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Molecular phylogeny and systematics of Australian ‘Irvadiidae’ (Caenogastropoda: Truncatelloidea)

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The family Irvadiidae is found to be polyphyletic in a molecular phylogenetic analysis using a subset of Australian taxa. Taxa previously assigned to *Irvadia* form a monophyletic clade, but *Nozeba topaziaca* clusters with *Auricorona queenslandica* n. gen. and n. sp. in an unnamed family related to Tornidae. *Aenigmula criscionei* n. gen. and n. sp., an irvadiid-like species from the Northern Territory, belongs to another unnamed family related to Caecidae, Calopiidae and Clenchiellidae. A systematic revision of some Australian ‘irvadiids’ raises the subgenera *Fluviocingula* and *Pseudomerelina* to full generic rank and reinstates two former synonyms of *Irvadia* (*Fairbankia*), *Pellamora* and *Wakauria*, as genera. The species formerly identified in Australia as *Irvadia quadrasi* is recognised as three allopatric species; *Irvadia pilbara* n. sp. and the reinstated species *Irvadia goliath* and *Irvadia quadrina*. *Pellamora splendida* n. sp., from Western Australia, is recognised as distinct from *Pellamora australis*, and *Fluviocingula superficialis* n. sp. from *Fluviocingula resima*. *Wakauria fukudai* n. sp. is recorded from central Queensland.

<http://zoobank.org/urn:lsid:zoobank.org:pub:1B9917F6-48B2-4597-85C1-F90BA9093475>

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Introduction

The Irvadiidae are a diverse group of microgastropods from the tropical to temperate Indo-West Pacific region. They occur in environments ranging from the deep ocean to shallow marine and estuarine waters, but are frequently associated with mangrove forests and rocky intertidal to shallow subtidal habitats. Ponder (1984) produced a morphology-based generic revision of Irvadiidae that recognised eight Recent genera (plus five subgenera) and one fossil genus, and subsequently Ponder (1994) described an additional monotypic genus from Hong Kong. The prevailing systematic classification of Irvadiidae divides the family into two groups: *Irvadia* Blanford, 1867, defined by several morphological characters and constituting the majority of the species-level diversity, and a heterogeneous assemblage of the other irvadiid genera (Ponder 1984; Ponder and de Keyser 1998). Starobogatov *et al.* (1989) subsequently removed all genera except *Irvadia* to either Hyalidae or an unnamed family group, although this classification is not generally used.

Most irvadiid species and several genera are known only from their shells, but others have been described in some anatomical detail (Ponder 1984; Fukuda 2000). The only apparent morphological feature that characterises the entire family is a flattened, unsculptured protoconch.

Ponder (1984) also noted that most (but not all) irvadiids lack a pallial or metapodial tentacle, but this situation is not unique in Truncatelloidea (sensu Criscione and Ponder 2012) so does not confirm a common origin for the group. Species in Irvadiidae are generally not well characterised and their taxonomy is sometimes inconsistently applied in the literature. There are several instances where irvadiids are recorded as undescribed or unidentifiable using the present resources (e.g. Robba *et al.* 2003; Japanese Association of Benthology 2012).

The paucity of available information for many irvadiids led Ponder (1984) to remark that his proposed classification was tentative and open to refinement with the benefit of additional evidence. Since that publication, several new irvadiid species have been recognised (Starobogatov *et al.* 1989; Ponder 1994; Fukuda 2000), but no further attempts have been made to address the higher classification of Irvadiidae. Criscione and Ponder (2012) generated the first molecular phylogenetic analysis to include multiple irvadiids, as part of a broader analysis of Risssooidea and Truncatelloidea. They included four irvadiids representing *Nozeba Iredale, 1915* and three subgenera of *Irvadia*. Significantly, Irvadiidae sensu lato (s. l.) was found to be paraphyletic because *Nozeba* was separated from the other species. This preliminary evidence high-

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lighted the need for a more inclusive molecular treatment of Iravadiidae.

There are currently 13 recognised iravadiid species occurring in Australia, representing all five subgenera of *Iravadia* and at least three other genera: *Rissopsis* Garrett, 1873, *Chevallieria* Cossmann, 1888, *Nozeba* and *Liroceratia* Ponder, 1984. Several of these species, such as *Iravadia quadrasi* (Böttger, 1893), have a broad Indo-West Pacific distribution that includes northern Australia but others are endemic to a specific region, such as *Chevallieria australis* Ponder, 1984, which occurs only in southern Australia. Some Australian iravadiids are abundant and widely distributed, particularly in mangrove forests throughout the tropical and subtropical regions.

The primary aim of this study was to conduct a preliminary phylogenetic analysis of available material of Iravadiidae using molecular data, and to reassess the present generic classification using this new line of evidence. A secondary objective was to test the apparent paraphyly of Iravadiidae (Criscione and Ponder 2012). Because iravadiids occur in many specific locations across the Indo-West Pacific and are often rare or have never been collected alive, many taxa could not be included in this study so it does not completely reflect the diversity in the family. Of necessity, this study therefore focuses on resolving the relationships of those Australian iravadiids for which material was available, the systematic redescription of named taxa and the description of new taxa.

Materials and methods

The majority of the material examined during this study was obtained from the collections of the Australian Museum or collected during field work in Queensland (September 2011) and northern Western Australia (June 2012) as part of a larger study of Australian mangrove microgastropods (see also Golding 2014). Material collected alive during fieldwork was photographed crawling in a Petri dish of salt water, using a microscope-mounted camera. Pigmentation and foot/tentacle morphology were observed and are included in descriptions (where available). Specimens were preserved for either molecular (95%–100% ethanol) or morphological (10% saltwater formalin or 70% ethanol) examination.

Penis morphology was observed and photographed (where possible) on living animals and examined on preserved specimens using a stereomicroscope with camera lucida. Radulae were removed from dissected buccal masses by dissolution overnight in a warmed solution of sodium hydroxide. Shells, radulae and opercula were cleaned in a sonic water bath, mounted on stubs and thinly coated with gold for examination by scanning electron microscopy (performed by Sue Lindsay, Microscopy and Microanalysis Laboratory, Australian Museum) using a Zeiss Evo LS-15 machine. Shell measurements were

made using a calibrated camera lucida, with whorl counts rounded to the nearest quarter whorl.

For molecular sampling, either entire animals or samples of foot tissue were processed using a DNeasy kit (Qiagen, Inc., Hilden, Germany) and QiaCube[®] robot to extract genomic DNA. Gene fragments from cytochrome oxidase subunit I (COI) and 16S genes from the mitochondrial genome and 28S from the nuclear genome were amplified using polymerase chain reactions (PCR). The PCR were performed in 25- μ l volumes containing 1 \times PCR buffer, 200 mM each dNTP, 2.0 mM MgCl₂, 0.5 mM forward and reverse primers, 1.25 units *Taq* polymerase, and approximately 50 ng DNA. Amplification followed a standard protocol with 35 cycles of 94°C for 1 minute, and primer-specific annealing conditions (see Golding 2014 for cycle conditions). Post-PCR products were purified using ExoSAP-IT proteinase solution (GE Healthcare, Pittsburgh, PA, USA) and sequenced in both directions by Macrogen Inc. (Seoul, Korea).

Sequences were compared to their electropherogram to correct misreads and compiled into contigs using BioEdit v7.0.9 (Hall 1999). All sequences were deposited in GenBank and their accession numbers are provided in Table 2 (KC439750–KC439959). Ribosomal sequences were aligned using the online MAFFT v.6 server (Katoh *et al.* 2002) with the E-INS-i option (Katoh *et al.* 2005) implemented for the 16S data set and Q-INS-i (Katoh and Toh 2008) for the 28S data set. Sequences of COI translated using the invertebrate mitochondrial code were unambiguously aligned by amino acid sequence. Data sets were compiled using Mesquite v2.75 (Maddison and Maddison 2011). Sequence divergence was estimated by uncorrected pairwise distances computed within and between taxa using MEGA5 (Tamura *et al.* 2011).

A subset of the Australian iravadiid fauna was sampled, with a focus on mangrove-affiliated species. Truly marine and subtidal taxa were not included due to the lack of suitable material. Hence, the genera known to occur in Australia, *Nozeba* and all subgenera of *Iravadia* except *Iravadia (Pseudonoba)*, were represented by one or more taxa in the molecular analysis, but *Chevallieria*, *Rissopsis* and *Liroceratia* were not sampled (Table 1) (Ponder 1984). Several new and unassigned taxa were collected and have been included in the molecular analysis (systematic descriptions are also provided). 16S and 28S sequence data from non-iravadiid taxa were sourced from Criscione and Ponder (2012) and additional COI sequences were produced during this study (see Golding 2014: Table 2). Details for the source of non-iravadiid sequences are provided in Table 1.

Two molecular data sets were constructed to test the monophyly of Iravadiidae and its relationship to other families in Truncatelloidea and also to test the internal relationships and molecular diversity of Australian Iravadiidae.

Table 1. Identity, location/source, registration and GenBank accession numbers for specimens included in the molecular analyses.

Family	Species	Locality/Source	AM reg.	COI	16S	28S
Iravadiidae	<i>Iravadia goliath</i> (Laseron, 1956)	River Heads, QLD	C.470845	KC439750	KC439872	KC439931
Iravadiidae	<i>I. goliath</i>	Dingo Beach, QLD	C.470916	KC439751	KC439873	KC439932
Iravadiidae	<i>I. goliath</i>	Magnetic Isl., QLD	C.470860	KC439752	KC439874	KC439933
Iravadiidae	<i>I. goliath</i>	Finch Bay, Cooktown, QLD	C.470872	KC439753	KC439875	–
Iravadiidae	<i>Iravadia quadrina</i> (Laseron, 1956)	Karumba, QLD	C.470896	KC439754	KC439876	–
Iravadiidae	<i>I. quadrina</i>	East Woody Beach, Arnhem Land, NT	C.175290	KC439755-6	KC439877-8	–
Iravadiidae	<i>I. quadrina</i>	Rapid Cr., Darwin, NT	C.475886	KC439757	KC439879	KC439934
Iravadiidae	<i>I. quadrina</i>	Dampier Creek, Broome, WA	C.476001	KC439758-9	KC439880-1	KC439935
Iravadiidae	<i>Iravadia pilbara</i> n. sp.	Four Mile Cr., Port Hedland, WA	C.476006	KC439760-1	KC439882-3	KC439936
Iravadiidae	<i>I. pilbara</i>	Nickol Bay, Karratha, WA	C.476027	KC439762	KC439884	KC439937
Iravadiidae	<i>Iravadia</i> cf. <i>capitata</i> (Laseron, 1956)	Horseshoe Bay, Bowen, QLD	C.470914	KC439763	KC439885	KC439938
Iravadiidae	<i>Wakauraiia fukudai</i> n. sp.	Tin Can Bay, QLD	C.426339	KC439764	KC439886	–
Iravadiidae	<i>W. fukudai</i>	Tannum Sands, QLD	C.470938	KC439765	KC439887	KC439939
Iravadiidae	<i>W. fukudai</i>	Finch Bay, Cooktown, QLD	C.470873	KC439766	KC439888	KC439940
Iravadiidae	<i>Pseudomerelina</i> cf. <i>mahimensis</i> (Melville, 1893)	Campwin Beach, QLD	C.470926	KC439767	KC439889	KC439941
Iravadiidae	<i>P.</i> cf. <i>mahimensis</i>	Rowes Beach, Townsville, QLD	C.470857	KC439768	KC439890	–
Iravadiidae	<i>P.</i> cf. <i>mahimensis</i>	Wallaby Isl., Weipa, QLD	C.470875	KC439769	KC439891	–
Iravadiidae	<i>P.</i> cf. <i>mahimensis</i>	Mapoon, QLD	C.470891	KC439770-1	KC439892-3	KC439942
Iravadiidae	<i>P.</i> cf. <i>mahimensis</i>	Karumba, QLD	C.470898	KC439772	KC439894	KC439943
Iravadiidae	<i>P.</i> cf. <i>mahimensis</i>	Nickol Bay, Karratha, WA	C.476019	KC439773	KC439895	–
Iravadiidae	<i>Pellamora australis</i> (Hedley, 1901)	Turkey Beach, QLD	C.470945	KC439774	KC439896	KC439944
Iravadiidae	<i>P. australis</i>	Magnetic Isl., QLD	C.470867	KC439775	KC439897	–
Iravadiidae	<i>P. australis</i>	Rapid Cr., Darwin, NT	C.475760	KC439776	KC439898	KC439945
Iravadiidae	<i>Pellamora splendida</i> n. sp.	Dampier Cr., Broome, WA	C.476000	KC439777	KC439899	KC439946
Iravadiidae	<i>Fluviocingula resima</i> (Laseron, 1956)	Karumba, QLD	C.470897	KC439778	KC439900	KC439947
Iravadiidae	<i>F. resima</i>	Rapid Cr., Darwin, NT	C.475759	KC439779	KC439901	KC439948
Iravadiidae	<i>Fluviocingula superficialis</i> n. sp.	Four Mile Cr., Port Hedland, WA	C.476013	KC439780-1	KC439902-3	KC439949-50
Clade A	<i>Nozeba topaziaca</i> (Hedley, 1908)	Woy Woy, NSW	C.475870	KC439782	KC439904	KC439951
Clade A	<i>N. topaziaca</i>	Salamander Bay, Port Stephens, NSW	C.472141	KC439783	KC439905	–
Clade A	<i>N. topaziaca</i>	Tin Can Bay, QLD	C.470999	KC439784	KC439906	KC439952
Clade A	<i>Auricorona queenslandica</i> n. gen. & n. sp.	Tin Can Bay, QLD	C.470951	KC439785	KC439907	KC439953
Clade A	<i>A. queenslandica</i>	Turkey Beach, QLD	C.470944	KC439786-7	KC439908-9	KC439954
?	<i>Aenigmula criscionei</i> n. gen. & n. sp.	Rapid Cr., Darwin, NT	C.475887	KC439788-9	KC439910-1	KC439955-6
Stenothyridae	<i>Stenothyra australis</i> Hedley, 1901	Magazine Cr., Bowen, QLD	C.470905	KC439692	KC439814	KC439915
Calopiidae	<i>Calopia imitata</i> Ponder, 1999	Woy Woy, NSW	C.475871	KC439790	KC439912	KC439957
Calopiidae	<i>Calopia minutissima</i> Ponder, 1999	Wallaby Isl., Weipa, QLD	C.470876	KC439791	KC439913	KC439958

(Continued)

Table 1. Continued.

Family	Species	Locality/Source	AM reg.	COI	16S	28S
Calopiidae	<i>Calopia laseroni</i> Ponder, 1999	Roebuck Bay, Broome, WA	C.475990	KC439792	KC439914	KC439959
Anabathridae	<i>Anabathron contabulatum</i> (Frauenfeld, 1867)	GenBank/AM tissue collections	C.466922	KC439793	KC109937	KC109989
Anabathridae	<i>Pisinna punctulum</i> (Philippi, 1836)	GenBank/AM tissue collections	C.463767	KC439794	KC109968	KC110020
Anabathridae	<i>Badepigrus pupoideus</i> (H. Adams, 1865)	GenBank/AM tissue collections	C.475761	KC439795	KC109942	KC109994
Anabathridae	<i>Nodulus contortus</i> (Jeffreys, 1856)	GenBank/AM tissue collections	C.463766	KC439796	KC109966	KC110018
Assimineidae	' <i>Assimineia</i> ' <i>capensis</i> (Sowerby, 1892)	GenBank/AM tissue collections	C.463732	KC439797	KC109939	KC109991
Falsicingulidae	<i>Falsicingula mundana</i> Yokoyama, 1926	GenBank/AM tissue collections	C.466899	KC439798	KC109957	KC110009
Truncatellidae	<i>Truncatella subcylindrica</i> (Linnaeus, 1767)	GenBank/AM tissue collections	C.463886	KC439799	KC109982	KC110035
Pomatiopsidae	<i>Coxiella striata</i> (Reeve, 1842)	GenBank/AM tissue collections	C.421184	KC439800	KC109948	KC110000
Hydrobiidae	<i>Hydrobia acuta</i> (Draparnaud, 1805)	GenBank/AM tissue collections	C.463786	KC439801	KC109959	KC110011
Tateidae	<i>Tatea rufilabris</i> (A. Adams, 1862)	GenBank/AM tissue collections	C.466927	KC439802	KC109980	KC110033
Clenchiellidae	<i>Clenchiella minutissima</i> (Wattlebled, 1884)	GenBank/AM tissue collections	C.475762	KC439803	KC109947	KC109999
Clenchiellidae	<i>Clenchiellid</i> sp.	GenBank/AM tissue collections	C.422679	KC439804	KC109946	KC109998
Caecidae	<i>Caecum trachea</i> (Montagu, 1803)	GenBank/AM tissue collections	C.463777	KC439805	KC109945	KC109997
Tornidae	<i>Pseudoliotia micans</i> (Adams A., 1850)	GenBank/AM tissue collections	C.466900	KC439806	KC109971	KC11002
Tornidae	<i>Elachorbis subtatei</i> (Suter, 1907)	GenBank/AM tissue collections	C.466923	KC439807	KC109953	KC110005
Tornidae	<i>Scrupus</i> sp.	GenBank/AM tissue collections	C.466910	KC439808	KC109974	KC110027
Rissoidae	<i>Rissoina fasciata</i> A. Adams, 1851	GenBank/AM tissue collections	C.466913	KC439809	KC109972	KC110025

Notes: Sample locations are within Australia unless otherwise stated. Sequences generated during this project are in bold, all other sequences were produced by [Criscione and Ponder \(2012\)](#). Taxa described or revised in this manuscript are named accordingly.

- (A) Concatenated COI (excluding third codon positions), 16S and 28S sequences with 100% coverage. Composed of 30 taxa, each represented by a single individual: 13 'Iravadiidae', 16 other truncatelloids and outgroup *Rissoina fasciata* (Rissoidae). Total of 2524 base pairs (bp), consisting of: 446 bp COI, 566 bp 16S, 1512 bp 28S.
- (B) Concatenated COI (including third codon positions), 16S and 28S sequences with 100% coverage of the mitochondrial genes but only partial coverage of 28S (35 of 50 individuals). Composed of 13 'Iravadiidae' (mostly represented by multiple individuals), representatives of several closely related families (three Calopiidae, two Clenchiellidae, two Tornidae, one Caecidae) ([Criscione and Ponder 2012](#)) and outgroups *Nodulus contortus* ('Anabathridae') and *Tatea rufilabris* (Tateidae).

Total of 2621 bp, consisting of: 669 bp COI, 565 bp 16S, 1387 bp 28S.

Maximum Likelihood (ML) and Bayesian Inference (BI) were used to construct phylogenetic trees from both data sets. ML analyses were performed using RAxML v7.3.2 ([Stamatakis 2006](#)) implemented in raxmlGUI v1.2 ([Silvestro and Michalak 2011](#)) with 1000 'thorough' bootstrap repetitions. Data sets were partitioned by gene and the GTRGAMMA model was implemented. BI analyses were performed using MrBayes v3.1.2 ([Ronquist and Huelsenbeck 2003](#)). Bayesian posterior probability support was estimated by running four Markov chains (10 million generations each, with trees sampled each thousand generations). The first 25% of trees were conservatively rejected as burn-in, and stationarity was confirmed by examination of the log likelihood plot using Tracer

(Rambaut and Drummond 2007). A summary consensus tree with support indices was generated by MrBayes. Data sets were partitioned by gene, with the GTR + G + I model of sequence evolution selected for both data sets by MEGA5. Trees were visualised using FigTree v1.3.1 and rooted using the outgroup. Support for individual clades was considered high for Bayesian probabilities > 95% and bootstraps > 80%, and moderate for Bayesian probabilities 90%–95% and bootstraps 70%–80%. Nodes with lower support values were not considered significant.

Systematic descriptions have been provided for the Australian taxa included in the molecular analysis. Many other taxa assigned to Iravadiidae are represented in the dry collections of the Australian Museum. However, since those taxa were addressed by Ponder (1984) and no new information has been gathered, they are not redescribed here. Unless otherwise stated, the location of type material and materials examined is Australia. Shell measurements were made using a calibrated camera lucida attached to a dissecting microscope or directly from scanning electron microscope images of entire shells. Materials examined have been summarised here, but full details are provided in a supplementary file.

Abbreviations

States of Australia: NSW—New South Wales; NT—Northern Territory; QLD—Queensland; VIC—Victoria; WA—Western Australia.

Institutions: AMS—Australian Museum, Sydney; NHMUK—Natural History Museum, London, UK; NTM—Northern Territory Museum; QM—Queensland Museum; WAM—Western Australian Museum.

Shell dimensions: SL—shell length; SD—diameter of last whorl; AL—aperture length; AW—aperture width; PWC—protoconch whorl count; SpP—number of spiral rows of pits on last whorl; SpR—number of spiral ribs on last whorl; SpRN—number of nodules on strongest spiral rib on last whorl (excluding varix); TWC—teleoconch whorl count.

