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Two new genera of land snail from dry subtropical forests of eastern Australia: Brigaladra gen. nov. and Euryladra gen. nov. (Eupulmonata: Camaenidae)

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Two new genera of land snail from dry subtropical forests of eastern Australia: *Brigaladra* gen. nov. and *Euryladra* gen. nov. (Eupulmonata: Camaenidae)

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ABSTRACT

Figuladra is a poorly understood genus of camaenid land snail endemic to subtropical eastern Australia, comprising species that inhabit either dry rainforests in the coastal hinterland or dry sclerophyll forests further inland. Given that the genus occurs in areas that have seen extensive land clearing, such as the inland brigalow scrub (savannah) and coastal vine thickets (dry rainforest), resolution of this genus is required to inform conservation efforts within these critical landscapes. Here we use an integrative approach based on comparative analyses of mitochondrial DNA sequences and key morphological features to review the systematic relationships within the group. Specifically, we performed Maximum Likelihood and Bayesian analyses of concatenated DNA sequences of two partial mitochondrial genes (*16S* and *COI*) to reconstruct the phylogenetic relationships of *Figuladra*. We subsequently examined features of the reproductive system that are considered to be useful in diagnosing genera (whole genitalia) and species (penial architecture) within the Camaenidae. Based on patterns of molecular differentiation and an assessment of the anatomy, we propose a more restrictive definition of *Figuladra* and describe two new monotypic genera for species that were previously assigned to *Figuladra*; *Euryladra* gen. nov. for *Varohadra incei mattea* Iredale, 1933 and *Brigaladra* gen. nov. for *Varohadra volgiola* Iredale, 1933. These two new genera differ from *Figuladra sensu stricto* in exhibiting distinctive epiphallic coiling patterns and anatomical differences of the penis–epiphallus configuration. The study shows that these three genera, and allied taxa, reveal contrasting patterns of diversity and distribution in two neighbouring habitat types: high levels of diversity and endemism in fire-sensitive seasonal subtropical forests juxtaposed against low diversity in large intervening areas of regularly burnt savannah and open woodlands.

Keywords: anatomy, camaenid, land snail, mitochondrial DNA, morphology, open woodland, Queensland, savannah, vine thicket.

Introduction

The Camaenidae is a family of rock, forest and woodland snails that are widespread across Australia, absent only from south-western Western Australia, Tasmania and the sandy deserts of central Australia (Stanisic *et al.* 2010, 2018; Hugall and Stanisic 2011). There are two centres of diversity for camaenids, the Kimberley region of the far north-west and the ranges of eastern Australia. Australian camaenids inhabit rainforests (moist tropical, sub-tropical and vine thickets) and woodlands (open eucalyptus forests) to drier savannahs (brigalow, scrub) (e.g. Hugall *et al.* 2002; Stanisic *et al.* 2010, 2018; Köhler 2011*a*; Parkyn and Newell 2013).

In eastern Australia, there are several genera of so-called 'large forest hadroid snails' (large, often striped camaenids). *Figuladra* Köhler & Bouchet, 2020 is one of these genera from north-eastern Australia (Queensland) with a distribution from the moister coastal areas to the drier interior west of the Great Dividing Range, mostly inhabiting dry vine thickets and open woodlands. Most species occur close to the coast, but two additional

species inhabit dry vine thickets in mid-eastern Queensland to the west of the mountains that run along Australia's east coast. Most *Figuladra* species are considered to be narrow range endemics (Stanisic *et al.* 2010). Currently, the identification and delineation of species in this genus rests predominantly on shell characters such as colour, size and banding patterns, but details of the reproductive anatomy and phylogenetic relationships are largely unknown. *Figuladra* taxonomy is complicated by a high intraspecific variation in shell colour and banding pattern in some of the species. Given that the genera occur in areas that have seen extensive land clearing, such as the inland brigalow scrub (savannah) and coastal vine thickets (dry rainforest), resolution of this genus is required to inform conservation efforts within these critical landscapes.

