January 2005

A remarkable radiation of hydrobiids in the caves and streams at Precipitous Bluff, south west Tasmania (Mollusca: Caenogastropoda: Hydrobiidae)

Stefan Eberhard

S. A. Clark

W. F. Ponder

ZOOTAXA

1074

A radiation of hydrobiid snails in the caves and streams at Precipitous Bluff, southwest Tasmania, Australia (Mollusca: Caenogastropoda: Rissooidea: Hydrobiidae *s.l.*)

W. F. PONDER, S. A. CLARK, S. EBERHARD & J. B. STUDDERT

Magnolia Press
Auckland, New Zealand

W. F. PONDER, S. A. CLARK, S. EBERHARD & J. B. STUDDERT

A radiation of hydrobiid snails in the caves and streams at Precipitous Bluff, southwest Tasmania, Australia (Mollusca: Caenogastropoda: Rissooidea: Hydrobiidae *s.l.*)

(*Zootaxa* 1074)

66 pp.; 30 cm.

1 Nov. 2005

ISBN 1-877407-32-1 (paperback)

ISBN 1-877407-33-X (Online edition)

FIRST PUBLISHED IN 2005 BY

Magnolia Press

P.O. Box 41383

Auckland 1030

New Zealand

e-mail: zootaxa@mapress.com

http://www.mapress.com/zootaxa/

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Zootaxa 1074: 1–66 (2005)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)
1074

A radiation of hydrobiid snails in the caves and streams at Precipitous Bluff, southwest Tasmania, Australia (Mollusca: Caenogastropoda: Rissooidea: Hydrobiidae *s.l.*)

W. F. PONDER[1], S. A. CLARK[2], S. EBERHARD[3] & J. B. STUDDERT[1]

[1] *Australian Museum, 6 College Street, Sydney, NSW, 2010, Australia.*
Email: winstonp@austmus.gov.au

[2] *Previously Australian Museum, now Department of Biological Sciences, Biodiversity and Systematics. University of Alabama, Box 870345, Tuscaloosa, AL 35487, United States of America*

[3] *Department of Conservation and Land Management, Science Division, PO Box 51, Wanneroo, WA 6065, Australia*

Table of contents

Accepted by D. Geiger: 15 Aug. 2005; published: 1 Nov. 2005

Abstract

A radiation of hydrobiid snails is described from caves at Precipitous Bluff, southern Tasmania. The radiation (10 species) comprises two closely related genera; *Pseudotricula*, endemic to the Precipitous Bluff caves, and *Nanocochlea* found in these caves and surface streams and seepages, but also known from elsewhere in southern Tasmania. Two Precipitous Bluff species of *Nanocochlea* inhabit streams outside the caves, while one is found within the caves; all three are new. Seven species of *Pseudotricula* are described, six being new. Up to five species, one *Nanocochlea* and four *Pseudotricula*, are found in single stream habitats characterised by diverse sediment and slow to moderate flows. One *Pseudotricula* species is found in a swifter, larger stream with cobbles and gravel and another on smooth limestone surfaces in fast flowing water and water falls. A cladistic analysis (based on morphology) confirmed the monophyly of *Pseudotricula*, but the monophyly of *Nanocochlea* is less robust.

Key words: karst, *Nanocochlea*, *Pseudotricula*, cladistics, anatomy, stygobite

Introduction

Endemism in cave faunas is well known with some well documented examples of speciation in northern hemisphere karst areas (overviews in Culver & Holsinger 1992; Wilkens *et al*. 2000). Radiations of hydrobiid and hydrobiid-like snails in karst and other groundwater environments have been described from other parts of the world e.g., New Zealand (Climo 1974), North America (e.g., Hershler & Longley 1986) and Europe (e.g., Giusti & Pezzoli 1977, 1981; Radoman 1983). However, only one obligate groundwater-dwelling species (stygobite) has been previously described from Australia, *Pseudotricula eberhardi* Ponder, 1992 from Precipitous Bluff, southwest Tasmania. One of us (SE) recollected from several caves within this karst area in 1991 and 1994 and found a number of additional species that are described herein. Samples were also collected by Arthur Clarke in 1988.

Recent molecular studies (Wilke *et al*., 2001) have shown that Hydrobiidae, as widely used, may not be monophyletic. In this paper the family name Hydrobiidae is used in the broad sense because the systematics of the family-group taxa involved require further studies before they are resolved.

The Precipitous Bluff caves and karst

Precipitous Bluff is located near the south coast of Tasmania in a remote and inaccessible part of the Tasmanian Wilderness World Heritage Area (Fig. 1). The area remains essentially undisturbed by human activities except for occasional visits by bushwalkers and cavers. The area lies within the perhumid precipitation effectiveness province of Gentilli (1972). The nearest meteorological station is at Hastings located 25 km

eastnortheast, where annual rainfall is 1416 mm. The cool, moist climate supports a dense vegetation cover of wet sclerophyll and cool temperate rainforest (Reid *et al*. 1999).

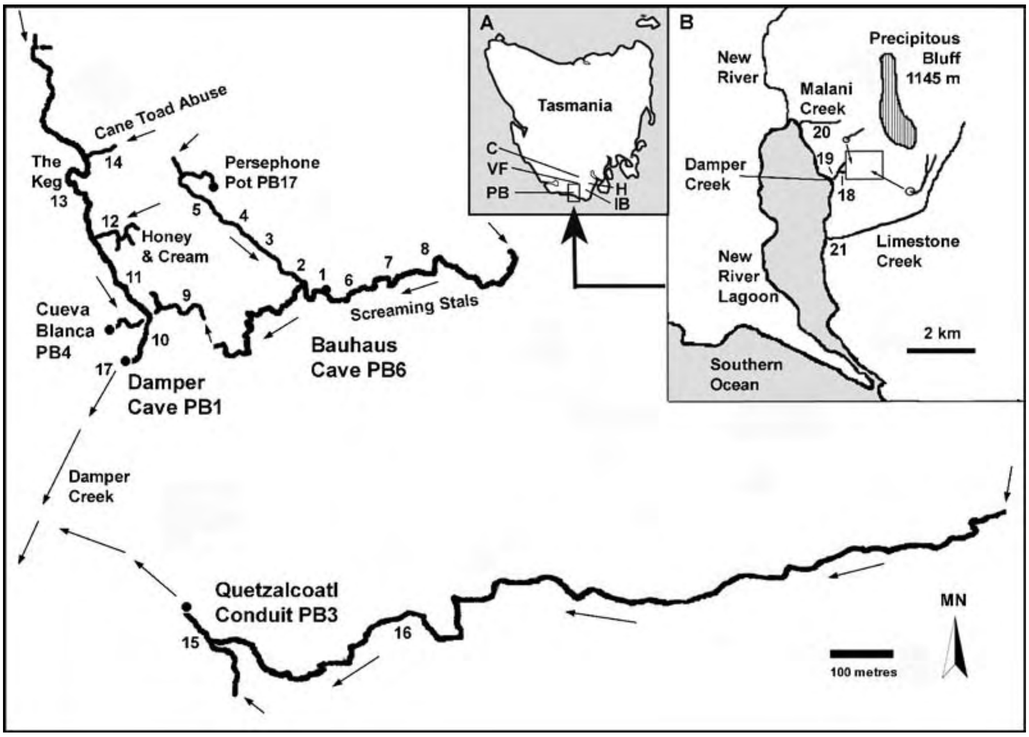

FIGURE 1. Schematic plan of mapped caves (black outline) at Precipitous Bluff showing hydrologic relationships (arrows indicate direction of stream flow paths), sample sites (numbered), cave entrances (black dots), and locations mentioned in text. Adapted from Hume (1989).
Inserts: **A**, Tasmania with location of Precipitous Bluff (PB in boxed area), Ida Bay (IB), Hastings (H), Vanishing Falls (VF) and Cracroft (C); **B**, Precipitous Bluff and New River Lagoon showing surface sample sites (numbered) and location of the caves (boxed area) in relation to dolines (open circles) with sinking streams that feed Damper Cave and Quetzalcoatl Conduit, which becomes Damper Creek upon resurging at the surface. Also shown (in B) is Precipitous Bluff. The numbers shown in B are explained below. The arrows in insert B and the main figure show the direction of water flow.
In the main map, the "PB" prefixed numbers refer to cave entrance numbers used by the Australian Speleological Federation. Sample sites shown in both the main map and in insert B are numbered as follows: 1 Bauhaus Cave (PB6) base of aven (stn PB6-1) and main streamway at downclimb (PB6-1A); 2 Bauhaus Cave (Persephone Pot PB17) lower streamway at first contact with stream stn 7; 3 Bauhaus Persephone middle streamway stn 8; 4 Bauhaus Persephone middle streamway stn 9; 5 Bauhaus Persephone upper streamway stn 10; 6 Bauhaus Screaming Stals streamway stn 11; 7 Bauhaus Screaming Stals streamway stn 12; and tributary seep near stn 12; 8 Bauhaus Screaming Stals streamway stn 13; 9 Cueva Blanca (PB4), Black Curtains streamway (=Inundation Passage); 10 Damper Cave (PB1) main streamway ca. 50 m inside entrance; 11 Damper Cave main streamway 100 m into cave; 12 Damper Cave, Honey and Cream; 13 Damper Cave seep near The Keg; 14 Damper Cave, Cane Toad Abuse; 15 Quetzalcoatl Conduit (PB3), 30 m into cave, stn PB3-1C; 16 Quetzalcoatl Conduit, beyond Pendulum Palace, stn PB3-2; 17 Damper Creek, 10 m downstream of Damper Cave entrance; 18 Damper Creek, first crossing; 19 Damper Creek at New River Lagoon; 20 Malani Creek; 21 Limestone Creek near New River Lagoon.

An extensive deposit of limestone occurs along the eastern flank of the New River valley and the western slope of Precipitous Bluff (Dixon & Sharples 1986). The Precipitous Bluff caves and karst are developed within Gordon Group Limestone of Ordovician age (Hughes 1957), the principal cave-bearing rock type in Tasmania. The limestone outcrops over about 10 km^2 between 0–300 m above sea level (asl) on the western and southwestern flanks of Precipitous Bluff (1120 m asl), which rises steeply from the shores of New River Lagoon, the estuary of the New River (Kiernan 1995).

The caves are developed on the lower flanks of Precipitous Bluff and receive allogenic recharge from streams descending from the upper slopes of the mountain which sink underground on contact with the limestone at about 300 m asl. Autogenic recharge is also received from rainfall directly on the limestone outcrop, which percolates downward via vertical shafts and fissures in the limestone. The descending subsurface flow paths coalesce at lower levels to form an integrated dendritic cave drainage network which discharges from resurgence caves situated at base level on the slope-plain juncture.

There are two resurgence caves associated with two drainage subsystems—Quetzalcoatl Conduit and Damper Cave (Fig. 1). The Quetzalcoatl Conduit subsystem is relatively simple and essentially consists of a single, linear base-level conduit, probably mostly fed by a sinking stream located to the northeast of Elusive Bluff. As a consequence of its relatively large surface catchment area draining from the higher slopes of Precipitous Bluff, combined with rapid conduit through-flow, this subsystem experiences a variable and flashy flow regime, which periodically floods the cave completely as well as mobilising and redistributing quantities of fine sediment.

In contrast to Quetzalcoatl Conduit the Damper Cave subsystem experiences flow regimes that are less variable and extreme, owing to a proportionately greater recharge contribution from diffuse sources. Inflows are smaller in size but numerous and these follow more intricate subterranean flow paths to base level. The Damper main stream, Cueva Blanca, and Bauhaus main stream are also quite responsive to rainfall events in the catchment, when surface runoff from the slopes of Precipitous Bluff rapidly sinks into the caves. However, the smaller, predominantly seepage fed streams (Persephone streamway, Hydrobiid Highway, Cane Toad Abuse) would have less variability in flow regime.

The Damper Cave subsystem encompasses considerable structural complexity with numerous tributary networks developed at different vertical levels, and between different caves. Nonetheless, they are hydrologically integrated via conduit connections. From upstream to downstream the hydrologic flow path is Persephone Cave to Bauhaus to Cueva Blanca to Damper Cave (Fig. 1).

The Quetzalcoatl Conduit and Damper Cave subterranean drainage subsystems lie adjacent to each other, and their resurging streams merge shortly downstream on the surface as Damper Creek before discharging into New River Lagoon. Hence, due to their close geographic proximity and downstream hydrologic connectivity, any observed faunal and hydrochemical similarities between the two subsystems may not be unexpected.

Certainly this appears to be the case in respect of a few measured hydrochemical parameters although very limited sampling has been undertaken. Water quality parameters in Damper Cave and Quetzalcoatl Conduit were measured on one occasion (Table 1) and both showed very similar water chemistry suggesting that any faunal differences between these two caves is likely to be due to other factors:

TABLE 1. Chemistry of water from Damper Cave and Quetzalcoatl Conduit sampled on 22nd November 1990 by R. Eberhard (data cited in Kiernan 1995).

	Damper Cave	Quetzalcoatl Conduit
pH	7.7	7.6
HCO_3^- mg/l	99.0	99.0
Cl^-mg/l	23.6	24.7
SO_4^{2-}mg/l	3.9	3.4
Ca^{2+}mg/l	26.0	26.0
Mg^{2+}mg/l	3.6	3.2
K^+mg/l	0.62	0.64
Na^+mg/l	11.9	12.0

The cave fauna at Precipitous Bluff was surveyed as part of a state-wide biodiversity survey of Tasmanian karsts undertaken by Eberhard *et al*. (1991b). This study discovered that the Precipitous Bluff karst supported the richest assemblage of locally endemic and obligate cave-dwelling species (> 12 spp.) in Tasmania (Eberhard 1992a). Most of this assemblage comprised terrestrial cave obligate species (troglobites) including described species of Coleoptera (Moore 1978), Opiliones (Hunt 1990; Hunt & Hickman 1993) and Araneae (Platnick & Forster 1989), in addition to other undescribed species of Opiliones, Araneae, Pseudoscorpionida, Oniscidea, and Collembola (Eberhard *et al*. 1991b).

An interesting aquatic cave fauna was suggested by the discovery of *Pseudotricula eberhardi* Ponder, 1992. Besides this snail, the sampled aquatic macrofauna included mayflies (Ephemeroptera), and crustaceans (Amphipoda, Syncarida) (Eberhard *et al*. 1991b; Eberhard 1992a). Of these other taxa at least two an undescribed species of paramelitid amphipod (*Antipodeus* sp.) and an undescribed species of psammaspid syncarid (*Eucrenonaspides* sp.) possessed clear stygomorphies (loss of eyes, pigment and elongation of appendages) indicating their status as obligate subterranean forms or stygobites (Eberhard *et al*. 1991b). Additional sampling may well increase the number of stygobites, particularly as the aquatic micro- and meiofauna have not been sampled.

Abbreviations

Repositories
AMS, Australian Museum, Sydney, New South Wales, Australia.
QVM, Queen Victoria Museum, Launceston, Tasmania, Australia.
TMAG, Tasmanian Museum and Art Gallery, Hobart, Tasmania, Australia

Other abbreviations
AL, aperture length.
AW, aperture width.
CV, convexity ratio.
SEM, scanning electron microscope.
SL, shell length.
SW, shell width.
TW, number of teleoconch whorls.

Materials and Methods

Collection of specimens took place between 18th December 1988 and 30th March 1994 during surveys of the limestone caves and adjacent surface streams in the Precipitous Bluff karst area in southern Tasmania (see Appendix for details). Specimens were collected using a combination of hand sieves to sweep the surface, washing of substrate, and picking them from the substrate by hand. A binocular microscope was used to sort material into relevant groups, whereby they were fixed in 10% formalin, buffered with sodium bicarbonate. Specimens were then preserved in 5% saltwater formalin.

Adult specimens were randomly picked from samples and were measured using a digitalised graphics tablet linked to a computer as described by Ponder *et al*. (1989). The convexity ratio (CV) was calculated using the method described by Ponder *et al*. (1989). A subset of the measured specimens, usually three males and females, were dissected using a binocular dissecting microscope with an attached drawing apparatus. The radula, operculum and anatomy, including pigmentation, mantle cavity, digestive system, male and female reproductive systems (see appendix for further details), were examined for all but *P. elongata* n. sp. These characters, together with the shell characters, were scored and entered into a DELTA (Dallwitz *et al*. 1993) file. DELTA was used to generate descriptions.

Shells and opercula used for SEM work were cleaned in freshwater using a small paint brush, fine jewellers, fine tipped tungsten wire, and in some cases using a sonicator. Cleaned specimens were then mounted on aluminium SEM stubs using either carbon tack, or carbon glue. Radulae (typically three per species) were extracted by dissolving the animal in a strong sodium hydroxide solution and incubating at approximately 60ºC for 6

–12 hours. Each radula was then washed four to five times in distilled water, and mounted on a glass cover slip using fine forceps to break and spread them. The cover slip was mounted on an aluminium SEM stub with double-sided carbon tape and carbon glue. All SEM stubs were gold-coated prior to SEM examination.

SYSTAT ver. 10 (SYSTAT Software Inc., Richmond, California, USA) was used for statistical analyses. PAUP* (ver. 4.0b10) (Swofford 1998) was used to perform maximum parsimony (cladistic) analyses.

Genus *Pseudotricula* Ponder, 1992

Type species: *Pseudotricula eberhardi* Ponder, 1992 (original designation).

Description

Shell. Moderate to large in size (adults 1.7 to 4.4 mm SL), conical. Protoconch of about 1.5 whorls, typically sculptured with small, close pustules with some coalesced into weak, irregular radial ridges; separation of protoconch from teleoconch distinct, with varix-like border. Teleoconch with spire much longer to slightly shorter than length of aperture. Aperture ovate, slightly angled and typically channelled posteriorly, inner lip attached to parietal wall or partially to completely detached, although never markedly so; usually lower part raised well above base. Outer lip usually prosocline, with terminal growth, typically markedly expanded and flared, simple in some species; weak external varix present in one species (*P. elongata* n. sp.). Periphery rounded, base simple, imperforate in both adults and juveniles. Usually semi-opaque to opaque, white, sometimes yellowish or brownish; with a thin pale yellowish periostracum.

Operculum. Ovate, paucispiral, flat, columellar edge slightly convex, outer edge strongly convex; outer surface simple, paucispiral, nucleus markedly eccentric; inner surface with weak ridges (probably representing reduced pegs) or (more often) white smear only.

Radula. Central teeth large, cutting edge broad, indented mid dorsally, with 4–5 cusps on either side of narrow sharp median cusp; narrow, thin lateral projections emerge at about 45º from mid laterally; base with short, rounded basal tongue not extending beyond lateral projections; two small to moderate basal cusps emerge from ventral face of tooth on either side of basal projection, innermost largest. Lateral teeth with short cutting edge, about 3–6 small cusps on inner side of narrow median cusp and 4–7 small cusps on outer side; neck prominent, near vertical; lateral flange about twice as long to slightly less than twice as long as cutting edge; prominent U-shaped projection on base below cutting edge; inner edge short, inner side of base excavated. Inner marginal teeth with 15–33 tiny cusps on rather wide cutting edge (ratio of cutting edge to shaft on inner marginal teeth about ¼; sides approximately parallel, outer edge thickened. Outer marginal teeth narrow, thickened on inner edge, distal end with 14–32 minute cusps; ratio of cutting edge to shaft about ¼.

Head-foot. Simple, unpigmented, with long cephalic tentacles, unpigmented eyes present in weak bulges at outer bases of tentacles; snout of moderate length, tapering, weakly bilobed distally. Foot short, rounded posteriorly.

Non-genital anatomy. Pallial cavity elongate, osphradium large and oval, towards posterior end of ctenidium; ctenidium with small ctenidial filaments and long efferent vein (ctenidium occupies only anterior ½ of pallial cavity). Hypobranchial gland variably developed. Kidney and pericardium usually about ½ in pallial roof; renal gland orientated longitudinally. Stomach with anterior and posterior chambers about equal or posterior smaller; style sac moderately long; no posterior caecum. Rectum with long S-shaped coil; overlying but not indenting pallial oviduct.

Male reproductive system. Prostate gland about ½ within pallial cavity; compressed to oval in section, with very thin ventral wall; pallial vas deferens opens at about ⅓–½ length of pallial portion. Penis located on right side of head well behind base of right tentacle; lacking glands but has an inconspicuous to moderately developed swelling in the distal portion just behind a papilla-like distal end; distal portion long and tapering; medial part simple and parallel sided; basal part wide to moderate.

Female reproductive system. Ovary simple sac; coiled oviduct smooth, firm, not embedded in connective tissue, initially inverted U-shaped, usually straight distal to seminal receptacle (one species with bend), usually reaching posterior end of bursa (sometimes a little more or less) then sharply bent to run anteriorly; Seminal receptacle ovoid to pyriform, with short duct, opening to oviduct, located opposite middle to ventral part of left side of bursa copulatrix. Bursa copulatrix rather large, ovoid to pyriform, posterior to albumen gland except for small overlap on right side, either just behind posterior pallial wall or extending in front of it; bursal duct arises from anterior or ventro-anterior wall, simple to undulating, joins oviduct dorsally at posterior pallial wall or in front of it as far anterior as junction of albumen and capsule glands. Common duct straight. Albumen gland ½ or more within pallial roof, shorter to longer than capsule gland. Capsule gland compressed-oval in section, divided into three glandular zones, short anterior and posterior translucent white zones and long yellowish to orange middle zone; anterior end blunt to steeply tapering; genital opening short, terminal to slightly anterior of capsule gland. Ventral channel extended into weakly to moderately developed vestibule anteriorly. No brood pouch.

Distribution and habitat

Species of *Pseudotricula* are restricted to stream and seep habitats in the Precipitous Bluff caves.

Remarks

The relationships of this genus with *Nanocochlea* Ponder and Clark, 1993 are now well established, with molecular data (Perez *et al*. 2005) showing they are sister taxa.

Anatomically the two genera are also very similar. They share the same type of ctenidium which only occupies the anterior half of the pallial cavity and with the filaments reduced in size and narrower than the normal broadly-triangular type. Other common features include the long, S-shaped rectal coil, unpigmented eyes, stomach morphology and genital anatomy. It could be argued that the fauna from Precipitous Bluff described herein shows a transition between the type species of *Nanocochlea* and *Pseudotricula*, both of which lie at the extremes of what perhaps could be regarded as a single genus. The main differences between *Nanocochlea* and *Pseudotricula* are shell characters. The shell in typical *Pseudotricula* is broadly conical in shape, rather than elongate conic to pupiform, with a relatively large aperture that typically bears an expanded, prosocline outer lip. Other differences are detailed below under *Nanocochlea*.

The shell differences between the type species of *Nanocochlea* and *Pseudotricula* are considerable and their close relationship was not fully realised at the time of their description. Anatomically the two genera are very similar and this similarity is reflected in their sister-group relationship (Perez *et al*. 2005). The paper describing *Pseudotricula* is listed as “in press” in Ponder *et al*. (1993), but it was actually published shortly before in 1992.

The species of *Pseudotricula* are rather uniform in anatomy, radular and opercular morphology, the latter differing only in the presence or absence of a peg on the inner surface. However, the species that we recognise here are readily discriminated on shell morphology (see below).

The penial swelling was not noted in the original description of *P. eberhardi* because it is very weakly developed in that species (confirmed by re-examination). It is, however, present in the other species of *Pseudotricula* and an identical structure is also seen in several species of *Nanocochlea*.

***Pseudotricula eberhardi* Ponder, 1992**

Figures 2A; 3A, B; 4A.

Synonymy

Pseudotricula eberhardi Ponder, 1992: 26, plate 1A–H, fig. 1A,B, fig. 2A,B, fig. 3A–C; Kierman & Eberhard, 1990, pl. 3.1.

Type material

Holotype: AMS C.165052, Black Curtain Streamway, Cueva Blanca, PB4, 31 MAR 1986.

Paratypes: AMS C.165053, same data (1 dry, 3 wet), TMAG E20151; AMS C.165054, same locality, 18 Dec. 1988 (9 dry, 20+ wet); TMAG E20152.

Other material examined

Cueva Blanca: AMS C.165390, PB4 (1 dry topotype); AMS C.203693, Black Curtain Streamway, PB4-1C (12 dry, 14 wet).

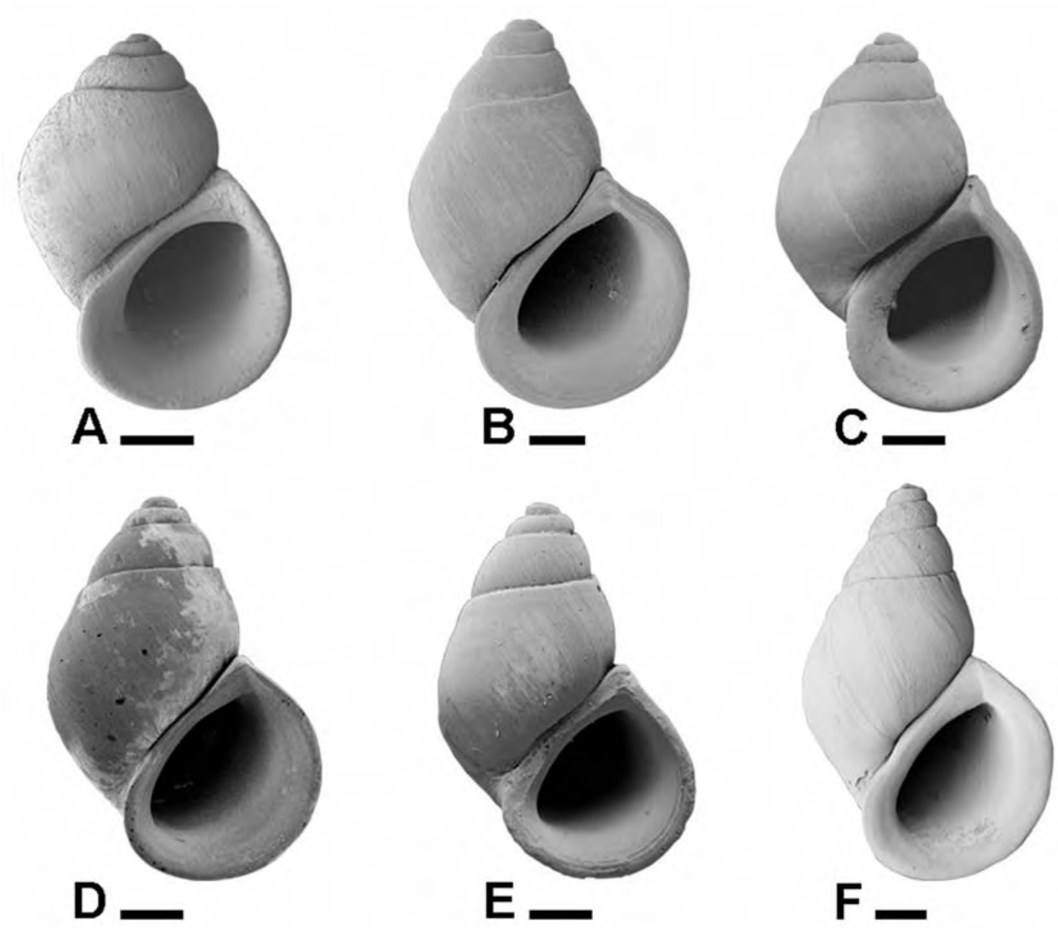

FIGURE 2. Shells of *Pseudotricula* species. **A**, *Pseudotricula eberhardi*, holotype, C.165052, Black Curtain Streamway, Cueva Blanca; **B–E**, *Pseudotricula expandolabra*, **B**, holotype, C.439673, Persephone Streamway, Bauhaus; **C**, paratype, C. 439674, Persephone Streamway, Bauhaus; **D**, C.201811, Persephone Pot, Bauhaus; **E**, C201495, Persephone Streamway, Bauhaus; *F*, *Pseudotricula auriforma,* holotype, C.439672, main streamway, Damper Cave. Scales: **A** **F**, 500 µm.