Results

Sequence divergence

Mean uncorrected pairwise distances (p-distances) of COI between individuals of each species examined in this study (i.e., within-species distances) ranged from 0.10% ($n = 3$, *Iravadia pilbara* n. sp.) to 2.42% ($n = 7$, *Pseudomerelina* cf. *mahimensis*) (Table 2). COI sequence divergence between pairs of species from different genera (as recognised in the Systematics section, below) was > 17.52% in every instance. The p-distance between the species pair in *Pellamora* was 12.46% and in *Fluviocingula* it was 15.62%. The three species comprising the taxon formerly recognised in Australia as *Iravadia quadrasi* (*Iravadia*

goliath, *Iravadia quadrina* and *I. pilbara* n. sp.) were separated by p-distances of between 8.51% and 18.11%. Sequence divergence from the most closely related species based on molecular phylogenies is given in the Remarks for each species in the Systematics section below.

Molecular phylogenies

The consensus trees produced by BI and ML analysis were very similar, and the few differences that were encountered are outlined in the following section. Only the BI summary trees are shown here, labelled with Bayesian posterior probabilities and bootstrap support values generated by ML analysis (Figs 1, 2).

The topology of the trees from BI and ML analyses of relationships within Truncatelloidea (including single representatives of all species in this study that were provisionally assigned to Iravadiidae) differed slightly (Fig. 1). The sister clade to *Fluviocingula* (lacking significant support) was *Pellamora* in the BI analysis, but *Pseudomerelina* in the ML analysis. Both analyses found strong evidence of paraphyletic structure in Iravadiidae. Three distinct clades were resolved: (1) ‘Clade A’, comprising *Nozeba topazica* and another new species (*Auricorona queenslandica* n. gen. and n. sp., described below); (2) the unclassified genus *Aenigmula* n. gen., with a single new species (*Aenigmula criscionei* n. gen. and n. sp., described below); (3) Iravadiidae s. str., containing the remaining iravadiid taxa. Each of these three groups was supported by very high support indices from both ML and BI analyses. ‘Clade A’ was found to be sister to Tornidae and *Aenigmula* was basal to a clade containing Clenchiellidae and Calopiidae, and this trio of families was sister to Caecidae. The clade comprising Iravadiidae, ‘Clade A’, *Aenigmula*, Tornidae, Caecidae, Clenchiellidae and Calopiidae received high support indices and was also characterised by the deletion of a single codon from the COI gene (Fig. 2). This deletion was found in all taxa in this group but was not observed in any other truncatelloid sequences. No clear sister taxon to this group was identified.

The phylogenetic analysis of a restricted subset of species, including multiple representatives of most ‘iravadiids’ and just two outgroup taxa, produced essentially the same topology (Fig. 2). Two differences were found between ML and BI analyses of this data set. (1) Three species formerly assigned to *Iravadia quadrasi* (*I. quadrina*, *I. goliath* and *I. pilbara* n. sp.) were sister to *Wakauraiia fukudai* n. sp. and *Iravadia* cf. *capitata* in the ML analysis (lacking significant support), but were more closely related to *Fluviocingula*, *Pellamora* and *Pseudomerelina* in the BI analysis (also lacking significant support). (2) The sister clade to *Fluviocingula* (lacking significant support) was *Pellamora* in the BI analysis, but *Pseudomerelina* in the ML analysis. Each multi-taxon genus recognised in the Systematic section

Table 2. Cytochrome oxidase subunit I sequence divergence (including third codon base positions) between species (sample size *n*) represented by mean uncorrected pairwise distances (%).

	<i>n</i>	<i>I. goliath</i>	<i>I. quadrina</i>	<i>I. pilbara</i>	<i>I. cf. capitata</i>	<i>W. fukudai</i>	<i>P. cf. mahimensis</i>	<i>P. australis</i>	<i>P. splendida</i>	<i>F. resima</i>	<i>F. superficialis</i>	<i>N. topaziaca</i>	<i>A. queenslandica</i>	<i>A. criscionei</i>
<i>Iravadia goliath</i>	4	0.30												
<i>Iravadia quadrina</i>	6	18.11	0.52											
<i>Iravadia pilbara</i> n. sp.	3	17.08	8.51	0.10										
<i>Iravadia cf. capitata</i>	1	24.66	22.05	23.02	—									
<i>Wakauria fukudai</i> n. sp.	3	24.79	23.37	23.02	24.58	0.80								
<i>Pseudomerelina cf. mahimensis</i>	7	23.40	19.12	20.80	21.06	23.90	2.42							
<i>Pellamora australis</i>	3	21.05	17.52	19.32	21.32	24.49	18.40	2.20						
<i>Pellamora splendida</i> n. sp.	1	21.25	20.95	20.77	24.47	25.13	21.15	12.46	—					
<i>Fluviocingula resima</i>	2	20.76	18.77	19.95	21.40	22.42	20.11	18.24	18.77	0.60				
<i>Fluviocingula superficialis</i> n. sp.	2	23.42	19.82	21.40	22.15	24.05	18.95	18.67	19.07	15.62	1.80			
<i>Nozeba topaziaca</i>	3	28.07	26.88	28.03	25.98	29.66	26.29	27.51	28.73	25.18	27.20	2.00		
<i>Auricorona queenslandica</i> n. gen. & n. sp.	3	28.59	27.13	26.28	26.68	29.13	26.01	27.81	28.98	27.03	29.66	23.77	0.90	
<i>Aenigmula criscionei</i> n. gen. & n. sp.	2	28.42	26.43	27.28	27.48	27.48	25.64	26.05	26.50	22.82	24.78	26.93	27.65	1.20

Notes: Values in bold are mean p-distance within each species. Taxa described or revised in this manuscript are named accordingly.

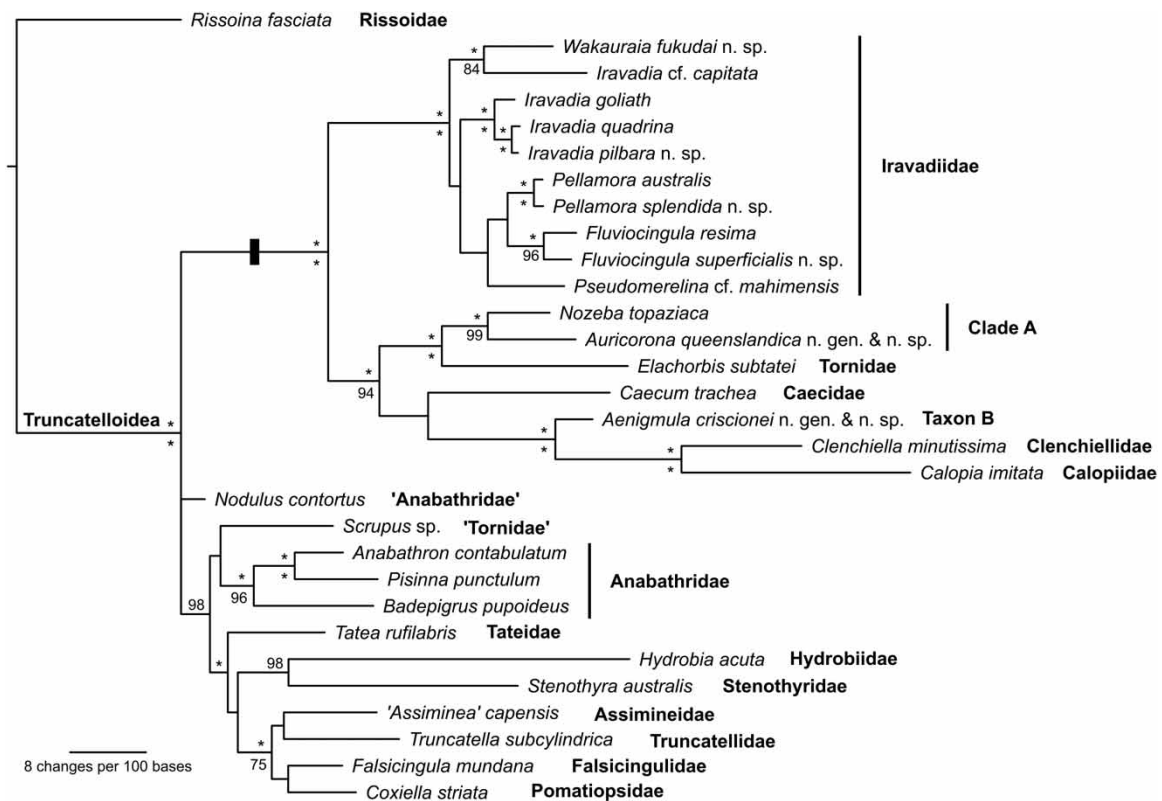


Figure 1. Summary tree from Bayesian analysis of concatenated cytochrome oxidase subunit I (COI; excluding third codon position bases), 16S and 28S sequences (10 million generations, trees sampled every 1000 generations). Support indices are Bayesian inference posterior probability (above nodes, > 90%) and maximum likelihood bootstraps (below nodes, > 70%); asterisks indicate a support value of 100%. Family and higher level names are in bold. Taxa described in this manuscript are named accordingly. Black bar indicates codon deletion from COI gene.

below was highly supported and monophyletic, except *Iravadia* in which *I. cf. capitata* was not sister to the other three species assigned to *Iravadia*. Species represented by more than one individual (all except *I. cf. capitata*) were reciprocally monophyletic with strong support by either bootstrap or Bayesian posterior probability indices or both.

Within *Iravadiidae* sensu stricto (s. str.), *Wakauria* + *I. cf. capitata* formed the most basal clade. The three species formerly recognised in Australia as *I. quadrasi* clustered together, although the relationships between this species group and other iravadiids were poorly supported and inconsistent between analysis methodologies. *Pseudomerelina*, *Fluviocingula* and *Pellamora* formed the crown group of *Iravadiidae* s. str., but the relationships between these genera remain uncertain.

Systematics

Gastropoda

Caenogastropoda

Truncatelloidea Gray, 1840

Iravadiidae Thiele, 1928

Iravadiinae Thiele 1928: 355. Type genus (original designation): *Iravadia* Blanford, 1867 [recognised as

Iravadiidae by Volkova and Pchelintsev (in Pchelintsev and Korobkov 1960): 144].

Fairbankiinae Thiele 1928: 354. Type genus (original designation): *Fairbankia* Blanford, 1868 [recognised as *Fairbankiidae* by Starobogatov 1970: 26].

Pseudomereliniinae Starobogatov, 1989 in Starobogatov *et al.* (1989): 36. Type genus (original designation): *Pseudomerelina* Ponder, 1984.

Remarks

Brandt (1968), as First Reviser, gave *Iravadiinae* precedence over *Fairbankiinae*. Ponder (1984) supported this decision, and synonymised the invalid name *Hyalidae* (a homonym of the amphipod family *Hyalidae* Bulycheva, 1957) with *Iravadiidae*. Starobogatov *et al.* (1989) reversed that decision, placing *Hyalia* H. & A. Adams, 1852 and *Nozeba* in *Hyalidae*, and removing *Rissopsis*, *Ceratia*, *Liroceratia* and *Aliceratia* Ponder, 1984 to a separate unknown family. *Hyalia* is characterised by a suite of characters (including a paucispiral operculum) that are more typical of 'Clade A' or *Aenigmula*, rather than *Iravadiidae* s. str., so *Hyalidae* is not here considered

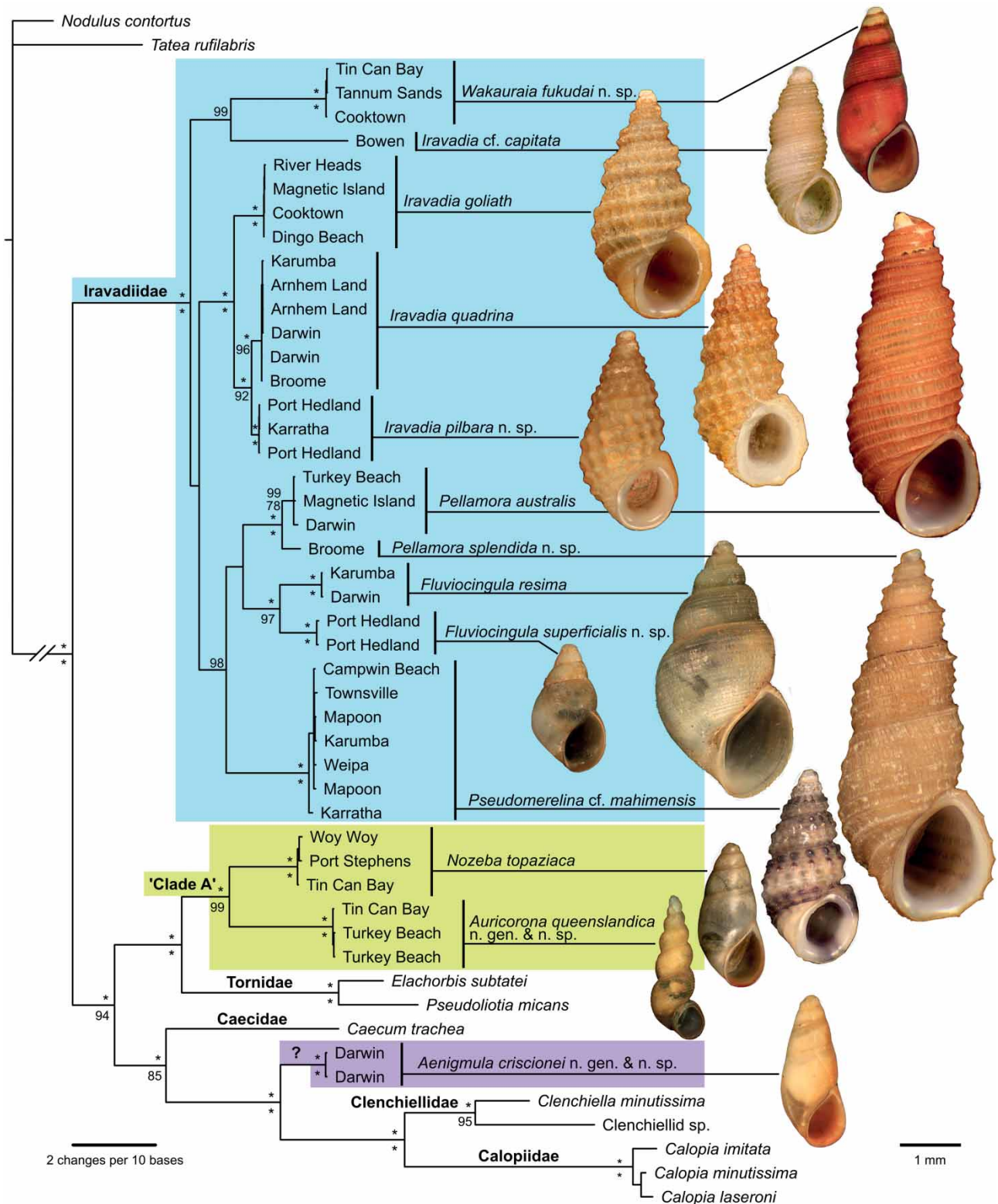


Figure 2. Summary tree from Bayesian analysis of concatenated cytochrome oxidase subunit I (COI; including third codon position bases), 16S and 28S sequences (10 million generations, trees sampled every 1000 generations). Support indices are Bayesian inference posterior probability (above nodes, > 90%) and maximum likelihood bootstraps (below nodes, > 70%); asterisks indicate a support value of 100%. Taxa described or revised in this manuscript are named accordingly, with locality data given for each sample. Family names are in bold and family-level groups examined here are shaded. Shell images are all to the same scale.

to be a synonym of Iravadiidae. Pseudomereliniinae was recognised as a synonym of Iravadiidae by Bouchet and Rocroi (2005).

Ponder (1984) recognised eight Recent genera (*Iravadia*, *Rissopsis*, *Chevallieria*, *Acliceratia*, *Hyalia*, *Ceratia*, *Liroceratia* and *Nozeba*) and one fossil genus (*Rhombostoma* Seguenza, 1876) in Iravadiidae. The genus *Lantauia* Ponder, 1994 was additionally described. The present study examines species of only two of these genera (*Iravadia* and *Nozeba*) and finds them to belong to different branches of the truncatelloid tree, preventing their unification in a single family. *Nozeba* has been removed from Iravadiidae (see 'Clade A', below). With the available material the affiliation of the unsampled genera to *Iravadia* cannot be tested using molecular data at this time. The inclusion of *Lantauia* in Iravadiidae is supported by opercular characters but the others must be regarded as tentative at best as their operculum is either paucispiral or unknown. On the basis of the information on these genera presented by Ponder (1984), they show more similarity to 'Clade A' or *Aenigmula* n. gen. than to *Iravadia* s. l., and therefore probably do not belong in Iravadiidae s. str. A molecular study including taxa from these ambiguous groups is sorely needed to resolve the true composition of Iravadiidae.

The taxon sampling in the molecular analysis and systematic sections of this study is too limited to provide a comprehensive diagnosis of Iravadiidae s. str. Based on the available information, it seems likely that Iravadiidae should be restricted to the group of taxa possessing an operculum with a nucleus on the umbilical margin (i.e., *Iravadia* s. l.) and an initially planar protoconch, excluding those with a paucispiral operculum and domed or tall protoconch. This separation has been validated for *Nozeba*, *Auricorona* n. gen. and *Aenigmula* n. gen. (see below), but not for *Lantauia*, *Rissopsis*, *Chevallieria*, *Acliceratia*, *Hyalia*, *Ceratia* or *Liroceratia*.

***Iravadia* Blanford 1867**

Iravadia Blanford 1867: 56–58. Type species (original designation): *Iravadia ornata* Blanford, 1867; Recent, India.

Remarks

Ponder (1984) recognised five subgenera within *Iravadia* s.l.; *Iravadia*, *Pseudomerelina*, *Fluviocingula*, *Fairbankia* and *Pseudonoba*. No species confirmed as belonging to *Iravadia* (*Fairbankia*) or *Iravadia* (*Pseudonoba*) was included in this study, so no definitive conclusions can be drawn on the status of those 'subgenera'. However, the concept of *Iravadia* has been substantially modified by the recognition in this study of *Fluviocingula* and *Pseudomerelina* as full genera, as well as the reinstatement of *Pellamora* Iredale, 1943 and *Wakauraia* Kuroda & Habe,

1954 for some taxa previously assigned to *Iravadia* (*Fairbankia*). It therefore seems likely that *Pseudonoba* and *Fairbankia* will also prove to be distinct genera.

Only four taxa in this study were retained in *Iravadia* s. str., three forming a group of species formerly identified in Australia as *Iravadia quadrasi* and one provisionally classified as *I.* cf. *capitata*. Other taxa currently assigned to *Iravadia* were not examined, including the type of the genus, *I. ornata*. Molecular phylogenetic analysis of Iravadiidae shows that the four sampled species of *Iravadia* do not form a monophyletic group, due to the nested position of *Wakauraia fukudai* n. sp. within the clade (sister to *I.* cf. *capitata*). On the basis of branch lengths and shell shape, it is likely that *I.* cf. *capitata* belongs to a distinct, unnamed genus (including similar taxa such as *Iravadia carpentariensis*, and perhaps some species currently assigned to *Pseudonoba*). At the present time, it is practical to retain *Iravadia* as a non-monophyletic group until further progress is made. No generic description is provided here for *Iravadia*, because it appears to be paraphyletic and because so few of its constituent taxa, including the type species, have been studied in detail.

***Iravadia goliath* (Laseron, 1956)**

Merelina goliath Laseron 1956: 436, fig. 137.

?*Merelina reversa* Laseron 1956: 435, fig. 134 [possible synonym].

Iravadia (*Iravadia*) *quadrasi* Ponder 1984 (not of Böttger, 1893), in part: 35, figs 4, 8B, 10A–E, 10C.

Material examined

Holotype of *Merelina goliath*: Hervey Bay, Queensland, 25°06' S, 152°49' E, coll. J. Laseron, 1955 (AMS C.102423). *Paratypes* of *Merelina goliath*. Hervey Bay, Queensland, 25°06' S, 152°49' E, coll. J. Laseron, 1955 (AMS C.109343, 7). Port Curtis, Queensland, 23°55' S, 151°23' E, C. Hedley, c.1900 (AMS C.061465, 5). *Holotype* of *Merelina reversa*. Bowen, Queensland, 20°01'00"S, 148°15'00"E, coll. J. Laseron, July 1952 (AMS C.102421). *Paratypes* of *Merelina reversa*. Bowen, Queensland, 20°01'00"S, 148°15'00"E, coll. J. Laseron, July 1952 (AMS C.109344, 8).

Other material. Twenty-three wet lots and 34 dry lots from Queensland between Moreton Bay and Cooktown. See supplementary data for full list of material examined.

Redescription

Shell (Figs 2, 3A–E). Elongate-conical, solid; moderately convex whorl profile with shallowly impressed suture; non-umbilicate; up to 6½ whorls including protoconch, SL = 3.05 – 4.86 mm, SD = 1.59 – 2.65 mm (Table 3). Pale beige to brown, often discoloured orange or black by

deposits; velvety periostracum corrugated by numerous fine spiral fringes, with longer fringing hairs on apices of nodules. Sculpture of strong spiral ribs (6 on last whorl, including weak subsutural and umbilical ribs) intersected by numerous axial ribs (14–18 on last whorl) to produce rounded nodules. Aperture oval, anterior margin rounded, posterior margin weakly angled; outer lip prosocline; external varix well developed.

Protoconch (Fig. 3E). First $1\frac{1}{2}$ whorls planar, then descending; $1\frac{3}{4}$ whorls total. Smooth or occasionally with very fine spiral grooves near transition to teleoconch; transitional varix weakly developed.

