

Three new genera and five new species of Helicarionidae from southeastern Australia (Pulmonata: Stylommatophora: Helicarionoidea)

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Abstract

Three new genera (*Brevisentis, Sheaia, Levidens*) and five new species (*Peloparion iridis, Brevisentis atratus, Nitor wiangariensis, Sheaia glenrockensis, Levidens ponderi*) of Australian Helicarionidae are described, based on morphological characters. The taxa can be distinguished primarily by features of the reproductive system, particularly the epiphallic retractor caecum and flagellum, the length of the vagina and the interior of the penis. Other important characters include the radular teeth, shell shape and body colouration. The phylogenetic relationships of these species are not clear, and further sampling and (where possible) DNA sequencing and analysis will be required to resolve their taxonomic positions.

Key words: Peloparion, Brevisentis, Nitor, Sheaia, Levidens, morphology, epiphallus, flagellum

Introduction

Helicarionidae is a group of land snails and semislugs recorded from Australia, the western Pacific, southeast Asia and Africa. Within Australia, the group is mostly confined to the eastern coast, with greatest diversity in northern Queensland. The most recent checklist recorded 52 genera and 107 species of Helicarionidae from Australia (Smith *et al.* 2002). Many of these are known only from shells and external morphology, characters which are known to be highly variable in this group (Stanisic 1993a, b; Hausdorf 1998). In addition to this suite of mostly poorly known species, there are ~140 undescribed species of Helicarionidae held in the collections of the Australian Museum and the Queensland Museum.

The relationships of Helicarionidae are also poorly understood. For many years the family has included subfamilies Helicarioninae, Ariophantinae, Urocyclinae, Euconulinae and Dyakiinae (Baker 1941; Solem 1966). However, a recent revision of Limacoidea sensu lato based on a phylogenetic analysis of morphological characters grouped Helicarionidae, Ariophantidae and Urocyclidae in Helicarionoidea, moved Euconulidae to Gastrodontoidea (along with several other families) and moved Dyakiidae to the monotypic Dyakioidea (Hausdorf 1998). The monophyly of Helicarionoidea sensu Hausdorf and the exclusion of Euconulidae from this group are supported by molecular data (Hyman et al. submitted). However, there are very few synapomorphies recognised for Helicarionoidea and none are known for Helicarionidae (Hausdorf 1998; Hyman and Ponder in preparation). This is due in part to the large number of characteristics that appear to have been reduced or lost multiple times in this group, notably the shell and associated structures (Stanisic 1993a, b; Hausdorf 1998; Smith 1998; Smith et al. 2002) and various parts of the reproductive system (stimulator, epiphallic retractor caecum, flagellum) (Solem 1966; Hausdorf 1998; Smith 1998).

The new taxa described in this paper are required for a revision of Australian Helicarionidae (Hyman and Ponder in preparation).

Materials and Methods

All material examined was from the collections of the Australian Museum and the Queensland Museum. All wet specimens were fixed and preserved in ethanol. Animals were dissected using a Leica MZ8 microscope and drawings were produced using a *camera lucida* attachment. Before dissecting, the shell and body were drawn. The animal was then dissected and features of the reproductive, digestive, nervous and excretory systems drawn. The radula was removed for SEM and if possible a spermatophore was also examined.

The radulae were cleaned by soaking in ~3.6M potassium hydroxide (KOH) for approximately one hour in a water bath at 60°C, sonicating for ten seconds, then soaking in fresh KOH. The radulae were then rinsed in distilled water, flattened out with forceps on a fragment of glass cover slip and air-dried. The fragment of glass was attached to a SEM stub using a carbon tab. Spermatophores were cleaned with distilled water and air-dried before being fixed onto SEM stubs using carbon tabs. The stubs were sputter-coated with gold and viewed using a Philips XL30 scanning electron microscope.

The taxonomic positions of the species described here were determined based on the results of a phylogenetic analysis of morphological data (Hyman and Ponder in preparation).

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Abbreviations

AMS: Australian Museum, Sydney; M: monotypy; NSW, New South Wales; OD: original designation; Qld, Queensland; QM: Queensland Museum, Brisbane; SD: subsequent designation.

Taxonomy

Family HELICARIONIDAE

Diagnosis

Snails or semislugs with caudal apparatus formed from curled up sole [Muratov's (1999) helicarionid type]. Kidney unilobed. Genital system oviparous; stimulator absent; bursa copulatrix inserted at vagina or if vagina absent, at junction of free oviduct and penis; penial tunica open at proximal end. Spermatophore soft capsule with long hard tail-pipe.

Description

Shell present, complete or reduced, ranging in diameter from ~5mm to 35mm. Shell shape and sculpture variable. Shell laps absent and shell lobes present or shell laps and lobes both present, ranging in size and degree of fusion. Sole of foot tripartite; caudal apparatus present, formed from curled up sole (Muratov's (1999) helicarionid type); caudal horn very small to large; caudal foss diamond-shaped or vertical slit. Kidney unilobed; minor venation on pallial cavity absent or present; pigmentation absent or present; mantle gland absent. Genital system oviparous; oviduct glandular. Bursa copulatrix variable in length; inserted on vagina or, if vagina absent, at junction of free oviduct and penis. Stimulator absent. Epiphallus enters penis through simple pore, fleshy lips or verge; interior of penis with no sculpture, or with pustules, ridges, longitudinal pilasters or circular pilasters. Penial tunica present, sometimes not covering entire penis; open at proximal end. Epiphallic retractor caecum absent or present; epiphallic flagellum absent or present. Spermatophore soft capsule with long hard tail-pipe; tail-pipe with varying sculpture. Radula narrow or wide; central tooth with small ectocones (except in Levidens n. gen.: ectocones absent); central tooth mesocone lanceolate (except in Parmellops Iredale, 1944 and Echonitor Iredale, 1937: small and rounded). Lateral and marginal fields distinguishable and tooth rows straight (except in Caldwellia H. Adams, 1873).

Remarks

The diagnosis and description of Helicarionidae given above are based on a detailed examination of the morphology of 33 Australian species, two New Caledonian species, four Mauritian species and two Madagascan species (Hyman and Ponder in preparation). This definition of Helicarionidae differs from that of Smith *et al.* (2002) by excluding Euconulidae (following Hausdorf 1998; for further details see Hyman and Ponder in preparation; Hyman *et al.* submitted).

Peloparion Iredale, 1937

Peloparion Iredale, 1937a: 8. Type species Helicarion helenae Godwin-Austen, 1883 (SD); see Iredale (1941).

Species included

Peloparion helenae (Godwin-Austen, 1883), Peloparion iridis n. sp.

Diagnosis

Shell reduced, whorl profile rounded. Shell laps moderately small to large, rounded or tapering slightly, fused at base, pale in colour with dark markings. Sides of body and shell laps and lobes speckled with iridescent pigment. Mantle with visible minor blood vessels. Oesophageal crop present. Vagina very short, internally with longitudinal pilasters. Epiphallus enters penis through simple pore or medium length verge; penis internally smooth or covered in faint longitudinal ridges, longitudinal and circular penis pilasters present. Epiphallic retractor caecum absent; epiphallic flagellum present; flagellum and distal part of epiphallus with small internal cryptae. Spermatophore tail pipe moderately long, narrow, sculptured at base of capsule with few short branching spines. Central and lateral radular teeth tricuspidate; marginal teeth multicuspidate.

Description

External morphology: Shell reduced, 2.5–2.7 whorls, glossy, spire and apex flattened. Protoconch smooth (*Peloparion iridis*) or sculptured with incised spiral grooves (*P. helenae*); teleoconch smooth. Whorl profile rounded above and below rounded periphery. Internal walls of early whorls complete; umbilicus closed. Right shell lap large, rounded; left shell lap moderately small, rounded (*P. iridis*) or tapering to slight point (*P. helenae*); shell laps fused at base, right shell lap with dark border around edge and left shell lap with dark stripe through middle, both laps with dark spots. Shell lobes small to medium, median and left lobe fused. Sides of body and shell laps and lobes covered with tiny specks of pale pigment iridescent in life (*P. iridis*; *P. helenae* not examined alive). Caudal apparatus as for family; caudal foss vertical slit in tail.