Description

Shell (Fig. 1A). Length up to 2.8 mm; broadly conical (SW/SL 0.71–0.80, mean 0.74, n = 10); spire low to moderate, straight to slightly convex in outline; last whorl evenly rounded; suture narrowly channelled; otherwise whorls evenly convex. Protoconch microsculpture small pits and pustules, with some weak spirally arranged wrinkles. Teleoconch up to 2.6 whorls in adult; aperture oval to pear-shaped; large, longer than spire (AL/SL 0.57–0.68, mean 0.63, n = 10); outer lip prosocline, straight to slightly sinuous, with strong reflection; external varix absent; notch present in posterior corner of aperture;

inner lip moderately thickened to thick and broad, adhering to, or narrowly separated from, parietal wall.

Dimensions. See Table 2.

TABLE 2. Shell dimensions and teleoconch whorl counts of *Pseudotricula eberhardi* Ponder.

	SL	SW	AL	AW	BW	CV	TW
Holotype	2.83	2.14	1.85	1.62	2.47	–	2.50
C.203693(9) paratypes							
Minimum	2.33	1.65	1.34	1.33	1.94	0.11	2.30
Maximum	2.66	1.96	1.69	1.65	2.35	0.16	2.62
Mean	2.50	1.86	1.57	1.46	2.14	0.13	2.52
Standard Dev.	0.12	0.12	0.11	0.11	0.13	0.02	0.10

Operculum. Yellowish; inner surface with white smear.

Pallial cavity. Ctenidium narrow; 9–13 very small filaments; osphradium between posterior end and middle of ctenidium; hypobranchial gland moderately developed; renal organ extends forward ca. ½ into pallial cavity; pericardium ½ in pallial roof.

Radula (Fig. 3A, B). *Central teeth* (Fig. 3B): dorsal edge with shallow indentation; 5 lateral cusps, median cusp of medium width, sharply pointed, less than twice as long as adjacent cusps. *Lateral teeth*: dorsal edge straight to lightly convex; with 3 cusps on inner and 4 on outer side; median cusp of medium width, sharply pointed, less than twice as long as adjacent cusps; ratio of cutting edge to shaft about ⅓–½; basal projection bluntly pointed. *Marginal teeth*: Inner with 15–17 cusps; outer with 14–20 cusps.

Stomach. Stomach with posterior chamber a little smaller than anterior chamber.

Male genital system. Testis of about 1 whorl; prostate gland oval to elongate pyriform; oval in section; pallial vas deferens straight to slightly undulating. Penis (Fig. 3A) with very weak swelling in mid-distal portion (hardly apparent); distal end tapering, similar to "papilla" in other taxa, medial section tapering; of medium length; penial duct in medial section of penis almost straight to undulating; base of penis moderately wide, with moderate folds; penial duct straight to undulating.

Female genital system. Ovary of 0.5–1.0 whorls; oviduct extends to posterior edge of bursa copulatrix; joins bursal duct at posterior pallial wall. Bursa copulatrix of medium size, not extending to posterior pallial wall; globular; with bursal duct arising from middle of anterior edge of bursa to antero-ventral edge; straight, wider at bursal end. Seminal receptacle at middle of inner wall of bursa copulatrix; pyriform. About ½ to more than ½ of albumen gland in front of posterior pallial wall; capsule gland about same to about ⅔ length of albumen gland; circular to oval in section; anterior end blunt; ventral channel simple, approximately parallel-sided throughout; vestibular area indistinct; genital opening subterminal.

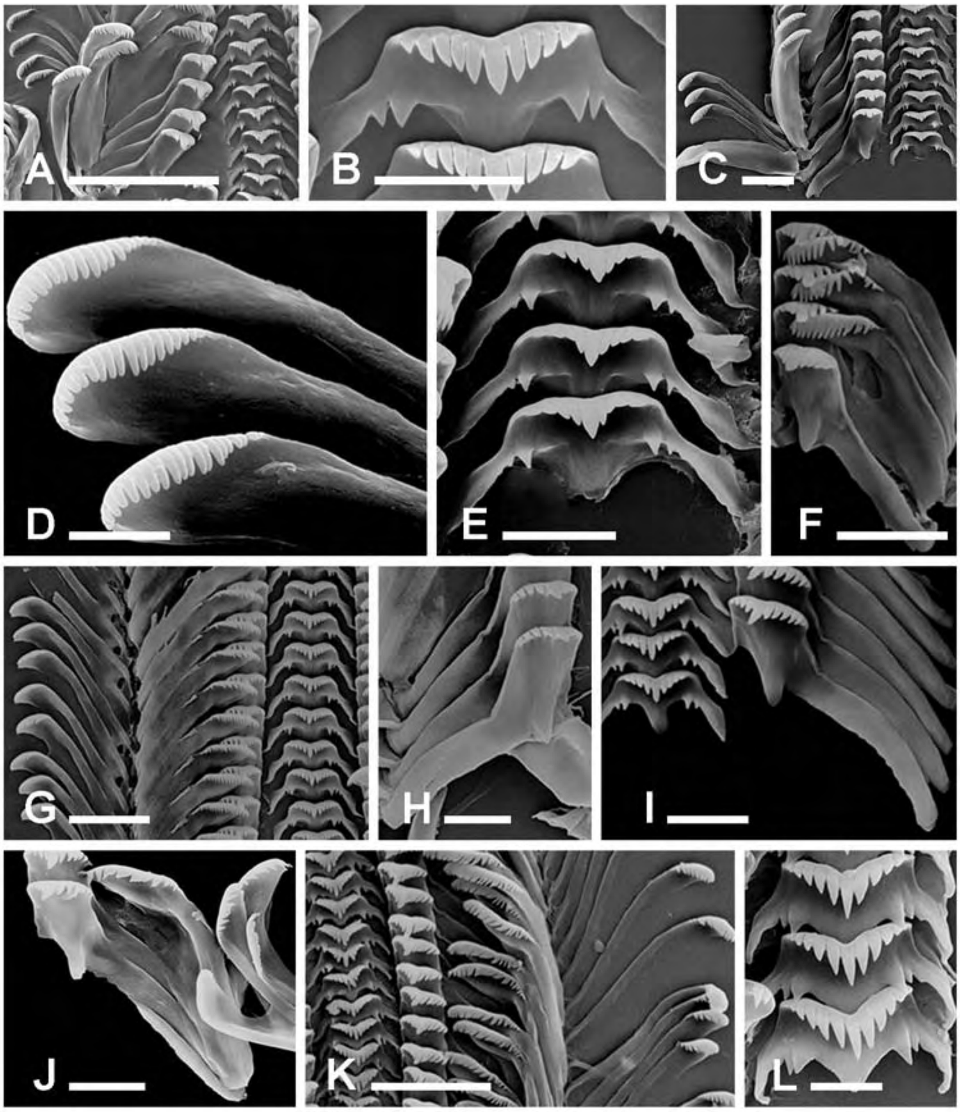

FIGURE 3: Radulae of *Pseudotricula* species. A, B, *Pseudotricula eberhardi*, C.165053, Black Curtain Streamway, Cueva Blanca; C–H, *Pseudotricula expandolabra*, C, D, C.201495, Persephone Streamway, Bauhaus, E, G, H, C.201811, Persephone Pot, Bauhaus, F, C.201822, main streamway, Bauhaus; I, *Pseudotricula arthurclarkei*, C.203671, paratype, Quetzalcoatl Conduit; J–L, *Pseudotricula conica*, C.203676, paratype, Cane Toad Abuse Streamway, Damper Cave. A, C, G, K, central, lateral inner and outer marginal teeth; B, E, L, central teeth; D, outer marginal teeth; F, J, lateral and inner marginal teeth; H, lateral tooth; I, central and lateral teeth. Scales: A, B, E, H–J, L 10 µm; C, F, G, K, 20 µm; D, 5 µm.

Distribution and habitat

Found only on smooth rock surfaces in fast-flowing falls and streams in Cueva Blanca.

Remarks

Pseudotricula eberhardi has only been found in very strongly flowing water in Cueva Blanca. A record of this species from Persephone Pot (Ponder 1992) are specimens of *P. expandolabra* n. sp. This species is distinguished from other congeners by its short, slightly convex spire and evenly convex whorls.

Pseudotricula expandolabra **n. sp.**

Figures 2B, E; 3C–H; 4B; 5A–F; 6A–D; 7A,B; 8A; 9C; 10A–C.

Type material

Holotype: AMS C.439673, Screaming Stals Streamway, Bauhaus, stn 12, 23 Dec, 1991.

Paratypes: AMS C.201493, same locality stn 12 (6 dry, 12 wet); QVM, 9:20536 (5 wet).

Figured (shell) paratypes: AMS C.439674, same locality stn 12.

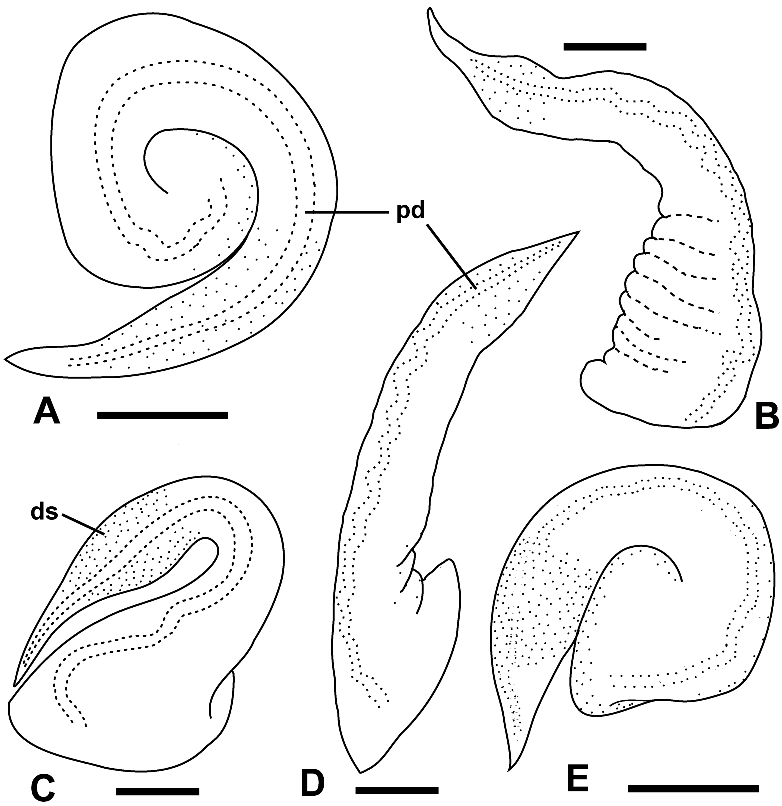

FIGURE 4. Dorsal views of penes of *Pseudotricula* and *Nanocochlea* species. A,. *Pseudotricula eberhardi*; B, *Pseudotricula expandolabra*; C, *Nanocochlea stylesae*; D, *Nanocochlea damperensis*; E, *Pseudotricula conica*. Scales A, B, E, 0.2 mm; C, D, 0.1 mm. Abbreviations: ds, distal swelling; pd, penial duct.

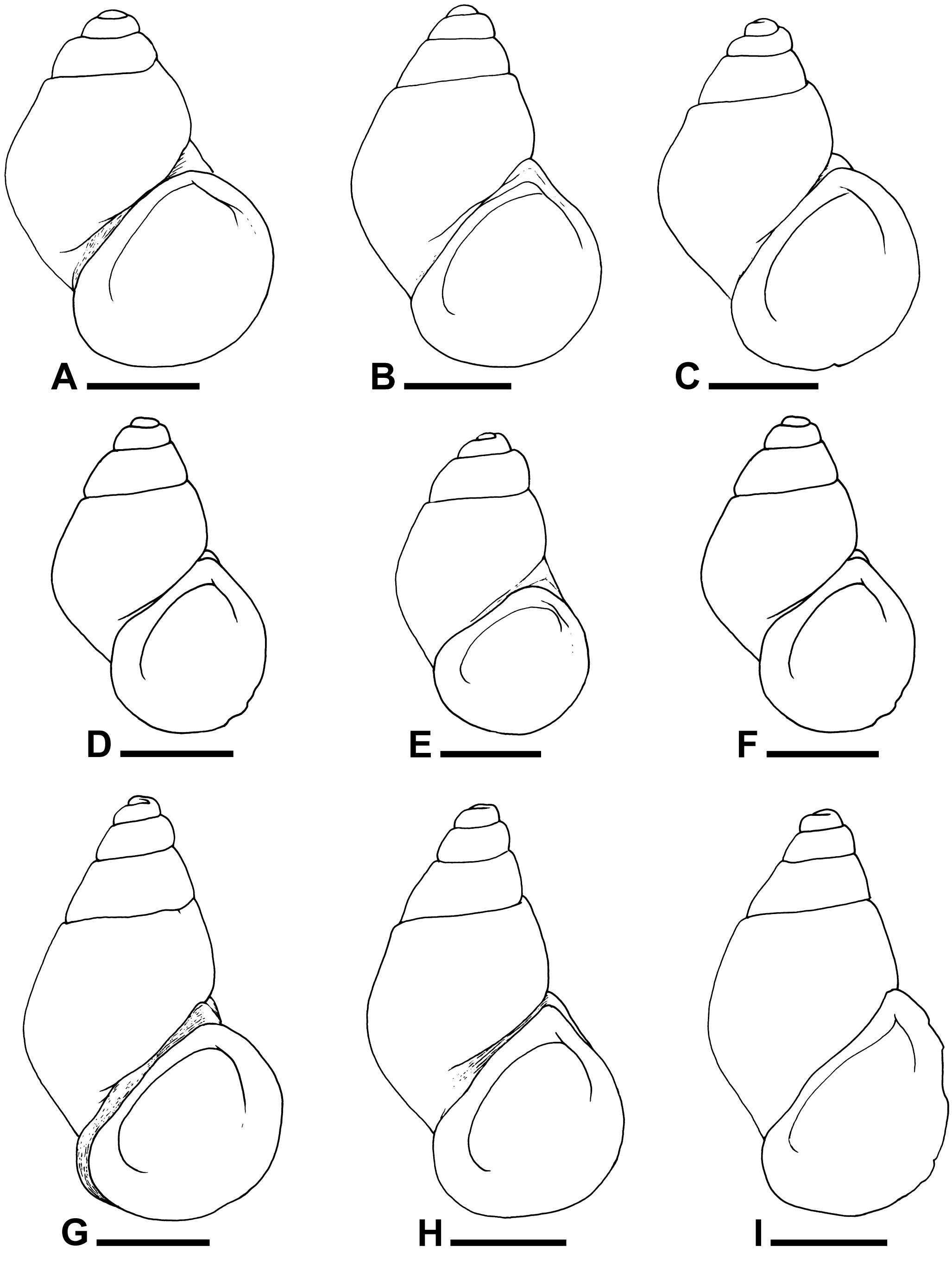

FIGURE 5. Shells of *Pseudotricula* species. A–F, *Pseudotricula expandolabra*, A–C, C.201489, Screaming Stals streamway, Bauhaus, D–F, Persephone Pot, Bauhaus, D, F, C.201811, E, C.201485, Persephone Pot, Bauhaus; G–I, *Pseudotricula auriforma* G, H, streamway near entrance, Damper Cave, I, main streamway, Damper Cave. Scales: 1 mm.

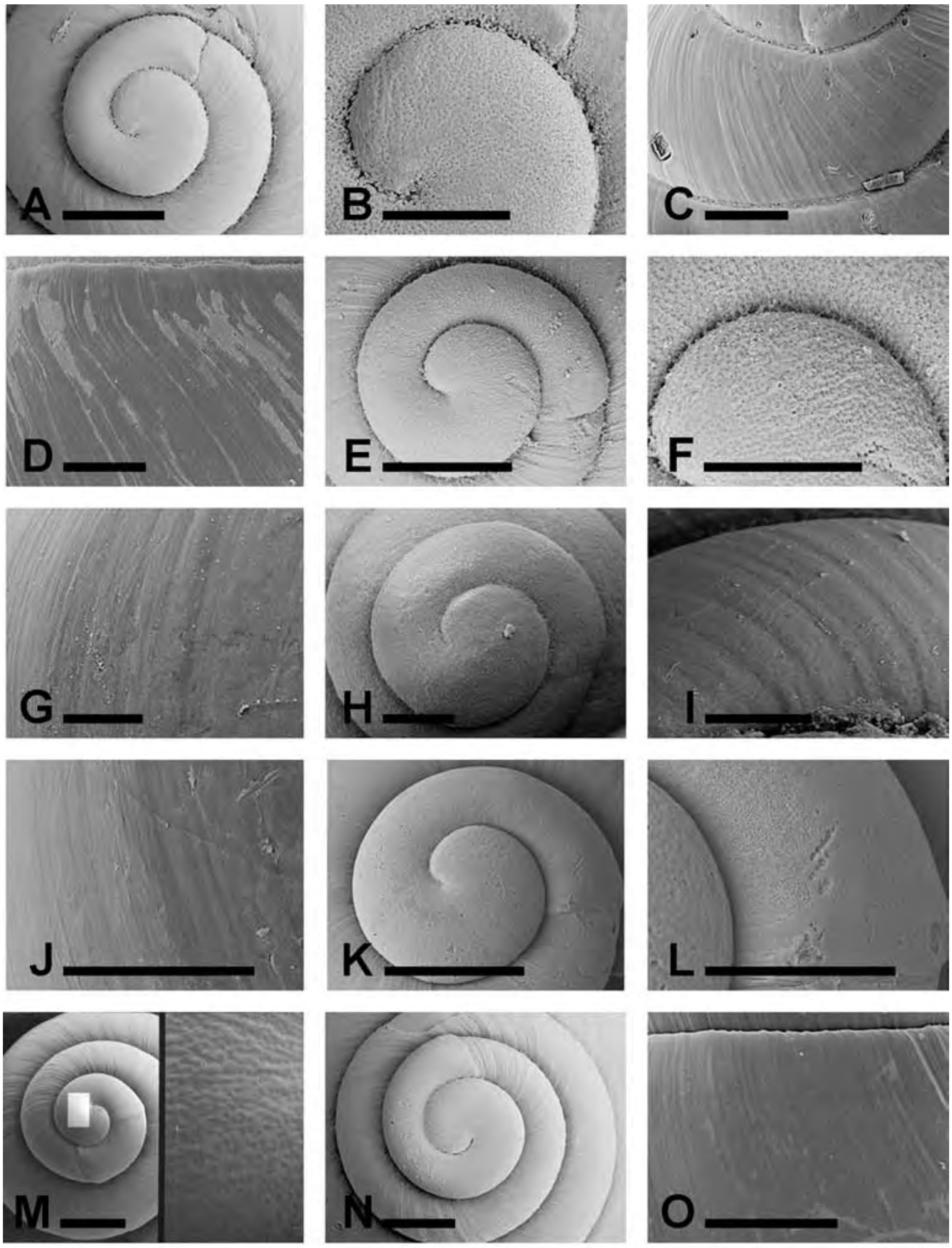

FIGURE 6. Protoconchs and teleoconch microsculpture of *Pseudotricula* and *Nanocochlea* species. A–D, *Pseudotricula expandolabra*, A, B, D, C.201493, paratype, main streamway, Bauhaus, C, C.201495, Persephone Streamway, Bauhaus; E–G, *Pseudotricula conica*, E, F, C.201464, Cane Toad Abuse Streamway, Damper Cave, G, Persephone Pot, Bauhaus; Honey and Cream Streamway, Damper Cave; H, *Nanocochlea exigua*, C.201475; I, J, *Nanocochlea stylesae*, C.201476, paratypes, Malani Creek; K–M, *Nanocochlea damperensis*, K, L, C.203685, paratypes, first crossing, Damper Creek, M, C.201282, Near New River Lagoon, E side, Limestone Ck, where tagged track crosses; N, O, *Pseudotricula progenitor*, C.201821, main streamway, Bauhaus. A, B, E, F, H, K–N, protoconch; C, D, G, I, J, O, microsculpture. Scales: A, C–E, J, K, M, O, 200 µm; B, F–I, L, N, 100 µm.

Other material examined

Bauhaus: AMS C.201822, main streamway, stn PB6-1A (16 dry, 18 wet); AMS C.201486, Screaming Stals streamway, stn 11 (8 dry 14 wet); AMS C.201489, same locality, stn 13 (15 dry, 20+ wet); C.201485, Persephone, stn 7 (4 dry, 11 wet); C.201491, Persephone streamway, stn 8 (8 dry, 10 wet); C.201492, same locality, stn 9 (9 dry); C.201495, same locality, stn 10 (8 dry, 6 wet); C.439676, same locality, stn 10, figured specimen; C.201811, Persephone Pot, stn PB17-8R (1 dry, 4 wet); same locality, middle and upper streamway, stn PB17-2a.2 (20+ dry, 20+ wet); C.439675, same locality, stn PB17-2a.2, figured specimen; C.201815, same locality, lower streamway, stn PB17-2a.1, (20+ dry, 20+ wet); C.165055.

Damper Cave: AMS C.201494, seep near The Keg, stn 3 (1 dry); AMS C.201490, Honey and Cream streamway, stn 4 (10 dry, 10 wet); AMS C.203678, Cane Toad Abuse streamway, stn PB1-2A (1 dry, 6 wet).

Etymology

Expando Latin, spread out, *labrum*, Latin, lip; refers to the expanded outer lip of the aperture.

Description

Shell (Fig. 2B, E; 5A–F; 6A–D). Length up to 3.8 mm; with conical spire and large, expanded aperture (SW/SL 0.61–0.74, mean 0.69, n = 43); spire low to moderate, straight to slightly convex in outline, last whorl evenly rounded; usually with shallow subshoulder depression on last two whorls. Protoconch microsculpture of distinct, small pits (Fig. 6B). Teleoconch of up to 3.6 whorls in adult; aperture oval to pear-shaped; large, about equal to spire or slightly longer (AL/SL 0.52–0.63, mean 0.57, n = 43); outer lip prosocline; straight to or weakly sinuous, with strong reflection; external varix absent; notch present in posterior corner of aperture; inner lip thick, broad, firmly adhering to, or narrowly separated from, parietal wall.

Dimensions. See Table 3.

TABLE 3. Shell dimensions and teleoconch whorl counts of *Pseudotricula expandolabra* n.sp.

	SL	SW	AL	AW	BW	CV	TW
Holotype	3.49	2.38	2.09	1.87	2.94	0.08	3.21
Figured Paratype	3.45	2.4	1.96	1.77	2.85	0.07	2.87
Figured specimen (D)	3.31	2.2	1.79	1.68	2.67	0.09	2.75
Figured Specimen (E)	3.14	1.99	1.72	1.58	2.49	0.1	3.00
C.201493 paratypes(15)							
Minimum	3.27	2.27	1.88	1.67	2.59	0.07	2.90
Maximum	3.82	2.71	2.27	2.04	3.06	0.16	3.50
Mean	3.62	2.53	2.11	1.89	2.90	0.10	3.11
Standard Dev.	0.14	0.13	0.11	0.10	0.11	0.02	0.16

......continued on the next page

TABLE 3 (continued)

	SL	SW	AL	AW	BW	CV	TW
C.201495(4)							
Minimum	3.02	2.12	1.71	1.60	2.45	0.06	2.90
Maximum	3.70	2.66	2.00	1.86	2.97	0.17	3.55
Mean	3.26	2.27	1.81	1.70	2.63	0.10	3.19
Standard Dev.	0.30	0.26	0.13	0.11	0.24	0.05	0.30
C.201811(20)							
Minimum	3.05	2.01	1.62	1.49	2.42	0.06	2.75
Maximum	3.61	2.48	1.97	1.86	2.90	0.13	3.30
Mean	3.24	2.20	1.79	1.65	2.58	0.10	3.01
Standard Dev.	0.15	0.12	0.09	0.11	0.12	0.02	0.15

Operculum (Fig. 7A, B). Yellowish; inner surface with or without white smear.

Pallial cavity (Fig. 8A). Ctenidium narrow; 12–16 very small filaments; osphradium between posterior end and middle of ctenidium; hypobranchial gland variably developed; renal organ extends forward ca. ⅓–½ into pallial cavity; pericardium more than ½ in pallial roof.

Radula (Fig. 3C–H). *Central teeth* (Fig. 3E): dorsal edge with shallow indentation; 4–5 lateral cusps, median cusp of medium to narrow, sharply pointed, less than twice as long as adjacent cusps. *Lateral teeth* (Fig. 3 F, H): dorsal edge with shallow indentation; with 3–4 (usually 4) cusps on outer and 3–5 on inner side; median cusp of medium width, sharply to bluntly pointed, less than twice as long as adjacent cusps; ratio of cutting edge to shaft about ¼; basal projection bluntly pointed. *Marginal teeth*: Inner (Fig. 3F) with 16–21 cusps; outer (Fig. 3D) with 17–26 cusps.

Stomach (Fig. 9C). Stomach with posterior chamber and anterior chamber about equal in size.