Operculum (Fig. 4B). Oval; growth striae concentric; nucleus positioned above midpoint on rounded umbilical margin. Exterior surface with coarse growth striae; interior surface with groove and thickened ridge along umbilical margin, and two low radial ridges emerging from nucleus.

Radula ($n = 3$) (Figs 4B, 5A). Central tooth 6 – 9 + 1 + 6 – 9/2 + 2; central cusp large, secondary cusps diminishing outwardly; paired basal denticles small, positioned just below cutting edge; lateral margins straight. Lateral teeth 3 + 1 + 4 – 5. Marginal teeth with subequal cusps; inner marginal teeth with ~20 cusps; outer marginal teeth with ~15 cusps.

External morphology and colouration in life (Fig. 4C). Head-foot cream or white; grey pigment on sides of neck and foot and dorsal surface of head, cream to yellow speckles between and behind eyes; snout either solid black (except for lips) or black on ventral and lateral surfaces with yellow and black patches on dorsal surface. Dorsal surface of propodium with diffuse, grey lateral stripes; posterior margin of foot pointed, lacking metapodial tentacle. Cephalic tentacles white to yellow with broad black bands at midpoint and $\frac{3}{4}$ length. Pallial tentacles absent.

Penis (Fig. 6A). Cylindrical with broad tip; duct opening on inner edge below inflated, transverse, glandular bulge on tip. Speckled white, with black flecks on inner margin.

Distribution (Fig. 7A)

Common in mangrove forests on the east coast of Australia from Brisbane northward at least as far as Cooktown, but not occurring west of the tip of Cape York.

Remarks

Irvadia quadrasi is generally considered to have a very broad Indo-West Pacific distribution including at least the Philippines, Thailand, Australia and Japan (Brandt 1968; Ponder 1984; Robba *et al.* 2003; Japanese Association of Benthology 2012). The discovery here of three genetically distinct Australian taxa strongly suggests that the use of the name *I. quadrasi* may not be applicable to any

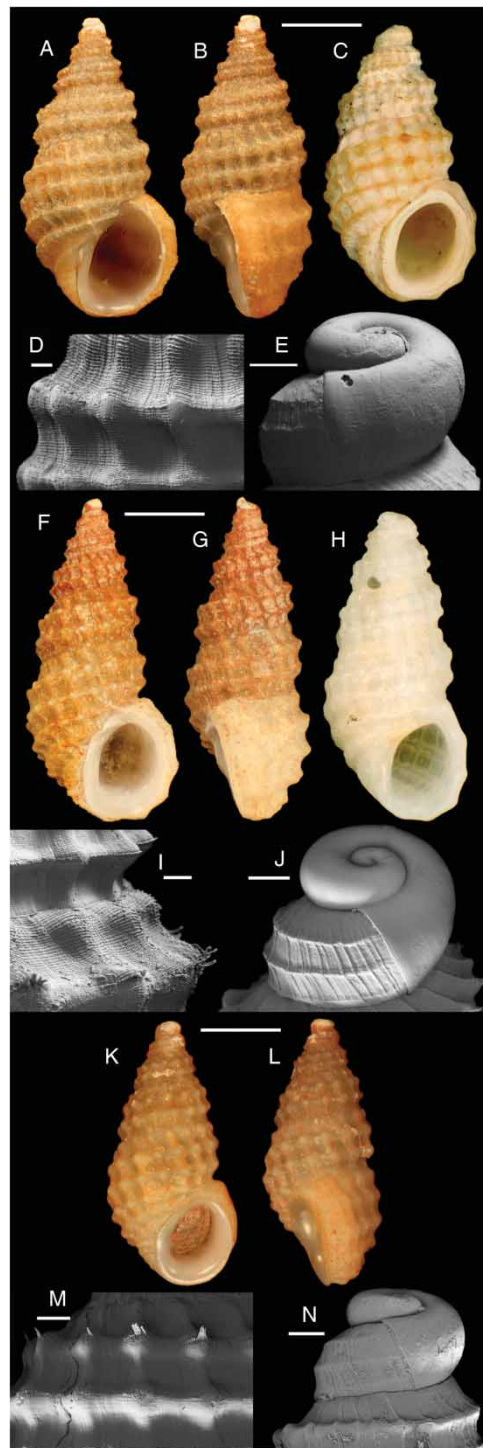


Figure 3. Cryptic species formerly recognised as 'Irvadia quadrasi'. A–E, *Irvadia goliath* (Laseron, 1956). A, B, Representative specimen, Tannum Sands, QLD, AMS C.470936; C, *Merelina goliath* Laseron, 1956 holotype, Hervey Bay, QLD, AMS C.102423; D, protoconch, Turkey Beach, QLD, AMS C.470941; E, shell sculpture with periostracum, AMS C.470941. F–J, *Irvadia quadrina* (Laseron, 1956). F, G, Representative specimen, Weipa, QLD, AMS C.470888; H, *Planapexia quadrina* holotype, Darwin, NT, AMS C.102399; I, protoconch, Broome, WA, AMS C.476001; J, shell sculpture with periostracum, Karumba, QLD, AMS C.470896. K–N, *Irvadia pilbara* n. sp. K, L, Holotype, Karratha, WA, WAM S.82651; M, protoconch, Port Hedland, WA, AMS C.470614; N, shell sculpture with periostracum, AMS C.470614. Scale bars: A–C, F–H, K, L, 1 mm; D, E, I, J, M, N, 100 µm.

Table 3. Shell measurements of type and other specimens of *Iravadia goliath*, *Iravadia quadrina* and *Iravadia pilbara* n. sp.

Registration no.	Status	SL (mm)	SD (mm)	AL (mm)	AW (mm)	TWC	SpR	SpRN	PWC
<i>I. goliath</i>									
AMS C.102423	Ht	4.06	2.23	1.51	1.45	4 ¹ / ₄	6	17	—
AMS C.470872	—	4.78	2.65	1.84	1.73	5	6	17	—
AMS C.470916	—	3.51	1.89	1.28	1.15	4 ¹ / ₄	6	18	—
AMS C.470916	—	3.05	1.59	1.16	0.98	4 ¹ / ₂	6	17	—
AMS C.470936	—	4.19	2.26	1.51	1.19	4 ³ / ₄	6	17	1 ³ / ₄
AMS C.470936	—	4.54	2.46	1.57	1.41	4 ³ / ₄	6	17	1 ³ / ₄
AMS C.470970	—	4.86	2.59	1.62	1.38	5	6	14	—
AMS C.470970	—	4.11	2.08	1.35	1.11	4 ¹ / ₂	6	17	—
Average or range (n = 8)	—	4.14	2.22	1.48	1.30	4 ¹ / ₄ –5	6	14–18	1 ³ / ₄
<i>I. quadrina</i>									
AMS C.102399	Ht	5.14	2.46	1.86	1.35	4 ¹ / ₂	6	20	—
AMS C.470888	—	4.62	2.24	1.51	1.22	4 ³ / ₄	6	19	—
AMS C.470888	—	4.81	2.41	1.62	1.43	4 ¹ / ₄	6	16	—
AMS C.470896	—	5.78	2.70	1.95	1.54	5 ¹ / ₂	6	17	—
AMS C.470896	—	6.28	2.93	2.21	1.66	5 ¹ / ₄	6	17	—
AMS C.476001	—	5.54	2.49	1.84	1.54	5 ¹ / ₂	6	17	1 ³ / ₄
AMS C.476001	—	5.70	2.54	1.89	1.49	5 ¹ / ₂	6	15	1 ³ / ₄
Average or range (n = 7)	—	5.41	2.54	1.84	1.46	4 ¹ / ₄ –5 ¹ / ₂	6	16–20	1 ³ / ₄
<i>I. pilbara</i> n. sp.									
WAM S.82651	Ht	3.28	1.51	1.13	0.98	4 ¹ / ₄	6	16	1 ¹ / ₂
AMS C.476027	Pt	3.45	1.68	1.15	1.00	4 ¹ / ₂	6	16	1 ³ / ₄
Average or range (n = 2)	—	3.36	1.60	1.14	0.99	4 ¹ / ₄ –4 ¹ / ₂	6	16	1 ¹ / ₂ –1 ³ / ₄

Notes: Only mature specimens with a varix were measured; note that many specimens were missing the protoconch, in which case shell lengths are underestimates and no protoconch whorl counts are provided. Ht, holotype; Pt, paratype.

Australian species. As there are no known morphological differences between *I. quadrasi* from the type locality in the Philippines and *I. goliath* from northeastern Australia, it is possible that they belong to the same taxon. The taxonomic divisions in this group are provisional pending further molecular testing to support the genetic separation of South East Asian *I. quadrasi* from the Australian taxa. Fortunately, previous authors have provided several names for Australian species in this group, two of which are reinstated here: *I. goliath* and *I. quadrina* (see Remarks for *I. quadrina*, below).

Although Laseron (1956) believed that the distribution of ‘*Merelina*’ *goliath* extended from the type locality at Hervey Bay (Queensland) to Darwin (Northern Territory), the molecular evidence suggests that the species is in fact restricted to the coastline east of the tip of Cape York. Ponder (1984) synonymised *Merelina reversa* Laseron, 1956 (type locality Bowen, Queensland) with *I. quadrasi*. However, the holotype of *M. reversa* (SL = 2 mm) is much smaller than adult specimens of *I. goliath* and may not be the same taxon.

There are no obvious shell characters to differentiate *I. goliath* from the closely related species *I. quadrina* and *I. pilbara* n. sp. Although the shells of the holotypes are clearly distinguishable (Fig. 3), examination of specimens from several populations shows considerable variation within each species. No reliable morphological characters have been identified, but *I. goliath* is generally intermediate in size and whorl count between the largest

species *I. quadrina* and the smallest *I. pilbara* n. sp (Table 3). *Iravadia goliath* usually has fewer axial ribs on the last whorl (14–18) than *I. quadrina* (16–20), although there is overlap between specimens from each species. The central radular teeth of *I. goliath* have a greater number of cusps (6–9) than *I. quadrina* and *I. pilbara* n. sp., and two pairs of basal denticles rather than one pair. Sequence divergence of the COI gene is 18.11% between *I. goliath* and *I. quadrina*, and 17.08% between *I. goliath* and *I. pilbara* n. sp. (Table 2). Where molecular or radular data are not available, *I. goliath*, *I. quadrina* and *I. pilbara* n. sp may be able to be reliably identified based on geographic location, as, so far as is known, their distributions do not overlap.

Iravadia quadrina (Laseron, 1956)

Planapexia quadrina Laseron 1956: 410, fig. 58.

Merelina goliath Laseron 1956, in part: 436, fig. 138.

Merelina humera Laseron 1956: 435, fig. 135.

Iravadia (Iravadia) quadrasi Ponder 1984 (not of Böttger, 1893), in part: 35, figs 1B.

Material examined

Holotype of *Planapexia quadrina*. Darwin, Northern Territory, 12°28’S, 130°50’E, coll. J. Laseron, 1942–1945 (AMS C.102399).

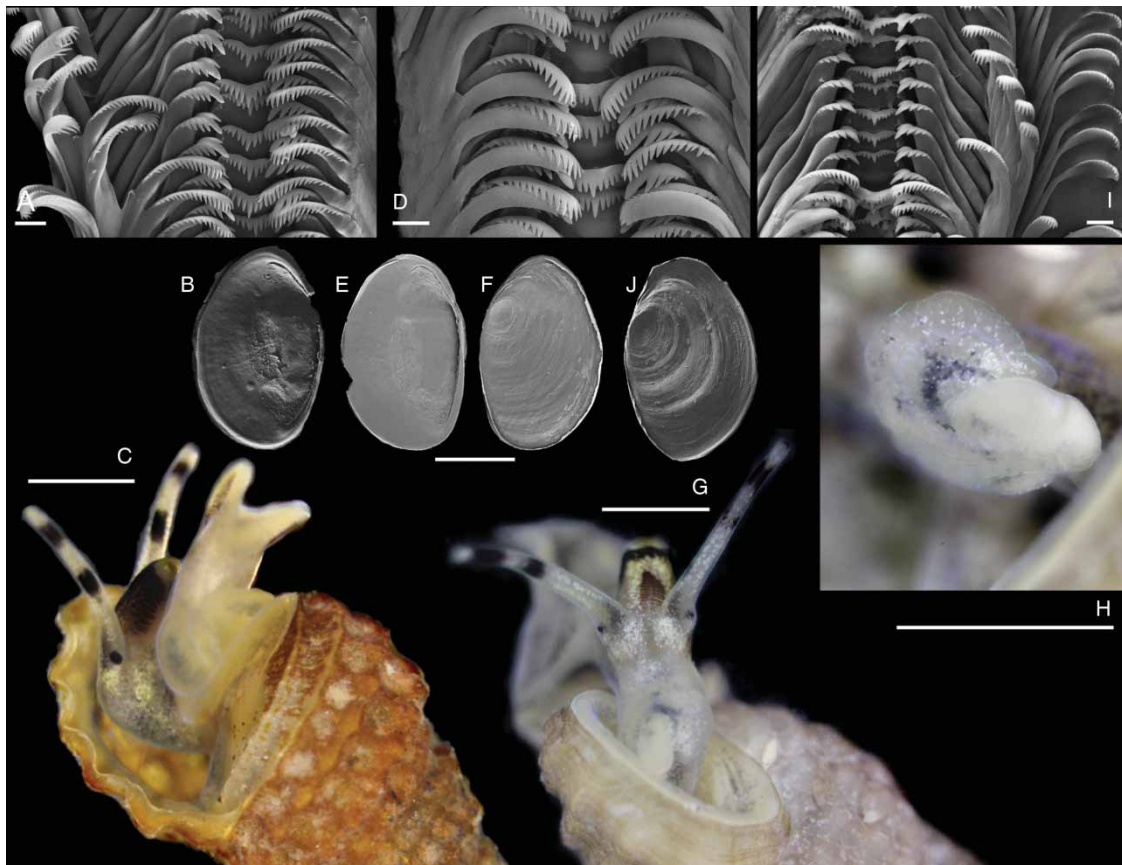


Figure 4. Cryptic species formerly recognised as '*Irvadia quadrasi*'. **A–C**, *Irvadia goliath* (Laseron, 1956). **A**, Radula, Nudgee Beach, QLD, AMS C.470970; **B**, interior surface of operculum, AMS C.470970; **C**, animal, Tin Can Bay, QLD, AMS C.470845. **D–H**, *Irvadia quadrina* (Laseron, 1956). **D**, radula, Karumba, QLD, AMS C.470896; **E**, **F**, interior and exterior surfaces of operculum; **G**, **H**, animal and penis, Broome, WA, AMS C.476001. **I**, **J**, *Irvadia pilbara* n. sp., Port Hedland, WA, AMS C.470614. **I**, Exterior surface of operculum; **J**, radula. Scale bars: **A**, **D**, **I**, 10 μ m; **B**, **C**, **E**, **F–H**, **J**, 500 μ m.

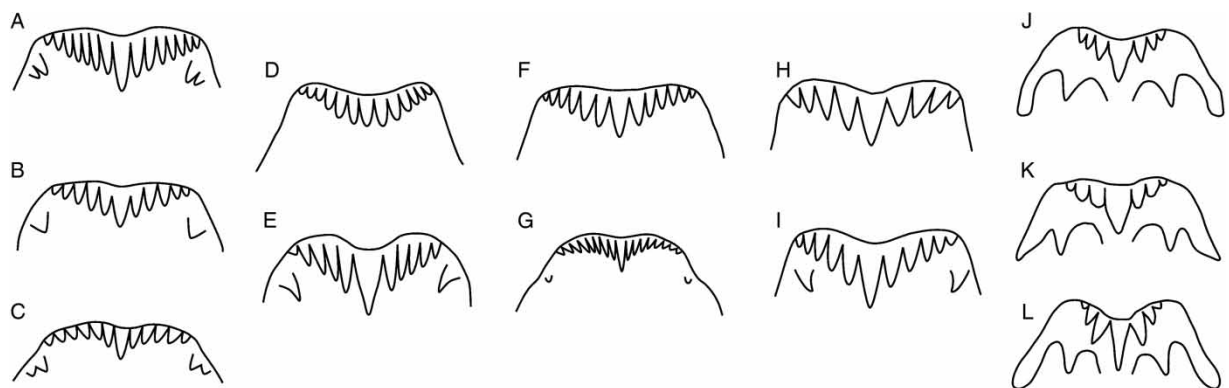


Figure 5. Comparative diagrams of the central tooth of the radula. **A**, *Irvadia goliath* (Laseron, 1956) and *Irvadia pilbara* n. sp.; **B**, *Irvadia quadrina* (Laseron, 1956); **C**, *Irvadia* cf. *capitata* (Laseron, 1956); **D**, *Wakauraiia fukudai* n. sp.; **E**, *Pseudomerelina* cf. *mahimensis* (Melvill, 1893); **F**, *Pellamora australis* (Hedley, 1901); **G**, *Pellamora splendida* n. sp.; **H**, *Fluviocingula resima* (Laseron, 1956); **I**, *Fluviocingula superficialis* n. sp.; **J**, *Nozeba topaziaca* (Hedley, 1908); **K**, *Auricorona queenslandica* n. gen. and n. sp.; **L**, *Aenigmula criscionei* n. gen. and n. sp.

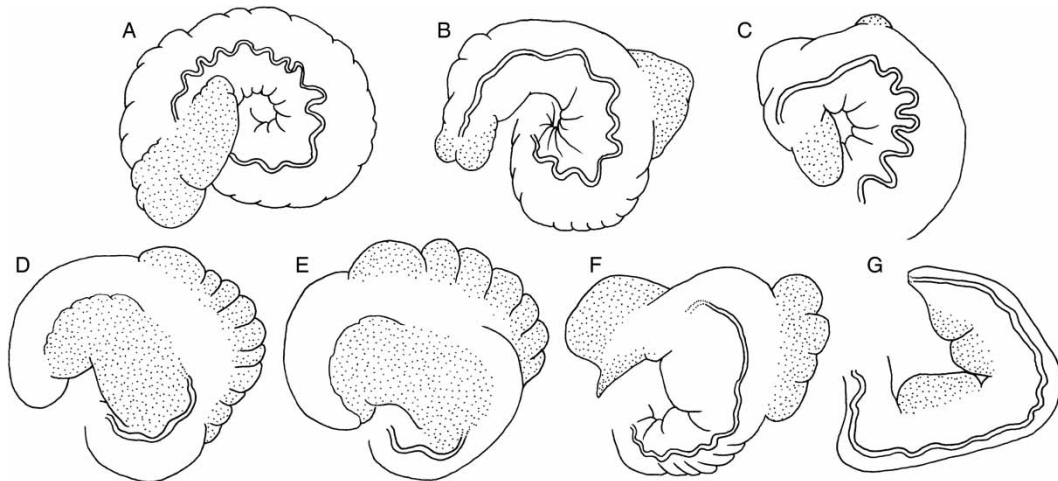


Figure 6. Comparative diagrams of penis morphology. **A**, *Irvadiaz goliath* (Laseron, 1956); **B**, *Wakauria fukudai* n. sp.; **C**, *Pseudomerelina* cf. *mahimensis* (Melvill, 1893); **D**, *Pellamora australis* (Hedley, 1901); **E**, *Pellamora splendida* n. sp.; **F**, *Fluviocingula resima* (Laseron, 1956); **G**, *Nozeba topaziaca* (Hedley, 1908).

Other material. Four wet lots and two dry lots from Queensland between Weipa and the Wellesley Group of Islands in the Gulf of Carpentaria; eight wet lots and five dry lots from Northern Territory between Gove Peninsula and the Tiwi Islands; two wet lots from Broome, Western Australia. See supplementary data for full list of material examined.

Redescription

Shell (Figs 2, 3F–J). As for *I. goliath*, except up to $7\frac{1}{4}$ whorls, SL = 4.62–6.28 mm, SD = 2.24–2.93 mm (Table 3). 16–20 axial ribs on last whorl.

Protoconch (Fig. 3J) and **operculum** (Fig. 4E, F). As for *I. goliath*.

Radula ($n = 3$) (Figs 4D; 5B). As for *I. goliath*, except central tooth 5 – 6 + 1 + 5 – 6/1 + 1; single pair of basal denticles.

External morphology, colouration in life (Fig. 4G) and **penis** (Fig. 4H). As for *I. goliath*.

Distribution (Fig. 7A).

Known from mangrove habitat between Weipa on the Gulf of Carpentaria coast of Queensland and Broome, in Western Australia. The species is not known west of Port Hedland or east of Cape York Peninsula.

Remarks

Laseron (1956) introduced *Planapexia quadrina* for a shell from Darwin, Northern Territory. Ponder (1984) placed '*P.*'*quadrina* in *Irvadiaz* in synonymy with *I. quadrasi*. On the basis of molecular and phylogeographic evidence, *I. quadrina* is here reinstated with its type

locality in Darwin, Northern Territory. *Irvadiaz quadrina* is slightly larger than either *I. goliath* or *I. pilbara* n. sp., based on limited shell measurements (Table 3). The radula has only a single pair of basal denticles, unlike the double pair present in *I. goliath*. Geographic information is useful in aiding the identification of *I. quadrina*, as morphological characters are mostly uninformative in separating species in this group. Molecular sequence divergence in the COI gene is 18.11% between *I. quadrina* and *I. goliath*, and 8.51% between *I. quadrina* and *I. pilbara* n. sp. (Table 2).

Irvadiaz pilbara n. sp.

