spired (**Fig. 444h**, mean H/D ratio 0.792), with an average number (mean 4 3/8) of rather loosely coiled whorls (**Fig. 444g**), the lip narrow and thin and umbilicus closed or a narrow crack. Body whorl evenly rounded. Shell brownish-yellow above, becoming lighter on the base. *Q. herberti* (**Figs 444d–f**) from Mt Herbert (**Map 46**) and *Q. monogramma* (Ancey, 1896) (Solem 1985: 848, 853, figs 213a–c, 215d–f) from the Napier and Oscar Ranges in the S Kimberley (**Map 42**) differ in their widely open umbilici and much lower spires. *Q. legendrei* (**Figs 442a–f**), from the Dampier Archipelago (**Maps 40, 46**), differs most obviously in the looser coiling of its whorls, obtusely angulated periphery, colour suffusion that stops at the periphery and nearly closed or closed umbilicus.

Anatomically (**Figs 446a–b**), *Q. turneri* has the vagina (V) slightly shorter than the penis sheath (PS), the penis (P) essentially equal in length to the sheath, the main pilaster (PT) fused on upper quarter, bifurcated and larger for lower three-quarters. Penis chamber wall mostly pustulose, simple longitudinal pilasters restricted to lower quarter. *Q. herberti* (**Figs 445a–b**) has a very short vagina and main pilaster, with corrugated longitudinal pilasters on lower half of the chamber wall. *Q. monogramma* (see Solem 1985: 852, figs 214a–c), from the Oscar and Napier Ranges, also has a

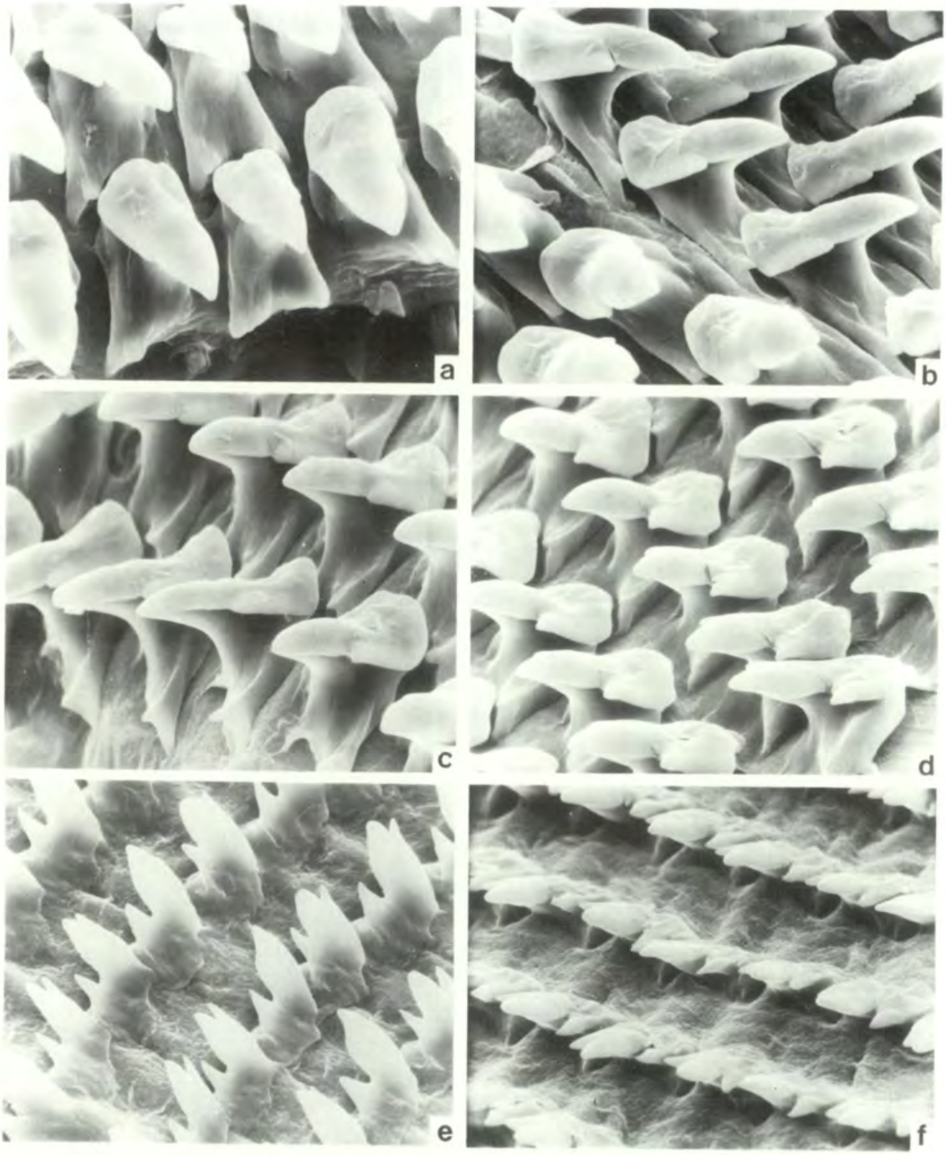


Plate 235: Radular teeth of *Quistrachia turneri* sp. nov.: WA–43, cliff on W bank of Kunagunarrina Pool, Turner River, S of Port Hedland, Pilbara, WA. 1 February 1974. FMNH 182551, Dissection D: (a) high angle view of central and first laterals at 730X; (b) early laterals at 720X; (c) mid laterals at 790X; (d) lateromarginal transition at 790X; (e) mid marginals at 730X; (f) outer marginals at 770X.

shortened main pilaster but has simple longitudinal pilasters on the lower penis chamber wall, a longer vagina and proportionately shorter albumen gland. In *Q. legendrei* (**Figs 443a–b**), the main pilaster is long and bifurcated for its entire length, the penis longer than the sheath and the vagina longer.

Holotype

WAM 770.87, WA–43, in rock cliff on W bank of Kunagunarrina Pool, Turner River, Pilbara, Western Australia. 21°15'S, 118°51'E. Collected 1 February 1974 by A. Solem and L. Price. Height of shell 14.0 mm, diameter 17.9 mm, H/D ratio 0.782, whorls 4 3/8+, umbilicus a very narrow lateral crack.

Paratopotypes

WAM 871.87, WAM 872.87, SAM D18208–9, AM C.200,765, MV F.59464, QM 52987, FMNH 182337, FMNH 182521, FMNH 182551, FMNH 182659, 51 LA, 13 DA, many LJ, 4 DJ.

Paratypes

WESTERN AUSTRALIA: Pilbara: Kunagunarrina Pool, Turner River (WA–183, rock cliffs on W bank above pool, WAM 873.87, WAM 874.87, SAM D18210–1, AM C.200,766, MV 46939, QM F.59479, FMNH 199227, FMNH 199784, FMNH 199890, FMNH 199898–9, 24 LA, 37 DA, many LJ, 13 DJ; WA–721, rock cliffs on W bank just N of pool, WAM 875.87, SAM D18212, FMNH 205361–2, 12 LA, 5 DA, 3 LJ, 2 DJ); Gallery Hill, Woodstock Station (K. & J. Tinley! 21 April 1988, WAM 448.88, WAM 449.88, FMNH 208788, 5 LA, 14 DA, 3 LJ, 20 DJ; P. Berry! 29 April 1988, WAM 444.88, WAM 445.88, 1 DA, 2 LJ; P. Berry! 30 April 1988, WAM 446.88, WAM 447.88, 1 LA, 1 DA, 2 LJ, 1 DJ).

Range

Quistrachia turneri has been collected only from two localities that are about 40 km apart (**Map 39**) – banks of Kunagunarrina Pool of the Turner River (21°15'S, 118°51'E) and Gallery Hill, Woodstock Station on the Yule River (*ca.* 21°40'03"S, 119°02'27"E). It is possible that the headwaters of these two rivers might merge temporarily under "flood of a century" conditions. Thus it is highly probable that other isolated colonies exist. *Q. herberti* from the lower Fortescue drainage (**Map 46**) and *Q. legendrei* from the Dampier Archipelago (**Maps 40, 46**) are the nearest congeneric species.

Diagnosis

Shell medium in size, adult diameter 13.25–18.95 mm (mean 17.23 mm), with 4 1/8– to 4 5/8– (mean 4 3/8) rather loosely coiled whorls (**Fig. 444g**). Apex and spire strongly elevated (**Fig. 444h**), shell height 10.0–15.65 mm (mean 13.65 mm), H/D ratio 0.716–0.870 (mean 0.792). Body whorl evenly rounded. Shell apex minutely pustulose, spire and body whorl with crowded radial ridgelets and anastomosing periostracal micro-ridgelets. Umbilicus (**Fig. 444i**) closed or a very narrow lateral crack. Body whorl descending moderately to strongly behind lip, which is thin, narrowly expanded, with pinkish tone in some live-collected specimens. Colour dark

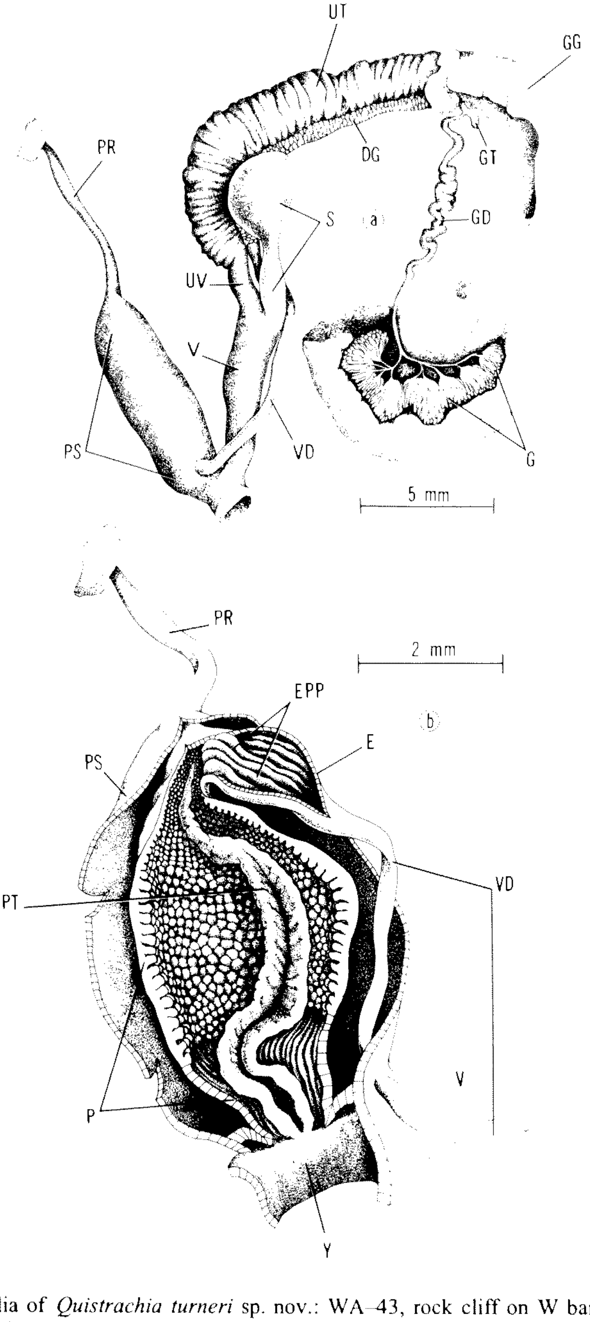


Fig. 446: Genitalia of *Quistrachia turneri* sp. nov.: WA–43, rock cliff on W bank of Kunagunarrina Pool, Turner River, Pilbara, WA. 1 February 1974. FMNH 182551, Dissection C: (a) whole genitalia; (b) interior of penis. Scale lines as marked. Drawings by Elizabeth A. Liebman.

yellow-brown above, gradually becoming lighter on shell base. Based on 165 measured adults.

Genitalia (**Figs 446a–b**) with albumen gland (GG) much shorter than prostate-uterus, spermatheca (S) medium length with globose head lying just above base of prostate-uterus. Free oviduct (UV) short, not curved. Vagina (V) slightly shorter than penis sheath (PS). Penis (P) about equal in length to sheath. Main pilaster (PT) large and bifurcated on lower three -quarters, fused and tapering in upper quarter. Most of penis chamber wall densely pustulose, lower quarter with simple longitudinal pilasters.

Central and early lateral teeth of radula (**Plate 235a–b**) with very prominent anterior flare, small ectocone and very small endoconal notch, normal cusp shaft angle, pointed and slightly curved cusp tip. Late laterals and lateromarginal transition (**Plate 235c–d**) with enlarged anterior flare and ectocone. Marginals (**Plate 235e–f**) and jaw typical.

Discussion

Both known colonies of *Quistrachia turneri* are from massive boulder jumbles that can receive wind-blown moisture from semi-permanent bodies of water. The snails seal to rocks or onto other snail shells with a mucoid epiphragm that shows no indication of calcification. Most of each population probably are deep within the jumbles. Dead examples occasionally can be seen washed out in the open at cliff bases. On the rare occasions that we were able to find "turnable rocks" or small talus accumulations, individuals were common.

Dissection showed no significant genital differences between the two colonies. They do differ in size:

Mean of:

	Height	Diameter	H/D ratio	Whorls
Gallery Hill (23)	11.63	14.98	0.777	4 1/2+
Kunagunarrina (142)	13.99	17.60	0.795	4 3/8–

The reduced whorl count of the larger Kunagunarrina Pool shells suggests that the populations may have been isolated for a considerable period. Normally in Australian camaenids, the smaller sized shells would have the lesser whorl count, suggesting that the size difference results merely from earlier cessation of growth. Higher whorl count at smaller size suggests actual dwarfing has taken place.

The name *turneri* refers to the Turner River.

QUISTRACHIA LEPTOGRAMMA (PFEIFFER, 1846)

(Plate 236a–d; Figs 447a–c, 448a–c, 449a–b, 450; Map 41)

Helix leptogramma Pfeiffer, 1846, *Proc. Zool. Soc. London,* **1845:** 127 – Cygnet Bay, Western Australia; Pfeiffer 1848, *Monog. Helic. viv.,* **1:** 322; Reeve 1852, *Conch. Icon.,* **7:** plt. LXXXII, fig. 437 – South Australia (error); Cox 1864, *Cat. Aust. Land Shells,* p. 15; Cox 1868, *Monog. Aust. Land Shells,* pp. 41–42, plt. 11, fig. 4 (copied from Reeve); E. A. Smith 1874, *Zool. of the Voyage of H. M. S. Erebus & Terror,* 1839–1843, 2: Mollusca, p. 2, plt. 4, fig. 18 (two views); Pilsbry 1889, *Man. Conch.*, (2) **4:** plt. 36, fig. 33 (copied from Reeve); Solem 1979, *Rec. Western Aust. Mus., Suppl.,* **10:** 10 – citation of name only.

Helix (*Rhagada*) *leptogramma* Pfeiffer, Pilsbry 1894, *Man. Conch.*, (2) **6:** 186; E. A. Smith 1894, *Proc. Malac. Soc. London*, **1:** 89 – Roebuck Bay, South of King Sound (J. J. Walker).

Thersites (*Rhagada*) *leptogramma* (Pfeiffer), Pilsbry 1894, *Man. Conch.*, (2) **9:** 136 – check list citation.

Rhagada leptogramma (Pfeiffer), Hedley 1916, *Jour. Roy. Soc. Western Aust.*, **1:** 70 – check list citation; Richardson, 1985, *Tryonia*, **12:** 265 – check list citation.

Globorhagada leptogramma (Pfeiffer), Iredale 1938, *Aust. Zool.,* **9** (2): 114 – check list citation; Iredale 1939, *Jour. Roy. Soc. Western Aust.,* **25:** 72–73, plt. V, fig. 18 – Broome, Western Australia.

Quistrachia leptogramma (Pfeiffer, 1846), Solem 1985, *Rec. Western Aust. Mus., Supplement* **20:** 847.

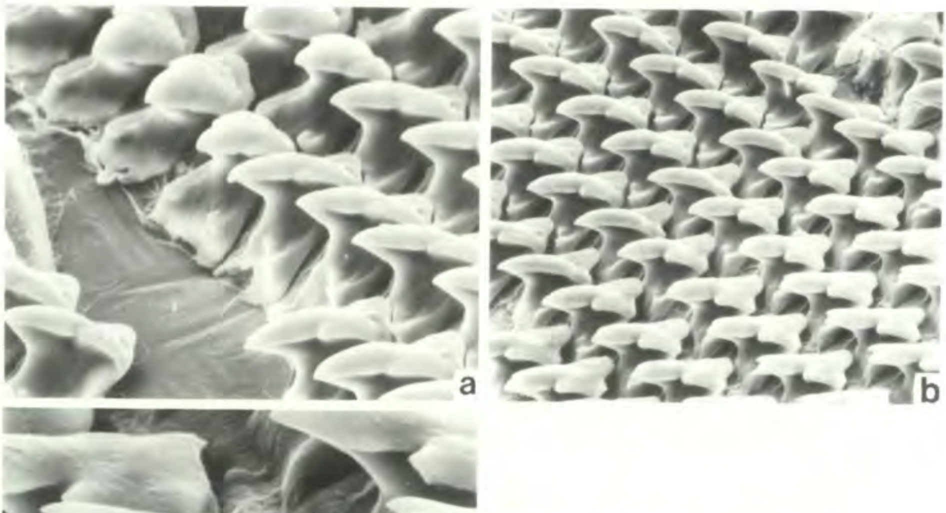


Plate 236: Radular teeth and jaw of *Quistrachia leptogramma* (Pfeiffer, 1846). WA–378, Wallis garden, Broome, WA. 23–25 February 1977. FMNH 199796: (a) central and early laterals at 640X; (b) latero-marginal transition at 495X; (c) early marginals at 1525X; (d) jaw at 55X.

Comparative remarks

Quistrachia leptogramma (Pfeiffer, 1846), which ranges throughout Dampier Land, WA (**Map 41**), is relatively large (mean diameter 17.50 mm), globose (**Fig. 447b**, mean H/D ratio 0.862), with an average count (mean 4 5/8+) of somewhat loosely coiled whorls (**Fig. 447a**), body whorl inflated (**Fig. 447b**), lip thin and moderately expanded and umbilicus usually narrowly open (mean D/U ratio 14.0). Body whorl evenly rounded. Shell with several red spiral bands, narrow to medium in width, ground colour yellow-white. Shell microsculpture not observed.

The widely umbilicated (mean D/U ratio 6.45), low spired (mean H/D ratio 0.599) *Q. monogramma* (Ancey, 1898) from the Napier and Oscar Ranges, S Kimberley (**Map 42**, Solem 1985: 848, 853, figs 213a–c, 215d–f) lacks an inflated body whorl and generally has only one faint red spiral colour band. *Q. herberti*, from the Pilbara (**Map 46**), has a narrower umbilicus and much lower spire (**Table 160**) and lacks the inflated

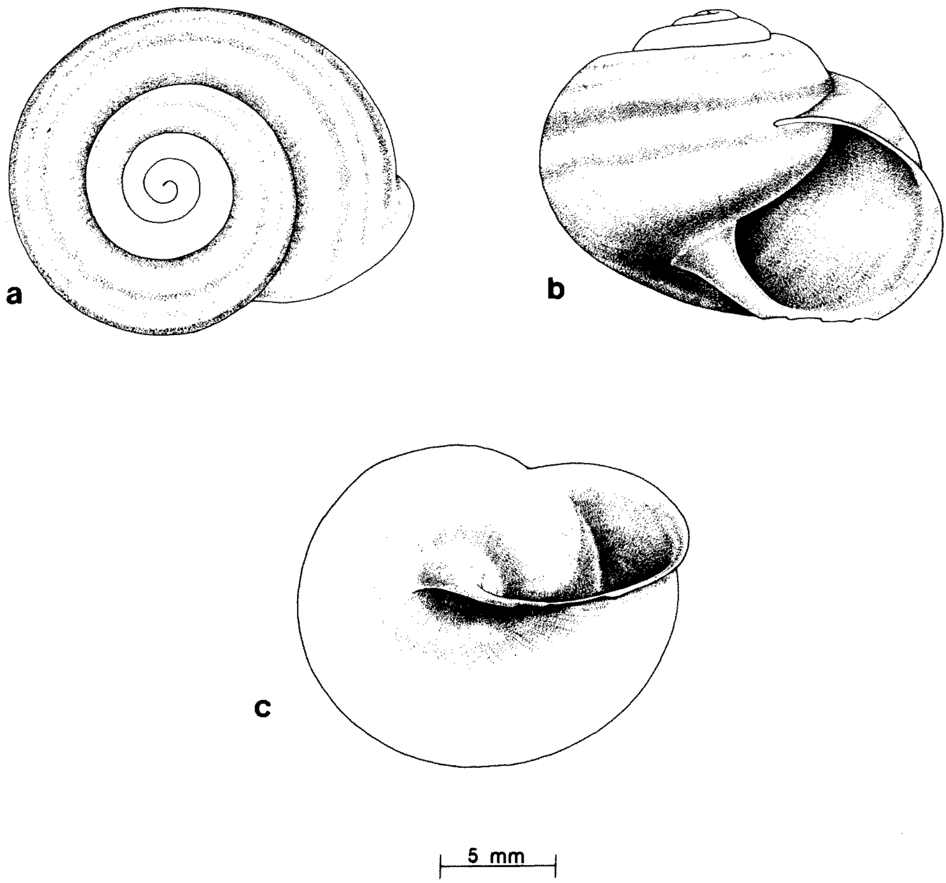


Fig. 447: Shell of *Quistrachia leptogramma* (Pfeiffer, 1846): Possible lectotype of *Helix leptogramma* Pfeiffer, 1846. BMNH 1844.17.11.55. Australia. Scale line equals 10 mm. Drawings by Linnea Lahlum.