Male genital system. Testis of 1.0–1.25 whorls; prostate gland oval to kidney-shaped to elongate pyriform; compressed in section. Pallial vas deferens straight to slightly undulating. Penis (Fig. 4B) weak swelling in mid-distal portion; distal end long, papilla-like; medial section tapering to parallel sided, of medium length; penial duct strongly undulating; base of penis moderately wide; with moderate folds; penial duct straight to undulating.

Female genital system (Fig. 10A–C). Ovary of 1.0 whorls; oviduct extends to posterior edge of bursa copulatrix; with one bend distal to seminal receptacle; joins bursal duct about half way between posterior pallial wall and capsule gland. Bursa copulatrix large, extending to posterior pallial wall or slightly in front; globular to elongately oval; with bursal duct arising from middle of anterior edge of bursa; straight or with undulations. Seminal receptacle at middle of inner wall of bursa copulatrix or near mid ventral edge; ovoid. More than ½ of albumen gland in front of posterior pallial wall; capsule gland longer than albumen gland; compressed oval in section; anterior end blunt;

ventral channel simple, approximately parallel-sided throughout; vestibular area indistinct to distinct; genital opening terminal to overlapping anterior end of capsule gland.

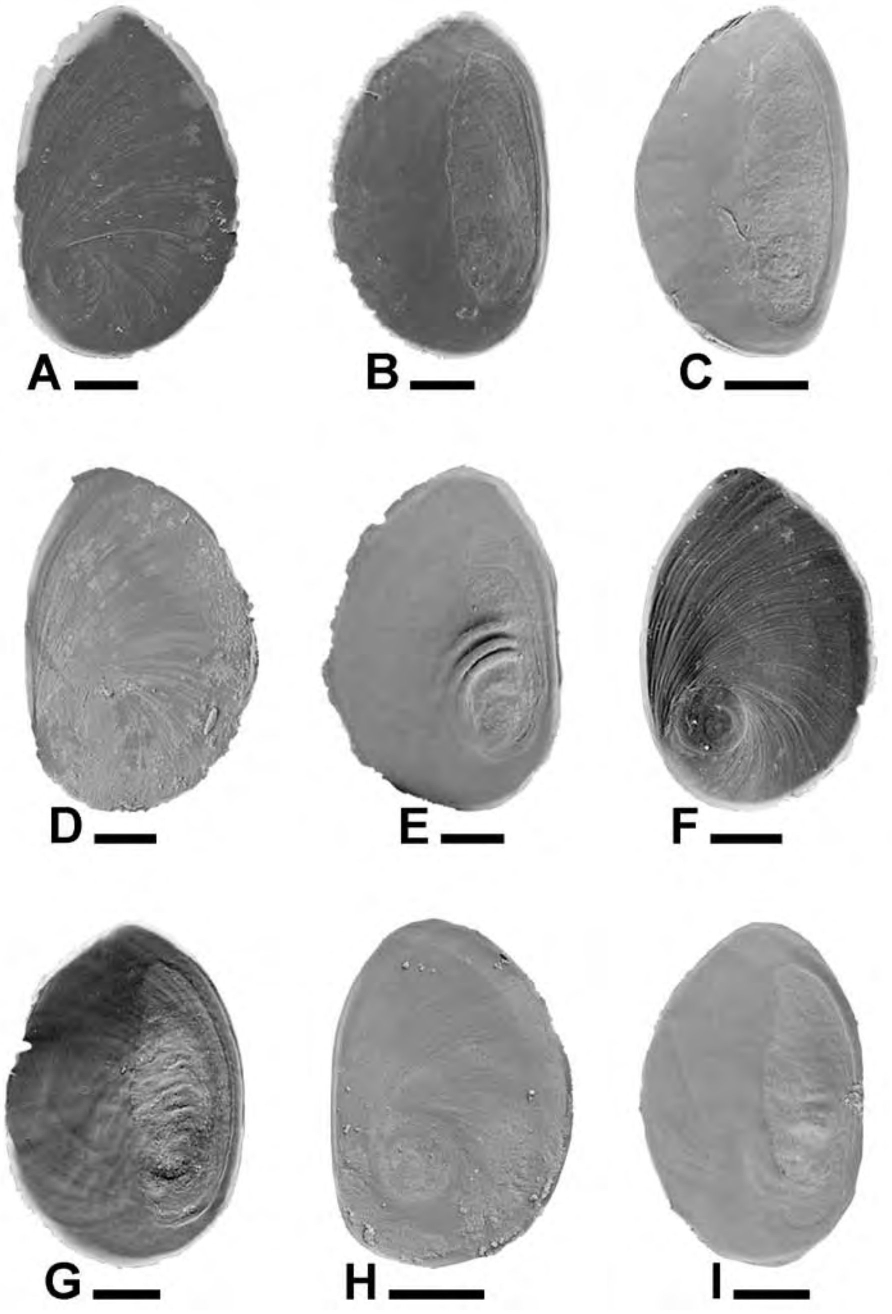

FIGURE 7. Opercula of *Pseudotricula* species. A, B, *Pseudotricula expandolabra*, C.201493, paratypes, main streamway, Bauhaus; C, *Pseudotricula auriforma*, C.201496, paratype, main streamway, Damper Cave; D, E, *Pseudotricula arthurclarkei*, C.203671, paratypes, Quetzalcoatl Conduit; F–I, *Pseudotricula conica*, F, G, C.203680, main streamway, near entrance, Damper Cave; H, I, C.201459, Screaming Stals streamway, Bauhaus; A, D, F, H, outer side; B, C, E, H, I, inner side; Scales: A–I, 200 µm.

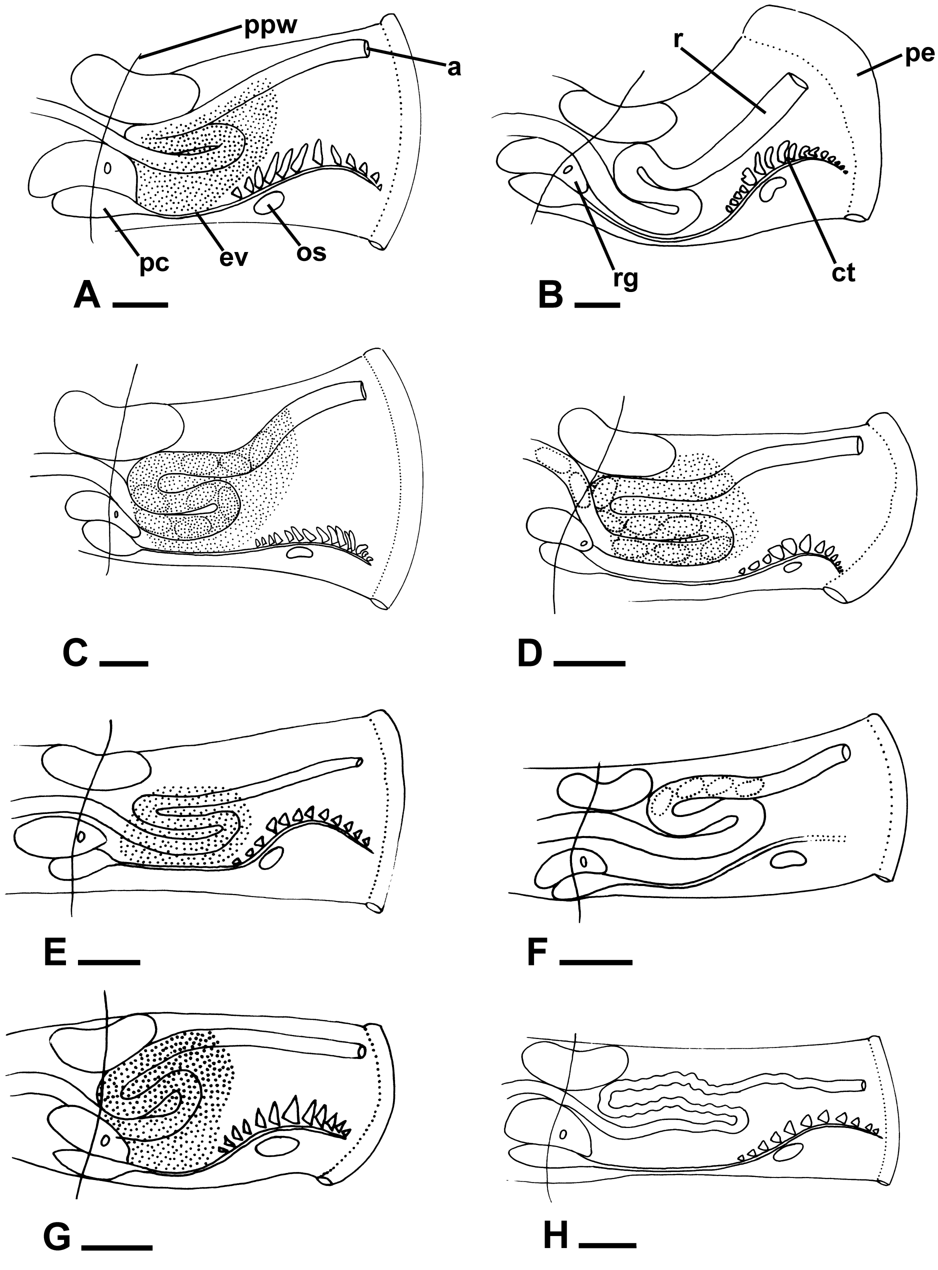

FIGURE 8. Pallial cavities of male specimens of *Pseudotricula* and *Nanocochlea* species. A, *Pseudotricula expandolabra*, C.201493, paratype, Persephone Streamway, Bauhaus; B, *Pseudotricula arthurclarkei*, C.203671, paratype, Quetzalcoatl Conduit; C, *Pseudotricula auriforma*, C.201496, paratype, main streamway, Damper Cave; D, E, *Pseudotricula conica*, D, C.203680, main streamway near entrance, Damper Cave, E, Cane Toad Abuse Streamway, Damper Cave; F, *Nanocochlea exigua*, C.203677, paratype, Cane Toad Abuse Streamway, Damper Cave; G, *Nanocochlea damperensis*, C.203685, paratype, first crossing, Damper Creek; H, *Pseudotricula progenitor*, C.201821, main streamway, Bauhaus. Scales: A–D, F–H, 500 µm, E, 1 mm. Abbreviations: a, anus; ct, ctenidium; ev, efferent vein; os, osphradium; pc, pericardium; pe, pallial edge; ppw, posterior pallial wall; r, rectum; rg, renal gland. The stippled area represents the hypobranchial gland.

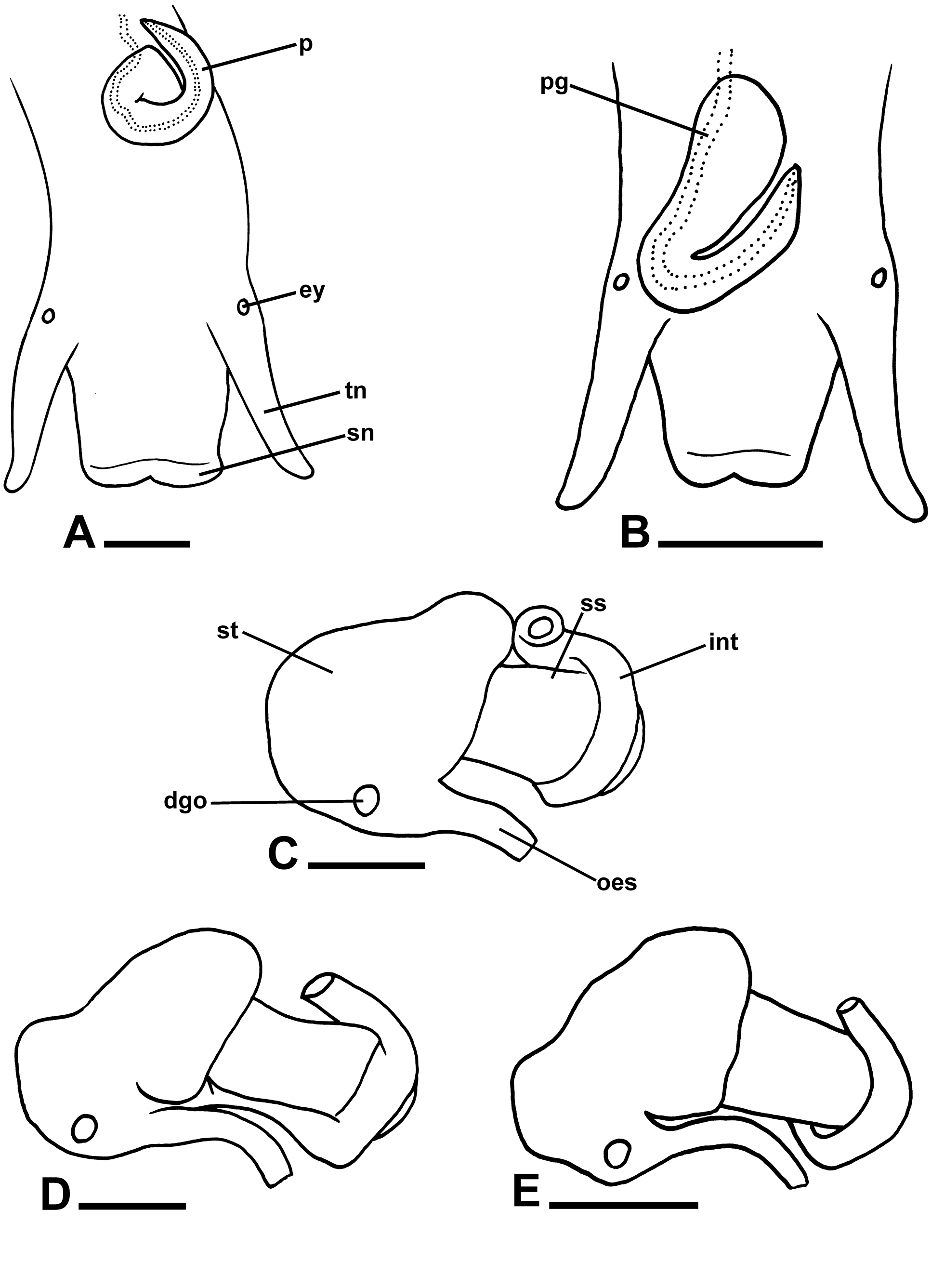

FIGURE 9. Head, penis and stomach of *Pseudotricula* species. A, D, *Pseudotricula conica*, C.203680, main streamway near entrance, Damper Cave; C, *Pseudotricula expandolabra*, C.201493, paratype, Persephone Streamway, Bauhaus; B, E, *Pseudotricula progenitor*, C.201821, main streamway, Bauhaus. A, B, head and penis; C–E, stomach. Scales: A–E, 500 µm. Abbreviations: dgo, opening from stomach to digestive gland; ey, eye; int, intestine; oes, oesophagus, p, penis; pg, penial duck; sn, snout; ss, style sack; st, stomach; tn, tentacle.

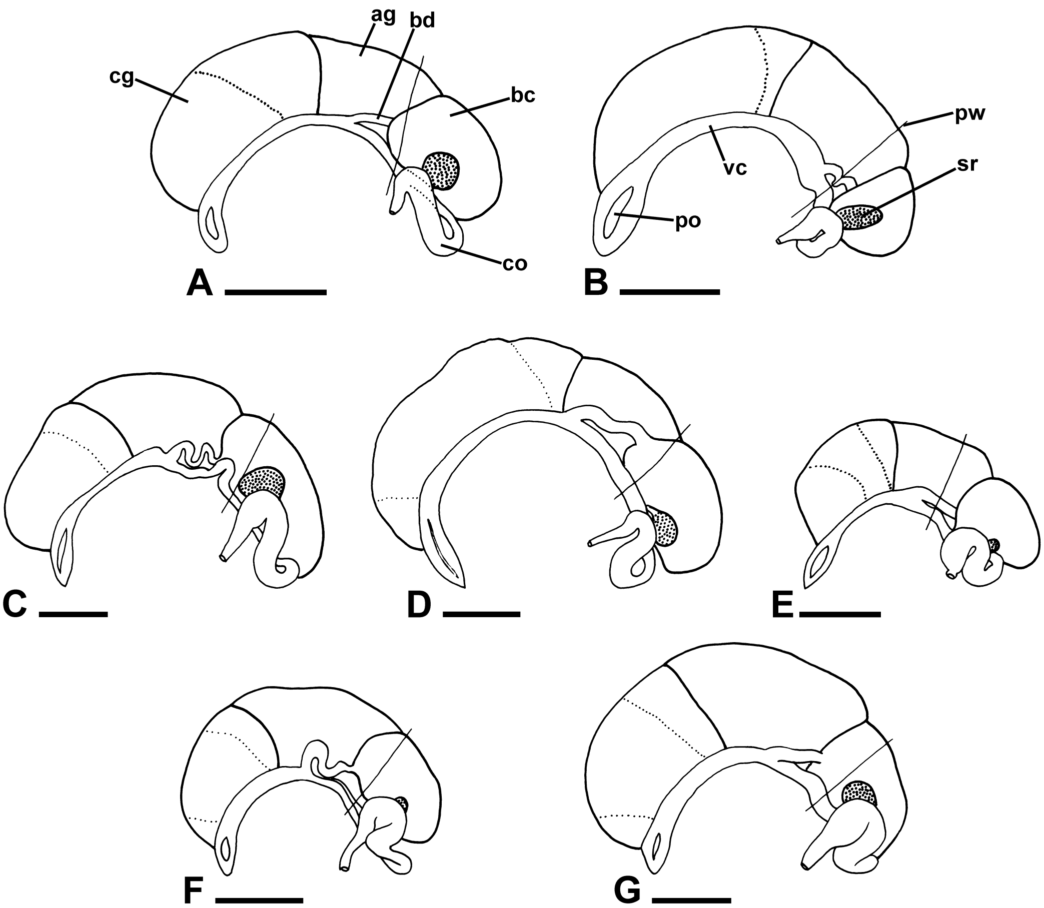

FIGURE 10. Female reproductive systems of *Pseudotricula* species. A - C, *Pseudotricula expandolabra*, A, B, C.201493, paratype, Persephone Streamway, Bauhaus, C, C.201815, Persephone Streamway, Bauhaus; D, *Pseudotricula auriforma*, C.201496, paratype, main streamway, Damper Cave; E, *Pseudotricula arthurclarkei*, C.203671, paratype, Quetzalcoatl Conduit; F, G, *Pseudotricula conica*, F, C203680, main streamway near entrance, Damper Cave, G, Cane Toad Abuse Streamway, Damper Cave. Scale: 500 µm. Abbreviations: ag, albumen gland; bc, bursa copulatrix; bd, bursal duct; cg, capsule gland; co, coiled oviduct; po, genital opening; pw, pallial wall; sr, seminal receptacle; vc, ventral channel.

Distribution and habitat

Damper Cave (Honey and Cream and Cane Toad Abuse streamways and seep near The Keg) and Bauhaus (Persephone and Screaming Stals streamways and Persephone Pot). This species is found in narrow (less than 1m in width) streams with gentle to moderate (<1L/s to about 5L/s estimated flows) within the caves. The substrate is mixed cobbles, gravel and silt and the microhabitats pools and riffles. Two samples were also found in seepages associated with this type of stream.

Remarks

Pseudotricula expandolabra is similar to *P. eberhardi* but its shell differs in having a straight spire outline, a taller spire ($P<0.001$) and the whorls are indented slightly below the shoulder. While it is rather constant in shape, it varies in size. Specimens from Persephone Pot are typically smaller (Fig. 5D–F) than those from the main Bauhaus cave. There also appears to be some notable anatomical variation; a specimen from Persephone Pot (Fig. 10C) has the bursal duct showing substantial undulations and the bursa copulatrix being larger and longer but a second specimen from this location is like some specimens from Bauhaus with only a single bend in the bursal duct (others have a straight bursal duct) and a smaller bursa. Given the continuity of these two systems and the similarity in the shells of specimens from the two localities, they are treated as a single species pending more detailed investigation.

Pseudotricula auriforma **n. sp.**

Figures 2F; 5G–I; 7C; 10D.

Type material

Holotype: AMS C.439672, Damper Cave, main streamway, stn 6, 22, DEC, 1991.

Paratypes: AMS C.201496, Damper Cave, main streamway, stn 6, 22, DEC, 1991 (3 dry, 2 wet); AMS C.203681, Damper Cave, streamway near entrance, stn PB1–1A, 28, MAR, 1994, 4 dry, 1 wet); QVM, 9:20537 (1 dry).

Etymology

Auris Latin, ear; *forma* Latin, shape; refers to the ear-shaped aperture.

Description

Shell. (Figs 2F; 5G–I). Length up to 4.4 mm; conical (SW/SL 0.59–0.65, mean 0.63, n = 6); spire moderate to high, straight in outline; last whorl evenly rounded, or angular to subangular in middle of whorl; suture indented/impressed, grooved/channelled or with very narrow shoulder above or below; subshoulder depression on last two whorls. Protoconch microsculpture unknown. Teleoconch up to 3.8 whorls in adult; aperture oval to pear-shaped; large, about equal to spire (AL/SL 0.47–0.55, mean 0.52, n = 6); outer lip prosocline, thin to weakly thickened in adult, straight, with strong reflection; external varix absent; notch usually present in posterior corner of aperture; upper half of inner lip thin to moderately thickened and moderately wide, thicker in lower half, in partial contact or narrowly separated from parietal wall. Translucent, semi-opaque; white (semi-opaque to opaque), or yellow.

Dimensions. See Table 4.

TABLE 4. Shell dimensions and teleoconch whorl counts of *Pseudotricula auriforma* n.sp.

	SL	SW	AL	AW	BW	CV	TW
Holotype	4.46	2.76	2.46	2.22	3.44	0.08	3.6
C.201496 paratypes (5)							
Minimum	3.64	2.31	1.71	1.67	2.72	0.07	3.50
Maximum	4.26	2.66	2.26	1.95	3.17	0.12	3.75
Mean	4.00	2.51	2.05	1.82	3.00	0.09	3.63
Standard Dev.	0.23	0.17	0.21	0.13	0.20	0.02	0.12

Operculum. Yellowish or brown; inner surface with or without white smear.

Pallial cavity (Fig. 8C). Ctenidium narrow; 14–15 very small filaments; osphradium between posterior end and middle of ctenidium to near middle of ctenidium; hypobranchial gland thick; renal organ extends forward ca. ⅓–½ into pallial cavity; pericardium more than ½ in pallial roof.

Radula (Fig. 7C). *Central teeth*: dorsal edge with shallow indentation; 4–5 lateral cusps, median cusp of medium width, sharply pointed, less than twice as long to about equal to adjacent cusps. *Lateral teeth*: dorsal edge with shallow indentation; with 3–4 cusps on outer and 3 on inner side; median cusp of medium width, sharply pointed, less than twice as long as adjacent cusps; ratio of cutting edge to shaft about ¼; basal projection bluntly pointed. *Marginal teeth*: Inner with 15–17 cusps; outer with 15–19 cusps.

Stomach. Stomach with posterior chamber and anterior chamber about equal in size, or with posterior chamber a little smaller than anterior chamber.

Male genital system. Testis of 1.5–2.0 whorls; prostate gland oval to kidney-shaped; compressed in section. Pallial vas deferens straight. Penis with weak swelling in mid-distal portion; distal end long, papilla-like; medial section parallel sided, of medium length; penial duct in medial section of penis straight to slightly undulating; base of penis moderately wide, or narrow; with weak to moderate folds; penial duct straight to undulating.

Female genital system. (Fig.10D). Ovary of 0.9–1.2 whorls; oviduct extends to posterior edge of bursa copulatrix or slightly anterior to that edge; with or without one bend distal to seminal receptacle; joins bursal duct in front of posterior pallial wall about half way between posterior pallial wall and capsule gland to about junction of albumen and capsule glands. Bursa copulatrix large, slightly in front of posterior pallial wall to slightly behind; pyriform to elongately oval; with bursal duct arising from middle of anterior edge of bursa; straight or with bend. Seminal receptacle at middle of inner wall of bursa copulatrix or near mid ventral edge; ovoid to pyriform. More than ½ of albumen gland in front of posterior pallial wall; capsule gland longer than albumen gland; compressed oval in section; anterior end tapering to blunt; ventral channel simple, approximately parallel-sided throughout; vestibular area distinct; genital opening overlapping anterior end of capsule gland.

Distribution and habitat

Known only from the main streamway in Damper Cave. This streamway is wider (about 2m) and has a faster flow (estimated at 10–20L/s) than the streams in which *P. expandolabra* occurs. The substrate consists of cobbles and gravel.

Remarks

Pseudotricula auriforma is similar to *P. expandolabra* but differs mainly ($P<0.001$) in its larger, more slender shell. It lives in a streamway that is wider and faster flowing than any of the habitats in which *P. expandolabra* occurs and the substrate lacks fine sediments.

***Pseudotricula elongata* n. sp.**
Figure 11A–C.

Type material

Holotype: AMS C.166854, Bauhaus, Persephone Pot, stn PB17–8R, 3, JAN, 1990.

Paratypes: AMS C.201809, same location, middle and upper streamway, stn PB17-2a.2, 27, March 94 (3 dry); AMS C.203713, same location, stn 9, 23, DEC, 1991 (1 dry, 1 wet).

Etymology

Elongatus Latin, prolonged; refers to the elongate shell.

Description

Shell (Fig. 11A–C). Length up to 2.8 mm; elongate-conic broadly conical (SW/SL 0.45–0.56, mean 0.49, n = 3);spire tall, straight in outline; last whorl evenly rounded, or angular to subangular in middle of whorl; suture grooved/channelled or with very narrow shoulder above or below. Protoconch microsculpture unknown. Teleoconch up to 4.4 whorls in adult; aperture oval to pear-shaped; small, much shorter than spire (AL/SL 0.37–0.44, mean 0.40, n = 3); outer lip orthocline, straight, with narrow reflection and thickened; notch present in posterior corner of aperture; inner lip thin to moderately thickened and narrow to medium width, in partial contact or narrowly separated from parietal wall.

Dimensions. See Table 5.

TABLE 5. Shell dimensions and teleoconch whorl counts of *Pseudotricula elongata* n.sp.

