

NEW CHAROPID LAND SNAILS CHIEFLY FROM LIMESTONE OUTCROPS IN NSW
(EUPULMONATA: CHAROPIDAE)

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Nineteen new species of Charopidae are described from mainly limestone habitats in eastern New South Wales. Eleven new genera are introduced and some existing genera and species revised. *Rhophodon* Hedley, 1924 is more clearly defined and *R. paethorpei* sp. nov., *R. silvaticus* sp. nov., *R. mcgradyorum* sp. nov. and *R. duplicostatus* sp. nov. are described from limestone and rainforest habitats in NE NSW; *Egilodonta* Iredale, 1937 (type species: *Charopa bairnsdalensis* Gabriel, 1930) is removed from the synonymy of *Rhophodon* and *E. wyanbenensis* sp. nov., *E. bendethera* sp. nov. and *E. paucidentata* sp. nov. are described from restricted limestone localities in SE NSW; *Letomola lanalittleae* sp. nov. is described from restricted limestone localities in the Macleay Valley, NE NSW; *Macrophallikoropa* gen. nov. is introduced for the widespread, moist forest dweller *Helix belli* Cox, 1864 and *M. stenoumbilicata* sp. nov. and *M. depressispira* sp. nov. are described from restricted localities in the Sydney Basin Bioregion; *Allocharopa* Iredale, 1937 (type: *Helix brazieri* Cox, 1868 from the Sydney Basin Bioregion) is shown to be a synonym of *Elsothera* Iredale, 1933; *Egilomen* Iredale, 1937 is redefined and a new diagnosis is presented for the type, *E. cochlidium* (Cox, 1868), which is restricted in distribution; *Whiteheadia* gen. nov. is introduced for *Egilomen globosa* Stanisic, 1990; *Coricudgia wollemiana* gen. et sp. nov. is described from Mt Coricudgy, Wollemi NP; *Decoriropa* gen. nov. is introduced for the widespread *Helix lirata* Cox, 1868; *Marilyniropa jenolanensis* gen. et sp. nov. is described from limestone localities near Jenolan, SE Oberon; *Cralopa* Iredale, 1941 is redefined and revised diagnoses and new distribution details are presented for the widespread *C. stroudensis* (Cox, 1864) and *C. kaputarensis* Stanisic, 1990 from the Nandewar Range; *Gouldiropa* gen. nov. is introduced for *C. carlessi* Stanisic, 1990 which is redefined and restricted in distribution to the northern New England Tableland; *Sharniropa* gen. nov. is introduced for *S. wollondillyana* sp. nov. and *S. borenorensis* sp. nov. from limestones in the Abercrombie and Orange areas of central NSW respectively, and *S. xanana* sp. nov. from limestone outcrops in the southern New England Tableland; *Acheronopa attunga* gen. et sp. nov. is described from limestones in the Manilla-Attunga region of the New England Tableland; *Hedleyropa yarrangobillyensis* gen. et sp. nov. is described from the Yarrangobilly limestones of SE NSW; *Scelidoropa* gen. nov. is introduced for the widespread *S. sarahjaneae* sp. nov. and the narrowly restricted *S. nandewar* sp. nov. from the Nandewar Range; *Diphyrropa* gen. nov. is introduced for *Helix saturni* Cox, 1868 from the Sydney Basin Bioregion and *D. macleayana* sp. nov. from the Macleay Valley, NE NSW. Patterns of morphological variation are analysed and discussed and a phylogenetic hypothesis for the species is presented based on 32 shell characters and 12 anatomical characters. Biogeographic discussions focus on the effects of climate-induced fragmentation and isolation of mesic communities since the Miocene on species distributions and the role of limestone outcrops as important secondary refugia (next to rainforest) for this biota. A conservation priority for these species is outlined. □ *Charopidae, systematics, new species, limestone, rainforest, biogeography, New South Wales.*

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The small to minute Charopidae form a significant part of the land snail fauna in Australia. The family occurs in many parts of Australia (Smith, 1984, 1992; Solem, 1983; 1984) but is particularly diverse along the eastern edge of the continent (here defined as the area

within approximately 200km of the coastline and stretching from the NSW – Vic Border to approximately Cooktown, NE Qld). In this region charopids are generally found in the litter zone of rainforests (moist and dry) with comparatively few species occurring in adjacent

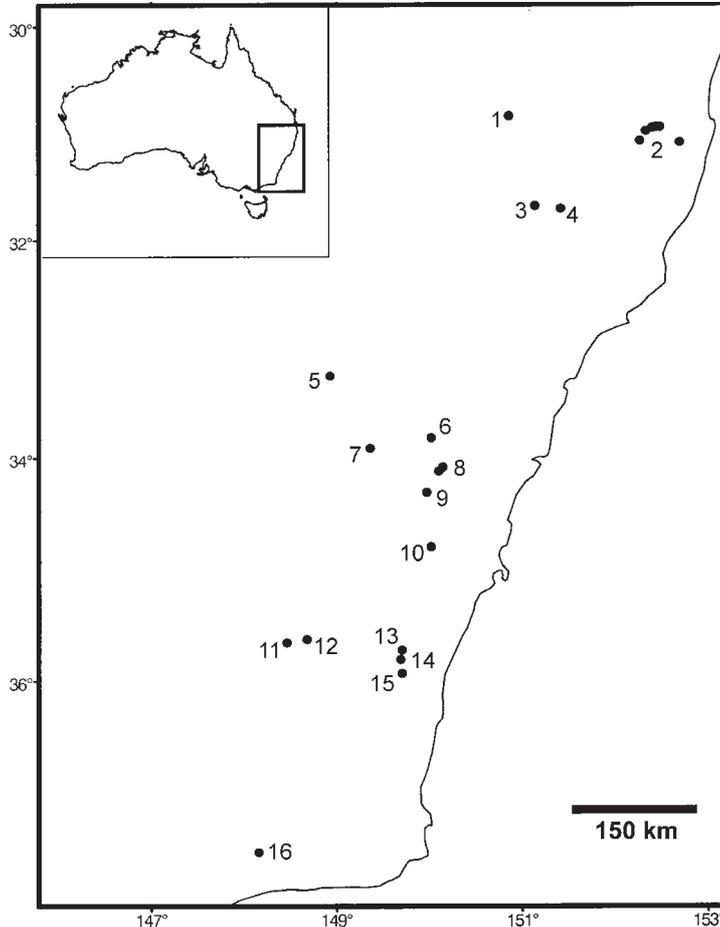


FIG. 1. Limestone localities. 1, Manilla-Attunga; 2, Macleay Valley; 3, Timor; 4, Glenrock; 5, Borenore; 6, Jenolan; 7, Abercrombie; 8, Church Creek-Colong; 9, Wombeyan; 10, Bungonia; 11, Cooleman; 12, Yarrangobilly; 13, Marble Arch; 14, Wyanbene; 15, Bendethera; 16, Buchan.

eucalypt forests (Stanisic, 1990, 1994a). However, within the drier zone of eucalypt forest and woodland, an archipelago of limestone outcrops forms an important secondary node of diversity for the family.

Stanisic (1990) reviewed 50 species (27 new) belonging to 18 genera from subtropical rainforests in eastern Australia and provided a summary of previous Australian and extralimital taxonomic studies on the group. Only minor additions to the Australian species inventory have occurred subsequently (Stanisic, 1993a,b; 1996). One of the major obstacles preventing more comprehensive reviews of the group in the

past has been the dearth of material available for study. These snails are very small (mostly <5mm, and often <3mm in diameter), extremely cryptic in their preferred microhabitat and, as experience has shown, usually very difficult to find alive in great numbers.

Since 1980, the Queensland Museum (QM) has been particularly focussed on collecting Charopidae in eastern Australia and through a program of leaf litter collecting and sorting (mainly to recover dead shells), it has been possible to gain some insight into the true diversity of the family in this region. The QM collections now contain more than 25,000 specimens of Charopidae from eastern Australia belonging to approximately 440 species of which more than 370 require description. [In contrast Smith (1992) listed 130 described species for the entire Australian continent]. The Australian Museum, Sydney (AMS) has important historical holdings of the family from eastern Australia as well as a significant amount of contemporary material but these collections are limited in their geographic scope.

However, in spite of the QM's intense collecting efforts (covering more than 2,000 sites) it is highly probable that there are major gaps in the charopid collection base. A significant number of species in the collections are still represented only by single lots and in some cases single specimens from single localities, flagging the possibility that many more species have yet to be discovered. A particularly critical problem for potential reviewers of material currently held in collections is the relative lack of spirit material for anatomical studies. Preserved animal material is available for less than 50% of species so that recollection of many sites is another necessary prerequisite to monographing the group.

A specialised component of the QM's wide-ranging collecting effort directed at the Charopidae was an investigation of the land snail fauna of limestone outcrops in eastern NSW. This was conducted mainly from 1992-1995 with casual follow-up collecting in the ensuing years. The main aims of that study were to obtain very detailed data on charopid diversity and distribution both within and between the many limestone outcrops that stretch chiefly along the Great Dividing Range from the Ashford Caves, NE NSW to the NSW-Vic Border (Lismund et al., 1986) (Fig. 1). These limestone formations vary in size from large tower-karst to small, barely discernible outcrops of very low relief, but all act as 'moisture sinks' in a sea of dry countryside. Many support rainforest in the form of well-developed dry vine thicket that contrasts markedly with the surrounding sclerophyll vegetation.

In numerous cases the surrounding landscape has been greatly altered by European settlers for farming activities whereas the outcrops have been left largely intact, sometimes even being fenced to prevent entry of cattle. In some examples however, such as those in the Cooma area, scattered Kurrajong trees are the only reminder of what vegetation may have been present on the outcrop in the past. But, even in these cases, charopids continue to eke out a living among the little microhabitat that remains. Consequently, it has been possible to obtain fairly robust data on both species presence and distribution across a wide range of these specialised habitats in spite of the fact that much of the surrounding countryside has been severely altered.

An important contributing factor to the continued survival of these snail communities has been the very nature of the limestone outcrops. Nestled amongst a vegetation community that these days is subject to almost perennial fires, the rock outcrop causes a fire shadow effect which contributes to the survival of both the fire sensitive rainforest vegetation and the associated invertebrate biota.

Many of the charopids occurring in these 'island-like' environments are morphologically, and possibly phylogenetically distant from those living in the adjacent countryside. Others have sister species in non-limestone habitats. Some are extremely localised 'limestone' endemics whereas others have broader and more widespread distributions among the archipelago of limestone

outcrops. Other species occur on the outcrops but have their main distribution in non-limestone habitats. This study examines a small subset of this diverse and somewhat enigmatic charopid fauna.

SCOPE OF STUDY

The charopids examined in this study were chosen on the basis of:

- 1) being well-differentiated on shell characters but covering a range of shell features (sculpture, rib spacing, umbilical width);
- 2) being well represented in collections so that the shell measurement datasets would be amenable to statistical analysis; and
- 3) being well represented by preserved material for dissection.

Beyond these basic criteria every attempt was made to include all available material that appeared to belong to the various grades of conchological organisation chosen for study (putative clades). Hence, in spite of trying to only deal with large and comprehensive datasets, some species are represented by shells only, sometimes in extremely limited numbers. The geographic limitation of the study (restricted to NSW) also means that some extralimital relatives (Qld in particular) have been excluded. Some chiefly non-limestone species have also been included in this study but only in as far as they contribute to a more comprehensive understanding of the systematics.

Due to the difficulty of assessing the relatively brief and comparatively imprecise descriptions of early authors such as Cox (1868) and Iredale (1933, 1937, 1941a,b), many of the detailed morphological comparisons in this study are made only with other taxa dealt with either in this study or with those in Stanisc (1990, 1993a,b, 1996). Where comparisons to charopid taxa outside these studies are made much of the data presented may include previously unpublished information and relies heavily on the observations of one of the authors (JS).

In attempting identification it should be kept in mind that the subset of species dealt with herein represents a small geographic and phylogenetic component of the total family diversity in eastern Australia and that taxonomic concepts may only have limited application. However, many of the species have restricted distributions and in most cases these are considered to be accurate reflections of the species' true range. Hence, given accurate collection data, the likelihood of mis-identification is considered to be low.

MATERIALS AND METHODS

All material used in this study came from the collections of the Australian Museum, Sydney or the Queensland Museum, Brisbane. Species descriptions were generally based on SEM data from 3 shells, measurements from these 3 shells plus 20 more empty shells, and anatomical and radular details from at least three spirit specimens. In addition, all the shells of a species were examined for major variation. However, in spite of careful selection 'wet' material was not available for all of the species, and for some species very few shells were available for SEM and quantitative analysis.

Shells were cleaned in warm dilute bleach, then mounted using silver tape and sputter-coated with gold. Shells were examined and photographed with a Leo 435VP Scanning Electron Microscope. Shells were measured using XTree Gold 2.51 (Johnson et al., 1989-1991). Variables measured were shell height (H) and diameter (D), spire height (SH), aperture height (AH) and width (AW) and umbilical width (U) (see Solem, 1976 for definitions).

Snails were dissected using a Leica MZ8 microscope. Drawings were made using a camera lucida attachment. Radulae were cleaned in warm potassium hydroxide, then mounted on glass slides using carbon tape, then gold-coated and photographed as for the shells. Anatomical and shell terminology largely follows Solem (1984).

Shell and anatomical data were scored using DELTA 1.03T (Description Language for Taxonomy) (Dallwitz et al., 2000). The DELTA files were analysed in PAUP* 4.08b (Phylogenetic Analysis Using Parsimony) (Swofford, 2001) using a heuristic search (100 replicates) with random selective addition and tree-bisection-reconnection. Bootstrap values were calculated using the 'fast stepwise-addition' function in PAUP* with 100 replicates. Trees were viewed in MacClade 3.08a (Maddison & Maddison, 1999). Only taxa for which both anatomical and shell data were available were included in the analysis. Outgroup taxa (*Aaadonta constricta constricta* and *Minidonta hendersoni*, Endodontidae) were scored from Solem (1976).

Unless otherwise stated classification follows Smith (1992).

ACRONYMS AND ABBREVIATIONS USED.

General: AMS, Australian Museum, Sydney; QM, Queensland Museum; NSW, New South

Wales; Qld, Queensland; Vic, Victoria; SF, State Forest; NP, National Park; NR, Nature Reserve; Ra, Range; R, River; SC, spirit or wet collection; RC, dry or reference collection; N, north; S, south; E, east; W, west; NE, northeastern; SE, southeastern.

Collectors: DP, Darryl Potter; GI, Glen Ingram; IL, Ian Loch; JC, Jan Chaseling; JS, John Stanistic; MS, Michael Shea; OG, Owen Griffiths; PHC, Phil Colman; WFP, Winston Ponder.

Habitat Data: cnvf, complex notophyll vine forest; drf, dry rainforest; ew, eucalypt woodland; Jct, junction; lm, limestone outcrop; lrf, littoral rainforest; mvf, microphyll vine forest; nvf, notophyll vine forest; rf, rainforest; ro, rocky outcrop; snvf, simple notophyll vine forest; strf, subtropical rainforest; trib., tributary; vt, vine thicket; wsf, wet sclerophyll forest; wtrf, warm temperate rainforest.

Anatomical Data: dg, prostate; e, epiphallus; g, ovotestis; gd, hermaphrodite duct; gg, albumen gland; gt, talon; h, heart; hv, principal pulmonary vein; i, intestine; kd1, primary ureter; kd2, secondary ureter; kp, pericardial lobe of kidney; kr, rectal lobe of kidney; mc, mantle collar; mg, mantle gland; p, penis; pp, penial pilaster; ppt, preputial tube; pv, penial verge; prm, penis retractor muscle; ss, spermathecal stalk; ut, uterus; v, vagina; vd, vas deferens.

SYSTEMATICS

Subclass EUPULMONATA
Family CHAROPIDAE Hutton, 1884
Subfamily CHAROPINAE Hutton, 1884
Rhophodon Hedley, 1924

Rhophodon Hedley, 1924: 219; Iredale, 1937: 329; Iredale, 1941b: 2, Kershaw, 1955: 30; Burch, 1976b: 133; Smith & Kershaw, 1979: 175; Stanistic, 1990: 114; Smith, 1992: 202.

TYPE SPECIES. *Rhophodon peregrinus* Hedley, 1924; by original designation.

DIAGNOSIS. Shell very small to minute, discoidal, flammulated to monochrome, with few to many apertural barriers; spire depressed to flat or very slightly elevated. Protoconch with prominent, slightly curved radial ribs that become more crowded toward the protoconch/teleoconch boundary and very fine, wrinkle-like, discontinuous spiral cordlets. Teleoconch sculpture of very crowded to widely spaced, straight to weakly protractively sinuated radial ribs; secondary sculpture of intersecting microradials and microspirals that form strong beads at their intersection. Umbilicus very wide

cup-shaped to saucer-shaped. Kidney weakly bilobed with pericardial lobe elongate, triangular, slightly reflexed at the apex. Penis internally with longitudinal pilasters, occasionally with additive circular pads.

DISTRIBUTION AND HABITAT. From Mt Booroon Booroon, SE Qld, to the Macleay Valley, NE NSW. Species are obligate closed-forest dwellers living among litter and rocks in warm temperate to subtropical (wet to dry) rainforest.

REMARKS. *Rhophodon* Hedley, 1924 was introduced for 3 Australian charopids with apertural barriers. *Letomola* Iredale, 1941 was subsequently introduced for *Rhophodon contortus* Hedley, 1924 but the author gave no convincing reasons for the separation from *Rhophodon*. Stanistic (1990) redefined *Rhophodon* as a genus of very small to minute charopids with apertural barriers, very wide umbilicus, primarily radial protoconch and prominent radial ribs on the teleoconch. Stanistic (1990) also included three new species and placed the monotypic *Egilodonta* Iredale, 1937 (type species: *Charopa bairnsdalensis* Gabriel, 1930) into its synonymy but maintained *Letomola* as a separate genus. A malleate protoconch, the presence of a supraperipheral sulcus and unusual radular features were considered to be sufficient reasons for its separation from *Rhophodon*.

Smith & Kershaw (1979) and Smith (1992) included the Victorian '*Charopa*' *problematica* Gabriel, 1947 in *Rhophodon* but this species was not examined by Stanistic (1990).

Following the examination of additional new material of '*C.* *bairnsdalensis*' and the discovery of several closely related species in the NSW/Vic Border area, *Egilodonta* is herein reinstated for a group of southern charopids with dentate apertures. These species are conchologically and anatomically cohesive. In particular the position and less exuberant development of the apertural barriers are features that combine to separate these species from *Rhophodon*. The position of '*C.* *problematica*' still needs to be determined. Smith & Kershaw (1979) mention the presence of apertural lamellae in the shell of this species, presumably a major reason for its generic placement by those authors, but these lamellae were not mentioned by Gabriel (1947). Hence, until the type specimen of '*C.* *problematica*' is re-examined this species should be regarded as a doubtful member of *Rhophodon*.

Rhophodon Hedley, 1924 is most similar to *Egilodonta* Iredale, 1937 in shell shape, in the protoconch sculpture (the radial ribs on the protoconch become increasingly crowded at the protoconch/teleoconch margin) and in the possession of apertural barriers. However, *Egilodonta* differs from *Rhophodon* in having consistently more widely spaced and thicker teleoconch ribs and consistently fewer apertural barriers that differ in their relative positions on both the palatal and parietal edges of the aperture. In *Egilodonta* there is only a single parietal barrier (positioned almost half way down the parietal wall), compared with at least two barriers (situated approximately one-half and two thirds down the parietal wall) and occasionally an infraparietal trace in *Rhophodon*. *Rhophodon* also usually has at least two palatal barriers (one in *R. silvaticus* sp. nov.) in contrast to the single palatal barrier in all *Egilodonta*.

Anatomically these two genera show little difference in general features of the pallial and reproductive systems (strong elongation) but this could be largely related to convergent shell shape. Shell design in both groups is characterised by many tightly coiled whorls and a very much reduced whorl cross-section. Elongation of structures such as the pericardial kidney lobe and epiphallus have may have developed as a spatial adjustment in response to this shared evolutionary trend in fundamental shell shape.

Rhophodon and *Egilodonta* are not only separated by considerable geographic distance (c.600km) but they are also ecologically distinct. *Rhophodon* is an obligate closed forest group inhabiting warm temperate to subtropical rainforest, albeit sometimes on limestone, whilst *Egilodonta* appears to be chiefly a calciphile group with a tendency to also occur in eucalypt woodland.

Letomola Iredale, 1941 from the Macleay Valley, NSW (which is sympatric with *R. kempseyensis*) also has apertural barriers. It also has an exsert protoconch and wide umbilicus (similar to *Rhophodon*) but has a more depressed spire, supraperipheral sulcus and malleate protoconch sometimes with fine, widely spaced, thin, curved, radial ridgelets. The teleoconch sculpture is degenerate consisting of broad, shingle-like overlapping sheets. *Letomola* also has fewer barriers than *Rhophodon*.

Decoriropa gen. nov. has the same general shell form as *Rhophodon* (discoidal shell with radial protoconch, wide umbilicus and prominent

radial ribs on the teleoconch) but lacks apertural barriers and has relatively evenly spaced radial ribs on the protoconch.

Solem (1983) showed that the shape of microprojections on the apertural barriers could be a useful means of elucidating phylogenetic relationships within those Pacific Island charopids with apertural barriers and Stanisic (1990) showed that this may also apply to Australian species. Specifically, *Letomola* was shown to have quite different apertural microprojections to those of *Rhophodon* spp., which correlated with fundamental differences in conchological and anatomical features between the two groups (Stanisic, 1990). However, the microsculpture of the apertural barriers was not investigated in the current study.

Rhophodon species can be distinguished from each other by a combination of shell size and rib spacing on the teleoconch, but most definitively, on the basis of apertural barrier conformation – number, form and position.

***Rhophodon kempseyensis* Stanisic, 1990**
(Figs 2-11; Table 1)

Rhophodon kempseyensis Stanisic, 1990: 125, figs 77-79; Smith 1992: 202.

TYPE LOCALITY. Natural Arch, Carrai SF, NSW.

MATERIAL. All NSW: AMSC168611, C308079, QMMO37076, MO37096, MO37151, MO56006, MO49295, MO52724.

DIAGNOSIS. Shell very small, chocolate brown with scattered, radially disposed lighter blotches. Teleoconch with extremely crowded, weakly protractively sinuated, narrow radial ribs. Mean ribs/mm 33. Aperture with three parietal barriers (infraparietal present only as a low trace); palatal barriers four, one at the baso-palatal margin. Penis internally with three to four longitudinal pilasters.

DISTRIBUTION AND HABITAT. W of Kempsey, from the Yessabah limestone outcrop to The Castles limestone outcrop in the Carrai SF; often found in great numbers in leaf and soil litter, or under logs and rocks, on limestone outcrops covered in rainforest.

REMARKS. *Rhophodon kempseyensis* Stanisic, 1990 has very fine and extremely crowded ribs (mean 34.56 ribs/mm on the last whorl). *R. consobrinus* (Hedley, 1924) and *R. peregrinus* (Hedley, 1924) also have crowded ribs, but only about half as many on the last whorl as *R. kempseyensis* (see Stanisic, 1990). *R. duplicostatus* sp. nov. has more crowded ribs

than *kempseyensis* (mean 142.3 ribs/mm) but these are very narrow, more like thickened micro-radials, and are grouped in pairs. *R. silvaticus* sp. nov. (mean 38.70 ribs/mm) also has a higher rib count but is smaller with a lower whorl count. *R. palethorpei* sp. nov. (mean 13.06 ribs/mm) and *R. mcgradyorum* sp. nov. (mean 8.04 ribs/mm) have considerably lower rib counts. The barrier arrangement in *R. kempseyensis* is very similar to that of *R. palethorpei* (three parietal barriers and four palatal barriers) but differs in having the infraparietal barrier present as a low trace rather than a high crescent shaped lamellae.

Additional fieldwork since the original description of this species has managed to extend the range of *R. kempseyensis* further westward (The Castles) in the Macleay Valley but still always in association with limestone covered in rainforest. *Rhophodon* spp. in general show a strong affinity with rainforest, suggesting that the present day restriction of *R. kempseyensis* to rainforest-covered limestone may be linked to the possible past restriction of this vegetation type to these rocky refugia. Although rainforest now flourishes elsewhere in the local countryside, *R. kempseyensis* has yet to disperse into these non-limestone associated habitats. Stanisic (1990) showed that the radula of *R. kempseyensis* has enlarged and almost spade-like mesocones on the lateral teeth rather than the more typical lanceolate, possibly an adaptation for scraping food from rock surfaces. This may be evidence that *R. kempseyensis* has become specialised to living on limestone.

***Rhophodon palethorpei* sp. nov.**
(Figs 2-11, 34; Table 1)

ETYMOLOGY. For Hugh Palethorpe.

MATERIAL. HOLOTYPE: QMMO70390, Werrikimbe National Park, at Youdales Hut on Kunderang Brook, NSW (31°04'45"S, 152°15'40"E), under fern roots, drf/lm, 4.i.1997, JS, JC. Height of shell=1.30mm, diameter=2.76mm, H/D=0.47, D/U=2.16, number of whorls=5.2, ribs on last whorl=89. PARATYPES: All same locality as holotype. QMMO60151, 3SC/73RC, under fern roots, drf/lm, 4.i.1997, JS, JC; QMMO55962, 10SC, on limestone, drf/lm, 7.i.1995, JS, JC; QMMO55961, 4RC, on limestone, drf/lm, 7.i.1995, JS, JC; QMMO59704, 110RC, AMSC205155, 10RC, on limestone, drf/lm, 7.i.1995, JS, JC; QMMO59706, 1RC, in litter, drf/lm, 7.i.1995, JS, JC.

DIAGNOSIS. Shell very small, dark golden brown with a wide umbilicus. Teleoconch with slightly sinuated, moderately crowded, relatively wide ribs. Mean ribs/mm 13.06. Aperture with

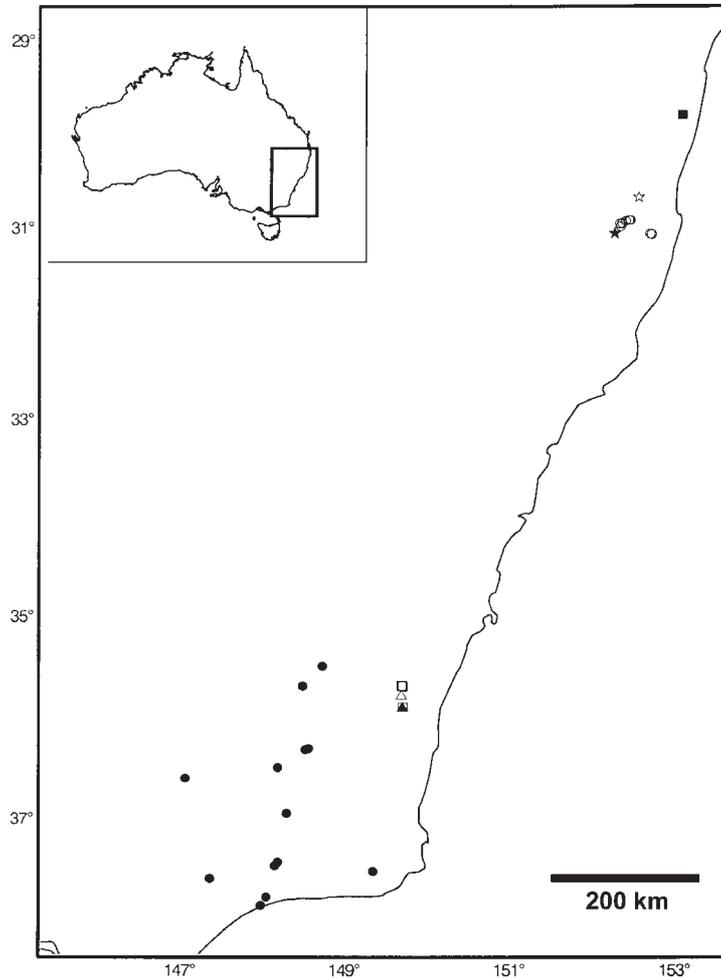


FIG. 2. Distribution of *Rhophodon* and *Egilodonta*. Key: ○ *Rhophodon kempseyensis*, ★ *Rhophodon palethorpei*, ☆ *Rhophodon silvaticus*, ■ *Rhophodon duplicostatis*, ● *Egilodonta bairnsdalensis*, Δ *Egilodonta wyanbenensis*, ▲ *Egilodonta bendethera*, □ *Egilodonta paucidentata*.

three parietal barriers; four palatal barriers, one at the baso-palatal margin. Penis internally with one round basal pilaster.

DESCRIPTION. Shell very small, brown to golden brown, with 4.3-5.1 (mean 4.65) tightly coiled whorls, the last descending more rapidly. Shell diameter 2.41-3.10mm (mean 2.67mm). Apex and early spire flat. Height of shell 1.05-1.40mm (mean 1.24mm), H/D 0.42-0.50 (mean 0.46). Protoconch exsert of 1.4-1.7 whorls. Apical sculpture of slightly curved, moderately spaced radial ribs, becoming more crowded toward the protoconch/teleoconch

border, width of interstices (in multiples of rib width) 7 at apex, 3 at post-nuclear boundary; secondary sculpture of moderately spaced, weak spiral wrinkles. Teleoconch sculpture of numerous slightly protractively sinuated radial ribs, 68-152 (mean 110) on last whorl. Ribs/mm 8.76-13.27 (mean 13.06). Ribs wide, height equal to width; straight in section, rounded on top. Rib interstices on first post-nuclear whorl equal to width of three major ribs; interstices on penultimate whorl equal to width of 2.5 major ribs. Interstitial sculpture of microradial riblets and fine microspirals cords. Microradial riblets low, 4-6 between major ribs on first post-nuclear whorl, 7-8 on penultimate whorls; microspirals cords low, crossing major radials, forming rounded beads at their intersection with microradials. Umbilicus very wide, saucer-shaped, diameter 1.00-1.28mm (mean 1.14mm), D/U 2.16-2.57 (mean 2.36). Sutures impressed, whorls evenly rounded above and below periphery. Aperture ovate; parietal callus present. Three parietal barriers and four palatal barriers present, all crescent-shaped lamellae. Based on 23 measured adults

(QMMO70390, MO60151).

Ovotestis containing two clumps of alveoli; with one alveolar lobe per clump. Talon stalk 1-3 times diameter of talon; talon circular. Penis retractor muscle half the length of penis or greater; inserting at junction of penis and epiphallus. Epiphallus longer than penis; wider than vas deferens; pilasters longitudinal; retractor muscle not entwined with epiphallus. Penis sheath present; penis tubular (with a large bulge on one side at base); internally with one round pilaster basally. Vagina shorter than penis.

Pallial cavity with unilobed kidney.

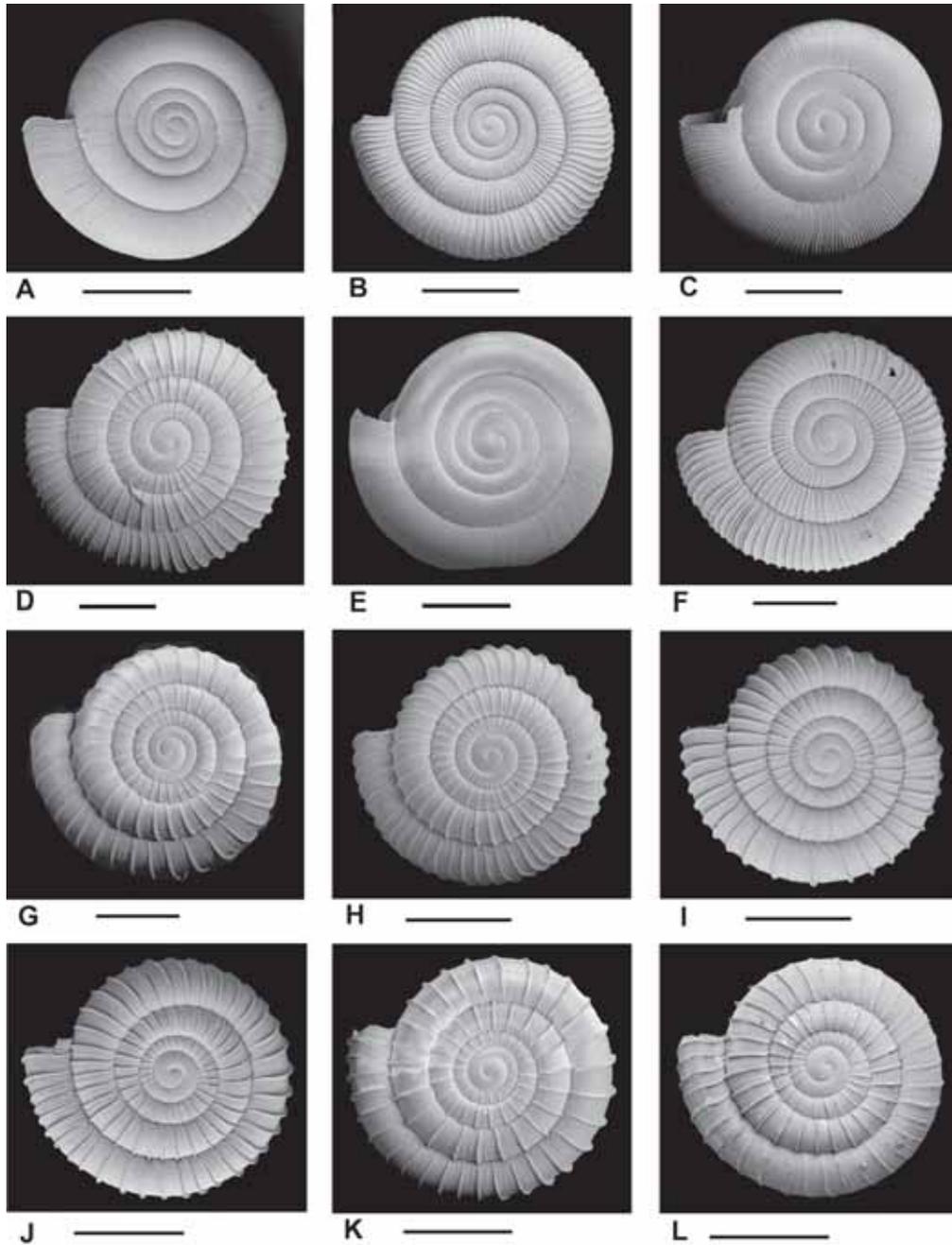


FIG. 3. Dorsal view of shells. A, *Rhophodon kempseyensis*, AMSC153720. B, *Rhophodon palethorpei*, QMMO70390. C, *Rhophodon mcgradyorum*, QMMO70392. D, *Rhophodon silvaticus*, QMMO70391. E, *Rhophodon duplicostatus*, QMMO70393. F, *Egilodonta wyanbenensis*, QMMO70394. G, *Egilodonta bendethera*, QMMO70395. H, *Egilodonta paucidentata*, QMMO49447. I, *Egilodonta paucidentata*, QMMO70396. J, *Egilodonta bairnsdalensis* (Yarrangobilly Caves, Kosciusko National Park), AMSC142959. K, *Egilodonta bairnsdalensis* (Lakes Entrance), AMSC153706. L, *Egilodonta bairnsdalensis* (Alpine Way, Kosciusko National Park), AMSC154808. Scale bars=0.5mm in C, D, E; 0.8mm in F-L; 1mm in A, B.

Radula with central tooth strongly tricuspid, considerably smaller than laterals; lateral teeth tricuspid; mesocone of first lateral tooth slender, slightly diamond-shaped; mesocone of marginal teeth rounded, spade-like; ectocone of outer marginal teeth split into three teeth; endocone occasionally split into two or more teeth. Number of lateral teeth: 7; marginal teeth: 7; radular rows: 123.

Based on 3 dissected specimens (QMMO55962).

DISTRIBUTION AND HABITAT. Known only from the type locality; living on limestone outcrops covered in dry rainforest (vine thicket).

REMARKS. *Rhophodon palethorpei* sp. nov. appears to be very closely related to *R. kempseyensis*. The barrier configuration of the two species is basically the same except that in *R. palethorpei* the infraparietal barrier is much more developed. *R. palethorpei* is also similar in to *R. kempseyensis* in most aspects of shell measurement, but differs most dramatically in having a lower rib count (13.06 ribs/mm compared with 34.56 ribs/mm in *R. kempseyensis*). *R. palethorpei* is readily distinguished from *R. silvaticus* sp. nov. by its larger size, lower rib count and in having a greater number of palatal barriers (four as opposed to one).

The many similarities between the shells of *R. kempseyensis* and *R. palethorpei*, in particular the configuration of the apertural barriers, suggest common ancestry. The two species are now geographically isolated in two different drainage systems: *R. kempseyensis* in the Macleay River valley and *R. palethorpei* in the Kunderang Brook watershed. This may be related to past restriction of rainforest habitats to refugia such as rocky outcrops and the consequent long-term isolation of once conjunct populations. Although *R. palethorpei* is currently known only from one locality, there is a possibility that it also exists on other, yet to be sampled, limestone outcrops along Kunderang Brook.

***Rhophodon silvaticus* sp. nov.**
(Figs 2-7; Table 1)

ETYMOLOGY. Latin *silvaticus*, pertaining to forests; referring to the forest habitat.

MATERIAL. HOLOTYPE: QMMO70391, Thumb Ck SF, slopes of Blue Knob, c.11.5km NW Burrupine, W Macksville, NSW (30°41'45"S, 152°33'15"E), under logs, wtrf, 29.ix.1993, JS, JC. Height of shell=0.67mm, diameter=1.39mm, H/D=0.48, D/U=ratio 2.36, number of whorls=4.1, ribs on last whorl=169. **PARATYPES:** QMMO49318, 2RC, same data as holotype;

QMMO37318, 4SC, same locality data as holotype, under logs on rocky hillside, wtrf, 15.i.1992, JS, JC.

DIAGNOSIS. Minute, golden brown shell with wide umbilicus. Teleoconch with narrow, slightly sinuated, very closely spaced ribs. Mean ribs/mm 38.70. Aperture with two parietal barriers and one palatal barrier. Anatomy unknown.

DESCRIPTION. Shell minute golden brown, with c.4.1 tightly coiled whorls, the last descending more rapidly; shell diameter c.1.39mm. Apex and early spire flat. Height of shell c.0.67mm, H/D c.0.48. Protoconch exsert of c.1.6 whorls. Apical sculpture of slightly curved, moderately spaced radial ribs, becoming more crowded toward the protoconch/teleoconch border, width of interstices (in multiples of rib width) 4 at apex, 3 at post-nuclear boundary; secondary sculpture of moderately spaced, weak spiral wrinkles. Teleoconch sculpture of numerous weakly protractively sinuated radial ribs, c.169 on last whorl. Ribs/mm c.38.70. Ribs narrow, height less than width; straight in section, rounded on top. Rib interstices on first post-nuclear whorl equal to width of 2 major ribs; interstices on penultimate whorl equal to width of 1.5 major ribs. Interstitial sculpture of fine microradial riblets and microspirals cords. Microradial riblets low, 2 between ribs on first post-nuclear whorl; 3 between ribs on penultimate whorl; microspirals cords low, crossing major radials, forming elongated beads at their intersection with the microradials. Umbilicus very wide saucer-shaped, diameter c.0.59mm, D/U c.2.36. Sutures impressed, whorls evenly rounded above and below periphery. Aperture ovately lunate; parietal callus present. Two parietal barriers and one palatal barriers present, all crescent shaped lamellae. Based on the measured holotype (QMMO70391).

Anatomy unknown.

DISTRIBUTION AND HABITAT. Known from the type locality; living under logs among volcanic rocks in temperate rainforest.

REMARKS. *Rhophodon silvaticus* sp. nov. is most similar to *R. kempseyensis* in rib spacing and general satin-like appearance of the shell surface, however it is much smaller, has the teleoconch ribs slightly more widely spaced (ribs/mm =38.70) and possesses only one palatal barrier (four in *R. kempseyensis*). *R. palethorpei* has the teleoconch ribs more widely spaced than those of *R. silvaticus* and like *R. kempseyensis*

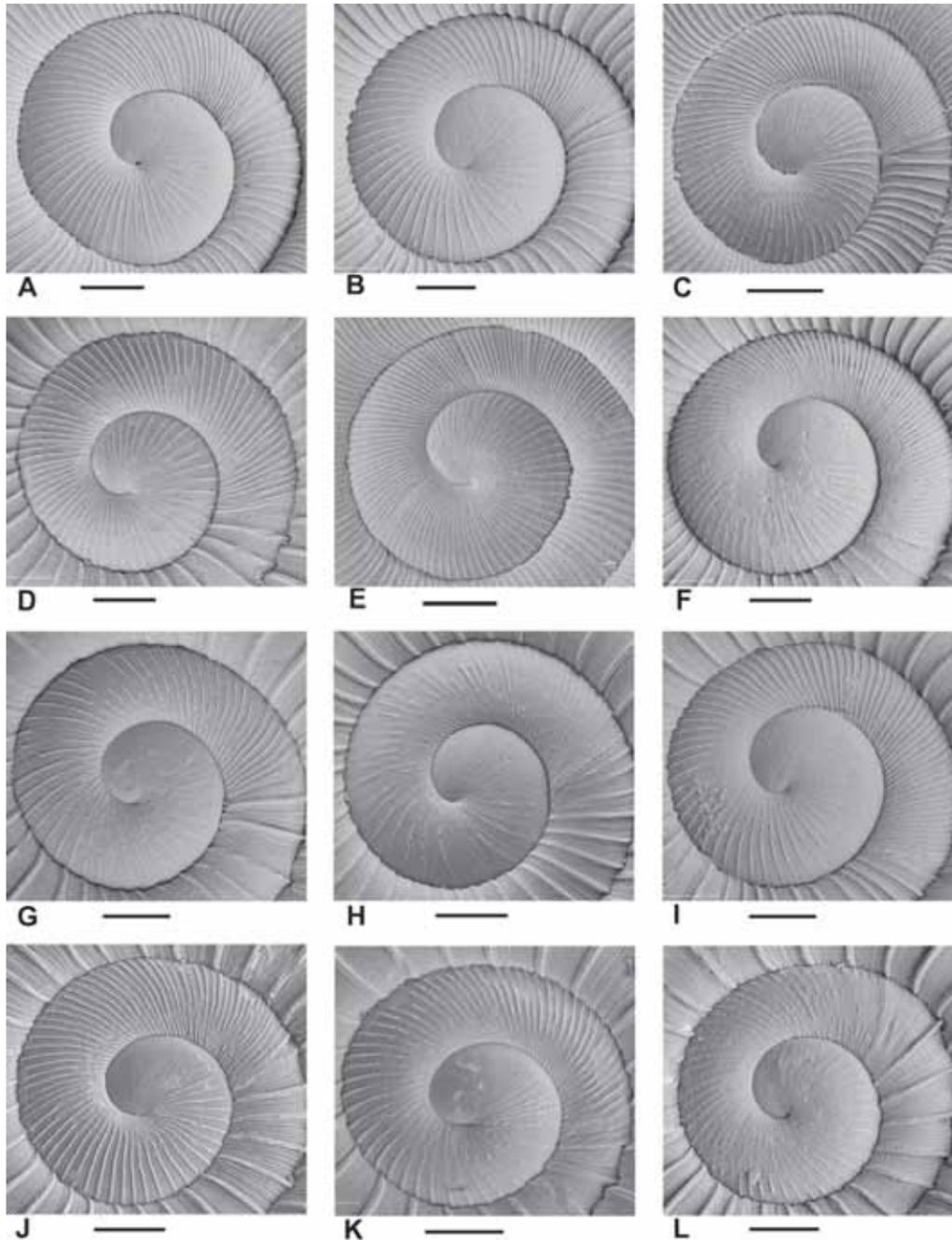


FIG. 4. Protoconch of shells from above. A, *Rhophodon kempseyensis*, AMSC153720. B, *Rhophodon palethorpei*, QMMO70390. C, *Rhophodon mcgradyorum*, QMMO70392. D, *Rhophodon silvaticus*, QMMO70391. E, *Rhophodon duplicostatus*, QMMO70393. F, *Egilodonta wyanbenensis*, QMMO70394. G, *Egilodonta bendethera*, QMMO70395. H, *Egilodonta paucidentata*, QMMO49447. I, *Egilodonta paucidentata*, QMMO70396. J, *Egilodonta bairnsdalensis*, AMSC142959. K, *Egilodonta bairnsdalensis*, AMSC153706. L, *Egilodonta bairnsdalensis*, AMSC154808. Scale bars=0.1mm.

also has four palatal barriers. This is the smallest of the *Rhophodon* group of species, and additional material is needed to adequately define the morphometrics of the shell and to detail the anatomy.

R. silvaticus is currently only known from the one locality in the Thumb Creek SF and more fieldwork is needed to confirm its range. There would appear to be no obvious reason why this species is not more widespread in the upper Taylors Arm watershed (Nulla Five Day SF) where similar habitats exist. The microhabitat data (on rocky hillside) suggests that it may have a patchy localised distribution confined to areas with rocky substrate.

***Rhophodon mcgradyorum* sp. nov.**
(Figs 2-7, 33; Table 1)

ETYMOLOGY. For Jim and Audrey McGrady.

MATERIAL. HOLOTYPE: QMMO70392, Bellbird Gully, Gibraltar Ra., NSW, 4.i.1988, G. Annabell. Height of shell=0.99mm, diameter=1.67mm, H/D=0.59, D/U=2.61, number of whorls=4.7, ribs on last whorl=47. PARATYPES: QMMO66108, 3RC, same data as holotype.

DIAGNOSIS. Shell minute, golden brown, with a wide umbilicus. Teleoconch with wide, straight (not sinuated) widely spaced ribs. Mean ribs/mm 8.04. Aperture with 3 parietal and 3 palatal barriers and a baso-columellar barrier; barriers thickened at the apex. Anatomy unknown.

DESCRIPTION. Shell very small, golden brown to yellow, with 4.5-4.9 (mean 4.7) tightly coiled whorls, the last descending more rapidly in front. Shell diameter 1.64-1.69mm (mean 1.67mm). Apex and early spire slightly concave to flat. Height of shell 0.82-0.99mm (mean 0.88mm), H/D 0.50-0.59 (mean 0.53). Protoconch exsert of 1.7-1.8 whorls. Apical sculpture of curved, moderately spaced, radial ribs, becoming more crowded toward protoconch/teleoconch boundary; width of interstices (in multiples of rib width) 6 at apex, 3 at post-nuclear boundary; secondary sculpture of weak, discontinuous spiral cords. Teleoconch sculpture of numerous, protractively sinuated widely spaced radial ribs; 35-47 (mean 42) ribs on last whorl. Ribs/mm 6.79-8.96 (mean 8.04). Ribs relatively broad, height less than width; straight in section, rounded on top. Rib interstices on first post-nuclear whorl equal to width of 4-6 ribs; interstices on penultimate whorl equal to width of 7 ribs. Interstitial sculpture of microradial riblets and fine microspirals. Microradial

riblets low, 12-13 between ribs on first post-nuclear whorl and 20 between ribs on penultimate whorl; microspirals low, crossing major radials, forming strong, round to square beads at their intersection with microradial riblets. Umbilicus widely open, saucer-shaped, diameter 0.61-0.64mm (mean 0.63mm). D/U 2.61-2.67 (mean 2.68). Sutures impressed, whorls evenly rounded above and below periphery. Aperture ovately lunate, parietal callus present. Three parietal barriers, one baso-columellar barrier and four palatal barriers present; barriers thickened. Based on 4 measured adults (QMMO70392, MO66108).

Anatomy unknown.

DISTRIBUTION AND HABITAT. Known only from the type locality in the Gibraltar Range NP, east of Glen Innes, NSW; habitat and microhabitat unknown.

REMARKS. The teleoconch ribs of *R. mcgradyorum* sp. nov. are relatively widely spaced compared with other NE NSW *Rhophodon* taxa and the shell bears a greater overall similarity to *R. minutissimus* Stanisic, 1990 from SE Qld. It is, however, distinguished from that species by having only two parietal barriers (three in *R. minutissimus*) and four palatal barriers (three in *R. minutissimus*). The barriers of *R. mcgradyorum* are also comparatively more thickened and lack the blade-like appearance of those in other found in other NE NSW *Rhophodon*. In this respect the barriers resemble those of *R. colmani* Stanisic, 1990 from the Kenilworth SF, SE Qld. However, the latter species differs dramatically from *R. mcgradyorum* in having many more apertural barriers (six palatal) and teleoconch ribs that are broader and much more widely spaced (mean ribs/mm 5.81).

***Rhophodon duplicostatus* sp. nov.**
(Figs 2-7, 34; Table 1)

ETYMOLOGY. Latin *duplico*, double and *costatus*, ribbed; referring to the major rib doublets on the teleoconch.

MATERIAL. HOLOTYPE: QMMO70393, Glenugie SF, slopes of Glenugie Peak (= Mt Elaine), SE Grafton, NSW (29°50'01"S, 153°04'47"E), under rocks on rocky hillside, remnant warm temperate rainforest, 16.i.1992, JS. JC. Height of shell=0.78mm, diameter=1.7mm, H/D =0.46, D/U =2.54, number of whorls=4.7, rib pairs on body 313. PARATYPES: QMMO37344, 7RC, same data as holotype.