Pallial cavity: As for family. Mantle with visible minor blood vessels; pigmentation of white spots.

Digestive system: Oesophageal crop present.

Genital system: As for family. Carrefour and talon both embedded in albumen gland. Free oviduct of medium length; capsular gland present; internal longitudinal pilasters absent. Bursa copulatrix inserted on vagina, short, less than half spermoviduct length (P. helenae), or moderately short, about half spermoviduct length (P. iridis); duct of bursa copulatrix wide (P. iridis) or narrow (P. helenae), distinguishable from bursa copulatrix, internally with longitudinal pilasters. Vagina internally with longitudinal pilasters. Epiphallus enters penis through simple pore (P. iridis) or medium length verge (P. helenae); penis internally smooth (P. helenae) or covered in faint longitudinal ridges (P. iridis), longitudinal penis pilasters present, circular pilasters also present (P.

helenae), diverticulum on penis absent. Penial tunica enclosing only penis; penis retractor muscle attached to epiphallus. Epiphallus internally without sculpture. Epiphallic retractor caecum absent. Diverticulum at junction of epiphallus and vas deferens in form of flagellum (thickwalled, glandular, with axial filament); flagellum and distal part of epiphallus with small internal cryptae forming external projections (*P. helenae*), or with internal cryptae hidden by thick external layer of muscle (*P. iridis*). Spermatophore (*P. helenae* only) soft capsule with hard tail pipe open at one end, tail pipe moderately long, narrow, sculptured at base of capsule with few short branching spines.

Radula: Relatively long and narrow. Central tooth with small ectocones; mesocone longer than tooth base. Lateral and marginal tooth fields distinguishable. Lateral teeth with endocone smaller than central tooth ectocone; ectocone equal in size to central tooth ectocone; mesocone shorter than tooth base, or longer than tooth base. Marginal teeth with endocones absent; ectocones approximately same length and breadth as mesocone, split into extra teeth.

Remarks

Peloparion was introduced as a subgenus of Helicarion Férussac, 1821 for Vitrina hyalina Pfeiffer, 1855, with Helicarion helenae Godwin-Austen, 1883 as a synonym (Iredale 1937). Later Iredale (1941) separated the two species, stated that the new subgenus name had been intended for helenae, not hyalina, and raised it to genus level, as well as describing a second species in the genus, Peloparion submissus Iredale, 1941. Two species, P. helenae and P. submissus, were recognised by Smith (1992) and Smith et al. (2002).

Examination of the original description and figures of Peloparion helenae has revealed that two different species are included in the figures (Godwin-Austen 1883). The colour drawings of the live animals (Godwin-Austen 1883, fig. 1, 1a), executed by Mrs H. Forde and sent to Godwin-Austen, have shells of 12-14mm in diameter and appear to depict the species currently known as Peloparion helenae. This species has grey to brown body colour; its major distinguishing anatomical characteristic is a reproductive system with a short, wide flagellum which has a thick muscular outer wall. However, the shell and anatomical drawings (Godwin-Austen 1883, figs 2-8) appear to depict the species described by Iredale (1941) as Peloparion submissus, a smaller species with a distinct red body colour and a reproductive system with a slender flagellum, longer than that of the grey-coloured animal. The shells of the two species differ primarily in size. The shell figured by Godwin-Austen (1883; fig. 2) is ~7mm in diameter, appearing to match the size of the smaller red-coloured animal. However, the type specimen has been lost.

Godwin-Austen's (1888) description was based primarily on the spirit specimens that he dissected, which appear to belong to the red-coloured species. As first revisor, I select this red-coloured species as the one described by Godwin-Austen. Thus, the two currently described species of

Peloparion (P. helenae and P. submissus) are synonyms with the name Peloparion helenae retained for the red-coloured species and the grey species requiring a new name. Peloparion helenae will be redescribed by Hyman and Ponder (in preparation) and Peloparion iridis n. sp. is described below.

Peloparion can be distinguished by its small, flattened, reduced shell of fewer than three whorls and by the dark border surrounding the distinctly rounded shell laps. Both species also have dark spots on the shell laps. In addition, specimens in alcohol exhibit tiny specks of pale pigment on the mantle laps and lobes and on the body. In live specimens of P. iridis these specks are iridescent, although this is only visible under magnification. Live specimens of P. helenae were not examined in detail, but it is likely that iridescence is also present in that species.

Peloparion belongs to a clade of semislugs and snails from southeastern Australia that is supported by morphological and molecular data (Hyman et al. submitted; Hyman and Ponder in preparation). The other genera in this clade (Helicarion, Mysticarion Iredale, 1941, Parmavitrina Iredale, 1937, Desidarion Iredale, 1941, Brevisentis n. gen.) share with Peloparion a very short vagina, a coiled flagellum with internal cryptae, a spiralling spermatophore with long branching spines, and the absence of an epiphallic retractor caecum.

Both species of *Peloparion* differ from the other southeast Australian genera in the shape of the flagellum and the spermatophore, although the latter was only observed in *P. helenae*. Internally, both species have cryptae in the flagellum and/or the distal epiphallus, indicating that the spermatophore does have spines; however, the cryptae are not externally visible. In *P. iridis* this is due to a thick muscular sheath around the flagellum, and in *P. helenae* the cryptae appear to be only in the distal end of the epiphallus and therefore the spermatophore only has a few short branching spines around the base of the tail-pipe. However, the presence of cryptae, absence of an epiphallic caecum and extremely short vagina still unite this genus with the southeast Australian group of genera.

Peloparion iridis n. sp. Figure 1, Table 1

Helicarion helenae; Godwin-Austen, 1883: 146, pl. 41, fig. 1 [live drawings only] (not of Godwin-Austin, 1883).

Material examined

Holotype. Sydney Harbour, Elizabeth Bay, **NSW**, **Australia**, 33°52' S, 151°14' E, pre 1877, AMS C456552.

Paratypes. Same data as holotype, AMS C103633 (n=4)

Other material. **Qld:** Upper Cedar Creek, foothills Mt Glorious, junction Cedar Creek and Love Creek, 27°19.1'S, 152°46.5'E, T. Carless, 3 Apr. 1994, attached to undersides of leaves of saplings and Hoya vines (to a height of at least 4m from ground), semi-evergreen vine thicket, QM

MO51026 (n=11; two specimens dissected, one radula examined). **NSW:** Sydney N, Bilgola Escarpment, between Barrenjoey & Wollombi Rds, 33°39' S, 151°19' E, M. Shea, 7 Jun. 1981, under fallen palm leaves in dense *Eucalypt &*

cabbage tree palm rainforest, AMS C162835 (n=9, one specimen dissected). Sydney S, Pittwater, Scotland Island, 33°39' S, 151°17' E, T. Gibbs, 14 Sep. 1999, AMS C368488 (n=6, one specimen dissected).