	SL	SW	AL	AW	BW	CV	TW
Holotype	2.83	1.32	1.05	0.82	1.77	0.08	4.4
C.201809(1)	1.38	0.77	0.61	0.48	0.95	0.09	2.50
C.203713(1)	2.31	1.04	0.90	0.68	1.53	0.10	3.65

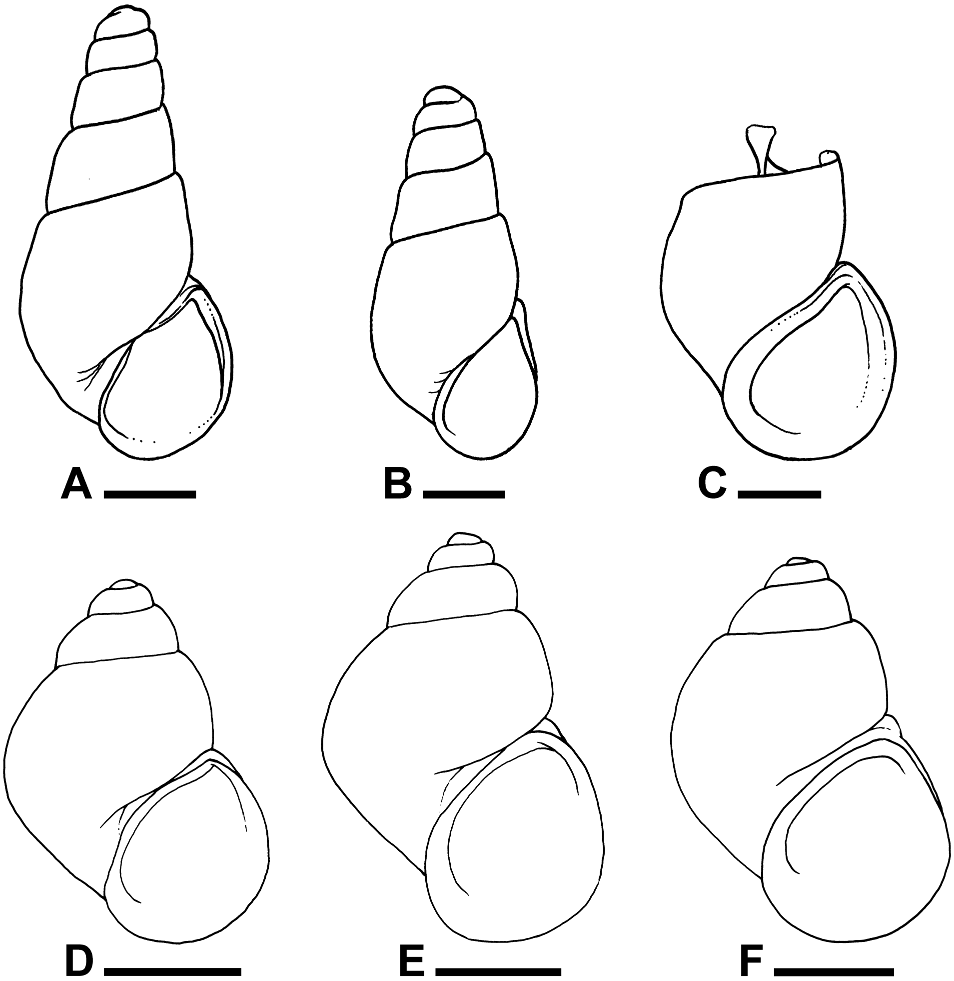

FIGURE 11. Shells of *Pseudotricula* species. **A - C**, *Pseudotricula elongata*, Persephone Pot, A, holotype, C.166854; B,C, paratypes, B, C.203713, C, C.201809; D–F, *Pseudotricula arthurclarkei*, C.203671, paratypes, Quetzalcoatl Conduit. Scales: A - C, 500 µm; D–F, 1 mm.

Distribution and habitat

Known only from Persephone Pot, Bauhaus, where it lives in a narrow (about 0.5m wide), slow flowing (estimated about 1L/s) stream. The substrate is composed of cobbles, gravel and silt.

Remarks

Pseudotricula elongata has a very distinctive, elongate shell shape and is known only from a few specimens. It is only known from Persephone Pot, where it is found living with several other species (Table 15). It is readily distinguished from all of the other species found in the caves by its large, elongate shell and distinctly sinuate outer lip.

***Pseudotricula arthurclarkei* n. sp.**

Figures 3I; 7E; 8B; 10E; 11D–F; 12A.

Type material

Holotype: AMS C.439656, Quetzalcoatl Conduit, stn PB3–1C, 29, MAR, 1994.

Paratypes: AMS C.203671, Quetzalcoatl Conduit, stn PB3–1C, 29, MAR, 1994 (20+ dry, 20+ wet); AMS C.203669, Quetzalcoatl Conduit, stn PB3–2B, 29, MAR, 1994 (12 dry, 20+ wet); QVM, 9:20538 (5 wet).

Etymology

Named for Arthur Clarke in recognition of his considerable contributions to the discovery and collection of cave fauna in Tasmania.

Description

Shell (Figs 11D–F; 12A). Length up to 3.1 mm; broadly conical (SW/SL 0.77–0.88, mean 0.81, n = 11); spire low to moderate, straight to slightly convex in outline; last whorl evenly rounded, or angular to subangular in middle of whorl; whorls distinctly convex; suture simple. Protoconch microsculpture of closely-spaced, distinct small pits. Teleoconch up to 2.5 whorls in adult; aperture oval to pear-shaped; large, little longer than spire (AL/SL 0.53–0.67, mean 0.61, n = 11); outer lip prosocline; weakly to moderately thickened in adult; outer lip straight; with or without slight reflection; external varix absent; posterior notch absent; inner lip moderately thickened and of narrow to medium width, firmly adhering to narrowly separated from parietal wall. Shell colour white or yellowish-brown to pale brown.

Dimensions. See Table 6.

TABLE 6. Shell dimensions and teleoconch whorl counts of *Pseudotricula arthurclarkei* n.sp.

	SL	SW	AL	AW	BW	CV	TW
Holotype	2.99	2.02	1.59	1.39	2.44	0.12	2.5
C203671 paratypes (10)							
Minimum	2.59	2.12	1.63	1.42	2.31	0.10	2.00
Maximum	3.07	2.66	1.91	1.74	2.70	0.15	2.45
Mean	2.88	2.38	1.79	1.65	2.54	0.12	2.22
Standard Dev.	0.16	0.15	0.10	0.09	0.12	0.02	0.12

Operculum (Fig. 7E).Yellowish; inner surface with white smear and 3–6 medium-sized pegs, or with pegs only.

Pallial cavity (Fig. 8B). Ctenidium narrow; 14–16 very small filaments; osphradium near posterior end to between posterior end and middle of ctenidium; hypobranchial gland moderately to poorly developed; renal organ extends forward ca. ⅓–½ into pallial cavity; pericardium more than ½ in pallial roof.

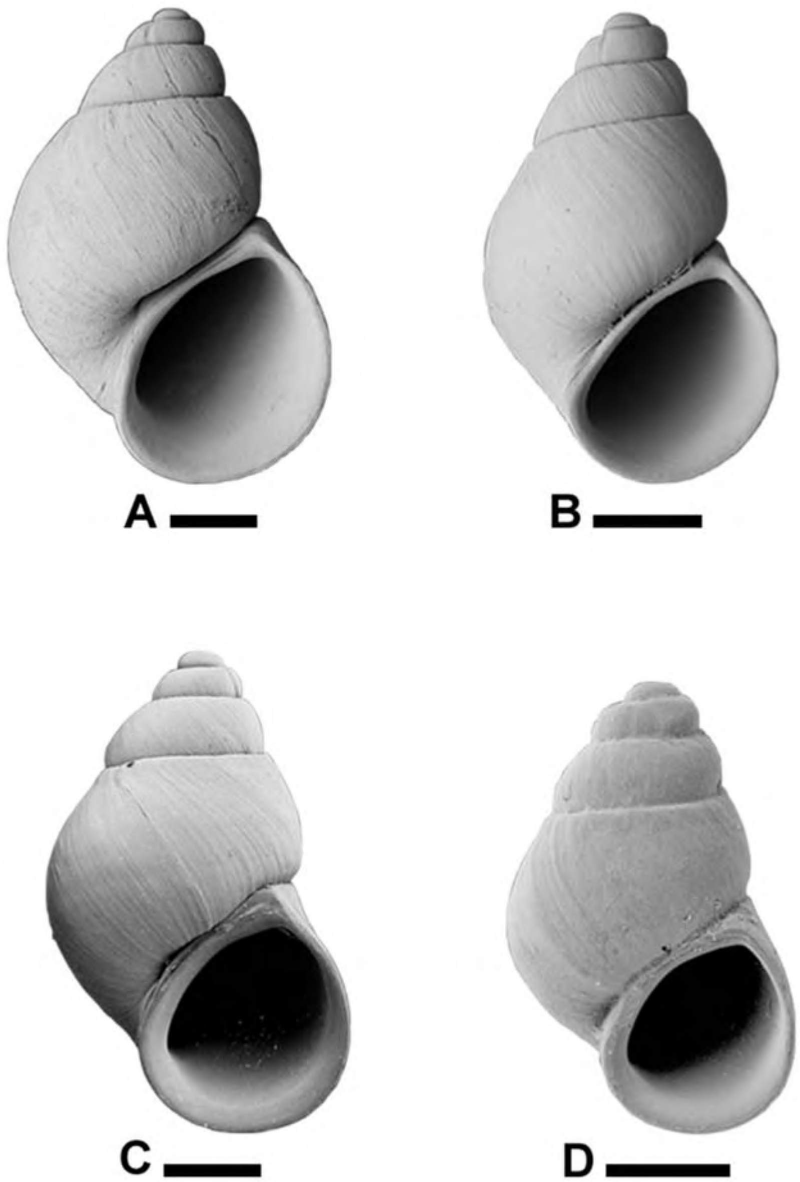

FIGURE 12. Shells of *Pseudotricula* species. A, *Pseudotricula arthurclarkei*, holotype, C.439656, Quetzalcoatl Conduit; B - D, *Pseudotricula conica*, B, holotype, Cane Toad Abuse Streamway, Damper Cave; C, C.203680, main streamway near entrance, Damper Cave; D, C.201813, Persephone Pot, Bauhaus. Scales: A–D, 500 µm.

Radula (Fig. 3I). *Central teeth*: dorsal edge moderately indented; 5–6 lateral cusps, median cusp narrow, sharply pointed, less than twice as long as adjacent cusps. *Lateral teeth*: dorsal edge straight to lightly convex or with shallow indentation; with 5–6 cusps on outer and 3–6 on inner side; median cusp of narrow to medium width, sharply pointed, less than twice as long as adjacent cusps; ratio of cutting edge to shaft about ¼–⅓; basal projection rounded to bluntly pointed. *Marginal teeth*: Inner with 28–33 cusps; outer with 23–27 cusps.

Stomach. Stomach with posterior chamber much smaller than anterior chamber.

Male genital system. Testis of 0.75–2.0 whorls; prostate gland oval to kidney-shaped, oval in section. Pallial vas deferens straight. Penis with weak swelling in mid-distal portion; distal end long, papilla-like; medial section parallel sided, of medium length; penial duct straight to undulating; base of penis moderately wide, with moderate folds; penial duct straight to undulating.

Female genital system (Fig. 10E). Ovary of 1.0 whorls; oviduct does not extend to posterior edge of bursa copulatrix; straight distal to seminal receptacle; joins bursal duct in front of posterior pallial wall about half way between posterior pallial wall and capsule gland to about junction of albumen and capsule glands. Bursa copulatrix of medium size, extending to posterior pallial wall; globular to pyriform; with bursal duct arising from middle of anterior edge of bursa; straight. Seminal receptacle at middle of inner wall of bursa copulatrix or near mid ventral edge; pyriform. About ½ to more than ½ of albumen gland in front of posterior pallial wall; capsule gland about same length as albumen gland; compressed oval in section; anterior end tapering to blunt; ventral channel simple, approximately parallel-sided throughout; vestibular area indistinct to distinct; genital opening overlapping anterior end of capsule gland.

Distribution and habitat

Known only from Quetzalcoatl Conduit, where it lives in a stream 3–4 m wide which has a strong flow (estimated at 15–30L/s) with sediments composed mostly of gravel and silt.

Remarks

Pseudotricula arthurclarkei and the next two species differ from “typical” members of *Pseudotricula* in having more cusps on both marginal teeth, a long lateral shaft on the lateral teeth and in lacking a strongly reflected outer lip. *Pseudotricula arthurclarkei* and *P. conica* n.sp. appear to be a sister taxa and also differ from other *Pseudotricula* species in having several weak to moderate curved ridges (reduced pegs) on the inside of the operculum, stronger and more complex protoconch microsculpture and the shell colour is often brown.

***Pseudotricula conica* n.sp.**

Figures 3J–L; 4E; 6E–G; 7F–I; 8D, E; 9A, D; 10F, G; 12B–D; 13A–F.

Type material

Holotype: AMS C.439649, Cane Toad Abuse Streamway Damper Cave, stn PB1–2A, 28 Mar 1994.

Paratypes: AMS C.203676, Damper Cave, same locality, stn PB1–2A (10 dry, 20+ wet); QVM, 9:20539 (5 wet).

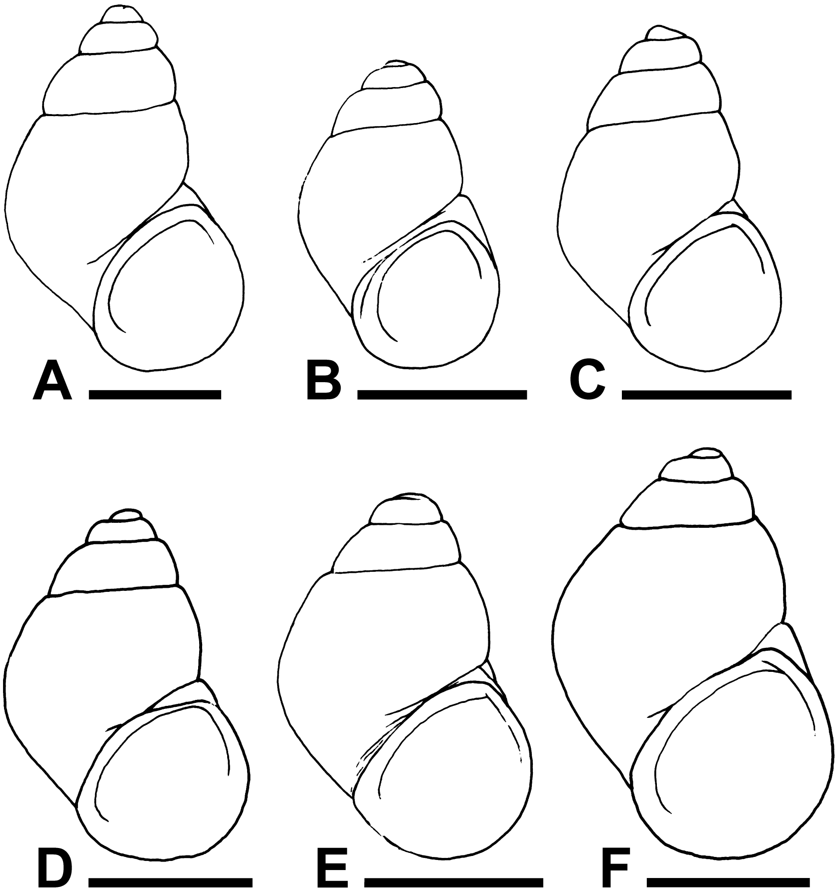

FIGURE 13. Shells of *Pseudotricula* species. A - F, *Pseudotricula conica*, A, C.203694, Black Curtain streamway, Cueva Blanca, B, Screaming Stals streamway, Bauhaus; C, C.201813, Persephone Pot, Bauhaus, D, C.203464, Cane Toad Abuse Streamway, Damper Cave, E, C.201488, main streamway, Damper Cave, F, C.203692, Damper Cave. Scales: 1 mm.

Other material examined (all AMS)

Bauhaus: C.201823, main streamway, stn PB6-1A, 14 dry); C.201824, same locality, stn PB6-1A (14 dry); C.201460, Screaming Stals streamway, stn 12 (2 dry, 17wet); C.201459, Screaming Stals streamway, stn 11 (12 dry, 20+ wet); C.201469, same locality, stn 13 (3 dry); C.439498, same locality, stn 12 (2 dry); C.201813, Persephone Pot, stn PB17-2a.2, middle and upper streamway (9 dry); C.201817, same locality, stn PB17-2.1, lower streamway (20+ dry, 20+ wet); C.439650, same locality, stn PB17-2a.1 (1dry) figured specimen; C.439496, Persephone Streamway, stn 8 (4 dry); C.439501, same locality, stn 9 (2 dry); C.439499, same locality, stn 9 (1 dry); C.439500, same locality, stn 10 (3 dry).

Damper Cave: C.203692, stn PB1-1B (1 dry, 3 wet); C.201488, main streamway, stn 6 (9 dry, 16 wet); C.203680, main streamway near entrance, stn PB1-1A (20+ dry, 20+ wet); C.439652, same locality, stn PB1-1A, (1dry), figured specimen; C.201464, Cane Toad Abuse streamway, stn 2 (11 dry, 20+ wet); C.201487, same locality, stn 2 (4 dry, 4 wet); C.201470, stn 2 (6 dry); *Cueva Blanca*: C.166967, no stn no. (2 dry, 6 wet); C.203694, Black Curtain Streamway, stn PB4-1C (5 dry).

Etymology

Conicus Latin adjective, cone-shaped; refers to the conical shape of the shell of this species.

Description

Shell (Figs 6E–G; 12B–D; 13A–F). Length up to 3.2 mm (usually less than 3 mm, mean 2.3 mm); conical to broadly conical (SW/SL 0.58–0.75, mean 0.67, n = 60); spire low to moderate, straight to slightly convex in outline; last whorl evenly rounded, or angular to subangular in middle of whorl; whorls very slightly convex; suture simple. Protoconch microsculpture of small, distinct, closely spaced pits (Fig. 6E, F). Teleoconch up to 3.3 whorls in adult; aperture oval to pear-shaped; moderately large, shorter to longer than spire (AL/SL 0.40–0.60, mean 0.50, n = 60); outer lip prosocline, straight, with or without slight reflection; external varix absent; posterior notch absent; inner lip thin to moderately thickened and narrow to medium width, firmly adhering to narrowly separated from parietal wall. Shell colour white or yellowish-brown to pale brown.

Dimensions. See Table 8.

TABLE 8. Shell dimensions and teleoconch whorl counts of *Pseudotricula conica* n.sp.

	SL	SW	AL	AW	BW	CV	TW
Holotype	2.26	1.43	1.05	1.06	1.76	0.11	2.75
Figured Specimen	2.07	1.28	1.01	0.89	1.58	0.14	2.60
Figured specimen	2.3	1.51	1.23	1.06	1.85	0.1	2.75
C.201459(20)							
Minimum	1.83	1.21	0.92	0.87	1.42	0.09	2.50
Maximum	2.52	1.63	1.20	1.12	1.94	0.18	3.00
Mean	2.22	1.46	1.07	1.01	1.71	0.13	2.76
Standard Dev.	0.16	0.11	0.09	0.07	0.12	0.02	0.15
C.201813(17)							
Minimum	1.65	1.01	0.67	0.57	1.18	0.01	2.12
Maximum	2.44	1.47	1.12	0.99	1.75	0.22	3.30
Mean	2.02	1.29	0.94	0.82	1.52	0.11	2.75
Standard Dev.	0.25	0.15	0.12	0.14	0.17	0.05	0.31
C.203680(20)							
Minimum	2.38	1.66	1.27	1.11	1.98	0.08	2.50
Maximum	3.23	2.07	1.57	1.39	2.45	0.16	3.10
Mean	2.61	1.84	1.41	1.26	2.15	0.12	2.66
Standard Dev.	0.20	0.12	0.09	0.07	0.13	0.02	0.16

Operculum (Fig. 7F–I). Yellowish; inner surface with white smear.

Pallial cavity (Fig. 8D, E). Ctenidium narrow; 10–14 very small filaments; osphradium between posterior end and middle of ctenidium; hypobranchial gland thick; renal organ extends forward ca. ⅓–½ into pallial cavity; pericardium more than ½ in pallial roof.

Radula (Fig. 3J–L). *Central teeth*: dorsal edge with moderate to deep indentation; 5 lateral cusps, median cusp of narrow to medium width, bluntly to sharply pointed, less than twice as long as adjacent cusps. *Lateral teeth*: dorsal edge lightly convex to moderately indented; with 4–7 cusps on outer and 4–6 on inner side; median cusp of medium to narrow, sharp to blunt, less than twice as long as adjacent cusps; ratio of cutting edge to shaft about ⅓; basal projection bluntly pointed. *Marginal teeth*: Inner with 21–32 cusps; outer with 22–32 cusps.

Stomach (Fig. 9D). Stomach with posterior chamber and anterior chamber about equal in size.

Male genital system. Testis of 1.25 whorls; prostate gland oval to elongate pyriform; compressed in section. Pallial vas deferens straight. Penis (Fig. 4E; 9A) with weak swelling in mid-distal portion; distal end long, papilla-like; medial section parallel sided; of medium length; penial duct in medial section straight to undulating; base of penis moderately wide; with weak to moderate folds; penial duct straight to undulating.

Female genital system (Fig. 10F, G). Ovary of 0.6–1.0 whorls; oviduct extends to posterior edge of bursa copulatrix or slightly anterior or posterior to edge; straight distal to seminal receptacle; joins bursal duct in front of posterior pallial wall about half way between posterior pallial wall and capsule gland to about junction of albumen and capsule glands. Bursa copulatrix large, extending to posterior pallial wall or into pallial roof; elongately oval to pyriform; with bursal duct arising from middle of anterior edge of bursa or from antero-ventral edge; straight or with undulations. Seminal receptacle at middle of inner wall of bursa copulatrix or near mid ventral edge; ovoid to pyriform. About ½ to more than ½ of albumen gland in front of posterior pallial wall; capsule gland about same length as albumen gland to about ⅓ length of albumen gland; compressed oval in section; anterior end tapering to blunt; ventral channel simple, approximately parallel-sided throughout; vestibular area indistinct; genital opening overlapping anterior end of capsule gland.

Distribution and habitat

This is one of the commonest and widely distributed species in the caves. It appears to prefer low energy streams with mixed substrates, although a few specimens have been found in high energy habitats, notably in Cueva Blanca.

Remarks

Pseudotricula conica exhibits considerable variation in shell size and shape in what

we have interpreted as a single species. In particular, samples from Cueva Blanca and Bauhaus caves are fairly consistently elongate (e.g., Fig. 12D; 13A, C), while those from Damper Cave are usually broader (Fig. 12B, C; 13D–F). At least some material from the latter cave shows a range of shell morphology tall to broad with intermediate shell shapes (as for example in Fig. 13B from Bauhaus). In addition, the anatomical and radular details of the broad and narrow forms are very similar. Because of this, and the existence of at least some apparent intermediates, we treat both forms as a single species pending more detailed studies. Specimens near the entrance to Damper cave (C.203680) are larger with rather dark-coloured shells than those from further inside the cave.

Pseudotricula conica is most similar to *P. arthurclarkei* from Quetzalcoatl Conduit but differs in its smaller size ($P<0.001$) although one lot from close to the entrance of Damper Cave (C.203680) is nearly as large as the former species. *P. conica* also tends to have less convex whorls and has weak to obsolete opercular ridges. The two taxa are not sympatric.

Pseudotricula progenitor **n.sp.**
Figures 6N, O; 8H; 9B,E; 14H, I; 15J, K; 16G, H; 17L–O; 18C, D.

Type material

Holotype: AMS C.439396, Bauhaus, Persephone streamway, stn 8, 23 DEC 1991.

Paratypes: AMS C.201463, same data, 30+ (11 dry, 20+ wet); QVM, 9:20540 (5 wet); AMS C.439397, same data (Fig. 14H).

Other material examined (all AMS)

Bauhaus: C.438369, stn PB6-1 (5 dry); C.201821, main streamway, stn PB6-1A (10 dry, 20+ wet); C.166856, Persephone Pot, stn PB17-8R (5 dry, 25 wet); C.201812, same locality, middle and upper streamway, stn PB17-2a.2 (20+ dry, 20+ wet); C.438370, C.201816, same data (20+ dry, 20+ wet); same locality, PB17-2A (20+ dry); C.201454, Persephone, stn 7 (4 dry, 20+ wet); C.201468, Persephone streamway, stn 9 (15 dry, 20+ wet); C.201484, same locality, stn 10 (6 dry, 20+ wet).

Damper Cave: C.203682, Main streamway near entrance, stn PB1-1A (3 dry, 5 wet); C.201458, main streamway, stn 6 (14 dry, 20+ wet).

Etymology

Progenitor Latin, founder of a family, ancestor. Refers to the apparently basal position (and plesiomorphic nature) of this species in relation to the other taxa included in *Pseudotricula*.

Description

Shell (Fig. 6N, O; 14H, I; 15J, K). Length up to 2.8 mm; elongate-conic (SW/SL 0.50–0.64, mean 0.56, n = 22); spire tall, straight to slightly convex in outline; subsutural

indentation on last two whorls; periphery of last whorl evenly rounded; suture simple. Protoconch (Fig. 6N) as for genus, microsculpture largely obscured in available material. Teleoconch up to 4.0 whorls in adult; umbilicus absent in juveniles; aperture oval to pear-shaped; small, shorter than spire (AL/SL 0.34–0.49, mean 0.40, n = 22); outer lip orthocline to opisthocline, weakly thickened in adult, straight, usually with slight reflection; posterior notch absent; inner lip thin to moderately thickened and of narrow to medium width, in partial contact or narrowly separated from parietal wall.

Dimensions. See Table 9.

TABLE 9. Shell dimensions and teleoconch whorl counts of *Pseudotricula progenitor* n.sp.

	SL	SW	AL	AW	BW	CV	TW
Holotype	2.64	1.35	0.95	0.86	1.77	0.13	3.6
Figured paratype	2.78	1.39	0.98	0.83	1.65	0.11	4.0
C.201468 (20)							
Minimum	1.91	1.22	0.89	0.80	1.39	0.06	2.75
Maximum	2.82	1.56	1.09	0.95	1.77	0.16	3.75
Mean	2.47	1.40	0.98	0.87	1.64	0.11	3.38
Standard Dev.	0.25	0.08	0.05	0.03	0.10	0.02	0.30

Operculum (Fig. 16G,H). Inner surface with or without white smear.

Eyes. Unpigmented.