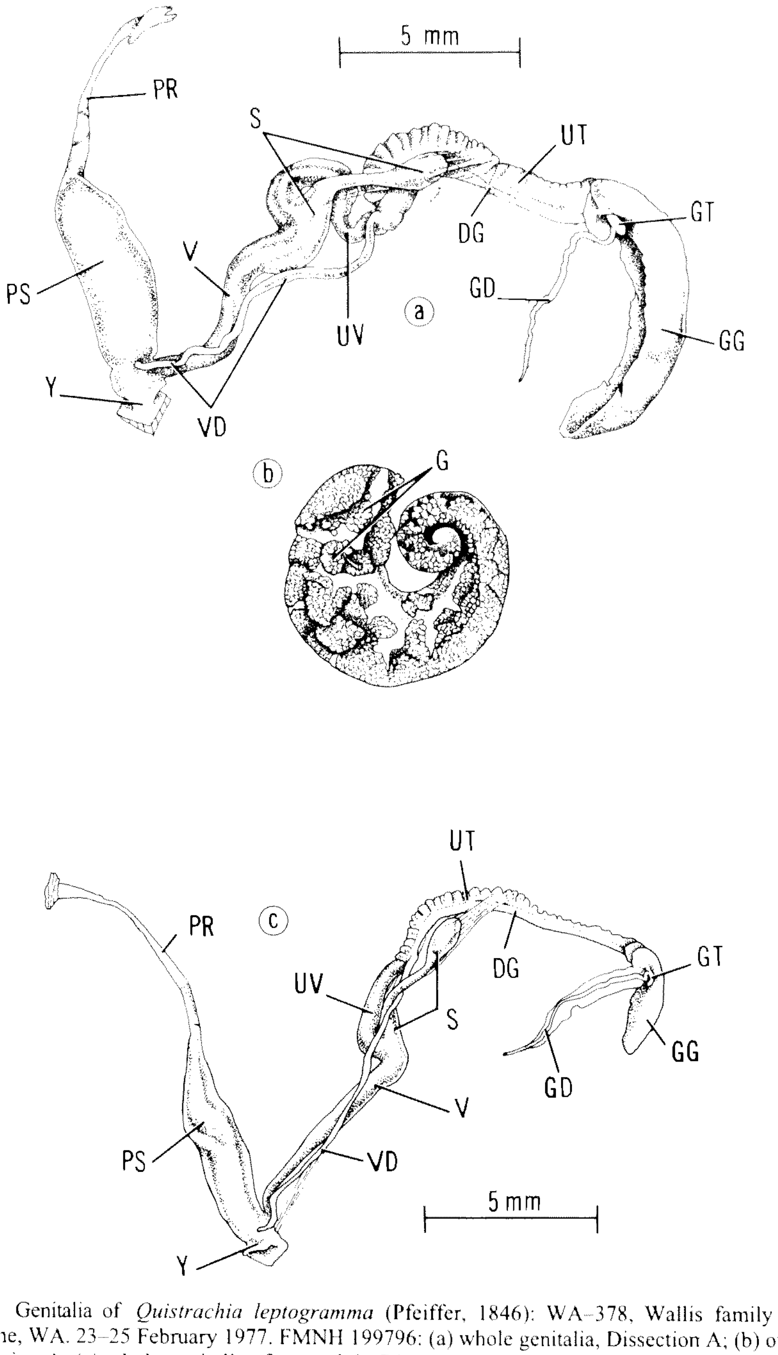


Fig. 448: Genitalia of *Quistrachia leptogramma* (Pfeiffer, 1846): WA–378, Wallis family garden, Broome, WA. 23–25 February 1977. FMNH 199796: (a) whole genitalia, Dissection A; (b) ovotestis, Dissection A; (c) whole genitalia of new adult, Dissection B. Scale lines equal 5 mm. Drawings by Elizabeth A. Liebman.

body whorl. The only species with an inflated body whorl (**Fig. 433e**), *Q. lefroyi* from the Cape Range (**Map 32**), has a closed or nearly closed umbilicus and colour banding restricted to the shell periphery.

Anatomically (**Figs 448a–c, 449a–b, 450**), *Q. leptogramma* has the vagina (V) slightly longer than the penis sheath (PS), which has thick lower walls, the penis (P) about 1.5 times the penis sheath length, the main pilaster (PT) fused basally and bifurcated on upper half, penis chamber wall with small to medium pustules, upper chamber (**Fig. 450**) sometimes with a verge-like structure developed. The other species with a thick-walled penis sheath, *Q. monogramma* (see Solem, 1985: 852, fig. 214b) has a shorter penis and short main pilaster that is not fused basally. The nearest WA species, *Q. herberti* (**Figs 445a–b**) and *Q. turneri* (**Figs 446a–b**) have the penis sheath thin-walled, with an all-pustulose walled penis chamber (*turneri*) with the main pilaster fused apically or with a part-longitudinal pilastered wall (*herberti*) and a very short, medially located main pilaster.

Possible lectotype

BMNH 1844.17.11.55. Australia. Height of shell 13.6 mm, diameter 17.5 mm, H/D ratio 0.777, whorls 4 1/4, umbilical width 1.3 mm, D/U ratio 13.5.

Syntype

BMNH 1844.17.11.56, 1 DA from the type locality.

Material studied

WESTERN AUSTRALIA: Dampier Land: Broome (WA–378, Wallis Garden, M. Wallis! 23–25 February 1977, FMNH 199796 7, 2 LA, 18 LJ, 3 DJ; WA–415, SE corner Herbert and Anne Streets, WAM 865.87, SAM D18204, AM, FMNH 199370, FMNH 199767, 3 LA, 5 DA, 9 LJ, 3 DJ; WA–719, Anne Street, between Herbert and Walcott Streets, FMNH 205357–8, 3 LA, 3 LJ, 2 DJ); Coulomb Point (W. H. Butler! July 1971, WAM 247.74, 1 DA, 2 DJ); Cape Bertholet (E of, B. R. Wilson and S. M. Slack-Smith! 5 September 1975, WAM 404.75, many fragments); Broome-Cape Leveque road (WA–403, 80 km in, FMNH 199349, 1 DA; WA–404, 90.3 km in, WAM 866.87, SAM D18205, AM, QM, MV, FMNH 199334, FMNH 199789, 3 LA, 22 DA, 7 DJ); Broome-Cape Leveque road, S of Beagle Bay turnoff (WA–283, 30.9 km S, FMNH 199521, 1 DA; WA–188, 26.2 km S, FMNH 199933, 1 DA, 2 DJ; WA–189, 16.1 km S, FMNH 199380, 2 DA, 3 DJ); Cape Leveque (AM C.64889, 1 DA; WA–185, Cape Leveque lighthouse, FMNH 199937, 2 DA; WA–186, Bulgan Creek, WAM 867.87, FMNH 199778, FMNH 200110, 10 DA); One Arm Point (WA–184, liana patch behind Cygnet Bay Pearl Fisheries, FMNH 199783, FMNH 200272, 3 DA, 2 DJ).

Range

Quistrachia leptogramma has been collected from gardens in Broome and then N to the tip of Dampier Land at Cape Leveque and One Arm Point (**Map 41**). No collections of land snails have been made in the area between Coulomb Point and Broome, so that this gap probably is an artifact. The nearest congeneric species is *Quistrachia monogramma* from the Oscar and Napier Ranges, on the S margin of

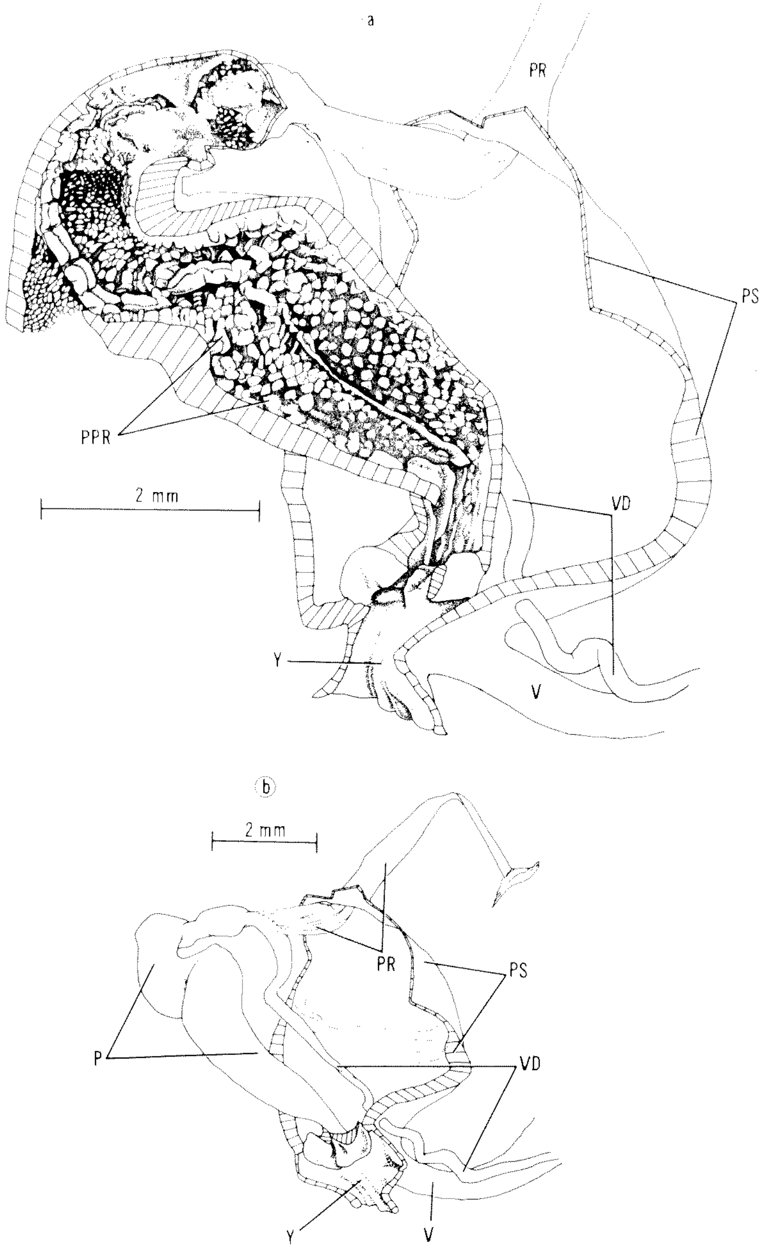


Fig. 449: Genitalia of *Quistrachia leptogramma* (Pfeiffer, 1846): WA–378, Wallis family garden, Broome, WA. 23–25 February 1977. FMNH 199796, Dissection A: (a) interior of penis; (b) opened penis sheath. Scale lines equal 2 mm. Drawings by Linnea Lahlum.

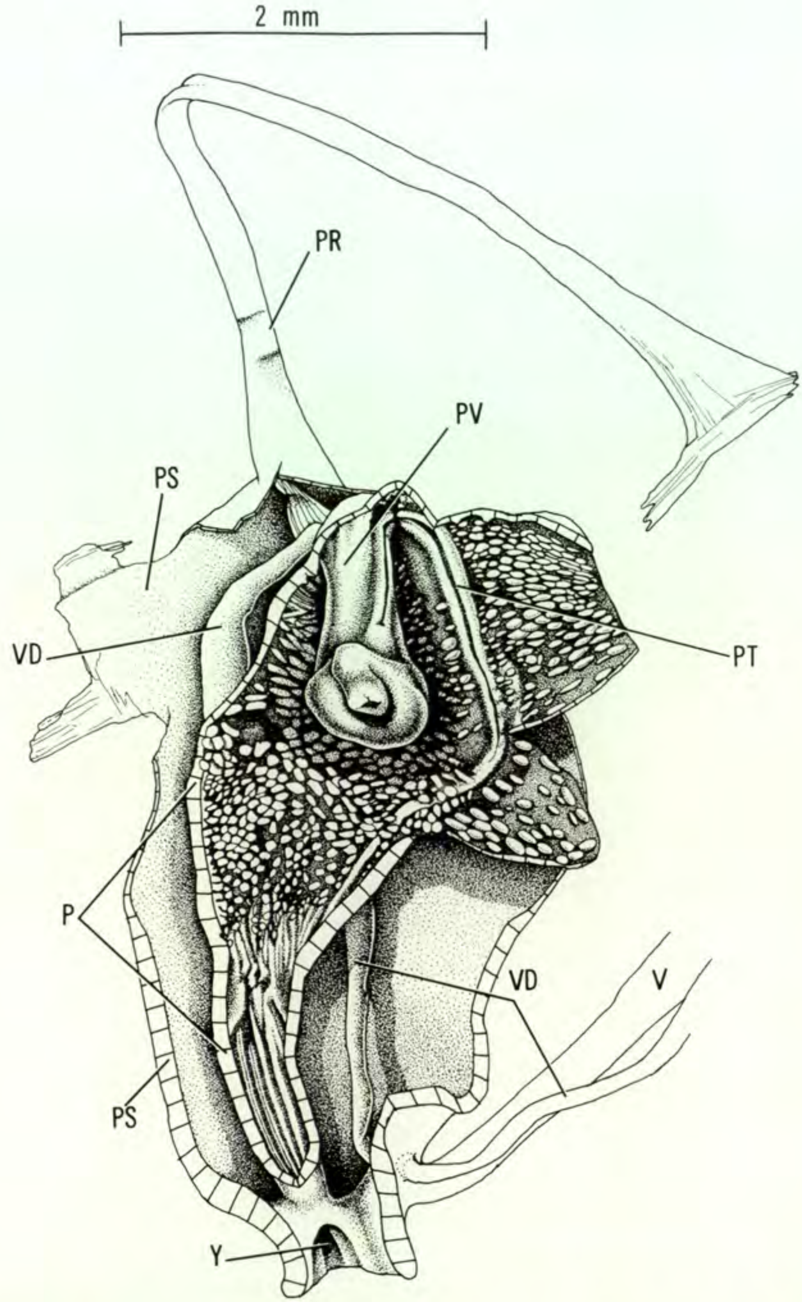


Fig. 450: Penis interior of new adult of *Quistrachia leptogramma* (Pfeiffer, 1846): WA–378, Wallis family garden, Broome, WA. 23–25 February 1977. FMNH 199796, Dissection B. Scale line equals 2 mm. Drawing by Linnea Lahlum.

the Kimberley to the E (**Map 42**) and then *Q. turneri* (**Map 39**) from the Yule and Turner River basins S of Port Hedland in the Pilbara and well S of the Great Sandy Desert.

Diagnosis

Shell relatively large, adult diameter 13.75–21.4 mm (mean 17.50 mm), with 4 1/4– to 5+ (mean 4 5/8+) somewhat loosely coiled whorls. Apex and spire moderately elevated (**Fig. 447b**), not rounded above, shell height 11.5–18.3 mm (mean 15.09 mm), H/D ratio 0.817–0.946 (mean 0.862). Body whorl evenly rounded. Shell microsculpture unknown, as all available material worn. Umbilicus (**Fig. 447c**) varying from narrowly open to a small lateral slit, width 0.9–1.9 mm (mean 1.30 mm), D/U ratio 9.87–19.6 (mean 14.0). Body whorl descending moderately behind lip, which is thin and moderately expanded. Several red spiral colour bands of varying width present. Based on 54 measured adults.

Genitalia (**Figs 448a–c, 449a–b, 450**) with albumen gland (GG) a little shorter than prostate-uterus, spermatheca (S) medium in length, head slightly expanded. Free oviduct (UV) long, curved, vagina (V) slightly longer than penis sheath (PS). Penis (P) about 1.5 times length of sheath, which has thickened walls on lower half. Main pilaster (PT) fused on lower half, bifurcated apically. Entire wall of penis chamber densely pustulose.

Central and early lateral teeth of radula (**Plate 236a**) with prominent anterior flare, small ectocone, normal cusp shaft angle, bluntly pointed and slightly curved cusp tip. Late laterals (**Plate 236b**) with more prominent anterior flare and enlarged ectocone. Lateromarginal transition and early marginals (**Plate 236c**) typical. Jaw (**Plate 236d**) with prominent vertical ribs that are reduced on side margins.

Discussion

The several spiral red bands found on the shell of *Quistrachia leptogramma* (**Figs 447a–c**) have resulted in its traditional placement in *Rhagada*.

Few live examples have been found except from the gardens and shrubs in Broome itself. Whether this is now a rare species in Dampier Land because of the frequent burning of forested areas, or whether we simply have not focused on its aestivation habits, is unknown.

Specimens from Broome (**Table 164**) and Coulomb Point are distinctly smaller than those from the northern part of Dampier Land. Only limited numbers have been collected at most stations. None of the available shells had sufficiently unworn surfaces so that observation of either apical or spire microsculpture was possible.

ADDENDUM TO SYSTEMATIC REVIEW

A few long-dead shells collected by William Turnbull and Ernest Lundelius are sufficiently worn so that no trace of shell colour or sculpture can be detected. They were found on top of a mesa located 22 km N of Skull Springs, Oakover River area (Nullagine 1:250,000 map SF 51–5 – 287:413).

They are very different from any known Pilbara or Kimberley species but are too worn to enable adequate description. There are intriguing similarities to the Flinders

Range of South Australia genus *Lacustrelix* Iredale, 1937 (see Solem 1992: 182–183) and to the Red Centre genus *Minimelon* Solem, 1993 (see Solem, 1993: 1217–1220). It thus has potentially important implications as to the possible origins of the Sinumeloninae radiation along the west coast and phylogeny within the subfamily.

Illustrations of the shell (**Figs 451a–c**) and a summary of shell features are presented below.

NEW GENUS, NEW SPECIES

(Figs 451a–c, Map 44)

Diagnosis

Shell small, adult diameter 9.7–10.5 mm (mean 10.07 mm), with 3 5/8 to 4 1/8– (mean 3 7/8–) normally coiled whorls (**Fig. 451a**). Apex slightly elevated, not rounded above (**Fig. 451b**), shell height 5.55–6.45 mm (mean 5.95 mm), H/D ratio 0.534–0.632 (mean 0.591). Body whorl evenly rounded. Umbilicus (**Fig. 451c**) open, last whorl with a columellar groove, decoiling more rapidly, width 1.5–1.95 mm (mean 1.70 mm), D/U ratio 5.30–6.56 (mean 5.96). Body whorl descending slightly to moderately behind lip, which is narrowly expanded and thickened on palatal and basal margins, more expanded on columellar margin with rolled edge. Parietal wall with thick callus. Shell sculpture and colour unknown because of extensive wear. Based on 8 measured adults.

Material studied

WESTERN AUSTRALIA: Pilbara: from top of mesa, 22 km N of Skull Springs, Oakover River (W. Turnbull and E. Lundelius! 27 September 1976, WAM 465.77, FMNH 199068, 8 DA, 2 DJ).

Discussion

Species of the Flinders Range sinumelonid genus *Lacustrelix* are much larger and more widely umbilicated, lack the heavy parietal callus and have tighter whorl coiling (see Solem 1992: 182–183, figs 77, 78), but agree in the umbilical groove on the columellar wall. *Minimelon colmani* Solem, 1993, from the Rawlinson to Blackstone Ranges in the Red Centre, agrees in size, but has an increased whorl count, much narrower umbilicus, higher spire and pattern of whorl increment.

Without dissection, the affinities of this unquestionably new genus and species cannot be determined, although recently dead examples that retained both shell colour and sculpture possibly would yield useful indications. Thus I am calling attention to this most interesting population (**Map 44**).

SUMMARY DISCUSSION

As briefly outlined at the beginning of the Systematic Review (pp. 1467–1468), patterns of distribution and structure found in the camaenids living in the areas from Dampier Land to Geraldton and then SE through the Nullarbor have been greatly influenced by the dramatic differences in moisture regimes that exist.

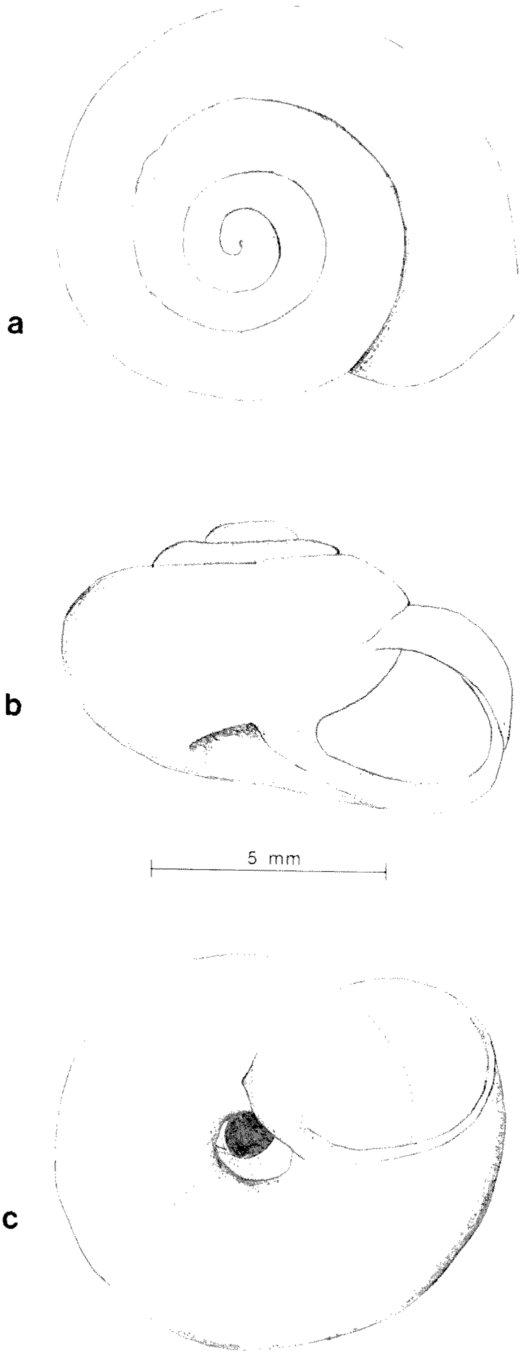


Fig. 451: Shell of probable gen. nov., sp. nov.: Stn 24, mesa 22 km N of Skull Springs, Oakover River, Pilbara, WA. WAM 465.77. Scale line equals 5 mm. Drawings by John Slapcinsky.

Table 165: List of taxa reviewed and material measured

GENUS & SPECIES	SPECIMENS	TOTALS
SUBFAMILY SINUMELONINAE		
Pleuroxia Ancey, 1887		
abstans Iredale, 1939	3	
bethana, sp. nov.	56	
elfina Iredale, 1939	583	
polypleura (Tate, 1899)	906	
oligopleura (Tate, 1894)	492	
TOTAL SPECIMENS		2,040
Sinumelon Iredale, 1930		
jimberlanensis, sp. nov.	31	
nullarboricum (Tate, 1879)	908	
kalgum Iredale, 1939	246	
tarcoolanum Solem, 1992	210	
vagente Iredale, 1939	88	
TOTAL SPECIMENS		1,483
Falspleuroxia, gen. nov.		
overlanderensis, sp. nov.	620	
species	1	
TOTAL SPECIMENS		621
Plectorhagada Iredale, 1933		
plectilis (Benson, 1853)	677	
rovina Iredale, 1939	1	
gascoynensis (E. A. Smith, 1894)	7	
carcharias (Pfeiffer, 1864)	1,160	
meilgana, sp. nov.	6	
scolythra, sp. nov.	375	
TOTAL SPECIMENS		2,226
Strepsitaurus, gen. nov.		
cardabius, sp. nov.	232	
milyeringus, sp. nov.	12	
williami, sp. nov.	146	
ningaloo, sp. nov.	463	
rugus (Cotton, 1953)	420	
TOTAL SPECIMENS		1,273
Promonturconchum, gen. nov.		
superbum, sp. nov.	253	
TOTAL SPECIMENS		253
Caperantrum, gen. nov.		
polygyrum, sp. nov.	229	
TOTAL SPECIMENS		229

TOTAL SINUMELONINAE = 8,125

Table 165 (continued).