DIAGNOSIS. Shell very small, golden brown, with a wide umbilicus. Teleoconch ribs slightly

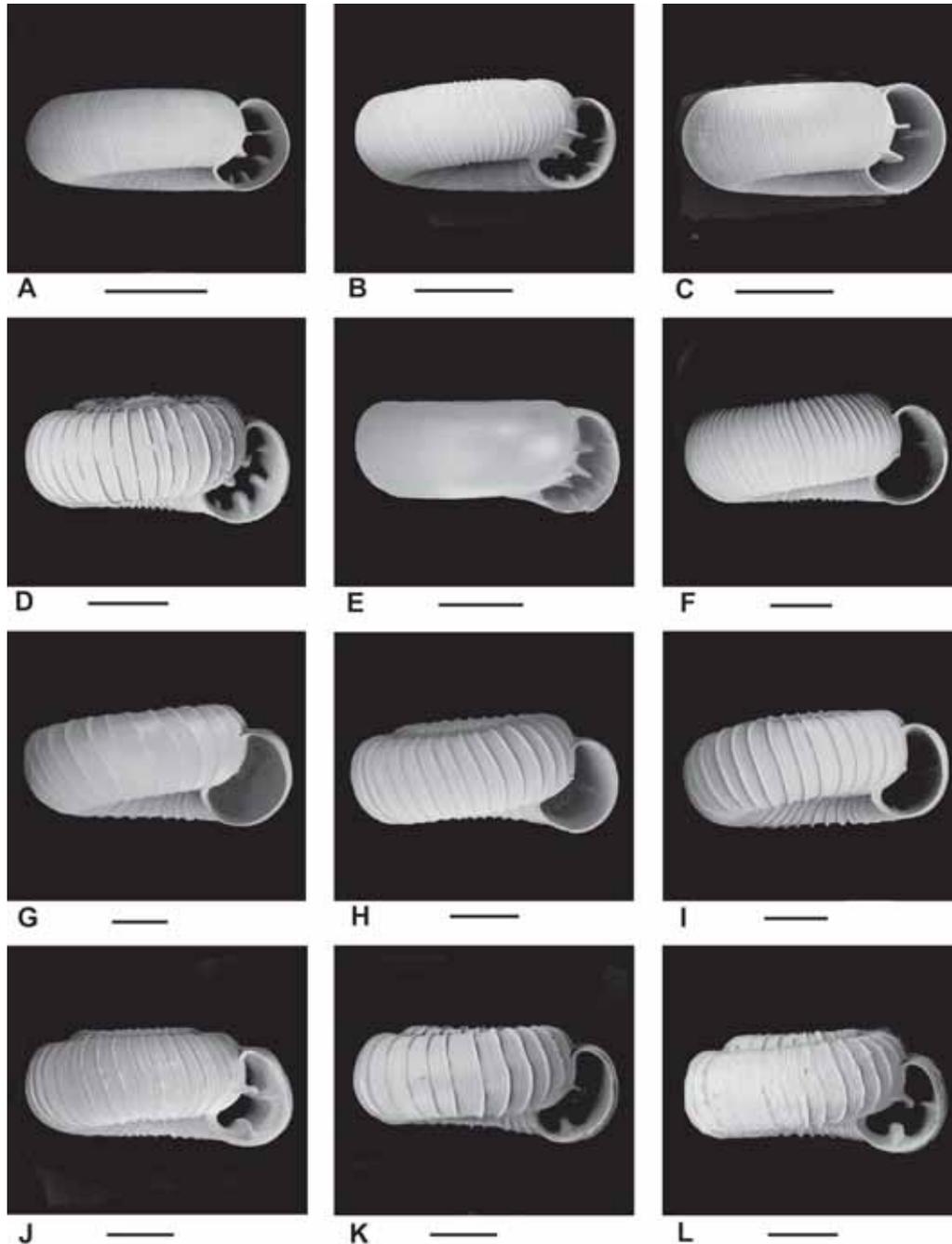


FIG. 5. Lateral view of shells. A, *Rhophodon kempseyensis*, AMSC153720. B, *Rhophodon palethorpei*, QMMO70390. C, *Rhophodon mcgradyorum*, QMMO70392. D, *Rhophodon silvaticus*, QMMO70391. E, *Rhophodon duplicostatus*, QMMO70393. F, *Egilodonta wyanbenensis*, QMMO70394. G, *Egilodonta bendethera*, QMMO70395. H, *Egilodonta paucidentata*, QMMO49447. I, *Egilodonta paucidentata*, QMMO70396. J, *Egilodonta bairnsdalensis*, AMSC142959. K, *Egilodonta bairnsdalensis*, AMSC153706. L, *Egilodonta bairnsdalensis*, AMSC154808. Scale bars=1mm in A, B; 0.5mm in C-L.

TABLE 1. Shell measurements for species of *Rhophodon*. (AH/AW, ratio of aperture height to aperture width; D, shell diameter; D/U, ratio of shell diameter to umbilicus width; H, shell height; H/D, ratio of shell height to diameter; N, number of specimens; NW, total number of whorls; PW, number of protoconch whorls; RIB, number of ribs on last whorl; RIBS/M, number of ribs per mm on the last whorl; SP, spire height; TW, number of teleoconch whorls; UMB, umbilicus width). * indicate actual number of measurements taken.

Measurement	<i>Rhophodon kempseyensis</i>	<i>Rhophodon palethorpei</i>	<i>Rhophodon silvaticus</i>	<i>Rhophodon duplicostatus</i>	<i>Rhophodon mcgradyorum</i>
N	23 (*22, **13)	23	1	3 (*1)	4
D	2.45-2.83 (2.628) ± 0.111	2.41-3.01 (2.674) ± 0.141	1.39	1.49-1.7 (1.627) ± 0.118	1.64-1.69 (1.672) ± 0.024
PW	1.3-1.6 (1.514) ± 0.064 *	1.5-1.7 (1.543) ± 0.059	1.6	1.5 *	1.7-1.8 (1.725) ± 0.05
TW	3.3-3.8 (3.582) ± 0.113 *	3.2-4.1 (3.704) ± 0.203	2.5	3.2 *	2.8-3.2 (2.95) ± 0.173
NW	4.8-5.3 (5.095) ± 0.143 *	4.9-5.6 (5.248) ± 0.175	4.1	4.7 *	4.5-4.9 (4.675) ± 0.171
H	1.03-1.24 (1.118) ± 0.059	1.05-1.4 (1.239) ± 0.095	0.67	0.72-0.83 (0.777) ± 0.055	0.82-0.99 (0.88) ± 0.075
SP	0	0-0.16 (0.083) ± 0.004	0.01	0-0.1 (0.003) ± 0.006	0-0.04 (0.018) ± 0.021
AH/AW	1.5-1.4 (1.4) ± 0.08	1.06-1.7 (1.32) ± 0.14	1.54	1.29-1.57 (1.42) ± 0.14	1.21-1.41 (1.3) ± 0.11
UMB	1-1.31 (1.169) ± 0.08	1-1.28 (1.136) ± 0.077	0.59	0.58-0.67 (0.633) ± 0.047	0.61-0.64 (0.625) ± 0.017
RIB	246-358 (288) ± 32.738 **	68-152 (110) ± 20.967	169	-	35-47 (42.25) ± 5.123
RIBS/MM	28.17-40.27 (34.56) ± 3.678 **	8.763-13.27 (13.06) ± 2.084	38.7	-	6.79-8.96 (8.035) ± 0.906
H/D	0.38-0.47 (0.43) ± 0.03	0.42-0.5 (0.46) ± 0.02	0.48	0.46-0.49 (0.48) ± 0.02	0.5-0.59 (0.53) ± 0.04
D/U	2.08-2.46 (2.25) ± 0.1	2.16-2.57 (2.36) ± 0.11	2.36	2.54-2.6 (2.57) ± 0.03	2.61-2.77 (2.68) ± 0.07

sinuated, very narrow and extremely crowded, complex, each consisting of a pair of ribs. Ribs/mm c.142.3. Aperture with three parietal and six blade-like palatal barriers present. Anatomy unknown.

DESCRIPTION. Shell minute, golden brown, with c.4.7 tightly coiled whorls, the last descending more rapidly in front. Shell diameter 1.49-1.70mm (mean 1.63mm). Apex and early spire slightly concave. Height of shell 0.72-0.83mm (mean 0.88mm), H/D 0.46-0.49 (mean 0.48). Protoconch exsert of c.1.5 whorls. Apical sculpture of moderately spaced, slightly curved radial ribs, becoming more crowded at protoconch/teleoconch boundary; width of interstices (in multiples of rib width) 5 at apex, 2.5 at post-nuclear boundary; secondary sculpture of weak, discontinuous spiral wrinkles. Teleoconch sculpture of very numerous and extremely crowded weakly protractively sinuated radial ribs that usually occur as doublets. Rib pairs on last whorl 313, ribs pairs/mm 142.3, giving the shell an appearance of being smooth. Height of ribs less than width; ribs straight in

section, rounded on top. Rib interstices on the first post-nuclear whorl about the size of the rib doublet (*i.e.* the size of two ribs). Interstitial sculpture of fine microradial riblets and thin microspiral cords. Microradial riblets low, 3-4 between ribs on first post-nuclear whorl and 2 between ribs on penultimate whorl; microspiral cords forming prominent elongate spiral beads at their intersection with the microradials. Umbilicus wide saucer-shaped, diameter 0.58-0.67mm (mean 0.63mm), D/U 2.54-2.60 (mean 2.57). Sutures impressed, whorls evenly rounded above and below the periphery. Aperture ovately lunate, parietal callus present. Three slender parietal barriers present; six very fine palatal barriers present, three in the baso-columellar region; barriers blade-like. Based on 3 measured adults (QMMO70393, MO37334).

Anatomy unknown.

DISTRIBUTION AND HABITAT. *Rhophodon duplicostatus* sp. nov. is known only from the type locality in Glenugie SF, NE NSW; found in litter among volcanic talus in a small patch of remnant warm temperate rainforest.

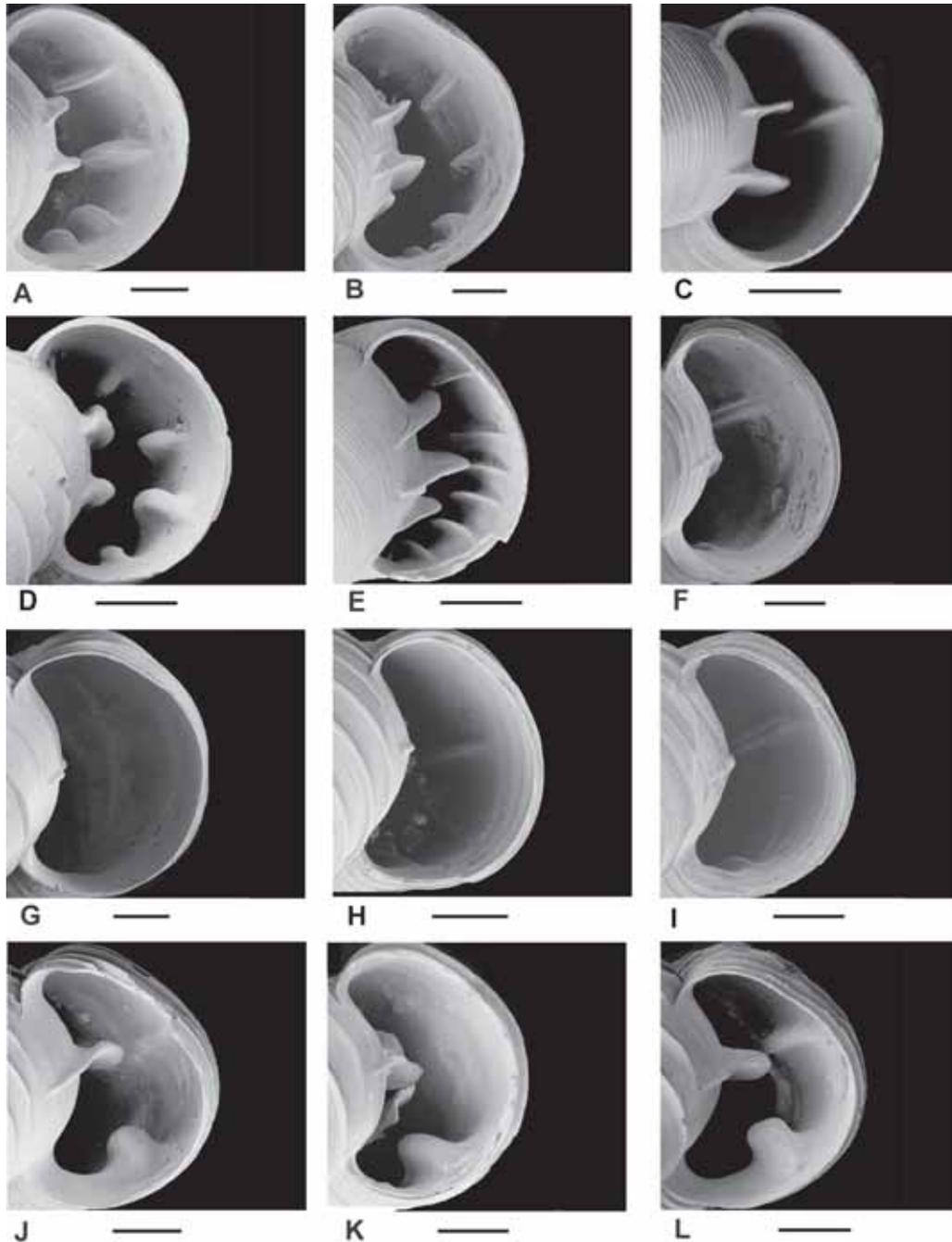


FIG. 6. Aperture of shells, showing apertural barriers. A, *Rhophodon kempseyensis*, AMSC153720. B, *Rhophodon palethorpei*, QMMO70390. C, *Rhophodon mcgradyorum*, QMMO70392. D, *Rhophodon silvaticus*, QMMO70391. E, *Rhophodon duplicostatus*, QMMO70393. F, *Egilodonta wyanbenensis*, QMMO70394. G, *Egilodonta bendethera*, QMMO70395. H, *Egilodonta paucidentata*, QMMO49447. I, *Egilodonta paucidentata*, QMMO70396. J, *Egilodonta bairnsdalensis*, AMSC142959. K, *Egilodonta bairnsdalensis*, AMSC153706. L, *Egilodonta bairnsdalensis*, AMSC154808. Scale bars=0.2mm.

REMARKS. *Rhophodon duplicostatus* sp. nov. has very fine and extremely crowded radial ribs that are almost too dense to count using light microscopy. Under SEM the ribs appear as doublets with each doublet separated by an interstice sculptured with fine, low microradials. In this respect the species cannot be confused with any of its congeners. The apertural dentition of *R. duplicostatus* is also diagnostic in having a proliferation of lamellae in the baso-columellar region. On the basis of having three parietal teeth the species is most readily associated with the *R. kempseyensis*-*R. palethorpei*-*R. peregrinus* group of species. The isolation of *R. duplicostatus*, a member of a closed forest group of land snails, on the unusual Glenugie Peak, suggests derivation from an ancestral population inhabiting once more widespread closed forests in NE NSW. Glenugie Peak (= Mt Elaine on early maps) is a pile of volcanic talus supporting a small patch of rainforest amidst an otherwise eucalypt dominated countryside. As a shift to more xeric climates restricted rainforest in the Tertiary (Kemp, 1981; Webb & Tracey, 1981; Adam 1992), mesic communities in the low coastal area around Grafton would probably have been cornered on such local topographic refugia. The refugial status of Glenugie Peak is reinforced by the fact that it is also home to 15 other species of land snails that include several possible endemic species (Stanisic, unpubl. data). This level of overall diversity is high in the context of the local area where site diversity is generally less than 10 species (Stanisic, 1994). According to Floyd (1987), Glenugie Peak is also floristically unusual, thus further emphasising the complex evolutionary history of this refugium. Geological data suggests that other similar refugia (yet to be investigated for land snails) exist closer to the coast in the vicinity of Glenugie SF (e.g. Brown's Knob) and it would not be surprising to find that *R. duplicostatus* has a broader local distribution among these.

***Egilodonta* Iredale, 1937**

Egilodonta Iredale, 1937: 328; Gabriel, 1947: 120; Gabriel & Macpherson, 1947:162; Kershaw, 1956a: 142; Burch, 1976b: 133; Smith & Kershaw, 1979: 174; Stanisic, 1990: 114 (in synonymy); Smith, 1992: 202 (in synonymy).

TYPE SPECIES. *Charopa bairnsdalensis* Gabriel, 1930; by original designation.

DIAGNOSIS. Shell minute, discoidal, monochrome golden brown, with relatively few apertural barriers; umbilicus very wide saucer-shaped. Protoconch with prominent, slightly

curved radial ribs that become more crowded toward the protoconch/teleoconch boundary and very fine, wrinkle-like, discontinuous spiral cords. Teleoconch sculpture consisting of bold, widely spaced radial ribs whose interstices are sculptured with fine microradial riblets; secondary sculpture of low microradial riblets and microspiral cords that form strong beads at their intersection. Kidney weakly bilobed with pericardial lobe long, triangular. Epiphallus thick and muscular and well differentiated from the vas deferens. Penis internally sometimes with vergic structures.

DISTRIBUTION AND HABITAT. *Egilodonta* ranges from the Bairnsdale region, SE Vic to just south of Braidwood, SE NSW. Species live in the litter and appear associated with limestone habitats, although *E. bairnsdalensis* (Gabriel, 1930) also shows some preference for surrounding eucalypt forest.

REMARKS. On the basis of limited material, Stanisic (1990) synonymised *Egilodonta* Iredale, 1937 with *Rhophodon* Hedley, 1924. The discovery of additional species of Charopidae with dentate apertures from the NSW-Vic Border area has enabled a reassessment of the status of *Egilodonta*. This group of charopids displays a number of consistent differences from the NE NSW species grouped in *Rhophodon*. Bolder and more widely spaced ribs in combination with fewer apertural barriers serve to circumscribe the SE NSW/NE Vic species. Consequently *Egilodonta* is restored to full generic status to include the type and three new species from this region. Inexplicably Solem (1972) placed '*C.* *bairnsdalensis* in *Dentherona* Iredale, 1933 (type species: *Helix dispar* Brazier, 1871) without formally documenting the implied generic synonymy.

Distinguishing characters that separate *Egilodonta* Iredale, 1937 and *Rhophodon* Hedley, 1924 have been discussed under the latter genus. Conchological differences among *Egilodonta* spp. are less dramatic than those among *Rhophodon* spp., which may indicate a relative recent separation of *Egilodonta* populations. Apertural dentition, rib spacing, and shell size vary marginally; however, genitalia show considerable variation compared with *Rhophodon* spp. These differences in penial chamber structure (verge and pilasters) most likely relate to species level interactions due to relatively recent microsympatry (see Solem, 1983). Significantly the one species that is truly

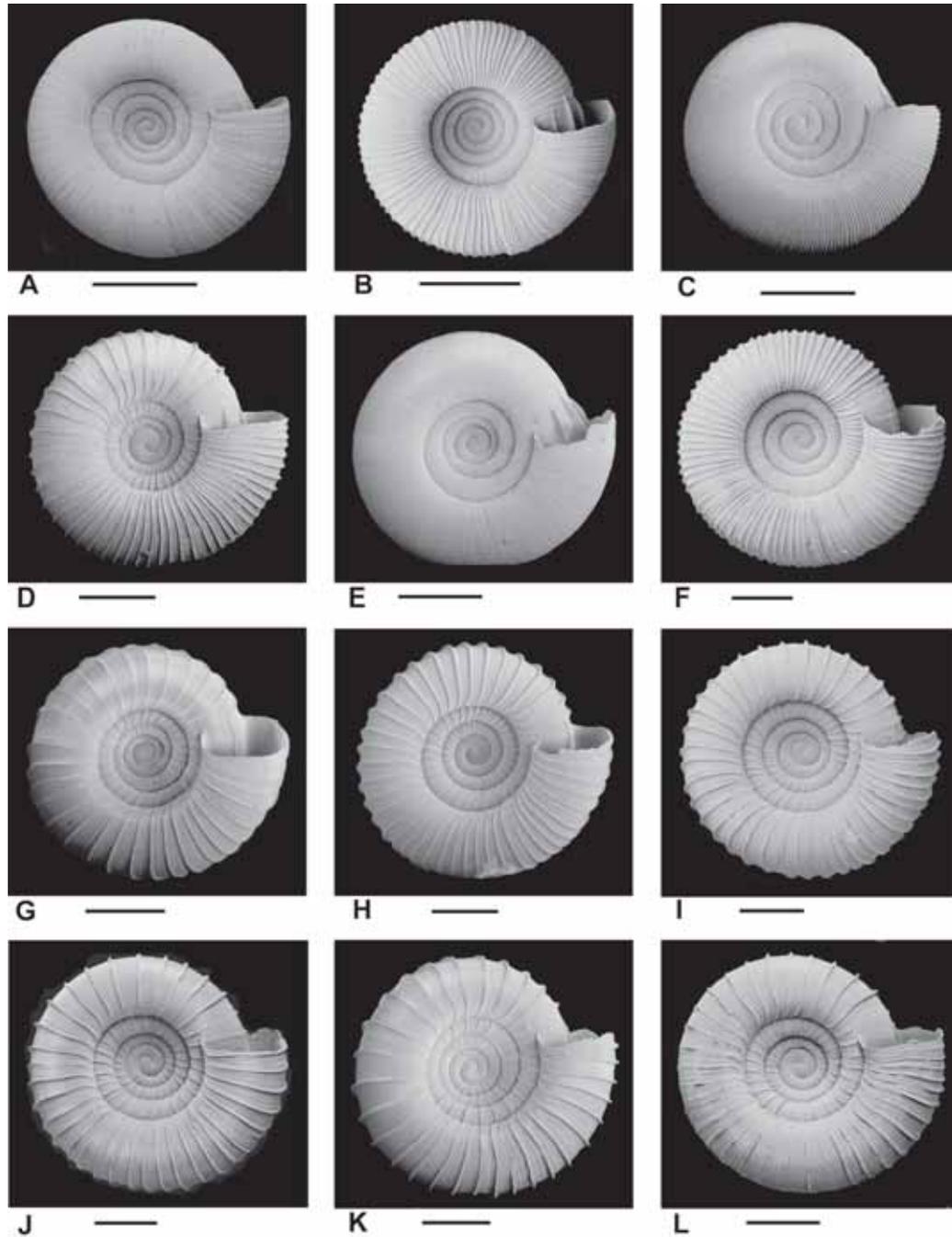


FIG. 7. Ventral view of shells. A, *Rhophodon kempseyensis*, AMSC153720. B, *Rhophodon palethorpei*, QMMO70390. C, *Rhophodon mcgradyorum*, QMMO70392. D, *Rhophodon silvaticus*, QMMO70391. E, *Rhophodon duplicostatus*, QMMO70393. F, *Egilodonta wyanbenensis*, QMMO70394. G, *Egilodonta bendethera*, QMMO70395. H, *Egilodonta paucidentata*, QMMO49447. I, *Egilodonta paucidentata*, QMMO70396. J, *Egilodonta bairnsdalensis*, AMSC142959. K, *Egilodonta bairnsdalensis*, AMSC153706. L, *Egilodonta bairnsdalensis*, AMSC154808. Scale bars=1mm in A, B; 0.5mm in C-L.

allopatric, *E. bairnsdalensis* (Gabriel, 1930), lacks a penial verge. It is probable that *Egilodonta* is still in a stage of comparatively exuberant speciation (in an historical context) compared with the environmentally restricted *Rhophodon*. The most widely collected species is *E. bairnsdalensis* which appears to be a eucalypt woodland species that also takes advantage of limestone habitats. *E. wyanbenensis* sp. nov., *E. bendethera* sp. nov. and *E. paucidentata* sp. nov. appear to be specifically associated with limestone environments based on current evidence, but more fieldwork in surrounding habitat needs to be completed before this association is firmly established.

***Egilodonta bairnsdalensis* (Gabriel, 1930)**
(Figs 2-7, 10-12, 34; Table 2)

Charopa bairnsdalensis Gabriel, 1930: 78, pl. 2, figs 11-12.
Endodonta bairnsdalensis (Gabriel). Kershaw, 1956a: 137.
Egilodonta bairnsdalensis (Gabriel). Iredale, 1937: 329;
Gabriel, 1947: 120; Gabriel & Macpherson, 1947:162;
Smith & Kershaw, 1979: 174.
Dentherona bairnsdalensis (Gabriel). Solem, 1972: 85, figs
17, 18.
Rhophodon bairnsdalensis (Gabriel). Stanisic, 1990: 138,
figs 89-91; Smith, 1992: 202.

TYPE LOCALITY. Bairnsdale, Vic.

MATERIAL. NSW: AMSC355056, C355058, QMMO65004, MO65017.

DIAGNOSIS. Shell minute, straw-coloured, with a wide saucer-shaped umbilicus. Teleoconch with wide, almost straight, relatively broad, very widely spaced ribs. Mean ribs/mm 5.32. Aperture with one strong parietal barrier, one basal barrier and one palatal barrier. Penis internally with 2-4 longitudinal pilasters; verge absent.

DISTRIBUTION AND HABITAT. The Great Dividing Range from the Bairnsdale area in SE Vic north to the Yarrangobilly Caves, Kosciusko NP, SE NSW; found living among litter in eucalypt woodland. Specimens cited in Stanisic (1990) from Marble Arch are now included in *E. paucidentata* sp. nov.

REMARKS. *Egilodonta bairnsdalensis* (Gabriel, 1930) can be distinguished from *E. bendethera* sp. nov. and *E. paucidentata* sp. nov. by its stronger apertural barriers, slightly wider ribs, the presence of two to four penial pilasters and the absence of a penial verge. *E. wyanbenensis* sp. nov. is readily distinguished by having more crowded ribs on the last whorl. Some individuals of *E. bairnsdalensis* (mostly from

around Lakes Entrance, Vic) have no palatal barrier, while others (mostly from around Kosciusko NP) have both basal and palatal barriers with the palatal weakly developed. However, in the absence of other shell (including shell size and shape) or anatomical differences between these populations, they are all included in *E. bairnsdalensis*.

***Egilodonta wyanbenensis* sp. nov.**
(Figs 2-11; Table 2)

ETYMOLOGY. From the type locality.

MATERIAL. HOLOTYPE: QMMO70394, Wyanbene Caves, S Braidwood, NSW (35°48'25"S, 149°41'20"E), lm, in litter, 6.i.1990, JS, JC. Height of shell=0.96mm, diameter=1.99mm, H/D=0.48, D/U=2.16, number of whorls=4.6, ribs on last whorl=66. PARATYPES: QMMO37793, 44RC, AMSC205156, 5RC, same data as holotype; QMMO29270, 34SC/3RC, Wyanbene Caves, S Braidwood, (35°48'25"S, 149°41'20"E), among litter on lm, 6.i.1990, JS, JC.

DIAGNOSIS. Minute straw-coloured shell with wide umbilicus. Teleoconch with moderately broad, slightly sinuated, moderately crowded ribs. Mean ribs/mm 10.32. Aperture with one parietal barrier, one basal barrier and one palatal barrier; barriers very weakly developed. Penis internally with a short verge and no pilasters.

DESCRIPTION. Shell very small, straw coloured, with 4.3-5.1 (mean 4.65) tightly coiled whorls, the last descending more rapidly in front. Shell diameter 1.78-2.39mm (mean 2.14mm). Apex and early spire flat to slightly concave. Height of shell 0.91-1.15mm (mean 1.03mm), H/D 0.43-0.52 (mean 0.48). Protoconch exsert of 1.4-1.7 whorls. Apical sculpture of curved radial ribs, becoming more crowded at protoconch/teleoconch boundary; width of interstices (in multiples of rib width) 6 at apex, 3 at post-nuclear boundary; secondary sculpture of discontinuous, very narrow, spiral wrinkles. Teleoconch sculpture of moderately crowded, slightly protractively sinuated radial ribs; 56-85 (mean 69) ribs on last whorl. Ribs/mm 8.49-13.05 (mean 10.32). Ribs moderately broad, height less than width; straight in section, rounded on top. Rib interstices on first post-nuclear whorl equal to width of 2.5 ribs; interstices on penultimate whorl equal to width of 3 ribs. Interstitial sculpture of fine radial riblets and crowded microspirals, about equal in strength. Microradials low, 3-6 between ribs on first post-nuclear whorl, 8 between ribs on penultimate whorl; microspirals crossing

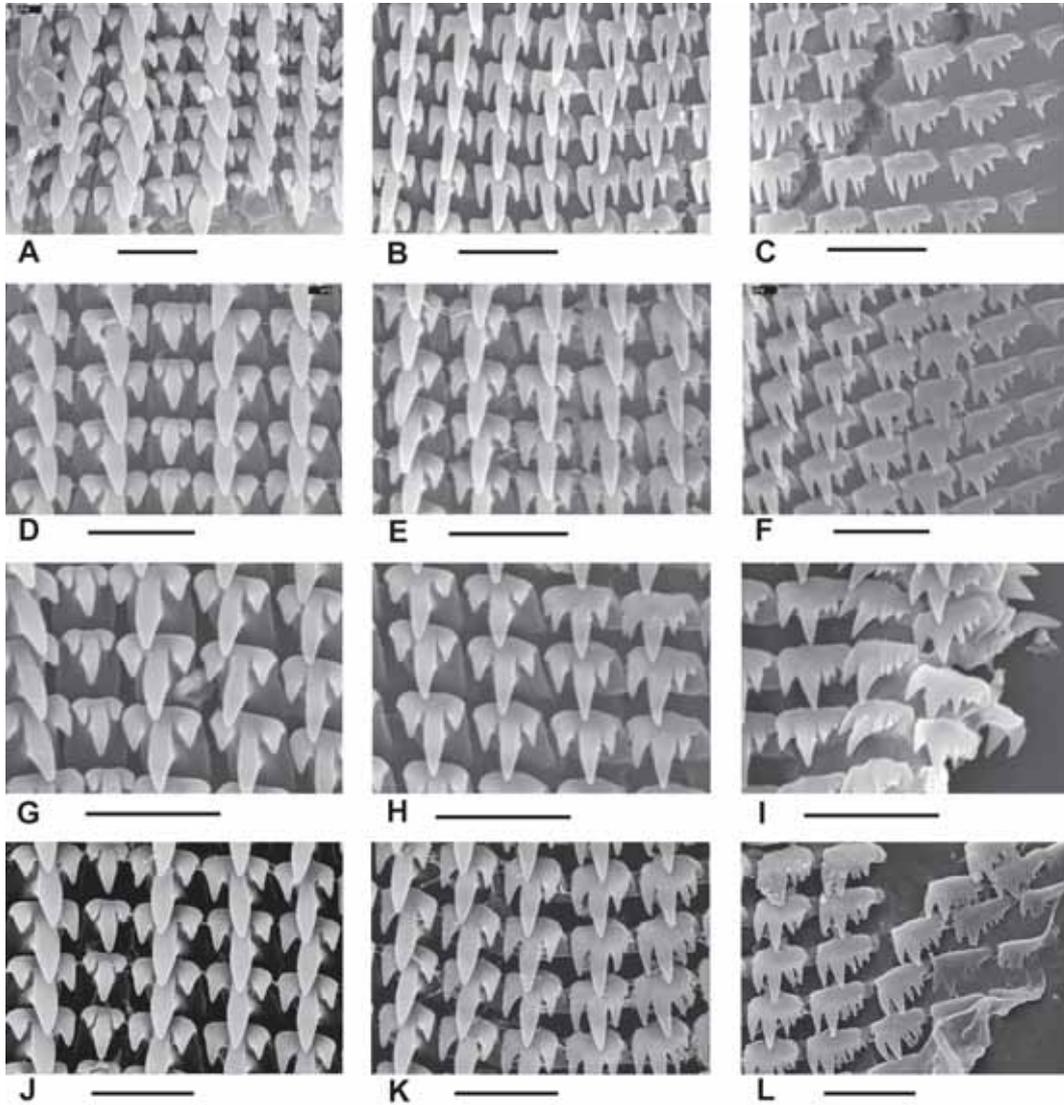


FIG. 8. Radula. A-C, *Rhophodon kempseyensis*, QMMO37096. D-F, *Rhophodon palethorpei*, QMMO55962. G-I, *Egilodonta wyanbenensis*, QMMO29270. J-L, *Egilodonta bendethera*, QMMO70395. Scale bars = 0.01mm.

major ribs and forming strong elongate beads at their intersection with microradials. Umbilicus very wide saucer-shaped, diameter 0.80-1.14mm (mean 0.48mm), D/U2.08-2.31 (mean 2.18). Sutures impressed, whorls evenly rounded above and below the periphery. Aperture ovately lunate, parietal callus present. One slender parietal barrier, a weak basal barrier and one palatal barrier present; all crescent shaped lamellae.

Based on 16 measured adults (QMMO70394, MO37793, MO37796).

Genitalia with ovotestis containing two clumps of alveoli; with more than two alveolar lobes per clump. Talon stalk more than 3 times diameter of talon; talon circular. Penial retractor muscle entwined with epiphallus, inserting at junction of the penis and epiphallus. Epiphallus longer than penis, entering penis through a verge; length of

verge less than half the length of penis. Epiphallus muscular, reflexed, wider than the vas deferens, internally with longitudinal pilasters. Penis tubular without internal pilasters; sheath present. Vagina tubular, longer than penis.

Pallial cavity with almost unilobed kidney; pericardial lobe elongate, triangular with apex slightly reflexed.

Radula with central tooth strongly tricuspid, considerably smaller than laterals; lateral teeth tricuspid; mesocone of first lateral tooth slender, slightly diamond-shaped; marginal teeth rounded; ectocone of outer marginal teeth split into four or more teeth; endocone occasionally split into two or more teeth. Number of lateral teeth 5; marginal teeth 6; radular rows 110.

Based on 3 dissected specimens (QMMO29270).

DISTRIBUTION AND HABITAT. Known only from the type locality; in litter on weakly vegetated limestone among open eucalypt woodland.

REMARKS. *Egilodonta wyanbenensis* sp. nov. is readily distinguished from *E. bairnsdalensis*, *E. bendethera* sp. nov. and *E. paucidentata* sp. nov. by the more crowded ribs on the teleoconch. Anatomically, *E. wyanbenensis* can be distinguished from its congeners by a combination of the presence of a short penial verge and absence of any penis pilasters. *E. bairnsdalensis* has two to four longitudinal pilasters and lacks a verge; *E. bendethera* has a long penial verge and a single longitudinal pilaster; and *E. paucidentata* has a short penial verge and several longitudinal pilasters.

The Wyanbene Caves locality has been relatively poorly surveyed, and the presence of *E. paucidentata* sp. nov. in the geographically proximate Bendethera and Marble Arch limestone outcrops might suggest that further fieldwork at this site could yet add this species to the inventory.

***Egilodonta bendethera* sp. nov.**
(Figs 2-11; Table 2)

ETYMOLOGY. For the type locality.

MATERIAL. HOLOTYPE: QMMO70395, Moruya, c.60km W at Bendethera Cave, NSW (35°55'54"S, 149°42'12"E), lm/Ficus, Acacia and eucalypt scrub, in litter on limestone rocks, 6.i.1994, JS, JC. Height of shell=0.91mm, diameter=1.64mm, H/D=0.55, D/U=2.34, number of whorls=4.3, ribs on last whorl=27. **PARATYPES:** QMMO68759, 14RC/14SC, same data as holotype; QMMO68760, 160RC, AMSC205157, 10RC, same data as holotype.

DIAGNOSIS. Shell very small, light golden brown with a wide umbilicus. Teleoconch with broad, widely spaced, protractively sinuated ribs. Mean ribs/mm 4.67. Aperture with one parietal barrier, and one weakly developed basal barrier and one weakly developed palatal barriers. Penis internally with long penial verge and one longitudinal pilaster.

DESCRIPTION. Shell very small, light golden brown, with 4.3-5.8 (mean 5.3) tightly coiled whorls, last descending more rapidly in front. Shell diameter 1.64-2.63mm (mean 2.34mm). Apex and early spire flat. Height of shell 0.91-1.38mm (mean 1.78mm), H/D 0.48-0.55 (mean 0.50). Protoconch exert of 1.5-1.7 whorls. Apical sculpture of slightly curved, moderately spaced radial ribs, becoming more crowded toward protoconch/teleoconch boundary; width of interstices (in multiples of rib width) 7 at apex, 3 at post-nuclear boundary; secondary sculpture of moderately spaced, discontinuous radial wrinkles. Teleoconch sculpture of bold, widely spaced, almost straight radial ribs, 27-47 (mean 34) on last whorl. Ribs/mm 3.92-6.08 (mean 4.67). Rib height greater than width; straight in section, rounded on top. Rib interstices on first post-nuclear whorl equal to width of 5-6 ribs; interstices on penultimate whorl equal to width of 6 ribs. Interstitial sculpture of fine radial riblets and crowded microspirals, about equal in strength. Microradials low, 12 between ribs on first post-nuclear whorl, 25 between ribs on penultimate whorl; microspirals crossing major ribs and forming strong round to elongate beads at their intersection with microradials. Umbilicus very wide saucer-shaped, diameter 0.7-1.5mm (mean 0.96mm), D/U 2.19-2.63 (mean 2.44). Sutures impressed, whorls rounded above and below periphery. Aperture ovately lunate; lip sinuous; parietal callus present. One very fine parietal barrier, one basal and one palatal barrier present; barriers low blade-like. Based on 10 measured adults (QMMO70395, MO68759).

Genitalia with ovotestis containing two clumps of alveoli; more than two alveolar lobes per clump. Talon stalk more than 3 times diameter of talon; talon circular. Penial retractor muscle inserting at the junction of the penis and epiphallus. Epiphallus longer than penis; wider than vas deferens, muscular, reflexed, entering penis through a verge; internally with longitudinal pilasters. Penis tubular, internally with one

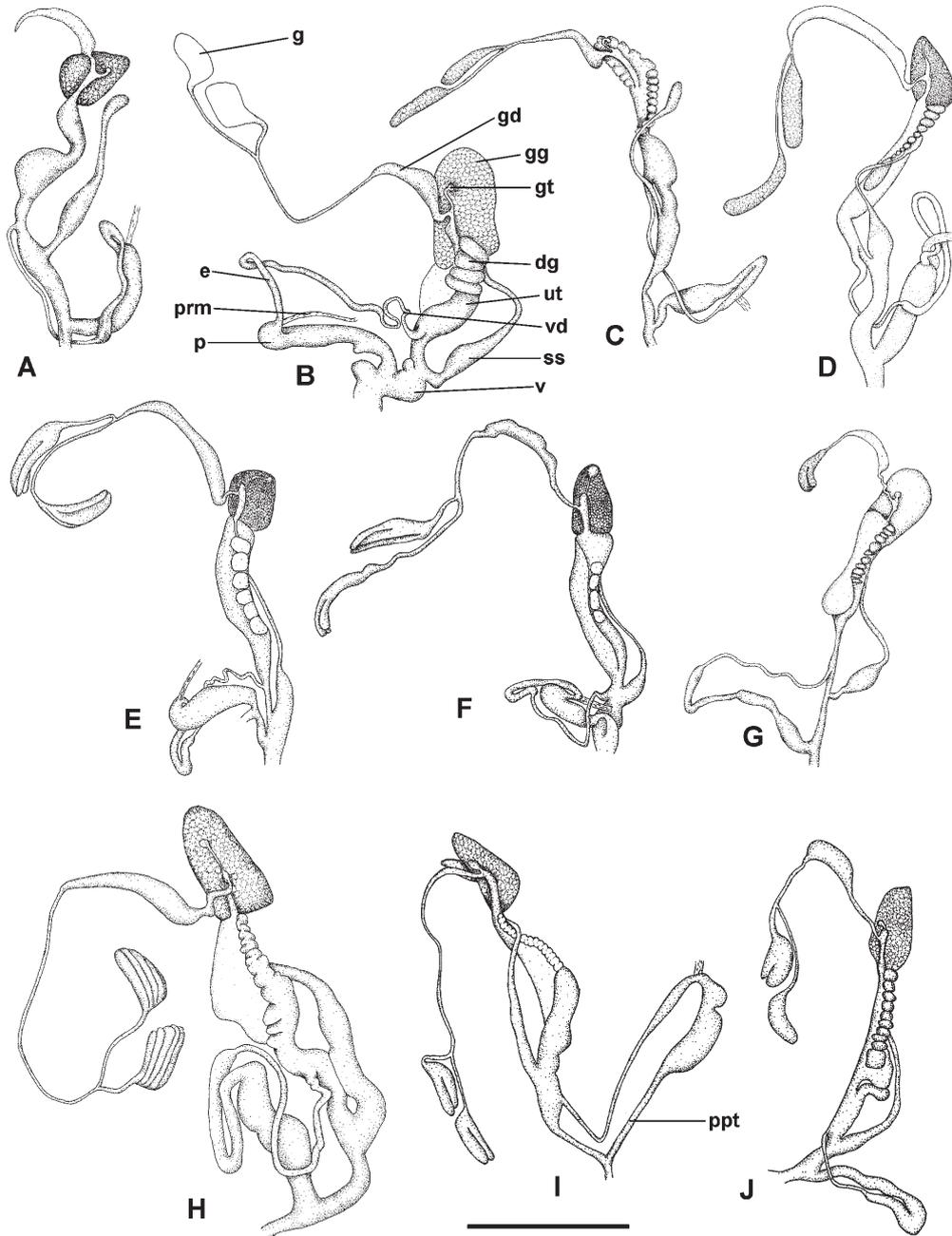


FIG. 9. Reproductive system. A, *Rhophodon kempseyensis*, QMMO37096. B, *Rhophodon palethorpei*, QMMO55962. C, *Egilodonta bairnsdalensis*, AMSC154770. D, *Egilodonta wyanbenensis*, QMMO29270. E, *Egilodonta bendethera*, QMMO70395. F, *Egilodonta paucidentata*, QMMO49447. G, *Letomola contortus*, QMMO56119. H, *Letomola lanalittleae*, QMMO56007. I, *Macrophallikoropa belli*, AMSC162176. J, *Macrophallikoropa stenoumblicata*, QMMO28661. Scale bar=2mm in A and D, and 1.6mm in all others. Abbreviations: dg, prostate; e, epiphallus; g, ovotestis; gd, hermaphrodite duct; gg, albumen gland; gt, talon; p, penis; ppt, preputial tube; prrm, penis retractor muscle; ss, spermathecal stalk; ut, uterus; v, vagina; vd, vas deferens.

longitudinal pilaster and long verge; length of verge greater than half the length of penis; sheath present. Vagina tubular, shorter than penis.

Pallial cavity with complete secondary ureter; kidney almost unlobed with rectal lobe vestigial and pericardial lobe elongate, triangular and with apex reflexed.

Radula with central tooth strongly tricuspid, considerably smaller than laterals; lateral teeth tricuspid; mesocone of first lateral tooth slender, slightly diamond-shaped; marginal teeth rounded; ectocone of outer marginal teeth split into four or more teeth; endocone not split. Number of lateral teeth 6; marginal teeth 7; radular rows 115.

Based on 3 dissected adults (QMMO68759).

DISTRIBUTION AND HABITAT. Known only from the type locality; living in litter on strongly vegetated limestone outcrop (including *Ficus* sp.) among open eucalypt woodland.

REMARKS. *Egilodonta bendethera* sp. nov. is microsypatric with *E. paucidentata* sp. nov., to which it bears a strong resemblance. The two species can be distinguished by a difference in shell colour (*E. bendethera* is lighter), and a difference in aperture shape. The whorls of *E. bendethera* are rounded above and below a flattened periphery, giving the aperture a less rounded appearance than *E. paucidentata*. *E. bendethera* is also larger, has wider rib spacing and has a narrower (wide cup-shaped instead of shallow saucer-shaped) umbilicus than *E. paucidentata*. Anatomically *E. bendethera* differs from *E. paucidentata* in that the epiphallus enters the penis through a long verge (more than half the length of the penis), and in having only one penial pilaster. In *E. paucidentata* the verge is considerably shorter (less than half the length of the penis), and there are six penial pilasters. Both species are similar to *E. bairnsdalensis*, but differ in having weaker apertural barriers and less widely spaced teleoconch ribs. *E. bendethera* is readily distinguished from *E. wyanbenesis* by having less crowded ribs on the teleoconch.

***Egilodonta paucidentata* sp. nov.**
(Figs 2-11, 33; Table 2)

ETYMOLOGY. Latin *paucus*, few, and *dentatus*, toothed; referring to the poor apertural dentition.

MATERIAL. HOLOTYPE: QMMO70396, Marble Arch, S of Braidwood, NSW (35°43'19"S, 149°42'12"E), limestone outcrop/remnant rainforest, under rocks and in

litter, 11.x.1992, JS, GI. Height of shell=0.95mm, diameter=1.92mm, H/D=0.49, D/U=2.06, number of whorls=4.8, ribs on last whorl = 37. **PARATYPES:** All NSW. QMMO42081, 5SC/49RC, same data as holotype; AMSC126761, 20+RC, W of Batemans Bay, Deua NP, Bendoura Ra, Reedy Ck, Marble Arch (35°43.6'S, 149°41.4'E), WFP, W.F. (Jr) Ponder; AMSC346063, 20+RC, W of Batemans Bay, Deua NP, Bendoura Ra, Reedy Ck, 5km E of Berlang Camping Ground, Marble Arch (35°43.6'S, 149°41.4'E), MS. **OTHER MATERIAL.** QMMO49447, MO68004.

DIAGNOSIS. Minute golden brown shell with a wide saucer-shaped umbilicus. Teleoconch with widely spaced, broad, protractively sinuated ribs. Mean ribs/mm 6.51. Aperture with one parietal, one basal and one palatal barrier; barriers weakly developed, blade-like. Penis internally with a short apical verge and six longitudinal pilasters.

DESCRIPTION. Shell discoidal, golden brown, with 4.5-5.5 (mean 5.0) tightly coiled whorls, the last descending more rapidly in front. Shell diameter 1.72-2.26mm (mean 1.99mm). Apex and early spire flat. Height of shell 0.80-1.11mm (mean 0.93), H/D 0.41-0.54 (mean 0.47). Protoconch exsert of 1.2-1.7 whorls. Apical sculpture with prominent, strongly curved radial ribs, becoming increasingly crowded toward protoconch/teleoconch boundary; width of interstices (in multiples of rib width) 7 at apex, 2 at post-nuclear boundary; secondary sculpture of moderately spaced, discontinuous radial wrinkles. Teleoconch sculpture of bold, widely spaced, protractively sinuated radial ribs; 28-57 (mean 41) ribs on last whorl. Ribs/mm 4.87-8.91 (mean 6.51). Rib height equal to width; straight in section, rounded on top. Rib interstices on first post-nuclear whorl equal to width of 4-5 ribs; interstices on penultimate whorl equal to width of 3-5 ribs. Interstitial sculpture of fine radial riblets and crowded microspirals, about equal in strength. Microradials low, 10-13 between ribs on first post-nuclear whorl, 15-21 between ribs on penultimate whorl; microspirals crossing major ribs and forming strong elongate beads at their intersection with microradials. Umbilicus very wide, saucer-shaped, diameter 0.85-1.07mm (mean 0.94mm), D/U 1.95-2.32 (mean 2.13). Sutures impressed, whorls rounded above and below a flattened periphery. Aperture ovately lunate; lip sinuous; shiny parietal callus present. One very fine parietal barrier, one basal and one palatal barrier present; barriers low blade-like. Based on 43 measured adults (QMMO70396, MO49447, MO68004, MO42081).