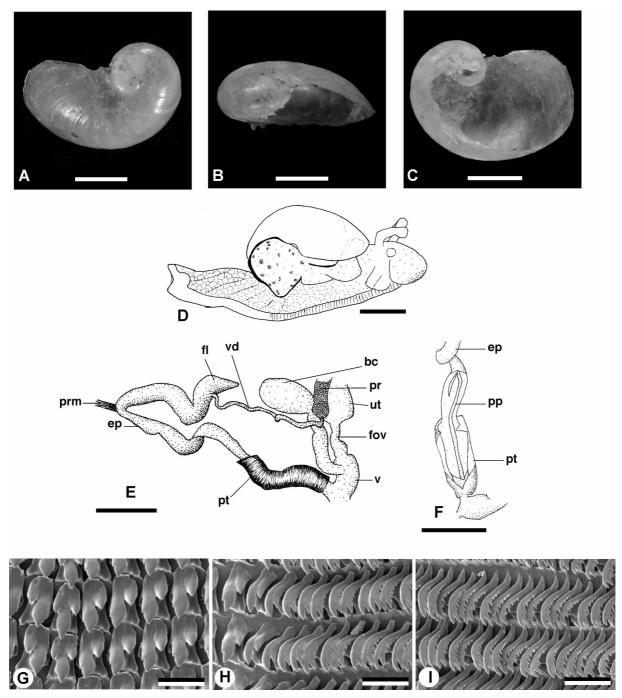


FIGURE 1. *Peloparion iridis.* **A–C**, Holotype, AMS C456552 (photographs by H. Barlow); **D**, External morphology, QMMO51026 (Mt Glorious, SE QLD); **E**, Reproductive system, QMMO51026; **F**, Penis interior, QMMO51026; **G–I**, Radula, QMMO51026. Scale bars: 3 mm (1–6), 20 mm (7–9). Abbreviations: bc — bursa copulatrix; ep — epiphallus; fl — flagellum; fov — free oviduct; pp — penial pilaster; pr — prostate; prm — penis retractor muscle; pt — penial tunica; ut — uterus; v — vagina; vd — vas deferens.

Description

External morphology: Shell (Fig. 1A–C) present, reduced, 2.5 whorls. Protoconch smooth. Shell shape and sculpture as for genus. Shell colour golden brown.

Dimensions of holotype. See Table 1.

Animal (Fig. 1D) beige with dark brown to grey markings; tiny specks of pale pigment cover mantle laps and lobes and sides of foot (iridescent in live specimens). Shell laps both rounded; otherwise as for genus. Right shell lobe of moderate size; left and median shell lobes fused, large in size. Caudal horn very large.

TABLE 1. Shell measurement data. Abbreviations: H — holotype; P — paratype.

Specimen	Number of	Shell	Shell
	whorls	diameter	height
		(mm)	(mm)
Peloparion iridis (H)	2.2	9.0	3.0
Brevisentis atratus (H)	4.5	7.7	3.6
Nitor wiangariensis (H)	5.7	10.6	5.2
Nitor wiangariensis (P)	5.5	11.2	6.2
Sheaia glenrockensis (H)	4.7	7.0	3.3
Levidens ponderi (H)	4.9	7.15	3.4

Pallial cavity and digestive system: As for genus.

Genital system (Fig. 1E–F): As for genus. Spermatheca moderately short, about half length of spermoviduct; spermathecal duct wide. Penis long, thin; epiphallus enters penis through simple pore; penis internally covered in faint ridges; one longitudinal penis pilaster present. Epiphallus slightly longer than penis; internally without sculpture. Epiphallic flagellum and distal part of epiphallus with internal cryptae hidden by thick external layer of muscle. Spermatophore not seen.

 $\it Radula$ (Fig. 1G–I): As for genus. Radular formula $(98.12.1.12.98) \times 140$.

Distribution

Previously Peloparion iridis (as P. helenae auct. in part) was thought to be restricted to the Sydney region, being found throughout Sydney from Randwick to the Kuringai Chase National Park. In this study, specimens from northern New South Wales and southern Queensland were identical to P. iridis. Thus, based on the known records, the species has a disjunct distribution, with some populations clustered around Sydney and others ranging from the Richmond River (northern New South Wales) to Brooyar State Forest, W of Gympie (Queensland). There is also a single lot collected in 1887 from near Monto, further to the north. There do not appear to be any similar species in this large gap and one possibility is that the species has been introduced to either Sydney or southern Queensland. Peloparion iridis was first recorded from southern Queensland in 1861 and from around Sydney in 1865 (Australian Museum collections). Much of the collected material from around Sydney, including the 1865 material, was found in or around gardens or built-up areas, whereas most of the southern Queensland material is from relatively undisturbed habitats. This indicates that the original population may have been derived from southern Queensland. The only evidence suggesting that the species may be a native of the Sydney area is that the clade to which Peloparion belongs is mainly distributed in southern Australia (Tasmania, Victoria, southern to middle New South Wales). However, Mysticarion porrectus (Iredale, 1941), another member of this clade, is also found in southern Queensland.

Peloparion iridis is found in rainforest, dry and wet sclerophyll forest and vine forest, often associated with palms. Specimens are found living in trees, on the underside of leaves, or under logs, fallen palm leaves and litter on the ground.

Remarks

Peloparion iridis has been recognised as Peloparion helenae for many years, based on the inclusion of colour drawings of the live animal of *P. iridis* in the original description of *P. helenae* (Godwin-Austen 1883, fig. 1). However, as noted above, the anatomical drawings that the description is based on (Godwin-Austen 1883; figs 2–8) are of a separate species. For this reason a new name (*P. iridis*) has been introduced for the relatively smaller, grey to brown species of *Peloparion*. This species can be distinguished from *P. helenae* by its smaller size and its grey to brown body colour, in contrast to the red body colour of *P. helenae*. Anatomically, *P. iridis* can be distinguished by the presence of a short, wide epiphallic flagellum with a thick muscular outer wall, the absence of a penial verge, and the presence of only longitudinal and not circular penial pilasters.

The function of the iridescent spots observed in this species is unknown. Terrestrial gastropods have poor vision (Chase 2001), so it seems unlikely that the iridescence could be used for recognition by other snails.

Etymology

Latin *iridis*, rainbow; referring to the iridescent specks of pigment in the skin.

Brevisentis n. gen.

Type species *Helix jacksoniensis* Gray, 1834 (OD).

Included species

Brevisentis jacksoniensis (Gray, 1834), Brevisentis atratus n. sp.

Diagnosis

Shell with rounded whorl profile. Shell laps small to moderately long, narrow, uniform in colour. Mantle with visible minor blood vessels. Oesophageal crop absent. Vagina very short to moderately long, internally with longitudinal pilasters. Epiphallus enters penis on one side, through short to medium length verge; epiphallus folded over top of penis. Penis interior variable, consisting of pustules at apical end (sometimes partially fused) and longitudinal (*B. jacksoniensis*) or irregular (*B. atratus*) ridges at basal end. Epiphallic retractor caecum absent; epiphallic flagellum present; flagellum and distal part of epiphallus with internal cryptae forming external projections. Spermatophore tail pipe short and spiralling, sculptured with moderately short branching spines at proximal end only. Central and lateral radular teeth tricuspidate; marginal teeth bicuspidate.

Description

External morphology: Shell 4.4–4.8 whorls, glossy, spire and apex slightly raised. Protoconch sculptured with

incised spiral grooves; teleoconch sculptured with microscopic spiral grooves. Whorl profile rounded above and below rounded periphery. Internal walls of early whorls complete; umbilicus open, very narrow U-shape. Shell laps small to moderately long, not fused, uniform in colour. Shell lobes small to very small, not fused. Caudal apparatus as for family; caudal foss vertical slit in tail.

Pallial cavity: Mantle with visible minor blood vessels; pigmentation of black and white spots (some specimens of *Brevisentis jacksoniensis* have orange spots).

Digestive system: Oesophageal crop absent.

Genital system: Carrefour embedded in albumen gland; talon shallowly embedded (B. jacksoniensis) or free (B. atratus). Free oviduct short (B. atratus) or short to long (B. jacksoniensis); capsular gland present; internal longitudinal pilasters absent. Bursa copulatrix inserted on vagina, short to moderately short, less than or equal to half spermoviduct length; duct of bursa copulatrix wide, distinguishable from bursa copulatrix, internally with longitudinal pilasters. Vagina very short (B. atratus, B. jacksoniensis) to moderately long (B. jacksoniensis), internally with longitudinal pilasters. Epiphallus enters penis on one side, through short to medium length verge; epiphallus folded over top of penis and attached by connective tissue. Penis interior variable, consisting of pustules at apical end (sometimes partially fused) and longitudinal (B. jacksoniensis) or irregular (B. atratus) ridges at basal end; diverticulum on penis absent. Penial tunica enclosing only penis; penis retractor muscle attached to epiphallus. Epiphallus internally with longitudinal pilasters. Epiphallic retractor caecum absent. Diverticulum at junction of epiphallus and vas deferens in form of flagellum (thick-walled, glandular, with axial filament); flagellum and distal part of epiphallus with internal cryptae forming external projections. Spermatophore soft capsule with hard tail pipe, open at one end; tail pipe short and spiralling, sculptured with moderately short branching spines at proximal end only.