GENUS & SPECIES	SPECIMENS	TOTALS
SUBFAMILY PLEURODONTINAE		
Rhagada Albers, 1860		
torulus (Ferussac, 1819)	347	
globosa, sp. nov.	269	
capensis, sp. nov.	488	
convicta (Cox, 1870)	721	
pilbarana, sp. nov.	55	
perprima Iredale, 1939	19	
richardsonii (E. A. Smith, 1874)	278	
radleyi Preston, 1908	135	
plicata Preston, 1914	70	
minima, sp. nov.	65	
intermedia, sp. nov.	104	
elachystoma (von Martens, 1878)	77	
aff. *elachystoma*	28	
angulata, sp. nov.	48	
dampierana, sp. nov.	109	
dringi (Pfeiffer, 1846)	218	
reinga (Pfeiffer, 1846)	64	
bulgana, sp. nov.	398	
cygna, sp. nov.	153	
TOTAL SPECIMENS		3,646
TOTAL PLEURODONTINAE = 3,646		
SUBFAMILY POSITION UNCERTAIN		
Quistrachia Iredale, 1939		
warroorana, sp. nov.	357	
lefroyi, sp. nov.	591	
species	7	
barrowensis, sp. nov.	105	
montebelloensis (Preston, 1914)	84	
legendrei, sp. nov.	23	
herberti, sp. nov.	46	
turneri, sp. nov.	165	
leptogramma (Pfeiffer, 1846)	54	
monogramma (Ancey, 1898)	662	
TOTAL SPECIMENS		2,094
TOTAL SUBFAMILY UNCERTAIN = 2,094		
GRAND TOTAL ADULT SPECIMENS MEASURED = 13,865		

The Kimberley and Dampier Land have a typical monsoon climate, with a well-defined and dependable summer wet season. In the wettest coastal areas, at Kalumburu and the Mitchell Plateau, the median annual rainfall is about 1,565 mm (Solem & Christensen 1984: 473, Table 1), of which 92.9% falls in November through March and 6.2% in April and October. Essentially no rainfall occurs normally from May

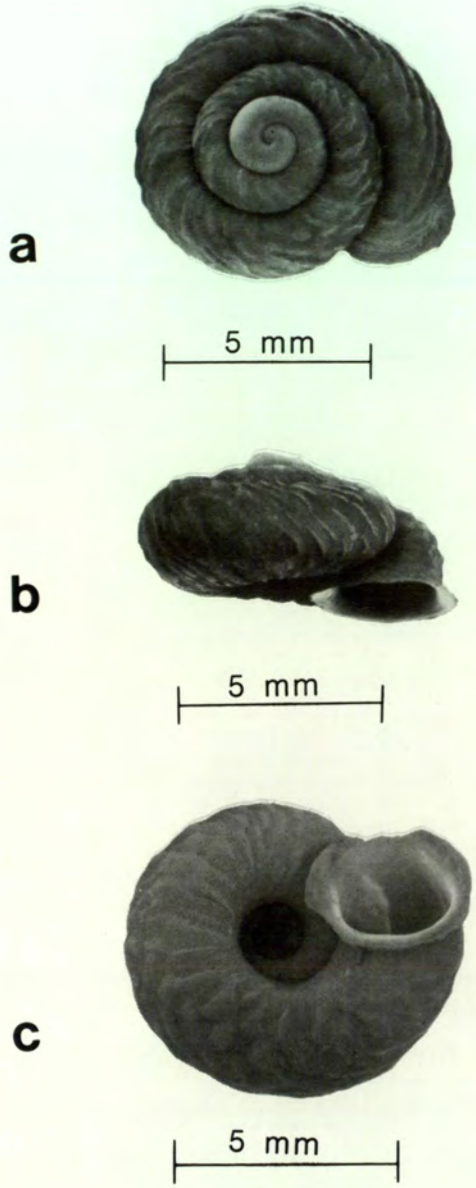


Fig. 452: Shell of *Strepsitaurus milyeringus* sp. nov.: WA–1084, Milyering Gorge, Cape Range, WA. Holotype. WAM 948.87. Scale lines as marked.

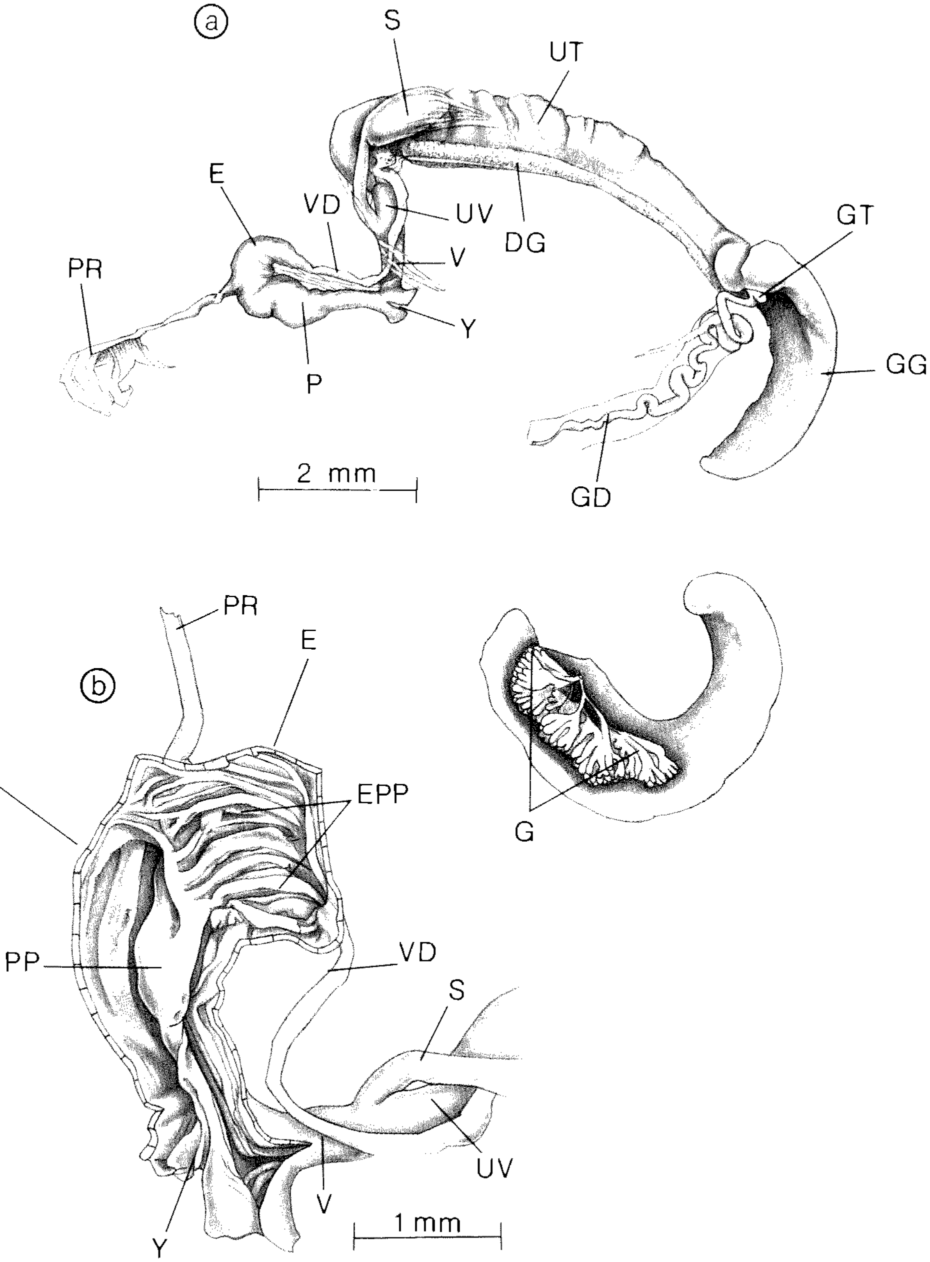


Fig. 453: Genitalia of *Strepsitaurus milyeringus* sp. nov.: WA–1084, Milyering Gorge, Cape Range, WA. 27 May 1989. FMNH 221762, Dissection A: (a) whole genitalia; (b) penis interior. Scale lines as marked. Drawings by Linnea Lahlum.

through September. On the margins of the Kimberley, at such stations as Napier Downs on the SE (Solem & Christensen 1984: 473, Table 1), Carlton Hill, Ivanhoe and Kununurra on the E margins (Solem, 1988b: 83, Table 1), the wet season is shorter, the number of rain days is reduced and the total wet season rainfall is only 640–735 mm. Further inland, on the S and SE margins of the Kimberley, at Lissadell and Halls Creek, the median annual rainfall drops to 581 mm and 497 mm, respectively (Solem 1988b: Table 1). To the NE, in the "Top End" of the NT, the wet season rainfall returns to the 1,500 mm level. All areas share the pattern of rainfall

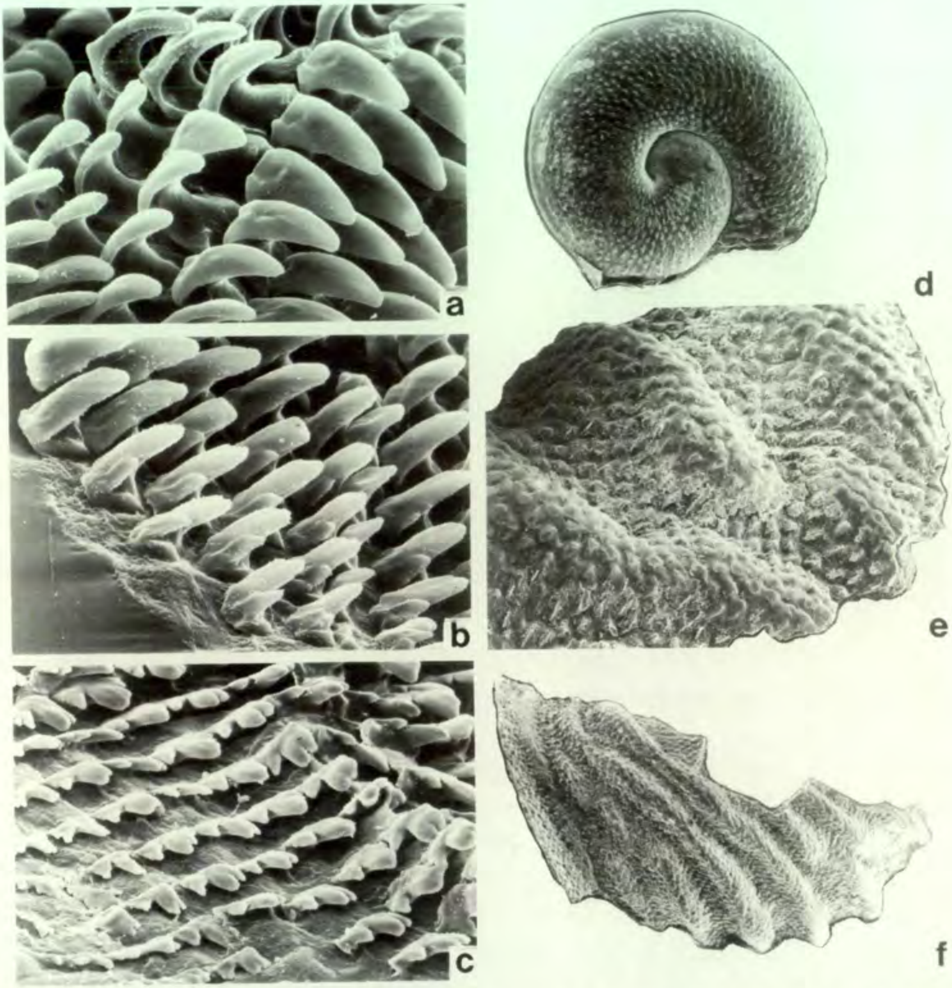


Plate 237: Radular teeth and shell sculpture of *Strepsitaurus milyeringus* sp. nov.: WA–1084, S side of Milyering Gorge, NW Cape Range, WA. 27 May 1989. FMNH 221762, Dissection A: (a) central and early lateral teeth at 690X; (b) latero-marghinal transition at 710X; (c) outer marginal teeth at 620X; (d) apex at 22X; (e) early spire at 35.5X; (f) body whorl sculpture at 12.4X.

concentrated into a defined wet season, the dryer areas having fewer and lighter falls than do the wet areas.

The camaenid land snails aestivate throughout the dry season. They have a pattern of reproductive maturation and seasonality that is adapted efficiently to this dependable wet season (Solem & Christensen 1984). To summarize briefly, the snails reach approximately half adult size in the wet season of their birth; complete shell growth and become male-mature near the end of their second wet season; function as males at the beginning of their third wet season and become female-mature late in the third wet season; function as males and females from their fourth wet season on and probably live in excess of 10 years. Marked adults (at least three years old) in the Napier Range were recaptured four years later, demonstrating a minimum seven year life span.

Seasonal variation also has a standard pattern. The ovotestis swells to functioning size late in the dry season and produces sperm. Activated by the first rains, the snails mate reciprocally and feed, then return to aestivation in the normal 10–40 day interval between first and second rains. Eggs are produced, fertilised and encapsulated, so that they can be deposited into the soil when the second set of rains reactivates the snails. Several matings and presumably egg layings occur during the first third of the wet season. About the middle of the wet season, the ovotestis and hermaphroditic duct shrink to about 5% of functioning volume, with the "digestive gland" or "liver" expanding into the vacated space as it swells with stored food. The prostate and uterus

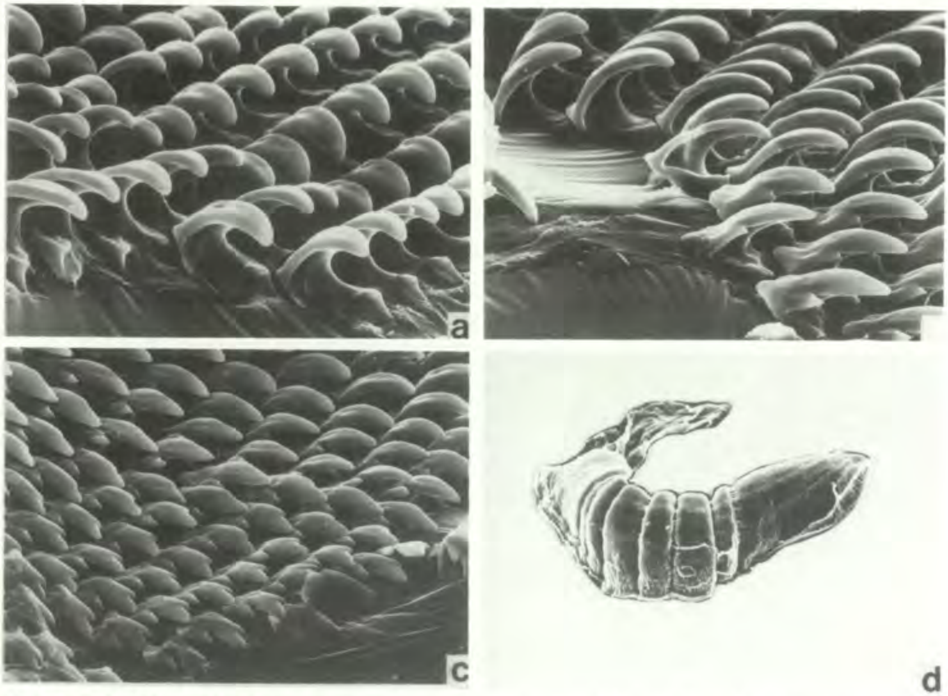


Plate 238: Radular teeth of *Strepsitaurus williami* sp. nov.: WA–1079, Thomas Carter Lookout, E side Cape Range, WA. FMNH 221744, Dissection A: (a) central and laterals at 550X; (b) latero-marginal transition at 580X; (c) marginals at 435X; (d) jaw at 96X.

also are reduced in diameter. Masses of allosperm are held in the spermatheca, seemingly little altered until until late in the dry season, when the reduction and disappearance of these masses coincides with the activation and size increase of the ovotestis.

The above pattern is adjusted to a predictable and seasonal wet season, followed by an extended dry season. Once the basic pattern evolved, the ability to survive a more extended dry period would have been a trivial adjustment. If the rainfall remained predictable as to season.

The graded climatic situation that exists along the W coast of WA presents an different pattern of moisture availability (**Table 166**). Three general trends are evident: 1) the total annual rainfall drops dramatically S of Broome, and does not increase again substantially until the latitude of Geraldton; 2) the number of rain days is greatly reduced between Wallal Downs and Mia Mia but increases dramatically at Carnarvon and Shark Bay; and 3) the percentage of the rain falling in the "wettest" set of months generally is significantly reduced.

What this table cannot demonstrate is the great variation and unpredictability from year to year. The median of 186 mm at Cardabia Station just S of North West Cape is based upon 57 complete years of records between 1913 and 1974. The year of greatest rainfall, 1918, had 611 mm, resulting from one massive storm system in February (309 mm) and a second one in May (217 mm). In contrast, ten years had 49–99 mm total rainfall; 19 years had 100–199 mm; 14 years had 200–299 mm; 11 years had 300–399 mm; two years had 400–449 mm and the one year had 611 mm.

Geraldton lies on the N fringe of the "winter rains" area. It thus shows a significant increment in total rain, rain days and a marked seasonality, although reversed from that of the Kimberley.

At Shark Bay and Carnarvon, there are many "dribbles of rain", whereas from Mia Mia to Wallal Downs there tends to be a few "drenchings" – but at unpredictable times. The coastal sites do benefit from heavy fogs, some of which may activate local populations for a few hours. But the parameters of life for the camaenids have changed drastically. Not only is there no set period for a wet season, there is no guarantee that the next rain will come within a few weeks – or even months.

Snails living in the area of reduced and unpredictable rainfall cannot afford to have a set season for reproduction. They cannot predict when it will rain and thus cannot have the ovotestis (G) and "liver" alternate in size. The seasonal pattern of ovotestis size in Kimberley camaenids is typified by *Amplirhagada burnerensis* (Solem 1981a: 241–242, figs 52a, d, f, 53), in which it reached a huge size when the wet season was late and was greatly decreased in size during the late wet and most of the dry season. In contrast, the number of lobes in the *Rhagada* and *Quistrachia* species is reduced and there is, at most, minor variation in the size of these lobes, regardless of the month of collection, in species found between 80 Mile Beach and the Shark Bay area (see **Figs 404–449**).

The W coast species also cannot afford the luxury of exchanging sperm after the first rain, then counting on being able to lay eggs at most a few weeks later when the second rains come (it may be up to a year or more later!). They must mate and reproduce whenever they have the chance. Whereas in the Kimberley, the number of "Snail Activity Nights" each year may number 78–104 (Solem 1988b: 69) and are

Table 166: Rainfall patterns, SW Kimberley to Geraldton

Station & years of record	Median annual in mm	Average rain days	Main months of rainfall: Months	mm	% of annual total
Napier Downs, Kimberley (1951–1976)	644	40	Dec-Mar	552	85.7%
Lombardina Mission, Dampier Land (1951–1973)	633	34	Dec-Mar	405	64.0%
Broome, Dampierland (1951–1976)	510	48	Jan-Mar	294	57.6%
Wallal Downs, 80 Mile Beach (1951–1976)	269	18	Jan-Mar	148	55.0%
Port Hedland (1951–1976)	313	31	Jan-Mar	110	35.1%
Learmonth, NW Cape (1950–1974)	271	21	Jan-Mar	151	55.7%
			May-Jul	113	41.7%
Cardabia, NW Cape (1913–1974)	186	21	May-Jul	82	44.1%
Mia Mia (1903–1972)	229	18	Jan-Feb	34	14.8%
			May-Jul	59	25.8%
Carnarvon (1945–1974)	239	45	May-Aug	125	52.3%
Hamelin Pool, Shark Bay (1885–1974)	194	39	May-Aug	112	57.7%
Geraldton (1942–1974)	472	89	May-Aug	360	76.3%

clustered through the wet season, at Ningaloo Station, just N of Cardabia, but with a mean annual rainfall of 272.3 mm, the number of SANs is 6.5–44.5 (mean 24.8), grouped into 2–8 (mean 5.2) events of activity time annually. They may be scattered through 11 months of the year.

Given the limited period of activity, the length of life for these snails probably is greatly expanded. We have no direct data, however, as to the actual change. The only records that are vaguely comparable refer to Sonoran Desert and fringe area snails in western North America (Walton 1963, 1970). These reports documented 10–15 year life spans for helminthoglyptid and polygyrid species.

The preliminary data given in the systematic reviews above show a pattern of structural change in the Sinumeloninae and Pleurodontinae inhabitants of the central west coast of Western Australia. The reduction in number of ovotestis lobes and the lack of significant size variation for these lobes holds for taxa S of Dampier Land and

N of Geraldton. Beginning with the Dampier Land species and accelerating to the S, species of the pleurodontid genus *Rhagada* show a rapid increase in size of the albumen gland (GG), compared with Kimberley taxa (Solem 1985b: figs 227, 229, 231, 232, 233). The albumen gland has become enormous in the southernmost species, *Rhagada torulus* from Shark Bay (**Fig. 404a**). An equivalent change is seen in the Sinumeloninae. The albumen gland is typical in the Nullarbor fringe species, such as *Pleuroxia elfina* (**Fig. 371a**), *Sinumelon jimberlanensis* (**Fig. 380**) and *S. kalgum*. It is somewhat enlarged in the Nullarbor Plain edge species, *Sinumelon nullarboricum* (**Fig. 381a**) and definitely enlarged in *S. vagente* (**Fig. 384a**) from the Geraldton-Mt Singleton area. In *Pleuroxia bethana* from the Kalbarri and Greenough River area near Geraldton, the albumen gland is huge (**Fig. 369a**), and continues greatly enlarged in the restricted endemic sinumelonid genera to the N (*Falspleuroxia*, *Plectorhagada*, *Strepsitaurus*, *Promonturconchum*, *Caperantrum*, see **Figs 387a, 391a, 392a, 393a, 396a, 397b, 400a, 402a**).

The functional significance of albumen gland size increase in this region remains to be determined. I hypothesize that it involves at least two aspects: 1) supplements or replaces part of the food storage function of the liver or digestive gland; and 2) maximises the number of young that can be produced during one of the infrequent rain events in this region. Since the ovotestis must remain "ready to function", there is less food storage space left in the apical whorls although the percentage of time spent in aestivation is considerably greater. The need for food storage space is greater and shifting this in part to the albumen gland is one of the few practical alternatives.