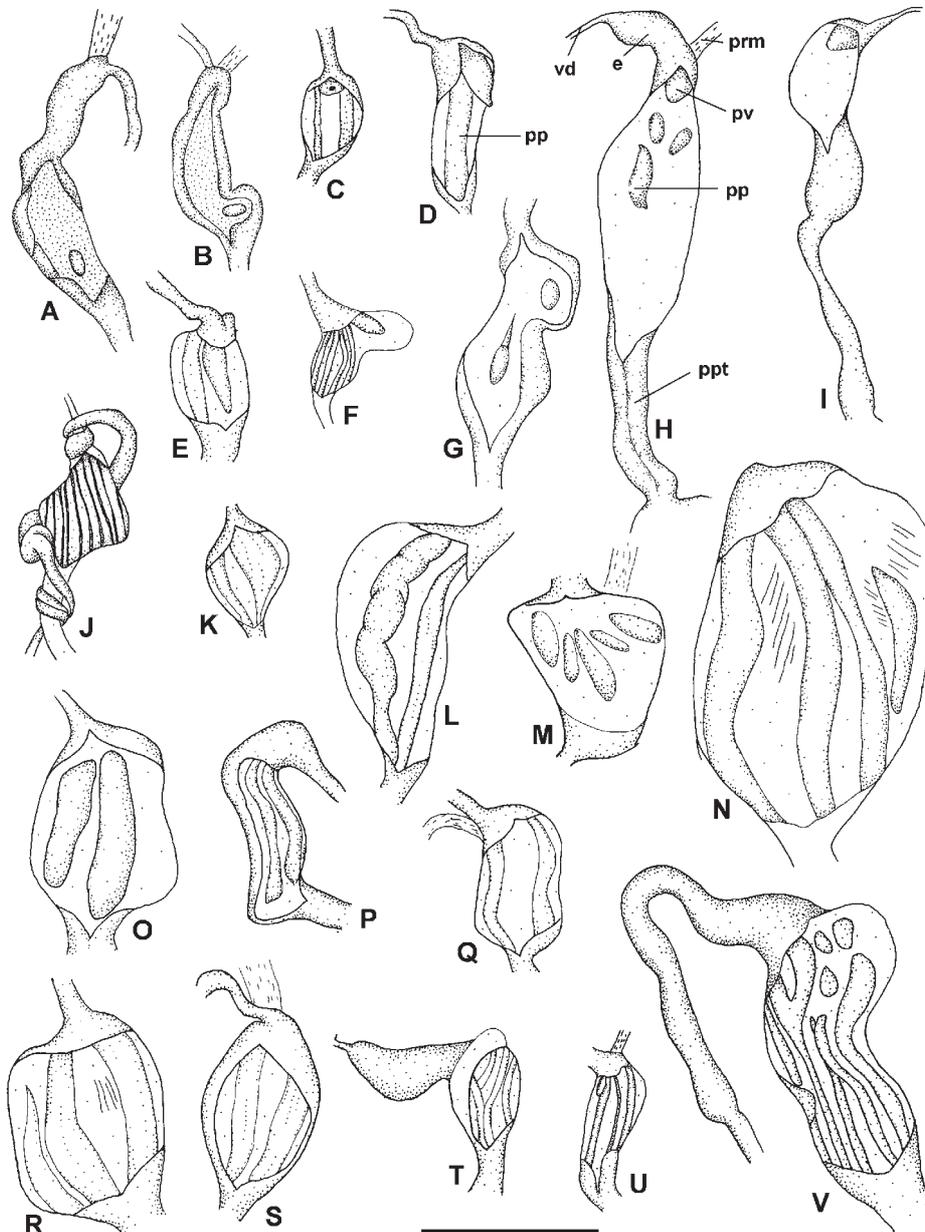


FIG. 10. Penis, dissected. A, *Rhophodon kempseyensis*, QMMO37096. B, *Rhophodon palethorpei*, QMMO55962. C, *Egilodonta bairnsdalensis*, AMSC154770. D, *Egilodonta wyanbenensis*, QMMO29270. E, *Egilodonta bendethera*, QMMO70395. F, *Egilodonta paucidentata*, QMMO49447. G, *Letomola lanalittleae*, QMMO56007. H, *Macrophallikoropa belli*, QMMO16867. I, *Macrophallikoropa stenoumbilicata*, QMMO28661. J, *Elsothera brazieri*, QMMO44810. K, *Decorioropa lirata*, QMMO42109. L, *Coricudgia wollemiana*, QMMO28659. M, *Marilyniropa jenolanensis*, QMMO37465. N, *Gouldiropa kaputarensis*, QMMO49175. O, *Cralopa stroudensis*, QMMO29722. P, *Gouldiropa carlessi*, MO32080. Q, *Sharniropa wollondillyana*, QMMO29241. R, *Acheronopa attunga*, QMMO49218. S, *Hedleyropa yarrangobillyensis*, QMMO39840. T, *Scleridoropa sarahjaneae*, QMMO39974. U, *Scleridoropa nandewar*, QMMO49158. V, *Diphyoropa macleayana*, AMSC162184. Scale bar=1.25mm in L, and 1mm in all others. Abbreviations: e, epiphallus; pp, penial pilaster; ppt, preputial tube; pv, penial verge, vd, vas deferens.

Genitalia with ovotestis containing two clumps of alveoli; more than two alveolar lobes per clump. Talon stalk 1-3 times the diameter of the talon; talon circular. Penis retractor muscle half the length of penis or greater; inserts at junction of penis and epiphallus. Epiphallus present; enters penis through a verge; length of verge less than half the length of penis. Epiphallus longer than penis; wider than vas deferens; pilasters longitudinal; retractor muscle not entwined with epiphallus. Penis sheath present; penis tubular; pilasters longitudinal; 6 pilasters present. Vagina shorter than penis; atrium shorter than penis; preputial tube absent. Pallial cavity with complete secondary ureter; primary ureter normal; kidney almost unilobed; apex reflexed. Mantle gland absent.

Radular morphology unknown.

Based on 1 dissected adult (QMMO49447).

DISTRIBUTION AND HABITAT. Known only from two limestone environments in the Bendoura/Minuma Ranges, S of Braidwood, SE NSW; living in litter on strongly vegetated limestone outcrops that support some remnant rainforest plant species; the surrounding countryside comprises open eucalypt woodland.

REMARKS. Features that differentiate *Egilodonta paucidentata* sp. nov. from other members of the genus are given above. The species is most similar to *E. bairnsdalensis* in general shell features and was mis-identified as that species by Stanisc (1990). *E. paucidentata* has comparatively weaker apertural barriers and slightly more crowded ribs than *E. bairnsdalensis*. Anatomically, the presence of a verge in *E. paucidentata* is a major difference from the vergeless condition in *E. bairnsdalensis*. The two species are allopatric and accurate locality data should eliminate the chance of misidentification.

Additional fieldwork needs to be conducted in the vicinity of the limestone localities in order to determine whether this species is an obligate calciphile.

***Letomola* Iredale, 1941**

Letomola Iredale, 1941a: 267; Stanisc, 1990: 109; Smith 1992: 110.

Letomala (error) Kershaw, 1956b: 9.

TYPE SPECIES. *Rhophodon contortus* Hedley, 1924; by original designation.

DIAGNOSIS. Small to minute charopids, with discoidal shells; colour brown with white radial streaks. Shell with or without apertural barriers;

spire flat to depressed. Protoconch strongly exsert with sculpture of irregular pits; sometimes with narrow, very widely spaced, curved radial ribs; spiral cords absent but discontinuous spiral grooves sometimes present. Teleoconch sculpture degenerate, without distinct radial ribs, instead with broad, shingle-like, overlapping radial thickenings; secondary sculpture of low microradial ridges and low spiral cords that form weak beads at their intersection. Umbilicus very wide saucer-shaped to broad V-shaped. Kidney moderately bilobed with apex of pericardial lobe slightly reflexed. Penis internally with longitudinal pilasters and with or without vergic structures.

DISTRIBUTION AND HABITAT. *Letomola* Iredale, 1941 is known only from the Macleay Valley, NE NSW. Species are obligate limestone dwellers usually living in litter or on the rock surface of outcrops among dry rainforest.

REMARKS. Iredale (1941a) introduced *Letomola* for *Rhophodon contortus* Hedley, 1924 without giving clear reasons for the separation from *Rhophodon* Hedley, 1924. Kershaw (1956b) briefly discussed the genus. Subsequently Smith & Kershaw (1979) added *Helix barrenensis* Petterd, 1879 (type locality: Furneaux Group of islands, Bass Strait) without detailed justification for this placement. These authors probably based their decision on the presence of apertural lamellae since other details of the shell do not agree with those of *Letomola*. Smith (1992) maintained this classification. *H. barrenensis* is not discussed here but the fact that it has well developed radial sculpture on the teleoconch (as opposed to the degenerate sculpture of *Letomola*) indicates strongly that it does not belong to *Letomola*. The generic status of this species most probably needs to be determined in a context of the Tasmanian charopids.

In spite of the absence of apertural barriers, the addition of *L. lanalittleae* sp. nov. does not alter the basic concept of *Letomola* as presented by Stanisc (1990). Barriers have developed independently in a number of Australian charopid genera and numbers of barriers vary from species to species. In the case of *L. lanalittleae* barrier loss merely represents an extreme example of reduction. Protoconch sculpture, teleoconch sculpture, and to a lesser degree, general shell form all agree with Stanisc's (1990) view of the genus. A slightly amended diagnosis is presented to accommodate the idiosyncrasies of the new species.

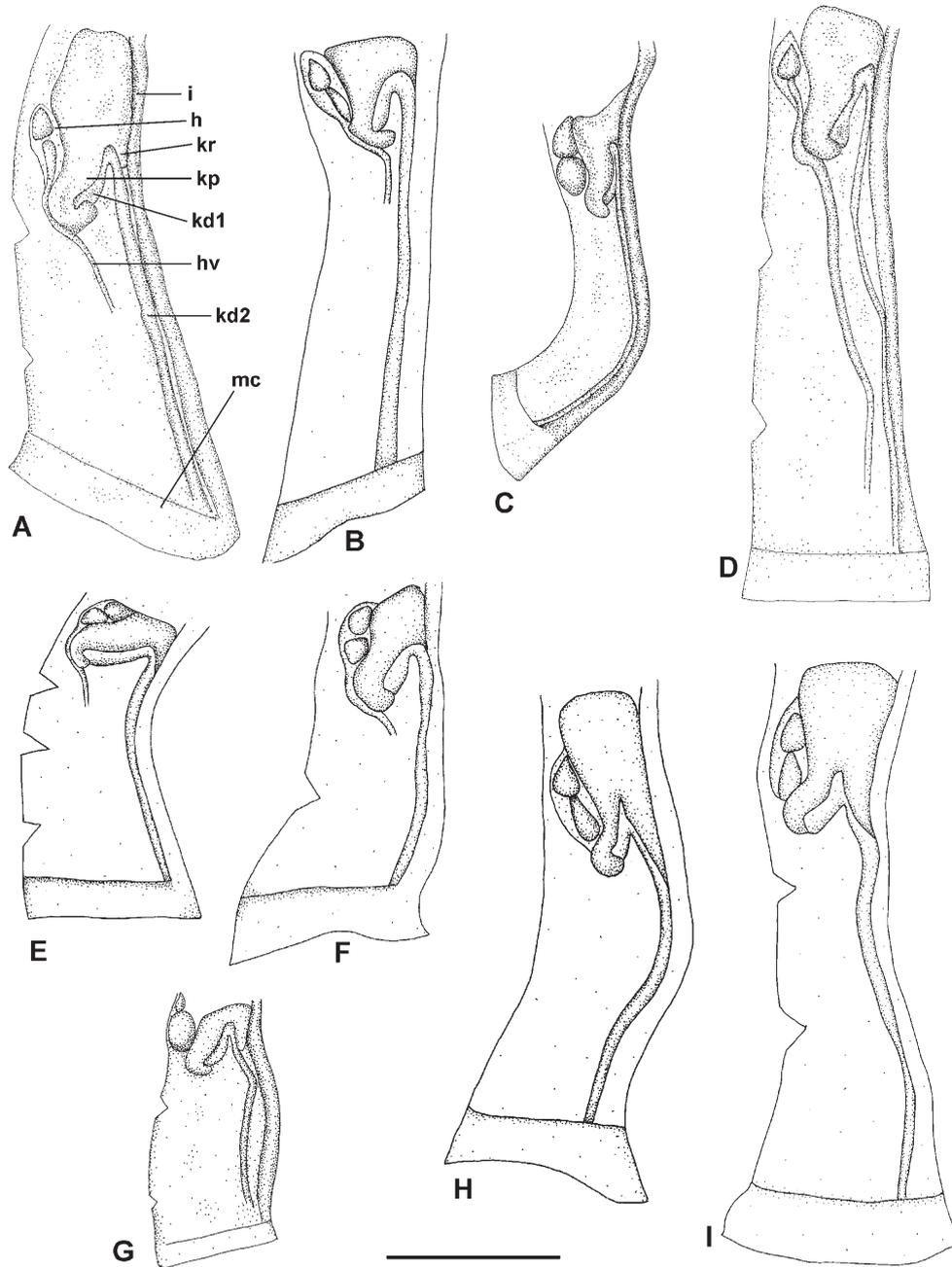


FIG. 11. Pallial cavity. A, *Rhophodon kempseyensis*, QMMO37096. B, *Rhophodon palethorpei*, QMMO55962. C, *Egilodonta bairnsdalensis*, AMSC154770. D, *Egilodonta wyanbenensis*, QMMO29270. E, *Egilodonta bendethera*, QMMO70395. F, *Egilodonta paucidentata*, QMMO49447. G, *Letomola contortus*, QMMO56119. H, *Macrophallikoropa belli*, AMSC162176. I, *Macrophallikoropa stenoumbilicata*, QMMO28661. Scale bar = 1.5mm in B, and 1.2mm in all others. Abbreviations: h, heart; hv, principal pulmonary vein; i, intestine; kd1, primary ureter; kd2, secondary ureter; kp, pericardial lobe of kidney; kr, rectal lobe of kidney; mc, mantle collar; mg, mantle gland.

Letomola Iredale, 1941 possesses a number of features that distinguish it from other charopid genera examined in this study. Having a shell with a pitted protoconch, supra-peripheral sulcus and degenerate teleoconch sculpture and a radula with greatly reduced central tooth are a unique combination of features that readily identify *Letomola* among all hitherto described eastern Australian Charopidae. Ecologically *Letomola* is distinguished by living on the limestone karst surface as well as in the interstitial litter. No other charopid is currently known to live on limestone karst in eastern Australia although this is common among groups such as the Hydrocenidae (*Georissa* spp.), Helicinidae (*Pleuropoma* spp.) and Pupillidae (*Gylotrachela* spp.) (Stanisic, pers. obs.). Solem (1974) suggested that ribs have a universal functional role among land snails of maintaining a dirt free shell surface for the snail as it crawls through moist, adherent litter. In which case the modified (reduced?) shell sculpture of *Letomola* may be related to its tendency to a non-litter lifestyle. A similar pattern is seen in the semi-arboreal charopids, *Lenwebbia protoscribiculata* Stanisic, 1990 and *Lenwebbia paluma* Stanisic, 1993. Both have a shell with pitted apical sculpture and reduced teleoconch sculpture.

***Letomola contortus* (Hedley, 1924)**
(Figs 9, 11-12, 14-18; Table 2)

Rhophodon contortus Hedley, 1924: 220, pl. 32, figs 35-37; Kershaw, 1955: 30.

Letomola contortus (Hedley). Iredale, 1941a: fig. 6; Iredale, 1941b: 2; Stanisic, 1990: 110, figs 67-69; Smith, 1992: 193.

Letomala (sic) *contortus* (Hedley). Kershaw, 1956b: 9.

MATERIAL. All NSW: QMMO37150, MO19796, MO56119, MO59998, MO52762, AMSC157303, C168612.

DIAGNOSIS. Shell minute, brown with white radial streaks. Whorls tightly coiled with a strong supraperipheral sulcus. Protoconch pitted, without any radial ribs or spiral cords, spire depressed. Teleoconch lacking distinct radial ribs, instead with broad, shingle-like, radially ridged, overlapping thickenings. Umbilicus wide and shallow saucer-shaped. Two apertural barriers (one parietal, one palatal) present. Ototestis consisting of one clump of alveoli with two alveolar lobes. Penis internally with an apical round pilaster and several longitudinal pilasters basally.

DISTRIBUTION AND HABITAT. Eastern end of the lower Macleay Valley, NE NSW on limestone outcrops among dry rainforest. Found

living on roof, walls and in floor litter of limestone caves, or sheltered vertical limestone rock faces.

REMARKS. *Letomola contortus* (Hedley, 1924) is readily identified by its degenerate adult sculpture, very wide umbilicus and the presence of a supraperipheral sulcus. Differences from *L. lanalittleae* sp. nov. are presented under that species (see below). Anatomically *L. contortus* is not very different from other 'dentate' charopids such as those grouped under *Rhophodon* Hedley, 1924 and *Egilodonta* Gabriel, 1930. However, the shell patterns are a dramatic departure from general charopid patterns seen in this study and probably relate to a slightly altered lifestyle not requiring the functional advantages of a ribbed shell. Interestingly this species lives on the limestone karst rather than the litter.

***Letomola lanalittleae* sp. nov.**
(Figs 9-10, 12, 14-18, 33-34; Table 2)

ETYMOLOGY. For Lana Little.

MATERIAL. All NSW. HOLOTYPE: QMMO70397, Kempsey, WNW, c.1.5km E Mt Sebastopol, Kempsey-Carrai Rd, NSW (30°57'00"S, 152°28'40"E), on rocks, drf/lm, 28.xi.1989, JS, DP. Height of shell=1.38mm, diameter=2.86mm, H/D=0.48, D/U=3.62, number of whorls=4.7. PARATYPES: QMMO32292, 19SC/44RC, same data as holotype; QMMO37761, 50RC, Kempsey, WNW, c.1.5km E Mt Sebastopol, Kempsey-Carrai Rd (30°57'00"S, 152°28'40"E), in litter, drf/lm, 28.xi.1989, JS, DP; QMMO56007, 20SC/42RC, Kempsey, WNW, c.1.5km E Mt Sebastopol, Kempsey-Carrai Rd (30°57'00"S, 152°28'40"E), on limestone and in litter, drf/lm, 8.i.1995, JS, JC. OTHER MATERIAL. QMMO49294.

DIAGNOSIS. Shell moderately small, chocolate brown with cream blotches. Whorls tightly coiled with a strong supraperipheral sulcus; Umbilicus wide V-shaped. Spire flat with exsert protoconch. Apertural barriers absent. Pitted protoconch with faint, curved, irregular radial ribs and discontinuous spiral grooves. Teleoconch without pronounced radial ribs, instead with broad, radially ridged, shingle-like overlapping thickenings. Ototestis containing two clumps of alveoli, with more than two alveolar lobes per clump. Penis internally with round to ovate pilasters.

DESCRIPTION. Shell small, chocolate brown with cream radial streaks, with 4.7-5.6 (mean 5.3) tightly coiled whorls, the last descending very rapidly in front; supraperipheral sulcus present. Shell diameter 2.81-3.74mm (mean 3.40mm).

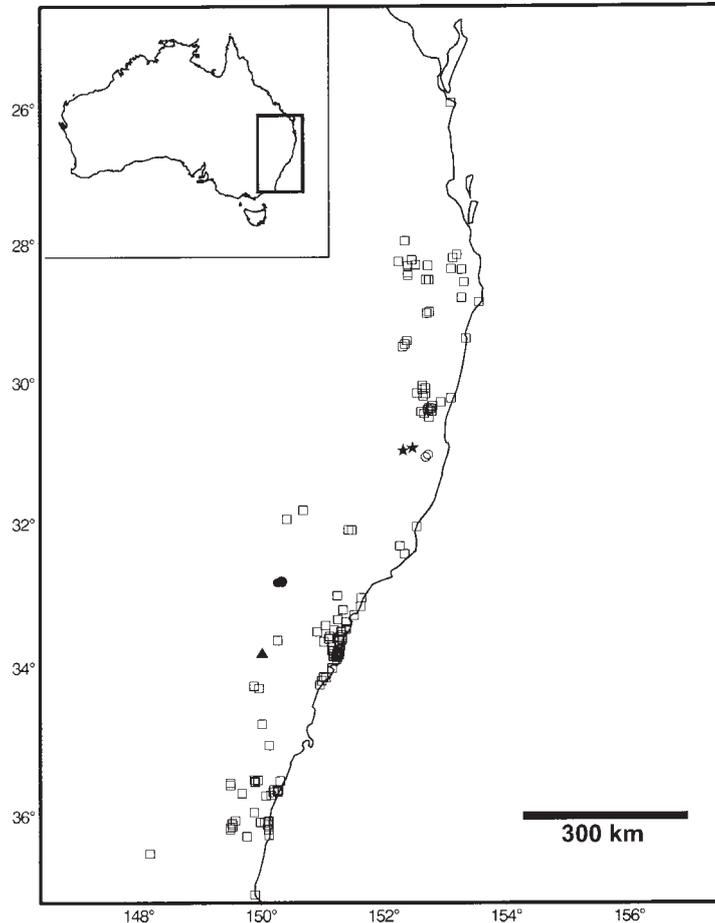


FIG. 12. Distribution of *Letomola* and *Macrophallikoropa*. Key: ○ *Letomola contortus*, ★ *Letomola lanalittleae*, □ *Macrophallikoropa belli*, ● *Macrophallikoropa stenoumblicata*, ▲ *Macrophallikoropa depressispira*.

Spire flat. Height of shell 1.30-1.74mm (mean 1.48mm), H/D 0.40-0.49 (mean 0.44). Protoconch strongly exsert of 1.5-1.7 whorls. Apical sculpture of irregular pits, with irregularly spaced, curved radial ribs; rib spacing variable, decreasing towards post-nuclear boundary (but not evenly); width of interstices (in multiples of rib width) 15 at apex; 2 at post-nuclear boundary. Scattered, discontinuous spiral grooves also present. Teleoconch sculpture consisting of broad, radially ridged, shingle-like overlapping thickenings. Microsculpture of low microradial radial ridgelets and microspiral cords, about equal in strength; forming weak round beads at their intersection. Umbilicus wide V-shaped, diameter 0.79-1.18mm (mean 1.02mm), D/U

3.08-3.74 (mean 3.35). Base flattened with microradial ridgelets becoming more bladeliike. Aperture ovately lunate; parietal callus present; apertural barriers absent. Based on 21 measured adults (QMMO37761, MO32292, MO70397).

Genitalia with ovotestis containing two clumps of alveoli; with more than two alveolar lobes per clump. Talon stalk more than 3 times diameter of talon; talon circular. Penial retractor muscle less than half the length of penis; inserting onto the penis apex. Epiphallus present, longer than penis; wider than vas deferens, entering penis through a simple pore. Penis tubular, pilasters modified (round); penial sheath present. Vagina shorter than penis.

Pallial cavity with kidney moderately bilobed; apex very slightly reflexed.

Radula with central tooth weakly tricuspid; lateral teeth tricuspid; first and second laterals equal in width; mesocone of first lateral tooth rounded at tip; marginal teeth flattened and rectangular; ectocone of outer marginal teeth split into three teeth; endocone not split. Number of

lateral teeth 7; marginal teeth 7; radular rows 119. Based on 4 dissected specimens (QMMO56007).

DISTRIBUTION AND HABITAT. *Letomola lanalittleae* sp. nov. is known from limestone outcrops among dry rainforest at the western end of the lower Macleay Valley; living on vertical limestone surfaces.

REMARKS. *Letomola lanalittleae* sp. nov. is distinguished from *L. contortus* by its larger size, flat spire (depressed in *L. contortus*), narrower umbilicus and the absence of apertural lamellae (two present in *L. contortus*). Anatomically, *L. lanalittleae* differs by having 2 clumps of alveoli in the ovotestis compared with only 1 in *L. contortus*. The radula of *L. lanalittleae* also has

TABLE 2. Shell measurements for species of *Egilodonta* and *Letomola*. (Abbreviations as in Table 1).

Measurement	<i>Egilodonta bairnsdalensis</i>	<i>Egilodonta wyanbenensis</i>	<i>Egilodonta bendethera</i>	<i>Egilodonta paucidentata</i>	<i>Letomola contortus</i>	<i>Letomola lanalittleae</i>
N	49 (*48)	16 (*15)	10	42	15	21 (*20)
D	1.51-2.19 (1.86) ± 0.09	1.78-2.39 (2.14) ± 0.157	1.64-2.63 (2.34) ± 0.32	1.72-2.26 (1.99) ± 0.11	1.78-2.23 (2.063) ± 0.133	2.81-3.74 (3.4) ± 0.28
PW	1.5-1.8 (1.66) ± 0.07 *	1.4-1.7 (1.573) ± 0.088 *	1.5-1.7 (1.55) ± 0.07	1.2-1.7 (1.56) ± 0.1	1.5-1.6 (1.527) ± 0.046	1.5-1.7 (1.61) ± 0.07
TW	2.9-4.9 (3.27) ± 0.3) *	2.7-3.4 (3.073) ± 0.215 *	2.8-4.2 (3.78) ± 0.46	3-4 (3.44) ± 0.2	2.2-2.7 (2.467) ± 0.172	3.1-4 (3.66) ± 0.25
NW	4.6-6.6 (4.93) ± 0.3 *	4.3-5.1 (4.647) ± 0.185 *	4.3-5.8 (5.33) ± 0.47	4.5-5.5 (5) ± 0.19	3.7-4.2 (3.993) ± 0.175	4.7-5.6 (5.26) ± 0.27
H	0.73-1.08 (0.89) ± 0.09	0.91-1.15 (1.033) ± 0.074	0.91-1.38 (1.18) ± 0.16	0.8-1.11 (0.93) ± 0.07	0.85-1.05 (0.979) ± 0.057	1.3-1.74 (1.48) ± 0.11
SP	0-0.12 (0.03) ± 0.04	0-0.02 (0.001) ± 0.005	0.01-0.18 (0.07) ± 0.06	0-0.14 (0.04) ± 0.04	0-0.01 (0.002) ± 0.004	0.08-0.42 (0.25) ± 0.1
AH/AW	1.1-1.62 (1.31) ± 0.12	1.29-1.76 (1.5) ± 0.13	1.13-1.57 (1.33) ± 0.14	1.14-1.76 (1.34) ± 0.12	0.97-1.31 (1.18) ± 0.08	0.71-1.05 (0.87) ± 0.09
UMB	0.67-0.95 (0.79) ± 0.06	0.8-1.14 (0.985) ± 0.082	0.7-1.15 (0.96) ± 0.13	0.85-1.07 (0.94) ± 0.05	0.64-0.88 (0.783) ± 0.067	0.79-1.18 (1.02) ± 0.11 *
RIB	23-50 (33.57) ± 6.53	56-85 (69.125) ± 7.83	27-47 (34.3) ± 7.04	28-57 (40.67) ± 7.07	-	-
RIBS/MM	2.78-7.27 (5.32) ± 1.11	8.49-13.05 (10.32) ± 1.271	3.92-6.08 (4.67) ± 0.71	4.87-8.91 (6.51) ± 1.02	-	-
H/D	0.43-0.55 (0.48) ± 0.03	0.43-0.52 (0.48) ± 0.03	0.48-0.55 (0.5) ± 0.03	0.41-0.54 (0.47) ± 0.03	0.43-0.53 (0.48) ± 0.03	0.4-0.49 (0.44) ± 0.03
D/U	2.11-2.58 (2.37) ± 0.11	2.08-2.31 (2.18) ± 0.07	2.19-2.63 (2.44) ± 0.12	1.95-2.32 (2.13) ± 0.09	2.38-2.79 (2.64) ± 0.13	3.08-3.74 (3.35) ± 0.21 *

the first lateral tooth the same size as the other lateral teeth, whereas in *L. contortus* the first lateral is considerably larger than the others. *L. contortus* and *L. lanalittleae* are allopatric within the lower Macleay Valley and the considerable shell differences point to either a long period of isolation or a major shift in environmental regime. The larger size of *L. lanalittleae* may be a reflection of its adaptation to a less insular lifestyle above the litter on the limestone rock where living conditions are harsher and requiring of a larger shell. A somewhat analogous phenomenon is seen in populations of littoral zone mollusks where larger individuals can exist higher up on the seashore because they are less prone to desiccation. In the case of *Letomola*, the evolution of a larger shell has probably allowed *L. lanalittleae* more flexibility in living space than *L. contortus*.

Macrophallikoropa gen. nov.

ETYMOLOGY. Greek *macro*, long and *phallikos*, penis; referring to the unusually long penial apparatus.

TYPE SPECIES. *Helix belli* Cox, 1864; herein designated.

DIAGNOSIS. Shell minute, discoidal, with tightly coiled whorls. Colour golden brown to very light golden brown, sometimes with darker

flamulations. Protoconch exsert; spire slightly elevated to depressed. Protoconch sculptured with narrow, high, continuous spiral lirae; number of lirae 13-20. Secondary apical sculpture of radial elements present as narrow, discontinuous ridgelets (= pressure folds) between the cords. Teleoconch with slightly sinuated to straight, very crowded ribs; interstitial sculpture with microradials and microspirals about equal in strength, forming strong rounded beads at their intersection. Umbilicus wide U-shaped to very wide saucer-shaped. Kidney strongly bilobed. Epiphallus moderately long to very short. Penis with long to very long preputial tube; internally with very short apical verge or apical pore; no other visible thickenings.

DISTRIBUTION AND HABITAT. *Macrophallikoropa* gen. nov. ranges from SE NSW to SE Qld. Species live under logs and rocks in temperate to subtropical rainforest (humid and dry), dry vine thicket and wet to dry sclerophyll forest and occur under a variety of geological regimes ranging from sandstone to basalt and limestone.

REMARKS. *Allocharopa* Iredale, 1937 (type species: *Helix brazieri* Cox, 1868) was introduced to accommodate a number of charopids

from New South Wales, Victoria and Tasmania, including *Helix belli* Cox, 1864. One of the key characters given in the generic diagnosis was that the protoconch should be 'radially ribbed as remainder of shell'. Closer inspection reveals that the conglomeration of species included in this genus represents a variety of protoconch types. This is a strong indication that the group is polyphyletic. *H. belli* has a prominent spirally lirate protoconch which immediately separates it from the other species listed by Iredale, 1937 under *Allocharopa*.

As will be shown below, *Allocharopa* is a junior synonym of *Elsothera* Iredale, 1933 and most of the species included in this genus by Smith (1992) will need reallocation. A major revision of all the species is beyond the scope of this study and only *H. belli* and *H. brazieri* (see below) are dealt with herein. It is highly probable that the other species (mostly Tasmanian) will need to be reviewed in the context of that local charopid fauna since many of the southern Charopidae (Tasmanian, Victorian) appear unrelated to the eastern NSW radiation (Stanisic, unpubl. data).

Smith & Kershaw (1979) placed *H. belli* in *Roblinella* Iredale, 1937 (type species *Helix roblini* Petterd, 1879) which was introduced to accommodate a series of species with 'spirally striated nuclear whorls'. These authors did so without giving reasons. As introduced by Iredale (1937), *Roblinella* contains species with dramatically different apical spiral lirae indicating that it is polyphyletic (possibly at least three genera [Stanisic, unpubl. data]). The spirally lirate protoconch of *H. belli* comes closest to that of the type, *R. roblini*, but differs in having more regular and crowded lirae. The very fine teleoconch ribs and coiling pattern of *R. roblini* (loose coiling with tiny umbilicus) are also features that indicate the two species are not congeneric.

On available evidence *H. belli* deserves generic recognition and *Macrophallikoropa* gen. nov. is introduced for this widespread rainforest charopid plus two additional new species from very restricted localities in the Sydney Basin Bioregion.

Macrophallikoropa gen. nov. can be distinguished from all other genera in this study by the presence of a spiral protoconch. The studies of Stanisic (1987, 1990, 1993a) show that spiral apical sculpture has developed independently in distantly related groups. In contrast to the apical sculpture of *Setomedeia* Iredale, 1941 (low,

narrow, moderately spaced, strongly to slightly wavy spiral cords with vague, scattered radial ridges); *Oreokera* Stanisic, 1987 (low, crowded, regular to wavy spiral cords with radial rugosities developing at the protoconch/ teleoconch boundary); *Mussonula* Iredale, 1937 (low, fine to bold, crowded to very crowded spiral cords with curved radial ridges appearing toward the protoconch/teleoconch border); *Sinployea* Solem, 1983 (low, widely spaced radial cords); and *Omphaloropa* Stanisic, 1990 (low, moderately spaced spiral cords that become indistinct toward the inner half of the embryonic whorls), that of *Macrophallikoropa* features spiral cords that are strongly developed, crowded, narrow and high in section. In each of the above genera the lirae and general protoconch appearance seem macroscopically similar, but when viewed by scanning electron microscopy they reveal subtle but significant differences in architectural detail. These seemingly minor differences in protoconch sculpture correspond with major differences in shell form, teleoconch sculpture and anatomy suggesting that they are phylogenetically significant. Iredale (1937, 1941a,b) and Smith & Kershaw (1979) list a number of Australian charopids with a spirally lirate protoconchs, but do not provide adequate detail on microstructural diversity for this level of interpretation.

An additional feature on the protoconch of *Macrophallikoropa* is the presence of short, discontinuous radial elements between the cords. These may represent shrinkage wrinkles associated with a dried periostracum (=pressure folds) in a manner similar to the discontinuous spiral elements shown by Solem (1984) to be present on the apices of species with predominantly radial protoconchs such as *Discocharopa aperta* (Möllendorff, 1888).

The biogeography of this group is intriguing with a widespread species, *M. belli* (Cox, 1864) occurring mainly in the rainforests along the Great Dividing Range from SE NSW to SE Qld, in the sandstone country around Sydney and in several southern limestone localities (Jenolan, Bungonia, Wombeyan, Marble Arch, Wyabene). Two additional species, *M. depressispira* sp. nov. and *M. stenoumbilicata* sp. nov., occur in restricted habitats at Jenolan Caves and Mt Coricudgy and environs respectively. Much of the area that encompasses these latter distributions is sandstone dominated by sclerophyll forests with rainforest occurring only as small refugia in damp gullies or on rocky outcrops. Jenolan Caves (limestone) and Mt

Coricudgy (a basalt capped peak) represent two unusual isolated topographies within this sandstone landscape. Both maintain remnant rainforest communities. Judging by the widespread distribution of *M. belli* within currently disconnected coastal rainforests blocks in eastern NSW and SE Qld, this species must have been present in these rainforests at a time when they were more extensive and more strongly interconnected. Presumably as rainforest became climatically restricted and fragmented in distribution from approximately the mid-Miocene onwards, *M. belli* would have continued to exist as isolated populations in widely separated refugia, probably along drainage lines, on mountain tops and in select topographic niches. Presumably also, climatically induced, shorter-term expansion of traditional *M. belli* habitat through the many wet climatic phases in the Plio-Pleistocene would have enabled *M. belli* to once again disperse and also occupy the wetter, non-rainforest habitats it now does in southern areas, including much of the Sydney Basin Bioregion. *M. depressispira* and *M. stenoumbilicata* appear to represent two climatically isolated derivatives of *M. belli* since they maintain many of the features of that species while also showing a number of significant departures from the ancestral pattern (depressed spire, narrower umbilicus, reduced length of preputial tube, lengthening of the umbilicus).

Macrophallikoropa belli (Cox, 1864) comb. nov.
(Figs 9-12, 14-18; Table 3)

Helix belli Cox, 1864: 22; Cox, 1868: 17, pl. 6, fig. 3.

Endodonta (Charopa) belli (Cox). Cox, 1909: 11.

Allocharopa belli (Cox). Iredale, 1937: 326; Iredale, 1941a: 261; Kershaw, 1956a: 141; Smith, 1992: 181.

Roblinella belli (Cox). Smith & Kershaw, 1979: 180.

MATERIAL. LECTOTYPE (herein designated): AMSC205161. Height of shell=0.84mm, diameter=1.67mm, H/D=0.5, D/U=3.04, number of whorls=4.5, ribs on last whorl=175. **PARALECTOTYPES**: AMSC136899, 26RC, same data as lectotype. **KEY MATERIAL**. AMSC162176,

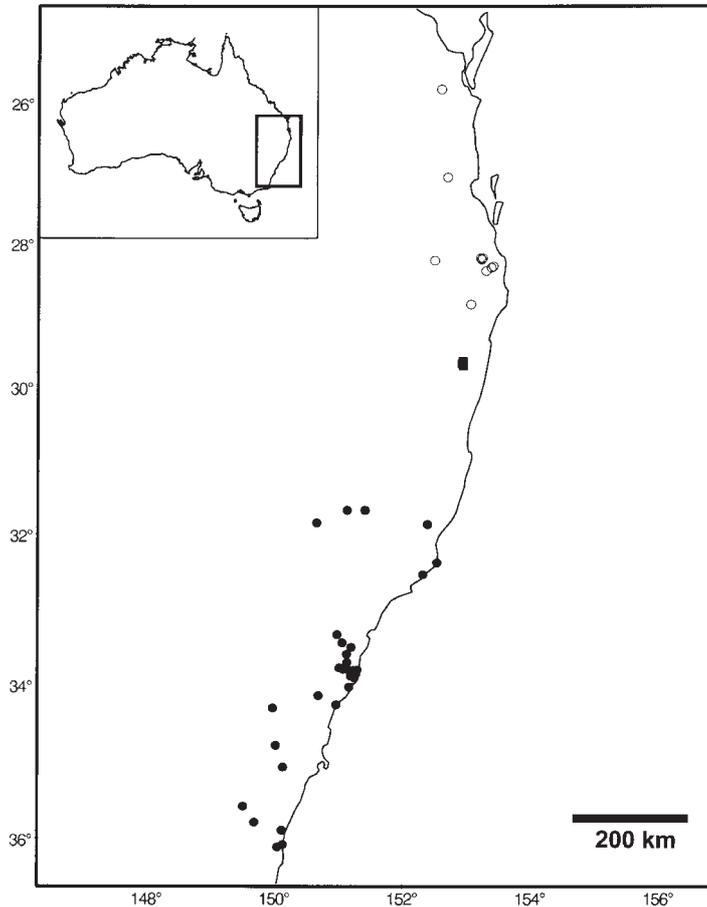


FIG. 13. Distribution of *Egilomen*, *Whiteheadia* and *Decorioropa*. Key: ■ *Egilomen cochlidium*, ○ *Whiteheadia globosa*, ● *Decorioropa lirata*.

16SC/2RC, S of Quirindi, Liverpool Ra. Cedar Brush Nature Res, Cedar Brush Gap, off Warrah Ck Rd, NSW, 4WD Track (31°50.54'S, 150°41.4'E), under logs, rf with broken canopy, 8.xi.1985, IL, JW; QMMO29277, 6SC, Misty Mt., c.19km along Bolaro Mtn Rd, off Batemans Bay-Braidwood Rd, NSW (35°37'S, 149°57'E), wtrf, under logs, 06.i.1990, JS, JC; QMMO16867, 3SC, Lamington NP, Binna Burra, Qld Mt Hobwee circuit, nvf, under logs, 01.x.1985, JS, DP, JC; AMSC171336, 20+RC, Sydney, Bellevue Hill, Cooper Park NSW (33°53.26'S, 151°14.9'E), wsf, 23.v.1982, MS; QMMO10760, 8RC, Durrumbidgee, ca.2.3km N, Durrumbidgee-Grafton Rd NSW (30°11'S, 152°34'E), mvf, 15.vi.1981, WFP, JS, OG, DP; QMMO42080, 15RC, Marble Arch, S of Braidwood NSW (35°43'S, 149°42'E), Isoc/rf, 11.x.1992, JS, GI; QMMO10512, 12RC, Mt Warning, NSW, summit (28°24'S, 153°16'E), nvf, 07.vii.1981, WFP, JS, OG, DP. **OTHER MATERIAL**. Southeastern NSW: QMMO29275, AMSC357398, C357402-4, C357410, C357415, C318486, QMMO29263, MO37985. Sydney Basin: AMSC377544, C318382, C318383, C318385, C318390, C318393, C318398,

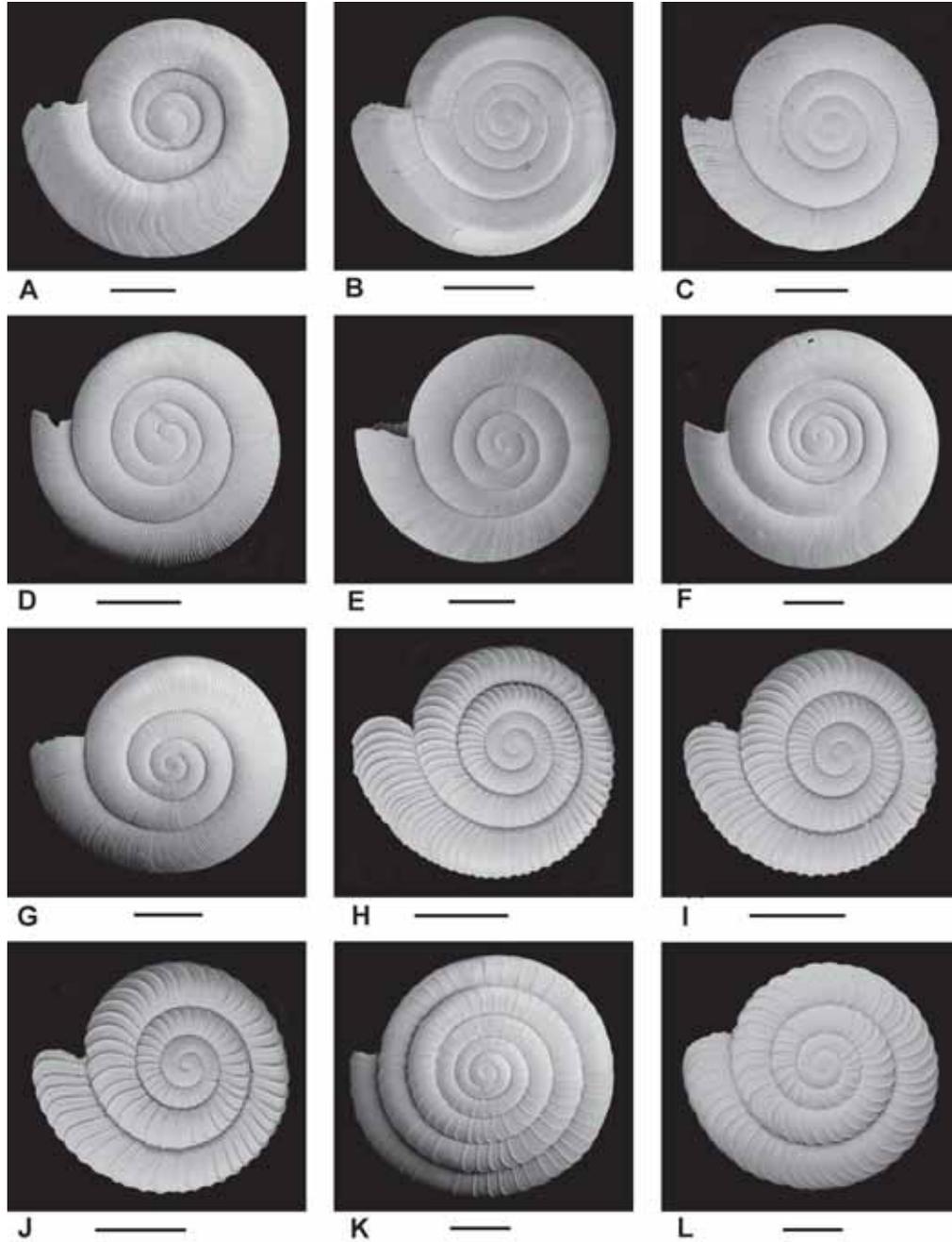


FIG. 14. Dorsal view of shells. A, *Letomola contortus*, AMSC119349. B, *Letomola lanalittleae*, QMMO70397. C, *Macrophallikoropa belli* (Sydney), AMSC171336. D, *Macrophallikoropa belli* (Mt Warning), QMMO10512. E, *Macrophallikoropa stenoumbilicata*, AMSC205162. F, *Macrophallikoropa depressispira*, AMSC205163. G, *Elsothera brazieri*, QMMO28775. H, *Decoriropa lirata* (Taree), AMSC135842. I, *Decoriropa lirata* (Kempsey), QMMO52755. J, *Decoriropa lirata* (Wombeyan Caves), QMMO64764. K, *Coricudgia wollemiana*, AMSC205164. L, *Marilyniropa jenolanensis*, AMSC205165. Scale bars=0.5mm in A, C-F, H; 0.8mm in I-L; 1mm in B,

C318403, C318407, C318422, C318412, C318416, C318417, C318419, C318420, C318425, C318435, C318430, C318431, C318439, C318444, C318432, C318433, C318442, C318438, C318440, C318441, C318443, C318483, C377468, QMMO37777, MO34782, MO31920. Northeastern NSW. QMMO31938, MO37517, MO29739, MO49246, MO52681, MO52699, MO29749, AMSC377871, C377941, C377867, C377840, C162009, QMMO10781, MO10804, MO10820, MO10753, MO16773, MO10892, MO9830, MO10539. SE Qld: AMSC136491, C129240, QMMO10992, MO12863, MO12697, MO6079, MO8364.

DIAGNOSIS. Minute, golden brown to very light golden brown shell, sometimes with darker flammulations. Spire flat, protoconch with crowded spiral lirae. Teleoconch with slightly sinuate to straight crowded ribs; interstitial sculpture with microradials and microspirals about equal in strength, forming strong beads. Umbilicus very wide cup-shaped, mean D/U 2.75. Penis internally with very short penial verge, very long preputial tube. Epiphallus very short.

DESCRIPTION. Shell tiny, golden brown (occasionally with darker flammulations), with 3.8-5.5 (mean 4.46) tightly coiled whorls, the last descending more rapidly in front. Sutures impressed, whorls evenly rounded above and below periphery. Shell diameter 1.43-2.22mm (mean 1.76mm). Apex and early spire flat. Height of shell 0.73-1.12mm (mean 0.92mm), H/D 0.48-0.56 (mean 0.52). Protoconch exsert of 1.5-1.8 whorls. Apical sculpture of crowded, narrow spiral lirae; number of lirae 14-20. Secondary apical sculpture of discontinuous radial ridglets that may be periostracal pressure folds. Teleoconch sculpture of very crowded, protractively sinuated radial ribs; 102-248 (mean 179) ribs on last whorl. Ribs/mm 14.69-42.19 (mean 32.65). Ribs medium to narrow; height equal to width; straight in section; rounded on top. Rib interstices on the first post-nuclear whorl equal to width of one to four major ribs; interstices on the penultimate whorl equal to one to three ribs. Interstitial sculpture of fine radial riblets and spiral cords, about equal in strength. Microradials low; 2-7 between ribs on first postnuclear whorl, 3-6 between ribs on penultimate whorl. Microspirals forming strong round to elongate beads at their intersection with the microradials; crossing major ribs. Umbilicus very wide, cup-shaped; diameter 0.42-0.84mm (mean 0.64mm), D/U 2.31-3.43 (mean 2.76). Aperture ovately lunate, with parietal callus. Based on 31 measured adults (AMSC171336, C318439, C205161, QMMO10760, MO10512, MO42080, MO32185).

Genitalia with ovotestis containing 2 clumps of alveoli with 2 alveolar lobes per clump. Talon stalk shorter than or equal to talon diameter; talon circular. Penial retractor muscle less than half the length of the penis inserting at or near the junction of the penis and epiphallus, on either the penis or epiphallus. Epiphallus short wider than epiphallus, entering penis through a verge; length of verge less than half the length of the penis. Penis tubular, internally with an apical verge but without any other noticeable thickenings. Vagina shorter than or equal in length to penis; atrium shorter than penis; long preputial tube present.

Kidney bilobed; apex of pericardial lobe slightly reflexed.

Radula with central tooth strongly tricuspid; lateral teeth tricuspid; first and second laterals equal in width. Mesocone of first lateral tooth slender, slightly diamond-shaped; marginal teeth skewed towards the centre; ectocone of outer marginal teeth split into two teeth; endocone not split. Number of lateral teeth 5; marginal teeth 6; radular rows 78-80. Based on 7 dissected specimens (AMSC162176, QMMO29277, MO16867, MO32185).

DISTRIBUTION AND HABITAT. *Macrophallikoropa belli* is a wide ranging species inhabiting a range of forest types from dry sclerophyll to rainforest on limestone, volcanics and sandstone; found living under logs and rocks.

REMARKS. *Macrophallikoropa belli* (Cox, 1864) comb. nov. is sympatric with *M. depressispira* sp. nov. at the Jenolan Caves limestone locality but can be distinguished from that species by its smaller size, less open umbilicus and flatter spire. *M. belli* differs from *M. stenoumbilicata* sp. nov. by its smaller size and more open umbilicus.