Material examined

Holotype. Nickol Bay, Karratha, Western Australia, 20°43'24"S, 116°52'16"E, coll. R. Golding and M. Hill, 5 July 2012, on leaf litter and filamentous mangrove roots in pools between mangroves (WAM S.82651). **Paratypes.** Same data (AMS C.476027, 3).

Other material. Three wet lots and one dry lot from Western Australia between the Port Hedland and Karratha. See supplementary data for full list of material examined.

Description

Shell (Figs 2, 3K–N). As for *I. goliath*, except $5\frac{3}{4}$ whorls, length 3.28–3.45 mm, diameter of last whorl 1.51–1.68 mm (Table 3); 16 axial ribs on last whorl.

Protoconch (Fig. 3N) and **operculum** (Fig. 4J). As for *I. goliath*.

Radula ($n = 1$) (Fig. 4I, 5A). As for *I. quadrina*.

External morphology and colouration in life, and penis. As for *I. goliath*.

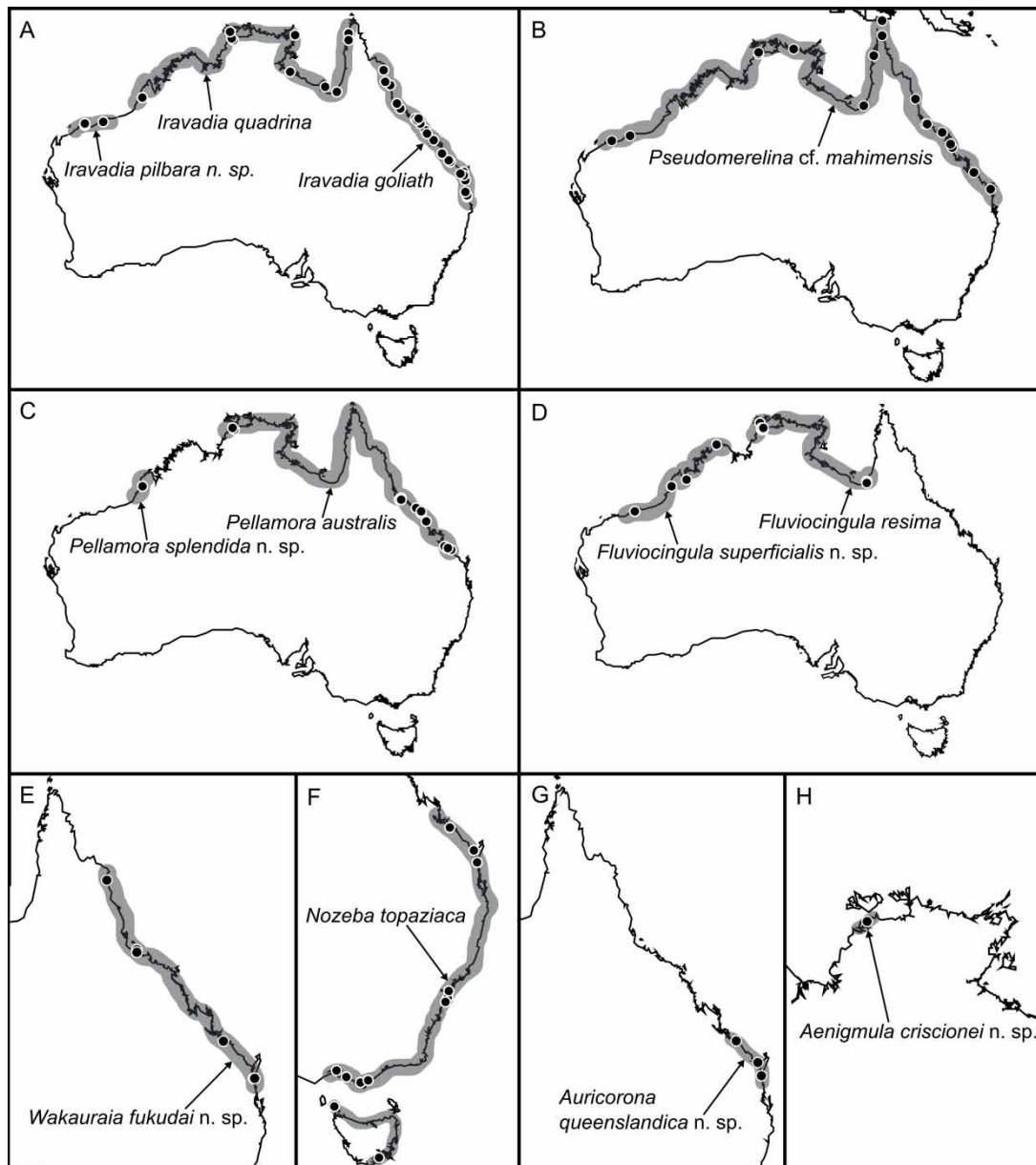


Figure 7. Distribution maps of species treated in the systematics section. Dots indicate samples examined during this study and labelled grey areas possible distributions based on known samples. **A**, Map of Australia with distributions of cryptic species formerly attributed to '*Iravadia quadrasi*' (Bottger, 1893): *I. goliath* (Laseron, 1956), *I. quadrina* (Laseron, 1956), and *I. pilbara* n. sp.; **B**, map of Australia with distribution of *Pseudomerelina* cf. *mahimensis* (Melville, 1893); **C**, map of Australia with distributions of *Pellamora australis* (Hedley, 1901) and *Pellamora splendida* n. sp.; **D**, map of Australia with distributions of *Fluviocingula resima* (Laseron, 1956) and *Fluviocingula superficialis* n. sp.; **E**, map of Queensland with distribution of *Wakauraia fukudai* n. sp.; **F**, map of southeastern Australia with distribution of *Nozeba topaziaca* (Hedley, 1908); **G**, map of Queensland with distribution of *Auricorona queenslandica* n. gen. and n. sp.; **H**, map of Northern Territory with distribution of *Aenigmula criscionei* n. gen. and n. sp.

Distribution (Fig. 7A)

Known only from two locations in the Pilbara, Western Australia; Port Hedland and the Dampier region (including Karratha).

Remarks

None of the several names introduced by earlier authors for species subsequently synonymised with *I. quadrasi*

are available for this new Western Australian species. Molecular phylogenetic analysis shows that *I. pilbara* n. sp. is most closely related to *I. quadrina*, with sequence divergence in the COI gene of 8.51%, versus 17.08% between *I. pilbara* and *I. goliath*. The distributions of *I. pilbara* n. sp. and *I. quadrina* are separated by a relatively short distance (600 km) between Broome and Port Hedland, Western Australia. Species identification in this group is difficult, and should be informed by geographic

information. Based on the small number of mature specimens available for shell measurement, it appears that *I. pilbara* n. sp. has fewer whorls and is smaller than other closely related species previously referred to *I. quadrasi*. It also seems to have fewer axial ribs on the last whorl than *I. quadrina*, although this is variable between individuals.

Etymology

Named after the Pilbara region of northwestern Australia, where the species occurs.

Iravadia c.f. *capitata* (Laseron, 1956)

?*Pellamora capitata* Laseron 1956: 425, figs 106, 107.

?*Pellamora spiralis* Laseron 1956: 426, figs 108, 109.

Material examined

Holotype of *Pellamora capitata*. Albany Passage, Cape York Peninsula, Queensland, 10°45'00"S, 142°37'00"E, coll. C. Hedley and A. McCulloch, 9 October 1907, on mud and sand (AMS C.102402). *Holotype* of *Pellamora spiralis*. Michaelmas Cay, Great Barrier Reef, Queensland, 16°36'00"S, 145°59'00"E, coll. T. Iredale and G. P. Whitley, May 1926 (AMS C.102406).

Other material. Horseshoe Bay, Bowen, Queensland, 19°58'41"S, 148°15'40"E, coll. R. Golding and S. A. Clark, 6 October 2011, under partially buried rocks and boulders in sandy gutter at low tide (AMS C.470914, 3).

Redescription

Based on AMS C.470914, not type material.

Shell (Fig. 8A–E). Elongate-ovate, solid; convex whorl profile with moderately deep suture; up to 5½ whorls including protoconch, SL = 3.03 – 3.24 mm, SD = 1.48 – 1.61 mm (Table 4). Pale beige to brown; periostracum thin. Sculpture of low spiral ribs (12–14 on last whorl, with additional secondary ribs between the first five major ribs) crossed by numerous weak axial riblets. Aperture oval to D-shaped, anterior margin rounded, posterior margin moderately angled; outer lip orthocline; external varix well developed.

Protoconch (Fig. 8E). Planar, 1½–1¾ whorls. Smooth; transitional varix strongly developed.

Operculum (Fig. 8F). Oval to D-shaped; growth striae concentric; nucleus positioned at midpoint on obtusely angled umbilical margin. Exterior surface with fine growth striae; interior surface with groove and thickened ridge along umbilical margin, and two low radial ridges emerging from nucleus.

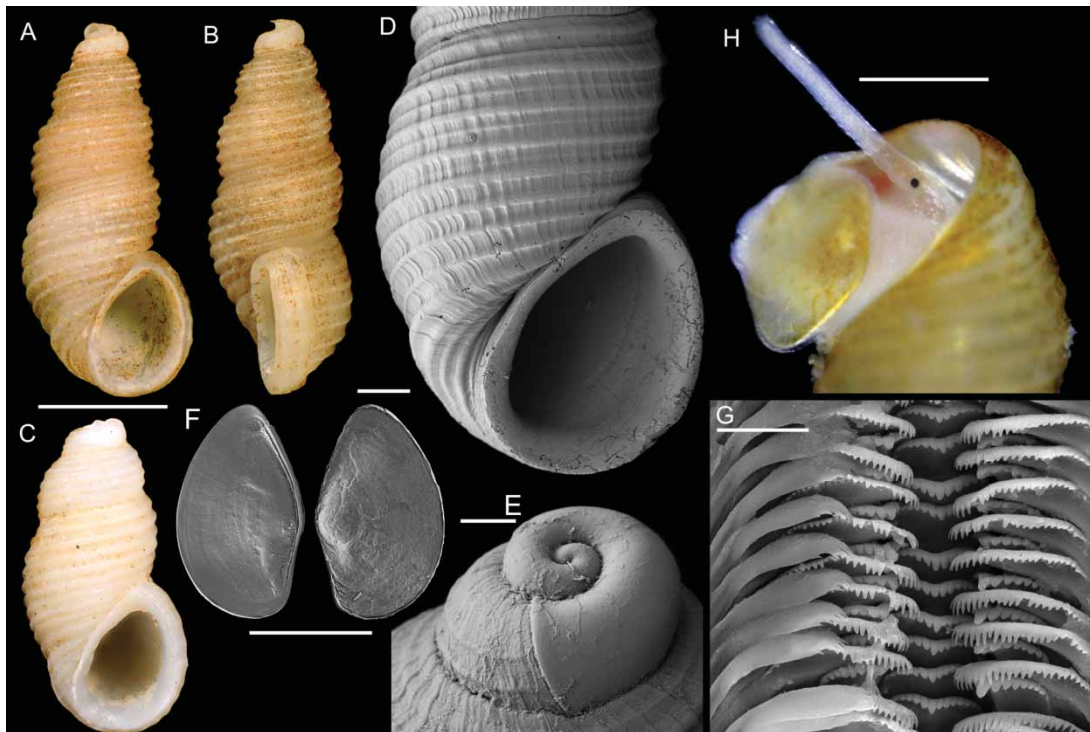


Figure 8. *Iravadia* cf. *capitata* (Laseron, 1956). A, B, Representative specimen; C, *Pellamora capitata* Laseron, 1956 holotype, Albany Passage, QLD, AMS C.102402; D, interior and exterior surfaces of operculum; E, last whorl with sculpture, periostracum removed; F, protoconch; G, radula; H, animal. A, B, D–H from Bowen, QLD, AMS C.470914. Scale bars: A–C, 1 mm; D, H, 500 µm; E, 200 µm; F, 100 µm; G, 10 µm.

Table 4. Shell measurements of type and other specimens of *Iravadia capitata* (and its synonym *Pellamora spiralis*), *Pellamora laseroni* and *Iravadia cf. capitata*.

Registration no.	Status	SL (mm)	SD (mm)	AL (mm)	AW (mm)	TWC	SpR	PWC
<i>P. spiralis</i>								
AMS C.102406	Ht	2.59	1.36	1.17	0.86	3	13	—
<i>P. laseroni</i>								
AMS C.476087	Nt	3.07	1.38	1.07	0.83	4 ¹ / ₂	10	1 ¹ / ₄
<i>P. capitata</i>								
AMS C.102402	Ht	2.38	1.26	1.02	0.81	3	13	—
<i>I. cf. capitata</i>								
AMS C.470914	—	3.24	1.48	1.14	0.86	4	12	1 ¹ / ₂
AMS C.470914	—	3.03	1.48	1.21	0.95	3 ³ / ₄	13	—
AMS C.470914	—	3.24	1.61	1.33	1.05	3 ³ / ₄	14	1 ³ / ₄
Average or range ($n = 3$)		3.17	1.53	1.22	0.95	3 ³ / ₄ -4	12-14	1 ¹ / ₂ -1 ³ / ₄

Notes: Ht, holotype; Nt, possible neotype.

Radula ($n = 1$) (Figs 5C, 8G). Central tooth 5 – 6 + 1 + 5 – 6/2 + 2; central cusp slightly larger than others, secondary cusps diminishing outwardly; double basal denticles small, positioned just below cutting edge; lateral margins straight. Lateral teeth 2 + 1 + 7 – 8. Marginal teeth with subequal cusps; inner marginal teeth with ~25 cusps; outer marginal tooth with ~20 cusps.

External morphology and colouration in life (Fig. 8H). Head-foot transparent white with opaque white speckles on sides of neck and behind eyes. Posterior foot margin simple, lacking metapodial tentacle. Cephalic tentacles with scattered white speckles but otherwise unpigmented. Pallial tentacle absent.

Penis. Not observed.

Distribution

Based on specimens in the collections of the Australian Museum, the distribution of *I. capitata* extends along the eastern coast of Australia from southern to northern Queensland, terminating in the region of Cape York. However, as the identity of the examined material is unclear due to confusion between several Australian species of *Iravadia* (see below), this distribution is speculative.

Remarks

The specimens used in the molecular analysis and in this redescription have been provisionally referred to *I. capitata*, but they are not a perfect match to the holotype of that species. The holotypes of *I. capitata* and its synonym *I. spiralis* are both small but mature shells with three teleoconch whorls. In contrast, the shells of lot AMS C.470914 (used for this description) have 3³/₄ teleoconch whorls and have proportionally longer shells. Both the holotypes and lot C.470914 have 13 spiral ribs on the last whorl. Examination of the Australian Museum collections revealed a possible lot of paralectotypes for *Pellamora laseroni*

Iredale, 1943. This lot was previously lost, and this species was not included in *Ponder's (1984)* revision of Iravadiidae. This material of *P. laseroni* have taller shells with 4¹/₂ whorls and are a similar size and proportion to the shells of C.470914, but the last whorl only has 10 spiral ribs (*Iredale 1943*). There are many lots in the Australian Museum collections that could be assigned to either *I. capitata* or *I. laseroni*, and it appears that the size and number of ribs on the spiral whorl vary considerably. Without molecular material or intact specimens, it is not possible to further delineate these forms.

Wakauraia Kuroda & Habe, 1954

Fairbankia (Wakauraia) Kuroda & Habe 1954: 75, figs 9–12. Type species (original designation): *Fairbankia (Wakauraia) sakaguchii* Kuroda & Habe, 1954; Recent, Wakaura, Japan.

Redescription

Shell. Elongate-conical, delicate; slightly convex whorl profile with moderately impressed suture; non-umbilicate; up to six whorls including protoconch, length 3–5 mm. Pale to dark, reddish brown. Sculpture of low, spiral ridges crossed by weak axial ridges. Aperture teardrop-shaped, anterior margin rounded and slightly sinuate, posterior margin moderately angled; outer lip orthocoline or prosocline; external varix absent or weakly developed.

Protoconch. Planar, 1¹/₂ whorls.

Operculum. Oval to D-shaped; growth striae concentric; nucleus positioned at midpoint on obtusely angled umbilical margin. Exterior surface with fine growth striae; interior surface with groove and thickened ridge along umbilical margin, and two low radial ridges emerging from nucleus, one parallel to umbilical margin.

Radula. Central tooth with subequal cusps diminishing in size outwardly; central cusp either slightly enlarged

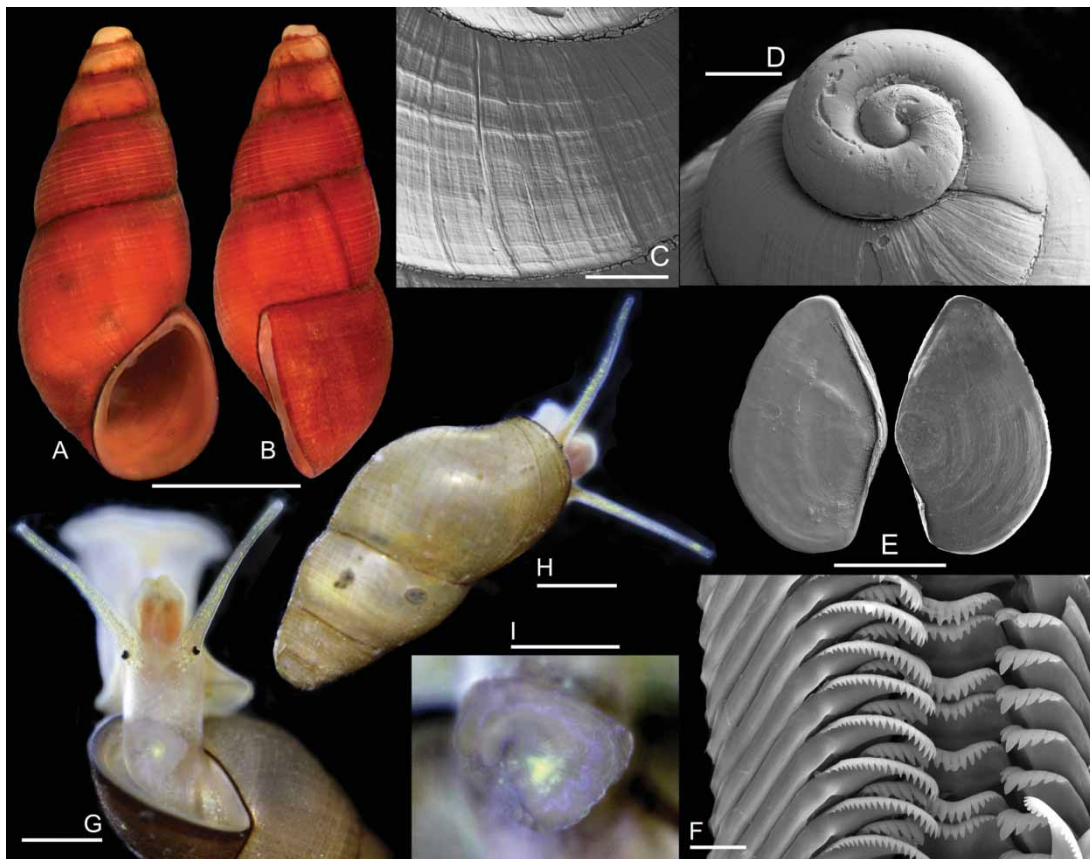


Figure 9. *Wakauria fukudai* n. sp. **A, B**, Holotype, Tin Can Bay, QLD, QM MO.80759; **C**, shell sculpture with periostracum; **D**, protoconch; **E**, interior and exterior surfaces of operculum; **F**, radula; **G**, animal, Tannum Sands, QLD, AMS C.470938; **H, I**, animal crawling and detail of penis, Cooktown, QLD, AMS C.470873. **C–F** paratypes from Tin Can Bay, QLD, AMS C.426339. Scale bars: **A, B**, 1 mm; **C, D**, 100 μ m; **E, G, H**, 500 μ m; **F**, 10 μ m; **I**, 200 μ m.

or equal; basal denticles absent; lateral margins of tooth straight. Marginal teeth with subequal cusps; inner marginal teeth with ~ 20 cusps; outer marginal teeth either present or (possibly) absent.

External morphology and colouration in life. Posterior foot margin simple, lacking metapodial tentacle. Cephalic tentacles with yellow pigmentation, lacking black bands. Pallial tentacles absent.

Remarks

[Kuroda and Habe \(1954\)](#) described the Japanese iravadiid *Fairbankia* (*Wakauria*) *sakaguchii* and erected a new subgenus for the species. They tentatively placed *Wakauria* as a subgenus of *Fairbankia* based on shell features, and the subgenus was subsequently synonymised with *Fairbankia* and further nested in *Iravadia* (*Fairbankia*) by [Ponder \(1984\)](#). The type of *Iravadia* (*Fairbankia*),

Table 5. Shell measurements of type and other specimens of *Wakauria fukudai* n. sp.

Registration no.	Status	SL (mm)	SD (mm)	AL (mm)	AW (mm)	TWC	PWC
QM MO.80759	Ht	3.64	1.60	1.34	1.02	4 $\frac{1}{2}$	1 $\frac{1}{2}$
QM MO.80760	Pt	3.55	1.72	1.36	1.11	4	1 $\frac{1}{2}$
QM MO.80760	Pt	3.45	1.49	1.23	0.94	4 $\frac{1}{4}$	1 $\frac{1}{2}$
AMS C.426339	Pt	3.40	1.55	1.21	1.00	4	—
AMS C.426339	Pt	3.34	1.57	1.30	1.06	4	1 $\frac{1}{2}$
AMS C.426339	Pt	3.23	1.53	1.23	0.96	4	1 $\frac{1}{2}$
Average or range ($n = 6$)		3.44	1.58	1.28	1.01	4–4 $\frac{1}{2}$	1 $\frac{1}{2}$

Notes: Ht, holotype; Pt, paratype.