Pallial cavity (Fig. 8H). Ctenidium narrow; 9–10 very small filaments; osphradium between posterior end and middle of ctenidium; hypobranchial gland thick to moderately developed; renal organ extends forward ca. ½ into pallial cavity; pericardium more than ½ in pallial roof.

Radula (Fig. 17L–O). *Central teeth*: dorsal edge with moderate to deep indentation; 5–6 lateral cusps, median cusp narrow, sharply pointed, about twice as long as adjacent cusps. *Lateral teeth*: dorsal edge with shallow indentation; with 5–6 cusps on outer and 4–5 on inner side; median cusp narrow, sharply pointed, less than twice as long as adjacent cusps; ratio of cutting edge to shaft about ¼; basal projection bluntly pointed. *Marginal teeth*: Inner with 25–29 cusps; outer with 22–28 cusps.

Stomach (Fig. 9E). Stomach with posterior chamber and anterior chamber about equal in size or posterior chamber a little smaller.

Male genital system. Testis of 0.9–1.5 whorls; prostate gland oval to kidney-shaped; compressed in section. Pallial vas deferens straight. Penis (Fig. 9B) with weak swelling in mid-distal portion; distal end long, papilla-like; medial section tapering to parallel sided; of medium length; penial duct in medial section of penis strongly undulating; base of penis moderately wide; with moderate folds; penial duct strongly undulating.

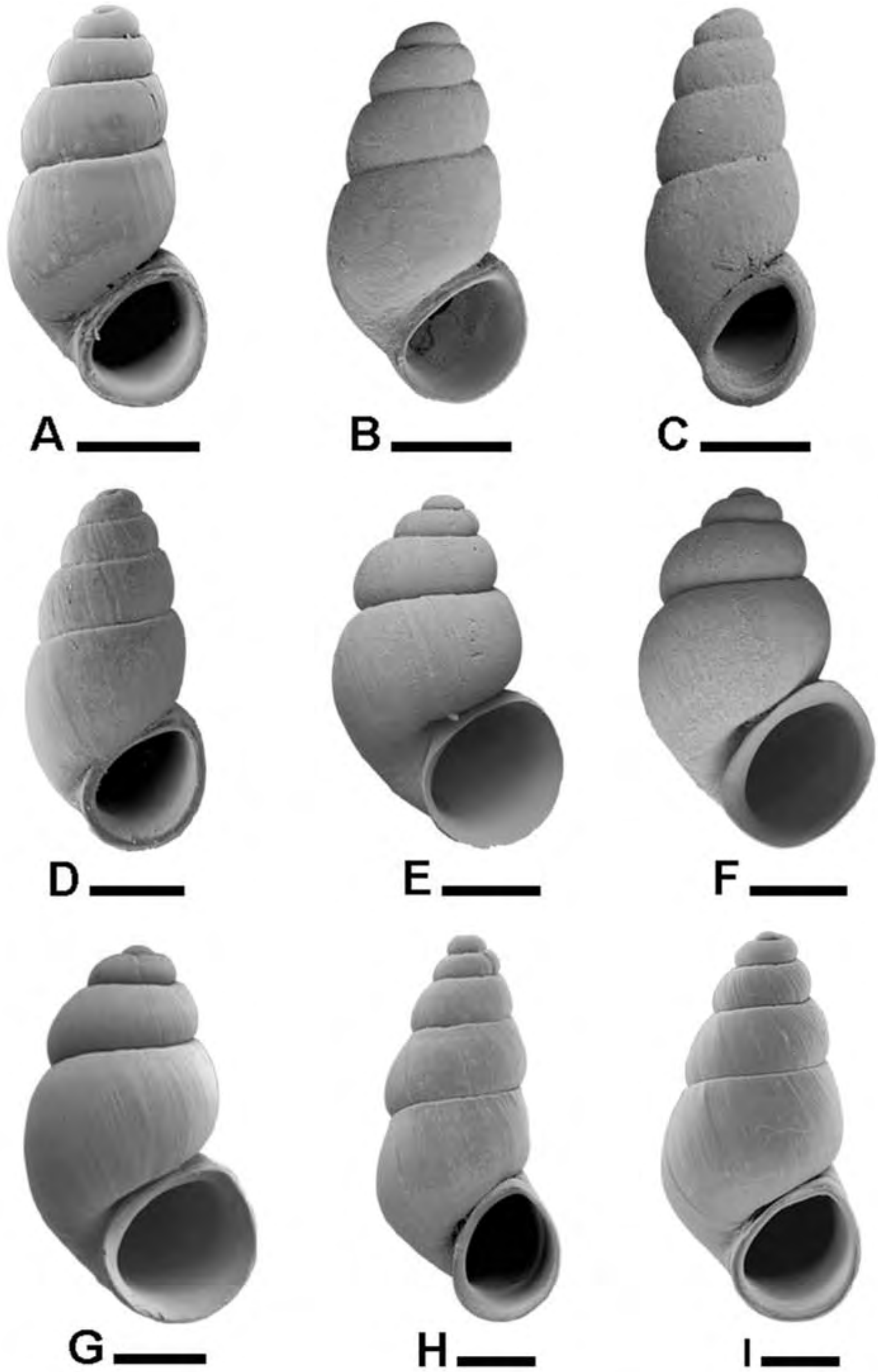

FIGURE 14. Shells of *Nanocochlea* species and *Pseudotricula progenitor*. A - C, *Nanocochlea exigua*, A, holotype, C.439393, Cane Toad Abuse Streamway, Damper Cave; B, C, C.201465, main streamway, Damper Cave; D, *Nanocochlea stylesae*, holotype, C.439398, Malani Creek; E–G, *Nanocochlea damperensis*, E, C.203685, paratype, first crossing, Damper Creek; F, holotype, C.439399, first crossing, Damper Creek, F, C.201282, Near New River Lagoon, E side, Limestone Ck, where tagged track crosses; H, I, *Pseudotricula progenitor*, H, paratype, C.439397, Persephone Streamway, Bauhaus; I, holotype, C.439396, Persephone Streamway, Bauhaus. Scales: 500 μm.

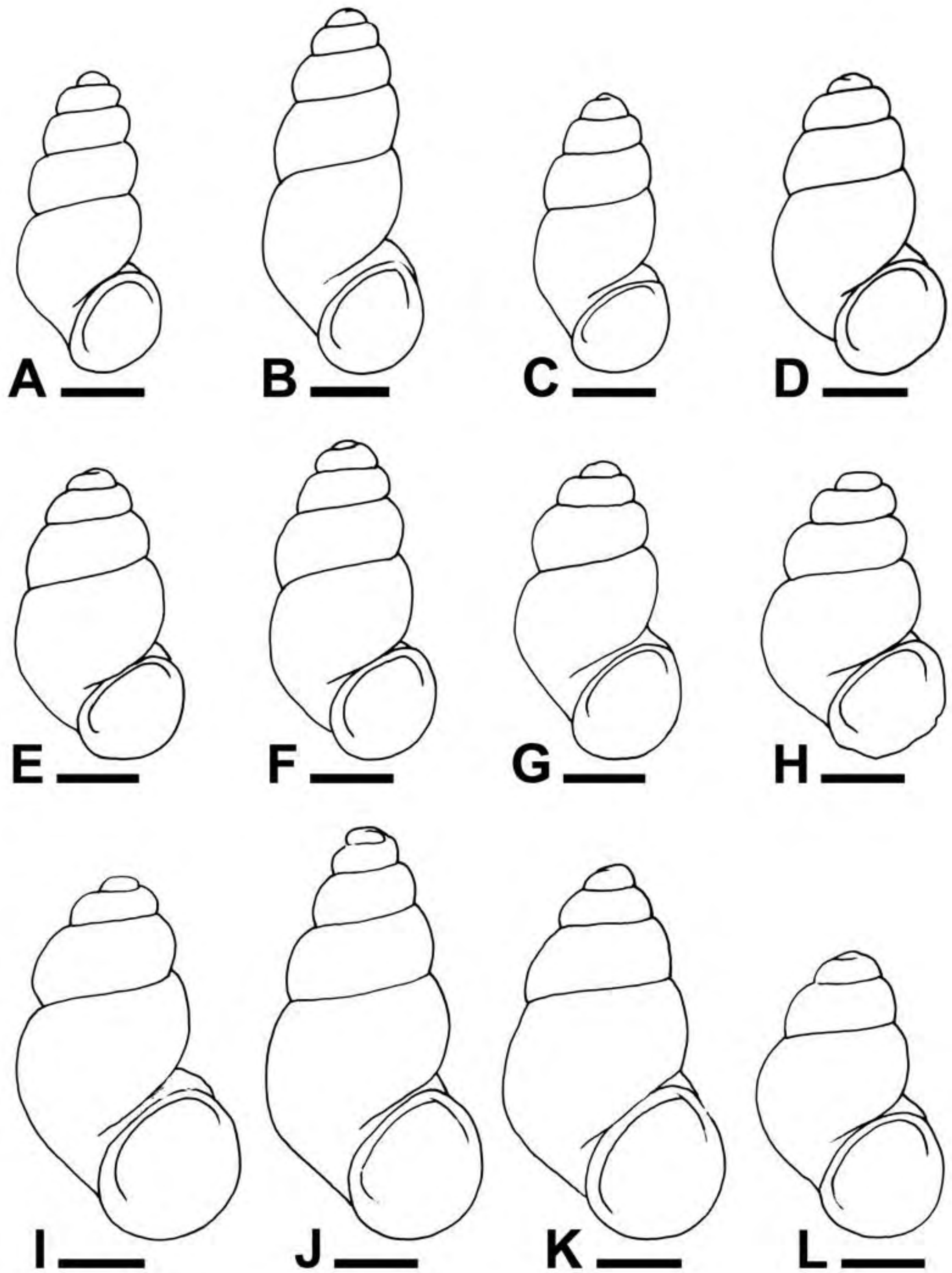

FIGURE 15. Shells of *Nanocochlea* species and *Pseudotricula progenitor*. A - C, *Nanocochlea exigua*, A, C.203674, outside Damper Cave, Damper Creek B, C.166855, Persephone Pot, Bauhaus, C, C.201465, main streamway, Damper Cave; D–F, *Nanocochlea stylesae*, D, C.201476, paratype, Malani Creek, E, F, C.203686, first crossing, Damper Creek; G-I, *Nanocochlea damperensis*, G,H, C.303685, seepages at Bauhaus entrance, I, C.203685, paratype, first crossing, Damper Creek; J–L, *Pseudotricula progenitor*, J, L, C.201463, paratype, Persephone streamway, Bauhaus, K, C.201454, Persephone, Bauhaus. Scales: 1 mm.

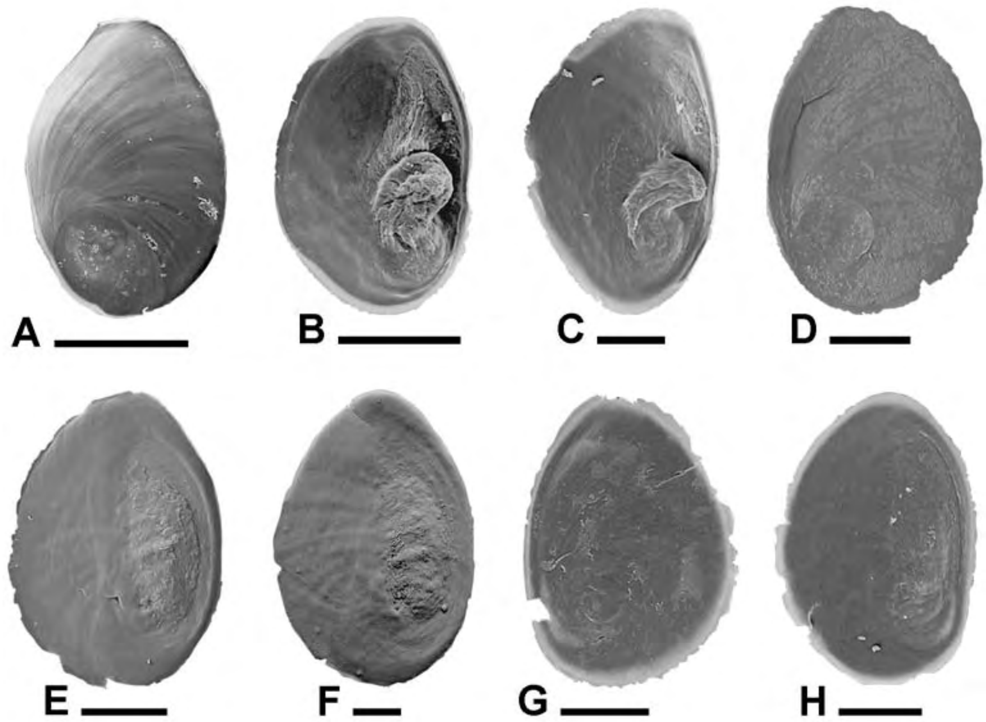

FIGURE 16. Opercula of *Nanocochlea* species and *Pseudotricula progenitor*. A - C, *Nanocochlea exigua*, C.203677, paratypes, Cane Toad Abuse Streamway, Damper Cave; D - F, *Nanocochlea damperensis*; C–E, C.203685, paratypes, first crossing, Damper Creek; F, C.201282, Near New River Lagoon, E side, Limestone Ck, where tagged track crosses; G, H, *Pseudotricula progenitor*, C.201821, main streamway, Bauhaus; A, D, G, outer side; B, C, E, F, H, inner side; Scales: A, B, D, 200 µm, C, E–H, 100 µm.

Female genital system (Fig. 18C, D). Ovary of 0.5–0.7 whorls; oviduct extends to posterior edge of bursa copulatrix; joins bursal duct in front of posterior pallial wall at junction of albumen and capsule glands to half way between posterior pallial wall and capsule gland. Bursa copulatrix large, extending to posterior pallial wall; globular to pyriform; with bursal duct arising from middle of anterior edge of bursa, straight or with undulations. Seminal receptacle at middle of inner wall of bursa copulatrix; pyriform. More than half of albumen gland in front of posterior pallial wall; capsule gland about same length as albumen gland; compressed oval in section; anterior end blunt; ventral channel with distinct muscular vestibule; genital opening overlapping anterior end of capsule gland.

Distribution and habitat

Bauhaus and Damper Cave in low energy small streams with mixed substrate.

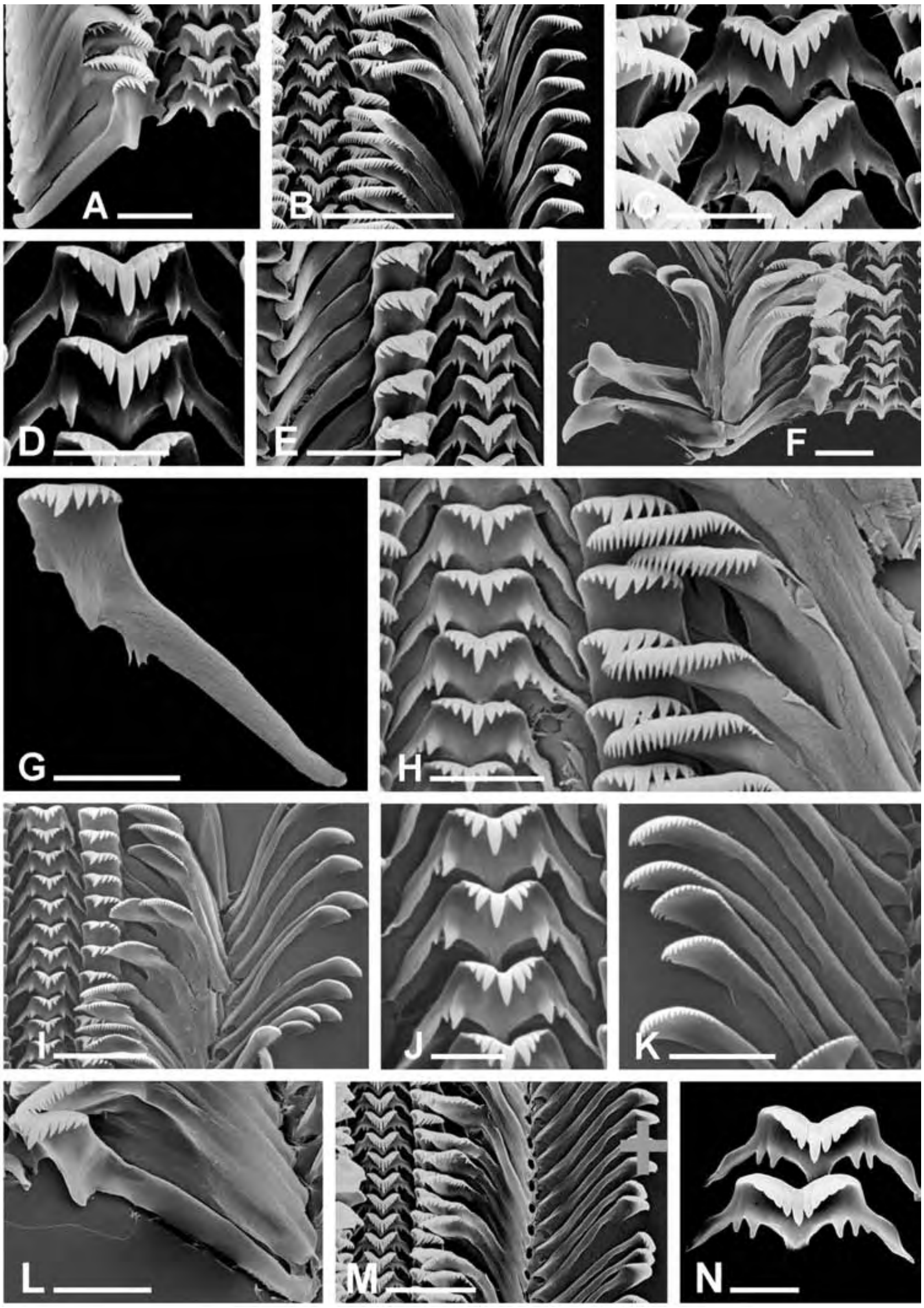

FIGURE 17. Radulae of *Nanocochlea* species *Pseudotricula progenitor*. A - C, *Nanocochlea exigua*, A, C.201475, Honey and Cream Streamway, Damper Cave, B, D, C.201465, main streamway, Damper Cave; D–E, *Nanocochlea stylesae*, C.201476, paratypes, Malani Creek; G–K, *Nanocochlea damperensis*, G, H, C.203685, paratypes, first crossing, Damper Creek, I–K, C.201282, Near New River Lagoon, E side, Limestone Ck, where tagged track crosses; L–O, *Pseudotricula progenitor*, C.201821, main streamway, Bauhaus. A, E, central and lateral teeth; B, F, I, M, central, lateral, inner and outer marginal teeth; C, D, J, N central teeth; G, L, lateral teeth; H, central lateral inner and outer marginal teeth; K, outer marginal teeth. Scales: A, G–H, K, L, 10µm; B, I, M, 20µm; C, D, J, N, 5 µm.

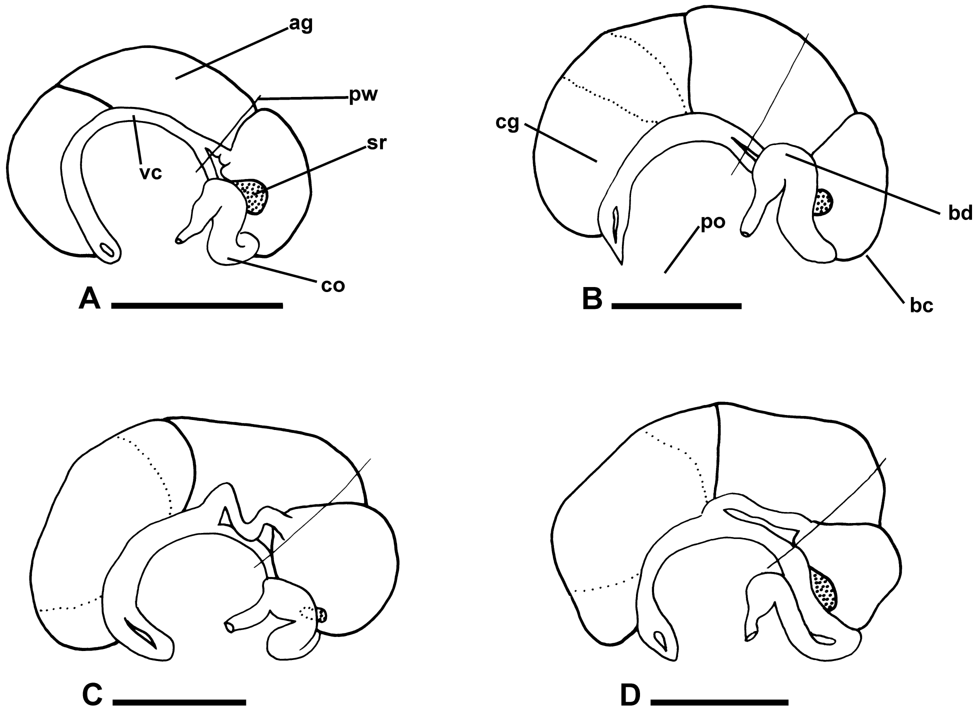

FIGURE 18. Female reproductive system of *Nanocochlea* species and *Pseudotricula progenitor.* A, *Nanocochlea exigua*, C.203677, paratype, Cane Toad Abuse Streamway, Damper Cave; B, *Nanocochlea damperensis*, C.203685, paratype, first crossing, Damper Creek; C, D, *Pseudotricula progenitor*, C.201821, main streamway, Bauhaus. Scales: 500 µm. Abbreviations: ag, albumen gland; bc, bursa copulatrix; bd, bursal duct; cg, capsule gland; co, coiled oviduct; po, genital opening; pw, pallial wall; sr, seminal receptacle; vc, ventral channel.

Remarks

Pseudotricula progenitor shares characters of both *Nanocochlea* and *Pseudotricula*. The small-sized, tall-spired shell is typical of *Nanocochlea* but the (narrowly) reflected outer lip, straight spire outline and subsutural indentation are characters found in typical *Pseudotricula* taxa. The protoconch microsculpture, while not able to be examined in detail, appears to be of the plesiomorphic type (shared by *Nanocochlea* and *Pseudotricula* s.s.), as are the radular characters, which are like those of *Nanocochlea* and *P. arthurclarkei* and *P. conica*. It is probable that this species most closely resembles the ancestral *Pseudotricula* that gave rise to the Precipitous Bluff cave radiation.

Genus *Nanocochlea* Ponder and Clark (in Ponder *et al*.), 1993

Type species: *Nanocochlea monticola* Ponder and Clark *in* Ponder *et al*., 1993 (original designation).

Description

Shell. Minute to small in size (adults range from 1.6 to 2.5 mm in length), pupiform to elongate pupiform or elongate-conic. Protoconch of about 1.4–1.5 whorls, typically sculptured with uniform pitting; separation of protoconch from teleoconch distinct, with varix-like border. Teleoconch with spire much longer than length of aperture. Aperture ovate, slightly angled posteriorly, inner lip attached to parietal wall or partially to completely detached, although not markedly so, usually lower part not much separated from base; outer lip orthocline to opisthocline, weakly thickened, simple or with very slight reflection. Periphery rounded, base simple, imperforate in adults, rarely narrowly umbilicate in juveniles. All species described below are semi-opaque to opaque, white with a thin pale yellowish periostracum.

Operculum. Ovate, paucispiral, flat, yellowish; columellar edge slightly convex, outer edge strongly convex; outer surface simple, paucispiral, nucleus markedly eccentric; inner surface usually smooth with white smear or (in one species) large, broad peg.

Radula. Central teeth large, cutting edge broad, indented mid dorsally, with 4–5 cusps on either side of narrow sharp median cusp; narrow, unthickened lateral projections emerge at about 45º from mid laterally; base with short, narrow, rounded basal projection not extending beyond lateral projections; two basal cusps emerge from ventral face of tooth on either side of basal projection, innermost longest. Lateral teeth with short cutting edge, about 4–5 small cusps on inner side of narrow median cusp and 4–6 small cusps on outer side; neck prominent, near vertical; lateral flange more than twice as long as cutting edge; prominent U-shaped projection on base below cutting edge; inner edge short, inner side of base excavated. Inner marginal teeth with 21–38 tiny cusps on rather wide cutting edge (ratio of cutting edge to shaft on inner marginal teeth about ¼); sides approximately parallel, outer edge thickened. Outer marginal teeth narrow, thickened on inner edge, distal end with 17–29 minute cusps; ratio of cutting edge to shaft about ¼.

Head-foot. Simple, unpigmented, with long cephalic tentacles, unpigmented to lightly pigmented eyes present in weak bulges at outer bases of tentacles; snout of moderate length, tapering, weakly bilobed distally. Foot short, rounded posteriorly.

Non-genital anatomy. Pallial cavity elongate, osphradium large and oval, towards posterior end of ctenidium; ctenidium absent or with small (reduced from normal triangular type) ctenidial filaments; efferent vein very short to long (ctenidium occupying nearly entire length of pallial cavity to about ½). Hypobranchial gland variably developed. Kidney and pericardium usually about ½ in pallial roof; renal gland orientated longitudinally. Stomach usually with anterior chamber larger than posterior; long style sac moderately long; no posterior caecum. Rectum with long S-shaped coil; overlying but not indenting pallial oviduct.

Male reproductive system. Prostate gland about ½ within pallial cavity; compressed to oval in section, with very thin ventral wall; pallial vas deferens opens at about ⅓–½ length of pallial portion. Penis located on right side of head well behind base of right

tentacle; lacking but has an inconspicuous to moderately developed swelling in the distal portion just behind a papilla-like distal end; distal portion long and tapering; medial part simple and parallel sided; basal part wide to moderate.

Female reproductive system. Ovary simple sac; coiled oviduct smooth, firm, not embedded in connective tissue, initially inverted U-shape, usually straight distal to seminal receptacle, usually reaching posterior end of bursa (sometimes a little more or less) then sharply bent to run anteriorly; Seminal receptacle ovoid to pyriform, with short duct, opening to oviduct, located opposite middle to ventral part of left side of bursa copulatrix. Bursa copulatrix medium to rather large, globular to pyriform, posterior to albumen gland except for small overlap on right side, either behind posterior pallial wall or extending to it; bursal duct arrises from anterior or ventro-anterior wall, simple to undulating, joins oviduct dorsally at posterior pallial wall or just in front of it. Common duct straight. Albumen gland with ½ or more within pallial roof, shorter to longer than capsule gland. Capsule gland compressed-oval in section, divided into three glandular zones, short anterior and posterior translucent white zones and long yellowish to orange middle zone; anterior end blunt to steeply tapering; genital opening short, terminal to slightly anterior of capsule gland. Ventral channel extended into weakly to moderately developed vestibule anteriorly. No brood pouch.