M. belli is readily distinguished from other co-habiting charopids through a combination of very small size, spiral protoconch, strongly curved, narrow and very crowded radial ribs, wide cup-shaped umbilicus and the lack of apertural lamellae. Some *Rhophodon* spp. are similar in general shell form (shape, teleoconch ribbing and umbilical width) but are distinguished by having radially ribbed protoconchs and apertural lamellae. *Decoriropa lirata* (Cox, 1864) comb. nov. also has a small discoidal shell with wide umbilicus but has a radial protoconch and widely spaced, bold ribs on the teleoconch. Anatomically the long penial apparatus of *M. belli* is unusual among the eastern Australian Charopidae and hitherto

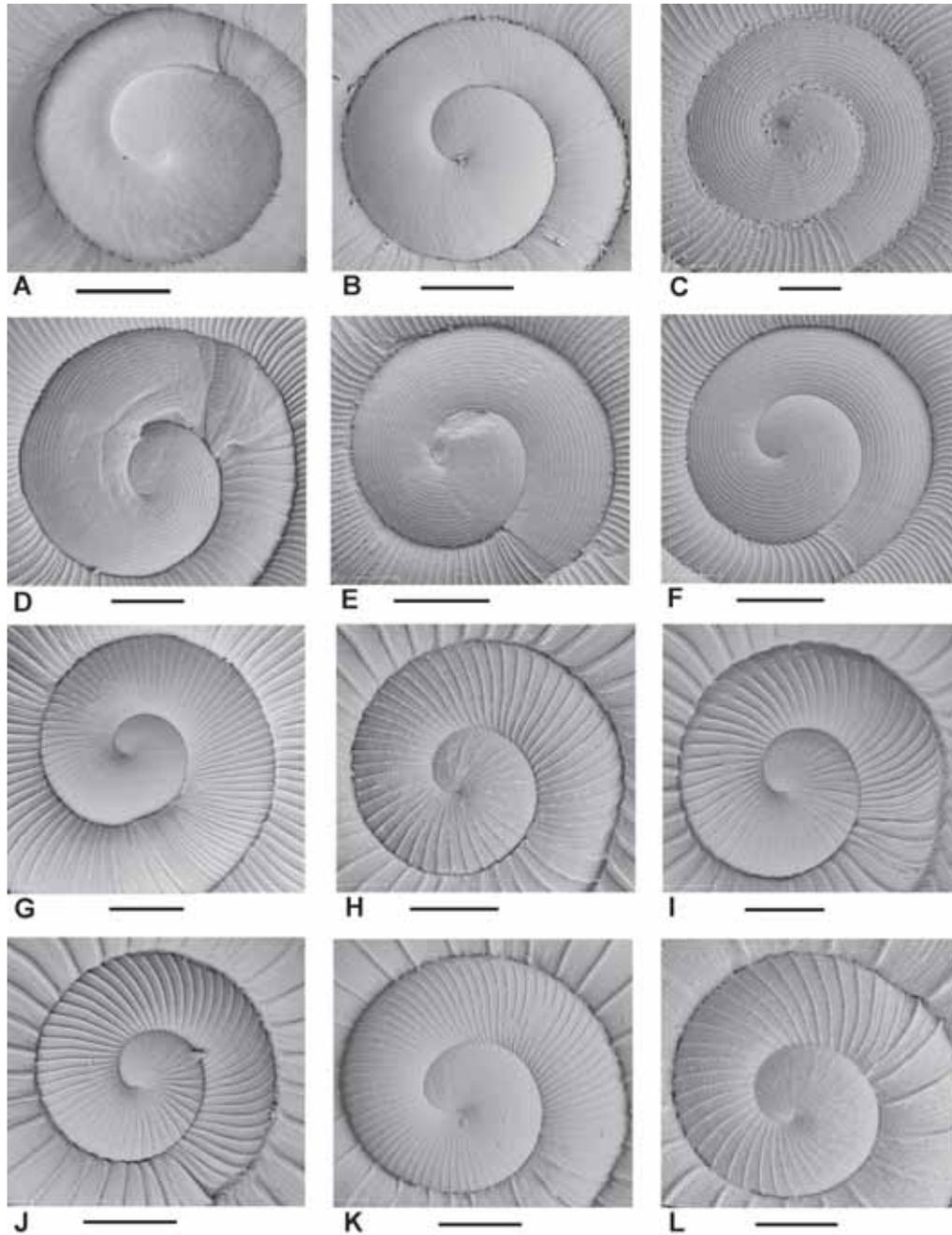


FIG. 15. Protoconch of shells from above. A, *Letomola contortus*, AMSC119349. B, *Letomola lanalittleae*, QMMO70397. C, *Macrophallikoropa belli* (Sydney), AMSC171336. D, *Macrophallikoropa belli* (Mt Warning), QMMO10512. E, *Macrophallikoropa stenoumbilicata*, AMSC205162. F, *Macrophallikoropa depressispira*, AMSC205163. G, *Elsothera brazieri*, QMMO28775. H, *Decoriropa lirata* (Taree), AMSC135842. I, *Decoriropa lirata* (Kempsey), QMMO52755. J, *Decoriropa lirata* (Wombeyan Caves), QMMO64764. K, *Coricudgia wollemiana*, AMSC205164. L, *Marilyniropa jenolanensis*, AMSC205165. Scale bars=0.15mm in A, E, F, H, I; 0.1mm in C, D; 0.2mm in B, G, J-L.

matched only by that of *Rotacharopa densilamellata* Stanisc, 1990. Stanisc (1990) suggested that in the case of *Rotacharopa* this development was organ elongation in response to a marked increase in whorl numbers from the clade average. However, this is not the case in *M. belli* where whorl numbers are fairly similar to both *M. stenoumblicata* and *M. depressispira* that lack this condition. It could be that this elongated condition is a retained ancestral feature. From a practical viewpoint it is difficult to understand how the penial apparatus could function as an eversible organ.

M. belli is a relatively widespread species in the context of eastern Australian charopids, especially for a species that inhabits moist rainforest. *Discocharopa aperta* (Mollendorff, 1888) has a wider distribution (Solem, 1989) than *M. belli* but that species also shows a greater environmental adaptability in preferring drier habitats such as deciduous vine thickets. But while *M. belli* distribution is largely restricted to wetter environments these do cross a wide range of floristic and geological boundaries, from sclerophyll forest to rainforest and through basalt, limestone and sandstone landscapes. *M. belli* has a significant presence in the Sydney Basin Bioregion where it persists in quite marginal habitats (e.g. Sydney Botanic Gardens) thereby also implying an inherent adaptability. That *M. belli* has been able to disperse into and adapt to this broad set of habitats across a wide geographic area indicates that the species has a long temporal history. In spite of the large amount of material in the AM and QM, few of these specimens are adult. Adult specimens are readily identifiable by the more rapid descension of the last whorl, which effectively elevates the remainder of the shell's spire. Hence, the shell datasets do not allow any rigorous analysis of geographic trends in shell variation. Of the specimens measured those from Marble Arch were distinctive in displaying a slightly more elevated spire and a more closed umbilicus.

Not all available material in the AM and QM has been listed herein. The listing is meant to be a guide to significant datasets, general distribution and key localities for the species. Additional lots, in many cases containing 1-3 specimens and duplicating many of the listed localities, are held in the AM and QM. The sheer quantity of material is a poignant indication of the widespread distribution of *M. belli* compared with other species discussed herein.

***Macrohallikoropa stenoumblicata* sp. nov.**
(Figs 9-12, 14-18; Table 3)

ETYMOLOGY. Greek *stenos*, narrow and Latin *umbilicus*; referring to the relatively narrow umbilicus.

MATERIAL. All NSW. HOLOTYPE: AMSC205162, Mt Coricudgy, E Rylstone, southern slope (32°50.82'S, 150°2'E), in litter off road, 2.x.1983, PHC. Height of shell=1.03mm, diameter=1.92mm, H/D=0.54, D/U=3.20, number of whorls=4.2, ribs on last whorl=197. PARATYPES: AMSC162008, 12RC, same data as holotype; AMSC162007, 2RC, Mt Coricudgy, E Rylstone, Hanging Swamp (32°50.2'S, 150°21.2'E), in litter, 2.x.1983, PHC; QMMO28661, 4SC/3RC, slopes of Mt Coricudgy, W of Rylstone (32°51'S, 150°21'E), under logs, temperate rainforest, 15.i.1990, JS, JC; QMMO44706, 1RC, summit, Mt Coricudgy, N Rylstone (32°49'48"S, 150°20'24"E), under rocks, remnant rainforest, 10.i.1993, JS, JC. OTHER MATERIAL. All NSW. QMMO44716, MO44724, MO59873, MO59860.

DIAGNOSIS. Shell minute, golden brown to very light golden brown, sometimes with darker flammulations; whorls tightly coiled. Spire and apex slightly elevated, protoconch with crowded spiral lirae. Teleoconch with almost straight, very crowded ribs. Umbilicus wide U-shaped, mean D/U 3.11. Penial verge absent; moderately long preputial tube present, epiphallus moderately long.

DESCRIPTION. Shell minute, light to golden brown (occasionally with darker flammulations), with 4.0-4.7 (mean 4.33) tightly coiled whorls, the last descending more rapidly in front. Sutures strongly impressed, whorls evenly rounded above and below the periphery. Shell diameter 1.61-1.22mm (mean 1.95mm). Apex and early spire slightly elevated. Height of shell 0.77-1.19mm (mean 1.00mm), H/D 0.48-0.54 (mean 0.51). Protoconch slightly exsert, of 1.5-1.8 whorls. Apical sculpture of crowded, narrow spiral lirae; number of lirae 17. Secondary apical sculpture of discontinuous radial ridglets that may be periostracal pressure folds. Teleoconch sculpture of very crowded, weakly protractively sinuated radial ribs; 147-197 (mean 171) ribs on the last whorl. Ribs/mm 26.43-32.66 (mean 28.94). Ribs narrow; height equal to width; straight in section, rounded on top. Rib interstices on the first post-nuclear whorl equal to width of three to four major ribs. Interstitial sculpture of fine radial riblets and spiral cords, about equal in strength. Microradials low, forming prominent, elongate beads at their intersection with the microradials. Umbilicus wide U-shaped, diameter 0.53-0.73mm (mean 0.63mm), D/U 3.04-3.20 (mean 3.11). Aperture ovately lunate. Based on 6 measured adults (AMSC162008, C205162).

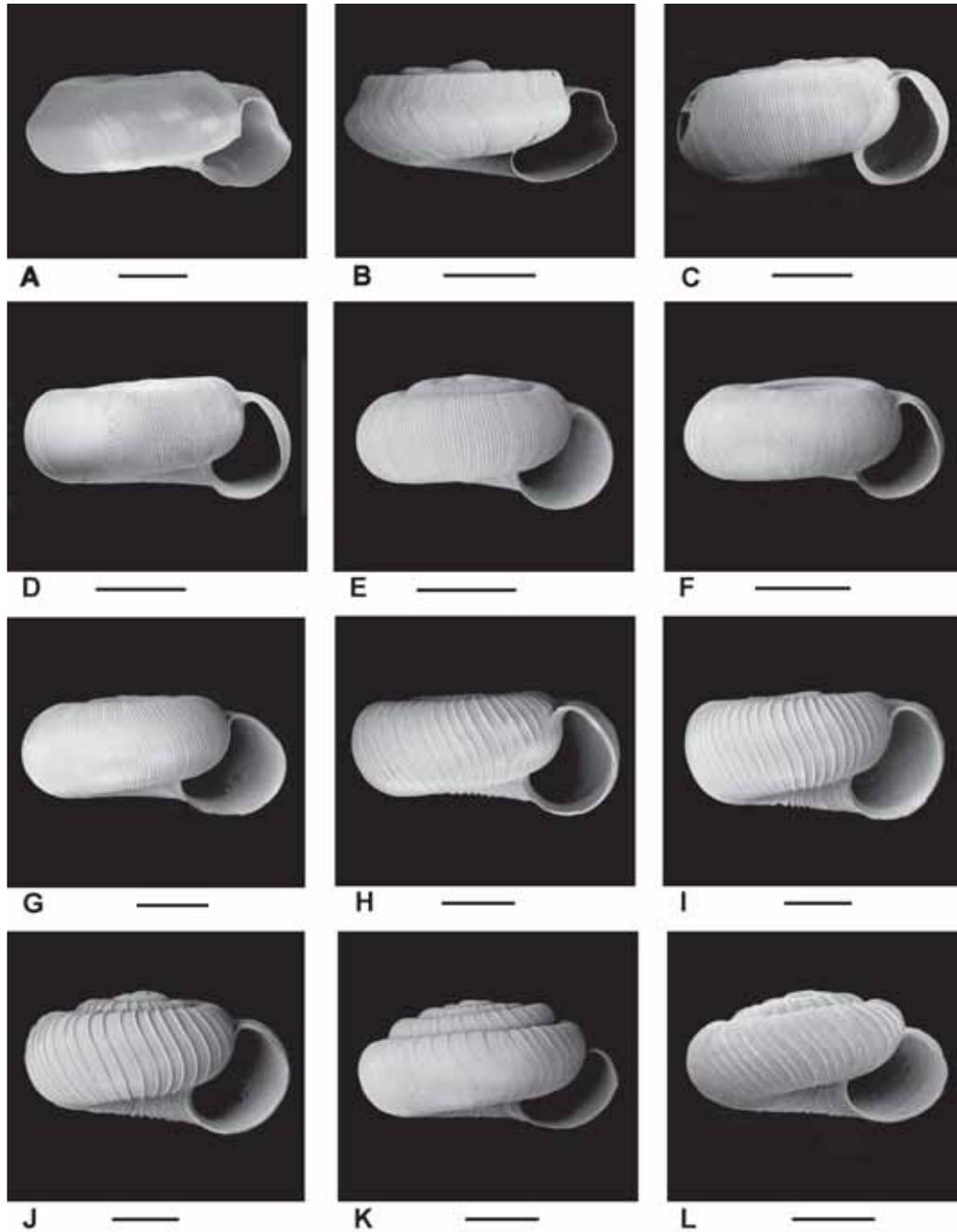


FIG. 16. Lateral view of shells. A, *Letomola contortus*, AMSC119349. B, *Letomola lanalittleae*, QMMO70397. C, *Macrophallikoropa belli* (Sydney), AMSC171336. D, *Macrophallikoropa belli* (Mt Warning), QMMO10512. E, *Macrophallikoropa stenoumbilicata*, AMSC205162. F, *Macrophallikoropa depressispira*, AMSC205163. G, *Elsothera brazieri*, QMMO28775. H, *Decoriropa lirata* (Taree), AMSC135842. I, *Decoriropa lirata* (Kempsey), QMMO52755. J, *Decoriropa lirata* (Wombeyan Caves), QMMO64764. K, *Coricudgia wollemiana*, AMSC205164. L, *Marilyniropa jenolanensis*, AMSC205165. Scale bars=0.5mm in A, C, D, H-J; 0.8mm in E, F; 1mm in B, G, K, L.

Genitalia with ovotestis containing two clumps of alveoli; with two alveolar lobes per clump. Talon stalk shorter than talon; talon circular. Epiphallus moderately long, shorter than penis; wider than the vas deferens, entering penis through a simple pore. Penial retractor muscle inserted on head of penis. Penis tubular, internally without any visible thickenings; moderately long preputial tube present. Vagina shorter than penis, without unusual features.

Kidney bilobed with apex of pericardial lobe weakly reflexed.

Radular morphology unknown.

Based on 3 dissected adults (QMMO42150, MO28661).

DISTRIBUTION AND HABITAT. *Macrophallikoropa stenoumbilicata* sp. nov. is known from rocky refugia on and in the vicinity of Mt Coricudgy at the northern end of the Wollemi NP; found living under logs and rocks in remnant rainforest and eucalypt forest.

REMARKS. The shell of *Macrophallikoropa stenoumbilicata* sp. nov. is larger in size than that of *M. belli*, and has a smaller umbilicus (wide U-shaped), slightly more elevated spire and radial ribs that are only weakly protractively sinuated. Anatomically *M. stenoumbilicata* differs from *M. belli* by lacking a penial verge, having a longer epiphallus and shorter preputial tube. *M. stenoumbilicata* differs from *M. depressispira* sp. nov. by having a smaller shell with more elevated spire (rather than flat to slightly elevated) and an umbilicus that is less excavate (wide saucer-shaped in *M. depressispira*).

M. stenoumbilicata is confined to the northern end of the Wollemi NP which is characterised by basalt capped peaks that are scattered among a landscape of Narrabeen sandstone. These peaks support rainforest and wet sclerophyll forest near their summits and southeastern aspects and were probably critical refugia for the survival of this species during the drier climatic phases of the Plio-Pleistocene. Much of this area still needs to be investigated in order to determine the full extent of the species range.

Macrophallikoropa depressispira sp. nov.
(Figs 12, 14-17, 33-34; Table 3)

ETYMOLOGY. Latin *depressus*, low and *spira*, spire; referring to the depressed spire.

MATERIAL. All NSW. HOLOTYPE: AMSC205163, Jenolan Caves, E side Grand Arch near Blue Lagoon, near Devils Coach house (33°49.3'S, 150°1.6'E), in litter,

among rocks and grass, 11.xii.1979, WFP, JS. Height of shell=1.14mm, diameter=2.21mm, H/D=0.52, D/U=ratio 2.60, number of whorls=5.0, ribs on last whorl=293. PARATYPES. AMSC124275, many RC, same data as holotype; AMSC63771, 1RC, Jenolan Caves, same data as holotype; QMMO9699, many RC, Jenolan Caves, entrance to the Devils Coachhouse, litter, 13.xii.1979, JS.

DIAGNOSIS. Shell minute, golden brown to very light golden brown, with tightly coiled whorls. Spire concave, protoconch with crowded spiral lirae. Teleoconch with very crowded radial ribs. Umbilicus very wide saucer-shaped, mean D/U 2.57. Anatomy unknown.

DESCRIPTION. Shell minute, golden brown with 4.6-5.2 (mean 4.96) tightly coiled whorls, the last descending more rapidly in front. Sutures weakly impressed, whorls evenly rounded above and below periphery. Shell diameter 1.97-2.37mm (mean 2.16mm) Spire depressed (concave). Height of shell 0.90-1.14mm (mean 1.06mm), H/D 0.46-0.52 (mean 0.49). Protoconch slightly exsert of 1.6-1.8 whorls. Apical sculpture of crowded, narrow spiral lirae; number of lirae 13. Secondary apical sculpture of discontinuous radial ridglets that may be periostracal pressure folds. Teleoconch sculpture of crowded, weakly protractively sinuated radial ribs; 165-293 (mean 222) ribs on the last whorl. Ribs/mm 37.97-26.39 (mean 28.94). Ribs narrow, height equal to width; straight in section; rounded on top. Rib interstices on the first post-nuclear whorl equal to width of two to three ribs. Rib interstices sculptured with low radial ridges and low microspirals forming elongate to round beads where they intersect. Microradials between ribs on first postnuclear whorl 3; between ribs on penultimate whorl 2-4. Umbilicus very wide saucer shaped, diameter 0.76-0.91mm (mean 0.84mm), D/U 2.34-2.72 (mean 2.57). Aperture ovately lunate; parietal callus present. Based on 19 measured adults (AMSC124275, C205163, C124275).

Anatomy unknown.

DISTRIBUTION AND HABITAT. *Macrophallikoropa depressispira* sp. nov. is known only from the type locality at Jenolan Caves; found in litter collected from among limestone rocks.

REMARKS. *Macrophallikoropa depressispira* sp. nov. differs from both *M. belli* and *M. stenoumbilicata* in having a larger shell with depressed spire (rather than flat to slightly elevated) and an umbilicus that is more excavate

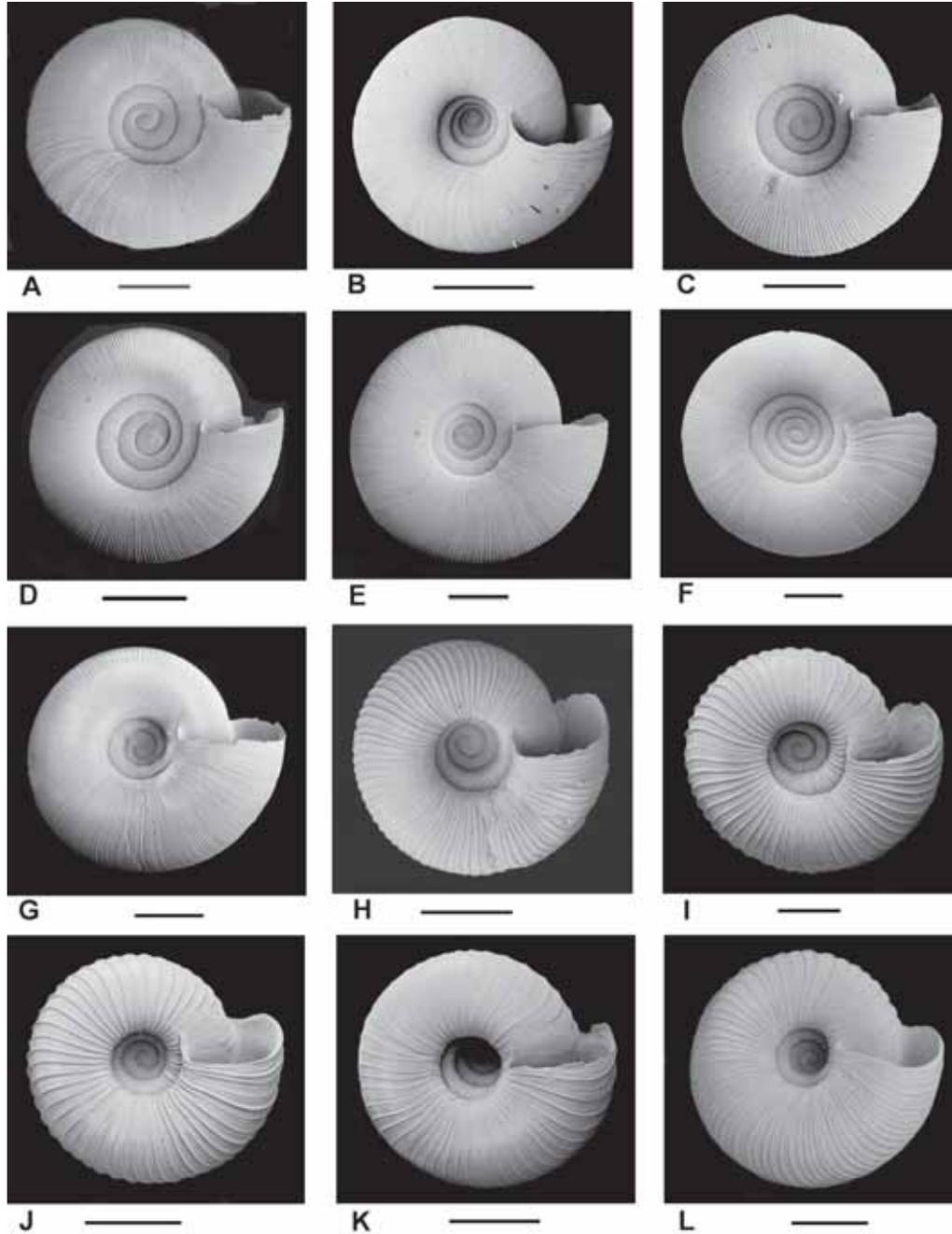


FIG. 17. Ventral view of shells. A, *Letomola contortus*, AMSC119349. B, *Letomola lanalittleae*, QMMO70397. C, *Macrophallikoropa belli* (Sydney), AMSC171336. D, *Macrophallikoropa belli* (Mt Warning), QMMO10512. E, *Macrophallikoropa stenoumbilicata*, AMSC205162. F, *Macrophallikoropa depressispira*, AMSC205163. G, *Elsothera brazieri*, QMMO28775. H, *Decoriropa lirata* (Sydney), AMSC427984. I, *Decoriropa lirata* (Kempsey), QMMO52755. J, *Decoriropa lirata* (Wombeyan Caves), QMMO64764. K, *Coricudgia wollemiana*, AMSC205164. L, *Marilyniropa jenolanensis*, AMSC205165. Scale bars=0.5mm in A, C-F, I; 0.8mm in H, J; 1mm in B, G, K, L.

(wide saucer-shaped). It can be readily distinguished from other sympatric charopids by its protoconch features.

There has been considerable land snail collecting undertaken in the Blue Mountains area and Jenolan Caves area in particular, suggesting that the distribution is accurate and that this species is a true, narrow limestone endemic. No live material of *M. depressispira*, which could be critical to a better understanding of character shifts within the genus, has yet been collected.

Elsothera Iredale, 1933

Elsothera Iredale, 1933: 53; Iredale, 1937: 324; Iredale, 1941a: 267; Kershaw, 1956a: 140; Burch, 1976b: 132; Staniscic, 1990: 160; Smith, 1992: 187; Staniscic, 1996: 345.

Allocharopa Iredale, 1937: 326; Iredale 1941a: 269; Kershaw, 1956a: 141; Burch, 1976b: 132; Smith, 1992: 181.

TYPE SPECIES. *Helix sericatula* Pfeiffer, 1850; by original designation.

DIAGNOSIS. Shell very small with evenly to loosely coiled whorls. Colour greyish brown with darker streaks or monochrome brown. Protoconch sculpture of thin, regularly spaced, curved radial ribs (sometimes absent) and with prominent to very weak, sometimes discontinuous, microspiral cords. Teleoconch with crowded to moderately widely spaced, protractively sinuated radial ribs. Microsculpture of bladed microradial ribs crossed by low microspiral cords; prominent beads formed at their intersection. Umbilicus ranging from widely open to closed. Epiphallus and vas deferens long and strongly coiled about penial retractor muscule and/or penis. Penis with numerous longitudinal pilasters.

DISTRIBUTION AND HABITAT. *Elsothera* Iredale, 1933 is widespread through central western Qld to eastern and central western NSW, Victoria and eastern South Australia. Records of the genus from Tasmania (Smith & Kershaw, 1979; 1981) need to be verified; living under rocks and logs in wet and dry sclerophyll forest, vine thickets and open eucalypt woodland.

REMARKS. In dealing with *Macrophallikoropa belli* (Cox, 1864) comb. nov. it became apparent that *Allocharopa* Iredale, 1937 was polyphyletic. The mixture of species placed here by Iredale (1937) comprised some with primarily radially ribbed protoconchs (sometimes accompanied by a secondary spiral sculpture) and some, such as *M. belli*, which had strong spiral lirae. While a

review of all the 'radially ribbed' species is beyond the scope of this study a cursory study of the type of *Allocharopa* (= *Helix brazieri* Cox, 1868) revealed that it has significant characters (shell and anatomy) in common with *Elsothera*. In particular the protoconch sculpture and unusual epiphallic coiling were similar to *E. sericatula* which is sympatric with the former in the Sydney Basin. These characters are also shared with *E. hewittorum* Staniscic, 1996 from the Qld Brigalow Lands. On these shared characters *H. brazieri* is reassigned to *Elsothera* and *Allocharopa* is relegated to synonymy with *Elsothera*.

In as much as *Helix brazieri* (Cox 1868) is placed in *Elsothera* Iredale 1933 it should be noted that as currently defined (Smith, 1992) this genus probably is polyphyletic and the generic diagnosis herein should be regarded as tentative. The protoconch sculpture within the genus comprises several distinct forms including crowded curved radials with weak, sometimes discontinuous microspiral wrinkles (pressure folds) as seen in in *E. brazieri* (Cox, 1868) comb. nov. and *E. sericatula* (Pfeiffer, 1850); curved radials with distinct continuous, crowded microspiral cords (*E. nautilodea*); and crowded microspiral cords with weak to obsolete microradials (*E. hewittorum* Staniscic, 1996, *E. funerea* (Cox, 1868). In the case of *E. genithecata* Staniscic, 1990 the radial ribs are stronger and more widely spaced and this species may yet be shown to belong to another clade (Staniscic, 1990; 1996; unpubl. data). There is also a considerable variation in shell colour within the genus ranging from grey to greyish brown with darker radial flecks to all brown. *Elsothera* requires revision but this is beyond the scope of this study. A key character that appears to bind the group is the extensive coiling of the epiphallus which in the case of *E. brazieri* is coiled around the penis. This feature has not been seen in any other eastern Australian charopid genus but because of the comparative dearth of anatomical studies within the group, its phylogenetic significance has yet to be fully determined.

Elsothera brazieri (Cox, 1868) comb. nov. (Figs 10, 14-18, 20-22, 33-34; Table 3)

Helix brazieri Cox, 1868: 14.

Endodonta (*Charopa*) *brazieri* (Cox). Cox, 1909: 13.

Allocharopa brazieri (Cox). Iredale, 1937: 326; Iredale 1941a: 269, fig. 6 (part); Kershaw, 1956a: 141; Smith & Kershaw, 1979: 161; Smith, 1992: 181.

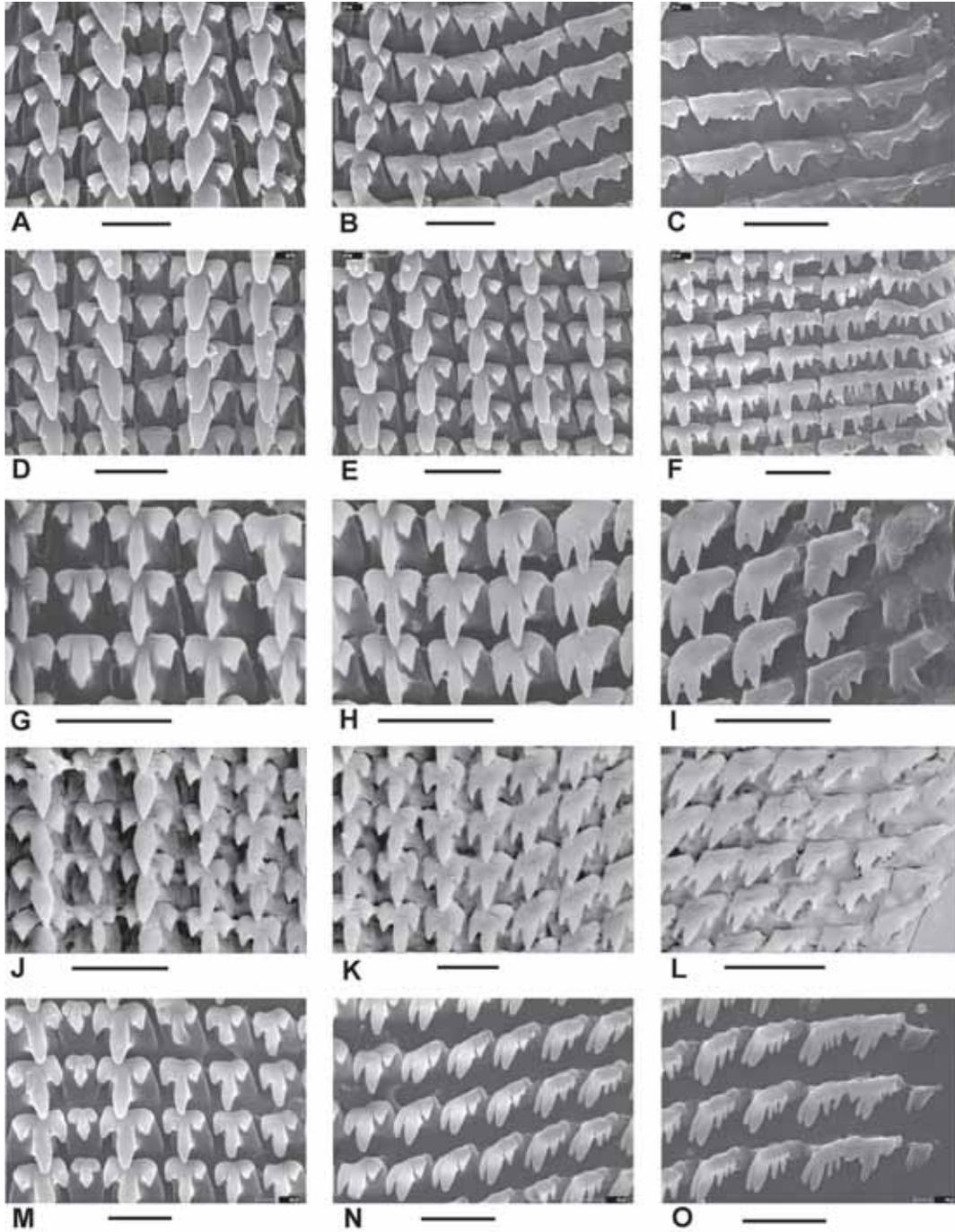


FIG. 18. Radula. A-C, *Letomola contortus*, QMMO56119. D-F, *Letomola lanalittleae*, QMMO56007. G-I, *Macrophallikoropa belli*, QMMO16867. J-L, *Elsothera brazieri*, QMMO44810. M-O, *Decoriropa lirata*, QMMO29722. Scale bars=0.01mm in A-I, M-O; 0.02mm in J-L.

MATERIAL. HOLOTYPE. AMSC63498, Cooks River, Sydney S (33°55'S, 151°70'E), under stones in dry places, 1868, J. Brazier. Height of shell=1.69mm, diameter=3.43mm, H/D=0.49, D/U=3.46, whorls=4.4, ribs on last whorl=138. KEY MATERIAL. All NSW. QMMO44810, SSC, Blue Mountains NP, Federal Pass, Echo Pt-Scenic Rwy, Katoomba, 33°44'06"S, 150°38'42"E, wt6rf/ro, under logs and rocks, 16.i.1993, JS, JC; QMMO28775, 2SC/7RC, Jenolan Caves (33°49'S, 150°01'E), lm, under rocks, 09.i.1990; JS, JC. OTHER MATERIAL. All NSW. Sydney Basin. AMSC159053, C174614, C346733, C348657, C368692, C109350, C154914, C154917, C154926, C318526, C319927, C319931, C319932, C319933, C319934, C319935, C319936, C319937, C319938, C319939, C346810, C148111, C346819, C367089, QMMO16940, MO28668, MO42139, MO42143, MO44782, MO71653, MO34741, MO71657.

DIAGNOSIS. Small very small with evenly coiled whorls. Protoconch with curved, crowded radial ribs that become more crowded at the protoconch/teleoconch boundary and weaker, sometimes discontinuous spiral cords. Teleoconch sculpture of numerous, crowded and prominent curved radial ribs, mean ribs/mm 15.32. Microsculpture of strongly bladed microradial ribs and low, crowded microspiral cords with beads formed at their intersection. Umbilicus wide V-shaped, mean D/U 3.58. Epiphallus long and coiled around penial retractor muscle and basal part of penis. Penis internally with five longitudinal pilasters.

DESCRIPTION. Shell very small, greyish brown in colour with darker radial streaks, 3.8-4.4 (mean 4.17) evenly coiled whorls. Shell diameter 2.72-3.99mm (mean 3.37mm). Spire flat. Height of shell 1.64-1.94mm (mean 1.80mm), H/D 0.49-0.58 (mean 0.52). Protoconch of 1.5-1.8 whorls with primarily radial sculpture consisting of 80-90 regularly spaced, weakly curved radial ribs that become more crowded at the protoconch/teleoconch boundary and very weak, low regularly spaced spiral lirae that cross the radial ribs. Ribs wide, height less than width; spacing uniform; width of interstices (in multiples of rib width) 4-5 at apex. Teleoconch sculpture of bold, protractively sinuated, crowded radial ribs; 136-206 (mean 162) ribs on the last whorl, ribs/mm 13.70-17.96 (mean 15.30). Ribs medium in size height greater than width, straight in section, rounded on top. Rib interstices on the first post-nuclear whorl equal to width of 6-8 ribs; interstices on the penultimate whorl equal to width of 6-7 ribs. Microsculpture of low microradial ribs and stronger microspiral cords that cross the

microradials and form strong elongate to round beads at their intersection. Microradials low; 6-8 between ribs on first postnuclear whorl; 10-12 between ribs on penultimate. Umbilicus wide V-shaped, diameter 0.80-1.31mm (mean 0.97mm), D/U 3.05-4.04 (mean 3.57). Sutures weakly impressed, whorls rounded above and rounded below a rounded periphery. Aperture roundly lunate, parietal callus present. Based on 10 measured specimens (QMMO28775, AMSC63498).

Genitalia with ovotestis containing 2 clumps of alveoli; with more than 2 alveolar lobes per clump. Talon stalk narrower than talon diameter; talon circular. Penial retractor inserting onto the penis head. Epiphallus longer than penis, coiled around basal part of penial retractor muscle and basal part of the penis; wider than the vas deferens. Penis tubular internally with numerous longitudinal pilasters.

Pallial cavity with kidney very weakly bilobed; apex slightly reflexed.

Radula with central tooth strongly tricuspid and smaller than the first lateral; lateral teeth tricuspid.; Ectocone of outer marginal teeth split into four or more teeth; endocone not split. Number of lateral teeth: 4, marginal teeth: 8; radular rows: 85. Based on 2 dissected specimens (QMMO44810).

DISTRIBUTION AND HABITAT. *Elsothera brazieri* is known only from the Sydney Basin and the northern part of the SE Highland Bioregions; living under logs and rocks in temperate rainforest and wet and dry sclerophyll forest.

REMARKS. *Elsothera brazieri* is micro-sympatric with *E. sericatulata* (Pfeiffer, 1850) but is distinguished by having a widely open rather than closed umbilicus, having the radial ribs more widely spaced (coarser sculpture) and in having the epiphallus more strongly coiled and twisted around the penis. *Diphyoropa saturni* (Cox, 1864) comb. nov., which is also widely sympatric with *E. brazieri* in the Sydney Basin, may be confused with the latter judging by identifications on existing museum material. However, *D. saturni* is readily distinguished by the bolder, more widely separate ribs on the teleoconch and in having a protoconch with a bimodal sculpture wherein initial spirals give way to radial ribs and ridges on the latter part of the embryonic whorls. Anatomically, *D. saturni* lacks the coiled epiphallus of *Elsothera* spp.

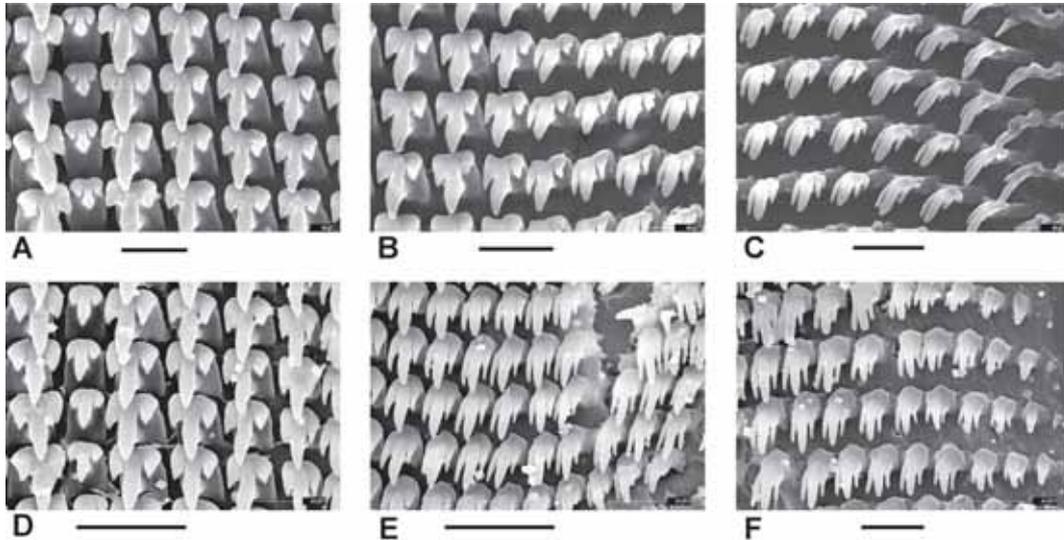


FIG. 19. Radula. A-C, *Coricudgia wollemiana*, QMMO28659. D-F, *Marilyniropa jenolanensis*, QMMO37465. Scale bars=0.01 in A-C, F; 0.02mm in D,E.

Most of the *Elsothera* group have an open umbilicus. *E. nautilodea* (Cox, 1866) and *E. genithecata* Stanisc, 1990 from NE NSW and *E. sericatula* from the Sydney Basin are exceptions. In the present case the major shift in umbilical width from closed in *E. sericatula* to widely open in the *E. brazieri* may be linked to underlying species recognition changes that have occurred under conditions of congeneric sympatry.

Also *E. brazieri* appears to be less abundant in the field than the sympatric *E. sericatula* based on the quantity of material in museum collections. Reasons for this are not immediately obvious.

Egilomen Iredale, 1937

Egilomen Iredale, 1937: 328; Iredale, 1941a: 267, 269; Kershaw, 1955: 29; Burch, 1976b: 132; Stanisc, 1990: 193; Smith, 1992: 187.

TYPE SPECIES. *Helix cochlidium* Cox 1868; by original designation.

DIAGNOSIS. Shell very small, colour white. Protoconch with relatively widely spaced, very bold, slightly curved radial ribs (approx. 30) that do not become more crowded, even at the protoconch/teleoconch boundary; spiral elements vague, consisting of discontinuous periostracal wrinkles (?=pressure folds). Teleoconch with broad, widely spaced, weakly protractively sinuated radial ribs; secondary sculpture of prominent crowded, low microspirals and relatively less prominent microradials

ribs that form strong beads at their intersection. Umbilicus moderately wide U-shaped. Anatomy unknown.

DISTRIBUTION AND HABITAT. *Egilomen* is restricted to the Clarence and Richmond River drainages in NE NSW. However, it would not be surprising if the range of the genus is extended beyond this area. Material in the collections of the QM from the Macleay Valley, NE NSW, appears to fall within *Egilomen* based on protoconch characters (Stanisc, unpubl. data). *Egilomen* prefers dry subtropical rainforest among litter and rocks; historical records suggest that it can also be found in riparian environments.

REMARKS. *Egilomen* was introduced by Iredale (1937) for Charopidae that had a wide umbilicus, smooth protoconch and radial ribs on the teleoconch. *Helix cochlidium* Cox, 1868, as type; *H. lirata* Cox, 1864, *H. barrenense* Pettard, 1879, *H. pexum* Cox, 1868 and *H. saturni* Cox, 1864 were included. However, species included here by Iredale do not have smooth protoconchs and in fact cover an assortment of protoconch sculptures ranging from bold radial ribs, to radial ribs crossed by spiral cords and in one case a uniquely bimodal pattern of spiral and radial elements (*H. saturni*). Stanisc (1990), on the basis of limited comparative material, redefined *Egilomen* to include taxa with a protoconch sculpture of prominent radial ribs with spiral

elements reduced or absent and a teleoconch sculpture of bold radial ribs. Anatomically, the defining features were a strongly bilobed kidney and one longitudinal penis pilaster with an accessory circular pad. Stanisc (1990) included only the type and a new species, *E. globosa*. Although not reviewed, Stanisc (1990) suggested that most other species included in *Egilomen* by Iredale (1937) belonged elsewhere.

A redefinition of *Egilomen* was considered necessary in order that other taxa dealt with herein could be placed into appropriate taxonomic context. During the course of this study it became apparent that Stanisc's (1990) interpretation of *Egilomen*, and in particular *E. cochlidium*, was somewhat expansive. In addition, closer inspection of the protoconchs of the types of both *E. cochlidium* and *E. globosa* revealed differences indicating that these two species are generically distinct on the basis of discriminatory criteria used in the current study. Hence, *Egilomen* is herein once again redefined and restricted to include only the type. Revised diagnoses of both *Egilomen* and *E. cochlidium* are presented together with a revised list of 'material studied' for the latter species. Consequently, the distribution of *E. cochlidium* is herein restricted to include only the region surrounding the Richmond and Clarence River drainages. *E. globosa* is not able to be placed in any existing genus and hence is herein reassigned to *Whiteheadia* gen.nov. Two additional species, *H. lirata* and *H. saturni*, previously placed here by Iredale (1941a), are also reviewed and generically re-assigned. *H. pexa* and *H. barrenense* are not considered to belong to any of these groupings but their re-allocation must await further study.

The protoconch of *Egilomen* Iredale, 1937 has bold, widely spaced ribs and vague, discontinuous spiral creases (=pressure folds?). Most significantly however, the ribs on the protoconch show no tendency to become more crowded toward the protoconch/teleoconch boundary. This is a characteristic of many local charopid genera that have radial elements on the protoconch and usually provides a convenient means for locating the nuclear/post-nuclear transition point. This boundary is less easily distinguished in the case of *Egilomen* wherein the apical rib spacing is confluent with the teleoconch rib spacing. In both *E. cochlidium* and *Whiteheadia globosa* (Stanisc, 1990) comb. nov. the spiral elements on the protoconch that are visible at low magnification consist of irregularly

spaced, periostracal wrinkles that do not cross the radial elements. However, and most significantly, the latter species has much more crowded radials on the protoconch, and the protoconch-teleoconch boundary is more apparent because the denser apical ribbing contrasts clearly with the more widely spaced teleoconch teleoconch. This is considered to represent a generic level difference between the two species. *W. globosa* also differs significantly from *E. cochlidium* in having a partially thickened lip and closed umbilicus.

The shell of *Egilomen* (bold teleoconch ribs and open umbilicus) is most similar to that of *Decoriropa* gen. nov. but the latter has distinct, continuous apical spiral cords and finer, much more crowded apical ribs. *Decoriropa* has shell whorls of a similar profile to that of *Egilomen* but has the umbilicus more widely open and a weak sutural sinus. The absence of apertural barriers readily separates *Egilomen* from both *Rhophodon* and *Egilodonta*, which also have similarly shaped, though much smaller and more widely umbilicate shells (cup to saucer shaped).

The difficulty in dealing with this genus highlights the general problems posed by the availability of very limited material of a series of very tiny species with radially sculptured white shells (Stanisc, unpubl. data). Many are represented by only a few dry specimens, a direct consequence of relying on 'litter-sorting' for recovery of material without having located the species' true microhabitat. Such constraints will need to be overcome before a comprehensive revision of this group can be completed.

***Egilomen cochlidium* (Cox, 1868)**
(Fig. 13; Table 3)

Helix cochlidium Cox, 1868: 13, pl. 8, fig. 1.

Egilomen cochlidium (Cox). Iredale, 1937: 138; Iredale, 1941a: 269; Smith 1992: 187; Stanisc, 1990: 103 (in part), fig. 128a-c, e-g (only).

MATERIAL. LECTOTYPE. AMSC63505, Clarence River, NSW. Height of shell=1.25mm, diameter=2.26mm, H/D=0.55, D/U=3.14, whorls=4.5, ribs on last whorl=30. PARALLECTOTYPES. AMSC153714, 2RC, same collection data as lectotype. OTHER MATERIAL. All NSW. AMSC57247, C8737, C152253, C153715, C154732, QMMO56176.

DIAGNOSIS. Shell white, very small, with regularly coiled whorls, mean whorl count 4.5. Apex and early spire flat to weakly elevated, mean H/D 0.55. Teleoconch with broad, widely spaced, weakly protractively sinuated radial ribs,

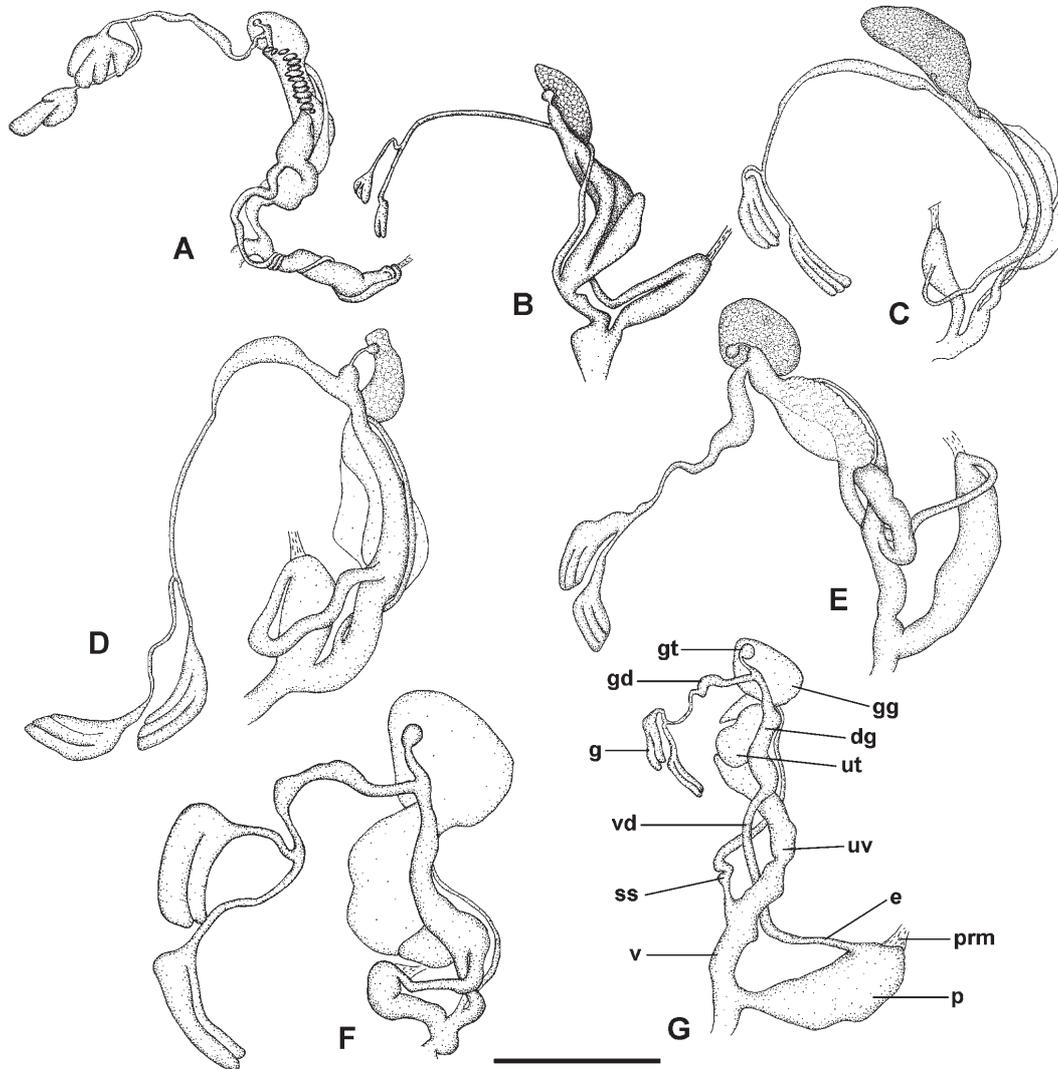


FIG. 20. Reproductive system. A, *Elsothera brazieri*, QMMO44810. B, *Decoriropa lirata*, QMMO42109. C, *Coricudgia wollemiana*, QMMO28659. D, *Marilyniropa jenolanensis*, QMMO37465. E, *Cralopa stroudensis*, QMMO29722. F, *Gouldiropa carlessi*, QMMO32080. G, *Gouldiropa kaputarensis*, QMMO49175. Scale bar=2.5mm in A, C and G, and 1.6mm in all others. Abbreviations: dg, prostate; e, epiphallus; g, ovotestis; gd, hermaphrodite duct; gg, albumen gland; gt, talon; p, penis; prm, penis retractor muscle; ss, spermathecal stalk; ut, uterus; uv, free oviduct; v, vagina; vd, vas deferens.

mean ribs/mm 5.57. Umbilicus moderately wide U-shaped, mean D/U 2.85. Anatomy unknown.