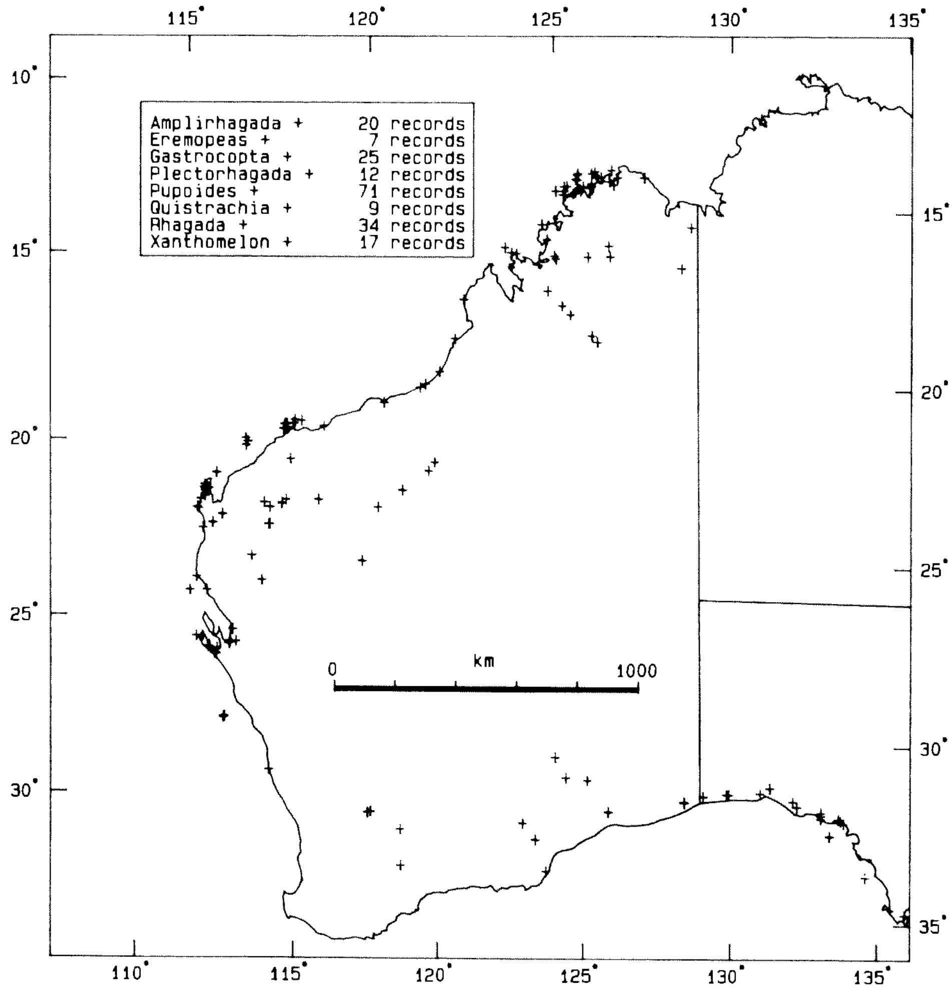
The presence of this modification in two unrelated subfamilies in the same region clearly is convergent. While it suggests a general pattern of coping with limited and unpredictable moisture supply, the situation in the third lineage present, *Quistrachia* (see **Figs 434a, 436a, 439a, 441a, 443a, 445a, 446a, 448a**), does not conform. The albumen gland in species of *Quistrachia* shows no pattern of size change from the Kimberley to Shark Bay. So much for simple universality!

A second pattern of change is shown by the species of *Rhagada*. In the Kimberley (Solem 1985b: figs 228a, c, 230a–b, 231d, 232c, 233b, 235a–b) and Dampier Land species (**Figs 428b, 430d, 432a–b**), the verge is large, nearly filling the penis chamber and often with a complex sperm groove. In the more southern species, the verge is greatly reduced in size and complexity. In the Cape Range species of *Quistrachia* and the endemic Sinumeloninae, *Strepsitaurus*, *Promonturconchum*, and *Caperantrum*, apparent secondary enlargement of the terminal genitalia has taken place but further study is needed to evaluate the patterns of change in relation to gross body size alterations.

In brief summary, three lineages of camaenid land snails are represented in at least part of the Dampier Land to Geraldton area. Both *Rhagada* (**Map 36**) and *Quistrachia* (**Map 44**) have taxa in the W and SW Kimberley, then extend S to Shark Bay in a series of allopatric species. The *Rhagada* show a clear pattern of graded change in the genitalia as drier conditions are encountered. Species ranges are larger, probably related to their ability to burrow effectively into sandy soil. Species of *Quistrachia* have shorter and often disjunct ranges, possibly relating to their pattern of rock association and do not show a pattern of change in genital structures from N to S.

Since there are no accessory dart sacs or mucous glands on the genitalia of the Camaenidae, as there are in the Helminthoglyptidae and Helicidae, *s. l.*, the pattern of organ loss demonstrated by Gregg (1960) for desert Helminthoglyptidae cannot exist, but the penis complex reductions in *Rhagada* are the functional and evolutionary equivalent.

The Sinumeloninae range extralimitally in the Red Centre (Solem 1993) and then the Gawler-Flinders-Eyre Peninsula section of SA. They follow the S fringes of the Nullarbor and two genera (*Pleuroxia*, *Sinumelon*) then extend (**Map 49**) NW through the Norseman-Kalgoorlie region to near Geraldton. From the S end of Shark Bay through the North West Cape (**Maps 29–31, 33, 35**), five endemic genera of Sinumeloninae with 13 named species (**Table 165**) have been recognised. Most of these species show significant structural modifications. Current data are inadequate to



Map 47: Collections of land snails in WA and the Nullarbor area made between 1 January 1900 and 31 December 1973, based on *Amplirhagada*, *Eremopeas*, *Gastrocopta*, *Plectorhagada*, *Pupoides*, *Quistrachia*, *Rhagada* and *Xanthomelon*.

decide if these genera are more closely related to Red Centre taxa or the *Sinumelon-Pleuroxia* complex to the SE. Resolution of this problem requires additional studies. Allozyme data concerning *Plectorhagada plectilis* (Benson, 1853) from near the 26th Parallel and *Sinumelon vagente* Iredale, 1939 from Bindoo Hill near Geraldton, give a Nei's 1978 genetic distance of 1.35 (Woodruff & Solem unpublished), suggesting that they are not closely related.

Radular and jaw variation in taxa from the central portion of the W coast is dramatic where microsympatry is involved, both among and within species. Feeding specialization to minimize competition during the very limited activity periods appears to correlate closely with radular and jaw changes. The differences are especially clear in the Cape Range area. *Strepsitaurus rugus* (Cotton, 1953), which feeds on algal-fungal films, has the jaw ribbing nearly lost (**Plates 200f, 201c**) where several species are present, but well developed (**Plate 201e**) elsewhere. Its central and early lateral radular teeth (**Plate 200a–b**) have a very high cusp shaft angle and a broadly rounded tip. *Quistrachia lefroyi*, which scrapes bark off small twigs of herbaceous plants, may have grossly enlarged anterior flares (**Plate 230a–c**) when several species are present, and yet only moderately enlarged flares (**Plate 231a–c**) when the diversity is less. *Rhagada capensis*, which has been observed favouring new green shoots and leaves, has a near vertical cusp shaft angle and greatly altered row interlock in the main portion of the Cape Range (**Plate 213a–c**), but less altered teeth elsewhere (**Plates 214, 231d–f**). Both *Promonturconchum superbum* (**Plate 203a–c**), with stomach contents of leaf and grass fragments, and *Caperantrum polygyrum* (**Plate 204a–b**), which has not been observed feeding, have generalised teeth and jaws (**Plate 202c–d, f**), although the cusp shaft angle is greater in the latter species. Preliminary mention of these differences was given in Solem (1974: 161, figs 7a–f). A more detailed analysis will be presented elsewhere.

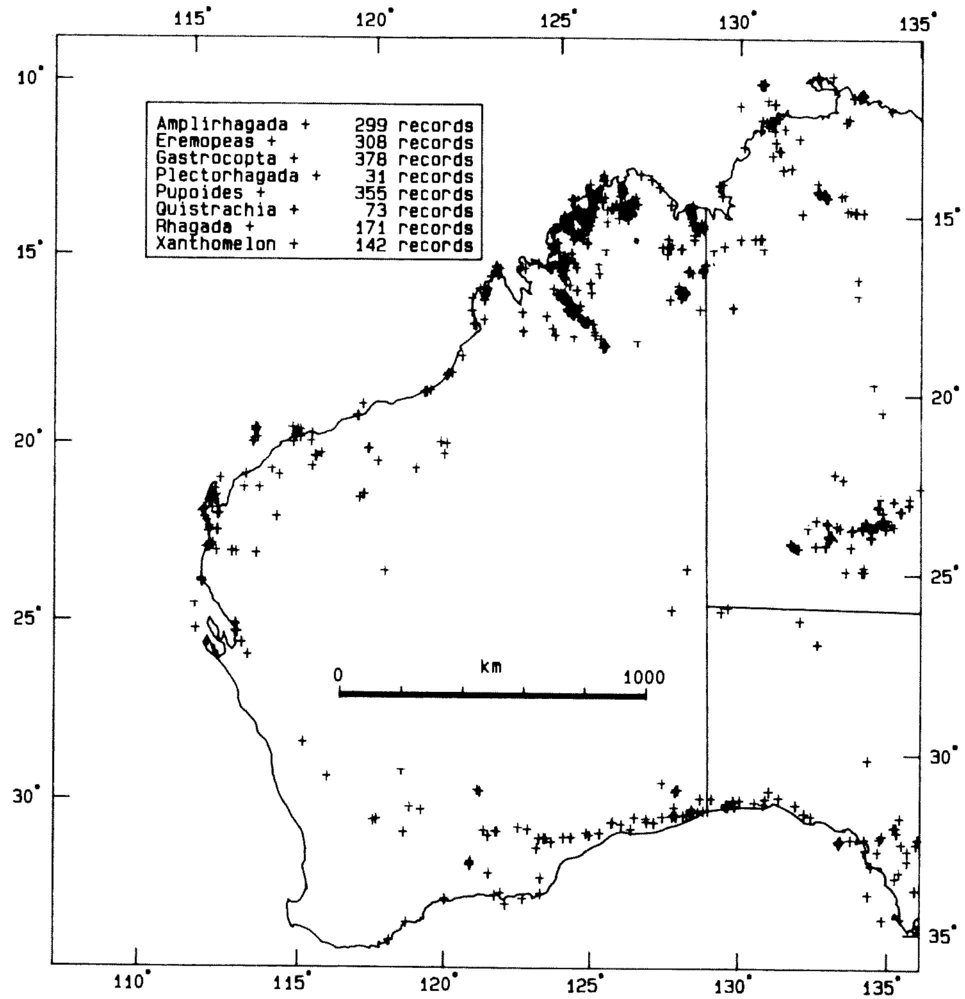
More than in any other area of Australia that I have studied, the structural variations in genitalia and feeding structures can be correlated with climatic factors. While this enables hypothesizing the functional significances of these changes, it makes any attempt at generating phylogenetic hypotheses more difficult.

BIOGEOGRAPHIC OVERVIEW

Publication of this volume completes the initially-proposed survey of **Camaenid land snails from Western and central Australia.** Previous monographs (Parts I–VI, Solem 1979, 1981a, 1981b, 1984b, 1985b) and supplemental papers (Solem 1988a, 1989c) have reviewed taxa from the Kimberley and adjacent hill systems in the NT and the Red Centre (Solem 1993). This report, covering the area from Dampier Land to Geraldton, SE to Norseman and then E along the Nullarbor coast to Yalata, SA, will be the last in this series.

A major extension in geographic coverage is represented by the survey of camaenids from southeastern SA recently published by the South Australian Museum (Solem 1992). It is intellectually part of the same study.

The initial focus, by necessity, has been to delineate species and then to cluster them into meaningful generic units. This basic work had not been accomplished previously. The classic monograph of all Australian land shells by Cox (1868) included virtually no material from WA or the Red Centre and only limited SA records. Only scattered descriptions are noted for these regions in his next catalogue (Cox 1909). Published studies, with few exceptions such as the brilliant pioneering reports of Tate (1896) and Hedley (1889, 1896, 1905), have been simple conchological descriptions (Bednall 1892, Clench & Archer 1937, Cotton 1953, Cotton & Godfrey 1932, Preston 1908, 1914, E. A. Smith 1874, 1893, Tate 1879, 1894, 1899), check list compilations (Hedley 1915, Burch 1976, Richardson 1985) and the annotated faunistic reviews of E. A. Smith (1894) and Iredale (1939). The latter report was preceded by a series of nomenclatural blatherings by an extreme



Map 48: Collections of land snails in western parts of Australia made between 1 January 1974 and 31 December 1988, based on *Amplirhagada*, *Eremopeas*, *Gastrocopta*, *Plectorhagada*, *Pupoides*, *Quistrachia*, *Rhagada* and *Xanthomelon*.

splitter (Iredale 1933, 1937a, 1937b, 1937c, 1938), based on very limited material and using pre-Darwinian concepts of species and genera. Iredale often named genera and species "to call attention to this unusual shell". Many of his *names* are valid but his *concepts* of species and genera have been almost universally altered or abandoned in these monographs.

Only casual collections had been made from most areas and the amount of well-localised material from, for example, WA was slight (**Map 47**). A series of trips by George W. Kendrick of the W.A. Museum produced significant collections from several areas and there were pioneering mid-1970's surveys of three areas in the Kimberley: the Prince Regent River area in 1974 (Wilson & Smith, 1975) and the Drysdale River region in 1975 (Merrifield, Slack-Smith & Wilson 1977) by staff of the W.A. Museum and other institutions, then a joint FMNH–WAM survey of the Mitchell Plateau in 1976. The results of these trips and my subsequent field activities have increased the material available significantly (**Map 48**). Similar increments were made for SA (Solem 1992: figs 102–105) and the Red Centre through field activities in the period since 1974.

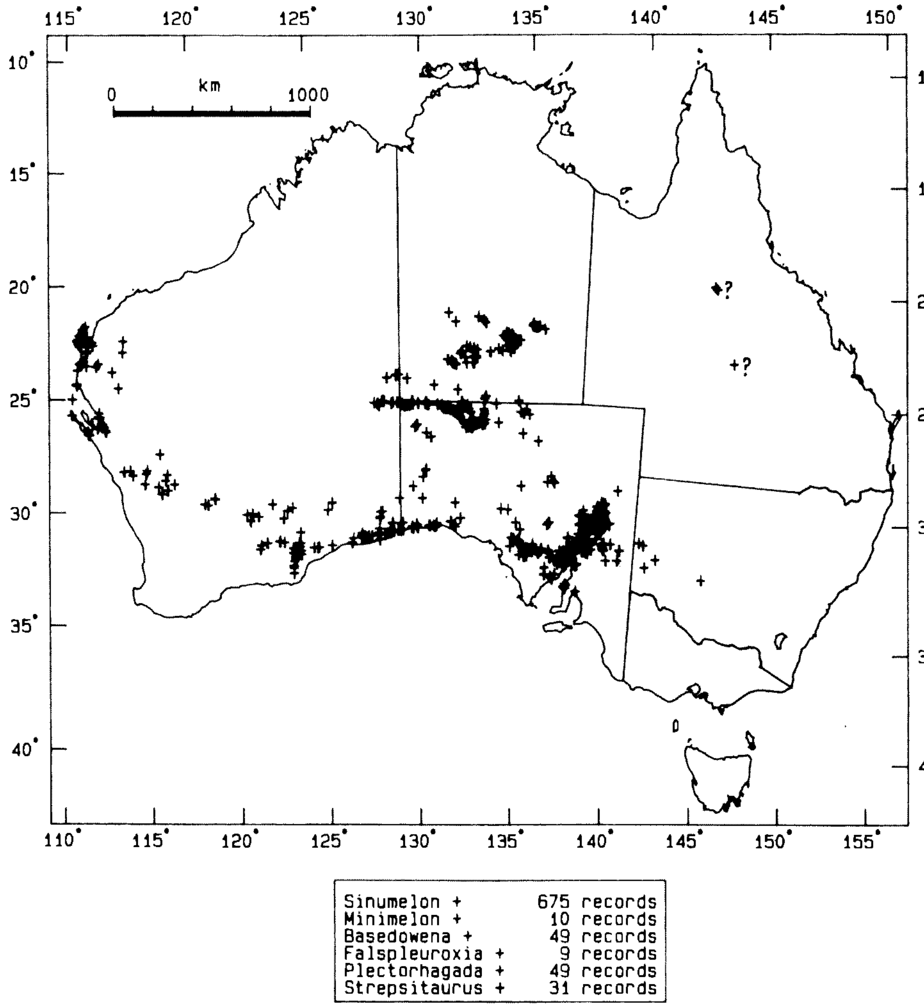
Although these monographs review 310 species (188 new) in 49 genera (22 new) (**Table 167**), much basic survey work remains to be accomplished. A June 1987 helicopter survey of 83 rainforest patches on the Kimberley mainland resulted in discovery of two new genera and more than 47 new species of camaenids (Solem 1991). These additions are reflected in **Table 168** but formal description will be presented elsewhere. Material from a mid-1988 expedition to islands along the Kimberley coast was still being processed at the time this was written but undoubtedly includes a number of previously unknown species.

Table 167: Taxonomic diversity of studied camaenids

Subfamily & range	Species Total	Species New	Genera Total	Genera New
Camaeninae (K, SA)	38	16	8	3
Pleurodontinae (RC, WA, K)	59	35	5	0
Sinumeloninae (RC, SA, WA)	79	36	15	8
Unknown (K, WA, NT)	181	148	23	13
TOTALS	**357**	**235**	**51**	**24**
Less Kimberley RFS new taxa	–47	–47	–2	–2
TOTALS	**310**	**188**	**49**	**22**

K – Kimberley; **NT** – Top End of Northern Territory; **RC** – Red Centre; **SA** – southeastern South Australia; **WA** – non–Kimberley areas of Western Australia.

In addition, several small but phyletically-significant, camaenid radiations, which occupy areas just outside the main regions, are yet to be described. For example, Kangaroo Island, SA has several restricted endemic species of *Cupedora* Iredale, 1933 and *Glyptorhagada* Pilsbry, 1890; the Roto area of western New South Wales has a minor radiation of Camaeninae, in which an anatomically monophyletic group of species has shells that converge with those of *Sinumelon* Iredale, 1930, *Cupedora* Iredale 1933 and *Damochlora* Iredale, 1938; an extensive radiation near Katherine, NT has species that are anatomically the same as *Torresitrachia* Iredale, 1939 but conchologically resemble *Pleuroxia* Ancey, 1887, *Mesodontrachia* Solem, 1985 and



Map 49: Distribution of Sinumeloninae in Australia, based on selected genera – *Basedowena, Falspleuroxia, Minimelon, Plectorhagada, Sinumelon* and *Strepsitaurus.*

Table 168: Diversity levels and distribution of camaenid genera

Genus	Number of species from: - Kimberley	Top End of NT	Red Centre	South Austr.	Western Austr.
SUBFAMILY CAMAENINAE					
Damochlora Iredale, 1938	5				
Hadra Albers, 1860	1 (+ N Qld)				
Cupedora Iredale, 1933				16	
Glyptorhagada Pilsbry, 1890				10	
Contramelon Iredale, 1937				1	
Cooperconcha Solem, 1992				3	
Pseudcupedora Solem, 1992				1	
Aslintesta Solem, 1992				1	
SUBFAMILY PLEURODONTINAE					
Semotrachia Iredale, 1933			25		
Dirutrachia Iredale, 1937			3		
Vidumelon Iredale, 1937			1		
Divellomelon Iredale, 1937			1		
Rhagada Albers, 1860	11				18
SUBFAMILY SINUMELONINAE					
Micromelon Solem, 1992				1	
Pleuroxia Ancey, 1887			4	4	5
Lacustrelix Iredale, 1937				3	
Sinumelon Iredale, 1930			10	13	4
Granulomelon Iredale, 1933			4		
Basedowena Iredale, 1937			9		

Table 168 (continued).

Genus	Kimberley	Top End of NT	Red Centre	South Austr.	Western Austr.
	Number of species from: -				
Minimelon Solem, 1993			1		
Tatemelon Solem, 1993			4		
Eximiorhagada Iredale, 1933			1		
Montanomelon Solem, 1993			2		
Plectorhagada Iredale, 1933					6
Strepsitaurus Solem, 199?					5
Promonturconchum Solem, 199?					1
Caperantrum Solem, 199?					1
SUBFAMILY POSITION UNKNOWN					
Xanthomelon von Martens, 1860	4	2 (also Qld)			
Torresitrachia Iredale, 1939	14	? (also Qld)			
Parglogenia Iredale, 1938		1			
Amplirhagada Iredale, 1933	55				
Ningbingia Solem, 1981	7				
Turgenitubulus Solem, 1981	8				
Cristilabrum Solem, 1981	12				
Prymnbriareus Solem, 1981	1				
Westraltrachia Iredale, 1933	21				
Mouldingia Solem, 1984	2				
Ordtrachia Solem, 1984	5				
Exiligada Iredale, 1939	1				
Prototrachia Solem, 1984	1				

Table 168 (continued).

Genus	Number of species from: - Kimberley	Top End of NT	Red Centre	South Austr.	Western Austr.
Setobaudinia Iredale, 1933	10	1			
Baudinella Thiele, 1931	4				
Retroterra Solem, 1985	5				
Kendrickia Solem, 1985	1				
Kimboraga Iredale, 1933	9				
Quistrachia Iredale, 1939	1				8
Carinotrachia Solem, 1985	2				
Mesodontrachia Solem, 1985	3				
New Genus 1	1				
New Genus 2	2				
TOTAL SPECIES (356)	**186**	**4**	**65**	**53**	**49**
TOTAL NEW SPECIES (234)	**150**	**2**	**39**	**20**	**24**
TOTAL GENERA (51)[1]	**25**	**4**	**12**	**10**	**8**
TOTAL NEW GENERA (24)	**13**	**0**	**3**	**4**	**4**

[1] Six genera occur in two or three areas (*Rhagada* – K & WA; *Pleuroxia* – RC, SA & WA; *Sinumelon* – RC, SA, & WA; *Xanthomelon* – K & NT; *Torresitrachia* – K & NT; and *Setobaudinia* – K & NT), thus the area numbers do not total 51.

Cristilabrum Solem, 1981; and there are several isolated species from the dry sections of western Queensland, including the *Quistrachia* from Black Mountain, near Boulia.

Many additional new species will be found in the Red Centre but coverage of the remaining regions probably is better and a higher portion of the extant taxa have been described.

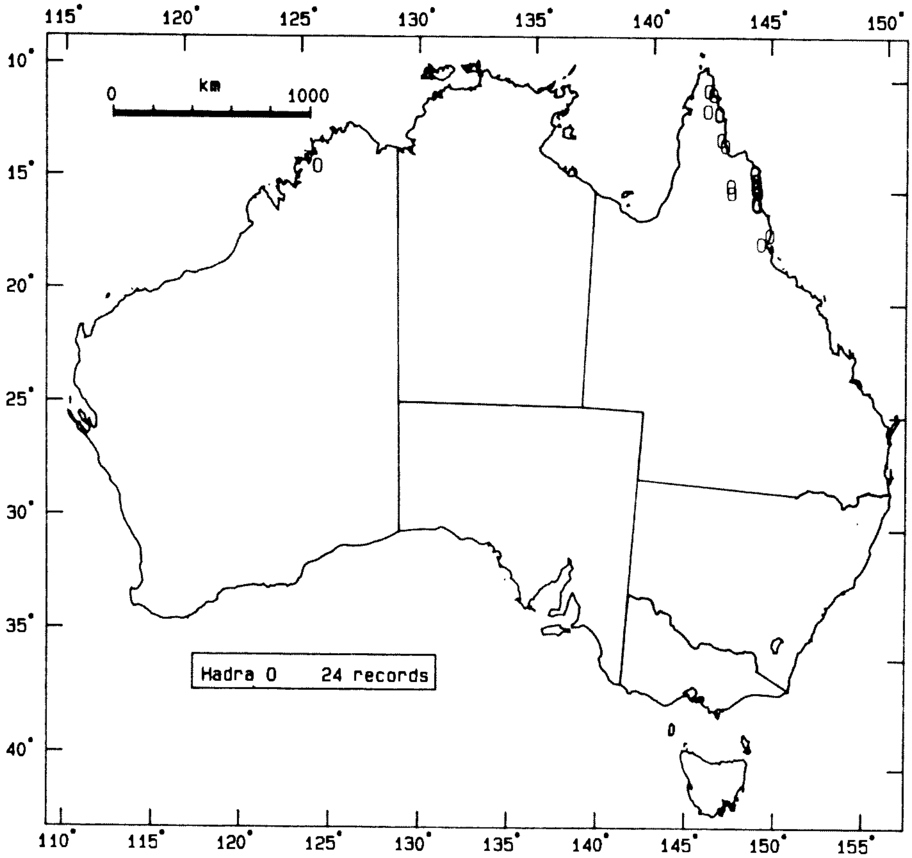
As material permitted, efforts were made to review the non-camaenid land snails (Solem 1981d, 1982, 1984a). Availability of massive collections made by Field Associate Vince Kessner in the "Top End" of the NT enabled the preparation of a summary account of non-camaenids from the Kimberley and all of the NT (Solem 1989a). The distributional data are summarised in **Table 169**. They provide considerable contrast with the camaenid distributional information.