Distribution and habitat

Members of the genus are known from mountain lakes, seepages, streams and caves in southern Tasmania.

Remarks

Nanocochlea differs from *Pseudotricula* in its small, tall-spired pupiform to elongate-conic shell with a thin, simple, orthocline to opisthocline, usually non-reflected outer lip. There are no obvious anatomical differences between the two genera and there is a rather minor radular difference—the basal tongue of the central teeth is narrower in *Nanocochlea*. The outer shaft on the lateral teeth is longer in species of *Nanocochlea* than in typical species of *Pseudotricula* but *P. conica*, *P. arthurclarkei* and *P. progenitor* also have a long shaft.

***Nanocochlea exigua* n. sp.**

Figures 6H; 8F; 14A–C; 15A–C; 16A–C; 17A–C; 18A.

Type material

Holotype: AMS C.439393, Cane Toad Abuse streamway, Damper Cave, PB1-2A, 28 MAR 1994.

Paratypes: AMS C. 203677, same data (20+ dry, 20+ wet); QVM, 9:20541 (5 wet).

Other material examined (all AMS)

Bauhaus: C.201820, stn PB6-1A (8 dry, 3 wet); C.201819, stn PB6-1A (1 dry); C,166855, Persephone Pot, stn PB17-8R (4 dry, 12 wet); C.201810, same locality, middle and upper streamway, stn PB17-2a.2 (7 dry); C.201814, same data (6 dry, 13 wet); C.201818, same locality, lower streamway, stn PB17-2a (1 dry); C.201274, Persephone, stn 7 (6 dry, 20+ wet); C.201461, Persephone streamway, stn 8 (7 dry, 20 wet); C.201455, same locality, stn 9 (6 dry, 20+ wet); C.201456, same locality, stn 10 (1 dry); C.201479, same locality, stn 10 (8 dry, 20+ wet); C.201462, Screaming Stals streamway, stn 12 (11 dry, 20+ wet); C.201480, same locality, stn 12 (5 dry); C.201457, same locality, stn 13 (1 dry).

Damper Cave: C.203683, main streamway near entrance, stn PB1-1A (3 dry); C.201465, main streamway, stn 6 (7 dry, 14 wet); C.439395, same data (2 dry, figd specimens); C.201482, Cane Toad Abuse streamway, stn 2 (8 dry, 20+ wet); C.201467, seep near The Keg, stn 3 (9 dry, 20+ wet); C.201475, Honey And Cream streamway, stn 4 (8 dry, 20+ wet); C.203679, Cane Toad Abuse streamway, stn PB1-2A (1 dry).

Damper Creek: C.203674, 10m outside Damper Cave, stn PBs-2A (2 dry, 1 wet).

Quetzalcoatl Conduit: C. 203672, stn PB3-1C (1 dry).

Etymology

Exiguus Latin, small, short.

Description

Shell (Fig. 6H; 14A–C; 15A–C). Length up to 2.2 mm; elongate-conic (SW/SL 0.39–0.61, mean 0.50, n = 37); spire tall, straight to slightly convex in outline; last whorl evenly rounded or with subshoulder depression; suture simple or indented/impressed. Protoconch microsculpture uniform (Fig. 6H). Teleoconch up to 3.7 whorls in adult; aperture oval to pear-shaped; small, shorter than spire (AL/SL 0.30–0.45, mean 0.36, n = 37); outer lip orthocline to opisthocline; weakly thickened in adult, straight; posterior notch absent; inner lip thin and narrow, in partial contact or narrowly separated from parietal wall.

Dimensions. See Table 10.

TABLE 10. Shell dimensions and teleoconch whorl counts of *Nanocochlea exigua n.*sp.

	SL	SW	AL	AW	BW	CV	TW
Holotype	2.03	0.8	0.73	0.51	1.34	0.1	3.3
Figured specimens C.201465	1.75	0.83	0.6	0.54	1.19	0.1	3.3
	1.73	0.85	0.65	0.6	1.2	0.11	3.4
C263677(20)							
Minimum	1.64	0.85	0.59	0.55	1.13	0.09	3.00
Maximum	2.18	0.99	0.78	0.69	1.41	0.18	3.70
Mean	1.89	0.92	0.67	0.62	1.24	0.12	3.37
Standard Dev.	0.14	0.04	0.04	0.04	0.07	0.02	0.21

......continued on the next page

TABLE 10 (continued)

	SL	SW	AL	AW	BW	CV	TW
C.201465(14)							
Minimum	1.10	0.73	0.48	0.43	0.84	0.05	2.55
Maximum	1.96	0.99	0.69	0.64	1.26	0.17	3.65
Mean	1.65	0.85	0.60	0.56	1.10	0.11	3.31
Standard Dev.	0.23	0.08	0.06	0.07	0.12	0.03	0.30

Operculum (Fig. 16A–C). Inner surface with white smear and 1 large peg.

Eyes. Unpigmented.

Pallial cavity (Fig. 8F). Ctenidium rudimentary with no filaments; osphradium present, as in other taxa; hypobranchial gland thick to moderately developed; renal organ extends forward ca. ⅓–½ into pallial cavity; pericardium more than ½ in pallial roof.

Radula (Fig. 17A–C). *Central teeth*: dorsal edge with deep indentation; 4–5 lateral cusps, median cusp narrow, blunt to sharply pointed, about twice as long as adjacent cusps. *Lateral teeth*: dorsal edge with shallow to moderate indentation; with 4–6 cusps on outer and 4–5 on inner side; median cusp narrow to medium width, blunt to sharply pointed, less than twice as long as adjacent cusps; ratio of cutting edge to shaft about ¼; basal projection bluntly pointed. *Marginal teeth*: Inner with 21–26 cusps; outer with 17–20 cusps.

Stomach. Stomach with posterior chamber a little smaller than anterior chamber.

Male genital system. Testis of 0.6–1.5 whorls; prostate gland about ⅔ in pallial roof, oval to kidney-shaped; compressed in section. Pallial vas deferens straight. Penis with weak swelling in mid-distal portion; distal end long, papilla-like; medial section parallel sided, of medium length; penial duct in medial section strongly undulating; base of penis very to moderately wide; with moderate folds; penial duct straight to weakly undulating.

Female genital system. (Fig. 18A). Ovary of 0.6–0.7 whorls; oviduct extends to posterior edge of bursa copulatrix or slightly less; joins bursal duct at posterior pallial wall. Bursa copulatrix large, extending to posterior pallial wall; elongately oval to pyriform; with bursal duct arising from antero-ventral to ventral edge of bursa; straight or with undulations. Seminal receptacle at middle of inner wall of bursa copulatrix or near mid ventral edge; ovoid to pyriform. Two thirds to all of albumen gland in front of posterior pallial wall; capsule gland about same length as albumen gland; oval in section; anterior end tapering to blunt; ventral channel simple, approximately parallel-sided throughout; vestibular area indistinct to distinct; genital opening overlapping anterior end of capsule gland to terminal.

Distribution and habitat

Found mainly in small, low energy streams and seepages in the caves. A few specimens were also found in Damper Creek 10 m outside Damper Cave.

Remarks

Nanocochlea exigua differs from other congeners in the operculum bearing a single large peg and in lacking a ctenidium (gill). In the former respect, it resembles some species included in *Austropyrgus* Cotton, 1942 (Clark *et al*. 2003), as well as a number of other hydrobiid genera, including some found outside Australia. There are, however, several important characters that link *N. exigua* with *Nanocochlea*. There is no gastric caecum (present in *Austropyrgus* and several other genera bearing similar opercular pegs), the rectum is strongly S-shaped whereas in other genera with opercular pegs it is usually straight to arched. The female genital anatomy and penial morphology is also very like other species of *Nanocochlea* and unlike that of *Austropyrgus*. Assuming that the lack of the ctenidium in *N. exigua* has evolved from the presumed apomorphic condition seen in the other Precipitous Bluff congeners, and that no other species of *Nanocochlea* are known to possess an opercular peg, it is possible that the peg in this species is a secondary condition.

***Nanocochlea stylesae* n. sp.**
Figures 4C; 6I, J; 14D; 15D–F; 17D, E.

Type material

Holotype: AMS C.439398, Malani Creek, stn 14, 28 DEC 1991.

Paratypes: AMS C.201476, same data, 1 dry, 20+ wet; QVM, 9:20542 (5 wet).

Other material examined

First crossing, Damper Creek: AMS C.203686, stn PBs-1A (2 dry, 1 wet).

Etymology

Named for Julie Styles who assisted one of us (SE) in the collection of the bulk of the material used in this paper.

Description

Shell (Fig. 6I–J; 14D; 15D–F). Length up to 2.0 mm; narrowly conical (SW/SL 0.47–0.56, mean 0.52, n = 21); spire tall, straight to slightly convex in outline; last whorl evenly rounded; suture simple or indented/impressed. Protoconch microsculpture not examined in detail. Teleoconch up to 3.5 whorls in adult; umbilicus closed in juveniles; aperture oval to pear-shaped; moderate size, shorter than spire (AL/SL 0.33–0.42, mean 0.37, n = 21); outer lip orthocline, weakly thickened in adult, straight, without reflection; posterior notch absent; inner lip thin and narrow, in partial contact or narrowly separated from parietal wall.

Dimensions. See Table 11.

TABLE 11. Shell dimensions and teleoconch whorl counts of *Nanocochlea stylesae* n.sp.

	SL	SW	AL	AW	BW	CV	TW
Holotype	2.04	1.01	0.75	1.13	1.37	0.13	3.5
C.201476 paratypes (20)							
Minimum	1.67	0.90	0.63	0.58	1.01	0.04	2.40
Maximum	2.00	1.07	0.78	1.09	1.41	0.12	3.50
Mean	1.90	0.99	0.71	0.69	1.25	0.09	3.19
Standard Dev.	0.09	0.06	0.05	0.12	0.11	0.02	0.25

Operculum. Inner surface simple or with small slightly thickened lump near nucleus (possibly rudimentary peg).

Eyes. Unpigmented.

Pallial cavity. Ctenidium narrow; 9–11 very small filaments; osphradium near posterior end of ctenidium; hypobranchial gland very weakly-developed to apparently absent; renal organ extends forward ca. ⅓ into pallial cavity; pericardium up to ⅓ in pallial roof.

Radula (Fig. 17D, E). *Central teeth*: dorsal edge with deep indentation; 5 lateral cusps, median cusp narrow, blunt to sharply pointed, about twice as long as adjacent cusps. *Lateral teeth*: dorsal edge with shallow to moderate indentation; with 5–6 cusps on outer and 5 on inner side; median cusp narrow, sharply pointed, less than twice as long as adjacent cusps; ratio of cutting edge to shaft about ⅓; basal projection pointed to bluntly pointed. *Marginal teeth*: Inner with 24–38 cusps; outer with 20–28 cusps.

Stomach. Stomach with posterior chamber and anterior chamber about equal in size.

Male genital system. Testis of about 2.0 whorls; prostate gland about ½ in pallial roof; oval to elongate pyriform; oval in section. Pallial vas deferens strongly undulating at prostate, straight between prostate and penis and at base of penis. Penis (Fig. 4C) with weak swelling in mid-distal portion; distal end long, papilla-like; medial section tapering to parallel sided; of medium length; penial duct straight to slightly undulating; base of penis moderately wide; with moderate folds; penial duct straight to weakly undulating.

Female genital system. Ovary of 0.7 whorls; oviduct extends to posterior edge of bursa copulatrix; joins bursal duct at posterior pallial wall. Bursa copulatrix of medium size, not extending to posterior pallial wall; globular; with bursal duct arising from middle of anterior edge of bursa; straight. Seminal receptacle at middle of inner wall of bursa copulatrix; ovoid. One third of albumen gland in front of posterior pallial wall; capsule gland about same length as albumen gland; circular in section; anterior end tapering to blunt; ventral channel simple, approximately parallel-sided throughout; vestibular area indistinct; genital opening terminal.

Distribution and habitat

This species is apparently restricted to surface streams flowing from Precipitous

Bluff—it is known from Malani Creek, approximately 1.3 km north of Damper Creek and in Damper Creek itself where a few specimens were found together with *N. damperensis.*

Remarks

Nanocochlea stylesae is somewhat similar in shape to *N. exigua* but has a short ctenidium, lacks a distinct opercular peg and tends to have more cusps on the inner marginal teeth. It differs from *N. damperensis* in its narrower shell ($P<0.001$) and less convex whorls and fewer ctenidial filaments.

***Nanocochlea damperensis* n. sp.**
Figures 4D; 6K–M; 8G; 14E–G; 15G–H; 16D–F; 17G–K; 18B.

Type material

Holotype: AMS C.439399, first crossing, Damper Ck, stn PBs-1A, 29 MAR 1994.

Paratypes: AMS C.203685, same data, 20+ dry, 20+ wet; QVM, 9:20543 (5 wet); AMS C.439400, same data (1 dry figured paratype).

Other material examined (all AMS)

Damper Creek: C.203673, 10m outside Damper Cave, stn PBs-2A (22 dry, 20+ wet); C.201282, near New River Lagoon, E side, Limestone Ck, where track crosses creek, JW 49, 15 FEB 1988; 20+ dry, 20 wet; figured specimen from same lot, C.343820.

Bauhaus: C.303685, cave entrance.

Etymology

Named after Damper Creek.

Description

Shell (Figs. 6K–M; 14E–G; 15G, H). Length up to 2.3 mm; conical (SW/SL 0.50–0.69, mean 0.61, n = 63); spire moderate to tall, convex in outline; last whorl evenly rounded; suture indented/impressed. Protoconch microsculpture of small shallow pits and pustules. Teleoconch up to 3.3 whorls in adult; umbilicus present only in juveniles; aperture oval to pear-shaped; moderate size, shorter than spire (AL/SL 0.37–0.47, mean 0.42, n = 63); outer lip, orthocline, weakly thickened in adult, straight to slightly convex, without reflection; notch usually present in posterior corner of aperture; outer lip orthocline to weakly opisthocline; inner lip thin and narrow, in partial contact or narrowly separated from parietal wall.

Dimensions. See Table 12.

TABLE 12. Shell dimensions and teleoconch whorl counts of *Nanocochlea damperensis* n. sp.

	SL	SW	AL	AW	BW	CV	TW
Holotype	2.05	1.36	0.92	0.86	1.53	0.2	2.9
Figured paratype	2.07	1.21	0.84	0.83	1.53	0.19	3.0
Figured specimen (C.440551)	1.97	1.17	0.86	0.77	1.49	0.18	2.6
C.203685, paratypes (20)							
Minimum	1.92	1.20	0.83	0.78	1.42	0.14	2.60
Maximum	2.29	1.45	1.00	0.93	1.68	0.19	3.10
Mean	2.08	1.31	0.90	0.85	1.55	0.16	2.81
Standard Dev.	0.10	0.06	0.04	0.05	0.08	0.01	0.12
C.201282(20)							
Minimum	1.87	1.16	0.80	0.72	1.41	0.14	2.60
Maximum	2.19	1.38	0.97	0.89	1.65	0.21	3.30
Mean	2.02	1.27	0.88	0.81	1.51	0.17	2.82
Standard Dev.	0.08	0.08	0.04	0.04	0.07	0.02	0.19
C.303685(20)							
Minimum	1.60	0.87	0.63	0.53	1.10	0.10	0.37
Maximum	2.08	1.16	0.08	0.81	1.42	0.21	4.90
Mean	1.84	1.05	0.73	0.71	1.27	0.15	4.69
Standard Dev.	0.13	0.07	0.05	0.06	0.08	0.03	0.13

Operculum (Fig. 16D–F). Inner surface with or without white smear and, in some, 3–5 weak ridges (reduced pegs).

Eyes. Slightly pigmented.

Pallial cavity (Fig. 8G). Ctenidium narrow; 12–13 very small filaments; osphradium between posterior end and middle of ctenidium; hypobranchial gland thick to moderately developed; renal organ extends forward ca. ⅓ into pallial cavity; pericardium more than ½ in pallial roof.

Radula (Fig. 17G–K). *Central teeth*: dorsal edge with moderate to deep indentation; 4–5 lateral cusps, median cusp narrow, sharply pointed, about twice as long as adjacent cusps. *Lateral teeth*: dorsal edge with shallow indentation; with 5–6 cusps on outer and 4–6 on inner side; median cusp narrow, sharply pointed, less than, to about twice as long as, adjacent cusps; ratio of cutting edge to shaft about ¼; basal projection pointed. *Marginal teeth*: Inner with 20–27 cusps; outer with 20–26 cusps.

Stomach. Stomach with posterior chamber a little smaller than anterior chamber.

Male genital system. Testis of 1.0–1.25 whorls; oval to kidney-shaped; oval in section. Pallial vas deferens straight to slightly undulating at prostate; straight between prostate and penis and at base of penis. Penis (Fig. 4D) with weak swelling in mid-distal portion; distal end long, papilla-like; medial section parallel sided; of medium length; penial duct in medial section strongly undulating; base of penis moderately wide; with moderate folds; penial duct straight to undulating.

Female genital system (Fig. 18B). Ovary of 1.0 whorls; oviduct extends to posterior edge of bursa copulatrix or slightly less; joins bursal duct just in front of posterior pallial wall. Bursa copulatrix of medium size, not extending to posterior pallial wall; globular; with bursal duct arising from middle of anterior edge of bursa; straight. Seminal receptacle at middle of inner wall of bursa copulatrix; ovoid or pyriform. More than ½ of albumen gland in front of posterior pallial wall; capsule gland up to ? length of albumen gland; oval to compressed oval in section; anterior end blunt; ventral channel with indistinct to distinct vestibule; genital opening overlapping anterior end of capsule gland.

Distribution and habitat

Found in Damper Creek near the entrance to Damper Cave but was not found in samples from inside Damper Cave (in the same creek). A sample of mainly empty shells from seepages at the entrance of Bauhaus cave (Fig. 15G, H) is also attributed to this species and a single dead shell (AMS C. 203714) from inside Bauhaus (Persephone Pot) is presumably washed in from a surface seepage. Specimens from the lower end of Limestone Creek on the eastern side of New River Lagoon are also attributed to this species (see remarks). The site in this creek is approximately 1.7 km S of the lower end of Damper Ck, although about 3.5 km separate the two locations where the samples were collected.

Remarks

Nanocochlea damperensis differs from the other *Nanocochlea* described to date in its broadly pupiform shell shape. Specimens from Limestone Creek are almost identical to the type material, although have more ctenidial filaments (14–17), 5–6 lateral cusps on the central teeth and the pallial vas deferens undulates rather than being straight. Other anatomical differences are the seminal receptacle is ovoid, not globular, the capsule gland has a terminal opening in some specimens and most specimens lack a distinct white smear on the operculum. Given their close geographic proximity and overall similarity, these two populations are considered to be conspecific pending more detailed investigation.

The very weak (rudimentary) multiple pegs on the operculum of this species resemble those seen in *P. conica* and *P. arthurclarkei* and have not been observed in other taxa included in *Nanocochlea*.

The shell-shape of this species resembles that of some taxa included in *Austropyrgus* (see Clark *et al*. 2003). Members of that genus have distinct pegs on the operculum, lack an S-shaped rectum and have three or more basal cusps on the central teeth.

Discriminant function analysis

A discriminant function analysis was performed separately on the species in each genus using the shell measurements, the convexity ratio and whorl counts to test the efficacy of

these data in defining the taxa. *Pseudotricula elongata* was excluded from the *Pseudotricula* analysis due to insufficient measurements, as was *P. progenitor*, which was included in the *Nanocochlea* analysis because of its similar shell shape to the other members of that group. Both these species are readily distinguished from their congeners using shell shape (see remarks under those taxa).

In the *Pseudotricula* analysis, involving 130 specimens, four of the five species were 100% discriminated while one specimen of *P. arthurclarkei* was misclassified as *P. conica* (Wilks lambda = 0.021, approx. F = 29.487, df = 28, 430, p-tail < 0.0001).

In the analysis involving the *Nanocochlea* taxa and *P. progenitor*, a total of 143 specimens, all *P. damperensis* were correctly classified, while *N. exigua* had five (of 37) specimens incorrectly classified with *N. stylesae*, *N. stylesae* had two classified as *N. exigua* and *P. progenitor* had one misclassified as *N. damperensis* (Wilks lambda = 0.025, approx. F = 47.548, df = 21, 382, p-tail < 0.0001). The plots of the first two discriminant scores are shown in Figures 19 and 20.

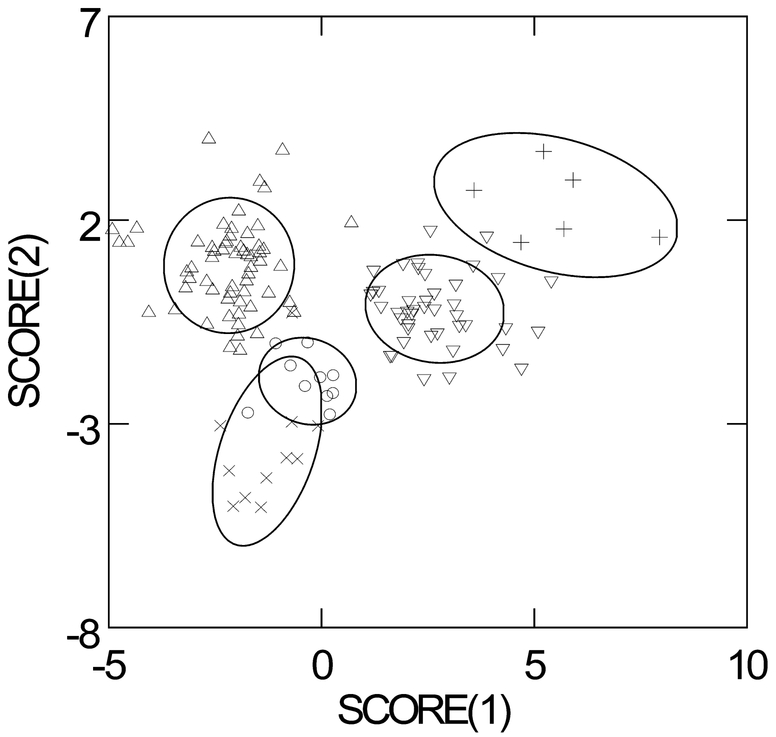

FIGURE 19. Plot of discriminant scores derived from shell measurements, convexity ratio and whorl counts for *Pseudotricula* species (*P. elongata* and *P. progenitor* excluded). ○—*P. eberhardi*; x—*P. arthurclarkei*; +—*P. auriforma*; △—*P. conica*; ▽—*P. expandolabra*. Gaussian bivariate ellipses are indicated for each sample (P=0.6827).

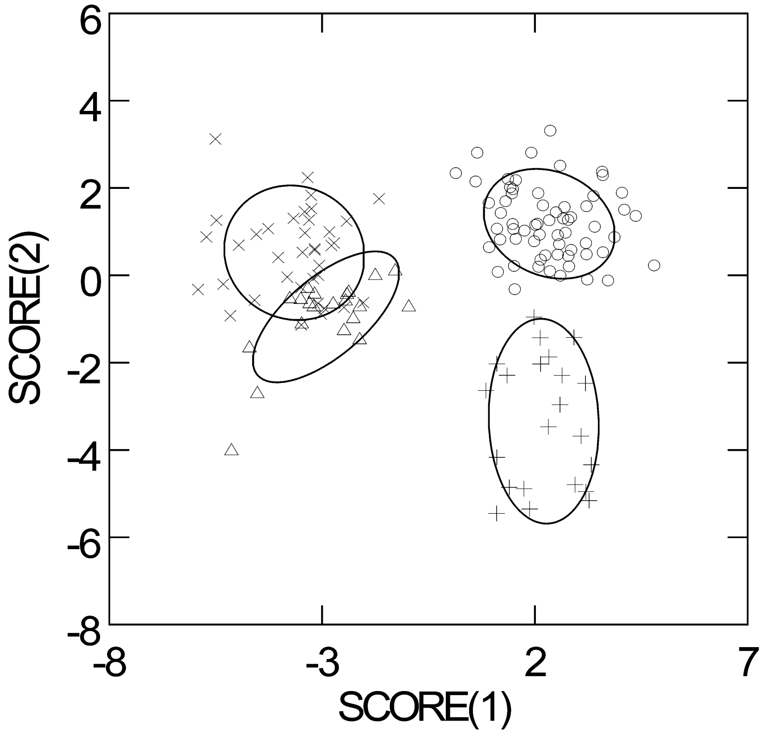

FIGURE 20. Plot of discriminant scores derived from shell measurements, convexity ratio and whorl counts for *Nanocochlea* and *Pseudotricula progenitor.* ○—*N. damperensis*; x—*N. exigua*; △—*N. stylesae*; +—*Pseudotricula progenitor.* Gaussian bivariate ellipses are indicated for each sample (P=0.6827).

Cladistic analysis

A maximum parsimony analysis was preformed on a dataset of 25 taxa (Table 13) and 60 characters (Table 14), all unordered and of equal weight (1). Two characters were parsimony-uninformative. A heuristic search of the dataset was undertaken with 100 random addition replicates (one tree held at each step) utilizing branch-swapping by tree-bisection-reconnection (TBR). The steepest descent option was not in effect and no constraints were enforced. The analysis resulted in six equally parsimonious trees of 215 steps (Consistency Index =0.502, Retention Index = 0.730, Rescaled Consistency Index = 0.367, Homoplasy Index = 0.498). The strict consensus tree is shown in Figure 21 with bootstrap (heuristic search, 1000 replicates) values of greater than 50% given.

The analysis included 15 taxa that were not part of the Precipitous Bluff fauna. Of these, the brackish-water genus *Tatea* Tenison Woods, 1879 (see Ponder *et al*. 1991) was used to root the tree. Other outgroup taxa included three species of *Austropyrgus* (see Clark *et al*. 2003) and four species of *Beddomeia* Petterd, 1889 and *Phrantela* Iredale, 1943 (see Ponder *et al*., 1993). The analysis also included the three previously described

species of *Nanocochlea* (Ponder *et al*. 1993). The tree obtained confirms the monophyly of the outgroup genera with the exception of *N. parva* Ponder & Clark, 1993 being included with *Phrantela*. This result is not unexpected, as there are several features of that taxon that are shared with *Phrantela* and it was only tentatively included in *Nanocochlea* by Ponder *et al*. (1993). Consequently, we include this taxon in *Phrantela* pending a more detailed analysis.