DESCRIPTION. (Amended from Stanisc, 1990). Shell very small, white to light straw yellow, with 4.0-5.1 (mean 4.5) evenly coiled whorls, the last descending in front. Shell diameter 1.91-3.07mm (mean 2.20mm). Apex

and early spire flat to slightly elevated. Height of shell 0.95-1.83mm (mean 1.26mm). H/D 0.49-0.61 (mean 0.55). Protoconch flat of 1.5-1.6 whorls. Apical sculpture of slightly curved, relatively widely spaced, broad radial ribs (approx 30), that do not become more crowded at the protoconch/teleoconch boundary; apical spiral elements vague, consisting of discontinuous

periostracal wrinkles (? = pressure folds). Teleoconch with bold, broad, widely spaced, protractively sinuated radial ribs, 30-47 (mean 37) ribs on the last whorl. Ribs/mm 4.22-5.99 (mean 5.07). Interstitial sculpture of prominent crowded, low microspirals cords and relatively less prominent microradial ribs that form strong beads at their intersection. Microradial riblets low, 8-12 between each pair of major ribs. Umbilicus moderately wide U-shaped, diameter 0.60-1.03mm (mean 0.82mm). D/U 2.59-3.47 (mean 2.85). Sutures strongly impressed. Whorls flattened below and rounded above a laterally compressed periphery. Aperture ovately lunate, lip simple. Based on 14 measured specimens (AMSC63505, C153714, C8737, C57247, C153715).

REMARKS. Stanisic's (1990) description of *E. cochlidium* included specimens from the Dorrigo area, NE NSW and the Border Ranges of NE NSW and SE Qld that had white shells with radially ribbed protoconchs, bold radials on the teleoconch and widely open umbilici. Although minor differences in coiling pattern, whorl profile and shell appearance were noted, these were considered variations in widespread populations. Specimen lots were small and spirit material was available in only one case. Little material has been added to this data set but in light of the emphasis on subtle differences in shell features, particularly the use of protoconch sculpture as a generic character, these specimens were subjected to closer scrutiny. Re-examination of this material (AMSC57247, C128524, C128637, C128618, C128319, C154735, QMMO10794, MO17291, MO16905, MO17290) has revealed several unrelated species (and possibly genera) on the basis of protoconch sculptural detail alone. These protoconch types are superficially similar to that of *E. cochlidium* in being macroscopically radial but differ in both rib architecture and spacing. In contrast to *E. cochlidium* these species have continuous spiral cords on the protoconch and more closely spaced and more curved apical ribs than that seen in *E. cochlidium*.

An important consequence of the above taxonomic rearrangement is that the anatomy of *E. cochlidium* remains unknown. The anatomical detail presented by Stanisic (1990) refers to an unnamed species from the Dorrigo area, W of Coffs Harbour, NE NSW that will be dealt with elsewhere.

Whiteheadia gen. nov.

ETYMOLOGY. For Thora Whitehead.

TYPE SPECIES. *Egilomen globosa* Stanisic, 1990; herein designated.

DIAGNOSIS. Shell minute, white. Protoconch with numerous, bold, relatively closely spaced, slightly curved radial ribs (approx. 50) that do not become more crowded toward the protoconch/teleoconch boundary; secondary apical sculpture of vague, discontinuous periostracal spiral wrinkles. Teleoconch with prominent, slightly protractively sinuated, moderately widely spaced radial ribs; secondary sculpture of prominent crowded, low microspirals cords and relatively less prominent microradial ribs that form strong beads at their intersection. Umbilicus closed or reduced to a tiny chink. Kidney evenly bilobed; pericardial lobe not reflexed. Penial retractor muscle inserted on the epiphallus some distance from the penis/epiphallus junction. Penis internally with a single longitudinal pilaster and accessory circular pad.

DISTRIBUTION AND HABITAT. From NE NSW to SE Qld; under logs and among rocks in closed forest.

REMARKS. Characters distinguishing *Whiteheadia* and *Egilomen* have been discussed under the latter genus but two unusual characters in *W. globosa* (Stanisic, 1990) comb. nov. require special mention. The baso-columellar thickening in *W. globosa* from Mt Guyra is interpreted as intraspecific variation in a disjunct population since all other characters fall within the species concept. Perhaps of greater significance though, is the epiphallic insertion of the penial retractor muscle. Most east Australian charopids hitherto dissected have the penial retractor muscle inserted on or very near to the penis/epiphallus junction. Relatively few exceptions have been noted (Stanisic, 1990) and no coherent phylogenetic pattern for this altered character state has yet emerged.

Whiteheadia globosa (Stanisic, 1990). comb. nov.
(Fig. 13)

Egilomen globosa Stanisic, 1990: 197, figs 131, 132; Smith, 1992: 187.

MATERIAL. All SE Qld: QMMO19460, MO23300, MO25968.

TYPE LOCALITY. Sidetrack off Mt Archer Rd, Mt Mee SF, SE Qld.

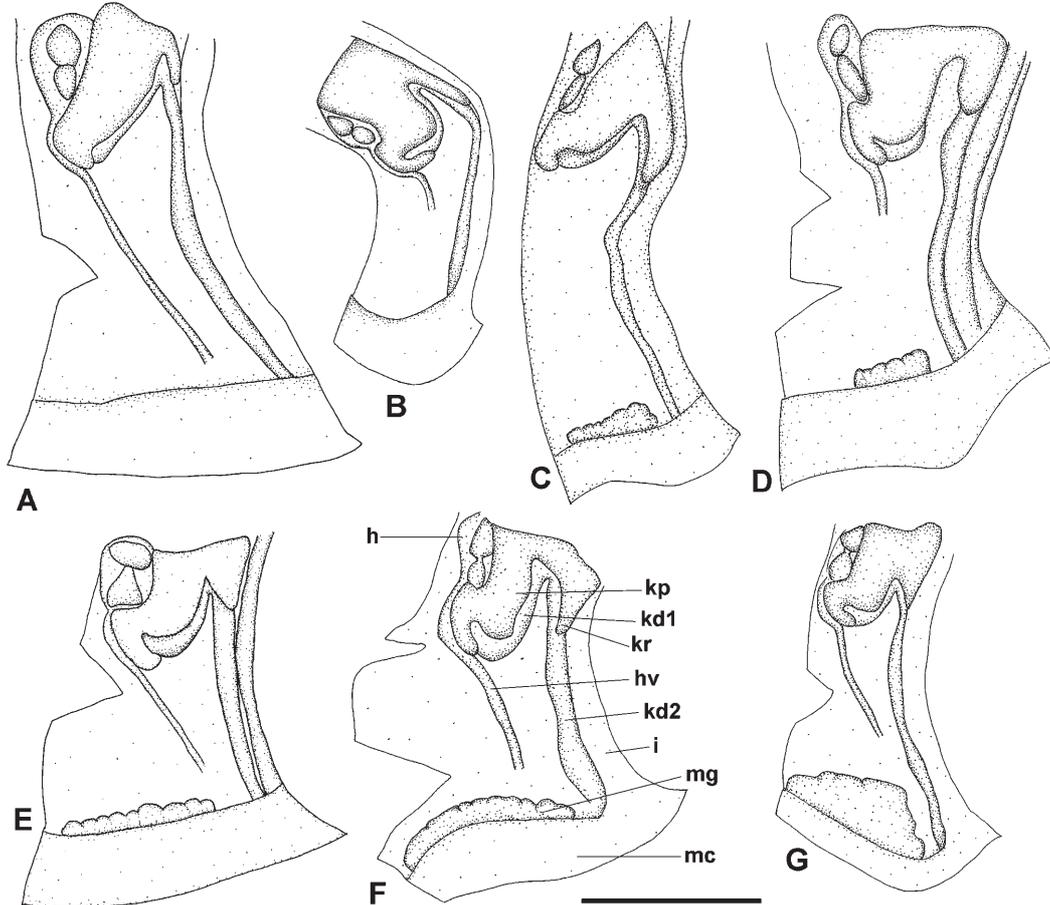


FIG. 21. Pallial cavity. Reproductive system. A, *Elsothera brazieri*, QMMO44810. B, *Decoriropa lirata*, QMMO42109. C, *Coricudgia wollemiana*, QMMO28659. D, *Marilyniropa jenolanensis*, QMMO37465. E, *Cralopa stroudensis*, QMMO29722. F, *Gouldiropa carlessi*, QMMO32080. G, *Gouldiropa kaputarensis*, QMMO49175. Scale bar=2mm in C and G, 1.6mm in D and F, and 1.28mm in all others. Abbreviations: h, heart; hv, principal pulmonary vein; i, intestine; kd1, primary ureter; kd2, secondary ureter; kp, pericardial lobe of kidney; kr, rectal lobe of kidney; mc, mantle collar; mg, mantle gland.

DIAGNOSIS. Shell minute, white, subglobose to globose with elevated spire, mean H/D 0.77. Whorls regularly coiled, mean whorl count 4.63. Teleoconch with numerous, prominent, slightly protractively sinuated, moderately widely spaced radial ribs, mean ribs/mm 9.04. Umbilicus closed or reduced to a tiny chink. Lip thickened, occasionally with a baso-columellar thickening. Penis with a centrally located longitudinal pilaster and an apical, accessory circular pad.

DISTRIBUTION AND HABITAT. From N of Casino (Richmond Range), NE NSW to S of Maryborough (Mt Guyra), SE Qld; under logs

and among rocks in subtropical notophyll vine forest, microphyll vine forest and vine thicket.

REMARKS. The combination of tiny, white, strongly ribbed, globose shell that has a predominantly radially ribbed protoconch and closed to almost-closed umbilicus readily distinguishes *W. globosa* from other eastern Australian charopids hitherto examined (Stanisic, unpubl. data). In general shell form, *W. globosa* resembles *Cralopa stroudensis* (Cox, 1864) but differs in lacking distinct spirals on the protoconch, having less sinuate, less numerous

TABLE 3. Shell measurements for species of *Macrophallikoropa*, *Elsothera*, *Egilomen* and *Decoriropa*. (Abbreviations as in Table 1).

Measurement	<i>Macrophallikoropa belli</i>	<i>Macrophallikoropa stenoumblicata</i>	<i>Macrophallikoropa depressispira</i>	<i>Elsothera brazieri</i>	<i>Egilomen cochlidium</i>	<i>Decoriropa lirata</i>
N	31 (*30)	6 (*5)	19 (*18; **17; ***16)	10 (*9; **8; ***7)	4	55 (*54, **53)
D	1.43-2.22 (1.76) ± 0.22	1.61-2.22 (1.945) ± 0.234	1.97-2.37 (2.161) ± 0.112	2.72-3.99 (3.37) ± 0.37	3.89-4.6 (4.203) ± 0.311	1.83-2.63 (2.19) ± 0.22
PW	1.5-1.8 (1.68) ± 0.1 *	1.5-1.8 (1.683) ± 0.117	1.6-1.8 (1.735) ± 0.07 **	1.5-1.8 (1.657) ± 0.098 ***	1.6-1.7 (1.65) ± 0.058	1.2-1.8 (0.63) ± 0.09
TW	2.1-3.7 (2.78) ± 0.44 *	2.2-3 (2.65) ± 0.327	3-3.4 (3.224) ± 0.13 **	2.3-2.7 (2.486) ± 0.168 ***	2.4-3.1 (2.85) ± 0.332	1.9-3.6 (2.56) ± 0.35
NW	3.8-5.5 (4.46) ± 0.43	4-4.7 (4.333) ± 0.273	4.6-5.2 (4.959) ± 0.173 **	3.8-4.4 (4.17) ± 0.21 **	4-4.8 (4.5) ± 0.383	3.6-5.3 (4.2) ± 0.36
H	0.73-1.12 (0.92) ± 0.11	0.77-1.19 (1.003) ± 0.147	0.9-1.14 (1.063) ± 0.068	1.64-1.94 (1.8) ± 0.1 *	2.29-2.67 (2.42) ± 0.175	0.92-1.4 (1.13) ± 0.12 **
SP	0-0.14 (0.06) ± 0.04 *	0.03-0.13 (0.085) ± 0.036	-	0-0.12 (0.015) ± 0.042 **	0-0.01 (0.005) ± 0.006	0-0.2 (0.08) ± 0.04
AH/AW	1.05-1.46 (1.27) ± 0.11 *	0.97-1.27 (1.09) ± 0.12	1.09-1.63 (1.33) ± 0.15	0.97-1.3 (0.14) ± 0.1 **	1.17-1.4 (1.29) ± 0.13	1.07-1.43 (1.22) ± 0.08
UMB	0.42-0.84 (0.64) ± 0.09	0.53-0.73 (0.627) ± 0.079	0.76-0.91 (0.84) ± 0.04 **	0.8-1.31 (0.97) ± 0.16 *	1.13-1.41 (1.278) ± 0.118	0.5-0.91 (0.69) ± 0.11 *
RIB	102-248 (179) ± 31.48	*147-197 (171) ± 20.671	165-254 (218) ± 20.607 ***	136-206 (162) ± 24.48 *	65-85 (73.5) ± 9.292	36-109 (57.82) ± 16.72
RIBS/MM	14.69-42.19 (32.65) ± 6.19	*26.43-32.66 (28.94) ± 2.601	37.97-26.39 (32.24) ± 3.172 ***	13.70-17.96 (15.32) ± 1.773 **	4.823-6.301 (5.571) ± 0.652	5.775-11.148 (8.310) ± 1.744
H/D	0.48-0.56 (0.52) ± 0.02	0.48-0.54 (0.51) ± 0.02	0.46-0.52 (0.49) ± 0.02	0.49-0.58 (0.52) ± 0.03 *	0.56-0.59 (0.58) ± 0.01	0.48-0.58 (0.52) ± 0.02 **
D/U	2.31-3.43 (2.76) ± 0.26	3.04-3.2 (3.11) ± 0.07	2.34-2.72 (2.57) ± 0.11 *	3.05-4.07 (3.57) ± 0.3 *	3.06-3.44 (3.3) ± 0.18	2.81-3.81 (3.19) ± 0.25 *

and more widely spaced ribs on the teleoconch and in lacking a true apertural sinus.

Material obtained subsequent to Stanistic (1990) has not altered either the concept of the species or details of its distribution. However, it has provided information for a more detailed analysis of the species' preferred habitat which shows that while *W. globosa* lives in moist forest in the south it is found in drier rainforest (microphyll vine forest, vine thicket) as its distribution attenuates northwards. And though this may initially suggest that the species has a relatively wide environmental tolerance, personal observation by one of us (JS) indicates that *W. globosa* is environmentally selective at the microhabitat level in the southern part of its distribution. For example, in the Lamington NP, SE Qld *W. globosa* has only been found on the Araucaria Circuit walking track, near Binna Burra which is a much drier rainforest (microphyll vine forest) than the moist notophyll vine forest dominating most parts of Lamington NP. Such local micro-environmental selectivity on the part of *W. globosa* may help explain the apparently patchy distribution of the species over its range.

Decoriropa gen. nov.

ETYMOLOGY. Latin *decorus*, beautiful; referring to the elegant shell.

TYPE SPECIES. *Helix lirata* Cox, 1868; herein designated.

DIAGNOSIS. Shell golden brown, with evenly coiled whorls and a weak apertural sinus. Protoconch with crowded, evenly spaced, curved radial ribs (approx. 60) and numerous regularly crowded, low, continuous spiral cords that cross the radial ribs. Teleoconch with numerous prominent, weakly to strongly protractively sinuated, moderately crowded to widely spaced radial ribs; secondary sculpture of low, thin microradial ribs that have weak periostracal blades, ribs continuous on the major ribs, crossed by generally more prominent microspirals that form rounded beads at their intersection with the microradials. Umbilicus moderately wide to very wide U-shaped. Kidney moderately bilobed with strongly reflexed pericardial lobe. Penis with two longitudinal pilasters.

DISTRIBUTION AND HABITAT. NE NSW (near Kempsey) in a broad range of habitats ranging from temperate and subtropical

rainforest (humid and dry) to dry vine thickets and wet and dry sclerophyll forest where it lives under logs and rocks.

REMARKS. *Decoriropa* has a similar shell profile to *Egilomen* but differs in having more crowded, thinner radials on the protoconch that are crossed by continuous spiral cords (discontinuous periostracal wrinkles in *Egilomen*), and a greater number of ribs on the teleoconch. The shell of *Decoriropa* also bears some similarity to those of *Rhophodon* and *Egilodonta* but lacks apertural barriers and has a smaller, less open (broad V-shaped) umbilicus (mean diameter 0.69mm). Most significantly the apical shell sculpture of these two 'dentate' groups differs from that of *Decoriropa* in having crowded radial ribs that become more crowded at the protoconch/teleoconch boundary (evenly spaced in *Decoriropa*); and apical spiral elements that consist of discrete cordlets that do not cross the radial ribs (continuous cords crossing the radials in *Decoriropa*).

The single species, *D. lirata* (Cox, 1868) comb. nov., occurs across a range of geologies from sandstone to volcanic rocks and limestone. In many ways it shows a similar environmental adaptability to *Macrophallikoropa belli* (Cox, 1864) comb. nov. However, in contrast to the range of that species *D. lirata* does not appear to extend into far northern NSW or SE Qld.

***Decoriropa lirata* (Cox, 1864) comb. nov.**
(Figs 10, 13-18, 20-21, 33-34; Table 3)

Helix lirata Cox, 1864: 38; 1868: 13, pl. 8, fig. 1.
Helix (Patula) lirata (Cox); Cox, 1909: 44.
Egilomen liratum (Cox); Iredale, 1937: 328; 1941a: 269.
Egilomen lirata (Cox); Smith, 1992: 187.

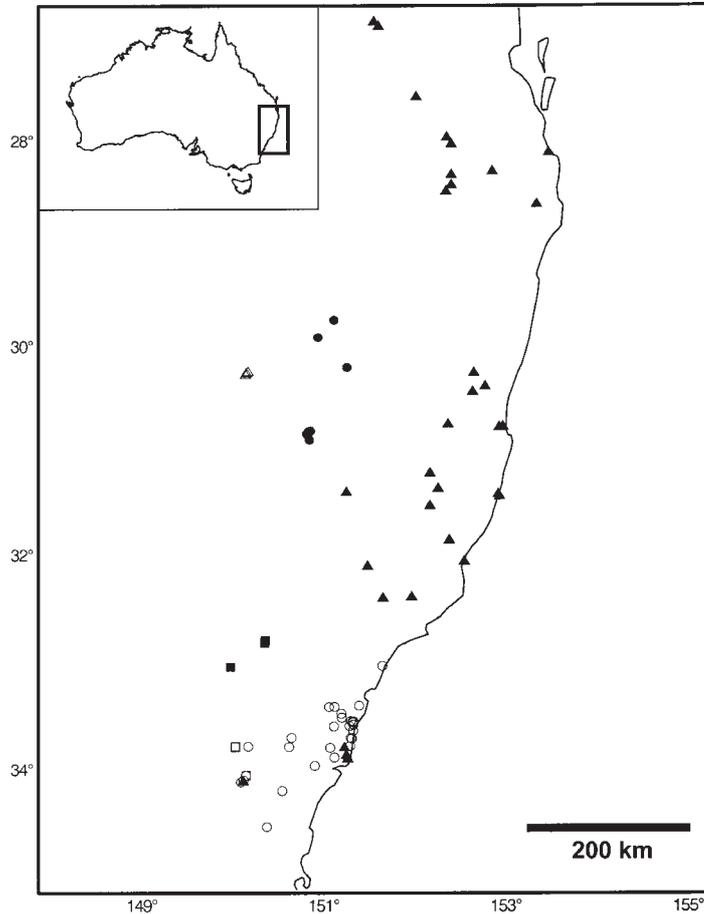


FIG. 22. Distribution of *Elsothera*, *Coricudgia*, *Marilyniropa*, *Cralopa* and *Gouldiropa*. Key: ○ *Elsothera brazieri*, ■ *Coricudgia wollemiana*, □ *Marilyniropa jenolanensis*, ▲ *Cralopa stroudensis*, ● *Gouldiropa carlessi*, ▲ *Gouldiropa kaputarensis*.

MATERIAL. NEOTYPE: AMSC427984. Height of shell=1.2mm, diameter=2.24mm, H/D=0.53, D/U=3.03, number of whorls=4.3, ribs on last whorl=70. **KEY MATERIAL.** All NSW. QMMO29722. 10SC/28RC, Georges R, banks, Warwick Farm (33°55'S, 150°56'E), degraded ew, under logs, bark and rubble, 31.xii.1989, JS, JC; QMMO42109, 8SC/8RC, Bungonia Gorge, ENE Goulburn (34°48'21"S, 150°00'47"S), lm/ew, 13.x.1992, JS GI; AMSC356052, 3RC, Sydney, Rose Bay, just S of Queens Bch, Hermitage Foreshore Park, off Hermitage Trail (33°51.75'S, 151°16.09'E), under litter at base of retaining wall, 07.i.1999, MS; AMSC154792, 20+RC, S of Braidwood, Wyanbene Caves (35°48.1'S, 149°40.9'E), lm, litter from cave entrance, 17.i.1981, WFP, W.F. Ponder (Jnr); AMSC136842, 12RC, W of Taree, Manning R, Wingham Brush (31°52.25'S, 152°22.85'E), rainforest, in litter, 26.viii.1982, JS; QMMO52755, RC, Kempsey, W, c.4km

W Sherwood, Sherwood-Willi Willi Rd (31°03'24"S, 152°41'06"E), drf/lm, 40m, litter, 28.xii.1993, JS, JC; QMMO64764, 20RC, Wombeyan Caves, NNE Goulburn (34°18'35"S, 149°57'46"E), lm/vt, litter, 13.x.1992, JS, GI; AMSC154791, 3RC, S of Forster, E of Smiths Lake, Bald Head (32.382°S, 152.531°E), under low scrub on dunes, in litter, x.1981, OG; AMSC157311, 13RC, W of Taree, Wingham, Wingham Brush (31.871°S, 152.381°E), leaf litter in subtropical lowland floodplain rf", 05.ii.1982, *MS. OTHER MATERIAL. Northeastern NSW: QMMO12745, MO44830 MO16758, MO16763, MO37514, MO17274, MO31909, MO31935, MO32066, MO37733, MO32072, MO49478, MO56147, MO52701, MO56136, MO56142, MO59891, MO32291, MO37106, MO49395, MO55875, MO55893, MO56012, MO56050, MO56080, MO59794, MO60143, MO60154, MO60477, MO60491, MO60498, AMSC168693, C339712, C411598. Sydney Basin: QMMO29640, MO34783, MO34973, MO37389, MO37818, MO42136, MO44783, AMSC63774, C140472, C319043, C319058, C319059, C319080, C319087, C319088, C319096, C319098, C319118, C319120, C319125, C319126, C345665, C356051, C356080. Southeastern NSW: QMMO29271, MO37791, MO37812, MO37980, MO42124, MO68010, AMSC318792, C63729, C157294, C168663, C157316, C168673, C168676, C358326, C358328, C358330, C346061.

DIAGNOSIS. Shell very small, golden brown with evenly coiled whorls and a weak apertural sinus. Spire and early apex flat to slightly elevated. Teleoconch with numerous prominent, weakly to strongly protractively sinuated, moderately crowded to widely spaced radial ribs (mean ribs/mm 8.31. Umbilicus moderately wide to very wide V-shaped, diameter range 0.50-0.91mm, mean D/U 3.19. Penis with two longitudinal pilasters.

DESCRIPTION. Shell very small, golden brown, with 3.6-5.3 (mean 4.2) evenly coiled whorls, the last descending in front; weak apertural sinus present. Shell diameter 1.83-2.63mm (mean 2.19mm). Apex and early spire flat to slightly elevated. Height of shell 0.92-1.40mm (mean 1.13mm), H/D 0.48-0.58 (mean 0.52). Protoconch of 1.2-1.8 whorls with sculpture of regularly spaced, moderately crowded, curved radial ribs, width of interstices (in multiples of rib width) 2-4 at apex. Secondary sculpture of low, continuous spiral cords (23-24), crossing radial ribs. Teleoconch sculpture of crowded, regularly spaced (increasing near end of last whorl), weakly protractively sinuated radial ribs; 36-109 (mean 58) ribs on the last whorl. Ribs/mm 5.78-11.15 (mean 8.31). Ribs wide, height less than or equal to width, straight in section, rounded on top. Rib interstices on the first post-nuclear whorl equal to width of 4-6

ribs; interstices on the penultimate whorl equal to width of 3-6 ribs. Interstitial sculpture of weak microradial ribs, 4-10 between ribs on first post-nuclear whorl; 7-13 between ribs on penultimate whorl; continuous on major radials, with weak periostracal blades. Secondary microsculpture of more prominent low, microspirial cords that cross the major ribs and form strong transversely elongate to rounded beads at their intersections with the microradials. Umbilicus very wide V-shaped, diameter 0.50-0.91mm (mean 0.69mm), D/U 2.81-3.81 (mean 3.19). Whorls flattened above and rounded below a weakly rounded periphery, sutures impressed. Aperture ovately lunate ovate, parietal callus present. Based on 55 measured specimens (AMSC356052, C154792, C136842, SC427984, QMMO52755, MO64764,).

Genitalia with ovotestis containing two clumps of alveoli, with two or more alveolar lobes per clump. Talon stalk 1-3 times the diameter of the talon; talon circular. Penial retractor muscle less than half the length of the penis; inserting at the junction of the penis and epiphallus. Epiphallus longer than penis, narrower than the vas deferens, entering penis through a simple pore; internally with longitudinal pilasters. Penis tubular with sheath, internally with two longitudinal pilasters. Vagina shorter or equal in length to penis.

Pallial cavity with moderately bilobed kidney, pericardial lobe strongly reflexed at apex.

Radula with central tooth strongly tricuspid; lateral teeth tricuspid; marginal teeth skewed towards the centre; ectocone of outer marginal teeth split into three teeth; endocone not split. Number of lateral teeth: 4; marginal teeth: 10; radular rows: 73. Based on 3 dissected specimens (QMMO29722, MO42109).

DISTRIBUTION AND HABITAT. *Decoriropa lirata* is widely distributed ranging from the Wyanbene Caves, SE NSW to the Macleay River valley, NE NSW. The species lives in a variety of forest-types ranging from humid subtropical rainforest to dry rainforest (vine thickets) and littoral rainforest, as well as dry and wet sclerophyll forest. The widespread nature of the distribution and habitat preference suggests an inherent adaptability that is probably a contributing factor to the species' continued survival in suburban Sydney.

REMARKS. *Decoriropa lirata* looks superficially like *Marilyniropa jenolanensis* sp. nov. but can be distinguished by its smaller shell that has narrower whorls (smaller cross section), a weak

apertural sinus, more dense ribbing and usually, a less elevated spire. *D. lirata* does not appear to occur on the Jenolan or Tuglow limestones but is found on the nearby Church Creek and Colong Caves limestones where it is sympatric with *M. jenolanensis*. Juveniles of the latter species are easily confused with *D. lirata* but are readily separated by having fewer (approx. 45), less crowded radials on the protoconch. *D. lirata* is also apparently absent from the nearby, Abercrombie limestones but is present on the more distant Wombeyan limestones. Specimens from Wombeyan Caves have a lower rib count, slightly higher spire and narrower umbilicus than usual, but otherwise agree with the general concept of the species which is remarkably stable across a wide and variable landscape.

In the absence of type material (Smith, 1992) a neotype was designated. The specimen chosen comes from inner Sydney close to the original type locality (Ruschcutters Bay). A key reason for choosing the Bellevue Hill locality was that the species is still readily found there alive.

Coricudgia gen. nov.

ETYMOLOGY. For Mt Coricudgy, NSW.

TYPE SPECIES. *Coricudgia wollemiana* sp. nov.; herein designated.

DIAGNOSIS. Shell white with a relatively large number of tightly coiled whorls and moderately elevated spire. Protoconch with very crowded (approx. 90) curved radial ribs and continuous crowded microspiral cords. Teleoconch with weakly sinuated, widely spaced, bold radial ribs; secondary sculpture of prominent microradial ribs with weaker microspiral cords that form rounded beads at their intersection. Umbilicus

open U-shaped. Kidney evenly bilobed with large wedge-shaped lobes; pericardial lobe only weakly reflected. Penis with 2 longitudinal pilasters.

DISTRIBUTION AND HABITAT. Restricted range centred on Mt Coricudgy, Wollemi NP, NSW. Mostly found living among rocks in rainforest.

REMARKS. *Coricudgia* gen. nov. displays several shell characters that distinguish it from other E Australian charopids with bold ribs and an open umbilicus. The high whorl count, large number of radial ribs and continuous spiral cords on the protoconch separate it from *Egilomen* (lower whorl number, few apical radials with

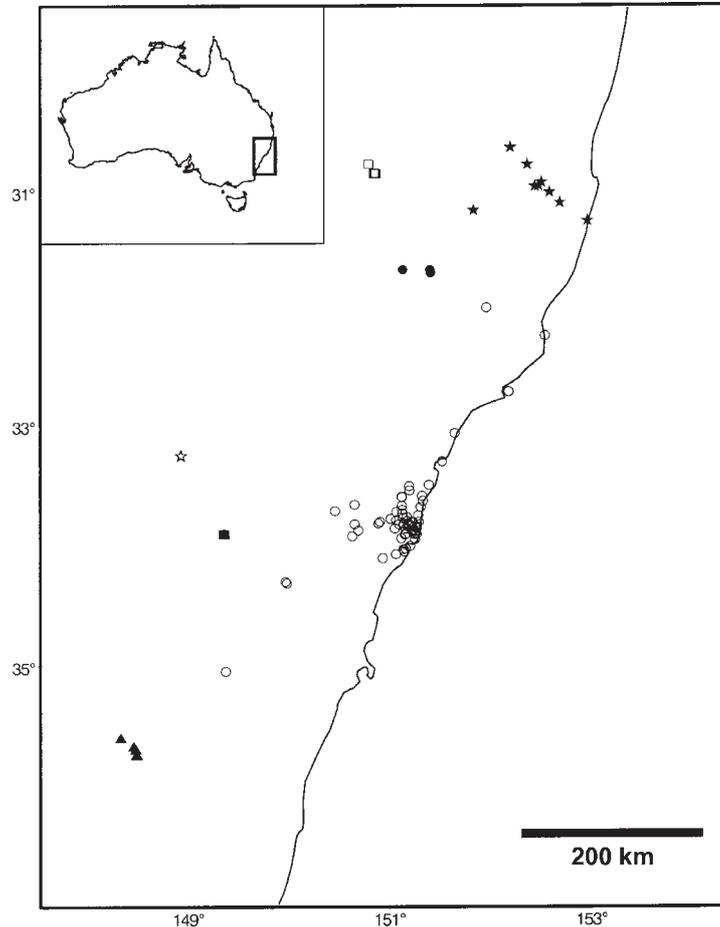


FIG. 23. Distribution of *Sharniropa*, *Acheronopa*, *Hedleyropa* and *Diphyoropa*. Key: ☆ *Sharniropa borenorensis*, ■ *Sharniropa wollondillyana*, ● *Sharniropa xanana*, □ *Acheronopa attunga*, ▲ *Hedleyropa yarrangobillyensis*, ○ *Diphyoropa saturni*, ★ *Diphyoropa macleayana*.

vague spiral wrinkles) which has a similarly coiled, whitish shell with moderately wide umbilicus and moderately elevated spire. It is distinguished from *Decoriropa* chiefly by the more elevated spire, the greater number of straighter ribs on the protoconch, a greater number of tightly coiled whorls and the much less sinuate ribs on the teleoconch. The greater number of tightly coiled whorls distinguish it from *Cralopa* Iredale, 1941, *Gouldiropa* gen. nov., *Sharniropa* gen. nov. and *Marilyniropa* gen. nov. which all have comparatively fewer whorls, bolder ribs and relatively looser coiling.

***Coricudgia wollemiana* sp. nov.**
(Figs 10, 14-17, 19, 33-34; Table 4)

ETYMOLOGY. For Wollemi NP, the type locality.

MATERIAL. HOLOTYPE: AMSC205164, E of Rylstone, Mount Coricudgy, southern slope, NSW (32°50.82'S, 150°21'E), in litter off road, 2.x.1983, PHC. Height of shell=1.95mm, diameter=3.73mm, H/D=0.52, D/U=3.59, number of whorls=6.1, ribs on last whorl=46. PARATYPES: All NSW. AMSC162143, 18RC, same data as holotype; QMMO28659, 13SC/9RC, slopes of Mt Coricudgy, W of Rylstone (32°51'S, 150°21'E), under rocks, 15.i.1990, JS, JC; QMMO44708, 1RC, Mt Coricudgy, NE Rylstone, summit (32°49'48"S, 150°21'24"E), remnant rainforest, under rocks, 10.i.1993, JS, JC; QMMO59868, 4SC/7RC, Rylstone, E, at Mt Coricudgy (32°51'25"S, 150°21'00"E), wtrf/basalt, under logs and rocks, 01.i.1996, JS, JC; QMMO44725, 1RC/11SC, Mt Coricudgy, NE Rylstone, c.0.1km E summit road, (32°51'00"S, 150°21'12"E), ws/wtrf, on roots of plants under rocks, 10.i.1993, JS, JC. OTHER MATERIAL. QMMO59859.

DIAGNOSIS. Shell very small, white, with moderately elevated spire (mean spire height 0.26mm) and a relatively large number of tightly coiled whorls (mean whorl count 4.9, range to 6.1 whorls). Protoconch with crowded (approx. 90) curved radial ribs and continuous crowded microspirals. Teleoconch with weakly sinuated, widely spaced, bold radial ribs, mean rib count 4.1 ribs/mm. Umbilicus open U-shaped, mean D/U 3.49. Penis with two longitudinal pilasters.

DESCRIPTION. Shell very small, white, with 3.6-6.1 (mean 4.9) tightly coiled whorls, the last descending more rapidly in front. Whorls weakly rounded above and rounded below a rounded periphery. Shell diameter 1.62-4.02mm (mean 3.30mm). Apex and early spire weakly elevated. Height of shell 0.83-2.21mm (mean 1.69mm), H/D 0.45-0.55 (mean 0.51). Protoconch of 1.7-1.8 whorls with sculpture of crowded,

regularly spaced, slightly curved radial ribs (approx. 90); width of interstices (in multiples of rib width) 3 at apex. Secondary sculpture of continuous spiral cords that cross the radials. Teleoconch with widely but regularly spaced, weakly protractively sinuated, bold radial ribs. Ribs on last whorl 28-47 (mean 40), ribs/mm 3.01-5.50 (mean 4.09). Height of ribs equal to width; straight in section; rounded on top, continuous on major radials. Rib interstices on the first post-nuclear whorl equal to width of 6-7 ribs. Interstitial sculpture of high microradial ribs, 9 between major ribs on first post-nuclear whorl; 16 between ribs on penultimate whorl. Secondary sculpture of low microspirals forming strong rounded beads at their intersection with the microradials. Umbilicus open, U-shaped, diameter 0.55-1.15mm (mean 0.94mm), D/U 2.95-3.80 (mean 3.49). Aperture broadly ovately lunate, parietal callus present. Based on 10 measured specimens (AMS C162143, C205164).

Genitalia with ovotestis containing two clumps of alveoli, with more than two alveolar lobes per clump. Talon stalk 1-3 times the diameter of the talon; talon circular. Penial retractor muscle less than half the length of the penis; inserting onto the penis head; entering penis through a simple pore. Penis tubular; with two longitudinal pilasters present, one very large and irregular in shape, the other much smaller and regular in shape. Vagina shorter than penis.

Pallial cavity with strong, evenly bilobed kidney; apex of pericardial lobe weakly reflexed. Mantle gland present.

Radula with central tooth strongly tricuspid; lateral teeth tricuspid; first and second laterals equal in width. Mesocone of first lateral tooth slender, slightly diamond-shaped; marginal teeth skewed towards the centre. Ectocone of outer marginal teeth not split; endocone not split; number of lateral teeth: 7; marginal teeth: 11; radular rows: 100. Based on 2 dissected specimens (QMMO28659).

DISTRIBUTION AND HABITAT. Known only from the Rylstone area, NSW but particularly the upper parts of Mt Coricudgy, Wollemi NP, NSW where the species lives among volcanic rocks in warm temperate rainforest.

REMARKS. *Coricudgia wollemiana* sp. nov. is easily recognisable by its white shell with very high whorl count, tightly coiled whorls and moderately elevated spire. Some specimens attain greater than 6 whorls which is a

comparatively high whorl count in the context of moderately sized (i.e. approx. shell diameter 3.5-4.5mm) eastern Australian charopids. However some other, smaller charopids, including some dealt with in this study, e.g. *Rhophodon* spp. and *Letomola* spp., have higher whorl counts. The discovery of this species on the heights of Mt Coricudgy once again points to the unusual nature of this rainforest/volcanic refugium among an otherwise dry sclerophyll/sandstone landscape. Mt Coricudgy is also home to the geographically restricted *Macrophallikoropa stenoumblicata* sp. nov. suggesting that the locality has broad significance as an historical refugium for mesic communities. A single specimen of *C. wollemiana* has also been found at a lowland locality near Capertee but the viability of any lowland populations needs to be more accurately assessed by undertaking additional collecting in the area. It is quite possible that the Capertee specimen was stream drift material washed from the mountain slopes. Relatively little land snail collecting has been undertaken in the Wollemi NP and the full extent of the distribution of *C. wollemiana* has yet to be determined.

Marilyniropa gen. nov.

ETYMOLOGY. For Marilyn Joy McGrady.

DIAGNOSIS. Shell very small, straw to beige in colour, with evenly coiled whorls; apertural sinus absent. Protoconch with evenly spaced, moderately crowded, curved radial ribs (approx. 55) that are crossed by crowded, low continuous spiral cords; radial ribs becoming bolder toward the protoconch/teleoconch boundary. Teleoconch with bold, widely spaced, strongly sinuate ribs (mean ribs/mm 4.62) that become more crowded on the latter half of the last whorl.

Umbilicus wide V-shaped. Kidney moderately bilobed, pericardial lobe reflexed. Mantle gland present. Penis with five longitudinal pilasters.

DISTRIBUTION AND HABITAT. Known only from limestone outcrops SSE Oberon, NSW. The single species, *Marilyniropa jenolanensis* sp. nov., lives among limestone talus.

REMARKS. *Marilyniropa* gen. nov. is grossly similar to *Decoriropa* in having an open umbilicus and bold ribbing but differs in having fewer, apical radial ribs, an elevated spire, no apertural sinus and fewer, variably spaced, more curved radial ribs on the teleoconch. Anatomically, *Marilyniropa* differs by having greater number of penial pilasters and shorter epiphallus than *Decoriropa*. Unfortunately it is not possible to

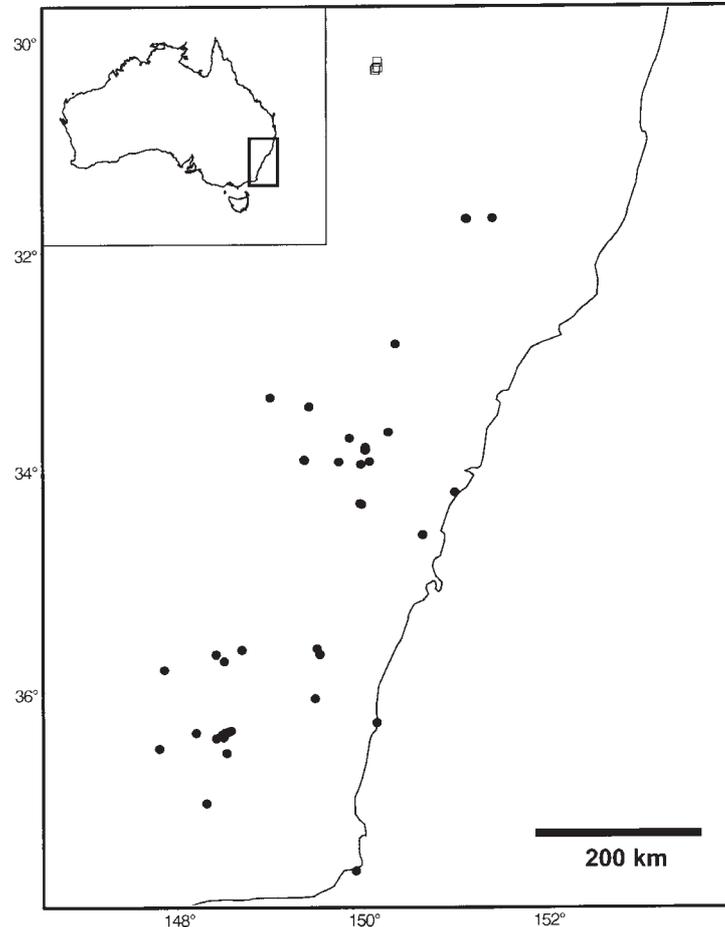


FIG. 24. Distribution of *Scleridoropa*. Key: ● *Scleridoropa sarahjaneae*, □ *Scleridoropa nandewar*.

put the significance of these character shifts in reproductive anatomy into phyletic context at this time except to say that they do represent major departures from the patterns seen in the somewhat conchologically similar species belonging to *Decoriropa*, *Sharniropa*, *Gouldiropa*, *Acheronopa* and *Cralopa*. The combination of more tightly coiled whorls and larger umbilicus differentiates *Marilyniropa* from the sympatric *Sharniropa* and *Gouldiropa*.

The current restriction of *Marilyniropa* to a few habitats surrounding and including Jenolan Caves, once again highlights the biogeographical importance of these limestones to land snail evolution.

***Marilyniropa jenolanensis* sp. nov.**
(Figs 10, 14-17, 19, 33-34; Table 4)

ETYMOLOGY. For the type locality.

MATERIAL. HOLOTYPE: AMSC205165, Jenolan Caves, NSW (33°49.3'S, 150°1.2'E), 6.vi.1982. O.L. Griffiths. Height of shell=1.77mm, diameter=3.46mm, H/D=0.51, D/U=3.33, number of whorls=4.5, ribs on last whorl=42. PARATYPES: All NSW. AMSC144224, many RC, same data as holotype; AMSC142966, Jenolan Caves, ridge on top of Grand Arch (33°49.24'S, 150°1.32'E), 12.xii.1979, JS. QMMO9730, 101RC, Jenolan Caves, above Grand Arch, lm, litter among rocks, 11.xii.1979, JS; QMMO28777, 2SC/4RC, Jenolan Caves, lm, under rocks, 9.i.1990, JS, JC; QMMO37776, 7RC, Jenolan Caves (33°49'S, 150°01'E), lm, in litter, 9.i.1990, JS, JC; QMMO37465, 4SC/36RC, Jenolan Caves (33°49'S, 150°01'E), lm, on limestone rocks among dirt, 10.i.1990, JS, JC. OTHER MATERIAL. All NSW. QMMO70485, MO70486, MO62450, AMSC63736, C63852, C121716, C124272, C154773, C154774, C154775, C154776, C154777, C157333, C168669, C346748, C346750.

DIAGNOSIS. Shell light brown to beige in colour with evenly coiled whorls, mean whorl count 4.51. Apex flat, early spire elevated, mean spire height 0.25mm, mean H/D 0.48. Protoconch with evenly spaced, moderately crowded, curved radial ribs (approx. 55) that are crossed by crowded, low continuous spiral cords. Teleoconch with bold, moderately widely spaced, strongly sinuate ribs (mean ribs/mm 4.62) that become more crowded on the latter half of the last whorl. Umbilicus wide V-shaped, mean diameter 0.89mm, mean D/U 3.67. Penis with 5 short, longitudinal pilasters.

DESCRIPTION. Shell very small, straw to light golden brown in colour with 4.1-4.8 (mean 4.5) evenly coiled whorls, the last descending in front; apertural sinus not developed. Shell diameter 2.96-3.65mm (mean 3.24mm). Apex

flat, early spire weakly elevated. Height of shell 1.33-1.97mm (mean 1.55mm), H/D 0.43-0.55 (mean 0.48). Protoconch with 1.4-1.7 whorls. Apical sculpture of crowded regularly spaced, slightly curved radial ribs (approx. 45); width of interstices (in multiples of rib width) 4-6 at apex. Secondary sculpture of narrow, continuous spiral cords that cross the microradial ribs; ribs becoming bolder toward the protoconch/teleoconch boundary. Teleoconch with prominent, regularly spaced, strongly protractively sinuated radial ribs, 35-61 (mean 47) ribs on the last whorl. Ribs/mm 3.76-6.08 (mean 4.62). Ribs greater in height than width; straight in section; rounded on top. Rib interstices on the first post-nuclear whorl equal to width of 4-7 ribs. Secondary microsculpture of more prominent low, microspirals that cross the major ribs and form strong transversely elongate to rounded beads at their intersections with the microradials. Whorls flattened above and rounded below a rounded periphery, sutures impressed. Umbilicus open, wide V-shaped. Umbilical width 0.73-1.07mm (mean 0.89mm), D/U 3.33-4.05 (mean 3.67). Based on 23 measured specimens (AMSC144244, C205165).

Genitalia with ovotestis containing two clumps of alveoli, with more than two alveolar lobes per clump. Talon stalk 1-3 times the diameter of the talon; talon circular. Penial retractor muscle less than half the length of the penis, inserting at the junction of the penis and epiphallus; epiphallus short. Penis tubular with 5 short, longitudinal pilasters. Vagina shorter than penis.

Pallial cavity with moderately bilobed kidney, pericardial lobe reflexed. Mantle gland present.

Radula with central tooth strongly tricuspid; lateral teeth tricuspid with first lateral slightly wider than second lateral. Mesocone of first lateral tooth slender, slightly diamond-shaped; marginal teeth skewed towards the centre. Ectocone of outer marginal teeth not split; endocone not split. Number of lateral teeth: 4; marginal teeth: 18; radular rows: 100. Based on 1 dissected specimen (QMMO37465).

DISTRIBUTION AND HABITAT. Known only from the Jenolan Caves region (Jenolan, Tuglow and Colong limestones), Blue Mountains, W of Sydney; living among limestone talus.