Detailed biogeographic commentaries on particular areas or phenomena are presented elsewhere. The incredible radiation of short-range species (median linear range of 28 restricted endemic camaenids is 1.65 km, median area range is 0.825 km^2) in the Ningbing-Jeremiah Hills area of WA (Solem 1988b) and the range patterns, sympatric diversity levels and area patterns of rainforest-patch snails in the wetter areas of the Kimberley (Solem 1991), are merely the first of several reviews.

Here it is appropriate to address general aspects of camaenid and non-camaenid distributions in the western two-thirds of Australia. Short accounts of endemism patterns, degree of local sympatric diversity and regional patterns precede discussions of convergences and possible faunal origins.

Endemism, specific and generic

Camaenids from four major geographic areas have been reviewed: 1) the Kimberley and adjacent NT hills; 2) Red Centre; 3) Flinders-Gawler-Eyre Peninsula; and 4)



Map 50: Distribution of *Hadra* in Australia.

Table 169: Distribution of Kimberley and Northern Territory non-camaenid land snails (Data from Solem, 1989a)

Taxon	Kimberley	Top End of NT	Red Centre	Extra-limital
HYDROCENIDAE				
Georissa obesa Solem, 1989	X*(S edge)			– 0 –
HELICINIDAE				
Pleuropoma walkeri E. A. Smith, 1894	X	(X)		– 0 –
CYCLOPHORIDAE				
Leptopoma minus von Martens, 1867		X		Indonesia
ACHATINELLIDAE				
Elasmias manilense (Dohrn, 1863)	X	X		Indo-Papua
Elasmias terrestris (Brazier, 1876)	X	X		Papua
PUPILLIDAE				
Pupisoma orcula (Benson, 1850)	X	X		India-Poly
P. circumlitum Hedley, 1897	X	X		Qld-NSW
P. species	X	X		– 0 –
Nesopupa mooreana (E. A. Smith, 1894)	X	X		– 0 –
N. novopommerana I. Rensch, 1932	(X)	X		Tanimbar-Bismarcks
Gastrocopta simplex Solem, 1989	X	X		– 0 –
G. deserti Pilsbry, 1917	(X) (S edge)	(X)	X	W Qld, WA W coast, N Flinders
G. larapinta (Tate, 1896)	(X) (S edge)		X*	– 0 –
G. tatei Pilsbry, 1917	(X)		X*	– 0 –
G. macdonnelli (Brazier, 1875)		X		Qld
G. mussoni Pilsbry, 1917	(X) (S edge)			Qld
G. macrodon Pilsbry, 1917	X			Papua
G. recondita (Tapparone-Canefri, 1883)	X (S edge)	X		Aru, Tanimbar, Haruku

Table 169 (continued).

Taxon	Kimberley	Top End of NT	Red Centre	Extra-limital
Pumilicopta kessneri Solem, 1989	X	X		– 0 –
Gyliotrachela napierana Solem, 1981	X*(S edge)			– 0 –
G. ningbingia Solem, 1981	X*(E edge)			– 0 –
G. catherina Solem, 1981		X*		– 0 –
Pupilla ficulnea (Tate, 1894)			X*	– 0 –
Glyptopupoides egregia (Hedley & Musson, 1891)	X			Qld, NSW
Pupoides ischnus (Tate, 1894)			X*	– 0 –
P. eremicolus (Tate, 1894)			X*	– 0 –
P. beltianus (Tate, 1894)			X*	W coast of WA
P. pacificus (Pfeiffer, 1846)	X	X		Qld, NSW
ENIDAE				
Amimopina macleayi (Brazier, 1876)	X	X		Papua, N Qld
SUBULINIDAE				
Eremopeas interioris (Tate, 1894)	X		X	W Qld
E. *tuckeri* (Pfeiffer, 1846)		X		Qld, NSW
BULIMULIDAE				
Bothriembryon spenceri (Tate, 1894)			X	– 0 –
HELICODISCIDAE				
Stenopylis coarctata (Mollendorff, 1894)	X	X	X	Philippine -Solomon Is & Qld
CHAROPIDAE				
Discocharopa aperta (Moellendorff, 1888)	X	X	X	Philippine -Society I & Qld
Pilsbrycharopa tumidus (Odhner, 1917)	X* (S edge)			– 0 –
Pillomena aemula (Tate, 1894)			X*	– 0 –

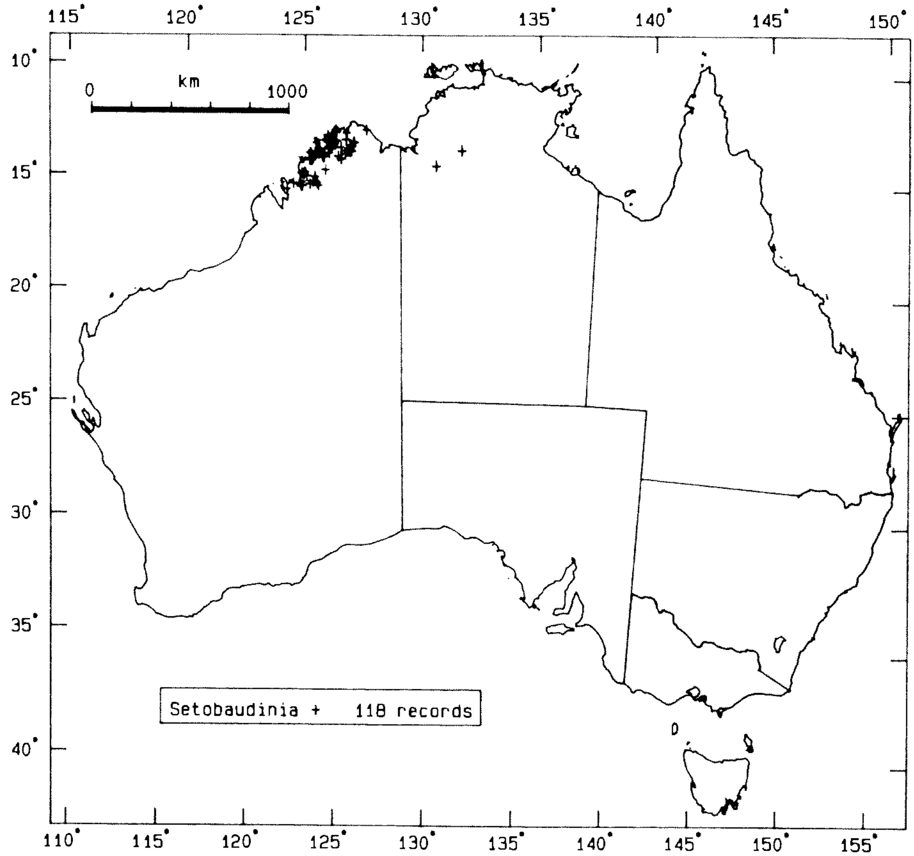
Table 169 (continued).

Taxon	Kimberley	Top End of NT	Red Centre	Extra-limital
PUNCTIDAE				
Paralaoma retinodes (Tate, 1894)			X	SE areas
SUCCINEIDAE				
Succinea species	X	X	X	??
HELICARIONIDAE				
Euconulinae				
Coneuplecta calculosa (Gould, 1852)		X		Indo-Poly
C. microconus (Mousson, 1865)	X	X		Indo-Poly
Wilhelminaia mathildae Preston, 1913	X	X		Indo-Micro
Microcystinae				
Liardetia doliolum (Pfeiffer, 1846)		X		Indo-Micro
L. scandens (Cox, 1872)	X	X		Qld-NSW
Queridomus grenvillei (Brazier, 1876)		X		Cape York
Helicarioninae				
Westracystis lissus (E. A. Smith, 1894)	X*			– 0 –
W. fredaslini Solem, 1982		X*		– 0 –
ZONITIDAE				
Trochomorphinae				
Trochomorpha melvillensis Solem, 1989		X*		– 0 –
TOTAL FAMILIES	**10**	**11**	7	
TOTAL GENERA	**20**	**20**	**10**	
TOTAL SPECIES	**30**	**30**	**14**	
* – **Restricted endemics**	5	3	7	
( ) – **Only on fringes**	4	3	0	

Indo = Indonesia; **Micro** = Micronesia; **NSW** = New South Wales; **Poly** = Polynesia; **Qld** = Queensland; **WA** = Western Australia

Dampier Land-Geraldton-Norseman-Nullabor all have major camaenid land snail faunas (**Table 168**). Despite the facts that only the comparatively small King Sound separates the two WA areas, and the distance between Ceduna and Yalata, SA is scarcely wider, only one of the 310 species, *Sinumelon tarcoolanum* Solem, 1992, is found in two of the areas – from the W end of the Gawler Range to the goldfields area E of Kalgoorlie and N of the Trans-Australian Railway line (**Map 26**). All of the remaining species are restricted to a single region and usually to a very small part of that region.

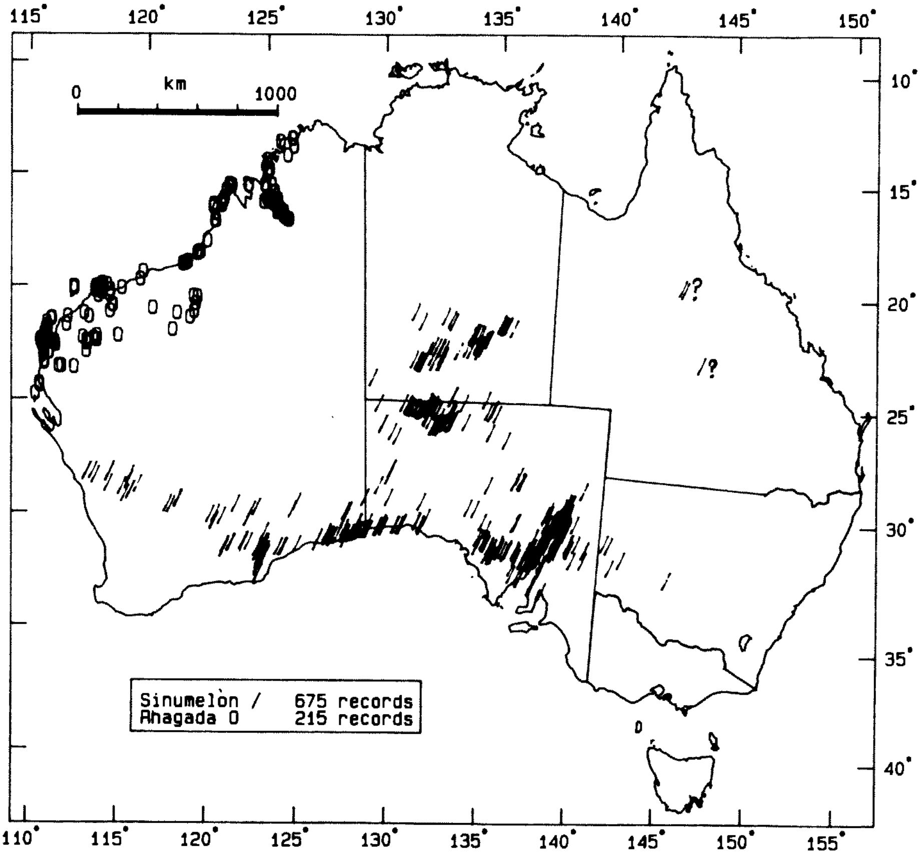
Generic endemism is almost as great. In the central and southern areas, two sinumelonid genera, *Pleuroxia* Ancey, 1887 (**Map 19**) and *Sinumelon* Iredale, 1930 (**Map 24**), are diverse in the Red Centre and Flinders-Gawler-Eyre Peninsula region and extend along the Nullarbor Coast to near Norseman and then NE to near Geraldton. Of the 25 Kimberley-NT area genera: 1) two "wet area" genera, *Xanthomelon* von Martens, 1860 and *Torresitrachia* Iredale, 1939, probably have a



Map 51: Records of the genus *Setobaudinia* in Australia.

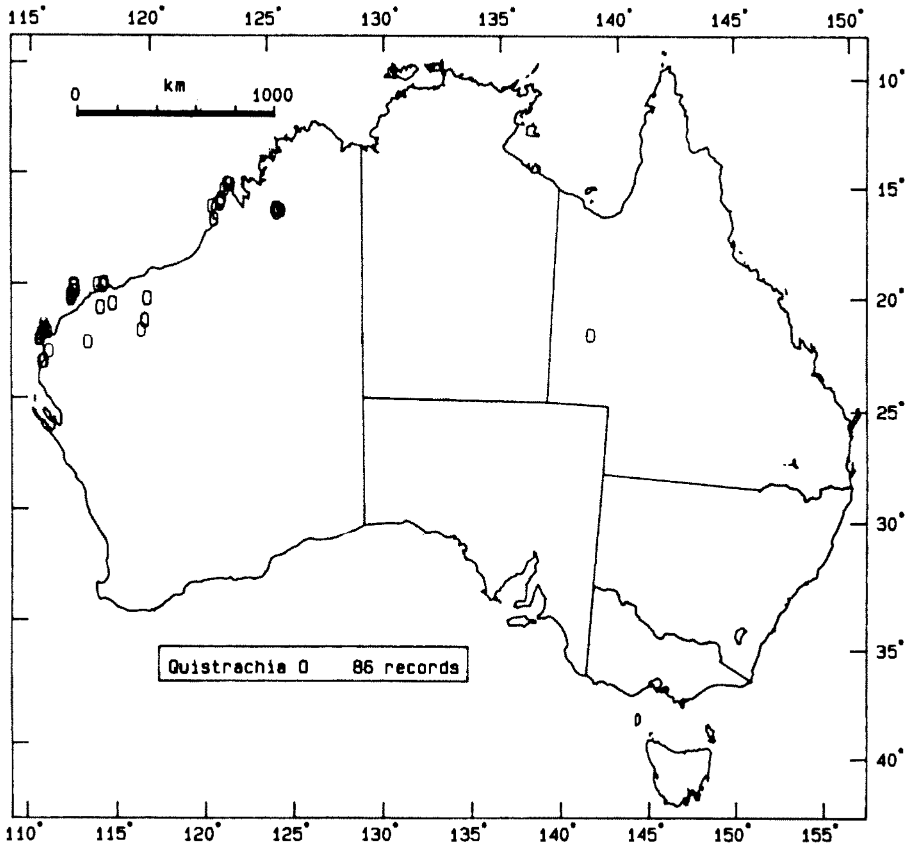
near-continuous range from the SW Kimberley across the "Top End" to Torres Strait and then S in Queensland for different distances; *Hadra* Albers, 1860 has one record (*Hadra wilsoni* Solem, 1979) in the Prince Regent River Reserve area and then a number of species in the N part of Queensland (**Map 50**); *Setobaudinia* Iredale, 1933 (**Map 51**) ranges in the Kimberley E to near Katherine, NT, a minor range extension; the pleurodontid genus *Rhagada* Albers, 1860 ranges (**Map 52**) through the SW Kimberley and then along the W coast as far S as Shark Bay; and *Quistrachia* Iredale, 1939 extends from the Oscar-Napier Range junction S through the Pilbara almost to Shark Bay, with a probable new species in W Queensland (**Map 53**). Thus 19 of the 25 camaenid genera found in the Kimberley are restricted endemics. It is possible that Indonesian-Melanesian or Queensland representatives may be discovered when the anatomy of taxa from these areas is investigated, but this is a future project. Of the 51 camaenid genera recognised in these reports, only eight are found in more than one region.

We do not have equally comprehensive data for the non-camaenid land snails for



Map 52: Comparative distribution of *Sinumelon* and *Rhagada* in Australia.

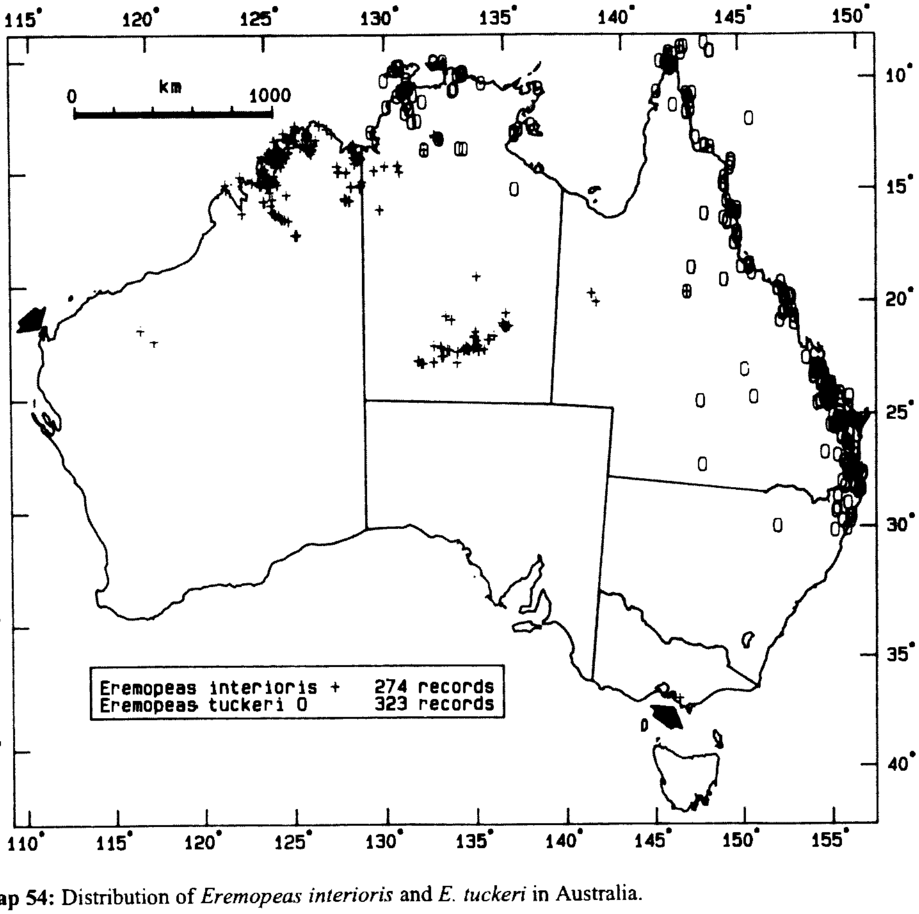
most regions, but the available records show a very different pattern of distribution. Data on the Kimberley and NT taxa (Solem 1981d, 1982, 1984a, 1989a), and a review of the pupilloid taxa from the S and midwestern coasts of Australia (Solem 1986), are available, with the former information summarised in **Table 169**. First, regional endemism at the species level is low: only five of 30 species recorded from the Kimberley (*Georissa obesa* Solem, 1989, *Gyliotrachela ningbingia* Solem, 1981, *G. napierana* Solem, 1981, *Pilsbrycharopa tumida* [Odhner, 1917] and *Westracystis lissus* [E. A. Smith, 1894]) are restricted endemics and all but the last one are found only in the E or S dry fringes. In contrast, seven (50%) of the Red Centre species are restricted endemics. The "Top End" has only three (of 30) restricted endemics (*Gyliotrachela catherina* Solem, 1981, *Westracystis fredaslini* Solem 1982 and Trochomorpha *melvillensis* Solem, 1989). Many non-camaenid (20), but no camaenid, species are shared by the Kimberley and "Top End" and many species (14) have been recorded from Indonesia and/or Papua. None of the non-camaenid genera are restricted endemic. Twenty genera have extended ranges in Indonesia and Melanesia, or are almost world-



Map 53: Distribution of *Quistrachia* in Australia.

wide (*Pupilla*, *Pupoides*). The remaining seven genera show varied patterns: only *Westracystis* (**Map 56**) is limited to the Kimberley and "Top End" (potential relatives elsewhere in Australia remain unstudied); *Eremopeas* (**Map 54**) and *Gyliotrachela* (**Map 57**) range over the northern half of Australia; *Glyptopupoides* and *Gastrocopta mussoni* have a disjunct Kimberley and Queensland-New South Wales (**Map 55**) range; *Queridomus* has a disjunct "Top End" and Cape York distribution; and three Red Centre records of the genera *Bothriembryon*, *Paralaoma* and *Pillomena* are northernmost records of southern groups.

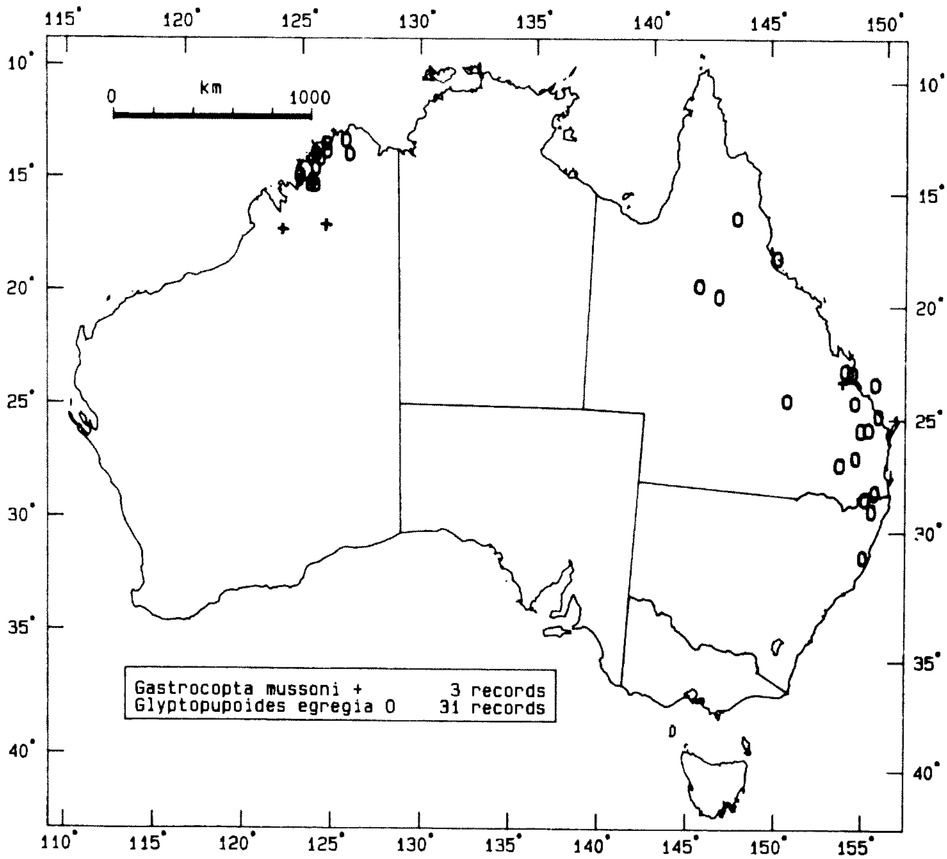
The non-camaenids, although far less diverse in the Kimberley area (30 species) than the camaenids (186 species), have much larger local ranges. Most of these genera and species have significant extralimital ranges and many taxa are shared with the "Top End". The camaenids, in contrast, are regionally restricted and have much smaller ranges.