The species that comprise the Precipitous Bluff radiation are included in a single well supported clade that is comprised of two subclades, one of *Nanocochlea* (the two previously described taxa form a subclade within this) and another clade that is here referred to as *Pseudotricula*. *Nanocochlea* is very weakly supported, with the only changes (both unambiguous) being shell size and the shape (in transverse section) of the prostate gland. *Pseudotricula* is a little better supported, with four unambiguous characters (although lacks bootstrap support): inner surface of the operculum with white smear (strongly convergent), the anterior location of the joining of the bursal duct and oviduct, relatively more of albumen gland in pallial roof and a small anterior shift in the position of the female genital opening. Ambiguous changes included: relative size of the stomach chambers, the position and shape of the bursa copulatrix, the shape of the capsule gland in section and the vestibule.

TABLE 13. Data matrix used in cladistic analysis. The list of characters is given in Table 14.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Tatea huonensis	3	1	1	1	1	1	2	2	1	1	1	3	2	1	3	3	1	1	1	2	1	1
Austropyrgus cooma	3	1	1	3	1	1	1	2	1	1	1	3	2	1	3	3	1	1	1	2	1	1
Austropyrgus niger	3	1	1,3	3	1	1	1	2	1	1	1	3	2	1	3	4	1	1	1	2	1	1
Austropyrgus petterdianus	1	1	1	3	1	1	1	2	1	1	1	3	2	1	3	3	1	1	1	2	1	1
Beddomeia launcestonensis	2	2	5	2	1	2	2	1	1	1	1	3	1,2	4	1	-	1	1	1	2	1	2
Beddomeia palludinella	3	3	5	3	1	2	2	1	1	1	1	3	3	4	1	-	1	1	1	2	1	2
Beddomeia hullii	2	2	1	2	1	2	2	1	1	1	1	3	1	1	1	-	1,2	2	1	2	1,2	2
Beddomeia bellii	2	3	5	2	1	2	2	1	1	1	1	3	1	2	1	-	2	2	1	2	1	2
Phrantela marginata	2	1	1	2	1	1	2	1	1	1	1	3	1	1	1	-	1	1	2	2	1	1
Phrantela conica	2	1	1	2	1	1	2	1	1	1	1	1,2	1	4	1	-	2	1	2	2	1	1
Phrantela warwicki	2	1	1	2	1	1	2	1	1	1	1	3	1	1	1	-	1	1	2	2	1	1
Phrantela pupiformis	2	1	1	2	1	1	2	1	1	1	1	3	1	1	1	-	1	1	2	2	1	1
Nanocochlea monticola	1	1	1	3	1	1	2	2	1	1	1	1	2	2	1	-	1	3	2	2	4	1
Nanocochlea pupoidea	1	1	1	3	1	1	2	2	1	1	1	2	2	2	1	-	1	3	2	2	4	1
"Nanocochlea" parva	1	1	1	2	1	1	2	1	1	1	1	3	1	4	1	-	1	1	2	2	4	1
Nanocochlea damperensis	1	1	1	2	1	3	1	2	1	1	1	1,2	2	2	2,3	3	1	3	3	2	4	1
Nanocochlea exigua	1	1	1	2	1,2	1	2	2	1	1	1	1,2	2	2	3	1	1	4	-	1,2	4	1
Nanocochlea stylesae	1	1	1	2	1	1	2	2	1	1	1	1	2	2	1	-	1	3	3	1	4	1
Pseudotricula progenitor	2	1	1	3	1,2	1	2	2	1	1	1	1,2	2	2	2	-	1	3	3	2	4	1
Pseudotricula eberhardi	2	3	4	2	1	1	3	2	2	1	2	3	3	2	2	-	1	3	3	2	4	1
Pseudotricula arthurclarkei	2	3	4	3	1	1	2	2	1	1	1	3	2	3	3,4	3	1	3	3	1,2	4	1
Pseudotricula auriforma	3	3	3	3	2	1	3	2	2	2	2	3	3	?	2	-	1	3	3	2,3	4	1
Pseudotricula conica	2	3	4	3	1,2	1	2	2	1	1	1	3	2	3	2,3	2	1	3	3	2	4	1
Pseudotricula expandolabra	2	3	4	3	2	1	3	2	2	2	2	3	3	2	2	-	1	3	3	2	4	1
Pseudotricula elongata	2	1	1	3	2	1	3	2	1,2	2	2	1	3	?	?	?	?	?	?	?	?	?

......continued on the next page

TABLE 13 (continied)

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Tatea huonensis	3	1	1,2	3	1	2	2	1,2	?	?	1,2	2	2	3	1	2	2	1,2	1	1	1	1
Austropyrgus cooma	3	2	1	2,3	1	1	2	2	2	?	2	2	1	3	3	3	2	2	1	1	1	1
Austropyrgus niger	3	1	1	2	1	1,2	2	2	2	?	2	2	1	3	3	3	2	2	1	1	1	1
Austropyrgus petterdianus	3	1,2	1	2	1	2	2	2	2	?	2	2	1	3	3	3	2	1	1	1	1	1
Beddomeia launcestonensis	1	2	1	3	1	3	1	2	2	?	2	2	2	2	1	3	1	1	1	1	2	2
Beddomeia palludinella	1	2	1	3	1	2,3	1	3	2	?	2	2	2	2	1	3	1	1	1	1	1	2
Beddomeia hullii	1	2	1	3	1	2	1	3	?	?	2	2	2	2	1	3	1	1	1	1	2	2
Beddomeia bellii	1	2	1	3	1	2	1	3	?	?	1,2	2	2	1	1	3	1	1	1	1	2	2
Phrantela marginata	1	2	2	3	1	3	3	1	1	?	2	2	2	2	3	2	1	2	1	1	3	2
Phrantela conica	1	2	1	3	1	2	3	2	2	?	2	2	2	2	3	2	1	1	1	1	3	2
Phrantela warwicki	1	2	2	3	1	2	3	1	2	?	2	2	2	2,3	1,2	3	1	1	1	1	1	2
Phrantela pupiformis	1	2	1	3	1	3	3	1	1	?	2	1,2	2	2	1	1	1	1	1	1	1	2
Nanocochlea monticola	2	2	2	3	1,2	2	3	1	2	?	2	2	2	1	2	2,4	2	2	2	3	3	1
Nanocochlea pupoidea	2	2	1,2	3	2	2	3	1	2	?	1,2	1,2	2	1	2	2	2	1	2	3	2	1
"Nanocochlea" parva	1	3	2	3	1	2	3	1	1	?	1	2	2	2	2	2	1	1	1	1	?	2
Nanocochlea damperensis	2	2,3	2	2	2	2	3	1	3	1	1,2	1,2	2	1	2	2	2	1	2	3	2	1
Nanocochlea exigua	2	3	2	1	2	2,3	3	1,2	2	1	1,2	1	2	1	3	2	2	1	2	3	2	1
Nanocochlea stylesae	2	3	2	2	2	2,3	3	1	2,3	1	2	1,2	1	1	2	2	2	2	2	3	2	1
Pseudotricula progenitor	2	2,3	2	2,3	2	2	3	1	2	1	2	2	1,2	1	3	2	2	1	2	3	2	1
Pseudotricula eberhardi	2	1	1	3	2	1	2	2	2	2	1	1	2	1	1,2	2	2	1	1,2	3	2	1
Pseudotricula arthurclarkei	2	2	2	3	2	1,2	3	1,2	1,2	1	2	2	3	1	2	2	2	1	2	3	2	1
Pseudotricula auriforma	2	1	1	3,4	2	2	2	2	2,3	2	1	1	1,2	1	3	2	2	1	2	3	2	1
Pseudotricula conica	2	2,3	1,2	3	2	1,2,33		1,2	2	1	2	2	1	1	3	2	2	1	2	3	2	1
Pseudotricula expandolabra	2	1	1,2	3	2	2	2	2	2	2	1	1	1	1	3	2	2	1	2	3	2	1
Pseudotricula elongata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Tatea huonensis	1	1	2	3	1	2,7	1	4	1	2	1	1	2	1,2	1	5
Austropyrgus cooma	1	1	1	2	1	7	1	2	1	1	1	3	2	1	-	3
Austropyrgus niger	2	1	1	2	1	7	1	1	1	2	2	3	2	1	-	2
Austropyrgus petterdianus	1	1	1	2	1	7	1	1	1	3	2	3,4	2	2	2	2
Beddomeia launcestonensis	2	2	2	1	1	6	1	4	1	2	3	1,2	2	1	-	1
Beddomeia palludinella	2	2	2	2	1	3	?	3	1,2	2	1	1	1	1	-	1
Beddomeia hullii	2	2	2	2	1	3	1	3	1,2	2	1,2,3	2	1	1,2	1	3
Beddomeia bellii	1,2	1	2	2	1	7	1	2	1	2	3	2	1	2	2	3
Phrantela marginata	1	1	2	3	3	4	2	5	2	4	2	3	1	1	-	2
Phrantela conica	2	3	2	3	2	4	2	5	2	2	1	2	1	1	-	3
Phrantela warwicki	1	2	2	3	2	4	1	5	2	4	2,3	2	1	1	-	4
Phrantela pupiformis	1	3	2	3	2	4	2	5	2	4	3	1	1	1	-	4
Nanocochlea monticola	1	2,3	2	2	1	6	1	4	1	2	3	1	1	1	-	3,4
Nanocochlea pupoidea	1	2	2	2	1	2	1	4	1	4	3	1	1,2	1	-	3
"Nanocochlea" parva	1	3	2	3	2	4	2	5	2	4	1	2	1	1	-	3
Nanocochlea damperensis	1	1,2	3	2	1	7	1	4	1	3	3	2,3	2	1	1,2	2
Nanocochlea exigua	1	1,2	2	3	2	7	1	4	1	4	2	2	1,2	1,2	-	2,3
Nanocochlea stylesae	1	2	2	2	1	1	1	4	1	2	2	1,2	1,2	1	-	3
Pseudotricula progenitor	1	2	4	2,3	2	1,6	1	4	1	3	2	3	2	2	2	2
Pseudotricula eberhardi	1	2	2	2	1	1	1	4	1	2,3	2,3	1,2	2	1	-	4
Pseudotricula arthurclarkei	1	1,2	4	2	1	1,6	1	4	1	2,3	2	3	1,2	1,2	1,2	2
Pseudotricula auriforma	1	1,2	4	3	1,2	1,5,6	1	4	1	3	1	3	1,2	1	2	2
Pseudotricula conica	1	1,2,3	4	3	2,3	5,6	1	2,4	1	2,3	2,3	3	1,2	1	-	2
Pseudotricula expandolabra	1	2	4	3	2,3	1,5	1	2,4	1	3	1	3	2	1,2	1,2	2,3
Pseudotricula elongata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

TABLE 14. The list of characters used in the cladistic analysis. The data matrix is given in Table 13.

1. Maximum dimension of shell: 1, very small (1.5-2.5 mm); 2, small (2.6-4.0 mm); 3, large 4.1-6 mm.
2. Aperture size: 1, less than to twice as short as spire; 2, about equal to spire; 3, 1 to less than 2x longer than spire.
3. Shell shape: 1, elongate; 2, medium conic; 3, broadly conic; 4, ovate.
4. Spire outline: 1, concave; 2, straight; 3, convex.
5. Sub-shoulder depression: 1, absent; 2, present.
6. Umbilicus: 1, absent in adults and juveniles; 2, present in adults (open); 3, present only in juveniles.
7. Aperture shape: 1, rounded; 2, oval to pear-shaped; 3, D-shaped.
8. Outer lip: 1, thin in adult; 2, weakly to moderately thickened.
9. Outer lip reflection: 1, absent or weak; 2, strong.
10. Aperture flaring: 1, not flared; 2, flared.
11. Posterior (anal) notch: 1, absent; 2, present.
12. Slope of outer lip: 1, orthocline; 2, opisthocline; 3, prosocline.
13. Inner lip: 1, thin; 2, moderately thickened and narrow; 3, thick and wide.
14. Protoconch microsculpture: 1, coarse pits; 2, small pustules; 3, pits and pustules; 4, very fine pitting.
15. Operculum inner surface: 1, simple; 2, with white smear only; 3, with white smear and pegs; 4, with pegs only.
16. Number of opercula pegs: 1, single large peg; 2, up to 2 small to medium pegs; 3, 3-5 pegs; 4, more than 5 pegs.
17. Posterior pallial tentacle: 1, absent; 2, present.
18. Ctenidium: 1, well developed, wide; 2, narrow; 3, rudimentary; 4, absent.
19. Ctenidium length relative to pallial cavity: 1, extends all or most of pallial cavity; 2, only in anterior ?; 3, only in anterior ½.
20. Osphradium position relative to ctenidium: 1, near posterior end; 2, between posterior end and middle, 3, near middle
21. Rectum: 1, straight or with slight arch; 2, with prominent arch; 3, short S-shape; 4, long S-shape.
22. Renal organ orientation: 1, longitudinal; 2, circular to transverse.
23. Basal cusps on central teeth: 1, one pair; 2, usually two pairs; 3, usually three or more pairs.
24. Dorsal edge of central teeth: 1, with shallow indentation; 2, moderately indented; 3, deeply V shaped.
25. Median cusp of central teeth: 1, medium width; 2, narrow.
26. Length of median cusp of central teeth (relative to adjacent cusps): 1, about 3 times longer; 1: about 2 times longer; 3, less than 2 times longer; 4, about equal.
27. Lateral edges of central teeth: 1, straight; 2, bent.
28. Dorsal edge of lateral teeth: 1, straight to lightly convex; 2, with shallow indentation; 3, moderately indented; 3, deeply V-shaped.
29. Shape of U-shaped basal tongue of central teeth: 1, wide; 2, medium; 3, narrow.
30. Median cusp of lateral teeth: 1, narrow; 2, medium; 3, broad.
31. Basal projection of lateral teeth: 1, U-shaped; 2, bluntly pointed; 3, pointed.
32. Cutting edge and shaft of lateral teeth: 1, shaft more than twice as long; 2, shaft twice or less than twice as long.
33. Cusps on inner marginal teeth: 1, up to 21 cusps; 22 cusps or more.
34. Cusps on outer marginal teeth: 1, up to 20 cusps; 21 cusps or more.

......continued on the next page

TABLE 14 (continued)

35. Stomach chambers: 1, posterior and anterior chambers about equal; 2, posterior chamber a little smaller; 3, posterior chamber much smaller; 4, with posterior chamber larger.
36. Stomach caecum: 1, absent; 2, small; 3, large.
37. Prostate shape in transverse section: 1, broadly oval to circular; 2, oval; 3, compressed; highly compressed.
38. Ventral wall of prostate: 1, ventral silt; 2, thin ventral wall; 3, thick ventral wall.
39. Vas deferens from pallial part of prostate: 1, emerges anteriorly; 2, emerges about half way ventrally.
40. Pallial vas deferens: 1, straight to slightly undulating; 2, moderately to strongly undulating.
41. Subterminal swelling on penis: 1, absent; 2, present.
42. Penial papilla (distal end): 1, no papilla; 2, short papilla; 3, long papilla.
43. Medial section of penis: 1, short and broad; 2, medium; 3, elongate and narrow.
44. Coiled oviduct: 1, firm, not embedded in connective tissue; 2, soft, in connective tissue.
45. Coiling of coiled oviduct: 1, simple U-shape; 2, coiled or with two or more folds or loops.
46. Posterior extent of coiled oviduct: 1, does not reach posterior edge of bursa; 2, extends to posterior edge of bursa; 3, extends behind bursa.
47. Point of joining of oviduct and bursal duct: 1, just behind pallial wall; 2, at posterior pallial wall; 3, just in front of posterior pallial wall; 4, well in front of posterior pallial wall.
48. Bursa copulatrix - size: 1, small; 2, medium; 3, large.
49. Bursa copulatrix extent: 1, lies behind posterior pallial wall; 2, extends to posterior pallial wall; 3, extends in front of posterior pallial wall.
50. Bursa copulatrix shape: 1, globular; 2, obliquely ovoid; 3, vertically ovoid; 4, horizontally ovoid; 5, elongately oval; 6, horizontally pyriform; 7, vertically pyriform.
51. Position of bursal duct emerging from bursa: 1, anterior edge; 2, ventral edge.
52. Seminal receptacle-position: 1, at anterior edge of bursa on left; 2, on middle of inner wall of bursa on left; 3, behind posterior edge of bursa on left; 4, at mid ventral edge of bursa on left; 5, on right side of bursa.
53. Seminal receptacle shape: 1, ovoid to pyriform; 2, narrow sac.
54. Albumen gland: 1, ¼ or less in pallial roof; 2, about ⅓ to ½ in pallial roof; 3, ½ to less than ⅔s in pallial roof; 3, more than ⅔s in pallial roof.
55. Length of capsule gland relative to albumen gland: 1, longer than albumen gland; 2, about equal to albumen gland; 3, up to about ? albumen gland; 4, less than ⅔s albumen gland.
56. Capsule gland - shape in transverse section: 1, circular in section; 2, oval in section; 3, compressed-oval in section; 3, elongate oval in section.
57. Anterior end of capsule gland: 1, tapering; 2, blunt; 3, rounded.
58. Ventral channel: 1, simple; 2, expanded anteriorly.
59. Vestibule: 1, indistinct or small; 2, moderate-sized, muscular; 3, large, muscular.
60. Genital opening position relative to anterior end of capsule gland: 1, anterior; 2, overlapping; 3, terminal; 4, subterminal; 5, well behind anterior end.

Pseudotricula is comprised of three subclades: *P. progenitor* is the sister to the remainder of the clade; *P. conica* and *P. arthurclarkei* form a separate clade from the remaining four *Pseudotricula* taxa, defined by a single unambiguous character (protoconch microsculpture). The third clade, which includes the typical species of *Pseudotricula*, has bootstrap support and is defined by 10 unambiguous character changes (see Fig. 21), notably, a D-shaped aperture, an expanded outer lip, posterior apertural notch and a reduction in the number of cusps on the marginal teeth.

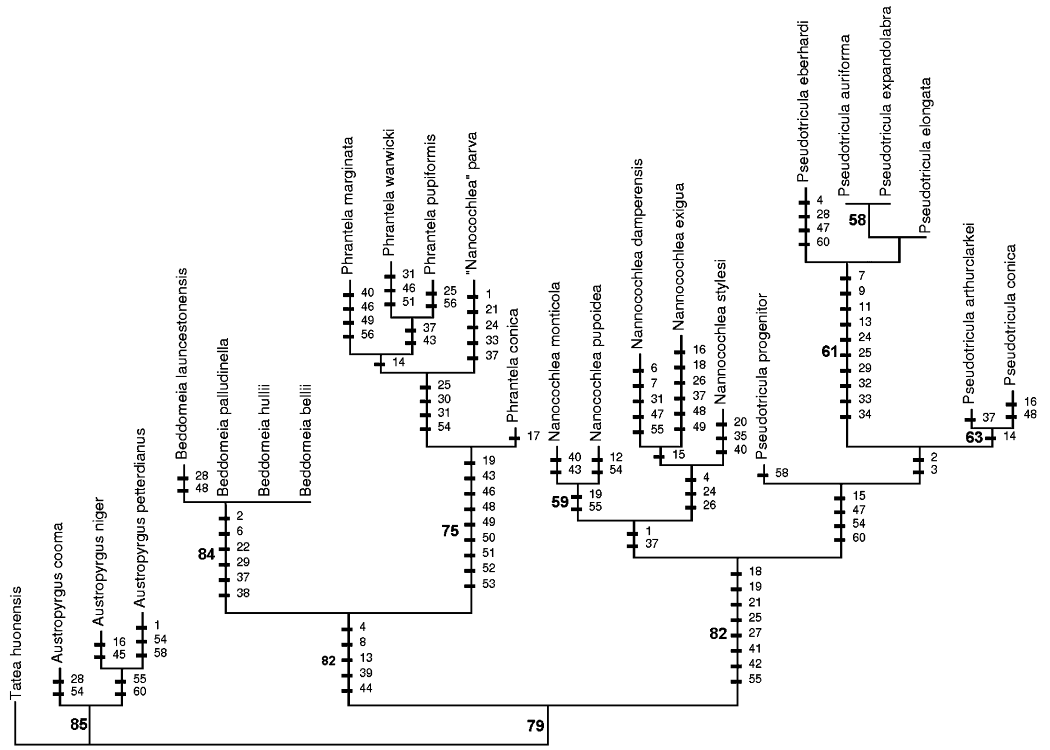

FIGURE 21. Strict consensus tree obtained from the 6 most parsimonious trees obtained from a cladistic analysis of the data in Table 13. The unambiguous character changes are listed on each branch (see Table 14 for list of characters). Bootstrap values of more than 50% are included next to the relevant branches on the left.

Discussion

This paper presents the first description of a significant radiation of closely-related freshwater molluscs occurring within a single karst area in Australia. The eight species of hydrobiids, in two closely related genera, in the Precipitous Bluff caves is a level of diversity that appears to be unique among Tasmanian (and Australian) karsts. This radiation mirrors the major radiation of hydrobiids in surface freshwaters in Tasmania and the southeastern mainland of Australia (Ponder *et al*. 1993, 1994; Colgan & Ponder 1994; Clark *et al*. 2003), albeit the Precipitous Bluff radiation involves fewer genera in a much smaller geographic area.

Sampling in dozens of other Tasmania karst areas has produced about 30 (mostly undescribed) hydrobiid taxa, many of which are also likely to be stygobites. These include species of *Austropyrgus*, *Beddomeia*, *Phrantela* and *Nanocochlea*, with no known additional species of *Pseudotricula* (Ponder *et al*. 1993, WFP and SAC pers. observ.). In all other Tasmanian caves, one to five species are known from each cave system and in most cases where multiple species are present they are not congeners. Two genera and five species have been found in both Gunns Plains/Mastyn Hardy and Junee Florentine/

Caryodes Cavern (W.F.P. S.A.C. and J.S. pers. observ.). The richness of the Precipitous Bluff radiation was revealed through repeated sampling at multiple sites and habitats within this karst area, thus demonstrating the need for intensive sampling to properly reveal subterranean biodiversity. While many other Tasmanian karsts have been sampled for hydrobiids no other major cave radiations have been revealed to date, including in other karst areas such as Vanishing Falls, Cracroft, Hastings and Ida Bay in the same geographic region of southern Tasmania (Clarke 1990, 1997; Eberhard *et al*. 1991a; Eberhard *et al*. 1991b; WFP unpublished data). Ida Bay in particular has been intensively sampled (see Eberhard 2001) and like Precipitous Bluff, the Ida Bay karst area is highly cavernous and contains a diverse array of aquatic and terrestrial habitats which harbour a rich assemblage of troglobites including many of the same genera (such as *Nanocochlea*) found at Precipitous Bluff (Eberhard *et al*. 1991b, 2001). Ida Bay therefore, might be considered a likely candidate for a major radiation of cave dwelling hydrobiids. However, intensive and repeated sampling in this karst has revealed only two hydrobiids, one a *Nanocochlea* and the other a *Phrantela* (Eberhard 2001; WFP, SAC and JS unpublished data).

Although not properly quantified, the diversity and heterogeneity in subsurface aquatic micro-habitats may be greater in the Precipitous Bluff caves than in other karst areas in Tasmania. The Precipitous Bluff karst is notable for the high density and development of caves, with more than 30 caves recorded and > 5 km of underground passages mapped within an area < 4 km^2 (Eberhard & Hume 1987; Hume 1989; Hume & Clarke 1989). Most of the underground passages contain perennially active streams of various physical dimensions, flow rates, and substrate characteristics. Hence there is a diverse range of aquatic subsurface habitats present. Within most caves there is considerable gradation and small-scale (< 1–10 m) heterogeneity in substrate and flow characteristics, which change in response to changes in the physical dimensions and gradient of the cave conduits which are highly non-uniform. Thus the Precipitous Bluff caves provide considerable diversity and heterogeneity of aquatic habitats at a range of spatial scales, from in-stream micro-habitat, to in-cave stream(s), to in-karst cave(s).

The aquatic subsurface habitats in the Precipitous Bluff caves range from tiny pools, seepages and trickles fed by diffuse vertical percolation, to small streams (< 0.5 m wide, < 0.1 m deep, flow < 1 L/s) formed from coalescing seepage flows, to larger streams (0.5–1 m wide, 0.1–1 m deep, flow 2–5 L/s), and finally major streams (2–4 m wide, 0.1–2 m deep, flow > 5 L/s). The benthic substrates of streams where the snails are found are also diverse. They include smooth limestone bedrock in sections of streams characterised by high flow velocities including chutes and waterfalls (e.g., Black Curtains Streamway in Cueva Blanca where *P. eberhardi* is found). Most other cave streams have a lower gradient than this particular site however, and their beds are cloaked in clastic sediments derived from higher up the slope of Precipitous Bluff. In streams with moderate-gradient and moderate to high-flow velocities (e.g., Bauhaus main streamway), the sediments typically

consist of cobbles and pebbles of dolerite, sometimes partially cemented within a matrix of gravel and silt. In low-gradient streams with lower flow velocities (e.g., Persephone Pot stream in Bauhaus, main streams in Damper Cave) the amount of gravel and silt increases proportionately, and these sediments may dominate the benthic substrate within some streams or caves (e.g., Quetzalcoatl Conduit). The clastic sediments on the beds of streams, which may be several metres deep in places, provide potential interstitial habitat which was not examined in detail. However, the single site sampled (Damper Cave) did yield hydrobiids. In general, the broader-shelled species appear to prefer faster-flowing water and their larger apertures may well be an adaptation to these environments. A large aperture is capable of housing a larger foot for clamping to the substrate than narrow-shelled taxa,

Based on the results of the cladistic analysis, the cave radiation represents two components an *in situ* radiation (*Pseudotricula*) derived from a common ancestor with *Nanocochlea* and a separate incursion (*N. exigua*). It is likely the radiation of *Pseudotricula* within the caves is the result of allopatric speciation with subsequent sympatry although there remains a possibility of sympatric speciation as a consequence of high habitat diversity and niche partitioning.