REMARKS. *Marilyniropa jenolanensis* sp. nov. most closely resembles *Decoriropa lirata* (Cox, 1864) comb. nov. in general appearance but can be distinguished from that species by its larger size, more elevated spire and fewer, more widely

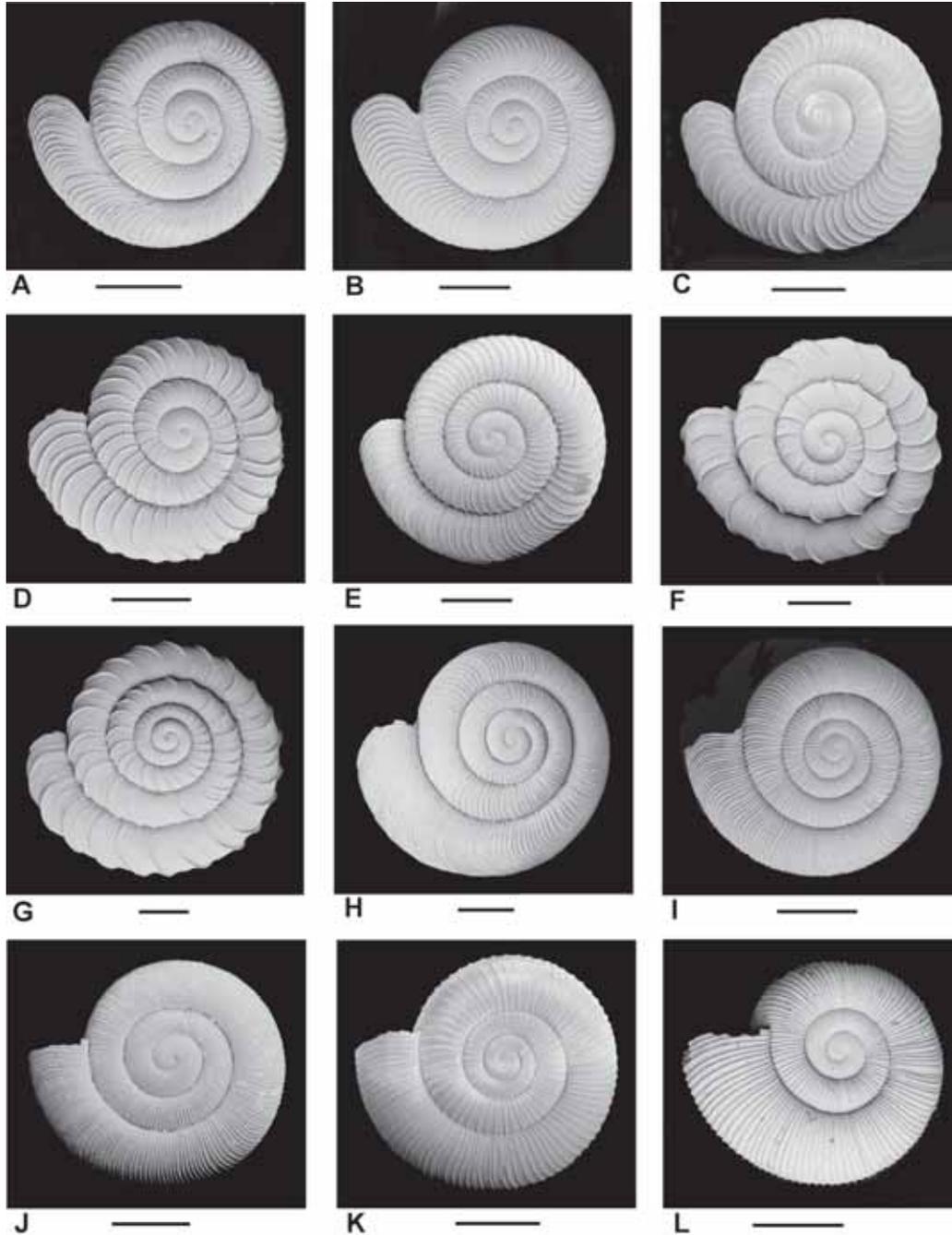


FIG. 25. Dorsal view of shells. A, *Cralopa stroudensis* (SEQ), QMMO16857. B, *Cralopa stroudensis* (Sydney), QMMO29638. C, *Gouldiropa carlessi*, AMSC003640. D, *Sharniropa wollondillyana*, QMMO70399. E, *Sharniropa borenorensis*, AMSC205166. F, *Sharniropa xanana*, QMMO70398. G, *Acheronopa attunga*, QMMO70400. H, *Hedleyropa yarrangobillyensis*, QMMO70401. I, *Scleridoropa sarahjaneae* (Yarrangobilly), QMMO70402. J, *Scleridoropa nandewar*, QMMO70403. K, *Diphyoropa saturni*, AMSC205167. L, *Diphyoropa macleayana*, AMSC168685. Scale bars = 0.5mm in J; 0.8mm in A-H, L; 1mm in K.

spaced, bolder apical radial ribs and fewer, less crowded ribs on the teleoconch. *M. jenolanensis* broadly resembles *Sharniropa wollondillyana* sp. nov. in general appearance of the shell (shape, sculpture) but the latter is larger, has more loosely coiled whorls, smaller umbilicus and bolder, more widely spaced ribs on the teleoconch.

Cralopa Iredale, 1941

Cralopa Iredale, 1941a: 267; Kershaw, 1956b: 8; Burch, 1976b: 132; Stanisc, 1990: 147 (in part); Smith, 1992: 184 (in part).

TYPE SPECIES. *Helix stroudensis* Cox, 1864; by original designation.

DIAGNOSIS. Shell very small with moderately loosely coiled whorls, deep sutures and a well-developed apertural sinus. Protoconch with very crowded, relatively narrow, curved radial ribs (approx. 80) crossed by numerous regularly spaced, crowded, low, continuous spiral cords. Teleoconch with numerous, prominent and very strongly protractively sinuated, crowded radial ribs that have weak periostracal blades. Secondary sculpture of prominent microspirals cords that cross the microradials and form round beads at their intersection. Umbilicus closed or only very slightly open. Kidney moderately to strongly bilobed with strongly reflexed pericardial lobe. Penis with two longitudinal pilasters.

DISTRIBUTION AND HABITAT. *Cralopa* Iredale, 1941 ranges from southern NSW to SE Qld. The single species lives under logs and rocks in moist rainforest and wet sclerophyll forest.

REMARKS. *Cralopa* was introduced by Iredale (1941a) for *Helix stroudensis* Cox, 1864. Iredale (1941b) added an additional species, *Cralopa intensa* Iredale, 1941. Stanisc (1990) revised *Cralopa* and in doing so reassigned *C. intensa* to *Sinployea* Solem, 1983 and included two additional new species (*C. kaputarensis*, *C. carlessi*) on the basis of shared shell and anatomical characters (closed to almost closed umbilicus, presence of an apertural sinus and large cylindrical penis). Analysis of protoconch sculpture consisted of noting the common presence of prominent radial ribs and low spiral cords. A difference in apical whorl size was noted between both *C. carlessi* and *C. kaputarensis* and *C. stroudensis*, the latter two species having a smaller protoconch than the former species. While conceding the cohesiveness of his new concept of *Cralopa*, Stanisc (1990) did however, make a number of observations relevant to a

possible future revision of the genus once additional material became available for study. Notable among these was firstly, that the biogeography of the genus was at odds (east-west) with the general pattern displayed by most other genera reviewed (north-south); secondly, that some individuals of *C. stroudensis* from the limestones of the Macleay Valley, W of Kempsey were unusual for their large size in what was an otherwise conchologically conservative, widespread species; and thirdly, that there was a large degree of variability displayed by *C. carlessi* in material from widespread localities (Wee Jasper area, SE NSW to Inverell, NE NSW). At the time this variability in shell features was considered to be local differences in a species with unusually widespread, disjunct populations. A number of these populations are herein excluded from the definition of *C. carlessi* (see below).

Cralopa Iredale, 1941 is redefined on the basis of protoconch sculpture. In contrast to both *C. carlessi* and *C. kaputarensis* and *C. stroudensis* have comparatively smaller protoconchs with more numerous and more crowded apical radial ribs (Stanisc, 1990). *Cralopa* is herein restricted to include only the type and *C. kaputarensis* (Nandewar Range Bioregion). *C. carlessi* (herein restricted to localities in the Attunga-Inverell area of the New England Bioregion, NSW) is reassigned to *Gouldiropa* gen. nov. Specimens of *C. stroudensis* from the limestone outcrops of the Macleay Valley, W of Kempsey cited in Stanisc (1990), viz. AMSC121680 [Yessabah], AMSC152198 [Natural Arch], are excluded from the revised definition of *C. stroudensis* and will be considered elsewhere (Stanisc, in prep.).

Cralopa Iredale, 1941 as redefined herein differs from that of Stanisc (1990) by the removal of *C. carlessi* Stanisc, 1990. Although the shell of this species bears a number of similarities to that of *C. stroudensis* these must be considered examples of convergent or parallel evolution. The smaller protoconch and denser apical ribbing of *C. stroudensis* and *C. kaputarensis* are considered key characters that serve to generically separate these species from *C. carlessi*. '*Charopa*' *colliveri* Gabriel, 1947 from SE Victoria was included here by Smith & Kershaw (1979) without detailed reasons but presumably on the basis of the reduced umbilicus and bold radial ribs on the teleoconch. A casual inspection of a co-type of '*C. colliveri*' in the QM (MO35761) from the Stan Colliver Collection reveals that there are characters such as the

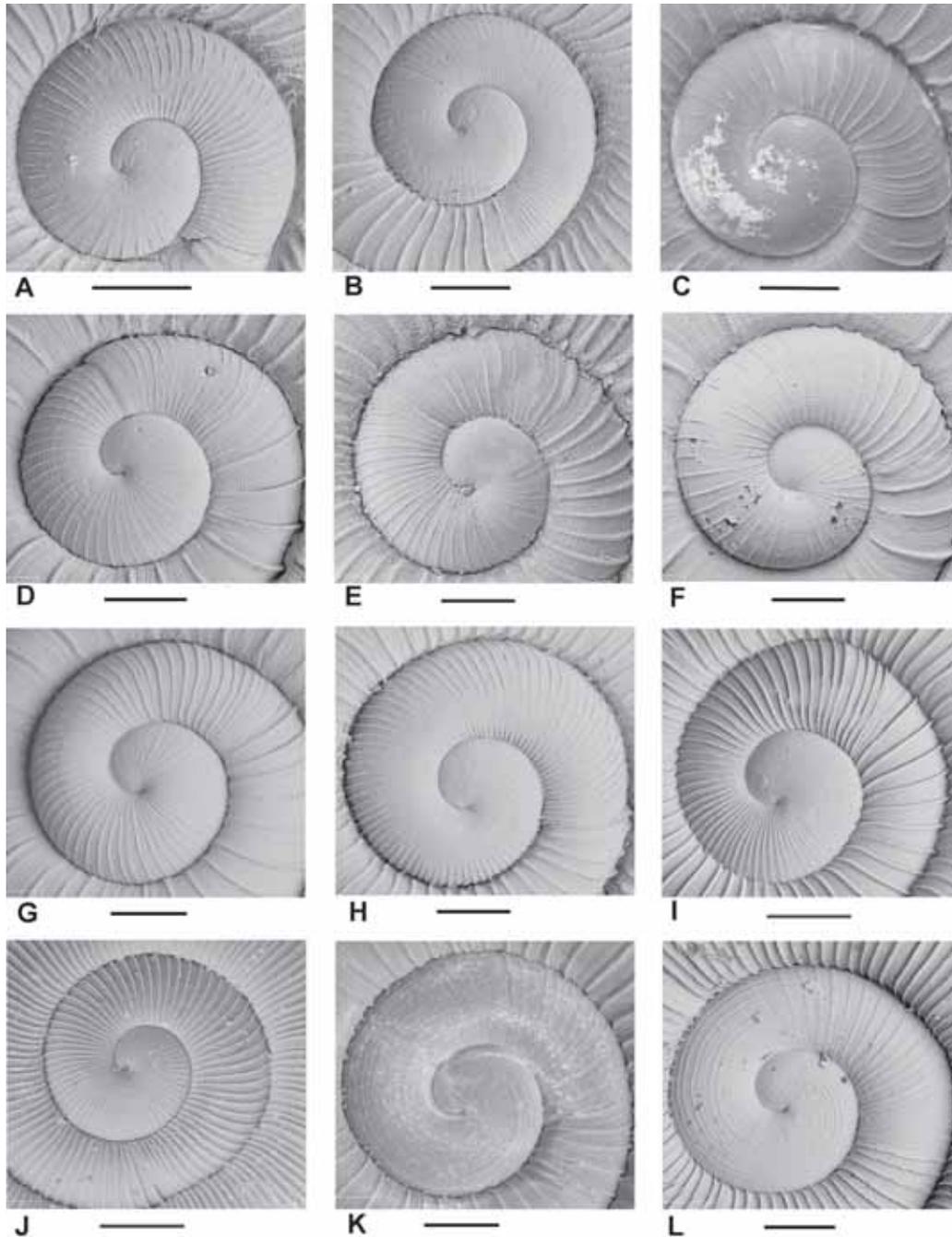


FIG. 26. Protoconch of shells from above. A, *Cralopa stroudensis* (SEQ), QMMO16857. B, *Cralopa stroudensis* (Sydney), QMMO29638. C, *Gouldiropa carlessi*, AMSC003640. D, *Sharniropa wollondillyana*, QMMO70399. E, *Sharniropa borenorensis*, AMSC205166. F, *Sharniropa xanana*, QMMO70398. G, *Acheronopa attunga*, QMMO70400. H, *Hedleyropa yarrangobillyensis*, QMMO70401. I, *Scleridoropa sarahjaneae* (Yarrangobilly), QMMO70402. J, *Scleridoropa nandewar*, QMMO70403. K, *Diphyoropa saturni*, AMSC205167. L, *Diphyoropa macleayana*, AMSC168685. Scale bars=0.15mm in K, L; 0.2mm in A-J.

considerably fewer number of radial ribs on the protoconch, the absence of an apertural sinus and less sinuated radial ribs that suggest this species is not congeneric with *C. stroudensis*. '*C. colliveri*' also differs from *C. stroudensis* in the nature of the umbilical closure which in the latter is partially due to relection of the columellar margin of the aperture over the umbilical opening rather than constriction as is the case in '*C. colliveri*'. All these differences indicate generic incompatibility, however, the generic placement of this species must await a future review that will probably need to include other Victorian and possibly Tasmanian charopids.

***Cralopa stroudensis* (Cox, 1864)**
(Figs 10, 20-22, 25-29, 34; Table 4)

Helix stroudensis Cox, 1864: 20; Tryon, 1887: 25, pl.4, figs 28-29.

Gyrocochlea stroudensis (Cox). Hedley, 1924: 217, pl. 3, figs 25-27; Iredale, 1937: 323.

Cralopa stroudensis (Cox). Iredale, 1941a: 269; Kershaw, 1956b: 8; Stanisc, 1990: 150, figs 95-97 (part); Smith, 1992: 184.

MATERIAL. HOLOTYPE: AMSC63500, E of Dungog, Stroud, NSW: (32°24.5'S, 151°58'E), Rev. R.L.King. Height of shell=1.62mm, diameter=2.56mm, H/D=0.63, D/U=8.30, ribs on last whorl =109, whorls=4. **PARATYPES.** AMSC225, 4, same data as holotype. **OTHER MATERIAL.** NSW: QMMO29638, MO12281, MO16857, MO49237, MO42140, MO20294, MO31855, MO32109, MO36809, MO37544, MO56140, MO38770, MO49239, MO55877, MO55931. SE Qld: QMMO29796, MO45173, MO28453.

DIAGNOSIS. Shell light golden brown, with moderately loosely coiled whorls, a well developed apertural sinus and strongly impressed sutures. Apex and early spire weakly elevated. Teleoconch with numerous, prominent and very strongly protractively sinuated, crowded radial ribs; mean ribs/mm = 10.08. Umbilicus closed or only very slightly open, mean D/U 7.81. Penis with two longitudinal pilasters.

DESCRIPTION. Shell very small, light golden brown, with 2.8-4.3 (mean 4.0) moderately loosely coiled whorls. Whorls weakly rounded to shouldered above and rounded below a weakly rounded periphery, well developed apertural sinus present. Shell diameter 1.63-1.33mm (mean 2.58mm). Apex and early spire very weakly elevated. Height of shell 1.02-1.73mm (mean 1.53mm), H/D 0.53-0.66 (mean 0.66mm). Protoconch of 1.5-1.7 whorls with very crowded, regularly spaced, curved radial ribs (approx. 80);

ribs of medium width; height less than or greater than width; spacing uniform; width of interstices (in multiples of rib width) 3-5 at apex. Secondary sculpture of low, crowded microspirals that cross the microradials. Teleoconch with prominent, crowded, strongly protractively sinuated, bold radial ribs. Ribs on the last whorl 68-126 (mean 88); ribs/mm 7.90-16.50 (mean 10.83); rib height less than to greater than width; straight in section; rounded on top. Rib interstices on the first post-nuclear whorl equal to width of 3-5 ribs; on the penultimate whorl equal to width of 4-5 ribs. Interstitial sculpture of weak, low to very low microradial ribs; 7-8 between ribs on first post-nuclear whorl; 6-13 between ribs on penultimate whorl. Microradial ribs with weak periostracal blades. Secondary microsculpture of prominent spiral cords that cross the microradials and form round beads at their intersection. Sutures strongly impressed. Umbilicus reduced to a pinhole and partially occluded by a reflection of the columellar edge of the aperture; occasionally closed. Umbilical width when open 0.14-0.44mm (mean 0.34mm), D/U 5.68-11-64 (mean 7.81). Aperture ovately lunate; parietal callus present. Based on 15 measured specimens (QMMO29638, MO16857, MO49237).

Genitalia with ovotestis containing two clumps of alveoli, with more than two alveolar lobes per clump. Talon stalk 1-3 times the diameter of the talon; talon circular. Penial retractor muscle less than half the length of the penis; insering onto the penis head, or at the junction of the penis and epiphallus; enters penis through a simple pore. Penis tubular; two longitudinal; pilasters present.

Pallial cavity with kidney moderately bilobed; apex of pericardial lobe reflexed. Mantle gland present.

Radula with central tooth strongly tricuspid; lateral teeth tricuspid; first and second laterals equal in width, or first lateral wider than second lateral. Mesocone of first lateral tooth triangular, or slender, slightly diamond-shaped; marginal teeth skewed towards the centre. Ectocone of outer marginal teeth not split; endocone not split; number of lateral teeth: 5-6; marginal teeth: 13-14; radular rows: 88-91. Based on 6 dissected specimens (QMMO12281, MO29638).

DISTRIBUTION AND HABITAT. Sydney area, west to the Blue Mountains, central NSW and N to the Bunya Mts, SE Qld; living under logs and rocks in subtropical and warm temperate rainforest.

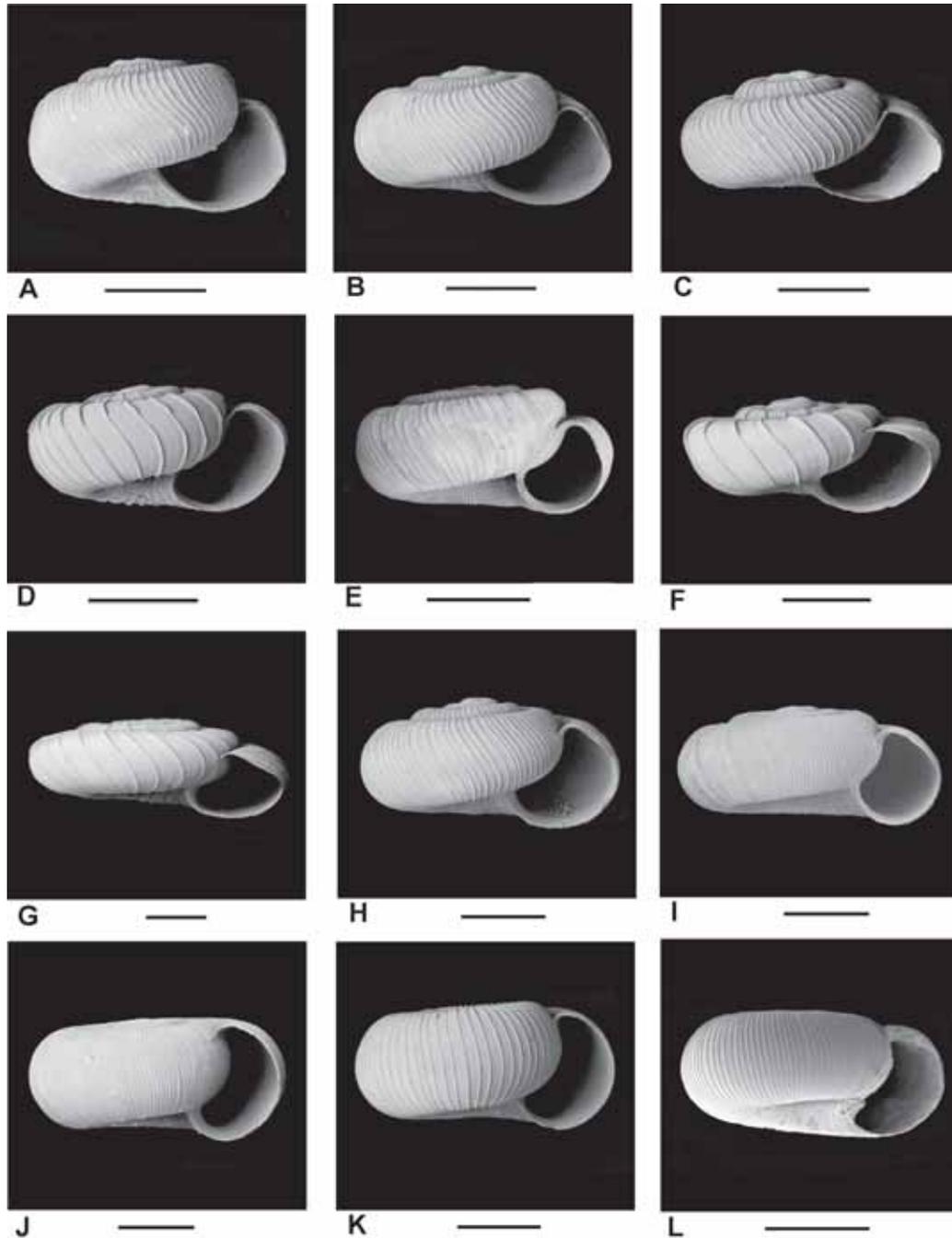


FIG. 27. Lateral view of shells. A, *Cralopa stroudensis* (SEQ), QMMO16857. B, *Cralopa stroudensis* (Sydney), QMMO29638. C, *Gouldiropa carlessi*, AMSC003640. D, *Sharniropa wollondillyana*, QMMO70399. E, *Sharniropa borenorensis*, AMSC205166. F, *Sharniropa xanana*, QMMO70398. G, *Acheronopa attunga*, QMMO70400. H, *Hedleyropa yarrangobillyensis*, QMMO70401. I, *Scleridoropa sarahjaneae* (Yarrangobilly), QMMO70402. J, *Scleridoropa nandewar*, QMMO70403. K, *Diphyoropa saturni*, AMSC205167. L, *Diphyoropa macleayana*, AMSC205274. Scale bars=1mm in A-I, K, L; 0.5mm in J.

REMARKS. The definition of *Cralopa stroudensis* presented herein differs from that of Stanisic (1990) by the exclusion of material from the limestones of the Macleay Valley, W of Kempsey, NSW (AMSC121680, C128902, C152198). The Macleay Valley specimens have much less crowded radials on the protoconch (possibly affiliated with *Gouldiropa*; Stanisic, pers. obs.) but are not dealt with in this study. *C. stroudensis* does, however, occur in the Kempsey region where it has been found in subtropical rainforest and wet sclerophyll forest adjacent to, but not on limestone outcrops.

Cralopa stroudensis shows some differences in shell features across its range (teleoconch rib spacing, shell size) but these variations display little geographic consistency and are also within the limits of observed intrapopulation variability. Most significantly this conchological variation is not reflected in any detectable change in reproductive anatomy. Shells of *C. stroudensis* can be distinguished from those of some other east Australian charopids with a closed to almost closed umbilicus eg. *Elsothera sericatula* (Pfeiffer, 1849) [Sydney region], *E. nautilodea* (Cox, 1866) [Grafton area, NE NSW], *Whiteheadia globosa* (Stanisic, 1990) comb. nov. [NSW/Qld Border Ranges] and *Gouldiropa* gen. nov. by a combination of the following features: numerous, very crowded radial ribs on the protoconch (fewer and more widely spaced in *W. globosa* and *Gouldiropa*); very crowded, strongly sinuated radial ribs on the teleoconch (more crowded and very weakly sinuated in *Elsothera*, widely spaced and almost straight in *W. globosa*); and a well-developed apertural sinus (absent in *Elsothera*, *W. globosa* and *Gouldiropa*).

***Cralopa kaputarensis* Stanisic, 1990**
(Figs 10, 20-22, 25-29)

Cralopa kaputarensis Stanisic, 1990: 153: 98; Smith 1992: 184.

MATERIAL. HOLOTYPE. QMMO16753, Mt Kaputar, summit, NSW (30°16'S, 150°10'E), among grass and litter, 9.xi.1983, JS, DP, PHC, J. Short. Height of shell=0.90mm, diameter=1.66, H/D=0.54, whorls=4.0, ribs on last whorl=80. PARATYPES. All NSW. QMMO16742, 1SC/2RC, Dawson Springs, Mt Kaputar (30°16'S, 150°10'E), under logs, in fern gully, alt. 1300m, 8.xi.1983, JS, DP, PHC, J. Short; QMMO16750, 1RC, Jokers Spring, Mt Kaputar (30°16'S, 150°10'E), edges of rocky creek bed, among lichens, alt. 1100m, 8.ix.1983, JS, DP, PHC, J. Short. OTHER MATERIAL. QMMO49167, MO49175.

DIAGNOSIS. Shell very small, dark brown with moderately loosely coiled whorls and a barely

visible apertural sinus; whorls flattened above a rounded periphery. Spire and early apex barely elevated. Teleoconch with numerous, crowded, prominent strongly protractively sinuated radial ribs (mean ribs/mm 13.94). Umbilicus reduced to a slight chink. Penis with two longitudinal and bifurcated pilasters present.

DISTRIBUTION AND HABITAT. From Mt Kaputar, Nandewar Ranges, NSW; in moist woodland living under rocks, logs and among lichen near springs.

REMARKS. *Cralopa kaputarensis* differs from *G. carlessi* by its smaller size, in having a more closed umbilicus and a greater number of radial ribs on the protoconch and teleoconch. *C. kaputarensis* is still only known from summit area of Mt Kaputar. However, this could be an artefact of collecting effort since most areas in and around these ranges still need to be investigated. Additional specimens collected since 1990 have not altered the species profile of Stanisic (1990).

***Gouldiropa* gen. nov.**

ETYMOLOGY. In honour of the late Stephen Jay Gould.

TYPE SPECIES. *Cralopa carlessi* Stanisic, 1990; herein designated.

DIAGNOSIS. Shell very small, dark brown, with moderately loosely coiled whorls and strongly impressed sutures; apertural sinus absent or only weakly developed. Protoconch with relatively widely spaced, crowded curved radial ribs (approx. 40) and numerous, regularly crowded, low continuous spiral cords that cross the radial ribs. Teleoconch with numerous, bold, weakly to very strongly protractively sinuated, moderately crowded to very widely spaced radial ribs. Interstitial sculpture with microspiral cords stronger than microradial ribs, beading at their intersection barely noticeable, obscured by strength of microspiral cords. Umbilicus closed or only slightly open. Columellar edge of aperture weakly reflected across the umbilical opening. Kidney moderately to strongly bilobed with reflexed apex on pericardial lobe. Penis with two longitudinal pilasters that may be divided.

DISTRIBUTION AND HABITAT. New England Bioregion. Species occur on limestone outcrops associated with vine thicket and in scattered moist refugia on volcanic rocks. The species live under rocks among vine thicket and in wet sclerophyll forest.

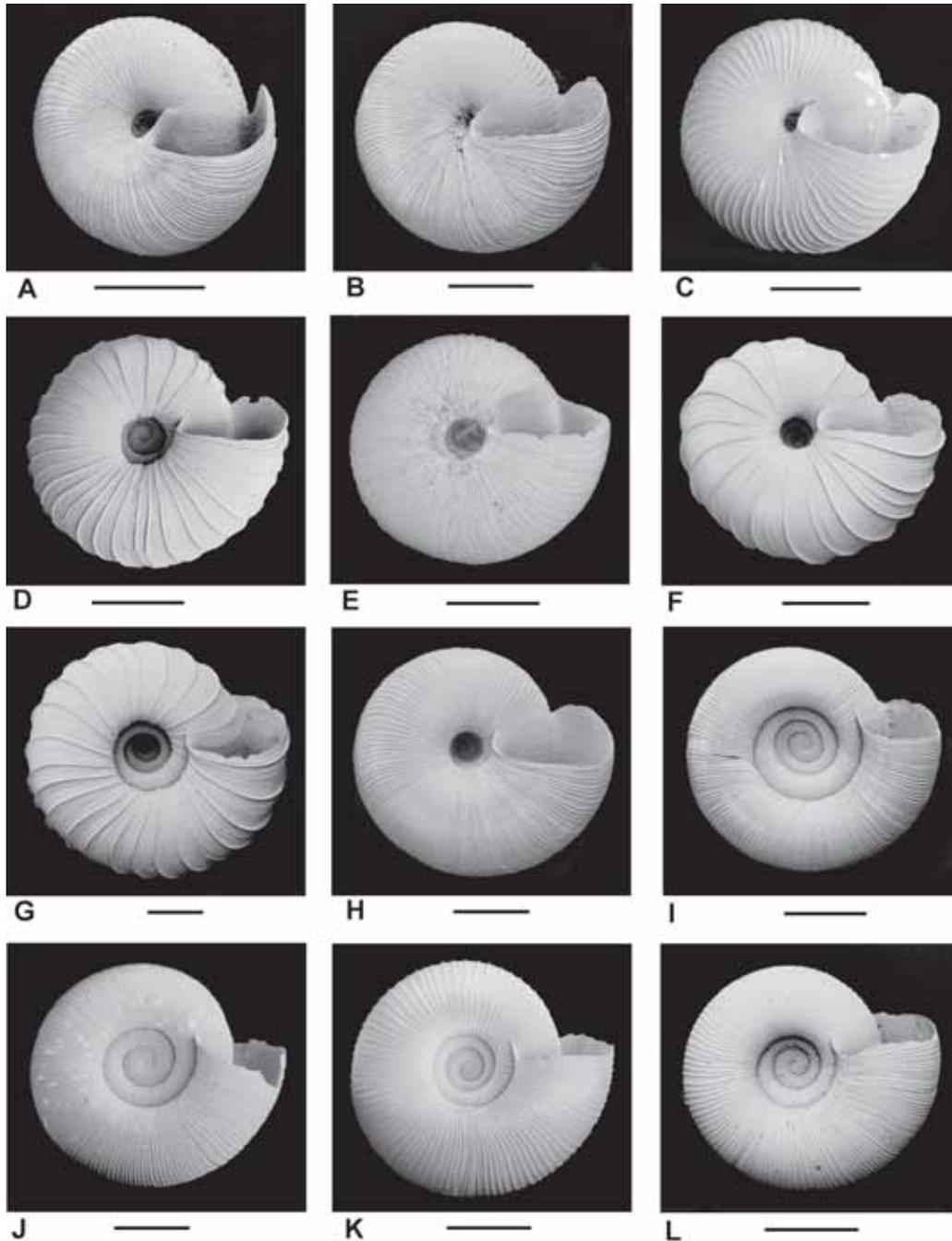


FIG. 28. Ventral view of shells. A, *Cralopa stroudensis* (SEQ), QMMO16857. B, *Cralopa stroudensis* (Sydney), QMMO29638. C, *Gouldiropa carlessi*, AMSC003640. D, *Sharniropa wollondillyana*, QMMO70399. E, *Sharniropa borenorensis*, AMSC205166. F, *Sharniropa xanana*, QMMO70398. G, *Acheronopa attunga*, QMMO70400. H, *Hedleyropa yarrangobillyensis*, QMMO70401. I, *Scleridoropa sarahjaneae* (Yarrangobilly), QMMO70402. J, *Scleridoropa nandewar*, QMMO70403. K, *Diphyoropa saturni*, AMSC205167. L, *Diphyoropa macleayana*, AMSC168685. Scale bars=0.5mm in J; 0.8mm in D; 1mm in A-C, E-I, K, L.

REMARKS. *Gouldiropa* sp. nov. is similar to *Cralopa* but differs most significantly in having fewer and less crowded ribs on the protoconch; fewer and less crowded teleoconch ribs that are bolder and much less sinuated than in *Cralopa*; and in lacking an apertural sinus.

Gouldiropa carlessi (Stanisic, 1990) comb. nov.
(Figs 10, 20-22, 25-29, 33-34; Table 4)

Cralopa carlessi Stanisic, 1990:156, figs 101-103 (in part);
Smith, 1992: 184 (in part).

MATERIAL. HOLOTYPE: NSW: AMSC123538, Inverell (29°46.5'S, 151°6.8'E), C.T.Musson. Height of shell=2.04, diameter=3.62, H/D=0.56, number of whorls=4.5, ribs on last whorl=70. PARATYPES. AMSC153716, C3640, C28496, C123610. OTHER MATERIAL. AMSC164886, QMMO49195, MO52694, MO32090, MO49207.

DIAGNOSIS. Shell very small, brown with moderately loosely coiled whorls and a barely visible apertural sinus; whorls flattened above a rounded periphery. Spire and early apex slightly elevated. Teleoconch with numerous prominent strongly protractively sinuated radial ribs (mean ribs/mm 6.03). Umbilicus very slightly open, diameter range 0.26-0.43mm, mean D/U 5.49. Penis with two longitudinal pilasters.

DESCRIPTION. (Amended from Stanisic, 1990). Shell very small golden brown with 3.8-4.1 (mean 4.0) moderately loosely coiled whorls; apertural sinus very weakly developed. Shell diameter 2.96-3.44mm (mean 3.20mm). Apex and early spire weakly elevated. Height of shell 1.61-1.88mm (mean 1.76mm), H/D 0.49-0.61 (mean 0.56). Protoconch with 1.5 whorls. Apical sculpture primarily radial consisting of approximately 40 regularly and widely spaced, curved radial ribs; ribs with height less than width; width of interstices (in multiples of rib width) 4-8 at apex. Secondary sculpture of continuous, regularly crowded spiral cords, crossing the radial ribs. Teleoconch with prominent strongly protractively sinuated, variably spaced radial ribs that become more spaced on the last whorl; 46-74 (mean 60) ribs on the last whorl. Ribs/mm 5.14-6.91 (mean 6.03). Ribs wide, height equal to width, straight in section, rounded on top. Interstices on the 1st post-nuclear whorl equal to width of 4-6 ribs; on the penultimate whorl, greater than or equal to width of 6 ribs. Interstitial sculpture of very low microradial ribs and stronger microspiral cords; 10-12 microradials between ribs on 1st post-nuclear whorl; 12-16 between ribs on penultimate whorl. Microspiral cords crossing

microradials but not forming distinct beads at their intersection. Umbilicus very narrowly open, U-shaped. Umbilical width 0.26-0.43mm (mean 0.32mm), D/U 5.21-5.77 (mean 5.49). Aperture ovately lunate. Whorls rounded above and below a weakly rounded periphery, sutures moderately impressed; parietal callus present. Based on 8 measured specimens (AMSC3640).

Genitalia with ovotestis containing two clumps of alveoli, with two alveolar lobes per clump. Talon stalk 1-3 times the diameter of the talon; talon circular. Penial retractor muscle less than half the length of the penis, inserting at the junction of the penis and epiphallus. Epiphallus entering penis through a simple pore; shorter than penis; narrower than the vas deferens. Penis tubular, internally with two longitudinal pilasters. Vagina shorter than penis. Based on 8 measured specimens (AMSC3640).

Pallial cavity with moderately bilobed kidney, pericarial lobe reflexed. Mantle gland present.

Radula: central tooth strongly tricuspid; lateral teeth tricuspid; ectocone of outer marginal teeth split into 2-3 teeth; endocone not split. Lateral teeth: 5; marginal teeth: 14; radular rows: 106. Based on 1 dissected specimen (QMMO32080).

DISTRIBUTION AND HABITAT. N New England Tableland, NSW; under rocks on limestone outcrops covered in vine thicket or in moist sclerophyll forest.

REMARKS. *Gouldiropa carlessi* Stanisic (1990) comb. nov. is herein restricted to include only populations from the northern part of the New England Tableland, NSW. Stanisic (1990) considered that this species had an extensive range from Wee Jasper, SE NSW to Inverell, NE NSW wherein intraspecific variability included considerable differences in rib spacing, spire protrusion and umbilical width. That study, however, was constrained by a paucity of material for examination. Since that time additional specimens have become available for scrutiny and have enabled a more detailed analysis of these characters to be undertaken. A closer inspection indicates that a number of species were involved. Unfortunately, and somewhat hastily, some of these were made paratypes for the nominal species, a salutary lesson for using only topotypes in the formal type series. Specimens cited by Stanisic (1990) as coming from limestones on Glenrock Station (AMSC340138, formerly AMSC144200) are assigned to *Sharniropa xanana*. Specimens from SE NSW (Tuglow Caves [AMSC124279],

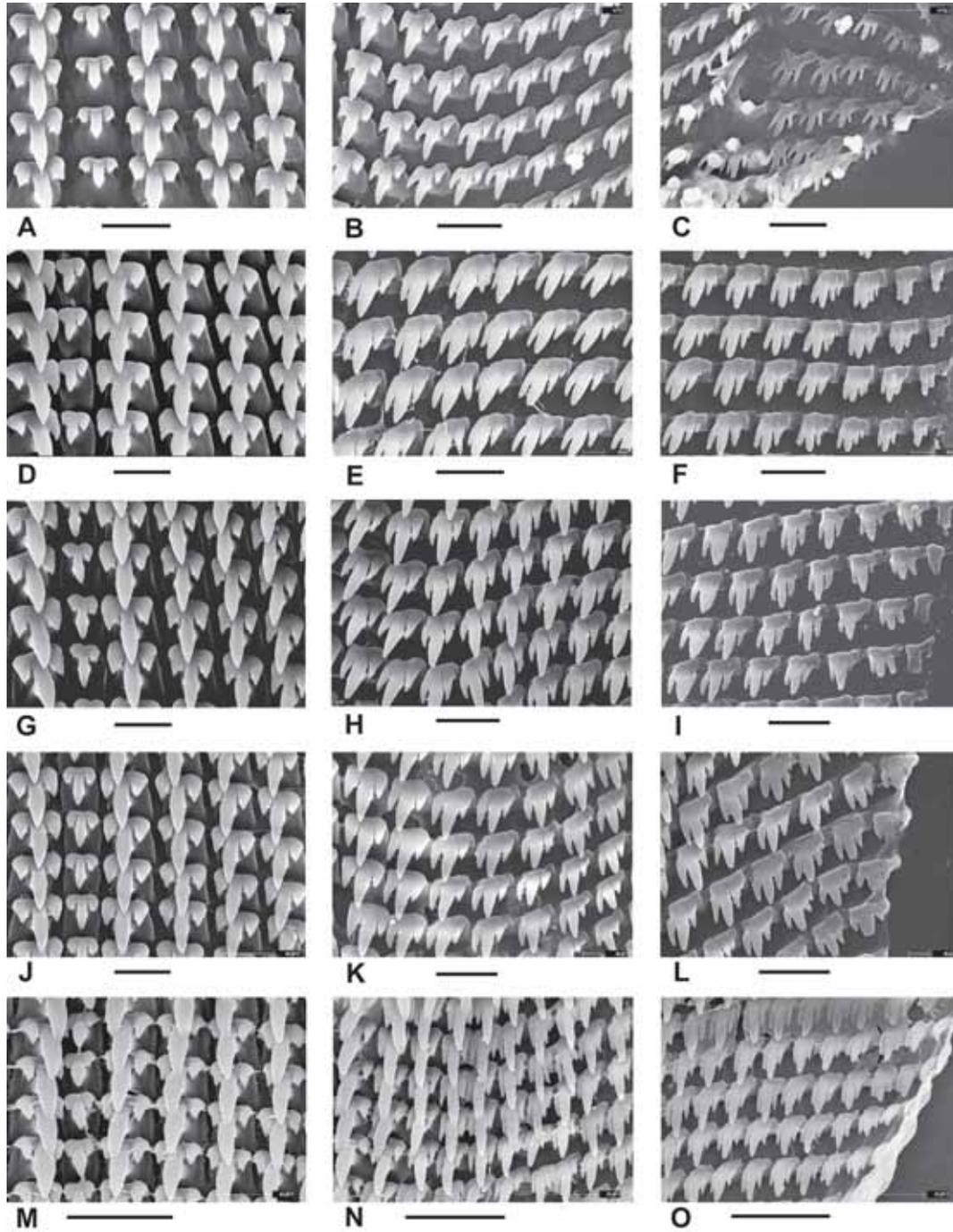


FIG. 29. Radula. A-C, *Cralopa stroudensis*, QMMO29638. D-F, *Gouldiropa carlessi*, QMMO32080. G-I, *Gouldiropa kaputarensis*, QMMO49175. J-L, *Sharniropa wollondillyana*, QMMO29241. M-O, *Acheronopa attunga*, QMMO49218. Scale bars=0.01mm in A-L; 0.02mm in M-O.

Jenolan Caves [QMMO17295], Wee Jasper [AMSC142961] and Wombeyan Caves [AMSC142967]) probably represent several species and are excluded. They will be dealt with elsewhere once more material becomes available for study.

Gouldiropa carlessi is distinguished from *G. kaputarensis* by its larger size, flatter whorls, slightly more open umbilicus, more elevated spire and by having fewer ribs on the teleoconch. *Sharniropa xanana* from the southern part of the New England Tableland has shouldered whorls, fewer ribs on the teleoconch and a more open umbilicus. *G. carlessi* is sympatric with the similarly shaped *Acheronopa attunga* but is readily distinguished from that species by its smaller size, almost closed umbilicus (widely open in *A. attunga*) and in having more crowded radial ribs on the teleoconch.

Sharniropa gen. nov.

ETYMOLOGY. For Sham Rose.

TYPE SPECIES. *Sharniropa wollondillyana* sp. nov.; herein designated.

DIAGNOSIS. Shell very small, dark brown, with moderately loosely coiled whorls and strongly impressed sutures; apertural sinus absent. Protoconch with relatively widely spaced, crowded curved radial ribs (approx. 45-50) and numerous, regularly crowded, low continuous spiral cords that cross the radial ribs. Teleoconch with numerous, bold, weakly to very strongly protractively sinuated, crowded to very widely spaced radial ribs. Interstitial sculpture with microspiral cords stronger than microradial ribs, beading at their intersection weak to barely noticeable, obscured by strength of microspiral cords. Umbilicus narrowly open U-shaped. Columellar edge of aperture not reflected across the umbilical opening. Kidney moderately to strongly bilobed with reflexed apex on pericardial lobe. Penis internally with two longitudinal pilasters.

DISTRIBUTION AND HABITAT. N part of the Southern Tableland Bioregion to the S end of the New England Tableland Bioregion; only on limestone outcrops living among limestone talus.

REMARKS. *Sharniropa* gen. nov. differs from *Gouldiropa* mainly in the coiling pattern of the shell. In *Sharniropa* narrowing of the umbilicus is caused by constriction, in *Gouldiropa* it is a combination of constriction and columellar reflection. *Acheronopa* differs in having a greater

number of apical radial ribs (approx. 60), a larger, flatter shell with evenly coiled whorls and a wider umbilicus caused by gradual decoiling.

Sharniropa wollondillyana sp. nov. (Figs 10, 23, 25-29, 31-34; Table 5)

ETYMOLOGY. For the Wollondilly River.

MATERIAL. HOLOTYPE. QMMO70399, Abercrombie Caves, SW Oberon, NSW, (33°54'42"S, 149°21'36"E), remnant vt/ lm, under logs and rocks, 13.i.1993, JS, JC. Height of shell=1.43mm, diameter=2.57mm, H/D=0.56, D/U=4.51, number of whorls=3.9, ribs on last whorl=31. PARATYPES. All NSW. QMMO44771, 48RC, same data as holotype; QMMO29241, 1RC, QMMO37781, 10RC, Abercrombie Caves, SW Oberon, lm, under rocks and in litter, 8.i.1990, JS, JC; AMSC157323, 7RC, SW of Bathurst, Bombah, 100m S of Abercrombie Caves camping ground (33°54.8'S, 149°21.5'E), lm, under rocks and soil on limestone hill, 6.vi.1982, MS; AMSC158364, many RC, S of Blayney, Abercrombie Cave, near Bushranger Cave (33°55'S, 149°21'E), vii.1982, O.L. Griffiths. OTHER MATERIAL. AMSC137245.

DIAGNOSIS. Shell very small, brown with moderately loosely coiled whorls; whorls weakly shouldered above a rounded periphery. Teleoconch with widely spaced, prominent, strongly protractively sinuated radial ribs (mean ribs/mm 3.93). Umbilicus open, very narrow U-shaped; umbilical diameter range 0.55-0.73mm, mean D/U 4.43. Penis with two longitudinal pilasters.

DESCRIPTION. Shell very small, colour brown with 3.7-4.3 (mean 4.0) moderately loosely coiled whorls. Shell diameter 2.27-3.34mm (mean 2.84mm). Apex and early spire barely elevated. Height of shell 1.21-1.54mm (mean 1.43mm), H/D 0.45-0.58 (mean 0.51). Protoconch of 1.5-1.8 whorls with sculpture of approximately 45-50, crowded, curved, regularly spaced radial ribs, ribs of medium width; height equal to width, width of interstices (in multiples of rib width) 6-8 at apex. Secondary sculpture of low continuous, croded and regularly spaced spiral cords that cross the radial ribs. Teleoconch sculpture of widely and regularly spaced (becoming more crowded at the end of the last whorl), strongly protractively sinuated radial ribs; 26-34 (mean 35) ribs on the last whorl, ribs/mm 2.79-5.00 (mean 3.93). Ribs wide; height greater than width; straight in section; rounded on top; interstices on the first post-nuclear whorl equal to width of 8-10 ribs; interstices on the penultimate whorl equal to width of 8 ribs. Interstitial sculpture of weak microradial ribs 20 between ribs on first post-nuclear whorl; 20 between ribs on

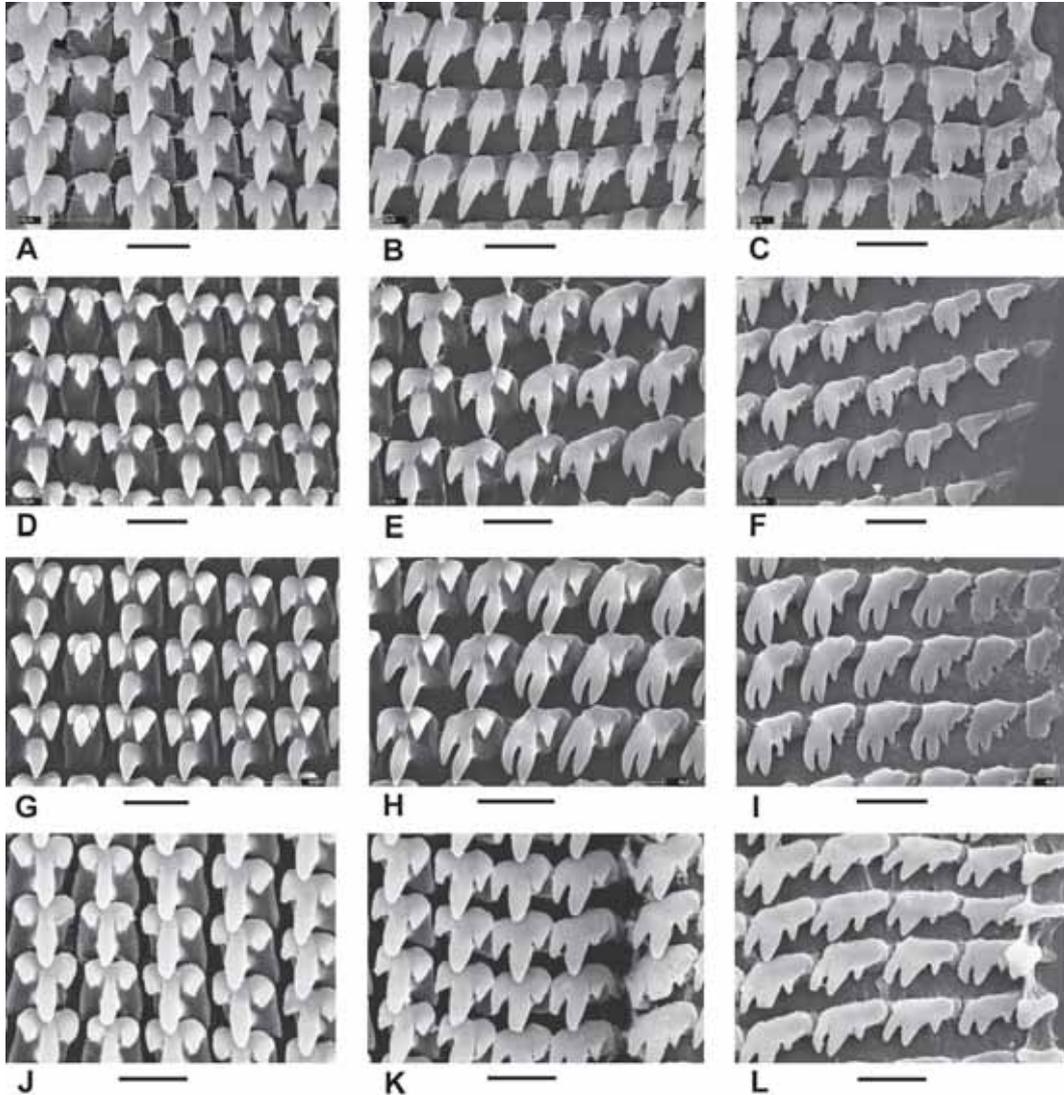


FIG. 30. Radula. A-C, *Hedleyropa yarrangobillyensis*, QMMO39840. D-F, *Scleridoropa sarahjaneae* (Yarrangobilly), QMMO39974. G-I, *Scleridoropa nandewar*, QMMO49158. J-L, *Diphyoropa macleayana*, AMSC162184. Scale bars=0.01mm.

penultimate whorl. Secondary sculpture of more prominent, low microspiral cords with weak beading at their intersection with the microradial ribs. Umbilicus moderately wide U-shaped, diameter 0.55-0.73mm (mean 0.64mm), D/U 3.99-5.03 (mean 4.43). Sutures impressed, whorls weakly shouldered above and rounded below a rounded periphery. Aperture ovately to roundly lunate. Based on 19 measured specimens (QMMO44771, MO70399).

Genitalia with ovotestis containing two clumps of alveoli, with two alveolar lobes per clump. Talon stalk 1-3 times the diameter of the talon; talon circular. Penial retractor muscle less than half the length of the penis, inserting at the junction of the penis and epiphallus. Epiphallus shorter than penis; narrower than the vas deferens; entering penis through a simple pore. Penis tubular, two longitudinal pilasters present.