Map 54: Distribution of *Eremopeas interioris* and *E. tuckeri* in Australia.

Sympatric diversity

The general pattern for camaenids is to have only one or two species living in the same rock pile. In the drier areas, higher diversity levels are a rare event. Throughout the Flinders-Gawler-Eyre Peninsula region (Solem 1992: table 37), there are 667 localities from which camaenids have been collected. There are 455 with one species recorded, 169 with two-species records, only 39 records of three species and four records of four species with microsympatry. Usually the two-species records consist of one Camaeninae and one Sinumeloninae, with the former species showing feeding specialisations. In the Nullarbor to Norseman area, generally a *Pleuroxia*, a *Sinumelon* and a *Bothriembryon* (Family Bulimulidae) will be found, together with one to three pupilloids. Between Shark Bay and the North West Cape, several two- and three-species records exist, but often with micro-ecological segregation of some species (sand versus red soil substrate). In the Cape Range, up to five species have been taken off or along the same 10 metres of exposed limestone. Dramatic local feeding specialisations have been demonstrated (see above).



Map 55: Disjunct distributions of *Gastrocopta mussoni* and *Glyptopupoides egregia* in Australia.

The Red Centre, in contrast, shows several areas of relative abundance – Palm Valley in the Krichauff Range, parts of the Musgrave Range and Maud Creek in the Hart Range. Three *Gastrocopta*, two *Pupoides*, occasionally *Pupilla ficulnea*, normally *Eremopeas interioris*, *Stenopylis coarctata*, *Discocharopa aperta*, *Succinea* sp. and up to five camaenids produce a respectable fauna of 10–15 species living under the same fig tree. Usually, at least some of the camaenids would show feeding specialisation structures.

The most extensive and quantifiable data are available for snails from the mainland rainforest patches of the Kimberley (Solem 1991: table 2). Of the 82 patches that yielded land snails, the camaenid numbers were 0–8 species (mean 3.68), non-camaenids 4–14 species (mean 9.03) and total land snail fauna 5–20 species (mean 12.5). In these wetter areas, no evidence was found of camaenid feeding specialisations. Along the dry S fringe of the Kimberley, in contrast, feeding specialisation in the area of overlap between *Westraltrachia* and *Amplirhagada* was extensive (Solem 1985a). The number of sympatric species in this region is less than in the wetter areas of the Kimberley (Solem, unpublished data).

Thus sympatric diversity of camaenids in the western two-thirds of Australia rarely reaches five species and for most areas would be only one or two species. This is very different from the patterns found in the most favourable areas of the world, where up to 70 species of land snails may exist microsympatrically but it conforms with the "world average" situation (Solem 1984c). Wetter areas have more species than drier areas. In the latter areas, where activity time of the snails is limited (see above), feeding specialisations are common, involving structure of the radula and/or jaw with specialisation as to preferred food resource. This is hypothesised to minimise competition during the limited activity periods.

The diversity of the Australian camaenids is based not upon evolution of many species that show overlapping ranges but upon evolution of many allopatric species with very short ranges. The Ningbing-Jeremiah Hills radiation, where the median linear range of 28 restricted endemic species is 1.65 km and the median area range is 0.825 km^2, is the most spectacular example (Solem 1988b) but the median linear range of all Kimberley rainforest-patch camaenids is only 20 km (Solem 1991: table 8). Very few species in any area have ranges than exceed 150 km and the exceptions either generally aestivate burrowed into sandy or loamy soil (*Rhagada*, *Xanthomelon*) or are "weed species" (some *Torresitrachia*).

The degree of diversification within genera varies greatly and is summarised in **Table 170**. The numbers are slightly misleading in that a few genera have extralimital records that are not recorded here. *Hadra* is monotypic in the area covered, but there is an unknown number of Queensland taxa; both *Torresitrachia* (14 species) and *Setobaudinia* (11 species) probably have several additional species; and *Quistrachia* (9 species) has at least one Queensland representative. Since all of these genera have been reviewed by the author and every attempt has been made to have an equivalent, albeit intuitive, "minimum difference" before a cluster of species was recognised as a genus, the results are comparable.

One genus, *Amplirhagada*, has 15.4% (55) of the total species of the family which are currently known (357). Eleven genera (21.6%) with 10–55 species account for 65.4% (233) of the species, while the 18 monotypic genera account for only 5.1% of the known species. Genera with two or three species (8) include 20 species (5.6%);

Table 170: Species numbers and generic distribution

Number of species in genus	Number of genera
1	18
2–3	8
4–5	7
6–7	3
8–9	4
10 (*Glyptorhagada*)	1
11 (*Setobaudinia*)	1
12 (*Cristilabrum*)	1
13 (*Pleuroxia*)	1
14 (*Torresitrachia*)	1
16 (*Cupedora*)	1
21 (*Westraltrachia*)	1
25 (*Semotrachia*)	1
27 (*Sinumelon*)	1
29 (*Rhagada*)	1
55 (*Amplirhagada*)	1
TOTAL GENERA = 51	

those with four or five species (7) include 32 species (8.7%); those with six or seven species (3) include 19 species (5.3%); and those with eight or nine species (4) included 35 species (9.8%).

Monotypic genera are found in each region and each subfamily unit:

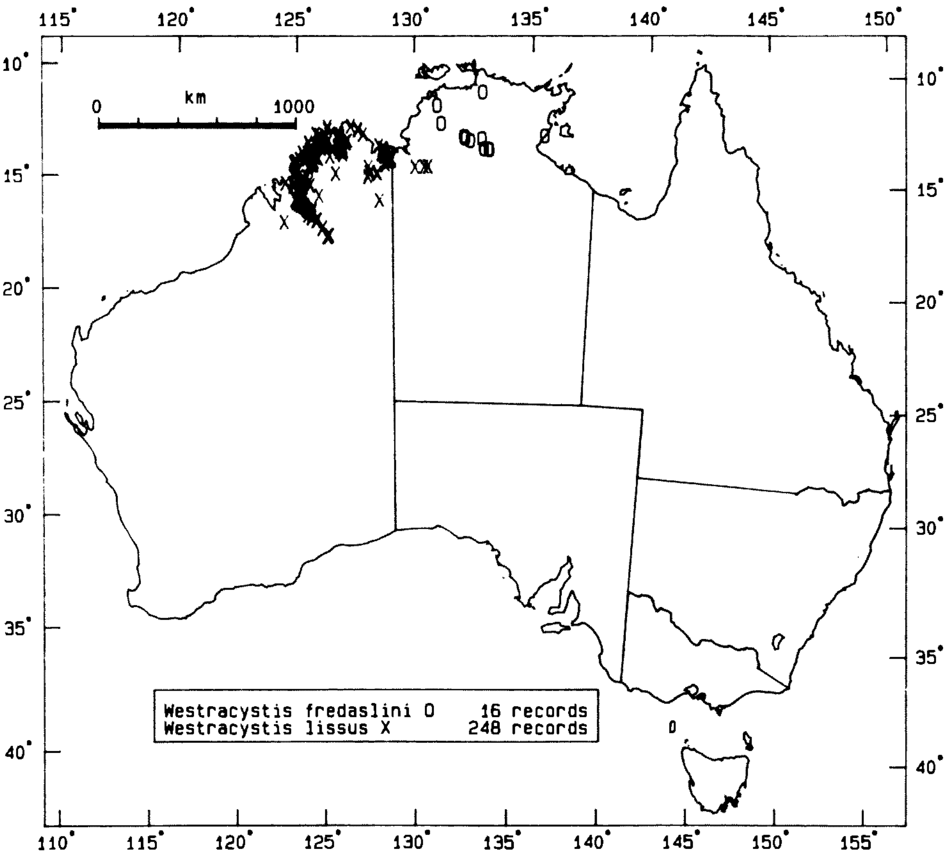
Kimberley	Red Centre	SE S Australia	W & S coasts
Parglogenia	*Vidumelon*	*Contramelon*	*Falspleuroxia*
Prymnbriareus	*Divellomelon*	*Pseudcupedora*	*Promonturconchum*
Exiligada	*Minimelon*	*Aslintesta*	*Caperantrum*
Prototrachia	*Eximiorhagada*	*Micromelon*	
Kendrickia			
Hadra			
New Genus 1			
(of 25)	(of 12)	(of 10)	(of 8)
(186 species)	(65 species)	(53 species)	(48 species)

The higher proportion of monotypic genera in the areas with lower total diversity will be commented on elsewhere. Here, it is sufficient to call attention to this situation.

There is no correlation between the number of species within a genus and the area occupied by that genus (**Map 58**). The 12 species of *Cristilabrum* all live in less than 75 km^2; the 13 species of *Pleuroxia*, in contrast, occur sporadically in that vast area from the mouth of the Murchison River on the W coast to the Barrier Range in Western New South Wales and from the Great Australian Bight N to the MacDonnell and Tomkinson Ranges in the Red Centre. The 21 species of *Westraltrachia* inhabit the very narrow southern limestone fringes of the Kimberley (**Map 59**); the 25 species of *Semotrachia* are restricted to the Red Centre (**Map 59**); the 27 species of *Sinumelon* have more continuous ranges and the generic range completely overlaps the range of *Pleuroxia* (**Maps 19, 24**). *Rhagada*, with at least 29 species, ranges (**Map 60**) from the W and SW Kimberley to Shark Bay and the 55 species of *Amplirhagada* are restricted to the Kimberley (**Map 61**).

Regional patterns

Except for the Kimberley, the camaenid fauna of each area has a relatively simple composition. These are summarised in **Tables 167–168**. The Red Centre has a mixture of Sinumeloninae and Pleurodontinae, each with moderate species radiations and at least some restricted endemic genera. The Flinders-Gawler-Eyre Peninsula region has a mixture of Sinumeloninae and Camaeninae, again with local generic and specific diversification. The Dampier Land to Nullarbor area has only Sinumeloninae along the S coast and in the goldfields section as far N as Geraldton. The Shark Bay to North West Cape area also has restricted endemic Sinumeloninae, while the Dampier Land to Shark Bay area has a mixture of two S Kimberley genera, the pleurodontid genus

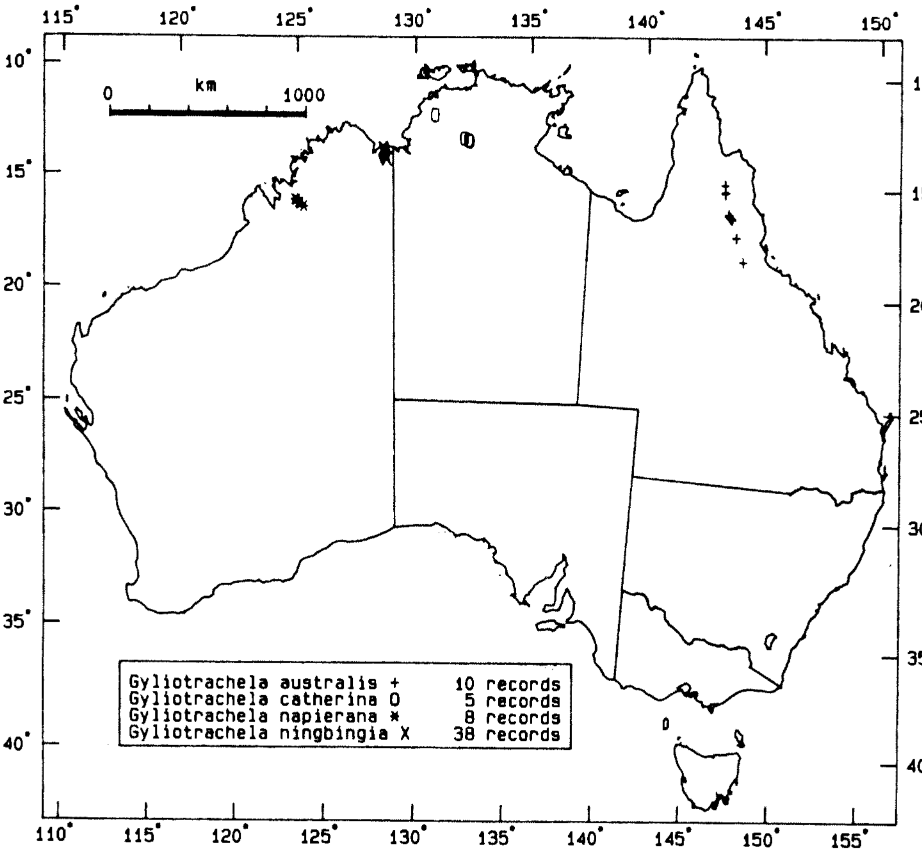


Map 56: Distribution of *Westracystis fredaslini* and *W. lissus* in Australia.

Rhagada and the "still unplaced in a subfamily" genus *Quistrachia*. The Kimberley has one pleurodontid genus on the SW margin (*Rhagada*) and two camaenine genera (*Hadra*, *Damochlora*).

These subfamilies are based upon highly distinctive patterns of reproductive structures and they show very different patterns of distribution. The Sinumeloninae (**Map 49**) are restricted to Australia, with the Red Centre, Flinders-Gawler-Eyre Peninsula and Nullarbor to Geraldton to North West Cape region defining the range. The Pleurodontinae (**Map 62**) are found in the Red Centre (4 genera), Mitchell Plateau to Shark Bay (*Rhagada*), Lesser Antilles (*Pleurodonte*) and probably in the China to Solomon Island axis. The Camaeninae (**Map 63**) range from China to the Solomon Islands, Queensland, New South Wales, the Flinders-Gawler-Eyre Peninsula area and has two genera (*Hadra*, *Damochlora*) in the Kimberley.

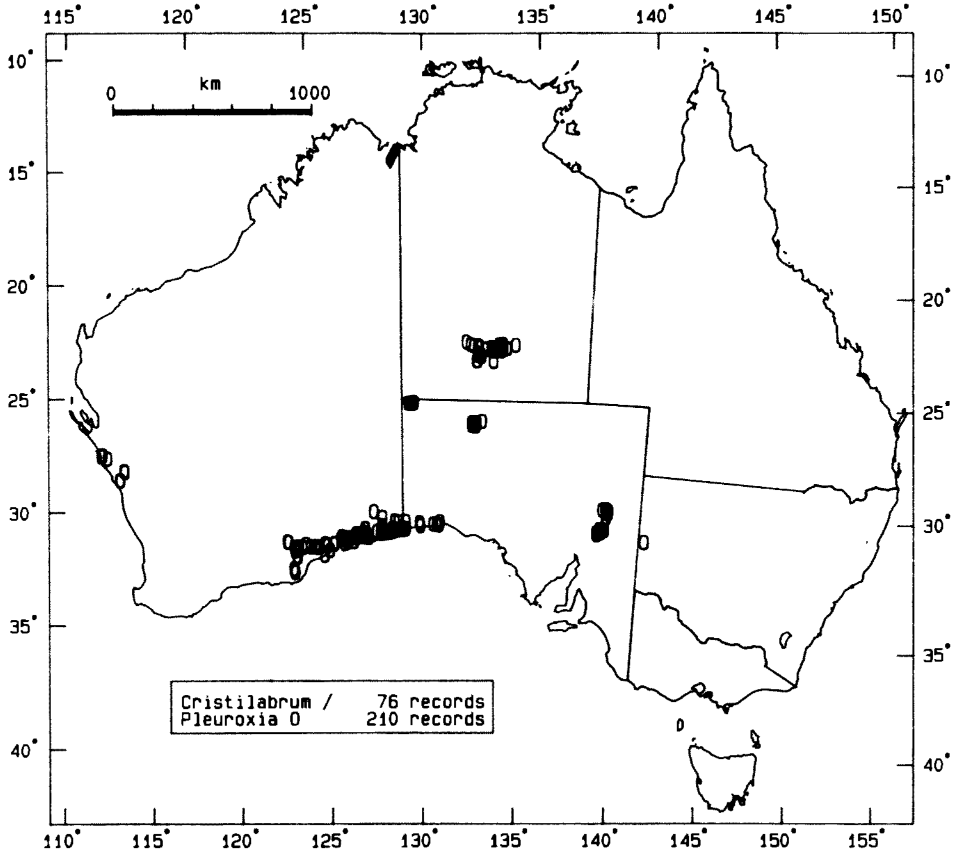
Thus only three (*Damochlora*, *Hadra*, *Rhagada*) of the 25 Kimberley camaenid



Map 57: Distribution of *Gyliotrachela australis*, *G. catherina*, *G. napierana* and *G. ningbingia* in Australia.

genera have been assigned to subfamilies at the time of writing. The remaining 22 genera are of problematic position. For 14 Kimberley genera, preliminary allozyme studies have been possible (Woodruff & Solem, in preparation). Both the allozyme data and studies of reproductive anatomy indicate that *Cristilabrum* is ancestral to *Turgenitubulus* – both genera are restricted to the Ningbing-Jeremiah Hills area. The suggestion of Solem (1984b: 693–699), that the S and E Kimberley genera *Westraltrachia, Mouldingia, Exiligada, Prototrachia* and *Ordtrachia* are related, is confirmed. The other genera "dangle" without clear relationships, since preliminary calculation of Nei's genetic distances, based on 15 allozymes, gives values so large that no relationships can be inferred (Solem, unpublished data). Both the anatomical and allozyme data suggest that these Kimberley genera are not closely related to each other.

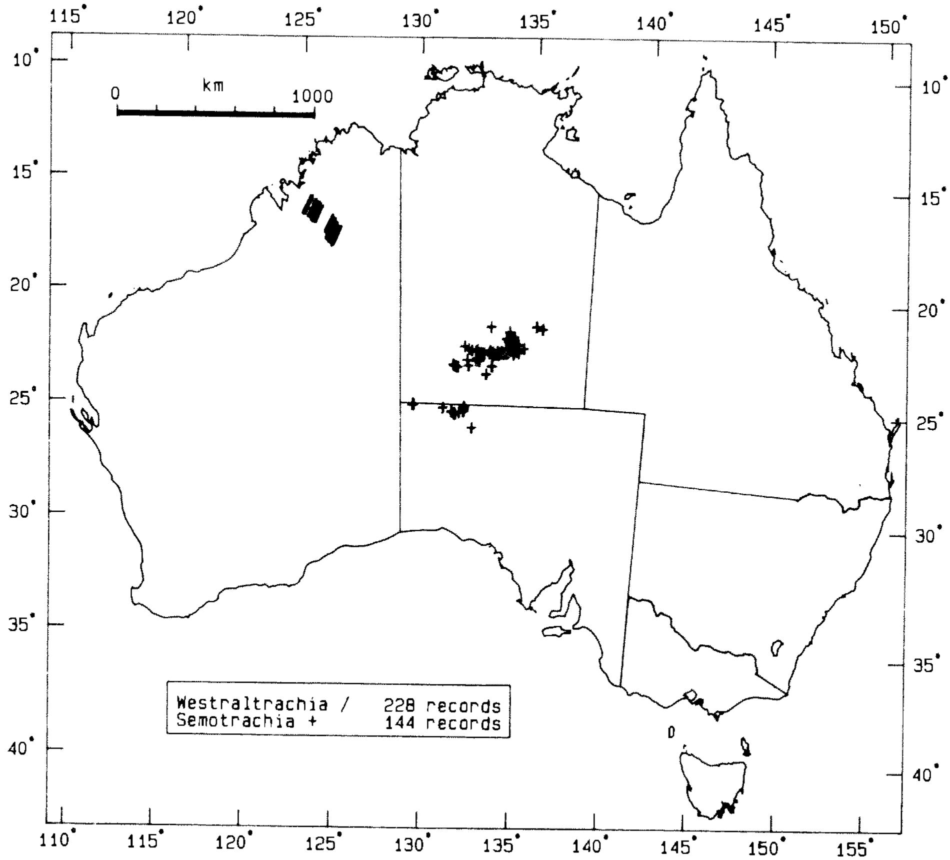
Cross regional patterns are few but intriguing. A few taxa show Kimberley-Queensland disjunctions – *Hadra* (**Map 50**), *Quistrachia* (**Map 53**), *Glyptopupoides egregia* (**Map 55**) and *Gastrocopta mussoni* (**Map 55**). *Georissa* also belongs in this category but the Queensland-New South Wales taxa have not been revised and accurate records are not available for mapping. *Gyliotrachela* has dry area taxa in the Kimberley



Map 58: Comparative distribution of *Cristilabrum* and *Pleuroxia* in Australia.

and northern Queensland (**Map 57**). The northern tip of the "Top End" (e.g. Cobourg Peninsula) Melville and Bathurst Islands have a small intrusion of "Indonesian wet area" taxa – *Trochomorpha melvillensis* Solem (1989a: 557–558), *Leptopoma minus* von Martens, 1867 (see Solem 1989a: 467–468) and the arboreal camaenid *Amphidromus cognatus* Fulton, 1907 (see Solem 1983). While *Leptopoma* also ranges into wet tropical Queensland, these are the only Australian records for *Trochomorpha* (Melanesian-Polynesian range) and *Amphidromus* (Khasi Hills of India to Timor and the Tanimbar Islands).

Other unusual non-camaenid records are the range (**Map 64**) of *Gastrocopta macrodon* Pilsbry, 1917 (see Solem 1989a: 495–496) from much of the Kimberley and from Milne Bay in Papua New Guinea and the Louisiade Archipelago, with no known intermediate occurrences; *Nesopupa novopommerana* Rensch, 1932 (see Solem 1989a: 476–477) from WA, NT, the Tanimbar Islands and Bismarck Archipelago; *Gastrocopta recondita* (Tapparone-Canefri, 1883) (see Solem 1989a: 496–497) from



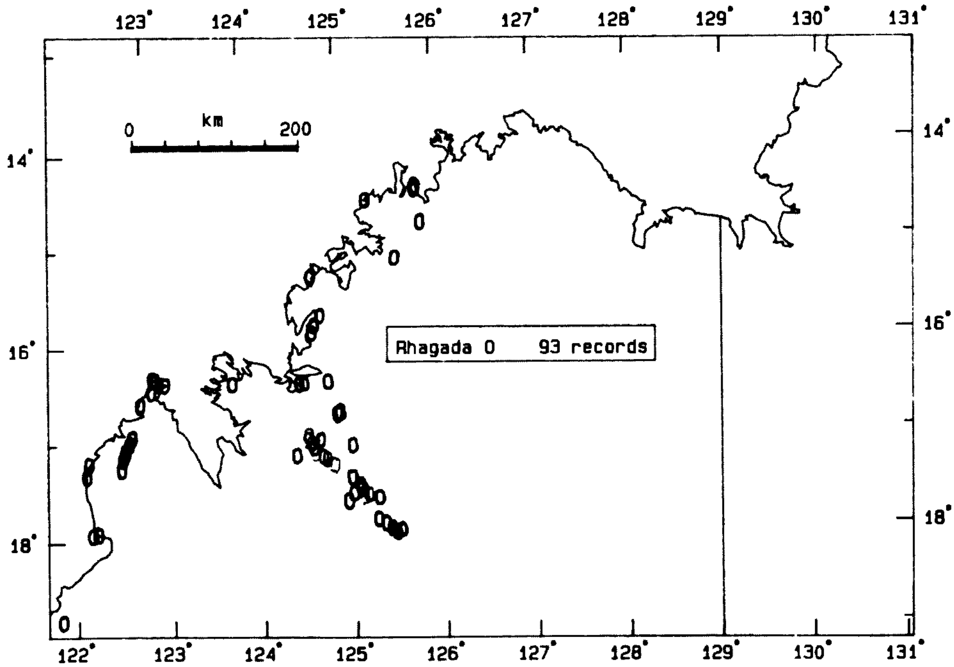
Map 59: Comparative distribution of *Westraltrachia* and *Semotrachia* in Australia.