Radula: Relatively long and narrow. Central tooth with small ectocones; mesocone lanceolate, longer than tooth base. Lateral and marginal tooth fields distinguishable. Lateral teeth with endocone smaller than central tooth ectocone; ectocone equal in size to central tooth ectocone; mesocone longer than tooth base. Marginal teeth with endocones absent; ectocones shorter and narrower than mesocone, not split into extra teeth.

Remarks

Brevisentis is created for some species previously included in Melocystis Iredale, 1937. Melocystis was introduced for Helix circumcincta Cox, 1868, with Helix jacksoniensis Gray, 1834 listed as a synonym (Iredale 1937). The genus was erected on the basis of Odhner's (1917) description of the radula of Helix marmorata Cox, 1864 (a synonym of Helix circumcincta); however, it is possible that Odhner's specimen was misidentified (Iredale 1941). Subsequently Iredale (1941) stated that jacksoniensis did not actually represent any Australian species but was the result of a mistake in localities. At the same time he described

Expocystis exclusus Iredale, 1941 in the family Microcystidae and removed *Melocystis* to Nitoridae.

Subsequent authors have followed Iredale's exclusion of *jacksoniensis* from the Australian fauna and have included two species in *Melocystis*, *M. circumcinctus* and *M. exclusus* (Smith 1992; Smith *et al.* 2002).

Examination of the syntypes of *Helix jacksoniensis* have indicated that the name belongs to a distinct species from the Sydney region which is very similar anatomically to *Melocystis exclusus*, but both species differ considerably from *M. circumcinctus*. In this study the latter species is placed in *Nitor*, and *Brevisentis* is introduced for *Helix jacksoniensis* (with *M. exclusus* as a synonym, *fide* Hyman and Ponder in preparation) and *Brevisentis atratus* sp. nov. Only *B. atratus* is described here; the morphology of *Nitor circumcinctus* and *B. jacksoniensis* will be described in a separate paper (Hyman and Ponder in preparation).

The new genus differs anatomically from all other Australian helicarionid snails, as it is the only group of snails to exhibit the short, wide and coiled flagellum, correspondingly spinose spermatophore, absent epiphallic caecum and extremely short vagina seen in semislug genera *Helicarion*, *Mysticarion*, *Parmavitrina*, *Desidarion* and *Peloparion*. *Brevisentis* can also be differentiated from *Nitor* Gude, 1911, the only confamilial snail genus with a range overlapping that of *Brevisentis*, by its rounded whorl profile and longer shell laps.

Etymology

Latin: *brevi*, short, and *sentis*, thorn; referring to the short spines on the spermatophore (gender: masculine).

Brevisentis atratus **n. sp.** Figure 2, Table 1

Material examined

Holotype. Coolah Tops NP, at lookout 1km S of Pinnacle Lookout at end of Pinnacle Rd, **NSW**, **Australia**, 31°41.8' S, 150°1.1' E, M. Shea, 26 May 2000, basalt rock pile at edge of escarpment, AMS C446473.

Paratypes. Same data as holotype, AMS C446452 (n=5).

Other material. NSW: Hunter region, Coolah Tops NP, Warung Forest Rd, 12.5km E of Hildegarde Rd junction, 31°45.8' S, 150°7.3' E, M. Shea, 30 Mar. 2001, tall dry eucalypt forest, AMS C446460 (n=4, two specimens dissected). Hunter region, Liverpool Ranges, Coulsons Creek Rd just below crest of range, 40.5km N of Merriwa (31°50.2' S, 150°30' E), M. Shea, 22 Apr. 2001, vine thicket on basalt scree, AMS C446458 (n=2, one specimen dissected). Hunter Region, Wollemi NP, upper Baerami Valley 300m upstreAMS of Baerami Oil Shale Mines & camping area alongside Reubens Creek Management Trail (32°34.2' S, 150°26' E), M. Shea, 13 May 2002, dense dry woodland on sandstone on S facing slope at Reubans Ck valley, AMS C446454 (n=2, one specimen dissected). Bowral, summit of Mt Gibraltar (850m), Oxley Drive,

34°28.33' S, 150°25.88' E, M. Shea, 3 Oct. 1999, crawling on wall of stone shelter during wet weather, sclerophyll forest,

AMS C205294 (n=1), one specimen dissected, radula examined).

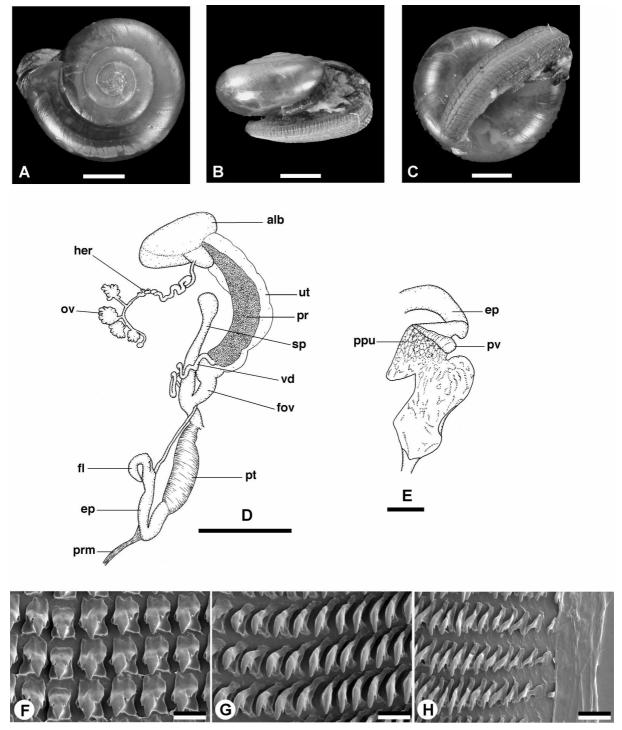


FIGURE 2. Brevisentis atratus. **A**, Holotype, AMS C446473 (photographs by H. Barlow); **B**, Reproductive system, AMS C205294; **C**, Penis interior, AMS C446460; **D**, Radula, AMS C205294. Scale bars: 2 mm (10–12), 5 mm (13), 1 mm (14), 20 mm (15–17). Abbreviations: alb — albumen gland; bc — bursa copulatrix; ep — epiphallus; fl — flagellum; fov — free oviduct; her — hermaphrodite duct; ov — ovotestis; ppu — penial pustules; pr — prostate; prm — penis retractor muscle; pt — penial tunica; pv — penial verge; ut — uterus; vd — vas deferens.

Description

External morphology: Shell (Fig. 2A) 4.5 whorls, golden brown, glossy, spire and apex slightly raised. Protoconch sculptured with incised spiral grooves; teleoconch sculptured with microscopic spiral grooves. Whorl profile rounded above and below rounded periphery.

Internal walls of early whorls complete; umbilicus open, very narrow U-shape. Animal dark grey to black, paler grey in middle of tripartite sole. Shell laps narrow, finger-shaped, not fused, uniform in colour. Caudal horn large, caudal foss vertical slit in tail.

Pallial cavity: As for genus. Pigmentation of black and white spots.

Digestive system: As for genus.