Pallial cavity with kidney moderately bilobed; apex of pericardial lobe reflexed. Mantle gland present.

Radula with central tooth strongly tricuspid; lateral teeth tricuspid; ectocone of outer marginal teeth not split; endocone not split. Number of lateral teeth: 6; marginal teeth: 12; radular rows: 97. Based on 3 dissected specimens (QMMO29241).

DISTRIBUTION AND HABITAT. Abercrombie limestones, NSW; under logs and rocks.

REMARKS. *Sharniropa wollondillyana* sp. nov. differs from *S. boronorensis* in having fewer radial ribs on the teleoconch and a larger umbilicus. *S. wollondillyana* is superficially similar to the sympatric *Decoriropa lirata* but differs primarily in having fewer apical radial ribs. *D. lirata* is also smaller than *S. wollondillyana*, has a relatively larger umbilicus and more crowded ribs on the teleoconch.

Sharniropa borenorensis sp. nov.
(Figs 23, 25-28; Table 4)

ETYMOLOGY. For the type locality.

MATERIAL. HOLOTYPE: AMSC205166, Borenore Caves, W side of large cave entrance W of Borenore, W of Orange, NSW (33°15.14'S, 148°56.19'E), in soil and grass among limestone boulders, vi.1983, MS. Height of shell=1.50mm, diameter=2.77mm, H/D=0.54, D/U=5.54, number of whorls=3.7, ribs on last whorl=50. **PARATYPES.** All NSW. AMSC157300, 13RC, same data as holotype; QMMO44745, 12RC, Borenore Caves, c.18.6km WNW Orange (33°15'06"S, 148°55'42"E), lm/ew, in litter under rocks, 11.i.1993, JS, JC; QMMO37496, 30RC, Borenore Caves, c.10km W Orange (33°15'S, 148°56'E), remnant vt/lm, among rocks, 13.i.1991, JS.

DIAGNOSIS. Shell very small, brown, with moderately loosely coiled; whorls weakly shouldered above a rounded periphery. Teleoconch with crowded, prominent, strongly protractively sinuated radial ribs (mean ribs/mm 7.13). Umbilicus open, very narrow U-shaped; umbilical diameter range 0.50-0.71mm, mean D/U 4.95. Anatomy unknown.

DESCRIPTION. Shell very small, brown, with 3.7-4.2 (mean 4.0) moderately loosely to evenly coiled whorls. Shell diameter 2.64-3.11mm (mean 2.84mm). Apex and early spire barely elevated. Height of shell 1.33-1.54mm (mean 1.42mm), H/D 0.45-0.54 (mean 0.50). Protoconch of 1.5-1.7 whorls with curved, regularly spaced radial ribs; ribs of medium width, height less than width, width of interstices

(in multiples of rib width) 5 at apex. Secondary sculpture of low, continuous regular spaced spiral cords that cross the radial ribs. Teleoconch sculpture of crowded, regularly spaced (but becoming more crowded toward the end of the last whorl), strongly protractively sinuated radial ribs; 50-79 (mean 64) ribs on the last whorl, ribs/mm 5.75-8.09 (mean 7.13). Ribs wide; height equal to width; straight in section; rounded on top. Rib interstices on the first post-nuclear whorl equal to width of 3-4 ribs. Interstitial sculpture of microradial ribs, 5-6 between ribs on first post-nuclear whorl; 8 between ribs on penultimate whorl. Secondary microsculpture of prominent low, regularly spaced microspiral cords that cross the microradial ribs without forming distinct beads. Umbilicus very narrow U-shaped, diameter 0.50-0.71mm (mean 0.58mm), D/U 4.34-5.54 (mean 4.95). Sutures impressed, whorls weakly shouldered above and rounded below a weakly rounded periphery; Aperture roundly to ovately lunate; parietal callus present. Based on 8 measured specimens (AMSC157300, C205166).

Anatomy unknown.

DISTRIBUTION AND HABITAT. Known only from the type locality at the Borenore Caves limestone outcrop; found under grass amongst limestone boulders.

REMARKS. *Sharniropa borenorensis* sp. nov. is similar to *S. wollondillyana* from the Wombeyan and Abercrombie limestone outcrops. It differs mainly from the latter species in having a greater number of radial ribs on the last whorl (50-79, mean 64 compared with 26-34, mean 35 for *S. wollondillyana*) and a smaller umbilicus.

Sharniropa xanana sp. nov.
(Figs 23, 25-28; Table 4)

Cralopa carlessi Stanisic, 1990:156 (in part), figs 101d-e; 102a-e; Smith, 1992: 184 (in part).

ETYMOLOGY. For Xanana Gusmao, President of East Timor.

MATERIAL. HOLOTYPE: QMMO70398, Timor Caves, via Murrurundi, NSW (31°41'S, 151°08'E), lm/remnant vt, in litter, 25.ix.1989, JS, DP. Height of shell=1.74mm, diameter=3.34mm, H/D=0.52, D/U=5.96, number of whorls=4.1, ribs on last whorl=18. **PARATYPES.** All NSW. QMMO37735, 29RC, AMSC205159, 5RC, same data as holotype; QMMO32065, 1 juvenile SC/6RC, in soil among rocks, otherwise same data as holotype. **OTHER MATERIAL.** QMMO56149, AMSC144200.

DIAGNOSIS. Shell very small, light golden brown, with moderately loosely coiled whorls

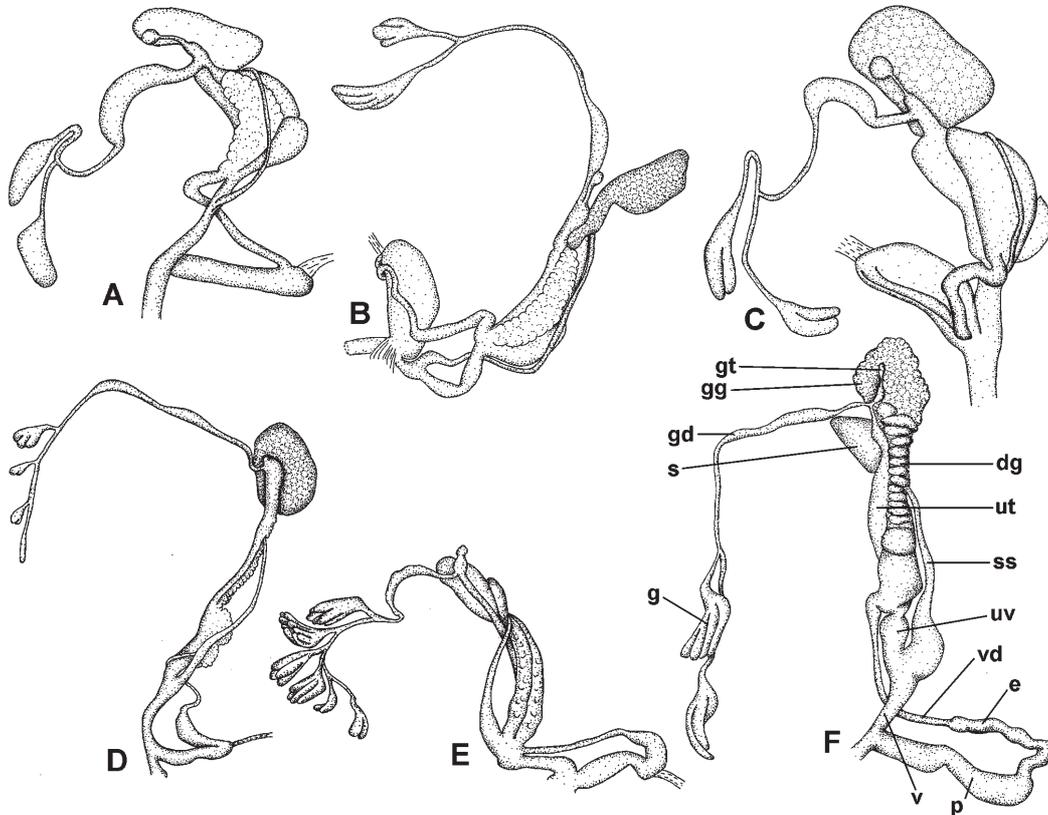


FIG. 31. Reproductive system. A, *Sharniropa wollondillyana*, QMMO29241. B, *Acheronopa attunga*, QMMO49218. C, *Hedleyropa yarrangobillyensis*, QMMO39840. D, *Scleridoropa nandewar*, QMMO49158. E, *Scleridoropa sarahjaneae* (Yarrangobilly), QMMO39974. F, *Diphyoropa macleayana*, AMSC162184. Scale bar=2.5mm in A and C, 2mm in B, and 1.6mm in all others. dg, prostate; e, epiphallus; g, ovotestis; gd, hermaphrodite duct; gg, albumen gland; gt, talon; p, penis; prm, penis retractor muscle; s, spermatheca; ss, spermathecal stalk; ut, uterus; uv, free oviduct; v, vagina; vd, vas deferens.

and a barely visible apertural sinus; whorls strongly shouldered above a rounded periphery. Spire and early apex flat to barely elevated. Teleoconch with relatively few, widely spaced, prominent, strongly protractively sinuated radial ribs (mean ribs/mm 1.86). Umbilicus open, very narrow U-shaped; umbilical diameter range 0.45-0.62mm, mean D/U 6.41. Anatomy unknown.

DESCRIPTION. Shell very small, light golden brown, with 3.9-4.5 (mean 4.09) loosely coiled whorls. Shell diameter 3.04-3.61mm (mean 3.31). Apex and early spire very weakly elevated. Height of shell 1.45-1.86mm (1.60mm), H/D 0.44-0.52 (mean 0.48). Protoconch relatively large with sculpture of approximately 40, regularly and widely spaced, weakly curved

radial ribs; ribs of medium width; height less than width; width of interstices (in multiples of rib width) 3-5 at apex. Secondary sculpture of crowded, continuous microspiral cords that cross the microradial ribs. Teleoconch with prominent, regularly spaced, strongly protractively sinuated, bold radial ribs, 16-25 (mean 19) ribs on the last whorl. Ribs/mm 1.65-2.20 (mean 1.86). Ribs greater in height than width; straight in section; rounded on top. Rib interstices on the first post-nuclear whorl equal to width of 13 ribs; on the penultimate whorl, equal to width of 13 ribs. Interstitial sculpture of very low microradial ribs and stronger microspiral cords; 30 microradials between ribs on first post-nuclear whorl, becoming almost impossible to count on penultimate whorl; beading indistinct due to

TABLE 4. Shell measurements for species of *Coricudgia*, *Marilyniropa*, *Cralopa*, *Gouldiropa* and *Sharniropa*. (Abbreviations as in Table 1).

Measurement	<i>Coricudgia wollemiana</i>	<i>Marilyniropa jenolanensis</i>	<i>Cralopa stroudensis</i>	<i>Gouldiropa carlessi</i>	<i>Sharniropa borenorensis</i>	<i>Sharniropa xanana</i>
N	10 (*9; **4; ***3)	23	15	10	8	9
D	1.62-4.02 (3.304) ± 0.75	2.96-3.65 (3.24) ± 0.194	1.63-3.13 (2.58) ± 0.35	2.66-3.84 (3.21) ± 0.32	2.64-3.11 (2.841) ± 0.186	3.04-3.61 (3.307) ± 0.204
PW	1.7-1.8 (1.775) ± 0.05 **	1.5-1.7 (1.587) ± 0.069	1.5-1.7 (1.59) ± 0.07	1.5	1.5-1.7 (1.563) ± 0.074	1.5-1.7 (1.589) ± 0.06
TW	1.8-4.3 (3.1) ± 1.253 ***	2.6-3.2 (2.922) ± 0.165	1.3-2.7 (2.38) ± 0.33	2.2-2.6 (2.43) ± 0.12	2.2-2.7 (2.425) ± 0.158	2.3-2.8 (2.5) ± 0.141
NW	3.6-6.1 (4.9) ± 1.253 ***	4.1-4.8 (4.509) ± 0.165	2.8-4.3 (3.97) ± 0.36	3.7-4.1 (3.93) ± 0.12	3.7-4.2 (3.987) ± 0.155	3.9-4.5 (4.089) ± 0.169
H	0.83-2.21 (1.691) ± 0.435	1.33-1.79 (1.549) ± 0.146	1.02-1.73 (1.53) ± 0.17	1.31-2.03 (1.74) ± 0.19	1.33-1.54 (1.421) ± 0.071	1.45-1.86 (1.6) ± 0.133
SP	0.06-0.47 (0.259) ± 0.14	0.11-0.41 (0.25) ± 0.084	0.05-0.18 (0.13) ± 0.04	0.1-0.33 (0.24) ± 0.07	0.09-0.21 (0.154) ± 0.038	0.06-0.3 (0.211) ± 0.079
AH/AW	0.75-1.14 (0.92) ± 0.11	0.78-0.98 (0.9) ± 0.05	0.81-1.11 (0.9) ± 0.08	0.77-0.93 (0.84) ± 0.06	0.77-0.91 (0.84) ± 0.05	0.65-0.79 (0.74) ± 0.05
UMB	0.55-1.15 (0.938) ± 0.177	0.73-1.07 (0.888) ± 0.087	0.14-0.44 (0.34) ± 0.07	0.26-0.54 (0.36) ± 0.1	0.5-0.71 (0.58) ± 0.083	0.45-0.62 (0.522) ± 0.059
RIB	28-47 (40.222) ± 6.36 *	35-61 (47.087) ± 7.366	68-126 (88.73) ± 16.45	28-74 (56.4) ± 13.62	50-79 (63.625) ± 8.193	16-25 (19.444) ± 3.206
RIBS/MM	3.008-5.502 (4.089) ± 0.695 *	3.764-6.078 (4.616) ± 0.588	7.904-16.50 (10.83) ± 2.241	3.35-6.85 (5.56) ± 1.13	5.746-8.086 (7.125) ± 0.735	1.649-2.204 (1.862) ± 0.201
H/D	0.45-0.55 (0.51) ± 0.03	0.43-0.55 (0.48) ± 0.03	0.53-0.66 (0.6) ± 0.04	0.49-0.58 (0.54) ± 0.02	0.45-0.54 (0.5) ± 0.03	0.44-0.52 (0.48) ± 0.03
D/U	2.95-3.8 (3.49) ± 0.23	3.33-4.05 (3.67) ± 0.22	5.68-11.64 (7.81) ± 1.63	5.22-13.23 (9.57) ± 2.55	4.34-5.54 (4.95) ± 0.4	5.29-7.85 (6.41) ± 0.91

strength of microspiral cords. Sutures impressed, whorls strongly shouldered above and rounded below a weakly rounded periphery. Sutures strongly impressed. Umbilicus very small, narrow U-shaped. Umbilical width 0.45-0.62mm (mean 0.52mm), D/U 5.29-7.85 (mean 6.41). Aperture ovately lunate, parietal callus present. Based on 9 measured specimens (QMMO32065, MO37735, MO70398).

DISTRIBUTION AND HABITAT. Limestone outcrops at Timor Caves and Glenrock Stn, NE of Scone, NSW; in litter among limestone talus.

REMARKS. *Sharniropa xanana* sp. nov. differs from its congeners by its strongly shouldered whorls, and relatively sparse teleoconch ribbing. Superficially the species bears a greater similarity to *Acheronopa attunga*. Both have a flattened shell with bold, widely spaced radial ribs. However, *S. xanana* is smaller, has a larger protoconch, fewer, more loosely coiled and more shouldered whorls, microsculpture with comparatively indistinct beading and a more closed umbilicus. This species was considered to be conspecific with *Gouldiropa carlessi* Stanistic, 1990 comb. nov. by Stanistic (1990).

The Timor and Glenrock limestone outcrops are among open woodland. Vegetation on the outcrops is degraded due mainly to human activity (fires, land clearing) but there is evidence that vine thicket may have been present on these in the past (Stanistic, pers. obs.).

Acheronopa gen. nov.

ETYMOLOGY. Greek *Acheron*, river in the nether world; alluding to the underground streams that have formed many of the caverns present in limestone formations.

TYPE SPECIES. *Archeronopa attunga* sp. nov.; herein designated.

DIAGNOSIS. Shell very small, brown, strongly depressed (mean H/D 0.40), with flattened, evenly coiled whorls. Apical sculpture of relatively crowded, curved radial ribs (approx. 60) and numerous, weaker, continuous low microspiral cords. Teleoconch with strongly sinuated, very widely spaced, bold radial ribs. Secondary microsculpture of low microspiral cords and microradial riblets forming beads at their intersection. Kidney moderately bilobed with apex of pericardial lobe reflexed. Umbilicus

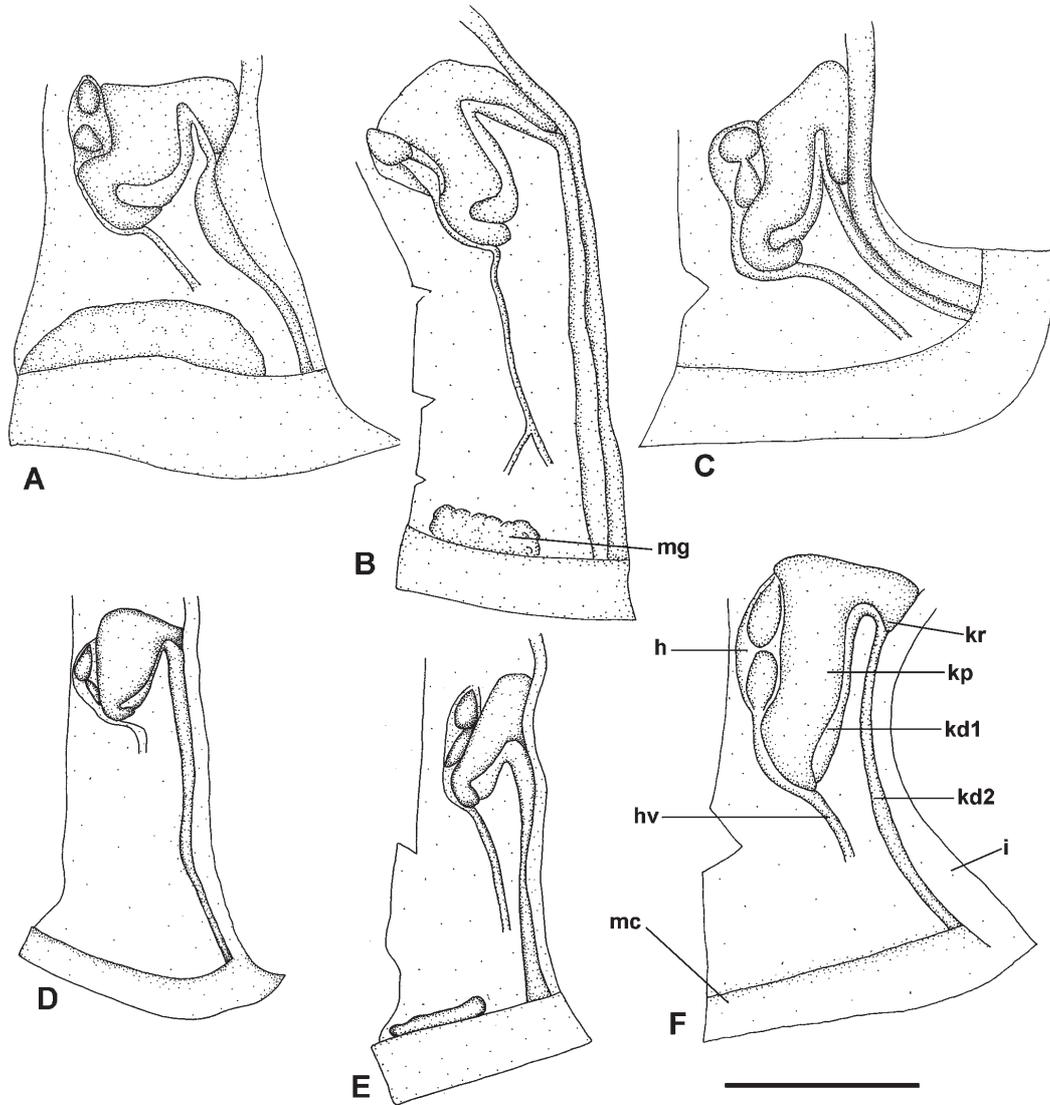


FIG. 32. Pallial cavity. A, *Sharniropa wollondillyana*, QMMO29241. B, *Acheronopa attunga*, QMMO49218. C, *Hedleyropa yarrangobillyensis*, QMMO39840. D, *Scleridoropa nandewar*, QMMO49158. E, *Scleridoropa sarahjaneae*, QMMO39974. F, *Diphyoropa macleayana*, AMSC162184. Scale bar=2mm in A and F, 1.6mm in B, and 1.28mm in all others. Abbreviations: h, heart; hv, principal pulmonary vein; i, intestine; kd1, primary ureter; kd2, secondary ureter; kp, pericardial lobe of kidney; kr, rectal lobe of kidney; mc, mantle collar; mg, mantle gland.

wide V-shaped. Penis with 3 longitudinal pilasters.

DISTRIBUTION AND HABITAT. Yarramanbully limestones near Attunga; between limestone talus on limestone karst covered in remnant vine thicket

REMARKS. *Acheronopa* gen. nov. is most similar to *Sharniropa* gen. nov. from the Timor/Glenrock limestone outcrops and *Gouldiropa* gen. nov. However, it differs significantly in having more crowded microradial ribs on the protoconch and in having more flattened whorls.

Acheronopa also differs from the sympatric *Gouldiropa* in having an open rather than closed umbilicus and in the more prominent, sparser teleoconch ribbing. The unusually depressed shell shape may be a functional adaptation to living between limestone slabs.

***Acheronopa attunga* sp. nov.**
(Figs 10, 23, 25-29, 31-34; Table 5)

ETYMOLOGY. For the New England town of Attunga.

MATERIAL. HOLOTYPE: QMMO70400, Manilla, c.20.4km ESE, Manilla-Yarramanbully Rd, NSW (30°51'00"S, 150°50'54"E), lm/vt, under rocks in talus pile, 25.ix.1993, JS, JC. Height of shell=1.81mm, diameter=4.27, H/D=0.42, D/U=3.21, number of whorls=4.9, ribs on last whorl=23. PARATYPES: All NSW. QMMO49218, 42SC/49RC, same data as holotype; QMMO49187, 7RC, Manilla, c.6.6km ESE at Amaroo Homestead (30°46'06"S, 150°47'36"E), vt/lm, under rocks abd logs and in litter, 24.ix.1993, JS, JC; QMMO49193, 8RC, Manilla, c.19.9km ESE, Manilla-Yarramanbully Ck Rd (30°50'42"S, 150°51'12"E), lm/vt, under rocks and logs, 24.ix.1993, JS, JC; QMMO52693, 18RC, Manilla, c.20.4km ESE, Manilla-Yarramanbully Rd, (30°51'00"S, 150°51'54"E), lm/vt, in litter, 25.ix.1993, JS, JC; QMMO32089, 100RC, AMSC205160, 10RC, Attunga, c.12km N, Woodburn-Yarramanbully Rd (30°51'S, 150°51'E), lm, under and between rocks, 26.xi.1989, JS, DP.

DIAGNOSIS. Shell very small, with strongly depressed, evenly coiled whorls. Teleoconch with strongly sinuated, very widely spaced, bold radial ribs, mean ribs/mm 1.72; secondary sculpture of prominent microspiral cords and low radial ridges, forming prominent beads at their intersection. Umbilicus wide V-shaped. Penis with three longitudinal pilasters.

DESCRIPTION. Shell very small, depressed, brown, with 4.6-5.2 (mean 5.0) evenly coiled whorls. Shell diameter 3.92-6.28mm (mean 4.65mm). Apex and early spire depressed. Height of shell 1.59-2.11mm (mean 1.85mm), H/D 0.30-0.48 (mean 0.40). Protoconch of 1.5-1.7 whorls with sculpture of crowded, regularly spaced, slightly curved radial ribs, width of interstices (in multiples of rib width) 5-7 at apex. Secondary apical sculpture of crowded, regularly spaced, continuous microspiral cords. Teleoconch sculpture of strongly sinuated, very widely spaced, bold radial ribs, increasing in spacing toward aperture, ribs on last whorl 20-31 (mean 25), ribs/mm 1.22-2.12 (mean 1.72). Ribs wide, height less than width; straight in section, rounded on top. Rib interstices on the first post-nuclear whorl equal to width of 3-5 ribs; interstices on the penultimate whorl equal to

width of 6-8 ribs. Interstitial sculpture of low microradial ribs, 7-9 between major ribs on first post-nuclear whorl; 16-20 between ribs on penultimate whorl. Secondary sculpture of prominent low microspiral cords that cross the major radial ribs and form very strong, raised beads where they intersect with the microradials. Sutures strongly impressed, whorls flattened above and weakly rounded below a flattened periphery. Aperture broadly ovately lunate. Umbilicus open, wide V-shaped, diameter 1.22-1.71mm (mean 1.48mm), D/U 2.89-4.21 (mean 3.16). Based on 23 measured specimens (QMMO49218, MO70400).

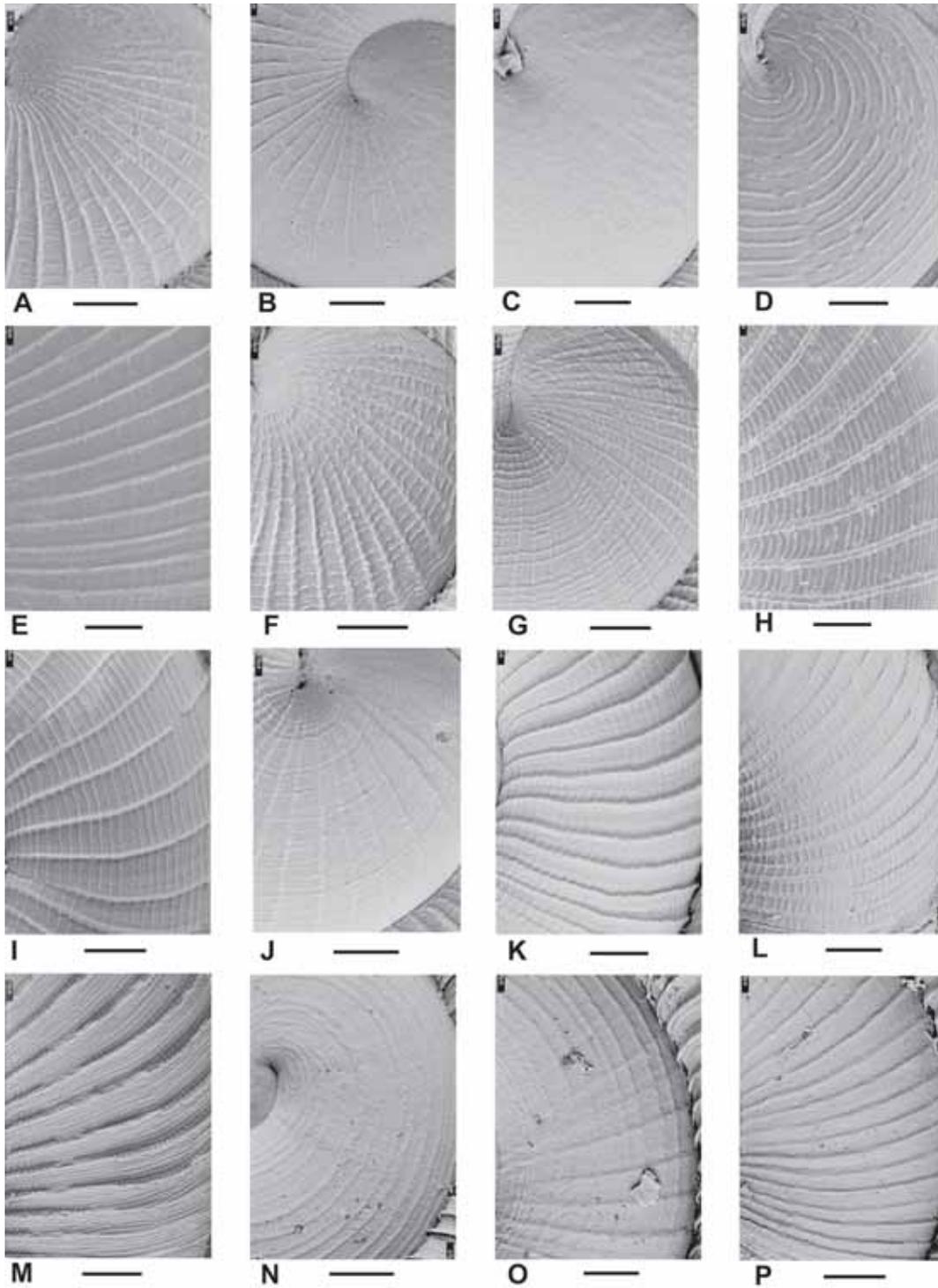
Genitalia with ovotestis containing two clumps of alveoli, with more than two alveolar lobes per clump. Talon stalk 1-3 times the diameter of the talon; talon circular. Penal retractor muscle less than half the length of the penis; inserting at the junction of the penis and epiphallus. Muscle fibres also attached to the base of the penis, close to the vagina/atrium. Epiphallus narrower than the vas deferens, entering penis through a simple pore; shorter than penis. Penis pear shaped, internally with three longitudinal pilasters, one much smaller than the other two. Vagina very short.

Pallial cavity with moderately bilobed kidney, apex of pericardial lobe reflexed. Mantle gland present.

Radula with central tooth strongly tricuspid; lateral teeth tricuspid; first and second laterals equal in width. Mesocone of first lateral tooth slender, slightly diamond-shaped; marginal teeth skewed towards the centre; ectocone of outer marginal teeth not split; endocone not split. Number of lateral teeth: 6; marginal teeth: 18; radular rows: 94. Based on 3 dissected adults (QMMO49218).

DISTRIBUTION AND HABITAT. *Acheronopa attunga* sp. nov. is known only from the Yarramanbully limestones near Attunga; living between limestone talus on limestone karst covered in remnant vine thicket.

REMARKS. *Acheronopa attunga* sp. nov. is most similar to *Sharniropa xanana* sp. nov. from the Timor/Glenrock limestone outcrops. However, it differs significantly from that species in being relatively much larger, having more crowded microradial ribs on the protoconch and in having more flattened whorls. *A. attunga* differs from the sympatric *Gouldiropa carlessi* (Stanisic, 1990) comb. nov. most noticeably in having an open rather than closed umbilicus and



in having more prominent, sparser teleoconch ribbing. The unusually depressed shell of *A. attunga* may be a functional adaptation to living between limestone slabs.

Hedleyropa gen. nov.

ETYMOLOGY. Named in honour of Charles Hedley.

TYPE SPECIES. *Hedleyropa yarrangobillyensis* sp. nov.; herein designated.

DIAGNOSIS. Shell very small, light brown in colour. Apex and early spire flat. Protoconch with very densely crowded, curved radial ribs (approx. 90), crossed by low, crowded spiral cords. Teleoconch with protractively sinuated radial ribs and a secondary sculpture of low radial ridglets and more prominent, crowded microspiral cords; microsculpture continuous on the major radials. Kidney moderately bilobed with weakly reflected pericardial lobe. Penis with two longitudinal pilasters.

DISTRIBUTION AND HABITAT. Yarrangobilly limestones, Kosciusko NP, SE NSW and surrounding environs. However, there are other undescribed species in the QM and AM collections from the region which may belong to this genus and it is quite probable that the range of the genus could be extended significantly particularly in other parts of the Kosciusko NP and NE Vic.

REMARKS. *Hedleyropa* gen. nov. is similar to *Cralopa* in having crowded apical radial ribs and numerous bold, relatively crowded sinuated teleoconch ribs, but differs in having a greater number of microradial ribs on the protoconch, no apertural sinus, finer and much less sinuate teleoconch ribs and a very narrow U-shaped umbilicus rather than one closed by columellar reflection. There is also a subtle difference in whorl profile between the two genera with *Hedleyropa* having more rounded whorls compared with that of *Cralopa*.

Hedleyropa yarrangobillyensis sp. nov.
(Figs 10, 23, 25-28, 30-34; Table 5)

ETYMOLOGY. For the type locality.

MATERIAL. HOLOTYPE. QMMO70401, Yarrangobilly, Yarrangobilly R, c.1km S bridge, NSW (35°39'28"S, 148°27'41"E), lm/ew, under rocks, 8.x.1992, JS, GI. Height of shell=2.20mm, diameter=3.74, H/D=0.54, D/U=4.35, number of whorls=4.5, ribs on last whorl=123. PARATYPES. All NSW. QMMO39973, 1SC/50+RC, same data as holotype; QMMO39840, 5SC, Tumut, c.42.3km SE, Tumut - Yarrangobilly Rd (35°35'16"S, 148°20'04"E), ew, under rocks, 8.x.1992, JS, GI; QMMO49419, IRC, Yarrangobilly, c.4.4km N turnoff to caves, Tumut - Kiandra Rd (35°41'00"S, 148°28'54"E), ew/lm, under logs and rocks, 03.i.1994, JS, JC; QMMO39975, 5SC/3RC, Yarrangobilly, Yarrangobilly Caves Reserve (35°43'45"S, 148°29'16"E), ew/lm, under rocks, 8.x.1992, JS, GI; AMSC162152, 6RC, Kosciusko NP, Yarrangobilly Caves, Village Cave System [?=Y-110] (35°43.5'S, 148°29.5'E), on wet moss in overhang, 6.vi.1980, Ken Keck.

DIAGNOSIS. Shell very small, with evenly coiled whorls and an almost flat spire. Teleoconch with bold, relatively crowded, protractively sinuated radial ribs mean ribs/mm 9.16). Umbilicus narrow U-shaped, mean D/U 4.3; whorls rounded at the periphery and evenly coiled. Penis with two longitudinal pilasters.

DESCRIPTION. Shell very small, light brown in colour with 4.2-4.7 (mean 4.5) evenly coiled whorls, the last weakly descending in front. Shell diameter 3.21-4.52mm (mean 3.82mm). Apex and early spire low to flat. Height of shell 1.63-2.51mm (mean 1.98mm), H/D 0.48-0.58 (mean 0.52). Protoconch of 1.6-1.9 whorls with sculpture of approximately 90, weakly curved, uniformly spaced radial ribs; ribs of medium width with height less than width; width of interstices (in multiples of rib width) 3-4 at apex. Secondary sculpture of much lower, narrow, low continuous spirals (approx. 37); height of spirals less than width. Teleoconch sculpture of strongly protractively sinuate, variably spaced radial ribs; spacing increasing towards aperture; 86-136 (mean 109) ribs on the last whorl. Ribs/mm 8.17-10.72 (mean 9.16). Rib height equal to width; straight in section; rounded on top; interstices on the first post-nuclear whorl equal to width of 4-6 ribs; interstices on the penultimate whorl equal to 4-5. Interstitial sculpture of low radial ridges, 8-9 between ribs on first

FIG. 33. Protoconch microsculpture. A, *Rhophodon mcgradyorum*, QMMO70392. B, *Egilodonta paucidentata*, QMMO70396. C, *Letomola lanalittleae*, QMMO70397. D, *Macrophallikoropa depressispira*, AMSC205163. E, *Elsothera brazieri*, QMMO28775. F, *Decoriropa lirata* (Taree), AMSC136842. G, *Coricudgia wolllemiana*, AMSC205164. H, *Marilyniropa jenolanensis*, AMSC205165. I, *Gouldiropa carlessi* (Inverell), AMSC3640. J, *Sharniropa wollondillyana*, QMMO70399. K, *Acheronopa attunga*, QMMO70400. L, *Hedleyropa yarrangobillyensis*, QMMO70401. M, *Scleridoropa sarahjaneae* (Abercrombie Caves), AMSC162165. N-P, *Diphyoropa macleayana*, AMSC168685. Scale bars=30µm in A, D; 40µm in B, C, E, F; 50µm in G, H, J, M, O; 60µm in I, K, L, N, P.

post-nuclear whorl; 8 between ribs on penultimate whorl; crossed by more prominent, very low microspiral cords. Beading weak. Umbilicus narrow U-shaped, diameter 0.70-1.20mm (mean 0.90mm), D/U 3.72-5.05 (mean 4.30). Sutures strongly impressed, appearing weakly channeled; whorls slightly shouldered above and rounded below a rounded periphery. Aperture roundly lunate. Umbilicus open, narrow U-shaped. Based on 20 measured specimens (QMMO39973, MO70401).

Genitalia with ovotestis containing two clumps of alveoli. Talon stalk slightly longer than the diameter of the talon; talon circular. Penial retractor muscle less than half the length of the penis; inserting at the junction of the penis and epiphallus. Epiphallus present; entering penis through a simple pore; slightly shorter than penis; narrower than the vas deferens. Penis tubular with two longitudinal pilasters. Vagina shorter than penis.

Pallial cavity with kidney moderately bilobed; apex reflexed.

Radula with central tooth strongly tricuspid; lateral teeth tricuspid; ectocone of outer marginal teeth not split (but the ectocone of the second last tooth is split into three); endocone not split. Number of lateral teeth: 4, marginal teeth: 15; radular rows: 85. Based on 1 dissected specimen (QMMO39840).

DISTRIBUTION AND HABITAT. Yarrangobilly limestones, SE Talbingo, SE NSW; living among limestone slabs.

REMARKS. *Hedleyropa yarrangobillyensis* sp. nov. is readily distinguished from other sympatric charopids by a combination of its dense radial ribbing on both the protoconch and teleoconch and the comparatively reduced umbilicus. *Scelidoropa sarahjaneae* sp. nov. has a radially ribbed teleoconch but differs in having a larger flammulated shell with wide cup-shaped umbilicus and a protoconch with microdaradial ribs in the interstices of the major ribs. Anatomically the two species are markedly distinct.

Hedleyropa yarrangobillyensis displays a tendency for reduction in the size of the umbilicus. The general shell form (weakly channelled sutures, bold ribbing, numerous apical radial ribs) recalls *Cralopa stroudensis* (Cox, 1864). However, the greater number of apical microradials, weaker sinuosity of the teleoconch ribs, lack of an apertural sinus and narrow but open U-shaped umbilicus all indicate

that *H. yarrangobillyensis* is a member of *Hedleyropa*.

Scelidoropa gen. nov.

ETYMOLOGY. Greek *skelidos*, rib; alluding to the interstitial microradial ribs on the protoconch.

TYPE SPECIES. *Scelidoropa sarahjaneae* sp. nov.

DIAGNOSIS. Small, light brown shell with darker radial flammulations with slightly tightly coiled whorls. Spire flat to slightly elevated. Protoconch with crowded, evenly spaced, slightly curved radial ribs (approx. 90). Secondary sculpture of low continuous microspiral cords and low slightly curved microradial ribs that form beads at their intersection. Teleoconch with slightly sinuated, crowded to very crowded ribs; microsculpture of microradial ribs and microspiral cords equal in strength, forming strong beads at their intersection. Umbilicus wide saucer-shaped. Penis with 0-4 pilasters. Kidney almost unilobed. Central radula tooth weakly tricuspid; lateral teeth with a smaller additional cusp between ectocones of the tooth.

DISTRIBUTION AND HABITAT. From SE NSW to the southern edge of the New England Tableland, NSW (Nundle area) and west to the Nandewar Range, NSW. The species live in litter among rocks.

REMARKS. The shell of *Scelidoropa* gen. nov. is quite distinctive among the east coast charopid genera. The flammulated shell with elevated spire, bold and prominent teleoconch ribs and very wide umbilicus are a combination of characters that are seen in other charopid groups. However, the microradial ribs on the protoconch immediately identify it among the east-coast fauna. Species in Victoria that are currently questionably classified in *Pernagera* Iredale, 1939 (Smith, 1992) series also have apical radial sculpture, bold teleoconch ribs and flammulated shells, but, and most significantly, lack the microradial ribs on the protoconch. Some species of *Elsothera* Iredale, 1933, superficially resemble *Scelidoropa* but the latter can be distinguished by its much larger size, bolder, weakly sinuated ribs, wider cup shaped umbilicus and most significantly, by the presence of intersitial microradials on the protoconch. Anatomically the two genera are immediately separable by the form of the epiphallus which is long and unusually coiled in *Elsothera* but shorter and more typically reflexed in *Scelidoropa*. The lateral teeth of the radula of

Scelidoropa are also distinctive in the context of all the other eastern Australian charopids hitherto reviewed in possessing an additional cusp.

The breadth of the range of *Scelidoropa* is matched only by that of *Macrophallikoropa* gen. nov. However, in contrast to the latter, the species' distributions do not include rainforests and encompass only very localised mesic refugia such as rocky outcrops (limestone and granite), and mountain tops (Mt Kaputar, Mt Coricudgy and Mt Canoblas). The species is absent from the Sydney Basin and the limestones of the Macleay Valley.

***Scelidoropa sarahjaneae* sp. nov.**
(Figs 10, 24-28, 30-34; Table 5)

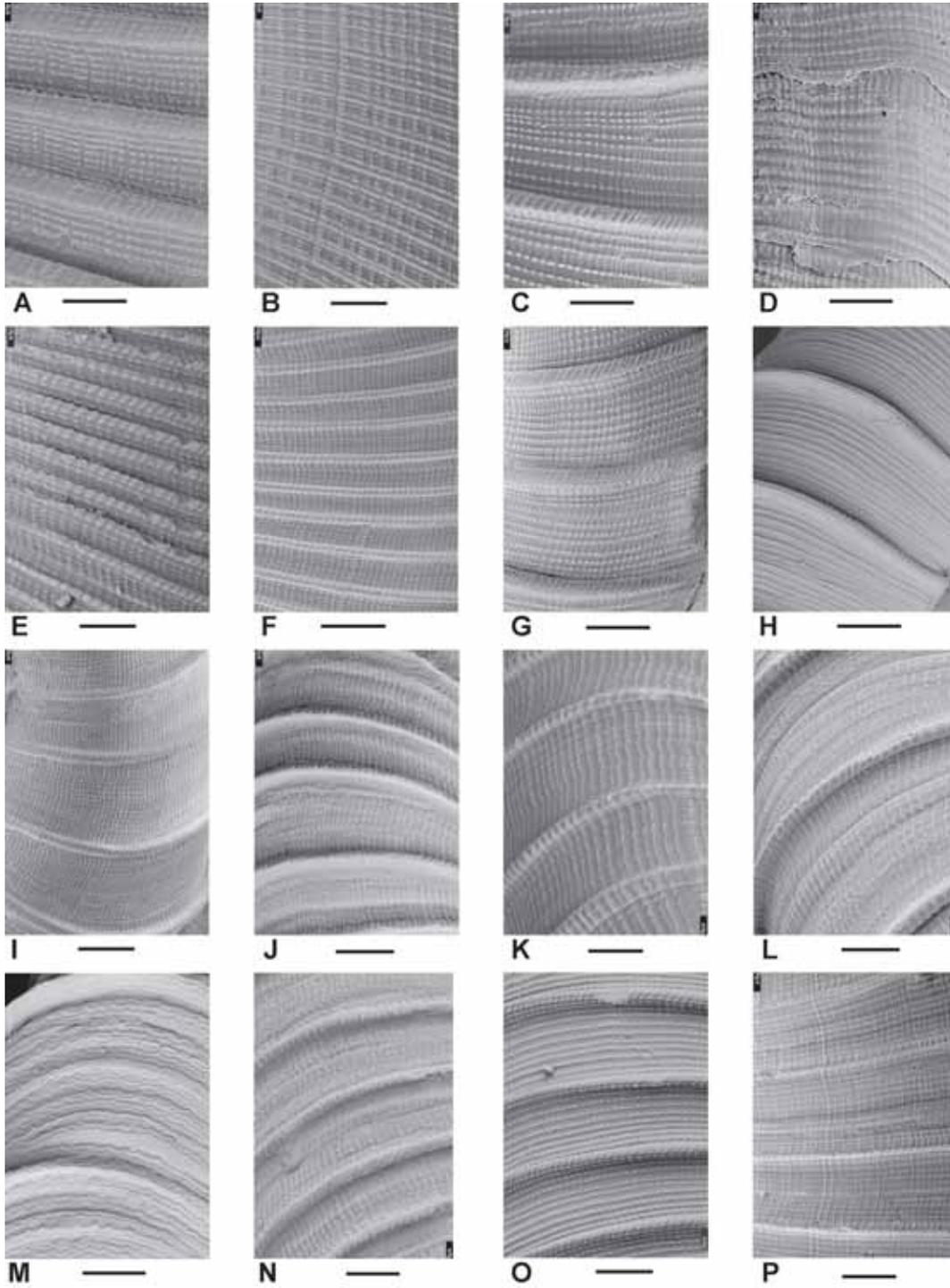
ETYMOLOGY. For Sarah Jane Roberts.

MATERIAL. HOLOTYPE. QMMO70402, Yarrangobilly, Yarrangobilly R, c.1km S bridge (35°39'28"S, 148°27'41"E), ew/lm, in litter, 08.10.1992, JS, GI. Height of shell=1.42mm, diameter=3.18mm, H/D=0.45, D/U=2.26, number of whorls=4.6, ribs on last whorl=122. PARATYPES. All NSW. QMMO39974, 13SC/50RC, same data as holotype; QMMO49418, 4RC, Yarrangobilly, c.1km S on Tumut - Kiandra Rd (35°39'30"S, 148°27'42"E), ew/lm, under rocks, 03.i.1994, JS, JC; QMMO49421, 5RC, QMMO52775, 34RC, Yarrangobilly, c.4.4km N T'off to caves, Tumut - Kiandra Rd (35°41'00"S, 148°28'54"E), ew/lm, under logs and rocks, 03.i.1994, JS, JC; QMMO39979, 7SC/50RC, Yarrangobilly, Yarrangobilly Caves Reserve (35°43'45"S, 148°29'16"E), ew/lm, in litter, 08.x.1992, JS, GI; QMMO68013, 50RC, Yarrangobilly, Yarrangobilly R, c.1km S bridge (35°39'28"S, 148°27'41"E), lm, in litter, 03.i.1994, JS, JC; AMSC153724, 1RC, Kosciusko NP, Yarrangobilly Caves, beside trail to River Cave (Y-27) (35.725°S, 148.492°E), in litter, 31.x.1980, WFP, J.Hall; AMSC168695, 1RC, Kosciusko NP, Yarrangobilly Caves, Village Cave System (?=Y-110) (35.725°S, 148.492°E), on wet moss in overhang, 06.vi.1980, Ken Keck; AMSC162150, many RC, Kosciusko NP, Yarrangobilly Caves, beside trail to River Cave (Y-27) (35.725°S, 148.492°E), in litter, 31.x.1980, WFP, J.Hall; AMSC162151, 1RC, Kosciusko NP, Yarrangobilly Caves (35.725°S, 148.492°E), 31.x.1980, WFP, J.Hall. OTHER MATERIAL. NSW: AMSC168626, C355262, C367084, C162140, C355269. Timor Caves: QMMO32063, MO37731, AMSC157326, C171504, C162162, C162185, C355267, C355268, C355266. Mt Coricudgy: QMMO44707, MO28663, MO44714, MO44722, MO59872, AMSC162144. Jenolan Caves: QMMO9687, MO16941, MO28778, MO37772, AMSC63851, MO62446, MO35764, MO44798, AMSC124276, C124277, C157334, C162157, C162168, C121717, C154813, C354933, C355270, C411537, C144225. Wombeyan Caves: AMSC319705, C157317, C355260, C384164. Abercrombie Caves: QMMO29242, MO37780, MO44766, AMSC157322, C158365, C162165. Orange district: QMMO37490, MO39782, AMSC168647, C168697. SE NSW: QMMO68018,

MO39986, MO39991, MO49429, AMSC162159, C354882, C168646, C354917, C354923, C354919, C354921, C354926, C355263, C355261, C355265, C357298, C357300, C357301, C162148, C355264, C162147.

DIAGNOSIS. Shell small, golden brown, with darker flammulations. Spire slightly elevated. Teleoconch with crowded, bold slightly sinuate ribs. Mean ribs/mm 10.43. Umbilicus very wide saucer-shaped, mean D/U 2.44. Penis with 4 longitudinal pilasters.

DESCRIPTION. Shell very small, golden brown, with darker flammulations (very faint to very dark), with 3.7-5.3 (mean 4.5) evenly coiled whorls. Shell diameter 2.65-4.27mm (mean 3.35mm). Apex and spire flat. Height of shell 1.30-2.17mm (mean 1.65mm). H/D 0.44-0.54 (mean 0.49). Protoconch: flat of 1.1-1.9 whorls. Apical sculpture of bold, regularly spaced slightly curved radial ribs. Ribs bold, medium to wide; height greater than or equal to width; interstices equal to the width of two to three ribs at apex; equal to the width of 4-6 ribs at post-nuclear boundary; ratio of rib spacing (apex to post-nuclear boundary): 0.3-0.5. Microradials with periostracal blades; 1-3 microradials between major ribs at apex; 6-8 microradials between ribs at post-nuclear boundary. Secondary sculpture of low (height less than width) microspirals crossing the major radials and forming beads at their intersection with the microradials. Teleoconch with bold prominent, closely and regularly spaced, slightly protractively sinuated radial ribs. Ribs on last whorl 70-176 (mean 109), ribs/mm 7.10-16.05 (10.43). Ribs medium size, straight in section, rounded on top. Rib interstices on the first post-nuclear whorl equal to width of 4-5 ribs; interstices on the penultimate whorl equal to width of 3-5. Microsculpture of microradial ribs and microspirals, about equal in strength. Microradials low, 7-11 between ribs on first postnuclear whorl; 7-11 between ribs on penultimate whorl. Microspirals low; crossing the microradials and forming strong beads at their intersection with the microradial ribs; beading strong, always round, or elongate on the first post-nuclear whorl, becoming round towards the aperture. Umbilicus wide saucer-shaped, diameter 0.93-1.79mm (mean 1.38mm), D/U 2.12-3.55 (mean 2.44). Sutures weakly impressed, whorls rounded above and below a rounded periphery. Aperture narrowly roundly ovate; parietal callus present. Based on 121 measured specimens (AMSC355266, C63851, C162165, C171504, C355260, QMMO39974, MO52781, MO70402).