I. (F.) bombayana (Stoliczka, 1868) has a larger, taller-spired shell with long periostracal hairs, coarse spiral sculpture and a strong varix on the outer apertural lip. It is unlikely that *W. sakaguchii* and *W. fukudai* n. sp. belong in the same genus as *I. (F.) bombayana*, on the basis of shell morphology, and therefore *Wakauraia* is here restored to genus-level. This decision needs to be tested by inclusion of *I. (F.) bombayana* in future molecular analysis of Iravadiidae. Only two species of *Wakauraia* are presently known, from Japan and Australia, but they share many features. *Wakauraia* has a distinctively reddish-brown periostracum, low, granular spiral ribs, a slightly sinuate anterior apertural lip, yellow pigment on the tentacles, subequal cusps on the central tooth and a distinctive configuration of ridges on the interior surface of the operculum.

***Wakauraia fukudai* n. sp.**

Material examined

Holotype. Toolara Esplanade Park, Tin Can Bay, Queensland, 25°55'23S, 153°0'28E, coll. W.F. Ponder and H. Fukuda, 4 March 2003, upper shore area, mangrove swamps (QM MO.80759). *Paratypes*. Same data (QM MO.80760, 2; AMS C.426339, 3).

Other material. Six wet lots from Queensland between Tin Can Bay and Cooktown. See supplementary data for full list of material examined.

Description

Shell (Figs 2, 9A–D). Length 3.23–3.64 mm, diameter of last whorl 1.53–1.72 mm (Table 5). Lustrous; pale beige with darker spiral bands to entirely dark, reddish, chestnut brown. Sculpture of ~30 irregularly spaced, low, granular, spiral ridges crossed by weak axial ridges; periostracum thick in grooves between spiral ridges. Outer lip prosocline; external varix absent.

Protoconch (Fig. 9D). First 1¼ whorls planar, then descending. Smooth; transitional varix weakly developed.

Operculum (Fig. 9E). As for genus.

Radula ($n = 2$) (Figs 5D, 9F). Central tooth with 11–13 subequal cusps; central cusp not enlarged. Lateral teeth 3 – 4 + 1 + 5 – 6. Outer marginal teeth absent from examined radulae.

External morphology and colouration in life (Fig. 9G, H). Head-foot semi-transparent white with opaque white and bright yellow speckles on sides of neck and between eyes. Cephalic tentacles transparent with yellow speckles.

Penis (Figs 5B, 9I). Cylindrical, rugose; duct opening at indentation on distal tip; one glandular swelling midway on outer edge. Bright yellow patch of pigment on inner edge near base.

Distribution (Fig. 7E)

Collected alive at several coastal localities in Queensland between Great Sandy Strait and Cooktown. Rare, found on damp or submerged leaf litter (in small, permanent pools) or under logs. The species seems to be associated with sandy (rather than muddy) substrate on the mid to high shore in estuarine mangrove forests.

Remarks

Wakauraia fukudai n. sp. has a finely sculptured shell that is distinct from any other Australian iravadiids. It closely resembles the Japanese species *W. sakaguchii* (originally placed in a subgenus of *Fairbankia*), but has a smaller, narrower shell and diffuse rather than banded yellow pigment on the tentacles (compared to *W. sakaguchii* figured by the [Japanese Association of Benthology 2012](#)). A peculiar feature of *W. sakaguchii* is the apparent absence of outer marginal teeth. There were few specimens available for morphological examination, so this may be a peculiarity of the two radulae mounted for scanning electron microscope examination.

Etymology

Named for my colleague Dr Hiroshi Fukuda, as a small note of appreciation for his efforts collecting the type specimens of this species and his many other contributions to the study of Australian mangrove microgastropods.

***Pseudomerelina* Ponder, 1984**

Iravadia (Pseudomerelina) Ponder 1984: 37–39. Type species (original designation): *Alvania mahimensis* Melvill, 1893; Recent, Bombay, India

Pseudomerelina. — Starobogatov, 1989 in Starobogatov *et al.* (1989): 36.

Remarks

Pseudomerelina was introduced by Ponder (1984) as a subgenus of *Iravadia* for a single species with a shell unlike that of other iravadiids. It was removed from *Iravadia* by Starobogatov *et al.* (1989) and recognised as a distinct genus, and this decision is supported by the molecular study presented here. *Pseudomerelina* is most closely related to *Fluviocingula* and *Pellamora*. No generic description is given here because material attributed to the only known species of *Pseudomerelina* is described below.

***Pseudomerelina* cf. *mahimensis* (Melvill, 1893)**

?*Alvania mahimensis* Melvill 1893: 241, pl. 1, fig. 17.

?*Merelina solida* Laseron 1956: 434, fig. 131.

?*Merelina sucina* Laseron 1956: 434, figs 132, 133.

?*Iravadia tuberculata* Brandt 1974: 137, pl. 10, fig. 78.

?*Iravadia (Pseudomerelina) mahimensis*. — Ponder 1984: 37, figs 1C, 5, 8C, 10F–J.

Material examined

Syntypes of *Alvania mahimensis*. Bombay (NMHUK 93.2.16.25–6, 2) [examined from photographs only].

Holotype of *Merelina solida*. Albany Passage, Cape York, 10°45'00"S, 142°37'00"E, coll. C. Hedley and A. McCulloch, 9–11 October 1907, on mud and sand (AMS C.102424).

Holotype of *Merelina sucina*. Darwin, Northern Territory, 12°28'00"S, 130°50'00"E, coll. J. Laseron, 1942–45 (AMS C.102425).

Paratypes of *Merelina sucina*. Darwin, Northern Territory, 12°28'00"S, 130°50'00"E, coll. J. Laseron, 1942–45 (AMS C.109345, 11).

Other material. Thirteen wet lots and four dry lots from Queensland between Hervey Bay and Torres Strait; three wet lots and two dry lots from Northern Territory between Arnhem Land and Darwin; three wet lots and two dry lots from Western Australia between Port Hedland and Karratha. See supplementary data for full list of material examined.

Redescription

Shell (Figs 2, 10A–D). Ovate-conical, solid; convex whorl profile with moderately impressed suture; non-umbilicate; up to 6¼ whorls including protoconch, length 2.57–3.16 mm, diameter of last whorl 1.28–1.48 mm (Table 6). Cream with broad, purple spiral bands above and below suture, also visible inside aperture; periostracum corrugated by numerous fine spiral fringes. Sculpture of strong spiral ribs (six on last whorl) intersected by numerous axial ribs (13–15 on last whorl) to produce nodules (on upper three spiral ribs only). Aperture oval to subcircular, anterior and posterior margins rounded; outer lip slightly prosocline; external varix strongly developed.

Protoconch (Fig. 10D). First whorl planar, then descending; 2–2¼ whorls. Smooth; transitional varix strongly developed.

Operculum (Fig. 10E). Oval; growth striae concentric; nucleus positioned at midpoint on rounded umbilical margin. Exterior surface with fine growth striae; interior surface with groove and thickened ridge along umbilical margin and two low radial ridges emerging from nucleus.

Radula ($n = 3$) (Figs 5E, 10F). Central tooth 4 – 5 + 1 + 4 – 5/1 + 1; central cusp large, secondary cusps diminishing outwardly; basal denticles large, positioned just below cutting edge; lateral margins straight. Lateral teeth 3 – 4 + 1 + 3 – 4. Marginal teeth with subequal cusps; inner marginal teeth with ~15 cusps; outer marginal teeth with ~10 cusps.

External morphology and colouration in life (Fig. 10G–I). Head-foot cream or white with opaque black and white speckles on neck, snout, head and dorsal surface of foot. Posterior margin of foot slightly indented with a short, broad pallial tentacle on the dorsal surface. Cephalic tentacles with white speckles and four to six narrow, uneven, irregularly spaced black bands.

Penis (Fig. 6C). Flattened, L-shaped; duct opening at distal end; two glandular swellings, on outer edge at midpoint and near tip.

Distribution (Fig. 7B)

The species described here is found commonly in Australia in mangrove forest and muddy/rocky estuarine habitat along the northern coast of Australia between Hervey Bay, Queensland and Port Hedland, Western Australia. *Pseudomerelina mahimensis* is also found throughout Asia, including India (the type locality is in Bombay) and Thailand (Brandt 1974), but it has not yet been determined that the Asian and Australian animals are conspecific. *Pseudomerelina* cf. *mahimensis* is sometimes found in very high densities, especially in mangrove forests where the substrate is rocky and subjected to a strong coastal influence.

Remarks

The species description is based exclusively on Australian specimens of *Pseudomerelina* cf. *mahimensis*. The tentative referral of this material to *P. mahimensis* is based on the lack of information in the literature about the Asian forms of this species, and the discovery in other iravadiids of significant geographical variation within supposedly homogeneous, wide-spread species (such as the *I. quadrasi* species complex). Molecular evidence shows that although the overall level of COI sequence divergence in *P. cf. mahimensis* across Australia is relatively low, samples from Western Australia are slightly divergent from those in other areas and the within-species divergence was higher than for other species (2.42%) (Table 2). It is likely that if Australian specimens were compared with those from the type locality in Bombay, India, genetic divergence would be higher still. Without that evidence, the Australian material examined here has been provisionally referred to *P. cf. mahimensis*. Specimens in good condition are easily distinguished from other iravadiids

Table 6. Shell measurements of non-type specimens of *Pseudomerelina* cf. *mahimensis*.

Registration no.	SL (mm)	SD (mm)	AL (mm)	AW (mm)	TWC	SpR	SpRN	PWC
AMS C.470857	3.16	1.43	0.91	0.90	4 ¹ / ₄	6	14	2
AMS C.470857	2.98	1.47	0.95	0.83	4	6	13	2 ¹ / ₄
AMS C.470857	2.84	1.48	1.03	0.83	3 ³ / ₄	6	15	2
AMS C.476026	2.72	1.40	0.93	0.79	3 ³ / ₄	6	15	2
AMS C.476026	2.62	1.31	0.86	0.78	3 ¹ / ₂	6	14	2
AMS C.476026	2.57	1.28	0.91	0.78	3 ¹ / ₂	6	15	2
Average or range (n = 6)	2.82	1.39	0.93	0.82	3 ¹ / ₂ –4 ¹ / ₂	6	13–15	2–2 ¹ / ₄

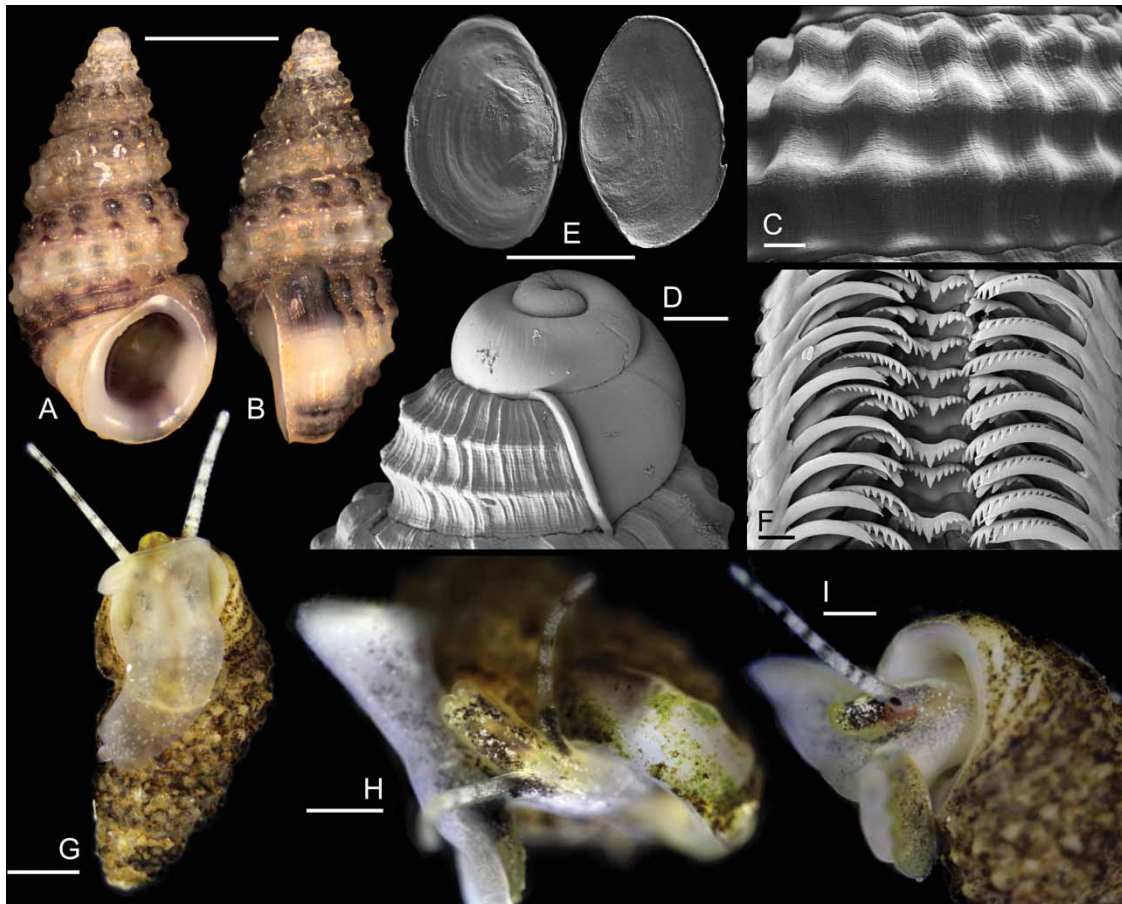


Figure 10. *Pseudomerelina* cf. *mahimensis* (Melville, 1893). A, B, Representative specimen; C, shell sculpture with periostracum; D, protoconch, Townsville, QLD, AMS C.470857; E, interior and exterior surfaces of operculum; F, radula; G, animal crawling on water meniscus, Mackay, QLD, AMS C.470919; H, I, animal, Bowen, QLD, AMS C.470850. A–C, E, F from Bowen, QLD, AMS C.470900. Scale bars: A, B, 1 mm; C, D, 100 µm; E, G–I, 500 µm; F, 10 µm.

by their purple banding, but worn shells resemble those of *I. goliath*, *I. quadrina* and *I. pilbara* n. sp., which are of a similar size and shape and also have nodular sculpture. Unlike the observations made by Ponder (1984), the operculum of *P.* cf. *mahimensis* was found to have radial ridges on the interior surface of the operculum.

Pellamora Iredale, 1943

Pellamora Iredale 1943: 206 Type species (by original designation): *Iravadia australis* Hedley, 1901; Recent, Australia.

Redescription

Shell. Elongate-conical, solid; slightly convex whorl profile with shallowly impressed suture; non-umbilicate; up to seven whorls including protoconch (estimated due to protoconch loss), length 3.5–8 mm. Brownish-orange to cream, slightly lustrous; periostracum thin, corrugated with numerous fine spiral fringes. Sculpture of low spiral ribs (eight or nine on last whorl) with numerous axial riblets in grooves between spiral ribs (but not crossing spiral ribs). Aperture subcircular to D-shaped, anterior margin angled near umbilicus, posterior margin moderately angled; outer lip prosocline; external varix present.

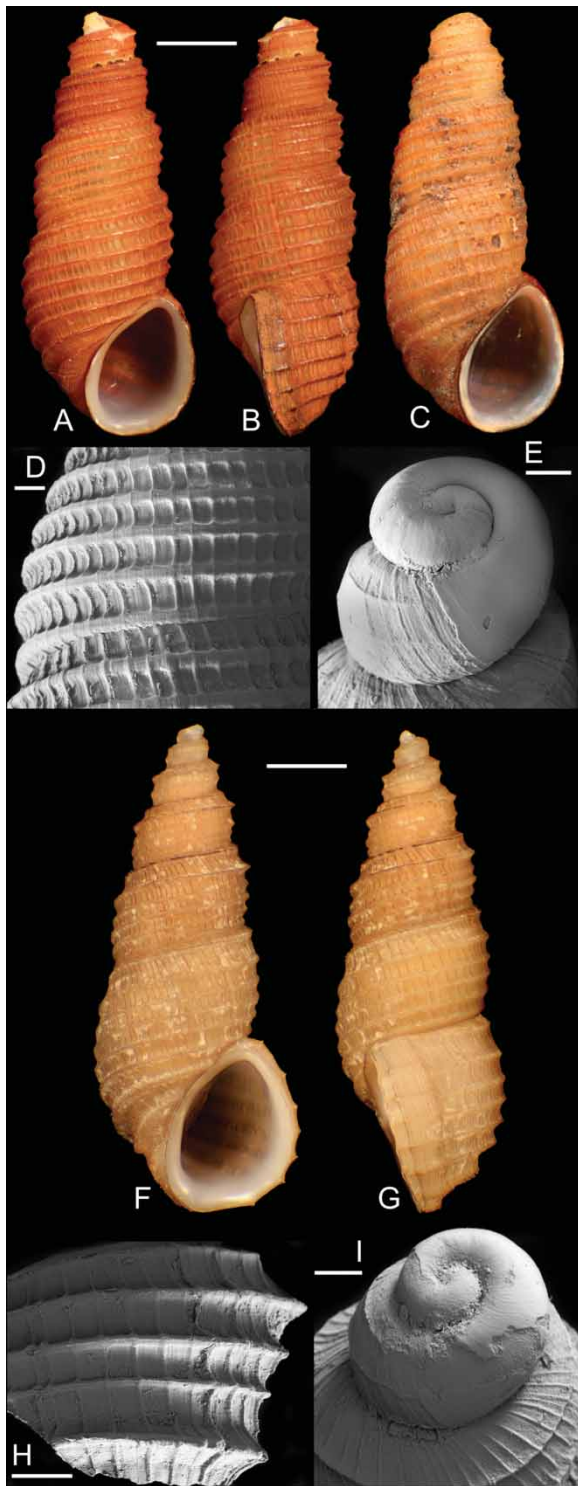


Figure 11. Australian species of *Pellamora*. A–E, *Pellamora australis* (Hedley, 1901). A, B, Representative specimen, Darwin, NT, AMS C.412376; C, syntype, Bowen, QLD, AMS C.008977; D, shell sculpture with periostracum, Magnetic Island, QLD, AMS C.459117; E, protoconch, Turkey Beach, QLD, AMS C.470945. F–I, *Pellamora splendida* n. sp. F, G, Holotype, Broome, WA, WAM S.82652; H, shell sculpture with periostracum, paratypes, Broome, WA, AMS C.476000; I, protoconch, AMS C.476000. Scale bars: A–C, F, G, 1 mm; D, H, 200 μ m; E, I, 100 μ m.

Protoconch. First whorl planar, then descending; $1\frac{1}{2}$ – $1\frac{3}{4}$ whorls total. Smooth; transitional varix weakly developed.

Operculum. Elongate oval, with flared anterior umbilical margin; growth striae concentric; nucleus positioned at midpoint on obtusely angled umbilical margin. Exterior surface with fine growth striae; interior surface with broad groove (abruptly terminating anteriorly), raised ridge on umbilical margin and two radial ridges emerging from nucleus, one parallel to umbilical margin.

Radula. Central tooth with large central cusp, secondary cusps diminishing outwardly; basal denticles either absent or single and minute; lateral margins of tooth straight. Lateral teeth 3 – 4 + 1 + 4. Marginal teeth with subequal cusps.

External morphology and colouration in life. Head-foot semi-transparent pinkish-white, with or without additional pigmentation. Posterior foot margin with shallow indentation, lacking metapodial tentacle. Cephalic tentacles with cream to bright yellow speckles, broad, black band at $\frac{3}{4}$ length and black tips. Pallial tentacle absent.

Penis. Relatively short, tapering towards tip; duct opening not determined; outer base and middle of penis encircled by row of glandular lobes, inner surface with broad glandular swelling. Opaque white, without pigmentation.

Remarks

Pellamora was introduced by Iredale (1943) to accommodate differences between Asian *Iravadia* and the Australian species *Iravadia australis* and *Pellamora procera* (the latter name is now regarded as a synonym of *P. australis*), but was synonymized with *Iravadia* (*Fairbankia*) by Ponder (1984). At present, there is little support for a close relationship between *P. australis* and the type species of *Fairbankia*, *I. (Fairbankia) bombayana*. The shell of *I. (F.) bombayana* has numerous weak spiral ridges and long, dense periostracal hairs, while *P. australis* and *P. splendida* n. sp. both have fewer strong spiral ridges and only minute fringes of periostracal hairs. Further examination of the type species and others belonging to *Iravadia* (*Fairbankia*) may support the synonymisation of *Pellamora*, but the latter name is here reinstated pending further discoveries.

The species pair *P. australis* and *P. splendida* n. sp. have been removed from *Iravadia* s. str. (as recognised here), based on both molecular and morphological data but pending further examination of the type species of *Iravadia*. They form a sister clade to *Fluviocingula*, and are characterised by their distinct shell shape and sculpture, tentacle pigmentation and penial morphology. Presently only two species, both Australian, are recognised in *Pellamora*.