Haruku, Ambon, Tanimbar and Aru Islands in Indonesia and then in drier parts of WA and the NT (**Map 64**); and *Gastrocopta macdonnelli* (**Map 64**) from the coastal NT eastward to Torres Strait.

Taken as an isolated instance, each of the above disjunctions or "only Australian records" can be viewed as "an interesting anomaly". However, collectively they are too numerous to ignore. They are discussed below as part of the speculation on the origins of this fauna.

Convergences

Perhaps the single most surprising result from this project was discovering the degree to which massive convergences in both structure and ecology have occurred. The basic *Pleuroxia* (sinumelonid) shell features (**Figs 368Aa–c, 370Aa–c, 370Bd–f, 372Aa–c, 372Bd–f, 374a–f**) – depressed shape, often-angulated periphery, often-anastomosing radial ribs, microsculpture of dense pustules, strongly deflected aperture, expanded lip that often is free of the parietal wall, lack of colour bands – have evolved in the Shark Bay area (*Falspleuroxia*, **Figs 386a–f**), Cape Range (*Strepsitaurus*, **Figs 394–395**), East Kimberley (*Cristilabrum kessneri* Solem, 1989b), near Katherine, NT the still undescribed radiation and the Red Centre (*Granulomelon arcigerens* [Tate, 1894] and *G. gilleni* Solem, 1993 [see Solem 1993: figs 265a–f]), in addition to the wide distribution of true *Pleuroxia*. The relatively similar *Glyptorhagada* (Camaeninae) pattern (Solem 1992: figs 45, 48, 50, 57) of SE South Australia is

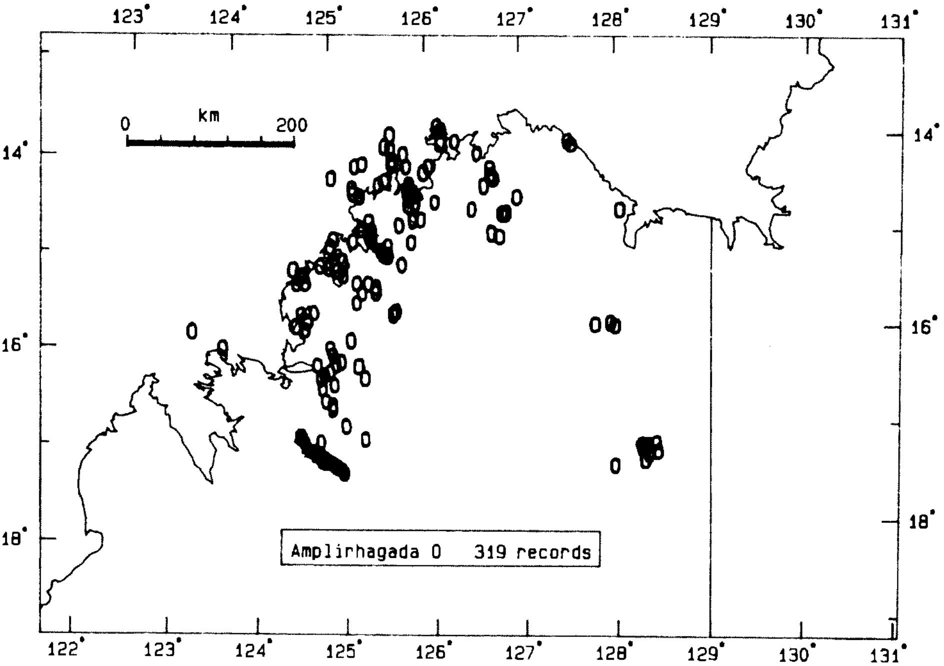


Map 60: Records of the genus *Rhagada* from the Kimberley and Dampier Land, WA.

closely duplicated by the Red Centre *Eximiorhagada* (Sinumeloninae, Solem 1993: figs 312a–c), Kimberley *Carinotrachia carsoniana* Solem (1985b: 860, figs 216a–c) and the Kimberley *Turgenitubulus pagodula* Solem (1985b: 957, figs 246d–f). All of the above taxa tend to aestivate sealed to a rock surface rather than in litter.

The speciose Red Centre genus *Semotrachia* (Pleurodontinae) is almost completely duplicated conchologically by the Red Centre *Montanomelon* (Sinumeloninae) (see Solem 1993: figs 313a–f, 319, 323, etc.). In the Flinders Range (Solem 1992: figs 68a–f), both a sinumelonid (*Micromelon*) and a camaenine genus (*Aslintesta*) have converged so completely to the *Semotrachia* size and structure that it requires SEM photos of shell microsculpture or genital dissection to separate them from each other or from *Semotrachia*. In the Kimberley, many species of *Setobaudinia* (subfamily position unknown) show nearly all of the *Semotrachia* features (Solem 1985b: plts 64–69, figs 181, 184, 187, 190, 192). The Mt Dryander, Queensland species, *Offachloritis dryanderensis* (Cox, 1872) (see Solem 1979: 118, figs 26d–f) is yet another convergent shell (subfamily Camaeninae, Solem, unpublished data). A third set of convergences, this time to a globose shape with narrowed lip and spiral colour zone, is found in the Shark Bay to Cape Range area and involves *Plectorhagada*, *Rhagada* and *Quistrachia*, representatives of three different subfamilies.

The above examples involve shape, whorl patterns, apertural features, very complex sculpture and colouration – shell features that show no necessary linkage. The taxa are differentiated by having genital anatomies that link them to "non-modified" taxa in the same areas. Thus the conchological similarities are hypothesised to be convergent with



Map 61: Records of the genus *Amplirhagada* from the Kimberley, WA.

taxa in the other regions.

Feeding changes involve both the jaw and the radula. Loss of the characteristic vertical ribbing on the jaw (**Plates 179e, 180f, 182d**, etc.) has been documented as a gradual process within the Kimberley genus *Westraltrachia* (see Solem 1984b, 1985a). Much of the change occurs in one species, *W. derbyi* (Cox, 1892) (see Solem 1984b: 454–455, plts 27–28). The same change is seen within populations of *Strepsitaurus rugus* (**Plate 201c–f**) and also among species of *Rhagada* (**Plate 215a–f**). The identical reduction change is thus documented in three subfamilies. It often correlates with a radular change but the latter does happen by itself in some situations.

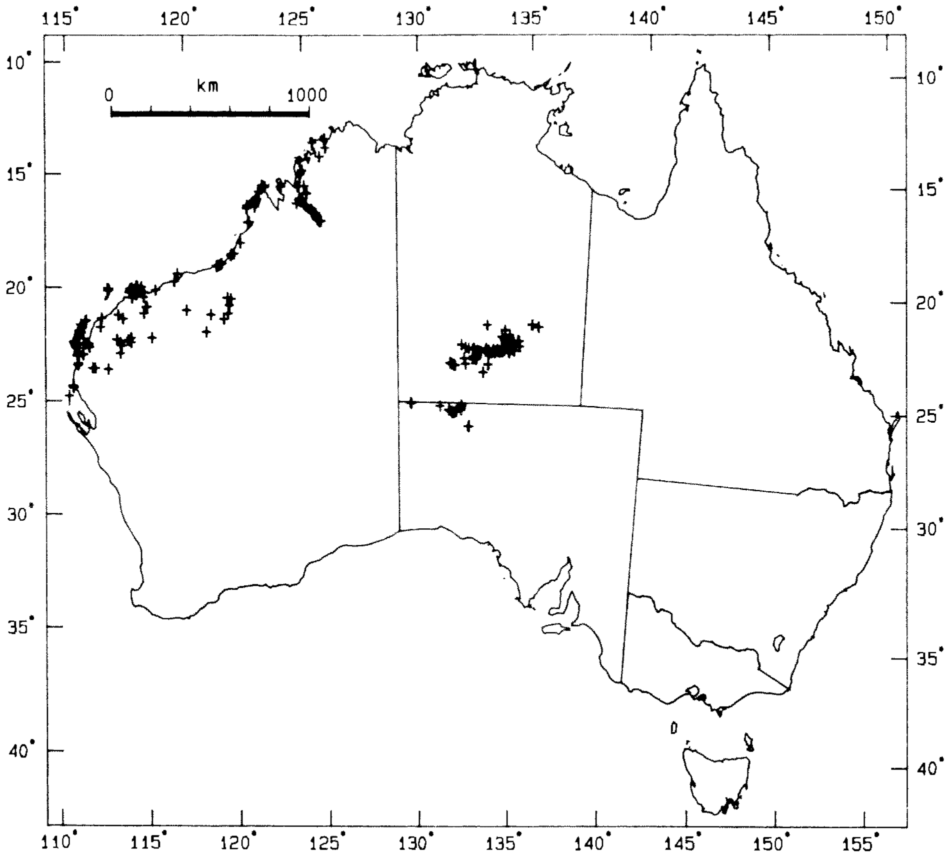
Radular specialisation is most easily noticed in the cutting teeth, central and laterals. The common modification pattern in the dry area camaenids is for: 1) great increase in cusp shaft angle; 2) very strong curvature of the cusp tip; 3) broad rounding of the cusp tip; and 4) shortening of the basal plate. These changes convert the feeding stroke from the typical "chop and cut into small pieces" pattern to one in which the tooth glides along a surface scraping attached particles loose. This shift was first documented as a gradual process involving several linear allopatric species in the Kimberley camaenid genus *Westraltrachia* (see Solem 1984b, 1985a). It is a general pattern in the SE South Australian Camaeninae, wherever they are sympatric with a species of Sinumeloninae. These changes have not been observed in Camaeninae from other parts of Australia. On the W coast, in the Geraldton to North West Cape area, where there is significant geographical overlap among Sinumeloninae (several genera), Pleurodontinae (*Rhagada*) and a third (undesignated) subfamily (*Quistrachia*), this shift in functioning is found in *Falspleuroxia overlanderensis* (**Plate 189a**), *Plectorhagada scolythra* (**Plate 195c**), *Strepsitaurus ningaloo* (**Plate 199a–b**) and *Strepsitaurus rugus* (**Plate 201d–f**). Interpopulational variation is found in the last-mentioned species. All species showing this change are members of the Sinumeloninae. It is not known why the SA Sinumeloninae maintain a generalised cutting tooth structure when sympatric, whereas the W coast Sinumeloninae have evolved the altered pattern in the area of extensive sympatry. This change has evolved several times in different parts of Australia. The common ecological factors are: 1) a medium to quite dry habitat; 2) geographic overlap with one or more different subfamilies of camaenids; and 3) availability of rock surfaces from which encrusting films could be scraped.

An entirely different pattern of radular specialisation is seen in wet forest arboreal taxa, such as *Amphidromus* and the papuinid complex (see Solem 1983: figs 2–19), which are adapted to feeding off leaf and twig surfaces. Although similar to the variation described above, when viewed from above at optical magnifications, the teeth are very different in shape (and function) when viewed laterally with the SEM.

Changes in the genital system are, at first, second, third, fourth, ... and last glance, bewildering. The reasons for this are comparatively simple; unraveling the results is a process still continuing.

My hypothesis is that the Australian camaenids are derived initially from monsoonal-climate ancestors, with the Kimberley providing a fringe monsoon climate. The semi-arid and arid zone camaenid taxa are descended from monsoonal-climate ancestors. Whether this resulted either from *colonisation* of the drier areas from wetter zones, or from arid climate *spread* to "dry out" formerly wetter areas, or from any combination of these processes is unknown and probably unknowable. Once a snail is able to aestivate through a several-month dry season in a monsoonal-climate, extension of time in aestivation for a year or more would be a trivial evolutionary adaptation. Monsoonal-climate snails are thus pre-adapted to desert survival.

In the wetter parts of Northern Australia, the wet season begins with a single soaking, during which the camaenids activate, mate, feed and then retreat again to shelter (Solem & Christensen 1984; Solem 1988b: 83, table 1). There is then a mean gap of 16–27 days until the second rain. I hypothesise that fertilisation and encapsulation of eggs occurs while the snails are inactive during this interval, so that egg laying can take place at the second activation. The first activation of the wet season may enable only one or two nights of activity by the snail. Hence the Kimberley camaenids show a "wham! bam! thank you, it!" pattern of 5–15 minute reciprocal

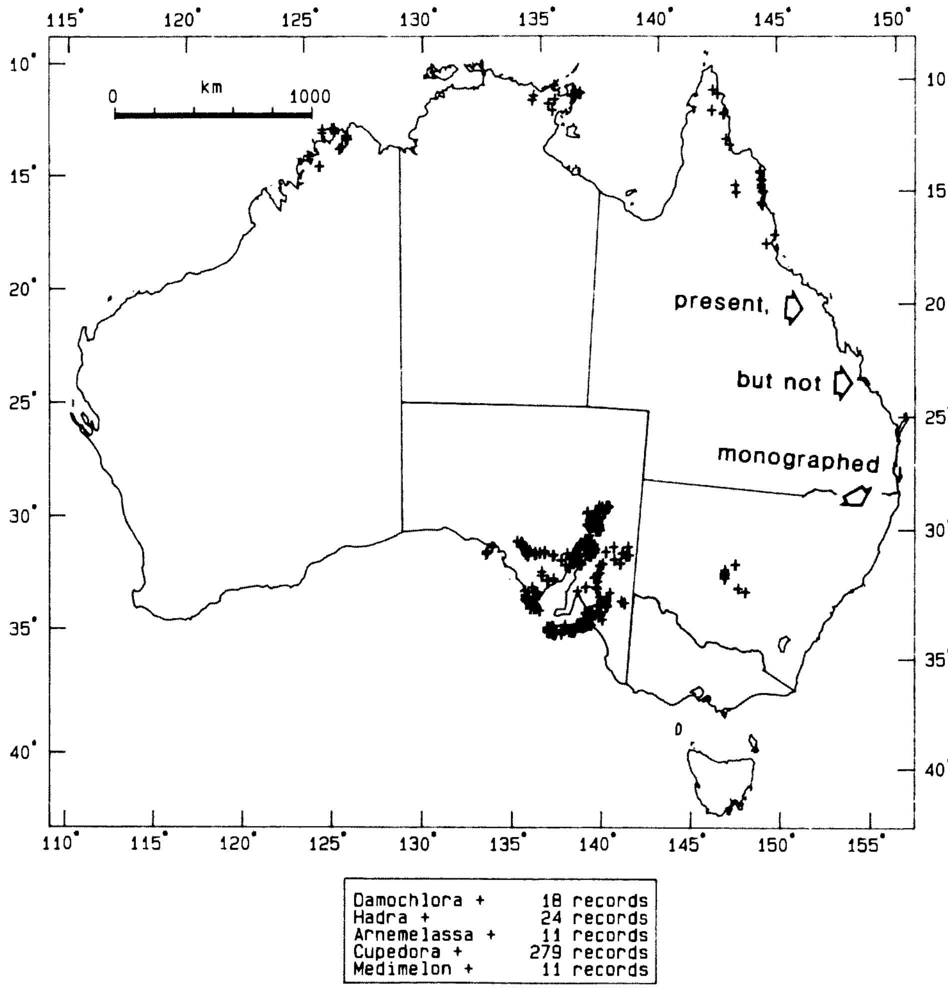


Rhagada +	215 records
Divellomelon +	4 records
Vidumelon +	2 records
Dirutrachia +	10 records
Semotrachia +	144 records

Map 62: Distribution of Pleurodontinae in Australia, based on *Dirutrachia*, *Divellomelon*, *Rhagada*, *Semotrachia* and *Vidumelon*.

mating (see Solem & Christensen 1984). This eliminates the use of lengthy courtship rituals and secretion of pheromones; it limits "species recognition" to altered structures in the terminal genitalia. It explains why the terminal genitalia of sympatric congeneric camaenids show gross differences. Indeed, the most striking differences are found in sympatric or contiguous allopatric species occurrences. The long courtship and 24–48 hour copulations of some European wet area slugs (Peyer & Kuhn 1928) stand in sharp contrast to the Kimberley mating patterns.

The above basic outline holds for taxa living in an area with a dependable wet season with a 800–1,500+ mm rainfall. As outlined above in the **Summary Discussion**, species living in areas with reduced and/or irregular rainfall have modified genital structures. This may involve shifts in organ functions, as with the enlarged albumen



Map 63: Distribution of Camaeninae in Australia, based on selected genera (*Damochlora, Hadra, Arnemelassa, Cupedora, Medimelon*).

gland in W coast *Rhagada* and Sinumeloninae, or size reduction/simplification in the terminal organs, such as the verge in *Rhagada* and the entire male system in the *Mouldingia-Westraltrachia-Prototrachia-Ordtrachia-Exiligada* complex (Solem 1984b: 693–699).

Interpretation of the above two examples as a "size reduction" sequence was relatively simple, because the species occupied linear sequences from a wetter to a drier zone. The changes were fairly simple and followed the geographic linearity. Unfortunately, we do not have equally simple systems elsewhere.

In the Camaenidae, there are a few constraints upon the size of the penis complex, relating to the attachment point of the penial retractor muscle at the mantle collar-neck junction. The muscle may attach to the epiphallus above the penis apex (Camaeninae and Pleurodontinae), or to the penis apex-epiphallus junction (Sinumeloninae, many Kimberley taxa). The total distance from external genital pore (atrium, Y) to where the penial retractor muscle reaches the mantle collar defines the maximum length of the penis complex – except when the presence of a penis sheath permits an elongated, coiled penis WITHIN the sheath, as in *Quistrachia lefroyi* (**Figs 437a–b, 438b**). Many Kimberley camaenids have elongated penes within penis sheaths.

Wet area helicoid land snails normally have an elongated foot and the head-neck extends considerably beyond the aperture of the shell when the snail is crawling. One way to reduce body size (and hence energy use) is to reduce the length and volume of the head-neck-foot region. This has occurred in a number of dry area camaenids. If the head and neck are both shortened and narrowed, this automatically shortens and compacts the penis complex. When this is combined with simplification or loss of terminal organs, strikingly similar structures can result, greatly confusing taxonomists, including this one.

Of the 25 Kimberley camaenid genera, 40% (10) are primarily or exclusively wet area (800–1,500 mm wet season rainfall) inhabitants, while 60% (15) are fringe of wet to dry, or exclusively dry, area (500–750 mm wet season) residents. The former have complex and obviously different terminal genitalia; many of the latter taxa have confusing small and simple genitalia. A good example of the common changes from wet to dry zone genitalia is shown by comparing the systems of the S China-Hong Kong species *Camaena cicatricosa* (Müller, 1774) (Solem 1992: figs 1–3) with the Flinders Range of SA species *Cupedora extensa* (Iredale, 1937) (Solem 1992: figs 18–20). Both have the characteristic head wart and tubular verge of the Camaeninae, but the smaller size and organ reduction in the *Cupedora* stands in great contrast. Indeed, the juvenile genitalia of *Camaena* (Solem 1992: fig. 1a) closely resembles the adult genitalia of the *Cupedora* (Solem 1992: figs 19a, c–e). Recognition of this reduction pattern was possible because the unique eversible head wart of the Camaeninae was present throughout the Australian Camaeninae.

Two of the above effects probably tend to counter each other and certainly cause additional confusion. Congeneric sympatric species will show major shifts in terminal genitalia to aid in species recognition, while dry region species will show simplification of structures. The shifting patterns caused by interactions of these two selective pressures may explain why there is such confusing and convergent genital system structural variation. Presence of a short spermathecal duct, for example, is a character found in a number of genera but *Rhagada*, *Baudinella*, *Retroterra* (see Solem, 1985b) all show different ways in which shortening can start. This strongly suggests that the change from a long to a short spermatheca has happened several times. The end results (short stalk) frequently cannot be differentiated.

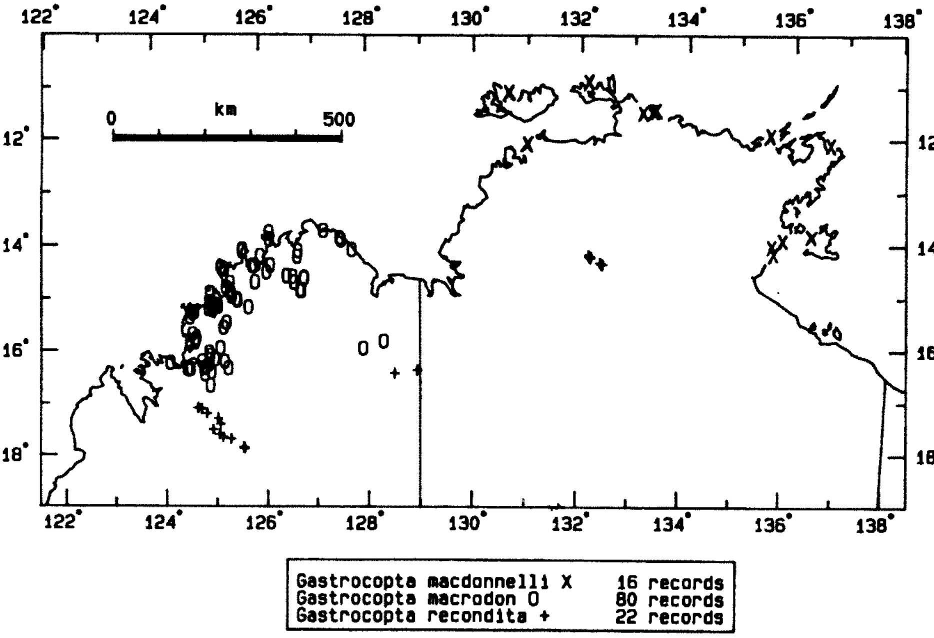
Similar statements can be made about most genital variations. These facts make identification of character polarity and change very difficult.

Possible faunal origins

It had been anticipated that this series would close with a testable phylogenetic hypothesis concerning the Camaenidae and that this would have produced a biogeographic scenario. These anticipations have foundered on the fact that only 28 of 51 genera have been allocated to subfamily units. The remaining 22 genera, all represented in the Kimberley, together with the NT *Parglogenia*, cannot yet, with assurance, be related to either Australian or extralimital subfamilal taxa. Part of this problem is caused, I suspect, by the many (secondary) simplifications that have taken place in the genital systems of dry-area camaenids. Part of the problem relates to the fact that preserved material from the China-Indonesia-Solomon Islands arc simply does not exist in museum collections.

Available evidence does permit advancing several hypotheses that could be tested by obtaining material from the China-Indonesia-New Guinea-Queensland-Solomon Islands arc for dissection and SEM observations.

Many factors mitigate against the possibility that the Camaenidae might be a



Map 64: Records of *Gastrocopta macdonnelli*, *G. macrodon* and *G. recondita* from the Kimberley, WA and NT.