Genital system (Fig. 2B–C): As for genus. Carrefour embedded in albumen gland, talon free. Free oviduct short. Spermatheca inserted on vagina, moderately short, about half length of spermoviduct. Vagina short, internally with longitudinal pilasters. Penis moderately long; epiphallus enters penis through short verge, less than half penis length; penis interior variable, consisting of pustules at apical end (sometimes partially fused) and irregular ridges at basal end. Spermatophore soft capsule with hard tail pipe; tail pipe open at one end, sculptured with branching spines towards capsule and smooth at tip.

 $\it Radula$ (Fig. 2D): As for genus. Radular formula $(34.10.1.10.34) \times 94$.

Distribution

Brevisentis atratus is known from the summit of Mt Gibraltar, near Bowral in southeastern New South Wales, to Coolah Tops National Park in the Hunter region. It is usually collected from dry woodland and vine thickets, in rock piles or leaf litter.

Remarks

Brevisentis atratus can be distinguished from B. jacksoniensis by the dark grey or black colouration of its body and by the absence of red mucus. Anatomically, it can also be distinguished by differences in the penial anatomy. B. atratus has a shorter, narrower penial verge than B. jacksoniensis. In addition, the interior of the penis has irregular pustules at the top and irregular ridges and indentations at the base, in contrast to the even circular rows of pustules and longitudinal ridges seen in the penis interior of B. jacksoniensis.

Etymology

Latin *atratus*, dressed in black; referring to the dark grey to black colouration of the body.

Nitor Gude, 1911

Thalassia Albers, 1860: 59. Type species *Helix subrugata* Reeve, 1852 (OD) (not *Thalassia* Gistel, 1848).

Nitor Gude, 1911: 270 [nom. nov. for Thalassia Albers, 1860]. Modonitor Iredale, 1937a: 3. Type species Helix pudibunda Cox, 1868 (M).

Melocystis Iredale, 1937a: 5. Type species *Helix circumcincta* Cox, 1868 (OD).

Included species

Nitor subrugatus (Reeve, 1852), Nitor pudibundus (Cox, 1868), Nitor circumcinctus (Cox, 1868), Nitor medioximus Iredale, 1941, Nitor graftonensis (Cox, 1864), Nitor wiangariensis n. sp.

Diagnosis

Shell with whorl profile flattened above and rounded or flattened below; rounded to angulate periphery. Shell laps short to absent, narrow, not fused, uniform in colour. Mantle with visible minor blood vessels. Oesophageal crop absent. Vagina moderately long, internally with longitudinal pilasters. Epiphallus enters penis through two fleshy lips (*N. circumcinctus*) or short verge (*N. pudibundus*, *N. subrugatus*); penis internally flat, longitudinal penis pilasters present. Epiphallic retractor caecum present, moderate in size, positioned in middle of epiphallus; penis retractor muscle attached to tip of caecum. Epiphallic flagellum present; flagellum and distal part of epiphallus without internal cryptae and externally smooth and slender. Spermatophore tail pipe long, sculptured with longitudinal rows of tiny narrow teeth. Central and lateral radular teeth tricuspidate; marginal teeth bicuspidate.

Description

External morphology: Shell 4.3–6.2 whorls, glossy, spire and apex slightly raised. Protoconch sculptured with incised spiral grooves; teleoconch sculptured with microscopic spiral grooves. Whorl profile flattened above and rounded (Nitor subrugatus) or flattened (N. circumcinctus, N. wiangariensis) below rounded to angulate periphery. Internal walls of early whorls complete; umbilicus closed (N. wiangariensis) or narrowly open (N. circumcinctus, N. subrugatus). Right shell lap short to very short, left shell lap short to absent, both shell laps narrow, finger-shaped, not fused, uniform in colour. Right and median shell lobes of moderate size, thick, left shell lobe very small. Caudal apparatus as for genus; caudal foss vertical or diamond-shaped slit in tail.

Pallial cavity: Mantle with visible minor blood vessels; pigmentation absent (N. subrugatus), or of white spots (N. wiangariensis), or of black and white spots (N. circumcinctus).

Digestive system: Oesophageal crop absent.

Genital system: Carrefour embedded in albumen gland, talon free (only observed in N. circumcinctus). Free oviduct of medium length; capsular gland present; internal longitudinal pilasters present. Bursa copulatrix inserted on vagina, short, less than half spermoviduct length; duct of bursa copulatrix wide, not distinguishable from bursa copulatrix, internally smooth (N. wiangariensis, N. subrugatus) or with longitudinal pilasters (N. circumcinctus). Vagina moderately long, internally with longitudinal pilasters. Epiphallus enters penis through two fleshy lips (N. circumcinctus) or short verge (N. pudibundus, N. subrugatus); penis internally flat, longitudinal penis pilasters present, diverticulum on penis absent. Penial tunica present, enclosing only penis (N. subrugatus, N. wiangariensis) or enclosing only base of penis (N. circumcinctus); penis retractor muscle attached to tip of epiphallic caecum. Epiphallus internally with longitudinal pilasters. Epiphallic retractor caecum moderate in size, positioned in middle of epiphallus. Diverticulum at junction of epiphallus and vas deferens in form of flagellum (thick-walled, glandular, with axial filament); flagellum and distal part of epiphallus without internal cryptae and externally smooth and slender. Spermatophore soft capsule with hard tail pipe, open at one

end; tail pipe long, sculptured with longitudinal rows of tiny narrow teeth.

Radula (only examined in N. circumcinctus): Relatively long and narrow. Central tooth with small ectocones; mesocone lanceolate, shorter than tooth base. Lateral and marginal tooth fields distinguishable. Lateral teeth with endocone smaller than central tooth ectocone; ectocone equal in size to central tooth ectocone; mesocone shorter than tooth base. Marginal teeth with endocones absent; ectocones not split into extra teeth.

Remarks

The preoccupied name *Thalassia* was introduced for *Helix subrugata* (Albers 1860) and *Nitor* was introduced as a replacement name (Gude 1911). Iredale (1937) included four species in *Nitor*: *Helix subrugata* Reeve, 1852, *Helix moretonensis* Reeve, 1854, *Helix kreffti* Cox, 1864 and *Helix pudibundus* Cox, 1868 (the latter two species separated in subgenera *Pravonitor* Iredale, 1937 and *Modonitor* respectively). Later Iredale (1941) removed *H. moretonensis* (thought to belong to a juvenile of another family) and added a new species, *Nitor medioximus*. Smith (1992) synonymised *Modonitor* with *Nitor* but raised *Pravonitor* to genus level, leaving three species in *Nitor*.

Iredale (1937) created the family Nitoridae for *Nitor*, but later (Iredale 1941) expanded it to include *Melocystis*, which was then defined as including only one species, *Melocystis circumcinctus*.

Three of the four currently recognised species of *Nitor* (*N. subrugatus*, *N. pudibundus*, *N. medioximus*) were described from locations relatively close together in northern New South Wales and all three are found in the Grafton-Casino area. A fifth species, *Nitor graftonensis* (treated by Smith 1992 as a synonym of *N. subrugatus*) is recognised in the collections of the AMS and QM (taxonomic decision: J. Stanisic); this species was described from the same locality as *N. subrugatus* and is also found in the Grafton-Casino area.

Melocystis is here synonymised with *Nitor* on account of its flattened shell profile, long, narrow flagellum, moderately long epiphallic caecum with the penis retractor muscle attached to its tip, moderately long vagina, the presence of longitudinal pilasters in the penis interior and the presence of small spines on the spermatophore tail-pipe. This expands the genus to include five described species. One new species, *Nitor wiangariensis* n. sp., is described in the current study. The genus diagnosis and description are based on an examination of *N. wiangariensis*, *N. subrugatus* and *N. circumcinctus*; the morphology of the latter two species will be described in full in a later paper (Hyman and Ponder in preparation).

Nitor can be separated from the new genera Brevisentis, Sheaia and Levidens by the presence of a long, slender flagellum. It can also be distinguished from other helicarionid snail genera by its moderately long vagina, the attachment of the penis retractor muscle to the tip of a moderately long epiphallic caecum, the presence of multiple distinct longitudinal pilasters in the penis and the presence of

very small, narrow teeth on the long tail-pipe of the spermatophore (see Hyman and Ponder in preparation for further details).