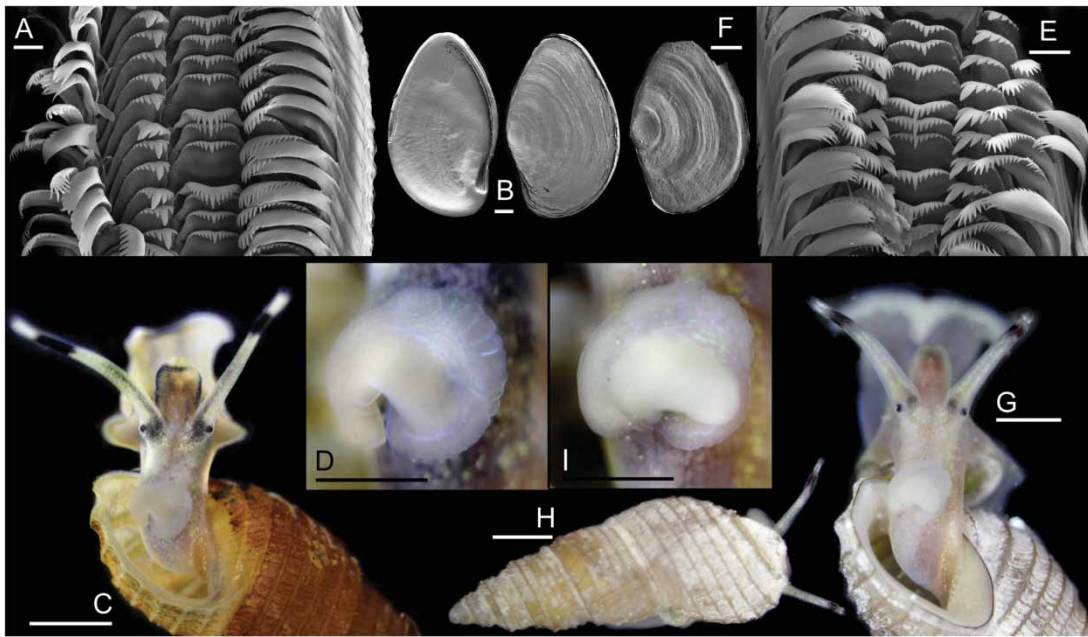


Figure 12. Australian species of *Pellamora*. **A–D**, *Pellamora australis* (Hedley, 1901). **A**, Radula, Darwin, NT, AMS C.468642; **B**, interior and exterior surfaces of operculum, AMS C.468642; **C**, **D**, animal and detail of penis, Turkey Beach, QLD, AMS C.470945. **E–I**, *Pellamora splendida* n. sp.. **E**, Radula, paratype, Broome, WA, AMS C.476000; **F**, exterior surface of operculum, AMS C.476000; **G–I**, holotype animal and detail of penis, Broome, WA, WAM S.82652. Scale bars: **A**, **C**, **E**, **G**, **H**, 10 μm ; **B**, **F**, 200 μm ; **D**, **I**, 500 μm .

***Pellamora australis* (Hedley, 1901)**

Iravadia australis Hedley 1901: 727, pl. xlvi, fig. 12.

Pellamora australis. — Iredale 1943: 206.

Pellamora procera Iredale 1943: 206.

Type material

Holotype of *Pellamora procera*. Darwin, Northern Territory, coll. J. Laseron, in shell sand, could not be located in the Australian Museum collections.

Material examined

Syntypes of *Iravadia australis*. Port Denison, Bowen, 20°01'00"S, 148°15'00"E, coll. J. Brazier, c. 1900, 'fresh-water' (AMS C.008977).

Other material. Thirteen wet lots and six dry lots from Queensland between Gladstone region and Townsville; five wet lots and three dry lots from Northern Territory around Darwin. See supplementary data for full list of material examined.

Redescription

Shell (Figs 2, 11A–E). Up to seven whorls including protoconch (estimated due to protoconch loss), length 3.76–5.68 mm (excluding lost protoconch), diameter of last whorl 1.62–1.92 mm (Table 7). Brownish-orange;

periostracum corrugated with numerous very fine spiral fringes between spiral ribs but worn away on ribs. Sculpture of evenly low spiral ribs (eight or nine on last whorl). Outer lip of aperture slightly prosocline; external varix moderately developed.

Protoconch (Fig. 11E). 1³/₄ whorls.

Operculum (Fig. 12B). As for genus.

Radula ($n = 3$) (Figs 5F, 12A). Central tooth 6 – 7 + 1 + 6 – 7/0 – 1 + 0 – 1; minute basal denticles absent or present. Inner marginal teeth with ~15 cusps; outer marginal teeth with ~12 cusps.

External morphology and colouration in life (Fig. 12C, D). Opaque grey speckles on sides of neck and dorsal surface of head; bright yellow speckles on neck and behind eyes; diffuse grey pigment behind and between eyes; ventral and lateral surface of snout black, dorsal surface of snout unpigmented.

Penis (Figs 6D, 12D). As for genus, with ~10 glandular lobes on outer surface.

Distribution (Fig. 7C)

Found uncommonly in mangrove habitat on the coast of Queensland between Gladstone region and Townsville, and also known from Darwin in the Northern Territory. There are no records in the Australian Museum from the coast of the Gulf of Carpentaria.

Table 7. Shell measurements of type and other specimens of *Pellamora* spp.

Registration no.	Status	SL (mm)	SD (mm)	AL (mm)	AW (mm)	TWC	SpR	PWC
<i>P. australis</i>								
AMS C.008977	St	5.46	2.30	1.92	1.38	4	9	—
AMS C.008977	St	5.68	2.57	1.92	1.59	3 ³ / ₄	8	—
AMS C.008977	St	4.46	1.95	1.49	1.27	4	8	—
AMS C.008977	St	4.41	1.97	1.46	1.19	3 ³ / ₄	8	—
AMS C.008977	St	3.76	1.62	1.41	1.08	3 ¹ / ₄	8	—
AMS C.412376	—	6.76	2.16	1.73	1.35	4 ¹ / ₂	9	—
AMS C.412376	—	7.59	2.11	1.76	1.49	5	8	—
AMS C.470945	—	—	—	—	—	—	—	1 ³ / ₄
Average or range ($n = 7, 1$)		5.44	2.10	1.67	1.34	3 ¹ / ₄ –5	8–9	1 ³ / ₄
<i>P. splendida</i> n. sp.								
WAM S.82652	Ht	7.93	3.28	2.72	2.03	5 ³ / ₄	8	—
AMS C.476000	Pt	—	—	—	—	—	—	1 ³ / ₄
AMS C.476000	Pt	—	—	—	—	—	—	1 ¹ / ₂
AMS C.476000	Pt	—	—	—	—	—	—	1 ¹ / ₂
Average or range ($n = 1, 3$)		7.93	3.28	2.72	2.03	5 ³ / ₄	8	1 ¹ / ₂ –1 ³ / ₄

Notes: Ht, holotype; Pt, paratype; St, syntype. Many specimens were damaged and had lost their protoconchs, so shell length is underestimated.

Remarks

The apparently discontinuous distribution of *P. australis* between Cape York Peninsula and Darwin may be an artefact of low collecting effort in this relatively inaccessible region, or patchy habitat. Molecular data support the continuity of *P. australis* between the two regions, with 2.20% within-species COI sequence divergence across its range. In contrast, *P. australis* and *P. splendida* n. sp. are separated by 12.46% COI sequence divergence (Table 2).

Pellamora splendida n. sp.

Material examined

Holotype. South of Streeters Jetty, Dampier Creek, Broome, Western Australia, 17°57'15"S, 122°14'45"E, coll. R. Golding and M. Hill, 29 June 2012, on leaf litter in pools around mangrove prop roots, in back of tall mangrove forest (WAM S.82652). *Paratypes*. Same data (AMS C.476000, 3).

Description

Shell (Figs 2, 11F–I). Up to 7¹/₂ whorls including protoconch, length 7.93 mm, diameter of last whorl 3.28 mm (only one adult specimen available, Table 7). Cream; periostracum corrugated with numerous very fine spiral fringes between spiral ribs and longer fringes on spiral ribs. Sculpture of moderately tall spiral ribs (eight on last whorl), first and second spiral ribs spaced further apart and taller than other ribs. Outer lip of aperture moderately prosocline; external varix strongly developed.

Protoconch (Fig. 11I). 1¹/₂–1³/₄ whorls.

Operculum (Fig. 12F). As for genus.

Radula ($n = 1$) (Figs 5G, 12E). Central tooth 8 + 1 + 8/1 + 1; minute basal denticles present. Inner marginal teeth with ~20 cusps; outer marginal teeth with ~17 cusps.

External morphology and colouration in life (Fig. 12G–I). Opaque yellow speckles on sides of neck and dorsal surface of head; diffuse grey pigment only at base of tentacle near eye; snout entirely unpigmented.

Penis (Figs 6E, 12I). As for genus, with ~7 glandular lobes on outer surface.

Distribution (Fig. 7C)

Known only from the type locality in Broome, Western Australia.

Remarks

Despite the similar shells of *P. australis* and *P. splendida*, n. sp., these two closely related species can be readily distinguished by the larger and paler shell of *P. splendida* n. sp., which also has more prominent and widely spaced first and second spiral ribs and more conspicuous periostracal fringing. *Pellamora splendida* n. sp. and *P. australis* are separated by 12.46% COI sequence divergence (Table 2). The distribution and adult anatomy of *P. splendida* n. sp. remain unknown, because only a single adult specimen (holotype) and three juveniles (paratypes) were collected from a single location in Broome, Western Australia.

Etymology

Named for its large, attractive shell.

***Fluviocingula* Kuroda & Habe, 1954**

Fluviocingula Kuroda and Habe, 1954: 73. Type species (by original designation): *Fluviocingula nipponica* Kuroda & Habe, 1954; Recent, Japan.

Mesodestea Laseron 1956: 451. Type species (by original designation): *Mesodestea resima* Laseron, 1956; Recent, Australia.

Iravadia (*Fluviocingula*) Ponder 1984: 41.

Redescription

Shell. Ovate to elongate-conical, delicate; convex to almost straight-sided whorls with deep or shallow suture; either non-umbilicate or with narrow umbilicus; up to eight whorls including protoconch, length 2–7 mm. Transparent grey, brown or orange; periostracum thin, either simple or with hairs. Sculpture of multiple, indistinct, spiral rows of minute, oblong pits. Aperture elongate oval, anterior margin rounded, posterior margin angled; outer lip strongly prosocline; external varix absent.

Protoconch. First whorl planar, then descending. $1\frac{3}{4}$ – $2\frac{1}{4}$ whorls. Smooth; transitional varix present.

Operculum. Elongate oval; growth striae concentric; nucleus positioned at midpoint on obtusely angled umbilical margin. Exterior surface with fine growth striae; interior surface either smooth or with U-shaped ridge.

Radula. Central tooth with large central cusp, secondary cusps diminishing outwardly; basal denticles absent or present just below cutting edge, single or double; lateral margins of tooth straight. Lateral teeth 3 – 4 + 1 + 3 – 4. Marginal teeth with subequal cusps; inner marginal teeth with ~15 cusps; outer marginal teeth with ~12–20 cusps.

Remarks

The Japanese type species of *Fluviocingula*, *F. nipponica*, was described in sufficient detail to be reasonably certain that the Australian species described here are congeneric. However, modern reports on micromolluscan fauna refer Japanese specimens to *Fluviocingula elegantula* (A. Adams, 1861) (Hasegawa 2000; Japanese Association of Benthology 2012). The most useful distinguishing feature of this group is the presence of spiral pitted sculpture on the shell. *Fluviocingula* was reduced to a subgenus of *Iravadia* by Ponder (1984), a decision that is reversed here on the basis of molecular evidence.

***Fluviocingula resima* (Laseron, 1956)**

Mesodestea resima Laseron 1956: 451, fig. 176.

Iravadia (*Fluviocingula*) *resima*. — Ponder 1984: 41, figs 1F, 12.

Material examined

Holotype. Darwin, Northern Territory, 12°28'00"S, 130°50'00"E, coll. J. Laseron, 1942–45 (AMS C.102478).

Other material. Three wet lots from Karumba, Queensland; six wet lots from Darwin and Tiwi Islands, Northern Territory. See supplementary data for full list of material examined.

Redescription

Shell (Figs 2, 13A–E). Ovate; convex whorls with deep suture; with narrow umbilicus; up to $7\frac{1}{4}$ whorls including protoconch, length 2.98–6.10 mm, diameter of last whorl 1.50–2.93 mm (Table 8). Transparent grey to orange; periostracum thin, with dense, short hairs in lines between spiral rows of pits, densest below suture and around umbilicus. Usually > 15 spiral rows of pits.

Protoconch (Fig. 13D). 2 – $2\frac{1}{4}$ whorls; transitional varix strongly developed.

Operculum (Fig. 14B). As for genus, except with groove and ridge on umbilical margin and broad, U-shaped ridge running longitudinally through centre of operculum.

Radula ($n = 4$) (Figs 5H, 14A). Central tooth 4 + 1 + 4; basal denticles absent.

External morphology and colouration in life (Fig. 14C, D). Head-foot grey; bright yellow speckles densely covering dorsal surface of head, neck and ventral surface of foot; dorsal surface of snout cream to yellow except for ring of black pigment behind white lips; ventral and lateral surfaces of snout black. Cephalic tentacles with cream speckles, broad black bands at $\frac{3}{4}$ length and black tips. Posterior foot margin indented, lacking metapodial tentacle. Pallial tentacles absent.

Penis (Figs 6F; 14E). Relatively short, broadest distally; duct opening not determined; outer middle of penis with lobate glandular swellings, tip of penis tapering to sharp, glandular point attached to broad, flat glandular appendage. Grey with bright yellow speckles.

Distribution (Fig. 7D)

Known only from two regions of northern Australia, based on the collections of the Australian Museum and recent fieldwork; Darwin (Northern Territory) and Karumba (Gulf of Carpentaria, Queensland). The distribution of *F. resima* may extend further east and west and is presumably continuous between these two regions based on genetic similarity.

Remarks

The holotype specimen is smaller than most adult specimens of *F. resima* and quite worn, but the shell shape

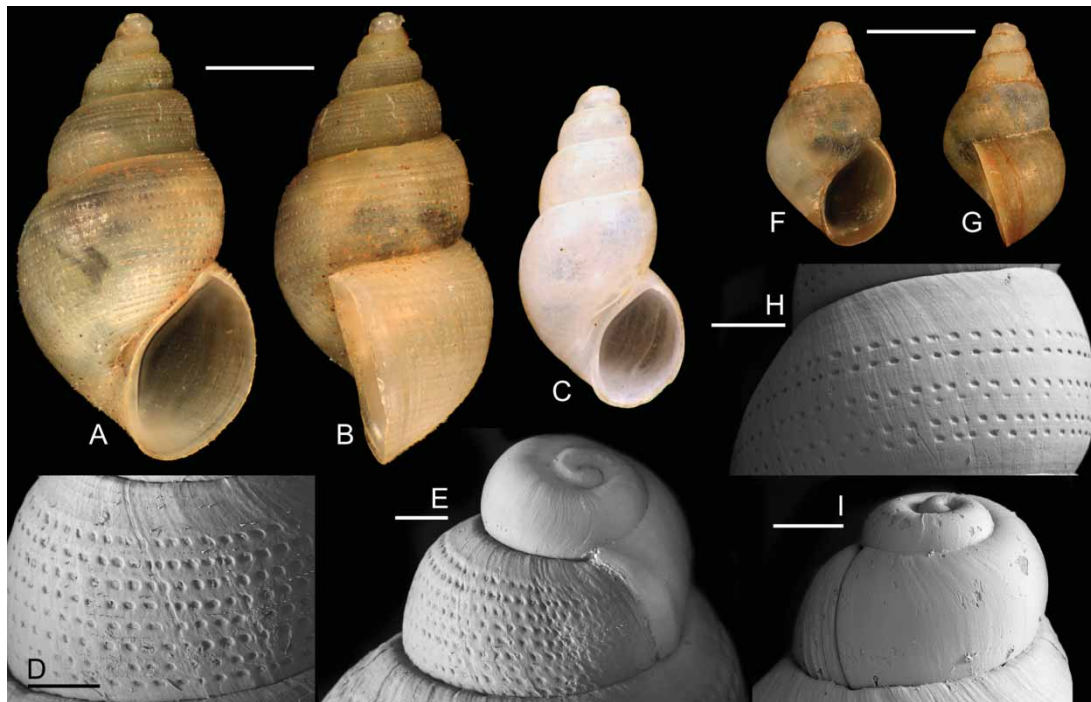


Figure 13. Australian species of *Fluviocingula*. A–E, *Fluviocingula resima* (Laseron, 1956). A, B, Representative specimen; C, holotype of *Mesodestea resima* Laseron, 1956, Darwin, NT, AMS C.102478; D, shell sculpture with periostracum; E, protoconch. A, B, D, E from Karumba, QLD, AMS C.470897. F–I, *Fluviocingula superficialis* n. sp. F, G, Holotype, Port Hedland, WA, WAM S.82653; H, shell sculpture without periostracum, AMS C.476013; I, protoconch of paratype, Port Hedland, WA, AMS C.476013. Scale bars: A–C, F, G, 1 mm; D, H, 200 µm; E, I, 100 µm.

Table 8. Shell measurements of type and other specimens of *Fluviocingula* spp.

Registration no.	Status	SL (mm)	SD (mm)	AL (mm)	AW (mm)	TWC	SpP	PWC
<i>F. resima</i>								
AMS C.459114	Ht	2.98	1.50	1.19	0.88	3½	>10	2¼
AMS C.102478	–	3.64	1.55	1.30	0.87	3½	>16	2¼
AMS C.102478	–	4.22	1.76	1.49	0.97	4½	>15	–
AMS C.470897	–	6.10	2.93	2.41	1.62	5	>17	2¼
AMS C.470897	–	5.00	2.45	2.00	1.41	4½	>16	2
AMS C.470897	–	4.11	2.16	1.78	1.19	4	>13	2¼
Average or range (n = 6)		4.34	2.06	1.70	1.16	3½–5	>10 – 17	2–2¼
<i>F. superficialis</i> n. sp.								
WAM S.82653	Ht	2.10	1.33	1.03	0.78	3	>8	1¾
AMS C.476013	Pt	2.83	1.52	1.26	0.86	3¼	>3	1¾
AMS C.476013	Pt	2.34	1.16	0.93	0.66	3½	>7	1¾
AMS C.476005	–	2.97	1.45	1.28	0.79	3¾	>5	1¾
Average or range (n = 4)		2.56	1.36	1.13	0.77	3–3¾	>3 – 8	1¾

Notes: Ht, holotype; Pt, paratype; SpP, spiral rows of pits on last whorl. Juvenile specimens were not measured.

and faint traces of spiral pitted sculpture confirm its identity. *Fluviocingula resima* can be distinguished from the other Australian species, *F. superficialis* n. sp., by its larger size, more convex whorls, greater number of spiral rows of pits, absence of basal denticles on the central tooth of the radula and presence of bright yellow pigmentation on the head-foot. COI genetic sequence divergence between *F. resima* and *F. superficialis* is 15.62%, but within-species divergence for *F. resima* is only 0.60% (Table 2).

Fluviocingula superficialis n. sp.

Material examined

Holotype. Four Mile Creek, Port Hedland, Western Australia, 20°19'19"S, 118°38'44"E, coll. R. Golding and M. Hill, 3 July 2012, on leaf litter from pools at back of dense mangrove forest beside road (WAM S.82653).

Paratypes. Same data (WAM S.82654, 10; AMS C.476013, 10).

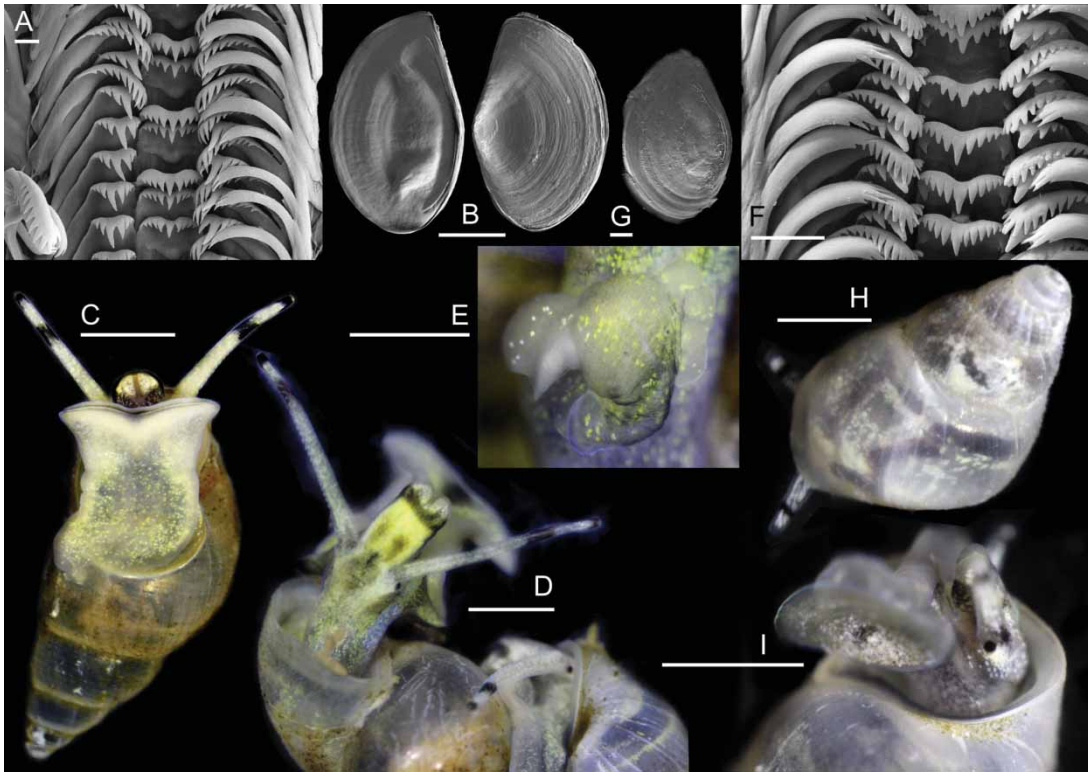


Figure 14. Australian species of *Fluviocingula*. A–E, *Fluviocingula resima* (Laseron, 1956), Karumba, QLD, AMS C.470897. A, Radula; B, interior and exterior surfaces of operculum; C, ventral view of animal; D, two live animals; E, detail of penis. F–I, *Fluviocingula superficialis* n. sp.. F, Radula of paratype AMS C.476013; G, interior surface of operculum, Port Hedland, WA, AMS C.476005; H, I, animal, Broome, WA, AMS C.475996. Scale bars: A, F, 10 μm ; B, 500 μm ; C, 1 mm; D, 500 μm ; E, H, I, 200 μm ; G, 100 μm .