Despite the high degree of hydrologic connectivity between the different caves and habitats within the caves, some species appear to have strict habitat preferences (Table 15). Most of the hydrobiid taxa prefer the small, gently flowing streams with a variety of substrate types, including silt. The most diverse assemblages (up to five sympatric species) occur in such streams as Persephone and the main streamway in Damper Cave. Two species appear to be specialised and restricted to the particular substrate and flow conditions in Cueva Blanca (Black Curtains Streamway: *P. eberhardi*) and Quetzalcoatl Conduit (*P. arthurclarkei*) respectively, whilst other species are excluded. The hydrobiid diversity in the caves is higher than usually seen in surface habitats in Tasmania, the highest diversity seen being six species (three genera) in one location, with single species being found in most locations (Ponder *et al*. 1993; Ponder & Colgan 2002; Clark *et al*. 2003).

While this probably contributes to the maintenance of biotic diversity it may not be the sole factor. Other factors that may contribute to hotspots of subterranean biodiversity in karstic regions include *inter alia* cave density, altitude, lateral extent and planar length of cave passage, and the degree of continuity or fragmentation between karst outcrops (see Holsinger & Culver 1988; Culver & Sket 2000; Culver *et al*. 2004). These factors have not been rigorously tested for Tasmanian karsts although it appears to be generally the case that larger karst areas, which are highly cavernous tend to harbour greater diversity (Eberhard *et al*. 1991b, Eberhard 1996).

As elsewhere in the world, historical biogeographic and geomorphic factors are also likely to have strongly influenced the evolution of Tasmanian cave faunas (Eberhard 1996), particularly Quaternary climate oscillations, which included peri-glacial and glacial

conditions that profoundly influenced the thermal and hydrologic regimes within virtually all Tasmanian karsts (Kiernan 1982). These climatic changes have been implicated in the isolation and speciation of populations in Tasmanian caves (Moore 1964; Kiernan & Eberhard 1990; Eberhard 1992a, 1996), consistent with the Pleistocene effect theory, which is the most widely accepted model for the evolution of terrestrial troglobites in the temperate latitudes of the Northern Hemisphere (see reviews in Barr & Holsinger 1985; Holsinger 2000). This model was invoked to explain why there is a general paucity of troglobites in Northern Hemisphere karst areas strongly affected by glaciation during the Pleistocene. This contrasts with the relatively rich troglobite faunas found in karst areas that experienced peri-glacial conditions beyond glacial margins. Beside the extirpation of faunas in karsts directly overridden by ice, this model assumed that cool climates during glacial periods favoured wide distribution of terrestrial invertebrates inhabiting moist, forest-floor litter and cave habitats. During warm interglacial climates, the forests retreated leaving populations isolated in cave habitats and the reduced gene flow between hypogean and epigean populations promoted the evolution of troglobites. Presumably aquatic faunas would also be affected by climatic changes and certainly in Tasmanian surface waters hydrobiids were apparently eliminated from highland areas, which were glaciated during the Pleistocene, whilst their low dispersal powers appear to have restricted their recolonisation after deglaciation (Ponder *et al*. 1993).

TABLE 15. Summary of habitats and hydrobiid species in the caves at, and in the general vicinity of, Precipitous Bluff.

Location	*damperensis*	*exigua*	*stylesae*	*progenitorr*	*arthurclarkei*	*conica*	*eberhardi*	*expandolabra*	*auriforma8*	*elongata*	*Potamopyrgus*
Outside caves											
Malani Ck			X								
Damper Ck, first crossing	X		X								
Damper Ck, 10 m outside cave	X	X									
Damper Ck, at New R Lagoon											X
Limestone Ck		X									
Inside caves											
Bauhaus		**X**		**X**		**X**		**X**		**X**	
main streamway								X			
Persephone streamway		X		X		X		X			
Screaming Stals streamway		X				X		X			
Persephone Pot	(X)	X		X		X		X		X	
Cueva Blanca						X	X				
Damper Cave		**X**		**X**		**X**		**X**	**X**		
main streamway		X		X		X		X	X		
main streamway near entrance		X		X		X			X		
cane toad abuse		X				X		X			
seep near the keg		X						X			
honey and cream streamway		X						X			
quetzalcoatl conduit		X			X						

A few specimens of one of the minute cave species (*N. exigua*) has been found in a stream flowing from Damper Cave a few metres outside the cave. Most species of *Nanocochlea* are typically associated with seepages and small streams and live in crevices, under stones and rocks or in moss and roots. Their bodies are unpigmented and they lack pigmented eyes (see also below). In contrast, none of the larger snails (*Pseudotricula*) have been found outside the caves.

Sampling suggests that streams outside the Precipitous Bluff caves, even close to a cave entrance (Damper Cave), have a different fauna with the one exception noted above. Thus, based on their absence from collections made in surface waters at Precipitous Bluff, we consider the cave-dwelling species stygobites, despite the retention of unpigmented eyes. The loss of body and eye pigment appears to have occurred in at least some of the apparently ancestral *Nanocochlea*, although *N. damperensis* has lightly-pigmented eyes. Unpigmented eyes are also found in some other stygobitic hydrobiids and are lost in others (e.g., Climo 1974).

Human-induced changes to water quality, flow regimes and benthic habitats can adversely impact cave dwelling hydrobiids such as resulted from quarrying operations at Ida Bay (e.g., Eberhard 1992b, 2001). Fortunately, the isolation of Precipitous Bluff and its containment within a National Park suggests that there are few obvious conservation concerns for this fauna. However, the presence of the introduced invasive *Potamopyrgus antipodarum* (Gray, 1843) at the lower end of Damper Creek (stn PBs-3) is of potential concern to the surface stream-living species. This parthenogenic, highly fecund New Zealand species appears to compete with native taxa to their detriment (e.g., Ponder 1988; Schreiber *et al*. 2002).

Extensive tracts of limestone remain partly explored in the Precipitous Bluff-Vanishing Falls-Cracroft areas and it is probable that other cave systems exist which may contain additional hydrobiid species.

Acknowledgements

This work was supported in part by ARC and ABRS grants. A small grant was also obtained from the Tasmanian Parks and Wildlife Service. Arthur Clarke, Janet Waterhouse, Vera Wong and Julie Styles assisted with collecting material. The map used in Fig. 1 is based on one drawn by N. Hume in 1989 for the TCC and is used with permission. Peter Middelfart assisted with some of the SEM work. Arthur Clarke assisted with the locality data and he and Martin Haase made useful comments on the manuscript.

References

Barr, T. & Holsinger J.R. (1985) Speciation in cave faunas. *Annual Review of Ecology and Systematics*, 16, 313–337.

Clark, S.A., Miller, A.C. & Ponder, W.F. (2003) Revision of the snail genus *Austropyrgus* (Gastropoda: Hydrobiidae). A morphostatic radiation of freshwater gastropods in southeastern Australia. *Records of the Australian Museum Supplement*, 28, 1–109.

Clarke, A. (1990) A summary of recent karst research in Tasmania. *Tasmanian Cave and Karst Research Group Journal*, 4, 1–6.

Clarke, A. (1997) Management prescriptions for Tasmania's cave fauna. Report to the Tasmanian Regional Forest Agreement Environment and Heritage Technical Committee. March 1997. 166 pp.

Climo, F. M. (1974) Description and affinities of the subterranean molluscan fauna of New Zealand. *New Zealand Journal of Zoology,* 1, 247–284.

Colgan, D.J. & Ponder, W.F. (1994) The evolutionary consequences of restrictions of gene flow: examples from hydrobiid snails. *Nautilus Supplement*, 2, 25–43.

Culver, D.C. & Holsinger, J.R. (1992) How many species of troglobite are there? *National Speleological Society Bulletin*, 54, 79–80.

Culver, D.C. & Sket, B. (2000) Hotspots of subterranean biodiversity in caves and wells. *Journal of Cave and Karst Studies*, 6, 11–17.

Culver, D.C., Christman, M.C., Sereg, I., Trontelj, P. & Sket, B. (2004) The location of terrestrial species-rich caves in a cave-rich area. *Subterranean Biology*, 2, 27–32.

Dallwitz, M.J., Paine, T.A. & Zurcher, E.J. (1993) Users guide to the DELTA System: a general system for processing taxonomic descriptions. 4th edition. http://biodiversity.uno.edu/delta/

Dixon, G., & Sharples, C. (1986) Reconnaissance geological observations on Precambrian and Palaeozoic rocks of the New and Salisbury Rivers, Southern Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*, 120, 87–94.

Eberhard, S. (1992a) *The invertebrate cave fauna of Tasmania: ecology and conservation biology.* MSc thesis, Zoology Department. University of Tasmania. 184 pp.

Eberhard, S. (1992b) *The effect of stream sedimentation on population densities of hydrobiid molluscs in caves*. Report to Tasmanian Dept. Parks, Wildlife and Heritage, Hobart. 8 pp.

Eberhard, S. (1996) Tasmanian cave fauna *In*: Juberthie, C. & Decu, V. (eds) *Encyclopedia Biospeologica*. Société Internationale de Biospeleologie, Moulis - Bucarest, pp. 2093–2103.

Eberhard, S. (2001) Cave fauna monitoring and management at Ida Bay, Tasmania. *Records of the Western Australian Museum Supplement*, 64, 97–104.

Eberhard, R., Eberhard, S. & Wong, V. (1991a) Karst geomorphology and biospeleology at Vanishing Falls, south-west Tasmania. *Helictite*, 30, 25–32.

Eberhard, S. & Hume, N. (1987) Report of the Tasmanian Caverneering Club 1986 speleological reconnaissance expedition to Precipitous Bluff. *Speleo Spiel (Newsletter of the Tasmanian Caverneering Club)*, 246, 1–15.

Eberhard, S., Richardson, A.M. & Swain, R. (1991b) *The invertebrate cave fauna of Tasmania.* Report to the National Estate Office, Canberra. Zoology Department, University of Tasmania. 174 pp.

Gentilli, J. (1972) *Australian climate patterns*. Thomas Nelson and Sons, Melbourne. 285 pp.

Giusti, F. & Pezzoli, E. (1977) Primo contributo alla revisione del genere *Bythinella* in Italia. *"Natura Bresciana" Annuario del Museo Civico di Storia Naturale di Brescia*, 14, 3–66.

Giusti, F. & Pezzoli, E. (1981) Notulae malacologicae XXV. Hydrobioidea nuove o poco conosciute dell'Italia appenninica. *Archiv für Molluskenkunde*, 111, 207–222.

Hershler, R. & Longley, G. (1986) Phreatic hydrobiids (Gastropoda: Prosobranchia) from the Edwards (Balcones Fault Zone) aquifer region, south-central Texas. *Malacologia*, 27, 127–172.

Holsinger, J.R. (2000) Ecological derivation, colonization, and speciation. *In*: Wilkens, H., Culver, D.C. & Humphreys, W.F. (eds) *Ecosystems of the World Vol. 30 Subterranean Ecosystems*. Elsevier, Amsterdam, pp. 399–415.

Holsinger, J.R. & Culver, D.C. (1988) The invertebrate cave fauna of Virginia and a part of Eastern Tennessee: zoogeography and ecology. *Brimleyana*, 14, 1–164.
Hughes, T.D. (1957) *Limestones in Tasmania.* Geological Survey and Mineral Resources 10. Tasmanian Department of Mines. Hobart. 291 pp.
Hume, N. (1989) 1988/89 Precipitous Bluff Expedition part 2. *Speleo Spiel (Newsletter of the Tasmanian Caverneering Club)*, 253, 1–14.
Hume, N. & Clarke, A. (1989) 1988/89 Precipitous Bluff Expedition part 1. *Speleo Spiel (Newsletter of the Tasmanian Caverneering Club)*, 252: 1–14.
Hunt, G.S. (1990) *Hickmanoxyomma*, a new genus of cavernicolous harvestmen from Tasmania (Opiliones: Triaenonychidae). *Records of the Australian Museum*, 42, 45–68.
Hunt, G.S. & Hickman, J.L. (1993) Revision of the genus *Lomanella* Pocock with implications for family level classification in the Travunoidea (Arachnida: Opiliones: Triaeononychidae). *Records of the Australian Museum*, 45, 81–119.
Kiernan, K.W. (1982) Glaciation and karst in Tasmania: review and speculations. *Helictite*, 20, 11–16.
Kiernan, K.W. (1995) *An atlas of Tasmanian karst*. Tasmanian Forest Research Council Inc., Research Report No. 10. 351 pp.
Kiernan, K.W. & Eberhard, S. (1990) Karst resources and cave biology. *In*: Smith, S.J. & Banks, M.R. (eds) *Tasmanian wilderness - world heritage values*. Royal Society of Tasmania, Hobart, pp 28–37.
Moore, B.P. (1964) Present day cave beetle fauna in perspective: a pointer to past climatic change. *Helictite*, 3, 3–9.
Moore, B.P. (1978) A new species of the Tasmanian cave carabid genus *Idacarabus* (Coleoptera). *Australian Entomology Magazine*, 5, 23–25.
Perez, K.E., Ponder, W.F., Colgan, D.J., Clark, S.A. & Lydeard, C. (2005) Molecular phylogeny and biogeography of spring-associated hydrobiid snails of the Great Artesian Basin, Australia. *Molecular Phylogenetics and Evolution*, 34, 545–556.
Platnick, N.I. & Forster, R.R. (1989) A revision of the temperate South American and Australian spiders of the family Anapidae. *Bulletin American Museum Natural History*, 190, 1–139.
Ponder, W.F. (1988) *Potamopyrgus antipodarum* - a molluscan coloniser of Europe and Australia. *Journal of Molluscan Studies*, 54, 271–285.
Ponder, W.F. (1992) A new genus and species of aquatic cave-living snail from Tasmania (Mollusca: Gastropoda: Hydrobiidae). *Proceedings of the Royal Society of Tasmania*, 126, 23–28.
Ponder, W.F., Clark, G.A., Miller, A. & Toluzzi, A. (1993) On a major radiation of freshwater snails in Tasmania and eastern Victoria - a preliminary overview of the *Beddomeia* group (Mollusca: Gastropoda: Hydrobiidae). *Invertebrate Taxonomy*, 7, 501–750.
Ponder, W.F. & Colgan, D.J. (2002) What makes a narrow range taxon? Insights from Australian freshwater snails. *Invertebrate Systematics*, 16, 571–582.
Ponder, W.F., Colgan, D.J. & Clark, G.A. (1991) The morphology, taxonomy and genetic structure of *Tatea* (Mollusca: Gastropoda: Hydrobiidae), estuarine snails from temperate Australia. *Australian Journal of Zoology*, 39, 447–497.
Ponder, W.F., Colgan, D.J., Clark, G.A., Miller A.C. & Terzis, T. (1994) Microgeographic genetic and morphological differentiation of freshwater snails—the Hydrobiidae of Wilsons Promontory, Victoria, south eastern Australia. *Australian Journal of Zoology*, 42, 557–678.
Ponder, W. F., Hershler, R. & Jenkins, B. (1989) An endemic radiation of Hydrobiidae from artesian springs in northern South Australia: their taxonomy, physiology, distribution and anatomy. *Malacologia*, 31, 1–140.
Radoman, P. (1983) Hydrobioidea, a superfamily of Prosobranchia (Gastropoda). I. *Serbian Academy of Sciences and Arts, Monograph*, DXLVII, 1–256.
Reid, J.B., Hill, R.S., Brown, M.J. & Hovenden, M.J. (eds) (1999) *Vegetation of Tasmania*. Flora of

Australia Supplementary Series 8. Australian Biological Resources Study, Canberra. i–xx, 1–453 p.

Schreiber, E.S.G., Lake, P.S. & Quinn, G. (2002) Facilitation of native stream fauna by an invading species? Experimental investigations of the interaction of the snail, *Potamopyrgus antipodarum* (Hydrobiidae) with native benthic fauna. *Biological Invasions*, 4, 317–325.

Swofford, D.L. (1998) *PAUP**. Phylogenetic analysis using parsimony (* and other methods). Version 4.* Sinauer Associates: Sunderland, Massachusetts, USA.

Wilke, T., Davis, G.M, Falniowski, A., Giusti, F., Bodon, M. & Szarowska, M. (2001) Molecular systematics of Hydrobiidae (Mollusca: Gastropoda: Rissooidea): testing monophyly and phylogenetic relationships. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 151, 1–21.

Wilkens, H., Culver, D.C. & Humphreys, W.F. (eds.) (2000) *Subterranean Ecosystems*. Ecosystems of the World, 30. Elsevier, Amsterdam. xiv + 791 pp.

Appendix: Station data

A. Outside caves

Malani Ck, Precipitous Bluff, in rocky seep/stream in mixed forest, stn 14, 43° 28'S, 146° 35'E , S. Eberhard & V. Wong 28 DEC 1991 (Note: Malani Ck drains the slopes of PB & is the next major creek to the north of the known caves).

Damper Ck tributary, first crossing, stn PBs-1A, 43° 29.25'S, 146° 34.5'E, S. Eberhard & J. Styles, 29 MAR 1994 (Stream width c. 2 m, depth < 0.2 m, flow est. 10–20 L/s, substrate cobbles-gravel, microhabitat gentle riffle).

Damper Ck, 10m outside Damper Cave, green filamentous algae, stn PBs-2a, 43° 29.06'S, 146° 34.96'E, S. Eberhard & J. Styles, 29 MAR 1994 (Stream width c. 2 m, depth < 0.5 m, flow est. 10–20 L/s, substrate green filamentous algae, stream bed of silt-gravel, microhabitat gentle riffle/pool (= run))

New River Lagoon, at Damper Ck, stn PBs-3, 43° 29.20'S, 136° 34.8'E, S. Eberhard, 30 MAR 1994 (Stream width c. 4 m, depth < 1–2 m, flow est. 10–20 L/s, stream bed of silt-gravel with logs, litter; *Potamopyrgus antipodarum* (AMS C.202667).

Limestone Ck, near New River Lagoon, where tagged track crosses creek, JW 49, 43° 29.2'S, 136° 34.8'E, J. Waterhouse, 15 FEB 1988. Shallow, flowing stream with gravel, sand and weeds.

Bauhaus, cave entrance, 43° 29.00'S, 146° 37.00'E, S. Eberhard, 26 MAR 1994, litter associated with small seepages.

B. Inside caves

Bauhaus (PB6) cave entrance 43° 29.01'S, 146° 35.28'E.

Bauhaus, in gravel, stn PB6-1, S.E. Eberhard & J. Styles, 27 MAR 1994 (Stream width < 1 m, depth < 0.3 m, flow est. < 5 L/s.)
Bauhaus, base of aven near shaft entrance - surface wash, stn PB6-1, S.E. Eberhard & J. Styles, 26 MAR 1994 (seepage close to surface, rocky substrate).

Bauhaus, Persephone streamway, stn 8, S. Eberhard & V. Wong, 23 DEC 1991
Bauhaus, Persephone streamway, further upstream, near dead possum, stn 9, S. Eberhard & V. Wong, 23 DEC 1991
Bauhaus, Persephone streamway, stn 9, S. Eberhard & V. Wong, 23 DEC 1991
Bauhaus, Persephone streamway, stn 10, S. Eberhard & V. Wong, 23 DEC 1991
Bauhaus, Persephone streamway, near end of passage, stn 10, S. Eberhard & V. Wong, 23 DEC 1991.
Collections for all these made progressively upstream from point of first entry into passage. Habitat details generally as: Stream width, 0.5 m, depth < 0.2 m, flow est. < 1 l/s. Substrate clastic sediments cobbles, gravel, silt, microhabitats gentle riffles & pools

Bauhaus, Screaming Stals streamway, stn 11, S. Eberhard & V. Wong, stn 23 DEC 1991
Bauhaus, Screaming Stals streamway, stn 12, S. Eberhard & V. Wong, 23 DEC 1991
Bauhaus, Screaming Stals streamway, tributary seep, stn 12, S. Eberhard & V. Wong, 21 DEC 1991
Bauhaus, Screaming Stals streamway, stn 13, S. Eberhard & V. Wong, 23 DEC 1991
Collections made progressively upstream from point of first entry into passage. Habitat details generally as: Stream width < 1 m, depth < 0.3 m, flow est. < 5 L/s. Substrate clastic sediments cobbles, gravel, silt, microhabitats gentle riffles & pools

Bauhaus, Persephone Pot, at first contact with stream, stn 7, S. Eberhard & V. Wong, 23 DEC 1991
Bauhaus, Persephone Pot, in stream, stn 7, S. Eberhard & V. Wong, 23 DEC 1991
Bauhaus, Persephone Pot, in stream, stn 9, S. Eberhard & V. Wong, 23 DEC 1991
Collections made progressively upstream from point of first entry into passage. Habitat details generally as: Stream width, 0.5 m, depth < 0.2 m, flow est. < 1 l/s. Substrate clastic sediments cobbles, gravel, silt, gentle riffles and pools.

Bauhaus, Persephone Pot, stn PB17-8R, slow flowing stream with silty substrate in deep zone, S. Eberhard, 3 JAN 1990.
Bauhaus, Persephone Pot, middle & upper streamway, in gravel, stn PB17-2, S. Eberhard & J. Styles, 27 MAR 1994
Bauhaus, Persephone Pot, lower streamway, stn PB17-2a.1, S. Eberhard, 26 MAR 1994
Bauhaus, Persephone Pot, middle and upper streamway, stn PB17-2a.2, S. Eberhard, 27 MAR 1994
Bauhaus, Persephone Pot, lower streamway, in gravel, stn PB17-1, S.E. Eberhard & J. Styles, 26 MAR 1994
(For all these: stream width 0.5 m, depth < 0.2 m, flow est. < 1 l/s, substrate clastic sediments cobbles, gravel, silt, microhabitats gentle riffles & pools)

Bauhaus, main streamway at downclimb, stn PB6-1A, S. Eberhard, 27 MAR 1994 (Stream width < 1 m, depth < 0.3 m, flow est. < 5 L/s, substrate cobbles, gravel, microhabitat riffle-pool).

Cueva Blanca cave (PB4) entrance 43° 29.00'S, 146° 34.95'E.

Cueva Blanca, clinging to smooth rock in turbulent shallow stream in dark zone, stn PB4, S. Eberhard, 31 MAR 1986 Cueva Blanca, A. Clarke & S. Eberhard, 18 DEC 1988.

Cueva Blanca, Black Curtain Streamway (= Inundation Passage), in torrents & waterfalls, 100-200m from entrance, stn PB4, A. Clarke & S. Eberhard, 18 DEC 1988.

Cueva Blanca, Black Curtain Streamway, stn PB4-1, J. Styles, 30 MAR 1994.

Cueva Blanca, Black Curtain Streamway, stn PB4-1C, S. Eberhard, 30 MAR 1994. (For all these: stream width ca. 1 m, depth highly variable chutes < 0.1 m to pools 1.5 m, Substrate smooth limestone bedrock. Flow high gradient streamway consisting of chutes and small waterfalls interspersed with plunge pools; flow ca. < 5 L/s.

Damper Cave (PB1) entrance 43° 29.06'S, 146° 34.96'E.

Damper Cave, main streamway, 100 m into cave, in dark zone, stn 6, S. Eberhard & V. Wong,

22–23 DEC 1991 (Stream width c. 2 m, depth < 0.2 m, flow est. 10 to 20 L/s, substrate cobbles-gravel, microhabitat gentle riffle).

Damper Cave, Cane Toad Abuse, stn PB1-2, S. Eberhard & J. Styles, 28 MAR 1994.

Damper Cave, Cane Toad Abuse, streamway, stn 2, A. Clarke, 22 DEC 1988.

Damper Cave, Cane Toad Abuse, streamway, stn PB1-2A, S. Eberhard & J. Styles, 28 MAR 1994. (All above: stream width ca. 1 m, depth, 0.1 m, flow est. < 1 L/s, substrate cemented cobbles, with gravel-silt. microhabitat gentle riffle).

Damper Cave, seep near The Keg, stn 3, S. Eberhard & V. Wong, 22 DEC 1991 (Small seepage fed by drip water from aven near The Keg. Located several hundred metres into cave, deep zone).

Damper Cave, main streamway near entrance (ca. < 50 m inside cave), in gravel, stn PB1-1 and PB1A (also listed as PB1-1A) S.E. Eberhard & J. Styles, 28 MAR 1994 (Stream width c. 2 m, depth < 0.2 m, flow est. 10 to 20 L/s, substrate cobbles-gravel, microhabitat gentle riffle).

Damper Cave, main streamway near entrance (ca. < 50 m inside cave), interstitial gravel, stn PB1-1B, S. Eberhard & J. Styles, 28 MAR 1994. (Stream width c. 2 m, depth < 0.2 m, flow est. 10 to 20 L/s, Substrate cobbles-gravel, microhabitat (interstitial gravel sampled using Karaman-Chapuis method)).

Damper Cave, streamway, Honey and Cream, stn 4, S. Eberhard & V. Wong, 22 DEC 1991 (Small tributary stream in Damper Cave. Stream width < 1 m, depth , < 0.1 m, flow est. < 1 L/s, substrate pebbles-gravel-silt. Microhabitat small stream, riffle).

Quetzalcoatl Conduit (PB3) entrance 43° 29.20’S, 146° 35.00’E.

Quetzalcoatl Conduit, stn PB2-1C, S. Eberhard & J. Styles, 29 MAR 1994.
Quetzalcoatl Conduit, 30m into cave, stn PB3-1, S. Eberhard & J. Styles, 29 MAR 1994. (Both: stream width 34 m, depth ranging from riffle/runs < 0.1 m to pools > 2 m, substrate limestone bedrock, sediments - cobbles, gravel, flow est. 1530 L/s, but cave floods severely. Collections made in shallow-riffle zones with hard (rocky) substrate).

Quetzalcoatl Conduit, 30m into cave, stn PB3-1C, S. Eberhard & J. Styles, 29 MAR 1994 (Stream width 34 m, depth ranging from riffle/runs < 0.1 m to pools 1.5 m, substrate limestone bedrock, cemented cobbles, in shallow-riffle zones with hard (rocky) substrate. Flow est. 15 30 L/s, but cave floods severely).

Quetzalcoatl Conduit, beyond Pendulum Palace, stn PB3-2, S. Eberhard & J. Styles, 29 MAR 1994 (Stream width 34 m, depth ranging from runs < 0.5 to pools > 2 m, substrate mostly soft sediments, gravel-silt, flow est. 1530 L/s, but cave floods severely).

Quetzalcoatl Conduit, stn PB3-2B, S. Eberhard & J. Styles, 29 MAR 1994 (Stream width 34 m, depth ranging from runs < 0.5 to pools > 2 m, substrate mostly soft sediments, gravel-silt, flow est. 1530 L/s, but cave floods severely).