Nitor wiangariensis n. sp.

Figure 3, Table 1

Material examined

Holotype. ca. 25km NE of Kyogle, off Forest Rd, Wiangarie State Forest, **NSW**, **Australia**, 28°23′ S, 153°6′ E, I. Loch & P. H. Colman, 17 May 1976, complex notophyll vine forest, AMS C446474.

Paratypes. Same data as holotype, AMS C334361 (n=20+, three specimens dissected, one shell measured).

Description

External morphology: Shell (Fig. A–C) 5.5–6.2 whorls; shape and sculpture as for genus; light yellow-brown; whorl profile flattened above and below rounded periphery; umbilicus closed. Animal yellow. Right shell lap small, finger-shaped; left shell lap a tiny stub; shell lobes as for genus. Caudal horn small; caudal foss diamond-shaped slit in tail.

Pallial cavity: As for genus. Mantle pigmented with white spots.

Digestive system: As for genus.

Genital system (Fig. 3D–F): As for genus. Spermatheca internally smooth. Epiphallus enters penis through short verge; penis internally smooth; seven to nine longitudinal penis pilasters present. Penial tunica present, enclosing only penis. Epiphallus longer than penis; internally with longitudinal pilasters. Spermatophore (Fig. 3F) as for genus.

Radula: Not examined.

Distribution

The complete range of this species is not known. The specimens examined were from Wiangarie State Forest in northern New South Wales. *Nitor pudibundus* and *N. subrugatus* have also been recorded from this region.

Remarks

Nitor wiangariensis was identified in the AMS collection as Nitor pudibundus; however, the specimens examined had shells of ~11-13mm in diameter with a rounded periphery (number of whorls ~5.5-6.2). The original description of N. pudibundus gives the diameter and height of a 6-whorl shell as 16.3mm and 13.8mm respectively. One of the possible syntypes of N. pudibundus (BMNH no registration number) has a diameter of 17.8mm and height of 11.0mm (6.0 whorls), indicating that N. wiangariensis is smaller than N. pudibundus. The two species also differ in whorl profile, with N. pudibundus exhibiting a more angular periphery. Furthermore, dissection of a specimen that closely matched the size and description of N. pudibundus (AMS C425191) showed a number of anatomical differences (data not shown), clearly indicating that N. wiangariensis and N. pudibundus are separate species. Nitor wiangariensis is also dissimilar to N.

subrugatus, which has a shell with a strongly keeled periphery. Finally, a comparison of the syntypes of *N. medioximus* with *N. wiangariensis* indicate that *N. medioximus* is smaller with a wider umbilicus. In addition, *N. medioximus* does not appear to occur in the Wiangarie State

Forest.

Etymology

This species is named after the type locality, Wiangarie State Forest.

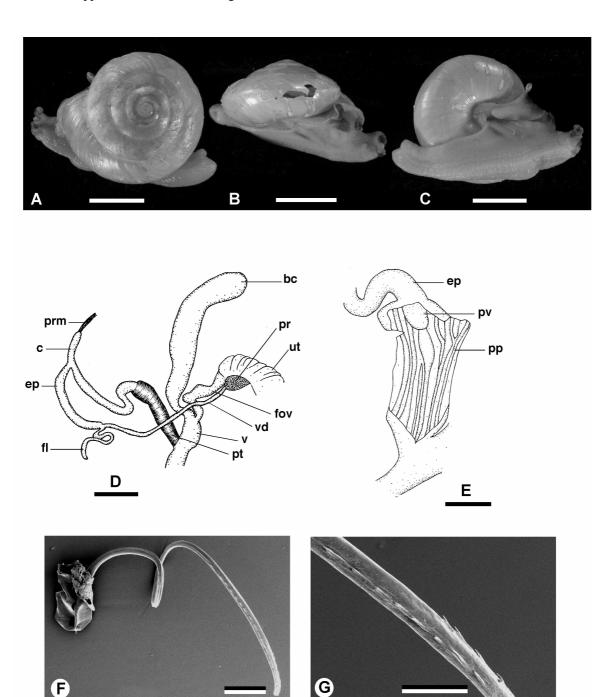


FIGURE 3. *Nitor wiangariensis*. **A–C**, Holotype, AMS C446474 (photographs by H. Barlow); **D**, Reproductive system, AMS C334361; **E**, Penis interior, AMS C334361; **F–G**, Spermatophore. Scale bars: 4 mm (18–21), 1 mm (22), 5 mm (23), 2 mm (24). Abbreviations: bc — bursa copulatrix; c — caecum; ep — epiphallus; fl — flagellum; fov — free oviduct; pp — penial pilaster; pr — prostate; prm — penis retractor muscle; pt — penial tunica; pv — penial verge; ut — uterus; v — vagina; vd — vas deferens.

Sheaia n. gen.

Type species Sheaia glenrockensis n. sp.

Included species

Sheaia glenrockensis n. sp.

Diagnosis

Shell with rounded whorl profile. Shell laps narrow, uniform in colour. Mantle with no visible minor blood vessels. Oesophageal crop absent. Vagina very short, internally smooth. Epiphallus enters penis through simple pore; penis internally smooth, longitudinal penis pilasters

present, pustular at apex and smooth at base of penis. Epiphallic retractor caecum absent; epiphallic flagellum absent; very small lime-sac present. Spermatophore not observed. Central and lateral radular teeth tricuspidate; marginal teeth bicuspidate.

Description

External morphology: Shell 5 whorls, pale golden, glossy, spire and apex slightly raised. Protoconch sculptured with incised spiral grooves; teleoconch smooth (spiral grooves not examined). Whorl profile rounded above and below rounded periphery. Internal walls of early whorls complete; umbilicus open, very narrow U-shape. Right shell lap narrow, finger-shaped, left shell lap not examined, shell laps not fused, uniform in colour. Sole of foot and caudal apparatus as for family; caudal horn moderately large; caudal foss vertical slit in tail.

Pallial cavity: As for family. Mantle with no visible minor blood vessels, pigmented with black and white spots.

Digestive system: Oesophageal crop absent.

Genital system: As for family. Carrefour embedded in albumen gland, talon free. Free oviduct long; capsular gland present but not visible externally; internal longitudinal pilasters present. Spermatheca inserted on vagina, short, less than half length of spermoviduct; spermathecal duct wide, not distinguishable from spermatheca, internally smooth. Vagina very short, internally smooth. Epiphallus enters penis through simple pore; penis internally smooth, longitudinal penis pilasters present, pustular at apex and smooth at base of penis, penial diverticulum absent. Penial tunica present, thin, enclosing penis and loop of epiphallus; penis retractor muscle attached to epiphallus. Epiphallus longer than penis, internally without sculpture. Epiphallic retractor caecum absent. Diverticulum at junction of epiphallus and vas deferens in form of very small lime-sac (thin-walled, no axial filament). Spermatophore not observed.

Radula: Relatively long and narrow. Central tooth with small ectocones; mesocone lanceolate, approximately equal in length to tooth base. Lateral and marginal tooth fields distinguishable. Lateral teeth with endocone much smaller than central tooth ectocone; ectocone equal in size to central tooth ectocone; mesocone approximately equal in length to tooth base. Marginal teeth with endocones absent; ectocones approximately same length and breadth as mesocone, not split into extra teeth until outer edge, where some teeth have 1-2 extra cusps.

Remarks

Sheaia lacks an epiphallic retractor caecum and a flagellum, as also present in *Echonitor*, *Periclocystis* Iredale, 1937, *Tarocystis* Iredale, 1937and *Levidens*. This could indicate that *Sheaia* should be placed in Euconulidae rather than Helicarionidae. However, the absence of spiral and radial ribs on the protoconch and teleoconch and the presence of incised spiral grooves on the protoconch (see Discussion) suggest inclusion in the Helicarionidae (Hyman and Ponder in preparation).