Other material. Five lots from Western Australia between Derby and Broome. See supplementary data for full list of material examined.

Description

Shell (Figs 2, 13F–I). Elongate-conical; almost straight-sided whorls with shallow suture; non-umbilicate; up to $5\frac{1}{4}$ whorls including protoconch, length 2.10–2.97 mm, diameter of last whorl 1.33–1.52 mm (Table 8). Transparent pale brown to orange; periostracum thin, simple. Usually more than six spiral rows of pits.

Protoconch (Fig. 13I). $1\frac{3}{4}$ whorls; transitional varix weakly developed.

Operculum (Fig. 14G). Adult operculum not observed; juvenile operculum as for genus, but without internal ridge.

Radula ($n = 1$) (Figs 5I, 14F). Central tooth 4 – 5 + 1 + 4 – 5/1 + 1; basal denticles large, triangular.

External morphology and colouration in life (Fig. 14H, I). Head-foot grey; white speckles behind eyes and on dorsal surface of head and snout; snout with black pigment

on ventral and lateral surface and black ring behind lips. Cephalic tentacles with white speckles, broad black bands at $\frac{3}{4}$ length and black tips. Posterior foot margin indented, lacking metapodial tentacle. Pallial tentacles absent.

Penis. Not observed.

Distribution (Fig. 7D)

Known from mangrove forests in northern Western Australia, between Port Hedland and the northern Kimberley region.

Remarks

Recent collections of this species from Port Hedland and Broome resulted in many live juveniles and several dead adult shells. The holotype was selected as a medium-sized specimen with an animal in the shell, but it may not be fully adult as there are larger dead shells among the paratypes. *Fluviocingula superficialis* can be distinguished from *F. resima* by its smaller shell with almost straight-sided whorls, absence of periostracal hairs, fewer rows of pitted spiral sculpture and white rather than yellow pigmentation on the head-foot. The central tooth of

the radula also has basal denticles, unlike *F. superficialis*. COI genetic sequence divergence between *F. superficialis* and *F. resima* is 15.62%, but within-species divergence for *F. superficialis* is only 1.80%.

Etymology

Named for the superficial resemblance of this species to a juvenile of the related species *Fluviocingula resima*.

Uncertain classification — ‘Clade A’

Remarks

Based on molecular phylogenetic analysis and morphological characterisation, *Nozeba* and *Auricorona* n. gen. do not belong in Iravadiidae s. str. However, these two genera are quite dissimilar to each other and also do not obviously belong in any other truncatelloid family. Ponder (1984) recognised a division within Iravadiidae s. l. between *Iravadia* and the other extant iravadiid genera with paucispiral opercula (*Nozeba*, *Rissopsis*, *Chevalieria*, *Acliceratia*, *Hyalia*, *Ceratia* and *Liroceratia*) (see Iravadiidae, Remarks). *Nozeba*, and perhaps some or all of these other genera with a paucispiral operculum, belong in ‘Clade A’. Although currently consisting of only two genera, it is anticipated that ‘Clade A’ will eventually comprise a large portion of the diversity previously assigned to Iravadiidae. A recently described Japanese species, *Ceratia nagashima* Fukuda, 2000, shares some anatomical and conchological features with *Auricorona queenslandica* n. gen. and n. sp. (see Remarks for *Auricorona*, below), suggesting that *Ceratia* (or at least *C. nagashima*) also belongs in ‘Clade A’ rather than Iravadiidae.

In the molecular analysis, ‘Clade A’ holds a highly supported sister relationship to Tornidae (although separated by moderately long branches), but the shell and soft-tissue anatomical characters of *Nozeba* and *Auricorona* do not closely resemble those of tornids. For example, tornids have short-spined to discoidal shells and a multispiral operculum (Ponder and de Keyser 1998) while *Nozeba* and *Auricorona* have tall-spined shells and paucispiral opercula. *Nozeba* and *Auricorona* n. gen. both have a single right (posterior) pallial tentacle and a simple posterior foot, unlike the paired posterior and single anterior pallial tentacles and indented posterior foot with a metapodial tentacle recorded in tornids (Ponder 1994). While ‘Clade A’ and Tornidae probably share a common origin, there is currently no basis for including *Nozeba* and *Auricorona* n. gen. in the latter family.

Elachisinidae was not represented in the molecular analysis, but this group of truncatelloid marine microgastropods shows some similarities to both ‘Clade A’ and *Aenigmula* n. gen.. Elachisinids have a moderately tall-spined (ovate-conic) shell, dome-shaped protoconch and

a posterior tentacle (sometimes with an additional anterior pallial tentacle) (Ponder 1985). Either ‘Clade A’ or *Aenigmula* n. gen. (or neither) may be synonymous with Elachisinidae, but this hypothetical relationship is speculative and untested. One species of elachisinid, *Elachisina ziczac* Fukuda & Ekawa, 1997, has been placed in *Nozeba* in at least one publication (Japanese Association of Benthology 2012), reflecting the possibility of a relationship between these two groups. The Hong Kong iravadiid *Lantauia taylori* Ponder, 1994 has a squat, ‘vitrinelliform’ shell shape, but lacks a pallial tentacle.

‘Clade A’ is distinguished from Iravadiidae s. str. by its paucispiral operculum, posterior pallial tentacle and domed protoconch. Although *Nozeba* and *Auricorona* n. gen. are not very similar to each other, they share a few morphological characters. They are both minute (< 3 mm shell height) and have a radula with a distinctive central tooth bearing prominent lateral branches and well-developed basal denticles on the lower margin, unlike Iravadiidae s. str. Despite strong molecular evidence, there are few characters to separate ‘Clade A’ and *Aenigmula* n. gen. (see Remarks), as the shells, opercula and radulae of *Nozeba* and *Aenigmula* n. gen. are remarkably similar. Due to my uncertainty about the inclusion of several species that have been placed in *Nozeba* by previous authors, I have not provided a description for this unnamed family group.

Nozeba Iredale, 1915

Nozeba Iredale 1915: 453. Type species (original designation): *Rissoa emarginata* Hutton, 1885; Plio-Pleistocene and Recent, New Zealand.

Antinodulus Cossmann, in Cossmann and Peyrot 1919: 568. Type species (original designation): *Bulimus globulus* Grateloup, 1827; Lower Miocene, France.

Syntharella Laseron 1955: 100. Type species (original designation): *Eulima topaziaca* Hedley, 1908; Recent, Australia.

Description

Modified from Ponder (1984), including only characters known to be shared by all Recent taxa currently assigned to *Nozeba* (see Remarks).

Shell. Conical to elongate-conical; straight-sided to slightly convex whorl profile with smooth suture; umbilicate or non-umbilicate; up to 5¼ (?) whorls including protoconch, length to ~3 mm. Smooth, or with raised spiral sculpture on initial whorls, entire shell or base of shell only. Aperture teardrop-shaped, anterior margin rounded or excavated, posterior margin sharply angled; outer lip orthocline; external varix absent.

Protoconch. Dome-shaped, each whorl slightly descending. Smooth; transitional varix absent.

Operculum. Teardrop-shaped; paucispiral; nucleus near anterior umbilical margin. Exterior and interior surfaces with paucispiral growth lines.

Radula. Central tooth either with few cusps including prominent central cusp, or numerous small cusps.

Remarks

Recent species currently recognised in *Nozeba* are *N. emarginata* (New Zealand), *N. mica* Finlay, 1930 (New Zealand), *N. topaziaca* (Hedley, 1908), ?*N. striata* Ponder, 1984 (Philippines, deep water) and ?*N. lignicola* Hasegawa, 1997 (Japan, deep water). Also, *Elachisina ziczac* was recently transferred from *Elachisina* to *Nozeba* (Japanese Association of Benthology 2012). *Nozeba? striata* and ?*N. lignicola* were hesitantly included in *Nozeba* by their describing authors, because their shell and radular characters differ from those of *N. topaziaca* and *N. emarginata* (Ponder 1984; Hasegawa 1997). Hasegawa (1997) remarked that the radula and shell of *N. lignicola* closely resemble those of *N. striata* (as figured by Ponder 1984), with raised spiral ribs and a distinct central radular tooth with numerous equal cusps. It is not yet clear whether these species should be placed in a new genus (or perhaps in *Auricorona* n. gen., see Remarks for that genus), but they do not appear to be congeneric with *N. topaziaca*.

The type species of *Nozeba*, *N. emarginata*, has a simple, conical shell that is somewhat similar to that of both *N. topaziaca* and *Aenigmula criscionei* n. gen. and n. sp.. It is therefore possible that *N. emarginata* is in fact congeneric with *Aenigmula criscionei* n. gen. and n. sp.. This possibility cannot be explored using the available information, so it is preferable to provisionally retain the current species composition of *Nozeba*. See Ponder (1984) for a discussion of other possible synonyms and the fossil history of *Nozeba*.

Nozeba topaziaca (Hedley, 1908)

Eulima topaziaca Hedley 1908: pl. x, fig. 29.

Estea amblycorymba Cotton 1944: 289, pl. 16, fig. 2.

Type material (not examined)

Holotype of *Estea amblycorymba*. 14 fathoms, Gulf of St Vincent, South Australia (SAM D.14185).

Material examined

Holotype of *Eulima topaziaca*. Balmoral Beach, Middle Harbour, Sydney, 33°49'42"S, 151°15'01"E, coll. C. T. Starkey, 1907 (AMS C.029112).

Other material. Two dry lots from D'Entrecasteaux Channel and King Island, Tasmania; two wet lots and four dry lots from Victoria between Port Albert and Western Port; > 200 dry lots from New South Wales and Queensland between southern border of New South Wales and Gladstone region. See supplementary data for full list of material examined.

Redescription

Shell (Figs 2, 15A–C, E, F). Ovate-conical, delicate; straight-sided to slightly convex whorl profile with smooth suture; non-umbilicate; up to 5¼ whorls including protoconch, length 2.29–2.79 mm, diameter of last whorl 1.10–1.36 mm (Table 9). Glossy, pale grey with orange sutures and apertural lip; initial whorl with ~10 fine spiral threads, remaining whorls smooth except for weak axial growth striae; periostracum thin. Aperture teardrop-shaped, anterior margin rounded, posterior margin sharply angled; outer lip orthocone; external varix absent.

Protoconch (Fig. 15E, F). Dome-shaped, each whorl slightly descending; 2–2¼ whorls. Smooth; transitional varix absent.

Operculum (Fig. 15D). Teardrop-shaped; paucispiral; nucleus near anterior umbilical margin. Exterior and interior surfaces with paucispiral growth lines.

Radula ($n = 3$) (Figs 5J, 15G). Central tooth 3 – 4 + 1 + 3 – 4/1 + 1; central cusp large, secondary cusps diminishing outwardly; basal denticles large, triangular, positioned on lower margin; lateral margins elongated to form curved branches. Lateral teeth 6 – 7 + 1 + 5. Marginal teeth with subequal cusps; inner marginal teeth with ~20 cusps; outer marginal teeth with ~10 cusps.

External morphology and colouration in life (Fig. 15H, I). Head-foot transparent, colourless with opaque grey speckles on all surfaces of head, neck and foot; bright yellow pigment around eye. Posterior foot margin simple, lacking metapodial tentacle. Cephalic tentacles with bright yellow speckles on proximal third; covered with short cilia. Single short, posterior (right) pallial tentacle present.

Penis (Fig. 6G). Wide, short; enclosed duct opening at distal end; three glandular swellings on inner edge. Covered with grey speckles, densest around base of penis.

Distribution

Distributed throughout eastern Australia, from southern Tasmania (D'Entrecasteaux Channel) through Bass Strait (King Island), central and eastern Victoria (as far west as Port Phillip), throughout New South Wales and as far north as Gladstone in Queensland (Fig. 6F). Most specimens were collected from estuarine seagrass habitat (either by sweeping or dredging), but some specimens were collected

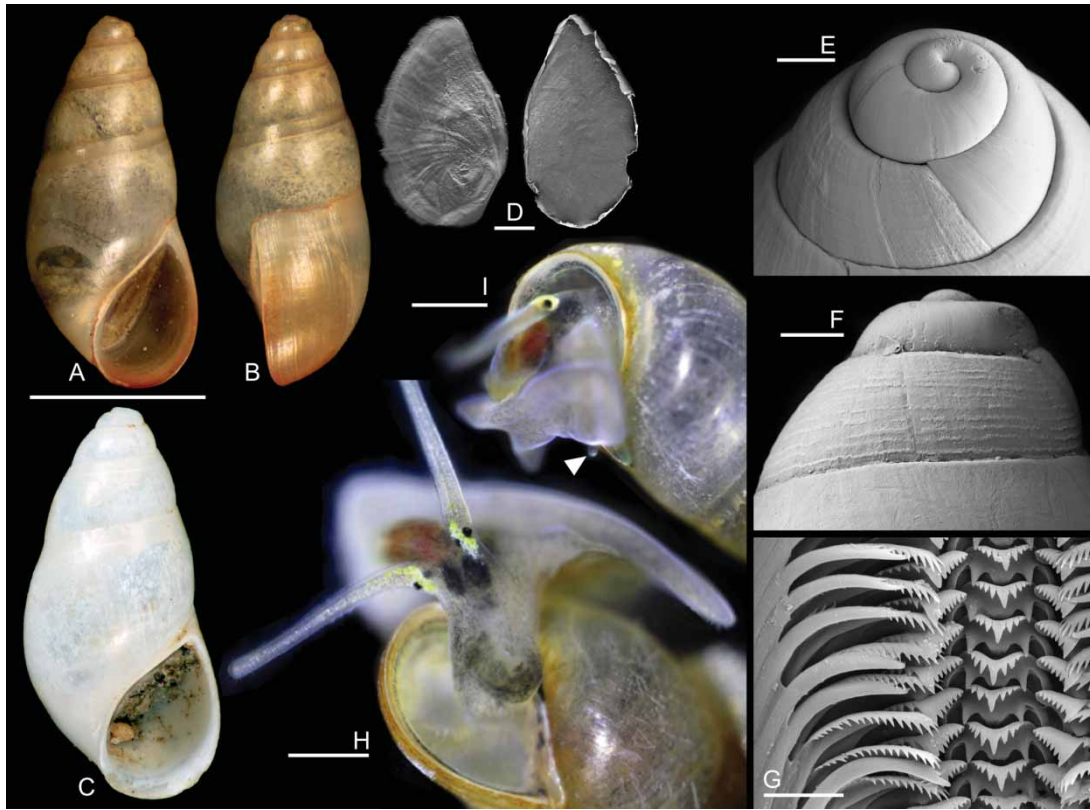


Figure 15. *Nozeba topaziaca* (Hedley, 1908). **A, B**, Representative specimen, Broken Bay, NSW, AMS C.327063; **C**, holotype of *Eulima topaziaca* Hedley, 1908, Balmoral Beach, NSW, AMS C.029112; **D**, interior and exterior surfaces of operculum, Port Phillip, VIC, AMS C.156452; **E**, protoconch, Gunnamatta Bay, NSW, AMS C.327101; **F**, shell sculpture with periostracum, AMS C.327101; **G**, radula, AMS C.156452; **H**, animal, Tannum Sands, QLD, AMS C.470937; **I**, animal with pallial tentacle (white arrow), Woy Woy, NSW, AMS C.475870. Scale bars: **A-C**, 1 mm; **D, H, I**, 200 μ m; **E, F**, 100 μ m; **G**, 10 μ m.

Table 9. Shell measurements of type and other specimens of *Nozeba topaziaca*.

Registration no.	Status	SL (mm)	SD (mm)	AL (mm)	AW (mm)	TWC	PWC
AMS C.029112	Ht	2.46	1.24	1.03	0.71	3	2
AMS C.327101	—	2.79	1.36	1.31	1.86	3 $\frac{1}{4}$	2
AMS C.327101	—	2.74	1.29	1.16	0.81	3	2 $\frac{1}{4}$
AMS C.327101	—	2.67	1.29	1.16	0.81	3 $\frac{1}{4}$	2
AMS C.327101	—	2.59	1.26	1.19	0.78	3 $\frac{1}{4}$	2
AMS C.327101	—	2.48	1.21	1.10	0.78	3	2
AMS C.327101	—	2.29	1.10	1.05	0.85	3	2
Average ($n = 7$)		2.58	1.25	1.14	0.80	3–3 $\frac{1}{4}$	2–2 $\frac{1}{4}$

Notes: Ht, holotype.

by washing mangrove leaf litter during recent fieldwork in Queensland.

Remarks

Despite a wide distribution across eastern Australia, molecular evidence from this study suggests that *N. topaziaca* has low sequence divergence between Queensland and southern New South Wales.

Auricorona n. gen.

Type species: Auricorona queenslandica n. sp.

Diagnosis

Shell minute, elongate, with convex whorl profile and coarse spiral ribs; aperture lacking external varix. Protoconch tall with weak spiral threads. Operculum subcircular, paucispiral, nucleus eccentric. Radula with

elongate lateral margins, single pair of basal denticles present. Opercular lobe decorated with ring of bright orange pigment; posterior foot lacking metapodial tentacle; posterior pallial tentacle present.

Remarks

A full description of the genus is not given because the description of the only known species of *Auricorona* is given below and can be taken as a description of the genus. Although provisionally placed here in the same group as *Nozeba* ('Clade A'), the only species currently included in *Auricorona* (*A. queenslandica* n. gen. and n. sp.) is unlike any of the other 'iravadiids' examined in this study. The most relevant comparisons are to the Japanese iravadiids *Ceratia nagashima* and *Nozeba lignicola*. The shells of those Japanese species have a similar size, shape and spiral sculpture to *A. queenslandica* n. gen. and n. sp. They all have paucispiral opercula, but that of *C. nagashima* is more elongate and has a distinct pattern on the internal surface, unlike *Auricorona* n. gen. *Ceratia nagashima* also has a shallow indentation in the posterior margin of the foot, a unique configuration of the central tooth and a shorter protoconch. Despite these differences, *C. nagashima*, *N. lignicola* and *A. criscionei* n. gen. and n. sp. are likely to belong in the same family-level group.

Etymology

Named for the externally visible pigmented ring around the opercular lobe, which resembles a golden (*auri-*) ring or the halo of light (*corona*) visible during a solar eclipse.

Auricorona queenslandica n. sp.

Material examined

Holotype. Mouth of Crab Creek, Tin Can Bay, Queensland, 25°55'52"S, 153°00'50"E, coll. R. Golding and S. A. Clark, 11 October 2011, on sandy mud in upper mangroves under damp leaf litter (QM MO.80761). *Paratypes*. Same data (QM MO.80762, 2; AMS C.470951, 4).

Other material. Queensland: Gatakers Bay, Point Vernon, Hervey Bay, 25°15'00"S, 152°49'00"E, coll. I. Loch, 23 October 1976, on dead green filamentous algal mat in clearing in beach mangroves (AMS C.175319, 4); near water treatment plant, Turkey Beach, 24°05'18"S, 151°38'51"E, coll. R. Golding and S. A. Clark, 10 October 2011, under moist leaf litter on surface of mud, back of mangroves (AMS C.470944, 9).

Description

Shell (Figs 2, 16A–D). Elongate, delicate; convex whorl profile with strongly impressed suture; umbilicate; up to 6³/₄ whorls including protoconch, height 1.98–2.54 mm, diameter of last whorl 0.72–0.91 mm (Table 10). Golden

to pale brown; ~25 coarse, narrow spiral ribs on last whorl, crossed by irregular axial threads; periostracum thick, velvety. Aperture subcircular, posterior margin weakly angled; outer lip prosocline; external varix absent; aperture sometimes slightly separated from shell at umbilical margin.

Protoconch (Fig. 16D). Tall, with initial whorl slightly descending, second whorl rapidly descending. Smooth, with ~10 weak spiral threads on last whorl; transitional varix absent.