Gondwanic element. Extralimitally, the absence of any actual or potential camaenids from southern South America, Southern Africa, Madagascar, New Zealand and other than the northern fringes of peninsular India, is highly significant. Within Australia, camaenids do not exist in the humid SW corner (roughly included in a Geraldton-Augusta-Esperance triangle), Tasmania and much of Victoria. There is no evidence that they ever existed in these regions. The large caryodid taxa of wet eastern areas (roughly Mackay, Queensland through Tasmania) are not at all similar in anatomy and cannot be cited as a potential ancestor to any of the camaenid subgroupings.

The fossil record of the Camaenidae, although subject to some controversy as to generic affinities, is substantial and indicative of a northern origin. Fossil camaenids are known from the Upper Cretaceous of Utah and China (Solem 1978). In the New World, there are subsequent Tertiary fossil records from Texas and New Mexico, an Oligocene record from Nebraska (Bishop, 1979), and Miocene records from Florida and Jamaica (Solem 1978). There are no significant Old World records outside of China, if the *Dentellocaracolus* Oppenheim, 1890 complex from the European Eocene is considered to be a helicid, not a camaenid.

Extant distribution in the New World shows that mainland camaenids range from Costa Rica S to the Dept. Cusco of Peru, with a few Amazonian Basin and Guiana records (Solem 1966). There is an extensive radiation on the Greater Antilles and Lesser Antilles (Wurtz 1955, Bishop 1979), but no North American or Nicaraguan through Mexico records (one Cuban-Bahaman species has been introduced into S Florida). Clearly the North American range no longer exists – except in so far as the Polygyridae and Oreohelicidae may be related to the Camaenidae. Old World distribution extends from China and Sri Lanka to Japan, Philippine Islands, Indonesia through New Guinea and the Solomon Islands and the major Australian radiation under review in this series together with the large Torres Strait S to middle New South Wales radiation.

All of the above data point to the Camaenidae as being a northern tropical group that was well established in the Cretaceous. There is no evidence for a southern origin.

The distribution of the identified subfamily units also provides suggestive data. The Sinumeloninae (**Tables 167–168, Map 49**) do not occur in northern or eastern Australia (W Queensland records require confirmation by dissection and may be based on shell convergences), have no known extralimital relatives and provide a number of unsolved problems. Is *Pleuroxia* a monophyletic unit, or has its separated species-clusters (**Map 19**) evolved independently from, most probably, *Sinumelon*? At least part of this puzzle could be solved by allozyme studies but more sophisticated molecular techniques probably will be required. Nearly all of the *Pleuroxia* species are microsympatric with either other *Pleuroxia* or *Sinumelon* species. I have not been able to find genital features that will indicate phylogeny, rather than just microsympatric species interactions. A second problem concerns the W coast endemic genera – *Falspleuroxia*, *Plectorhagada*, *Strepsitaurus*, *Promonturconchum* and *Caperantrum*. They inhabit perhaps the most stressful environment of any Australian camaenids and do have the enlargement of the albumen gland and shortened neck and body features mentioned above. Are they derived from the *Pleuroxia-Sinumelon* stock from the SE, represented by *Pleuroxia bethana* and *Sinumelon vagente* in the Geraldton hinterland? Or are they more closely related to some of the Red Centre genera? Preliminary allozyme studies (unpublished data) indicate a very substantial difference between

Plectorhagada plectilis and *Sinumelon vagente*, too wide for allozyme evidence to be useful. This suggests that the W coast radiation is independent of the Eastern Goldfields-Nullarbor taxa. However this does not begin to answer the question as to whether the W coast taxa are derived from the Red Centre through colonization from the E, or if they are related to neither area and are of independent origin, presumably from the N where they subsequently were replaced by other camaenids.

The Pleurodontinae (**Map 62**), distinguished by the exposed head wart, short penis complex and complex verge with a long sperm groove (unless secondarily reduced in dry area habitats), have a disjunct Australian distribution. *Rhagada* occurs along the W coast from the Mitchell Plateau to Shark Bay, inland in the Napier-Oscar Range area of the Kimberley and to the Oakover River area in the Pilbara (**Map 36**); then *Semotrachia* and its derivative genera in the Red Centre (**Map 62**). This subfamily may have some Queensland relatives but the material needed to answer this question has not been available to me. The same head wart and basic genital system has been confirmed as present in species of *Pleurodonte* from the Lesser Antilles (Solem unpublished). The same type of head wart has been seen in Philippine Islands taxa (Solem unpublished). Taki (1935), who initially observed this structure, found such warts not only in Japanese camaenids, but also in the Bradybaenidae. This may indicate a phyletic link between the two families. If confirmed, this could establish the Camaenidae as the base group of the Helicoidea. The available evidence is tenuous but dissection of Asian-Indonesian-Melanesian-Queensland taxa can provide critical data to determine whether pleurodontid taxa exist in this region and also the probable affinities with other family level taxa.

The Camaeninae, distinguished by an *eversible* head wart, long tubular verge, elongated penis complex and altered pattern of terminal female organs, are confirmed from S China, Queensland, two genera (*Hadra*, *Damochlora*) in the Kimberley (**Map 63**), New South Wales and southeastern SA (Solem 1992). In addition, I have dissected Philippine, Indonesian and Solomon Islands taxa that belong here. At present, I have not confirmed any New World representation. Although it is logical to suggest that there might be a close pleurodontine-camaenine link, with invagination of the head wart and closure of the sperm groove on the verge to form a tubular verge producing a camaenine from a pleurodontine ancestor (the reverse process is equally probable), I doubt that evolution has been that simple. There are too many other differences in "wet area" taxa for me to be confident of such an evolutionary pattern.

The overlap of Sinumeloninae and Camaeninae in the Gawler-Flinders-Eyre Peninsula region has been discussed previously (Solem 1992: figs 145-146), the latter hypothesised as colonizing from the E, the former from the N.

The data on these three subfamilies does account for the Red Centre and southeastern SA taxa, the Nullarbor and Goldfields taxa of WA and many of the midwestern coast and Queensland taxa, suggesting basically northern origins and dispersal. Certainly they show no evidence of vicariance on a generic or higher level, although vicariant events almost certainly account for many of the speciation events after initial waves of colonization.

There then remain the 22 Kimberley genera that have not been assigned to subfamily units. Genital anatomy and allozyme data (unpublished) do link a few of these taxa but most are too differentiated for allozyme data to provide answers. They show a variety of genital structures that suggest a considerable degree of differentiation. Such differentiation could be the result of: 1) local evolution that occurred long ago; or 2) multiple colonizations by stocks that had evolved elsewhere.

The latter pattern seems the more probable, based in part on the data provided by Kimberley and NT non-camaenid land snail distribution patterns. As outlined above, essentially the entire non-camaenid land snail fauna has Indonesian roots (except possibly *Amimopina*, see Solem 1988a: 516–519). Individual species ranges include intriguing disjunctions, with a Kimberley or NT range associated with a Queensland, E New Guinea, or Bismarck Archipelago presence.

It might be argued that a few taxa may have spread N and W from Australia after collison of the Australian and Asian plates, but it seems that most taxa will fit a model of: 1) colonizing the Kimberley or NT from Timor or neighbouring islands, as waves of immigration from SE Asia passed through Indonesia; 2) subsequently reaching Queensland and/or the Bismarck-Solomon Islands; 3) being replaced in Indonesia-New Guinea by later migrants; thus 4) producing a Kimberley-"other area" disjunction. Evidence of this exists for several non-camaenids, but not yet for the camaenids themselves.

Preserved material is needed from China, the Philippines, Japan, Indonesia, New Guinea, Queensland and the Bismarck and Solomon Islands to see how many of the "Kimberley 22" can be related to Old World taxa. At the same time, further study of the New World genera, based upon materials currently available, will reveal whether there are other bi-hemispheric linkages. While Wurtz (1955) provides much useful data, many phylogenetically significant characters in Australian camaenid genera are neither discussed nor illustrated for New World species. The main groups must be re-examined and several potential cross-hemisphere links investigated. For example, the genital structures of the Kimberley endemic *Amplirhagada* and some North American Polygyridae have striking similarities but more study is needed.

Work on the 51 monographed genera (plus a number of additional Queensland-New South Wales genera) indicates structural patterns into which extralimital taxa can be slotted or quickly identified as yet another variant. The convergences in shell structure encountered during these studies give me a permanent scepticism concerning shell features only. At the same time I have gained a deep appreciation of the genital conservatism of wet-area taxa.

The monographic work summarised here has outlined the camaenid fauna in the western two-thirds of Australia, has identified the patterns or structural changes involved in "desertification" as the climate ranges from monsoonal to semi-arid or arid, has linked more than half of the genera into subfamily units (two of which show intercontinental ranges) and has pointed out where studies must be undertaken in order to link the remaining taxa and then to develop an overall phyletic and biogeographic portrait of these intriguing organisms.

Answers must be sought by study of taxa living in the monsoonal tropics to the N, including faunas from both the New World and the Old World.

REFERENCES

BEDNALL, W. T. (1892)–Land and Fresh-water Mollusca (Elder Exploring Expedition). *Trans. Roy. Soc. S. Aust.* **16** (1): 62–67, pl. I.

BISHOP, M. J. (1979)–A new species of *Caracolus* (Pulmonata: Camaenidae) from the Oligocene of Nebraska and the biotic history of the American camaenid land snails. *Zool. Jour. Linnean Soc.* **67**: 269–286, figs 1–22.

BURCH, J. B. (1976)–Outline of Classification of Australian Terrestrial Molluscs (Native and Introduced). *J. Malac. Soc. Aust.* **3** (3–4): 127–156.

CLENCH, W. J. & ARCHER, A. A. (1937)–Some new Australian *Thersites*. *J. Conch.* **21** (1): 20–24, pl. 1.

COTTON, B. C. (1953)–New species and records of Mollusca from South Australia. *Trans. Roy. Soc. South Austr.* **76**: 21–26, plts II–III.

COTTON, B. C. & GODFREY, F. K. (1932)–South Australian Shells (Including descriptions of New Genera and Species). Part V. *S. Aust. Nat.* **13** (4): 127–176, pls 1–3.

COX, J. C. (1868)–A Monograph of Australian Land Shells. Sydney: William Maddock. pp. i–v, 1–111, pls 1–20.

COX, J. C. (1909)–An alphabetical list of Australian land shells. Part I. Sydney: Frederick W. White. pp. 1–84.

GREGG, W. O. (1960)–Derivation of the Helminthoglyptidae with Particular Reference to the Desert Forms (Abstract). *Annual Reports for 1959, Amer. Malac. Union* **26**: 45–46.

HEDLEY, C. (1889)–Anatomical Notes on the Helicidae. *Proc. Roy. Soc. Queensland* **6** (1): 62–63, pl. 3.

HEDLEY, C. (1896)–Appendix [to Mollusca]. Notes on Anatomical Characters. in Spencer, B. (ed.), *Report on the work of the Horn Scientific Expedition to Central Australia. Part II. Zoology. Mollusca:* 220–226, figs A–P.

HEDLEY, C. (1905)–Report on the Mollusca Collected by Mr. Herbert Basedow on the South Australian Government North-west Expedition, 1903. *Trans. Proc. Rep. Roy. Soc. S. Aust.* **29**: 161–165, 4 text figs, pl. XXX.

HEDLEY, C. (1915)–A preliminary index of the Mollusca of Western Australia. *Jour. Roy. Soc. Western Aust.,* **1**: 1–77.

IREDALE, T. (1933)–Systematic Notes on Australian Land Shells. *Rec. Aust. Mus.* **19** (1): 37–59.

IREDALE, T. (1937a)–A Basic List of the Land Mollusca of Australia. *Aust. Zool.* **8** (4): 287–333.

IREDALE, T. (1937b)–An Annotated Check List of the Land Shells of South and central Australia. *S. Aust. Nat.* **18** (2): 6–57, pls 1–2, 1 map.

IREDALE, T. (1937c)–A Basic List of the Land Mollusca of Australia. Part II. *Aust. Zool.* **9** (1): 1–39, pls I–III.

IREDALE, T. (1938)–A Basic List of the Land Mollusca of Australia. Part III. *Aust. Zool.* **9** (2): 83–124, pls XII–XIII.

IREDALE, T. (1939)–A Review of the Land Mollusca of Western Australia. *J. Roy. Soc. Western Aust.* **25**: 1–88, pls 1–5, 1 map.

KENDRICK, G. W. (1978)–New species of fossil nonmarine molluscs from Western Australia and evidence of late Quaternary climatic change in the Shark Bay district. *Jour. Roy. Soc. West. Aust.* **60**(2): 49–60, figs. 1–8.

MERRIFIELD, H. E., SLACK-SMITH, S. M., & WILSON, B. R. (1977)–Report on the mollusc fauna of the Drysdale River National Park, North Kimberley, Western Australia. Part X. Kabay, E. D. & Burbidge, A. A. A Biological Survey of the Drysdale River National Park, North Kimberley, Western Australia. *Western Australian Wildlife Research Centre. Department of Fisheries and Wildlife. Wildlife Research Bulletin* **6**: 110–120, tables 1–2, figs 1–3.

PEYER, B. & KUHN, E. (1928)–Die Kopulation von Limax cinereoniger Wolf. *Vierteljahrsch. Naturfor. Gessell. Zürich* **73**: 485–521, plts XVI–XX, text figs 1–9.

PILSBRY, H. A. (1895)–Guide to the Study of Helices. *Manual of Conchology* (2) **9**: vii–xlviii.

PILSBRY, H. A. (1900)–*Manual of Conchology* (2) **13**: 1–253, plts 1–72.

PRESTON, H. B. (1908)–Description of a new species of *Rhagada* from Western Australia. *Proc. Malac. Soc. London* **8** (2): 120, 2 figs.

PRESTON, H. B. (1914)–Description of new species of land and marine shells from the Montebello Island, Western Australia. *Proc. Malac. Soc. London* **11** (1): 13–18, 11 figs.

RICHARDSON, L. (1985)–Camaenidae: Catalog of Species. *Tryonia* **12:**1–479.

SMITH, E. A. (1874)–Mollusca. In Richardson, J. & Gray, J. E. (eds), *The Zoology of the Voyage of H. M. S. Erebus & Terror, under the command of Captain Sir James Clark Ross, R. N., F. R. S., during the years 1839 to 1843.* Vol. 2, Part 21, pp. 1–7, pls 1–4. London: E. W. Johnson.

SMITH, E. A. (1893)–Descriptions of new species of *Helix*, *Rissoina* and *Acteon*. *Conchologist* **2**(5): 97–100.

SMITH, E. A. (1894)–On the land-shells of Western Australia. *Proc. Malac. Soc. London* **1**(2): 84–99, pl. 7, figs 8–32.

SOLEM, A. (1966)–The Neotropical land snail genera *Labyrinthus* and *Isomeria* (Pulmonata, Camaenidae). *Fieldiana: Zoology* **50:** 1–226, figs 1–61, tables I–XVI.

SOLEM, A. (1974)–*The Shell Makers: Introducing Mollusks.* New York: John Wiley & Sons. pp. xii, 1–289, plts 1–12, many text figs.

SOLEM, A. (1978)–Cretaceous and Early Tertiary Camaenid Land Snails from Western North America (Mollusca: Pulmonata). *J. Paleont.* **52** (3): 581–589, figs 1–3.

SOLEM, A. (1979)–Camaenid Land Snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). I. Taxa with Trans-Australian Distributions. *Rec. Western Aust. Mus., Suppl.* **10:** 1–142, figs 1–35, pls 1–11, tables 1–10.

SOLEM, A. (1981a)–Camaenid Land Snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). II. Taxa from the Kimberley, *Amplirhagada* Iredale, 1933. *Rec. Western Aust. Mus., Suppl.* **11:** 147–320, figs 36–73, pls 12–14, tables 11–33.

SOLEM, A. (1981b)–Camaenid Land Snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). III. Taxa from the Ningbing Ranges and Nearby Areas. *Rec. Western Aust. Mus., Suppl.* **11:** 321–425, figs 74–110, pls 15–18, tables 34–42.

SOLEM, A. (1981c)–Land Snail Biogeography: a true snail's pace of change. *In "Vicariance Biogeography: A Critique"* (Eds G. Nelson and D. E. Rosen). New York: Columbia University Press. pp i–xvi, 1–593.

SOLEM, A. (1981d)–Small Land Snails from Northern Australia. I. Species of *Gyliotrachela* Tomlin, 1930 (Mollusca: Pulmonata: Vertiginidae). *J. Malac. Soc. Aust.* **5:** 87–100, figs 1–19.

SOLEM, A. (1982)–Small Land Snails from Northern Australia. II. Species of *Westracystis* Iredale, 1939 (Mollusca: Pulmonata: Helicarionidae). *J. Malac. Soc. Aust.* **5:** 175–193, figs 1–19.

SOLEM, A. (1983)–First record of *Amphidromus* from Australia, with anatomical notes on several species (Mollusca: Pulmonata: Camaenidae). *Rec. Aust. Mus.* **35:** 153–156, figs 1–24.

SOLEM. A. (1984a)–Small land snails from Northern Australia. III. Species of Helicodiscidae and Charopidae. *J. Malac. Soc. Aust.* **6:** 155–179, figs 1–45.

SOLEM, A. (1984b)–Camaenid Land Snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). IV. Taxa from the Kimberley, *Westraltrachia* Iredale, 1933 and Related Genera. *Rec. Western Aust. Mus., Suppl.* **17:** 427–705, figs 111–180, pls 19–63, tables 43–75.

SOLEM, A. (1984c)–A world model of land snail diversity and abundance. In "*World-wide Snails: Biogeographical Studies on Non-marine Mollusca* (Eds A. Solem & A. C. van Bruggen). Leiden: E. J. Brill. pp. 6–22.

SOLEM, A. (1985a)–Simultaneous character convergence and divergence in Western Australian land snails. *Biol. Jour. Linnean Soc. London* **24:** 143–163, figs 1–8 tables 1–3.

SOLEM, A. (1985b)–Camaenid Land Snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). V. Remaining Kimberley Genera and Addenda to the Kimberley. *Rec. Western Aust. Mus., Suppl.* **20:** 707–981, figs 181–256, pls 64–94, tables 76–94.

SOLEM, A. (1986)–Pupilloid land snails from the south and mid-west coasts of Australia. *J. Malac. Soc. Aust.* 7 (3–4): 95–124, figs 1–36.

SOLEM, A. (1988a)–New Camaenid Land Snails from the Northeast Kimberley, Western Australia. *J. Malac. Soc. Aust.* **9:** 27–58, text figs 1–34, pls 1–3.

SOLEM, A. (1988b)–Maximum in the Minimum: Biogeography of Land Snails from the Ningbing Ranges and Jeremiah Hills, Northeast Kimberley, Western Australia. *J. Malac. Soc. Aust.* **9:** 59–113, tables 1–10, maps 1–25.

SOLEM, A. (1989a)–Non-Camaenid Land Snails of the Kimberley and Northern Territory, Australia. Part 1. Systematics, Affinities and Ranges. *Invert. Tax.* **2** (4): 455–604, figs 1–217, tables 1–2.

SOLEM, A. (1989b)–*Cristilabrum kessneri*, a new camaenid land snail from the Jeremiah Hills, Western Australia. *Jour. Malac. Soc. Aust.* **10:** 97–107, 2 tables, 5 text figs, 2 plates.

SOLEM, A. (1991)–Land snails of the Kimberley rainforest patches and biogeography of all Kimberley land snails. *In*: *Kimberley Rainforests of Australia* N.L. McKenzie, R.B. Johnston & P.G. Kendrick (eds.), Surrey Beatty & Sons, Chipping Norton, pp 145–246, 1 text fig, 64 maps 16 tables.

SOLEM, A. (1992)–Camaenid Land Snails from Southern and Eastern South Australia, excluding Kangaroo Island. Part 1. Systematics, Distribution and Variation. *Rec. South Aust. Mus. Monograph Series* **2**: 1–1338, text figs 1-105, tables 1-36, plates 1-72. Ibid. Part 2. Biogeography and covariation. *Rec. South Aust. Mus. Monograph Series* **2**: 339-395, text figs 106-146, tables 37-40. Appendix 1, pp. 397-421. Index to land snails, pp. 422-425.

SOLEM, A. (1993)–Camaenid Land Snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). VI. Taxa from the Red Centre. *Rec. Western Aust. Mus., Suppl.* **43:** 983–1459, figs 257–367, plts 95–176, maps 1–18.

SOLEM, A. & CHRISTENSEN, C. C. (1984)–Camaenid Land Snail Reproductive Cycle and Growth Patterns in Semi-Arid Areas of Northwestern Australia. *Aust. J. Zool.* **32** (4): 471–491, figs 1–2, tables 1–5.

TAKI, I. (1935)–Notes on a Warty Growth on the Head of Some Land Snails. *Jour. Sci. Hiroshima Univ.* Series B, Div. 1, **3** (14): 159–183, plts I–V, figs 1–7.

TATE, R. (1879)–Description of new species of South Australian pulmoniferous snails. *Trans. Proc. Philosophical Soc. Adelaide* **1878–1879:** 133–136, plt. V, figs 1 a, b, 2 a, b, 7 a, b.

TATE, R. (1894)–Brief Diagnoses of Mollusca from central Australia. *Trans. Roy. Soc. S. Aust.* **18:** 191–194.

TATE, R. (1896)–Mollusca. *In* Spencer, B. (ed.): *Report on the work of the Horn Scientific Expedition to Central Australia. Part II. Zoology:* 181–219, pls 17–19. London: Dulan & Co.

TATE, R. (1899)–Definitions of New Species of Land Shells from South Australia. *Trans. Roy. Soc. South Austr.* **23:** 245–248, plts VI–VII.

VON IHERING, H. (1912)–Analyse der Süd–Amerikanischen Heliceen. *J. Acad. Nat. Sci. Philadelphia* (2) **15:** 475–500, pls XLI–XLII.

VON MARTENS, E. (1878)–Übersicht der während der Reise um die Erde in den Jahren 1874–1876 auf S. M. Schiff *Gazelle* gesammelten Land- und Süsswasser-Mollusken. *Monatsber. Königl. Akad. Wissen. zu Berlin* **1877:** 263–291, pls 1–2.

WALTON, M. L. (1963). Length of Life in West American Land Snails. *Nautilus* **76** (4): 127–131.

WALTON, M. L. (1970). Longevity in *Ashmunella, Monadenia* and *Sonorella*. *Nautilus* **83** (3): 109–112.

WILSON, B. R. & SMITH, P. R. (1975)–Mollusc Fauna. *In* J. M. Miles and A. A. Burbidge, (eds). A biological survey of the Prince Regent River Reserve, North-west Kimberley, Western Australia. *Western Australian Department of Fisheries and Wildlife, Wildlife Research Bulletin* 3 Part IX: 97–100.

WURTZ, C. B. (1955)–The American Camaenidae (Mollusca: Pulmonata). *Proc. Acad. Nat. Sci. Philadelphia* **107:** 99–143, pls 1–19.

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Valid names in *italics*; synonyms and homonyms in Roman; family-group names in **bold**.

[1] Compiled by Jane Griffiths, Department of Aquatic Zoology, Western Australian Museum