Sheaia can be distinguished from Echonitor, Periclocystis, Tarocystis and Levidens by the distinctive form of the longitudinal penis pilasters, which are formed of pustules at the apex of the penis and become smooth towards the base. This species also has a very short vagina and a long free oviduct.

Etymology

Sheaia (gender: feminine) is named for Michael Shea, both in thanks for his support in providing specimens and assistance over the last five years and in acknowledgement of his contribution to the collection and identification of land snails in Australia.

Sheaia glenrockensis n. sp. Figure 4, Table 1

Material examined

Holotype. Hunter region, beside Great North Walk in rainforest on northern side of Glenrock lagoon, Glenrock State Recreation Area, **NSW**, **Australia**, 32°57.61'S, 151°43.77'E, M. Shea, S. Clark, 3 Sep. 1999, under loose bark on dead standing tree, AMS C446470.

Paratypes: Same data as holotype, AMS C205298 (n=7; one specimen dissected, radula examined).

Description

External morphology: Shell (Fig. 4A–C) 5 whorls, pale golden, glossy, spire and apex slightly raised. Shell shape and sculpture as for genus. Animal pale cream; caudal horn grey. Shell laps and lobes and caudal apparatus as for genus. Pallial cavity and digestive system: As for genus.

Genital system (Fig. 4D–E): As for genus. Free oviduct long; 3–4 internal longitudinal pilasters present. Spermatheca inserted on vagina, short. Vagina very short. Penis long; epiphallus enters penis through simple pore; penis internally smooth, ~5 longitudinal penis pilasters present, pustular at apex and smooth at base of penis. Epiphallus longer than penis; internally without sculpture. Epiphallic retractor caecum absent. Diverticulum at junction of epiphallus and vas deferens in form of very small lime-sac (thin-walled, no axial filament). Spermatophore not examined.

 $\it Radula$ (Fig. F–H): As for genus. Radular formula $(35.10.1.10.35) \times 113$.

Distribution

Sheaia glenrockensis has only been collected alive from the northern side of Glenrock lagoon in the Hunter region. It was found in rainforest, under loose bark on a dead standing tree.

Remarks

Sheaia glenrockensis has the smallest range of the species described in the current study. It is also usually present in very low numbers and has rarely been collected alive, perhaps indicating that this species could be vulnerable to extinction.

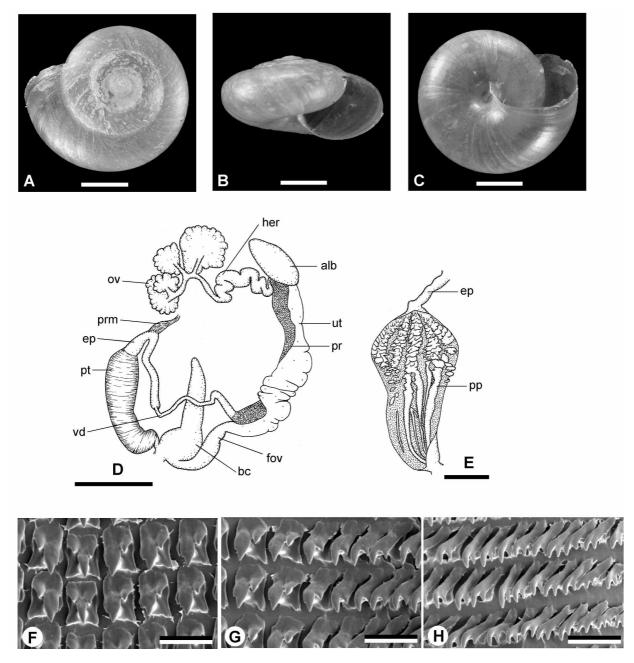


FIGURE 4. Sheaia glenrockensis. **A–C**, Holotype, AMS C446470 (photographs by H. Barlow); **D**, Reproductive system, AMS C205298; **E**, Penis interior, AMS C205298; **F–H**, Radula, AMS C205298. Scale bars: 2 mm (25–28), 1 mm (29), 20 mm (30–32). Abbreviations: alb — albumen gland; bc — bursa copulatrix; ep — epiphallus; fov — free oviduct; her — hermaphrodite duct; ov — ovotestis; pp — penial pilasters; pr — prostate; prm — penis retractor muscle; pt — penial tunica; ut — uterus; vd — vas deferens.

Etymology

Named after the type locality, Glenrock.

Levidens n. gen.

Type species Levidens ponderi n. sp.

Included species

Levidens ponderi n. sp.

Diagnosis

Shell with rounded whorl profile. Shell laps narrow, very short, not fused, uniform in colour. Mantle with no visible minor blood vessels. Oesophageal crop absent.

Vagina very short, bulbous, thick-walled, internally smooth. Epiphallus enters penis through simple pore; penis internally covered in pustules arranged in zig-zag rows, longitudinal penis pilasters present. Epiphallic retractor caecum absent; epiphallic flagellum absent. Spermatophore not examined. Central radular tooth unicuspidate; lateral and marginal teeth bipcuspidate.

Description

External morphology: Shell 5.1 whorls, glossy, spire and apex slightly raised. Protoconch sculptured with incised spiral grooves; early whorls of teleoconch sculptured with microscopic spiral grooves. Whorl profile rounded above and below rounded periphery. Internal walls of early whorls

complete; umbilicus open, narrow U-shape. Right and left shell laps narrow, finger-shaped, very short, not fused, uniform in colour. Sole of foot and caudal apparatus as for family; caudal horn small; caudal foss vertical slit in tail.

Pallial cavity: As for family. Mantle with no visible minor blood vessels, pigmented with white spots.

Digestive system: Oesophageal crop absent.

Genital system: Free oviduct long; capsular gland present with irregular pilasters; internal longitudinal pilasters present. Spermatheca inserted on vagina, short, less than half length of spermoviduct, spermathecal duct bulging at base, then narrow, distinguishable from spermatheca, internally with longitudinal pilasters. Vagina very short, bulbous, thickwalled, internally smooth. Epiphallus enters penis through simple pore; penis internally covered in pustules arranged in zig-zag rows, longitudinal penis pilasters present, penial diverticulum absent. Penial tunica present, moderately thick, folded at base, enclosing only penis; penis retractor muscle attached to epiphallus. Epiphallus shorter than penis, internally with longitudinal pilasters. Epiphallic retractor caecum absent. Diverticulum at junction of epiphallus and vas deferens absent. Spermatophore not examined.

Radula: Relatively long and narrow. Central tooth with no ectocones; mesocone triangular, very long, narrow, much longer than tooth base. Lateral and marginal tooth fields distinguishable. Lateral teeth with endocone absent; ectocone highly reduced, much smaller than central tooth ectocone; mesocone much longer than tooth base. Marginal teeth with endocones absent; ectocones on early marginal teeth reduced to tiny stub, increasing in size towards outer edge where they are approximately same length and width as mesocone, not split into extra teeth.

Remarks

Levidens, like Sheaia, lacks an epiphallic retractor caecum and a flagellum and has a very short vagina and long free oviduct. The penis interior differs in the presence of a single smooth penial pilaster and V-shaped rows of pustules. In addition, Levidens ponderi has a very distinctive and unusual radula. It is the only Australian helicarionid known to have a central tooth lacking endocones (Hyman and Ponder in preparation). The lateral teeth also have no endocones and very small ectocones, and both central and lateral teeth have very long and pointed mesocones.

Etymology

Latin *levis*, smooth, and *dens*, tooth; referring to the smooth radular teeth with greatly reduced cusps (gender: masculine).

Levidens ponderi n. sp.

Figure 5, Table 1

Material examined

Holotype. NE Tamworth, Oxley Park, Kamilaroi Walking Track, 250m E of Oxley Lookout, **NSW**, **Australia**, 31°5.18′ S, 150°57′ E, M. Shea, Apr. 1992, under loose rocks beside track in dry woodland, AMS C446472.