Ovotestis containing three to seven clumps of alveoli, with more than two alveolar lobes per clump. Talon stalk shorter than talon, or absent; talon circular. Penial retractor muscle half the length of the penis or greater, inserting onto the penis head or at the junction of the penis and epiphallus. Epiphallus present; shorter than or equal to the penis length, wider than the vas deferens; equal in width to penis; internally with two longitudinal pilasters. Penis tubular with 4 longitudinal pilasters. Vagina shorter than or equal length to penis.

Pallial cavity with kidney almost unilobed; apex slightly reflexed. Mantle gland absent, or present (present in one specimen; orange, thick).

Radula with central tooth weakly tricuspid; lateral teeth tricuspid, with an additional smaller cusp formed between the two ectocones. Ectocone of outer marginal teeth split into three teeth, or split into four or more teeth; endocone not split. Number of lateral teeth: 4-6, marginal teeth: 10-11; radular rows: 90-94. Based on 10 dissected specimens (QMMO39974, MO39991, MO32063, AMSC354933, C354923).

DISTRIBUTION AND HABITAT. From the Kosciusko NP in S NSW to the S New England Region, N NSW but is rare in the Sydney Basin.

REMARKS. *Scelidoropa sarahjaneae* sp. nov. differs from *S. nandewar* sp. nov. (Nandewar Range) in having a coarser shell sculpture, elevated rather than flat spire and a relatively smaller umbilicus. *Marilyniropa jenolanensis* gen. et sp. nov. from the Jenolan Caves area bears some superficial resemblance to this species but has more widely spaced ribs, smaller umbilicus and a protoconch without microradial ribs.

The wide distribution of *S. sarahjaneae* broadly mirrors that of some other species discussed in this study. However in contrast to widespread species such as *Macrophallikoropa belli* (Cox, 1864), *Cralopa stroudensis* (Cox, 1864) and *Egilomen lirata* (Cox, 1868) this species is barely represented in the Sydney Basin. Reasons

for this are not obvious but *S. sarahjaneae* may have a disliking for sandstone habitats.

***Scelidoropa nandewar* sp. nov.**
(Figs 10, 24-28, 30-32; Table 5)

ETYMOLOGY. For the Nandewar Range.

MATERIAL. HOLOTYPE: NSW. QMMO70403, Nandewar Ra, Mt Dowe (30°16'54"S, 150°09'48"E), snow gums, 1440m, under logs and bark, 23.ix.1993, JS, JC. Height of shell=1.38mm, diameter=3.07mm, H/D=2.22, D/U=2.21, number of whorls=4.9, ribs on last whorl=189. PARATYPES. NSW: QMMO49158, 4SC/5RC, same data as holotype, Nandewar Ra, Mt Dowe (30°16'54"S, 150°09'48"E), snow gums, 1440m, under logs and bark, 23.ix.1993, JS, JC; QMMO16743, 3SC/3RC, Dawsons Spring, Mt Kaputar (30°16'S, 150°10'E), 1300m, under moss, 08.xi.1983, JS, DP, PHC, J. Short; QMMO16754, 1RC, Mt Kaputar, summit (30°16'S, 150°10'E), among rocks, grass and litter, 1500m, 09.xi.1983, JS, DP, PHC, J. Short; QMMO49166, 8RC/4SC, Nandewar Ra, c.1.2km SW Mt Kaputar, summit (30°16'36"S, 150°08'48"E), dsf, 1420m, under bark and rubbish, 23.ix.1993, coll JS, JC; QMMO65450, 1SC, Nandewar Ra, Mt Kaputar NP, E of Bark Hut Camping Ground (30°17'30"S, 150°08'18"E), dsf, 1180m, under logs, 23.ix.1993, JS, JC.

DIAGNOSIS. Small golden brown shell with darker flammulations. Teleoconch with very crowded, bold slightly sinuate radial ribs. Ribs/mm c.19.60. Umbilicus very wide saucer-shaped, D/U c.2.21. Penis with four longitudinal pilasters.

DESCRIPTION. Shell very small, light brown, with darker flammulations, having c.4.9 slightly tightly coiled whorls. Shell diameter c.3.07mm, spire and apex flat. Shell height c.1.38mm, H/D c.2.22. Protoconch of c.2.0 whorls with apical sculpture of bold, regularly spaced slightly curved radial ribs. Ribs bold, medium to wide; height greater than or equal to width; interstices equal to the width of 2.5 ribs at apex; equal to the width of 3 ribs at post-nuclear boundary; ratio of rib spacing (apex to post-nuclear boundary): 0.3-0.5. Microradials present; 4 between each pair of major ribs. Secondary sculpture of low (height less than width) microspirals that

FIG. 34. Teleoconch microsculpture. A, *Rhophodon palethorpei*, QMMO70390. B, *Rhophodon duplicostatus*, QMMO70393. C, *Egilodonta bairnsdalensis* (Yarrangobilly Caves, Kosciusko National Park), AMSC142959. D, *Letomola lanalittleae*, QMMO70397. E, *Macrophallikoropa depressispira*, AMSC205163. F, *Elsothera brazieri*, QMMO28775. G, *Decorioropa lirata* (Taree), AMSC136842. H, *Coricudgia wollemiana*, AMSC205164. I, *Marilyniropa jenolanensis*, AMSC205165. J, *Cralopa stroudensis*, Sydney. K, *Gouldiropa carlessi* (Inverell), AMSC3640. L, *Sharniropa wollondillyana*, QMMO70399. M, *Acheronopa attunga*, QMMO70400. N, *Hedleyropa yarrangobillyensis*, QMMO70401. O, *Scelidoropa sarahjaneae* (Abercrombie Caves), AMSC162165. P, *Diphyoropa saturni*, AMSC142234. Scale bars=30µm in B and E; 40µm in A, C; 50µm in O; 60µm in D, G, K, L, N, P; 70µm in J; 80µm in H; 100µm in F; 130µm in I, M.

cross the major radials and form beads at their intersection with the microradials. Teleoconch with bold prominent, very crowded and regularly spaced, slightly protractively sinuated radial ribs. Ribs on last whorl c.189, ribs/mm c.19.60. Ribs medium; in size; straight in section, rounded on top. Rib interstices on the first post-nuclear whorl equal to width of 2-3 ribs; interstices on the penultimate whorl equal to width of 2-3 ribs. Microsculpture of microradial ribs and microspiral cords, about equal in strength. Microradials low, 4-5 between ribs on first postnuclear whorl; 3-4 between ribs on penultimate whorl. Microspirals low; crossing the microradials and forming strong beads at their intersection with the microradial ribs; beading strong, always round. Umbilicus wide saucer-shaped, diameter c.3.07mm, D/U c.2.21. Sutures weakly impressed, whorls rounded above and below a rounded periphery. Aperture narrowly roundly ovate; parietal callus present. Based on the measured holotype (QMMO70403).

Genitalia with ovotestis containing 6 clumps of alveoli, with 2-8 alveolar lobes/clump. Talon stalk very short; talon circular. Penial retractor muscle <1/2 penis length; inserting at junction of the penis and epiphallus. Epiphallus shorter than penis; wider than the vas deferens; equal in width to penis; internally with 2 longitudinal pilasters. Penis tubular with 4 longitudinal pilasters. Vagina equal length to penis.

Pallial cavity with kidney almost unilobed; apex reflexed. Mantle gland present (orange in colour).

Radula with central tooth weakly tricuspid; lateral teeth tricuspid, with a smaller additional cusp present between the ectocones. Ectocone of outer marginal teeth split into three teeth; endocone not split. Number of lateral teeth: 4, marginal teeth: 11; radular rows: 88. Based on 1 dissected specimen (QMMO49158).

DISTRIBUTION AND HABITAT. From Mt Kaputar, NSW; wet sclerophyll forest among rocks.

REMARKS. *Scelidoropa nandewar* sp. nov. is similar to the widespread *S. sarahjaneae* but can be distinguished by the more closely spaced ribs, flatter spire and relatively smaller umbilicus. The geographical restriction of *S. nandewar* contrasts with that of *S. sarahjaneae* and highlights the refugial significance of the Nandewar Ranges in land snail evolution.

Diphyoropa gen. nov.

ETYMOLOGY. Greek *diphyes*, double nature; referring to the dual nature of the protoconch sculpture.

TYPE SPECIES. *Helix saturni* Cox, 1864

DIAGNOSIS. Very small brown shell with evenly coiled whorls and flat spire. Protoconch sculpture bimodal with the first two-thirds of the protoconch having broad, irregularly spaced spiral lirae that weaken in the last third whorl broad, curved radial ridges develop and eventually dominate. Teleoconch sculpture of prominent, almost straight, moderately widely to closely spaced radial ribs. Umbilicus wide to very wide V-shaped. Kidney moderately bilobed. Epiphallus long. Penis tubular up to five longitudinal pilasters.

DISTRIBUTION AND HABITAT. Southern Tablelands Bioregion to the Macleay Valley, W of Kempsey, NE NSW. Species live under logs, rocks and leaf litter chiefly in eucalypt forest.

REMARKS. *Diphyoropa* gen. nov. is characterised by its unusual apical sculpture that features an initial prominence of spiral cords which give way to a dominance of curved radial ribs and ridges on the last 1/3 of the protoconch. This protoconch sculpture is unusual in the context of apical sculptures of Australian Charopidae (Iredale, 1937, 1941a,b; Kershaw 1955, 1956a,b; Smith & Kershaw, 1979, 1981; Stanisc, 1990) and as such is diagnostic for the genus. However, considering the many intricate variations on grossly similar apical sculptural themes that have been reported in this study, care needs to be taken in interpreting the condition seen in *Diphyoropa* as monophyletic. This peculiar apical sculpture may be merely a grade of organisation similar to the reticulate, spiral or radial patterns that have thus far been reported for many charopid species.

Undescribed taxa in the collections of the QM from other parts of NSW and SE Qld have grossly similar protoconch sculpture to *D. saturni* and *D. macleayana*. These may or may not belong to this clade.

Diphyoropa saturni (Cox, 1864) comb. nov. (Figs 23, 25-28; Table 5)

Helix saturni Cox, 1864a: 35; 1868: 14, pl.6, fig.11.

Helix costulata Cox, 1864b:184; non *costulata* Lamarck, 1822.

Endodonta (Charopa) saturni (Cox). Cox 1909: 69.

Egilomen saturni (Cox). Iredale, 1937: 328; Iredale, 1941a: 269.

Dentherona saturni (Cox). Smith & Kershaw, 1979: 173.

Dentherona (*Dentherona*) *saturni* (Cox). Smith, 1992: 187.

MATERIAL. LECTOTYPE. AMSC205167. Height of shell=1.18mm, diameter=2.22mm, H/D=0.53, D/U=3.08, number of whorls=4.2, ribs on last whorl=59. **PARALECTOTYPE.** AMSC136900, same data as lectotype. **OTHER MATERIAL.** All NSW, Sydney Basin: AMSC8899, C11809, C136900, C154787, C154909, C154919, C154920, C154921, C154924, C154956, C318793, C377420, C318807, C318811, C318908, C318911, C318912, C318913, C318914, C318916, C318918, C318926, C318931, C318932, C318933, C318934, C318935, C318941, C318942, C318943, C318944, C318946, C318947, C319714, C345664, C345675, C345720, C345721, C346756, C346761, C346765, C346767, C346769, C346773, C348735, C354869, C318928, C318929, C318936, C318938, C346771, C63819, C154954, QMMO28233, MO29635, MO29639, MO29721, MO37970, MO34784, MO34785, MO34809, MO34974, MO37390, MO60057, MO28224, MO42125. Lord Howe I: QMMO64125, MO64218, MO64133, AMSC204488, C204496, C204581, C397669, C398539, C400485, C389819, C389821, C389824, C389825, C389826, C389827, C389828, C389829, C389830, C389831, C389832, C389833, C389834, C389835, C390217. Vic.: AMSC155319.

DIAGNOSIS. Shell very small, with evenly coiled whorls and flat spire. Protoconch sculpture bimodal, with the 1st 2/3 of protoconch having broad, irregularly spaced, spiral lirae weakening in the last 1/3 where broad, curved radial ridges develop and eventually dominate. Teleoconch sculpture of prominent, almost straight, widely spaced radial ribs. Umbilicus very wide V-shaped. Penis with several longitudinal pilasters. Epiphallus about half penis length.

DESCRIPTION. Shell very small, light brown in colour with 4.2-4.6 (mean 4.33) evenly coiled whorls. Shell diameter 3.02-3.59mm (mean 3.26mm). Spire flat. Height of shell 1.18-2.03mm (mean 1.70mm), H/D 0.54-0.57 (mean 0.55). Protoconch of 1.6-1.7 whorls with sculpture consisting of broad irregularly spaced, spiral lirae for the first two-thirds of the protoconch; weakening in the latter third of the protoconch where broad curved radial ridges develop and gradually become more prominent than the spirals; spirals crossing radial ridges. Ridges wide height less than width; spacing uniform; width of interstices (in multiples of rib width): 2-3. Teleoconch sculpture of bold, almost straight, moderately widely spaced radial ribs; 58-85 (mean 72) ribs on the last whorl, ribs/mm 6.11-7.93 (mean 7.00). Ribs medium in size, height equal to width; straight in section, rounded

on top. Rib interstices on the first post-nuclear whorl equal to width of 6-8 ribs; interstices on the penultimate whorl equal to width of 6-7 ribs. Microsculpture of microradial ribs and stronger microspirals that cross the microradials and form strong elongate to round beads at their intersection. Microradials low; 9-11 between ribs on first postnuclear whorl; 11-12 between ribs on penultimate whorl. Umbilicus very wide V-shaped, diameter 0.72-1.27mm (mean 1.04mm), D/U 2.82-3.17 (mean 2.9). Sutures weakly impressed, whorls shouldered above and rounded below a rounded periphery. Aperture roundly lunate, parietal callus present. Based on 6 measured specimens (AMSC142234, C318912, C205167).

Genitalia (not figured) with ovotestis containing two clumps of alveoli; with more than two alveolar lobes per clump. Talon stalk equal to talon diameter; talon circular. Penial retractor muscle less than half the length of the penis; inserting onto the penis head. Epiphallus wider than the vas deferens, equal to a half to two thirds the length of the penis. Penis tubular with a prominent tapering distal; internally, upper chamber with several longitudinal pilasters.

Pallial cavity (not figured) with kidney moderately bilobed; apex slightly reflexed.

Radular morphology unknown.

Based on four dissected specimens (QMMO28233, MO60057, MO28244, MO37390).

DISTRIBUTION AND HABITAT. Sydney Basin Bioregion but extending to the N South-eastern Tablelands Bioregion (Wombeyan Caves). Presumed introduced populations in Victoria and on Lord Howe Island; under rocks, litter and logs, or discarded household debris in urban situations.

REMARKS. *Diphyrora saturni* (Cox, 1864) comb. nov. was placed in either *Egilomen* or *Dentherona* by various authors (Iredale, 1937; Smith & Kershaw, 1979) without explanation. The protoconch of *Egilomen* has widely spaced thick radial ribs with weak spiral creases while that of *Dentherona* (type: *Helix* (*Charopa*) *dispar* Brazier, 1871) is reticulate with comprising strong radials and somewhat weaker (less raised) spirals. *D. saturni* is almost exclusively confined to the Sydney Basin where it persists in urban situations. Neither sculptural pattern is considered to be generically compatible with the condition in *D. saturni*.

The almost exclusive occurrence of *D. saturni* within the Sydney basin suggests strongly that the extralimital records from Victoria and Lord Howe Island are introductions. A single record from a Gloucester garden, N of Barrington Tops (AMSC154954) could also be a translocation since it is the only record N of the Hunter River in an area where much collecting has taken place in surrounding forests.

Diphysoropa saturni has spread prolifically in Lord Howe Island, even outdoing introduced European species such as *Cantareus aspersus* (Muller, 1774) and *Vallonia pulchella* (Muller, 1774). A single specimen of *D. saturni* has been recorded from inner Melbourne, Vic but it could be more prominent in that city and an examination of material in the Museum of Victoria is needed to establish its local abundance more accurately.

Populations do not show much conchological variation throughout the natural range of the species. Locally the species is most likely to be confused with *Elsothera brazieri* (Cox, 1868) which differs from it primarily in having a protoconch with dominant radial ribs throughout that are crossed by weak, continuous spiral cords.

The decision not to figure the anatomy of this species was made to expedite publication. Very little spirit material of this species was available for study, and while this material was of sufficient quality to allow for observation of major anatomical features, it was not suitable for illustration.

***Diphysoropa macleayana* sp. nov.**
(Figs 10, 24-28, 30-34; Table 5)

ETYMOLOGY. For the Macleay Valley.

MATERIAL. HOLOTYPE. AMSC205274, Kempsey, WNW, c.1.5km E Mt Sebastopol, Kempsey-Carrair Rd, NSW (30°57'00"S, 152°28'40"E), drf/lm, 350m, on rocks/in litter, 28.xi.1989, JS, DP. Height of shell=1.59mm, diameter=2.81mm, H/D=0.57, D/V=3.35, number of whorls=4.1, ribson last whorl=106. PARATYPES. All NSW. QMMO56395, 1RC, same data as holotype; QMMO56011, 2RC, Kempsey, WNW, c.1.5km E Mt Sebastopol, Kempsey-Carrair Rd (30°57'00"S, 152°28'40"E), drf/lm, 350m, in litter, 08.i.1995, JS, JC; AMSC168685, 5RC, W of Kempsey, on W side Yessabah Caves limestone outcrop (31.095°S, 152.689°E), in soil under leaf litter in Lantana infested rainforest, iii.1983, MS. OTHER MATERIAL. QMMO37098, MO56399, MO49382, MO55876, MO56392, MO60236, AMSC140247, C140258, C162184.

DIAGNOSIS. Shell very small, with evenly coiled whorls and flat spire. Protoconch sculpture

bimodal with the first 2/3 of the protoconch having broad, irregularly spaced spiral lirae weakening in the last 1/3 where broad, curved radial ridges develop and eventually dominate. Teleoconch sculpture of prominent, almost straight, moderately widely spaced radial ribs. Umbilicus very wide V-shaped. Penis tubular with upper chamber muscular and lower part short, thin, tapering; internally with 5 longitudinal pilasters; epiphallus as long as main section of penis.

DESCRIPTION. Shell very small, light brown, with c.4.1 evenly coiled whorls. Shell diameter c.2.8mm. Spire flat to slightly depressed. Height of shell c.2.81mm, H/D c.0.57. Protoconch of c.1.8 whorls with bimodal sculpture consisting of broad irregularly spaced, weakly curved, spiral lirae for the first two-thirds of the protoconch; weakening in the latter third of the protoconch where broad curved radial ridges develop and become more prominent than the spirals; spirals crossing radial ridges. Ridges wide, height less than width; spacing uniform; width of interstices (in multiples of rib width): 3-6. Teleoconch sculpture of bold, almost straight, closely spaced radial ribs; c.106 ribs on the last whorl, ribs/mm c.13.4. Ribs medium in size, height equal to width; straight in section; rounded on top. Rib interstices on the first post-nuclear whorl equal to width of 4-5 ribs; interstices on the penultimate whorl equal to width of 3-4 ribs. Microsculpture of microradial ribs and stronger microspiral cords that cross the microradials and form strong elongate to round beads at their intersection. Microradials low; 36 between ribs on first post-nuclear whorl; 48 between ribs on penultimate whorl. Umbilicus very wide V-shaped, diameter c.0.84mm, D/U c.3.35. Sutures weakly impressed, whorls shouldered above and rounded below a rounded periphery. Aperture roundly lunate, parietal callus present. Based on the measured holotype.

Genitalia with epiphallus equal to penis length. Penis tubular internally with 2 longitudinal pilasters. Pallial cavity with kidney moderately bilobed; apex slightly reflexed.

Radula with central tooth strongly tricuspid, only slightly smaller than first lateral tooth; lateral teeth tricuspid. Mesocone of lateral teeth slender, slightly diamond-shaped. Marginal teeth tricuspid; ectocone of outer marginal teeth not split; endocone not split. Number of lateral teeth: 8; marginal teeth: 5; radular rows: 98.

Based on 2 dissected specimens (AMSC162184).

TABLE 5. Shell measurements for species of *Acheronopa*, *Hedleyropa*, *Scleridoropa* and *Diphyrora*. (Abbreviations as in Table 1).

Measurement	<i>Acheronopa attunga</i>	<i>Hedleyropa yarrangobillyensis</i>	<i>Scleridoropa euryscopa</i>	<i>Diphyrora saturni</i>	<i>Diphyrora macleayana</i>
N	23	20 (*19; **17)	119	5	1
D	3.92-6.28 (4.654) ± 0.468	3.21-4.52 (3.82) ± 0.354	2.65-4.27 (3.35) ± 0.32	3.02-3.59 (3.264) ± 0.274	2.81
PW	1.5-1.7 (1.6) ± 0.067	1.6-1.9 (1.671) ± 0.077 **	1.1-1.9 (1.71) ± 0.09	1.6-1.7 (1.66) ± 0.055	1.8
TW	3-3.6 (3.37) ± 0.177	2.3-3.1 (2.806) ± 0.205 **	2-3.6 (2.78) ± 0.27	2.5-2.9 (2.7) ± 0.187	2.3
NW	4.6-5.2 (4.97) ± 0.172	4.2-4.7 (4.476) ± 0.156 **	3.7-5.3(4.48) ± 0.26	4.2-4.6 (4.36) ± 0.219	4.1
H	1.59-2.11 (1.845) ± 0.159	1.63-2.51 (1.981) ± 0.209	1.3-2.17 (1.65) ± 0.18	1.62-2.03 (1.806) ± 0.182	1.59
SP	0.11-0.41 (0.263) ± 0.078	0.12-0.41 (0.208) ± 0.076	0-0.32 (0.11) ± 0.07	0-0.01 (0.002) ± 0.004	-
AH/AW	0.65-0.88 (0.74) ± 0.05	0.83-1.07 (0.96) ± 0.07	1.09-1.45 (1.26) ± 0.07	1.18-1.44 (1.3) ± 0.11	1.23
UMB	1.22-1.71 (1.477) ± 0.142	0.7-1.2 (0.896) ± 0.125	0.93-1.79 (1.38) ± 0.18	0.98-1.27 (1.102) ± 0.145	0.84
RIB	20-31 (25) ± 3.162	86-136 (108.9) ± 13.408 *	70-176 (109.29) ± 21.34	58-85 (74.2) ± 11.032	106
RIBS/MM	1.216-2.118 (1.721) ± 0.238	8.170-10.72 (9.156) ± 0.736 *	7.102-16.05 (10.43) ± 2.082	6.113-7.933 (7.216) ± 0.699	13.4
H/D	0.3-0.48 (0.4) ± 0.04	0.48-0.58 (0.52) ± 0.03	0.44-0.54 (0.49) ± 0.02	0.54-0.57 (0.55) ± 0.01	0.57
D/U	2.89-4.21 (3.16) ± 0.27	3.72-5.05 (4.3) ± 0.36	2.12-3.55 (2.44) ± 0.18	2.82-3.17 (2.98) ± 0.16	3.35

DISTRIBUTION AND HABITAT. Macleay River Valley, NE NSW; living in litter in a range of vegetation types including eucalypt woodland and dry rainforest on limestone. Closer to the coast *D. macleayana* occurs in eucalypt forest and littoral rainforest.

REMARKS. *Diphyrora macleayana* sp. nov. is smaller than *D. saturni* and has more crowded ribs on the teleoconch. However a key difference exists in the reproductive anatomy in which the epiphallus of *D. macleayana* is as long as the penis compared with an epiphallus half to two-thirds the length of the penis in *D. saturni*. *D. saturni* also has a distal tapering extension of the penis which is not seen in *D. macleayana*. Elongation of both the penis and in particular the epiphallus together with the bimodal protoconch sculpture are key departures from the more typical patterns seen in eastern Australian charopids hitherto investigated. An analoguous situation of combined conchological/anatomical character shifts was reported for *Rotacharopa* Stanisc, 1990 by Stanisc (1990). However, with so much of the charopid fauna yet to be studied, it is difficult to gain a true phylogenetic perspective of the significance of these features.

PHYLOGENETIC ANALYSIS

The characters and character states (Table 6) forming the data matrix (Table 7) lead to the strict consensus tree of the 250 most parsimonious trees (length 127, consistency index 0.56, retention index 0.65) (Fig. 35), with bootstrap values shown for each clade.

In the strict consensus tree, the *Rhophodon*, *Letomola*, *Elsothera* and *Scleridoropa* clades were well supported, with bootstrap values of 90% or greater. *Macrophallikoropa* was also moderately well supported (bootstrap value of 80%). These groups were therefore accepted as genera. Most other clades in the tree were poorly supported. The remaining taxa were either placed into monotypic genera, or united in genera with taxa not included in the analysis (based on shell characters).

Two exceptions to this are *Cralopa* and *Egilodonta*. *Cralopa* was not well supported by bootstrap values. One species (*carlessi*) was removed from this group into a new genus; however, the other two taxa were retained in *Cralopa*. There are at least two undescribed species that appear to be closely related to *C. kaputarensis* (JS, pers. obs.), and a study of these,

TABLE 6. List of characters and character states used in the phylogenetic analysis.

Character number	Character	States
1	Shell colour	1: absent, 2: flecked, 3: flammulated, 4: plain
2	Coiling pattern	1: loose, 2: even, 3: tight.
3	Whorl profile above periphery	1: flattened, 2: rounded, 3: shouldered
4	Supraperipheral sulcus	1: absent, 2: present
5	Apertural sinus	1: absent, 2: shallow, 3: deep
6	Spire height	1: apex and early spire elevated, 2: apex depressed and early spire elevated, 3: apex and early spire flattened, 4: apex and early spire depressed
7	Protoconch shape	1: exsert, 2: flattened
8	Umbilicus shape	1: cup or saucer shaped, 2: V-shaped, 3: U-shaped, 4: closed
9	D/U ratio	1: less than 3, 2: 3-4, 3: 4-4.5, 4: more than 4.5
10	Protoconch radial ribs	1: absent, 2: present
11	Protoconch – regular radial ribs	1: absent, 2: present
12	Protoconch microradials	1: absent, 2: present
13	Protoconch spirals	1: absent, 2: present
14	Protoconch pits	1: absent, 2: present
15	Protoconch radial ribs – spacing	1: evenly spaced, 2: increasing towards teleoconch, 3: decreasing towards teleoconch
16	Protoconch radial ribs – number	1: 45 or fewer, 2: 46-65, 3: 66-85, 4: 85 or more
17	Protoconch spirals – form	1: wrinkles, 2: threads, 3: lirae
18	Protoconch spirals – crossing radial ribs	1: spirals do not cross radial ribs, 2: spirals cross radial ribs
19	Teleoconch radial ribs	1: absent, 2: present
20	Teleoconch rib count	1: low (69 or fewer), 2: medium (70-149), high (149 or more)
21	Teleoconch radial rib width	1: narrow, 2: medium, 3: wide
22	Teleoconch rib curvature strength	1: strong, 2: weak
23	Teleoconch rib situation	1: convex, 2: concave, 3: straight
24	Kidney	1: almost unilobed, 2: moderately bilobed, 3: strongly bilobed
25	Secondary ureter	1: closed, 2: open
26	Epiphallus and vas deferens junction	1: bulbous, 2: no-bulbous
27	Epiphallus coiling	1: simple, 2: complex
28	Penis pilasters	1: simple longitudinal, 2: circular, 3: absent
29	Number of longitudinal pilasters	1: 1 pilaster, 2: 2 pilasters, 3: 5 or more pilasters, 4: 3-4 pilasters
30	Vergic structure	1: absent, 2: present
31	Ovotestis – general shape	1: many follicles in line along duct; 2: few follicles arranged in clumps (usually 2)
32	Ovotestis lobes	1: 1 lobe, 2: 2 lobes, 3: more than 2 lobes
33	Preputial tube	1: absent, 2: present
34	Radula – lateral tooth structure	1: continuous, 2: discontinuous
35	Radula – central tooth structure	1: tricuspid, 2: almost unicuspid
36	Radula – marginal teeth	1: saw-like (Rectangular), 2: similar in shape to laterals
37	Apertural barriers – microdentition	1: triangular, 2: rectangular
38	Parietal barrier A	1: absent, 2: present
39	Parietal barrier B	1: absent, 2: present
40	Parietal barrier C	1: absent, 2: present
41	Palatal barrier A	1: absent, 2: present
42	Palatal barrier C	1: absent, 2: present
43	Palatal barrier E	1: absent, 2: present
44	Basal barrier A	1: absent, 2: present

TABLE 7. Data matrix for the phylogenetic analysis.

Species	Character																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
<i>Minidonta hendersoni</i>	4	2	2	1	1	1	1	2	2	2	1	2	2	2	1	?	2	?	2	2	?	-	-	
<i>Aaadonta constricta constricta</i>	3	3	-	2	1	1	1	3	4	1	1	1	2	1	-	-	2	-	2	?	1	?	3	
<i>Rhophodon kempseyensis</i>	3/4	3	2	1	1	4	1	1	1	2	1	1	2	1	3	2	1	1	2	3	1	2	2	
<i>Rhophodon palethorpei</i>	4	3	2	1	1	3	1	1	1	2	1	1	2	1	3	2/3	1	1	2	2	3	2	2	
<i>Egilodonta bairnsdalensis</i>	4	3	2	1	1	3/4	1	1	1	2	1	1	2	1	3	4	1	1	2	1	3	2	2	
<i>Egilodonta wyanbenensis</i>	4	3	2	1	1	3/4	1	1	1	2	1	1	2	1	3	4	1	1	2	1	2	-	2	
<i>Egilodonta bendethera</i>	4	3	2	1	1	3	1	1	1	2	1	1	2	1	3	2	1	1	2	1	3	2	2/3	
<i>Egilodonta paucidentata</i>	4	3	2	1	1	3	1	1	1	2	1	1	2	1	3	1/3	1	1	2	1	3	2	2/3	
<i>Letomola contortus</i>	3	1	-	2	1	3	1	1	1	1	1	1	2	-	-	-	-	1	-	-	-	1	2	
<i>Letomola lanalittae</i>	3	1	-	2	1	4	1	2	2	2	1	1	2	3	?	-	-	1	-	-	-	1	2	
<i>Macrophallikoropa belli</i>	3	3	2	1	1	3	1	1	1	2	1	2	1	2	1	-	-	3	-	2	3	1/2	2	2
<i>Macrophallikoropa stenoumbilicata</i>	2	3	2	1	1	1	3	2	1	2	1	2	1	-	-	-	3	-	2	3	1	-	1	
<i>Elsothera brazieri</i>	2	2	3	1	1	3	2	2	2	2	1	1	2	1	1	3/4	2	2	2	3	2	2	2	
<i>Elsothera sericatala</i>	1	2	3	1	1	1/3	2	4	-	2	1	1	2	1	1	?	2	2	2	3	2	?	2/3	
<i>Whiteheadia globosa</i>	1	2	3	1	1	1	2	4	-	2	1	1	2	1	1	?	1	1	2	1	3	1	1/3	
<i>Coricudgia wollemiana</i>	4	3	2	1	1	1	2	3	2	2	1	1	2	1	1	4	2	2	2	1	3	1	3	
<i>Decoriropa lirata</i>	4	2	1	1	2	1/3	2	2	2	2	1	1	2	1	1	2	2	2	2	1	3	1	1	
<i>Marilyntropa jenolanensis</i>	4	2	1	1	1	2	2	2	2	2	1	1	2	1	1	2	2	2	2	1	3	1	3	
<i>Cralopa stroudensis</i>	4	1	3	1	3	1	2	3/4	?	2	1	1	2	1	1	3	2	2	2	2	3	1	1	
<i>Gouldiropa carlessi</i>	4	1	2	1	2	1	2	3	4	2	1	1	2	1	1	1	2	2	2	1	3	1	1	
<i>Gouldiropa kaputarensis</i>	4	1	1	1	2	1	2	3/4	?	2	1	1	2	1	1	1	2	2	2	2	3	1	1	
<i>Sharniropa wollondillyana</i>	4	1	3	1	1	1	2	3	3	2	1	1	2	1	1	2	2	2	2	1	3	1	1	
<i>Acheronopa attunga</i>	4	2	1	1	1	4	2	2	2	2	1	1	2	1	1	2	2	2	2	1	3	1	1/3	
<i>Hedleyropa yarrangobillyensis</i>	4	2	3	1	1	1/3	2	3	3	2	1	1	2	1	1	4	2	2	2	?	1	1	1	
<i>Scleridoropa sarahjanae</i>	3	2	2	1	1	3	2	1	1	2	1	2	2	1	2	4	2	2	2	2	3	2	2/3	
<i>Scleridoropa nawdewar</i>	3	2/3	2	1	1	3	2	1	?	2	1	2	2	1	2	4	2	2	2	?	3	-	2/3	
<i>Diphyropa saturni</i>	4	2	3	1	1	3	2	2	2	1	1	2	1	1	1	3	1	2	2	3	-	3	3	

Species	Character																						
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	
<i>Minidonta hendersoni</i>	2	2	2	1	1	2	1	1	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
<i>Aaadonta constricta constricta</i>	1	2	2	1	1	?	?	1	?	1	?	?	?	1	?	?	?	?	?	?	?	?	?
<i>Rhophodon kempseyensis</i>	1	1	2	1	1	4	1	2	2	1	1	1	2	2	2	2	2	2	2	2	2	1	1
<i>Rhophodon palethorpei</i>	1	1	2	1	2	-	1	2	2	1	1	1	2	2	2	2	2	2	2	2	2	2	1
<i>Egilodonta bairnsdalensis</i>	1	1	2	1	1	2	2	2	2	1	1	1	2	2	1	2	1	2	1	2	1	2	1
<i>Egilodonta wyanbenensis</i>	1	1	2	1	3	-	2	2	2	1	1	1	2	2	1	2	1	2	1	1	2	1	1
<i>Egilodonta bendethera</i>	1	1	2	1	1	1	2	2	2	1	1	1	2	2	1	2	1	2	1	2	1	2	1
<i>Egilodonta paucidentata</i>	1	1	2	1	1	3	2	2	2	1	1	1	2	2	1	2	1	2	1	2	1	2	1
<i>Letomola contortus</i>	2	1	2	1	1/2	4	1	2	1	1	1	2	1	2	2	1	1	1	1	1	2	1	
<i>Letomola lanalittae</i>	2	1	2	1	2	-	1	2	2	1	1	2	1	-	1	1	1	1	1	1	1	1	1
<i>Macrophallikoropa belli</i>	3	1	2	1	3	-	2	2	2	2	1	1	2	-	1	1	1	1	1	1	1	1	1
<i>Macrophallikoropa stenoumbilicata</i>	3	1	2	1	3	-	-	2	2	?	?	?	-	1	1	1	1	1	1	1	1	1	1
<i>Elsothera brazieri</i>	1	1	1	2	1	2	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	3
<i>Elsothera sericatala</i>	1	1	1	2	2	-	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	?
<i>Whiteheadia globosa</i>	3	1	2	1	1/2	1	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	?
<i>Coricudgia wollemiana</i>	3	1	2	1	1	2	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	3
<i>Decoriropa lirata</i>	2	1	2	1	1	2	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	1/2
<i>Marilyntropa jenolanensis</i>	2	1	2	1	1	3	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	3
<i>Cralopa stroudensis</i>	2	1	2	1	1	2	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	2
<i>Gouldiropa carlessi</i>	2	1	2	1	1	2	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	3
<i>Gouldiropa kaputarensis</i>	2	1	2	1	1	2	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	3
<i>Sharniropa wollondillyana</i>	2	1	2	1	1	2	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	3
<i>Acheronopa attunga</i>	2	1	2	1	1	4	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	4
<i>Hedleyropa yarrangobillyensis</i>	2	1	2	1	1	2	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	4
<i>Scleridoropa sarahjanae</i>	1	1	2	1	1	4	1	2	2	1	2	1	2	-	1	1	1	1	1	1	1	1	3
<i>Scleridoropa nawdewar</i>	1	1	2	1	1	4	1	2	2	1	2	1	2	-	1	1	1	1	1	1	1	1	2
<i>Diphyropa saturni</i>	2	1	2	1	1	3	1	2	2	1	1	1	2	-	1	1	1	1	1	1	1	1	4

when more material becomes available, may show that the latter should be in a separate genus, leaving *Cralopa* as a monotypic taxon.

Egilodonta had a bootstrap value of 46%. There was greater support for the group

[*Egilodonta* + *Rhophodon*], which had a bootstrap value of 74%. These groups have been united before (Stanisic, 1990). However, the 4 *Egilodonta* taxa are united by characters such as wide rib spacing on the teleoconch and a penial

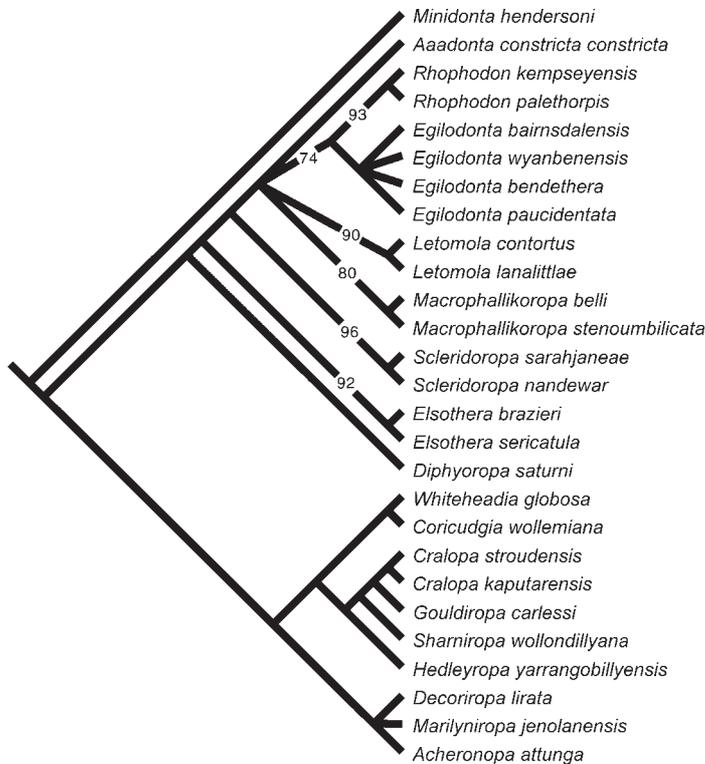


FIG. 35. Strict consensus tree of 27 taxa comprised of the 250 most parsimonious trees (length 127, consistency index 0.56, retention index 0.65). Bootstrap values are marked at the base of each clade.

verge, and are widely separated geographically from the other *Rhophodon* taxa. For these reasons, *Egilodonta* is established as a separate genus.

This study contains only a small cross-section of the Australian charopid fauna, and some of the low branch support may be due to the fact that key taxa are missing from the analysis. Until more Australian charopid taxa are described or thoroughly revised, many relationships within the group will remain unresolved.

DISCUSSION

The study of the eastern Australian Charopidae is still in its infancy and the descriptive task that faces researchers cannot be overstated. Stanistic (1990) analysed conchological and anatomical variation in 50 species of eastern Australian Charopidae and attempted to place these into regional and local context. In doing so the inadequacy of many previous species descriptions

and generic diagnoses based solely on comparatively gross shell characters (Iredale, 1937, 1941a,b; Smith & Kershaw, 1979, 1981) was exposed. Only the studies of Solem (1984) [on two northern Australian species] and Smith & Kershaw (1985) [on three Tasmanian species] were considered of sufficient standard to enable detailed comparisons to be undertaken with species extralimital to that study. The current study has attempted to build on the work of Stanistic (1990) and consequently has resulted in a change in some of the taxonomic concepts developed in the earlier study.

The species included in the current study were specifically selected on the basis that the species were generally well differentiated on shell features. As a result, they comprise only a limited range of morphotypes among a very large east-coast fauna. Remarks on the relative significance of patterns of morphological variation need to be tempered by the knowledge that additional 'unusual' forms will emerge as this fauna is investigated. This is especially

so in regard to the many species occurring on the high mountains of the Wet Tropics, NE Qld (Stanistic et al., 1994b) which display a range of shell variation greater than seen in the remainder of the east coast fauna (Stanistic, 1993a; unpubl. data).

Intergeneric variation is discussed under the relevant generic treatments but inferred relationships between genera are still largely tentative. In summary, it would appear that quite different lineages appear to have developed grossly similar patterns of shell form (size, shape and sculpture) probably in response to environmental selection. Living among seasonally dry, limestone talus would seem to favour species with dentate apertures and those with bold postnuclear sculpture. Anatomical variation was largely conservative with little in the way of identifiable character shifts. Where such shifts did occur (*Macrophallikoropa*, *Diphyoropa*) these coincided with major shifts in shell

patterns, particularly protoconch sculpture. Subtle differences in shell features such as fine structure of protoconch sculpture, architecture of post-embryonic sculpture, whorl profile and coiling pattern provided a means of discriminating between the grossly convergent patterns and in identifying significant generic level trends. Most useful was the difference in protoconch sculpture. A casual review of the generic taxa previously reviewed by Stanisc (1990, 1993a, b; 1996) shows that in nearly all cases, this feature is generically diagnostic. In two exceptions, *Cralopa* and *Egilomen*, greater attention to differences in protoconch sculpture would have avoided some of the problems rectified in this study. It would appear that this single feature will be a key guide to generic level classification within this family but needs to be interpreted in microscopic rather than macroscopic detail. Hence, terms such as radial or spiral are in themselves of limited use.

BIOGEOGRAPHY

The Charopidae are a Gondwanan group (Stanisc, 1998a) which has historically been regarded as having greatest diversity in the moist forests of southeastern Australia. However, significant charopid faunas have been reported from the high mountains of the Queensland Wet Tropics (Stanisc et al., 1994) and the semi-arid Brigalow Lands of Qld (Stanisc, 1998b). In each of these cases though, the charopids are associated with rainforest refugia reinforcing the contention of Stanisc (1990) that the association of charopids and rainforests in eastern Australia has had a long history, probably extending beyond the Miocene. Our knowledge of rainforest evolution since the Miocene (A.P. Kershaw, 1981; Webb & Tracey, 1981; Kershaw & Nix, 1988; Nix, 1991) suggests that rainforest has been contracting in the face of increased continental aridity. Rainforests were more widespread when Australia was wetter, possibly extending into the interior of the continent (Martin, 1981), and hence it is reasonable to speculate that the charopid fauna would have been more widely distributed. Martin (1987, 1997) has shown that rainforest was present in the inland Lachlan and Darling Rivers as recently as the early to mid-Pliocene. As climatic conditions on the Australian continent shifted to a drier regime, rainforest receded into moist refugia and the overall range of the Charopidae would have contracted. At the individual species level this climate-induced restriction of

rainforest would have led to the fragmentation of populations in the first instance and extinctions in many cases. The surviving Charopidae are now found mainly in suitable refugia.

This longterm isolation of such fragmented charopid populations would have provided numerous opportunities for allopatric speciation. Subsequent dispersal and recolonisation may have occurred as climatic conditions (and hence vegetation systems) fluctuated between wet and dry. Allopatric speciation in the Charopidae has been documented in the larger rainforest massifs (Stanisc 1987, 1993a,b). But the phenomenon should be even more pronounced in areas where small patches of rainforest were separated by the rapidly developing, drier eucalypt communities. Hitherto there has been little published evidence to show the effects of climatic change on the distribution of snails that exist in the 'drier' areas of eastern Australia.

Rainforest is used here in a broad sense to include dry vine thickets and scattered remnants sometimes represented by only a few key floristic elements. In semiarid areas rainforest survives chiefly on rocky outcrops, in gully heads and along watercourses mainly because these habitats provide a more stable moisture supply than the surrounding countryside. Rock outcrops in particular are important microhabitats for both rainforest plants and land snails. These 'rock piles' may consist of basalt talus, granite boulders or limestone karst, and preserve environmental moisture in the crevices between the rocks. They also provide important shelter from fire. Limestone outcrops are particularly significant for land snails in eastern Australia (Stanisc, 1997 a,b). Besides providing shelter and moisture, the limestone also provides a ready supply of calcium for shell production. Collecting has shown that in the majority of cases these outcrops are snail-rich 'islands' in a sea of otherwise snail-poor countryside. They often support quite distinctive land snail communities of which examples have been highlighted by Stanisc (1997a,b).

The rainforest on many of these outcrops may be the result of recent opportunistic seeding but in others the association may have greater continuity. Such is probably the case in the Macleay Valley where rainforest, besides growing on the limestone outcrops, is also a dominant floristic feature of the surrounding countryside. And, probably not through mere coincidence, here there is a proliferation of land

snails in numbers not seen elsewhere in eastern Australia (Stanisic, 1997a). Not all limestone outcrops have as spectacular faunas as those in the Macleay Valley, but they are distinctive nonetheless. In some cases, less than half a dozen species may be present, but they may still include restricted endemics.

Because this study covers a very small component of a much larger and undescribed charopid fauna, biogeographic hypotheses emerging from this work remain limited. Nevertheless one fact is evident from this study and that is that limestone outcrops have been important historical refugia for the Charopidae in E NSW. They have been of primary importance where some genera have relied on this archipelago of habitats for survival. This appears to be true for *Egilodonta*, *Letomola*, *Achenoropa*, *Sharniropa* and *Marilyniropa*. In both *Letomola* and *Sharniropa* allopatric speciation following fragmentation of a wider ancestral population that probably encompassed non-limestone areas is indicated. Isolation of species has probably been longterm. In contrast *Achenoropa attunga* and *Marilyniropa jenolanensis* are localised limestone endemics, in each case scattered across several geographically proximate, but nonetheless isolated limestone outcrops. They may be recently fragmented populations of limestone dwellers that have yet undergone speciation. In contrast, *Egilodonta* exemplifies the principle of population fragmentation followed by allopatric speciation.

In other groups the limestone outcrops appear to have formed a small but nonetheless integral part of a wider network of mesic refugia in which these tiny litter snails were able to withstand the vagaries of a drying landscape. Such is the case with *Macrophallikoropa*, *Scelidoropa* and *Rhophodon* where species also occur outside the limestone outcrop archipelago. *Macrophallikoropa belli* has the most widespread distribution of the species investigated herein, yet has restricted sister species on the Jenolan Caves limestones and on the volcanically capped Mt Coricudgy. The biogeographic importance of the Jenolan outcrops is further highlighted by the presence of the restricted *Marilyniropa jenolanensis*.

The widespread distributions of such species as *Decorioropa lirata*, *Macrophallikoropa belli* and *Scelidoropa sarahjanae* across the limestone archipelago suggests that the adaptability of individual species may also have been influential

in the determination of some of the distribution patterns discussed herein.

At a regional level, general trends are few. Perhaps such trends will become more obvious when additional species are studied. The absence of the otherwise widespread *Scelidoropa sarahjanae* from much of the Sydney Basin (in contrast to situation with *D. lirata*, *Cralopa stroudensis* and *M. belli*) is unusual and needs to be further investigated.

Secondary areas of biogeographic significance appear to be volcanic peaks such as Mt Coricudgy (*Macrophallikoropa stenoumbilicata*, *Coricudgia wollemiana*), Mt Kaputar (*Scelidoropa nandewar*, *Cralopa kaputarensis*) and Glenugie Peak (*Rhophodon duplicostatus*). Again these refugia preserve mesic communities chiefly because they are largely rocky outcrops that conserve moisture.

The lack of many major radiations within this study is probably a function of the choice of species chosen for study whereby highly differentiated forms were selected. However, it probably also reflects the relictual nature of this fauna. Many charopids have quite localised distributions and opportunistic survival in such small refugia appears to have been relatively commonplace. At the same time there would have been many instances of extinction.

CONSERVATION

Some of the larger limestone outcrops (e.g. Jenolan, Wombeyan) mentioned in this study have been afforded legislative protection because of their value as caving sites and this security has provided an inadvertent safe haven for the resident biota. But many lesser known outcrops have no formal protection at all and the plight of their fauna, including the unusual charopids, is uncertain. As this study has shown, many of the limestone-associated charopids are localised endemics, often restricted to single outcrops. A conservation strategy that aims to preserve this fauna by listing all limestone outcrops on the National Estate should be considered.

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