Operculum (Fig. 16E). Subcircular with slightly pointed posterior margin; paucispiral; nucleus eccentric. Exterior and interior surfaces with paucispiral growth lines.

Radula ($n = 2$) (Figs 5K, 16F). Central tooth 2 – 3 + 1 + 2 – 3/1 + 1; cutting edge triangular; central cusp large, secondary cusps diminishing outwardly; basal denticles large, triangular; lateral margins elongated to form straight branches. Lateral teeth 3 – 4 + 1 + 7. Marginal teeth with subequal cusps; inner marginal teeth with ~14 cusps on tip and distal half of outer edge; outer marginal teeth with many cusps on distal third of inner edge.

External morphology and colouration in life (Fig. 6G–I). Head-foot semi-transparent, colourless; opaque white speckles behind eyes and on ventral and lateral surfaces of body; perimeter of opercular lobe encircled by ring of bright orange dots. Posterior foot margin simple, lacking metapodial tentacle. Cephalic tentacles unpigmented. Single, short, posterior (right) pallial tentacle present.

Penis. Not observed.

Distribution (Fig. 7G)

Known from only three locations in the Great Sandy Strait region of central Queensland. *Auricorona queenslandica* lives in the back of muddy mangroves and during recent field work was found living beneath mangrove leaves that had settled on the damp surface of the mud, rather than in pools.

Remarks

Auricorona queenslandica is a minute species that might easily be overlooked when sampling micromolluscs in mangrove habitat across its distribution in central Queensland. When examined alive it is instantly recognisable by the ring of vivid orange pigment that encircles the opercular lobe. This feature is visible externally through the delicate and transparent operculum.

Etymology

Named for the narrow distribution of this species on the coast of central Queensland.

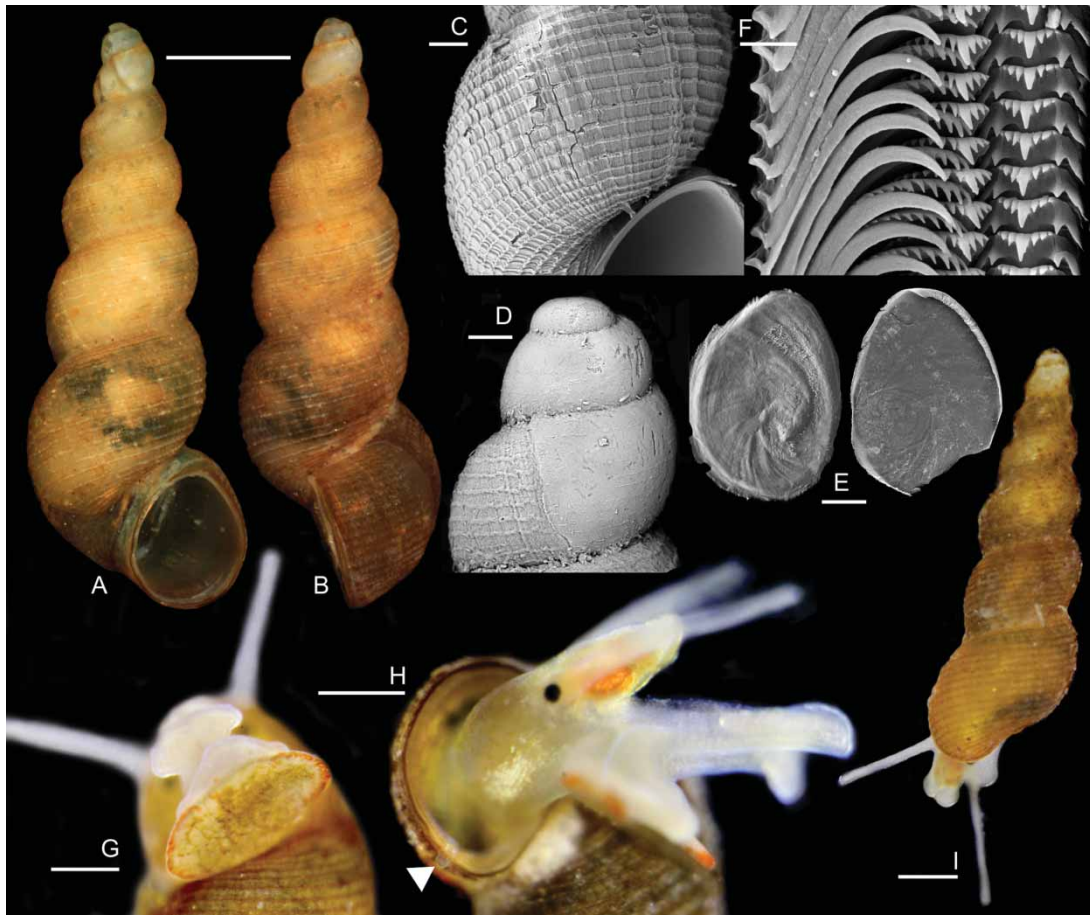


Figure 16. *Auricorona queenslandica* n. gen and n. sp.. **A, B**, Holotype, Tin Can Bay, QLD, QM MO.80761; **C**, shell sculpture with periostracum; **D**, protoconch, Turkey Beach, QLD, AMS C.470944; **E**, interior and exterior surfaces of operculum; **F**, radula; **G**, animal showing ring of pigment on opercular lobe (visible through operculum); **H**, animal showing pallial tentacle (white arrow); **I**, animal crawling. **C, E–I** paratypes from Tin Can Bay, QLD, AMS C.470951. Scale bars: **A, B**, 500 µm; **C, E**, 100 µm; **D**, 50 µm; **F**, 5 µm; **G–I**, 200 µm.

Table 10. Shell measurements of type and other specimens of *Auricorona queenslandica* n. gen. and n. sp.

Registration no.	Status	SL (mm)	SD (mm)	AL (mm)	AW (mm)	TWC	PWC
QM MO.80761	Ht	2.50	0.91	0.59	0.50	4 ³ / ₄	2
QM MO.80762	Pt	2.54	0.87	0.64	0.51	5	—
QM MO.80762	Pt	2.52	0.88	0.64	0.47	5	2
AMS C.470951	Pt	2.48	0.88	0.64	0.53	4 ¹ / ₂	2 ¹ / ₄
AMS C.470951	Pt	2.34	0.81	0.55	0.45	4 ¹ / ₂	—
AMS C.470951	Pt	1.98	0.72	0.53	0.40	4	—
AMS C.470944	—	—	—	—	—	—	2 ¹ / ₄
Average (<i>n</i> = 7)		2.39	0.85	0.60	0.48	4–5	2–2 ¹ / ₄

Notes: Ht, holotype; Pt, paratype.

Uncertain higher classification

Remarks

Aenigmula criscionei n. gen. and n. sp. described below is the sole representative of an unknown family or higher ranked group. *Aenigmula criscionei* was included in this study because it closely resembles the ‘iravadiid’ *Nozoba*,

with its minute, smooth, ovate-conic shell. Molecular analysis provides strong support for the position of *Aenigmula* n. gen. in a section of the truncatelloid phylogeny separate from any recognised iravadiids. The surprising discovery that *Aenigmula* n. gen. is, on the basis of the molecular analysis, not closely related to either Iravadiidae

s. str. or *Nozeba* ('Clade A') presents a challenge for assigning this taxon to a particular truncatelloid family.

Aenigmula n. gen. is nested in a well-supported section of the molecular phylogeny between Caecidae and a clade composed of Calopiidae and Clenchiellidae. The position of *Aenigmula* n. gen. on a discrete branch of the tree precludes its placement in any of these related families, and there are no evident characters to contradict this conclusion. As discussed above (see Remarks for 'Clade A'), there may be a relationship between Elachisinidae and 'Clade A' or *Aenigmula* n. gen., based on morphological and conchological characters (but not yet tested by molecular data). While this identity is possible, it is speculative and requires testing using molecular data.

This taxon is distinguished from Iravadiidae s. str. by its paucispiral operculum, configuration of the central radular tooth and domed (rather than flat) protoconch. Few morphological characters have been identified to distinguish *Aenigmula* n. gen. from 'Clade A', despite strong molecular support for the separation of these groups from each other and related taxa. As this taxon is monotypic, no description has been given for the unknown group of higher rank or *Aenigmula* n. gen. (see instead the description of *A. criscionei* n. gen. and n. sp.).

Aenigmula n. gen

Type species: *Aenigmula criscionei* n. sp.

Diagnosis

Small, glossy, ovate-conic, unsculptured, non-umbilicate shell; teardrop-shaped aperture lacking external varix. Protoconch dome-shaped. Operculum paucispiral, nucleus eccentric. Radula with curved, elongate lateral margins, single pair of basal denticles present.

Remarks

Only one species is recognised in *Aenigmula* n. gen., and there is little morphological or ecological information available to characterise the genus. It is necessary to recognise a new genus for *Aenigmula criscionei* n. gen. and n. sp., based on its position in the molecular phylogeny of Truncatelloidea in which it is not closely related to any other iravadiid and shows little morphological similarity to other non-iravadiid taxa to which it is apparently related.

Etymology

Named for the 'little puzzle' (Latin, puzzle = *aenigma*) that the only known species brings to our understanding of truncatelloid evolution.

Aenigmula criscionei n. sp.

Material examined

Holotype. Rapid Creek, Darwin, 12°23'03"S, 130°51'57"E, coll. F. Criscione, 14 August 2010, on dead mangrove leaves in pools, LT (NTM P.50626).

Paratypes. Same data (NTM P.50627, 3; AMS C.475887, 5).

Description

Shell (Figs 2, 17A–C, E). Ovate-conical; straight-sided to slightly convex whorl profile with smooth suture; non-umbilicate; up to 5³/₄ whorls including protoconch, length 2.14–2.93 mm, diameter of last whorl 0.91–1.36 mm (Table 11). Glossy, golden; smooth except for very faint axial growth striae; periostracum thin. Aperture teardrop-shaped, anterior margin rounded, posterior margin sharply angled; outer lip slightly prosocline; external varix absent.

Protoconch (Fig. 17C, E). Dome-shaped, each whorl slightly descending; 1³/₄–2 whorls. Smooth; transitional varix absent.

Operculum (Fig. 17D). Teardrop-shaped; paucispiral; nucleus near anterior umbilical margin. Exterior and interior surfaces with paucispiral growth lines.

Radula ($n = 1$) (Figs 5L, 17F). Central tooth 3 – 4 + 1 + 3 – 4/1 + 1; central cusp large, secondary cusps diminishing outwardly; basal denticles large, triangular, positioned on lower margin; lateral margins elongated to form curved branches. Lateral teeth 4 – 5 + 1 + 5 – 6. Marginal teeth with subequal cusps; inner marginal teeth with ~20 cusps; outer marginal teeth with ~20 cusps.

External morphology and colouration in life, and penis. The bodies of specimens preserved in 95% ethanol are entirely white, but no other morphological features could be determined.

Distribution (Fig. 7H)

Known from a single location in mangrove forest at Rapid Creek, Darwin, living on mangrove leaf litter in pools.

Remarks

This species is an unanticipated discovery and requires further work. Not only is it currently unassignable to a truncatelloid family, nothing is known about its soft-tissue anatomy, and little about its ecology or mode of life. From the limited information available, it appears in most respects to be a 'typical' truncatelloid gastropod. Molecular evidence suggests that it is most closely related to Caecidae, Clenchiellidae and Calopiidae, with which it has little in common except its minute size (like the other

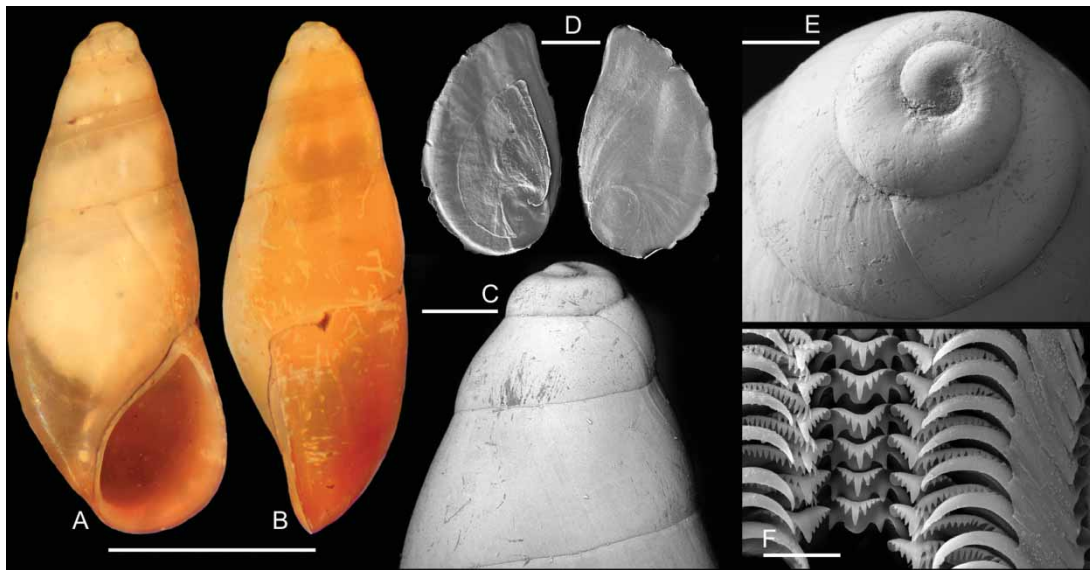


Figure 17. *Aenigmula criscionei* n. gen and n. sp.. **A, B**, Holotype, Darwin, NT, NTM P.50626; **C**, apical shell; **D**, interior and exterior surfaces of operculum; **E**, protoconch; **F**, radula. **C–F**, paratypes from Darwin, NT, AMS C.475887. Scale bars: **A, B**, 1 mm; **C, D**, 200 μ m; **E**, 100 μ m; **F**, 10 μ m.

Table 11. Shell measurements of type specimens of *Aenigmula criscionei* n. gen. and n. sp.

Registration no.	Status	SL (mm)	SD (mm)	AL (mm)	AW (mm)	TWC	PWC
NTM P.50626	Ht	2.93	1.24	1.07	0.78	4	1 ³ / ₄
NTM P.50627	Pt	2.86	1.36	1.05	0.79	4	1 ³ / ₄
NTM P.50627	Pt	2.59	1.14	0.95	0.70	3 ¹ / ₂	2
NTM P.50627	Pt	2.22	0.98	0.76	0.60	3 ¹ / ₄	2
AMS C.475887	Pt	2.67	1.24	1.00	0.79	3 ¹ / ₂	2
AMS C.475887	Pt	2.53	1.08	0.90	0.70	3	2
AMS C.475887	Pt	2.17	0.91	0.76	0.57	3	—
AMS C.475887	Pt	2.14	1.02	0.90	0.64	3	2
Average ($n = 8$)		2.51	1.12	0.92	0.70	3–4	1 ³ / ₄ –2

Notes: Ht, holotype; Pt, paratype.

three families) and presence in a mangrove habitat (like most Clenchiellidae).

Etymology

Named for my colleague Dr Francesco Criscione, who collected the type (and only known) specimens of this species and kindly contributed the material to this study.

Discussion

This study has recorded six new species and two new genera from Australia. Two formerly synonymised species and two genera have also been reinstated. This newly recognised diversity is a significant addition to the known iravadiid fauna and presents an opportunity to re-evaluate the classification of the group. This is particularly necessary because while some of the new species are closely related to known iravadiid taxa, others are phylogenetically distinct. An interesting and unexpected

outcome of this study was the discovery that some taxa that were believed to be widespread throughout Australia or the Indo-Pacific region actually have two or three molecularly distinct species represented in Australia. The taxon previously recognised as *Iravadia quadrasi* is now, with the benefit of molecular data, known to comprise three allopatric but morphologically similar species, each restricted to a different region of the northern Australian coastline. Likewise, the species formerly known as '*Iravadia*' *australis* and '*Iravadia*' *resima* are composed of species pairs with northern/eastern and western distributions. These findings increase the number of known species, but do not significantly alter our understanding of iravadiid evolution. In contrast, the discovery of *Auricorona queenslandica* and *Aenigmula criscionei* introduces a new element to our knowledge of Iravadiidae, and demands a critical re-evaluation of the classification and evolutionary interpretation of the group.

The generic classification established by Ponder (1984) provided a valuable framework for interpreting the morphological and systematic diversity of Iravadiidae. With the benefit of molecular data, it is now possible to revise some elements of the classification to reflect this new line of evidence. This study is limited by its focus on Australian species and the absence of several key groups, in particular *Iravadia* (*Fairbankia*), *Iravadia* (*Pseudonoba*), *Chevallieria*, *Lantauia*, *Ceratia*, *Aliceratia*, *Liroceratia* and *Rissopsis*, the last of which is only known from shell characters. However, the sampling was sufficiently broad to test some aspects of the current classification scheme. At the genus level, the changes proposed here are conservative and provisional on the addition of further sequences from other iravadiids.

Fluviocingula and *Pseudomerelina*, previously subgenera of *Iravadia*, have been elevated to full genus level. This reflects the narrower definition of Iravadiidae s. str. and the discovery of additional species diversity in *Fluviocingula*. Despite the absence of the type species of *Fairbankia* from the analysis, two previously synonymised genus-level names were reinstated to accommodate the phylogenetic structure of Iravadiidae. *Pellamora* is used for the Australian species formerly included in *Fairbankia*, and *Wakauraia* includes the original Japanese species and a newly discovered species from Australia. These decisions should be verified in future by the inclusion of the molecular data from the type species of *Fairbankia*, *F. bombayana*. *Iravadia* s. str. was found to be paraphyletic and the internal branches were poorly supported and inconsistent between analyses. The paraphyly arose because *Iravadia* cf. *capitata* clusters with *W. fukudai* n. sp. rather than with the '*I. quadrasi*' species group. This is unsurprising, because they do not share many distinguishing features (for example, tentacle pigmentation or shell sculpture). The decision to retain the paraphyletic genus *Iravadia* is based on the absence in the analysis of the type species, *I. ornata* and many other species presently included in this group. It is unfortunate that *Pseudonoba*, the most divergent subgenus of *Iravadia*, could not be included in this study. Species in that group are rare and difficult to collect because they most probably live on soft-bottomed subtidal habitats (Ponder 1984). On the basis of the morphological evidence presented by Ponder (1984), it is likely that *Pseudonoba* should be considered a distinct genus in Iravadiidae s. str., because it shares some key characters of that family such as the operculum having a marginal nucleus.

The most significant outcome of this study is the confirmation of polyphyly in 'Iravadiidae'. Both 'Clade A' and *Aenigmula* are phylogenetically isolated from Iravadiidae s. str., but cannot be united with any of the other truncatelloid families to which they are related. As discussed in the Remarks for 'Clade A', the possibility remains that either family could be connected to Elachisinidae, which could

not be included in the molecular analysis, but shares some morphological features. Another interesting outcome of the molecular phylogeny was the well-supported cluster of families comprising of Iravadiidae s. str.: 'Clade A', *Aenigmula*, Tornidae, Clenchiellidae and Calopiidae. This group was highly supported as a monophyletic unit and at each internal node, and was also recovered in the analyses of Criscione and Ponder (2012) ('Clade I') using similar species but a narrower data set of genes. The addition of COI sequence data in this study showed the unique deletion of a single codon in this group alone in Truncatelloidea, providing further support for the validity of this unnamed group. All members of this group are small and predominantly inhabit estuarine or brackish water. Further work is needed to better characterise the significance of this evolutionary unit.

The anatomical descriptions presented by Ponder (1984) are more comprehensive than the data used here, but it is useful to consider the systematic value of each character system. The 'iravadiid' shell is always small, but sculpturally diverse. Sculpture is generally unique to each genus recognised here, but fails to differentiate the divergent genera *Nozeba* and *Aenigmula* n. sp. The flat, simple protoconch that was previously the sole unifying character of 'Iravadiidae' is shown here to be more diverse in shape. The protoconch of Iravadiidae s. str. is planar for the first whorl, then descends slightly and sometimes has a strong transitional varix. In *Nozeba* and *Aenigmula* n. gen., the initial whorl is not planar and the protoconch is dome-shaped, while in *Auricorona* n. gen. the protoconch is tall and multispiral. Ponder (1984) found some significance in the presence of ridges on the interior surface of the operculum but ridges were found to be present on the interior surface of the operculum of most species in Iravadiidae s. str. While there were differences in the angle of the ridges, it remains to be seen whether they are phylogenetically informative. The overall shape of the central tooth of the radula is significant in separating Iravadiidae s. str. from 'Clade A' and *Aenigmula* n. gen.. The attenuation of the lateral margins of the central tooth in *Nozeba*, *Auricorona* n. gen. and *Aenigmula* n. gen. differentiates these groups from the true iravadiids. Soft-tissue anatomy is difficult to interpret because it is missing from some key species, such as *Aenigmula* n. gen. The most useful aspect, in terms of genus and species discrimination, is tentacle pigmentation. The presence of single, double or multiple black bands on the tentacles is restricted to a monophyletic subset of Iravadiidae s. str., excluding *Wakauraia* and *I.* cf. *capitata*. Ponder (1984) recognised the potential phylogenetic utility of reproductive morphology in Iravadiidae. Unfortunately, no new data on the reproductive system were produced during this study, except for descriptions of diverse penis morphologies. This is just one area of future research that will contribute to a greater understanding of the evolution of Iravadiidae.

Supplementary data

Supplementary file 1. Full list of material examined.

Acknowledgements

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