Paratypes. Same data as holotype, AMS C367488 (n=2).

Other material. NE Tamworth, Oxley Park, Kamilaroi Walking Track, 250m E of Oxley Lookout, **NSW**, 31°5.18' S, 150°57' E, I. Loch & J. H. Waterhouse, 9 Nov. 1985, sclerophyll on rocky hill, under wood on ground, AMS C340408 (n=9, one specimen dissected).

Description

External morphology: Shell (Fig. 5A-C) 5.1 whorls, glossy, dull fawn. Shell shape and sculpture as for genus. Animal beige. Shell laps and lobes and caudal apparatus as for genus.

Pallial cavity and digestive system: As for genus.

Genital system (Fig. 5D–E): As for genus. Free oviduct long. Spermatheca inserted on vagina, short. Vagina very short. Penis moderately long; epiphallus enters penis through a simple pore; penis internally covered in pustules arranged in zig-zag rows; one longitudinal penis pilaster present. Epiphallus shorter than penis, internally with longitudinal pilasters. Epiphallic retractor caecum absent. Diverticulum at junction of epiphallus and vas deferens absent. Spermatophore not examined.

Radula (Fig. 5F–H): As for genus. Radular formula (30.13.1.13.30) x at least 133.

Distribution

Levidens ponderi is found from just north of Scone to around Ashford in northern New South Wales, in dry sclerophyll woodland or remnant rainforest. It has been collected from under rocks and logs on the ground.

Remarks

Levidens ponderi has a very distinctive radula, unique among helicarionids due to the long, pointed mesocones and extreme reduction of the endocones and ectocones, perhaps indicating an unusual diet.

Etymology

Levidens ponderi is named for Winston Ponder, in thanks and appreciation for his support and inspiration over many years.

Discussion

The five species described here make up only a small part of the Australian helicarionid land snail fauna, which probably includes at least 200 species. The phylogenetic relationships of Helicarionidae are poorly understood (but see Hyman *et al.* submitted; Hyman and Ponder, in preparation). However, two of the species described here (*Peloparion iridis* and *Brevisentis atratus*) belong to a clearly defined group of genera that is supported by both morphological and molecular data (Hyman *et al.* submitted; Hyman and Ponder, in preparation). This clade, which also includes *Helicarion* (the type genus of Helicarionidae), *Mysticarion*, *Parmavitrina* and *Desidarion*, is restricted to the

southeastern part of Australia (Tasmania, Victoria, NSW, southern Queensland).

Nitor wiangariensis belongs to a genus that ranges from southern NSW to southern Qld. In a recent molecular phylogenetic analysis of Helicarionidae (Hyman *et al.* submitted), the genus *Nitor* (represented by *Nitor*

circumcinctus) was consistently placed as the sister taxon to a clade comprising all Helicarionidae from Lord Howe Island. This indicates that the Lord Howe Island taxa may have evolved from an ancestor of *Nitor*. No further details about the relationships of this group could be confirmed.

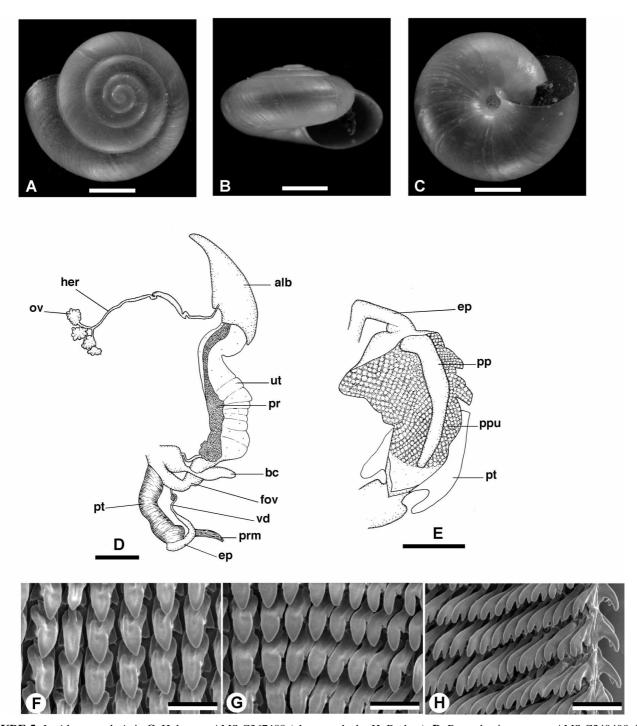


FIGURE 5. *Levidens ponderi*. **A–C**, Holotype, AMS C367488 (photographs by H. Barlow); **D**, Reproductive system, AMS C340408; **E**, Penis interior, AMS C340408; **F–H**, Radula, AMS C340408. Scale bars: 2 mm (33-36), 1 mm (37), 20 um (38-40). Abbreviations: alb — albumen gland; bc — bursa copulatrix; ep — epiphallus; fov — free oviduct; her — hermaphrodite duct; ov — ovotestis; pp — penial pilasters; ppu — penial pustules; pr — prostate; prm — penis retractor muscle; pt — penial tunica; ut — uterus; vd — vas deferens.

The relationships of *Levidens* and *Sheaia* are poorly understood. Molecular data are not available for either taxon and it is difficult to resolve their phylogenetic positions using morphological data alone (Hyman and Ponder in

preparation), in large part due to the absence of several key characters.

There are no known synapomorphies for Helicarionidae, but two of the synapomorphies of

Helicarionoidea (which includes Helicarionidae, Ariophantidae and Urocyclidae) are the presence of an epiphallic caecum and a flagellum with an axial filament (Hausdorf 1998). Levidens ponderi and Sheaia glenrockensis both lack these two characters. They also lack the presence of visible minor blood vessels on the mantle, a character present in most Helicarionoidea (Hausdorf 1998). While the absence of these character states could indicate that these species belong to Euconulidae rather than Helicarionidae, all three have been lost by some members of undoubted Helicarionoidea. For example, all members of the southeastern Australian helicarionid clade lack the epiphallic retractor caecum, as do Australian helicarionids Malandena suturalis (Odhner, 1917) and Parmellops etheridgei Hedley, 1890 (Hyman and Ponder in preparation). Another Australian helicarionid, Expocystis rustica (Pfeiffer, 1852), lacks visible minor blood vessels on the mantle (Hyman and Ponder in preparation). Finally, it is thought that several members of Urocyclidae have lost the epiphallic flagellum (Van Mol 1973; Van Goethem 1977). All these examples indicate that it is probable Levidens and Sheaia are helicarionids that have lost these taxonomically important structures.

The only positive character to link these species to Helicarionidae is the presence of incised spiral grooves on the shell. This character is present in most Helicarionidae (but not all species: for example, spiral grooves are absent in *Epiglypta howeinsulae* (Cox, 1873); Hyman and Ponder in preparation). In contrast, all Euconulidae have raised spiral (and often radial) striation and lack spiral grooves (Schileyko 2002). While I provisionally include *Levidens* and *Sheaia* in Helicarionidae, their phylogenetic relationship will require confirmation with molecular data.

Currently *Sheaia* and *Levidens* are both monotypic, but considering their restricted distributions and the often low numbers in which they are collected it is quite possible that with further sampling more species could be discovered. To gain a wider understanding of these species, further sampling (particularly of fresh material suitable for DNA extraction) is required. This would help to resolve not only the taxonomic positions of these species, but also increase our knowledge of their conservation status.

Acknowledgements

This research was carried out as part of a project supervised by Winston Ponder and Lars Jermiin. Material was provided by the Australian Museum (Sydney, Australia) and the Queensland Museum (Brisbane, Australia), and I would like to thank the collection managers and staff of these institutions. Some specimens were donated by Michael Shea and were gratefully received. Thanks are also due to Winston Ponder, Lars Jermiin and Michael Shea for commenting on an early version of the manuscript.

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