Figuladra has a particularly convoluted taxonomic history. The eastern Australian hadroids were once all placed in a single genus, *Sphaerospira* Mörch by Smith (1992). However, Stanisic *et al.* (2010) restricted *Sphaerospira* to some species more closely associated with rainforests along the eastern seaboard and allocated many species to other genera. This subdivision of *Sphaerospira* was made with main emphasis on animal colour, particularly that of the mantle, and shell morphology. Unpublished details of the reproductive anatomy formed an additional tier for the separation of these genera (Stanisic *et al.* 2010, p. 7). *Figuladra* in the current configuration was delineated by Stanisic *et al.* (2010) using a name first introduced by Iredale (1933). However, Köhler and Bouchet (2020) found that Iredale's original name was unavailable due to the lack of a formal diagnosis (Art. 13.4 of the Code; International Trust for Zoological Nomenclature 2012) and that this name had not been made available subsequently. To maintain the previous treatment of Stanisic *et al.* (2010), these authors described *Figuladra* as a new genus with the type species *Helix curtisiana* Pfeiffer, 1864. Prior to Stanisic's treatment, Iredale (1937, p. 30) placed *Figuladra* Iredale, 1933 in synonymy of *Varohadra* Iredale, 1933. However, *Varohadra* Iredale, 1933 is also an unavailable name (Köhler and Bouchet 2020). Smith (1992) correctly recognised *Figuladra* and *Varohadra* as *nomina nuda* and placed all species previously classified under these names as members of *Sphaerospira* Mörch, 1867 citing Bishop's (1978) anatomical study of *S. fraseri* Griffith and Pidgeon, 1833 as the reason for this taxonomic decision. Stanisic and Stanisic (2020) resolved historical taxonomic confusion surrounding *Figuladra* species described before 1900 thus allowing for revisions of *Figuladra* to be undertaken unencumbered by taxonomic ambiguity.

Molecular phylogenetic data for eastern Australian camaenids were limited until the landmark study by Hugall and Stanisic (2011). The phylogenetic tree of Hugall and Stanisic (2011, fig. 7) covered ~90% of the eastern Australian camaenid species accepted at the time and demonstrated that the traditional, largely shell-based classification was misled by convergence in shell characters. Shell morphology has proven to be of limited value as a taxonomic marker when used to delimit taxa in camaenids without regard to other sources of evidence (Köhler and Johnson 2012; Perez *et al.* 2014; Köhler and Criscione 2015). Similarly, Hugall and Stanisic (2011) concluded that the taxonomic classification of east coast camaenids had been misdirected by parallelism in shell form, but also stated that comparative shell morphology has a place within the framework of an integrative taxonomy. In contrast to the limited use of shell morphology, comparative anatomy of the terminal reproductive organs has been shown to be taxonomically informative in distinguishing genera (whole genitalia) and species (penial architecture) within the Camaenidae (e.g. Solem 1979, 1985, 1992; Stanisic 1996, 2013, 2016; Köhler 2011*a*, 2011*b*; Criscione and Köhler 2014*a*).

Hugall and Stanisic (2011) showed that there were four major clades within the 'hadroid complex' of camaenids (Clades 1–4). Clades 1 and 4 have overlapping distributions from far north-eastern Australia down to north-eastern New South Wales. However, the distributions are somewhat complementary, with Clade 1 taxa tending to occur in dry seasonal forest habitats (often referred to as vine thickets, scrub or dry rainforest in Australia), whereas Clade 4 taxa tend to occur in wetter rainforest habitats. Clade 2 comprised species that are concentrated in north-eastern Australia whereas Clade 3 comprised species in south-eastern Australia. *Sphaerospira*, as previously construed, represented a polyphyletic group spanning lineages in both Clade 1 and Clade 4 (Fig. 1). Hugall and Stanisic subsequently confirmed that the type species, *Sphaerospira fraseri* (Griffith & Pidgeon, 1833), belonged to Clade 4. This phylogeny illustrated that many species from Clade 1, thought to belong to *Sphaerospira*, were no longer in that genus. *Figuladra* was applied to the lineage containing *mattea*, *volgiola* and *incei curtisiana* (see Fig. 1) within Clade 1 by Stanisic *et al.* (2010). The apparent closest relative to this clade is the genus *Billordia* that comprises two species that occur in vine thickets on rocky screes in south-central Queensland.

The taxonomy of *Figuladra* clearly needs revision. The phylogeny of Hugall and Stanisic (2011) provides the basis for further investigations and a starting point for an in-depth examination of the *Figuladra* lineage containing the species *F. mattea*, *F. volgiola* and *F. incei curtisiana* (type species), and the related genus *Billordia*. The aim of this study was to test the taxonomic status of the *Figuladra* lineage by means of molecular phylogenetic and comparative morphological analyses. We use an integrative approach initially based on comparative analyses of mitochondrial phylogenetics by analysing fragments of two partial mitochondrial genes, *16S* rDNA (*16S*) and cytochrome *c* oxidase subunit I (*COI*). We used key morphological features (shell, radular morphology and reproductive anatomy) to review the systematic relationships of *Figuladra* more comprehensively.
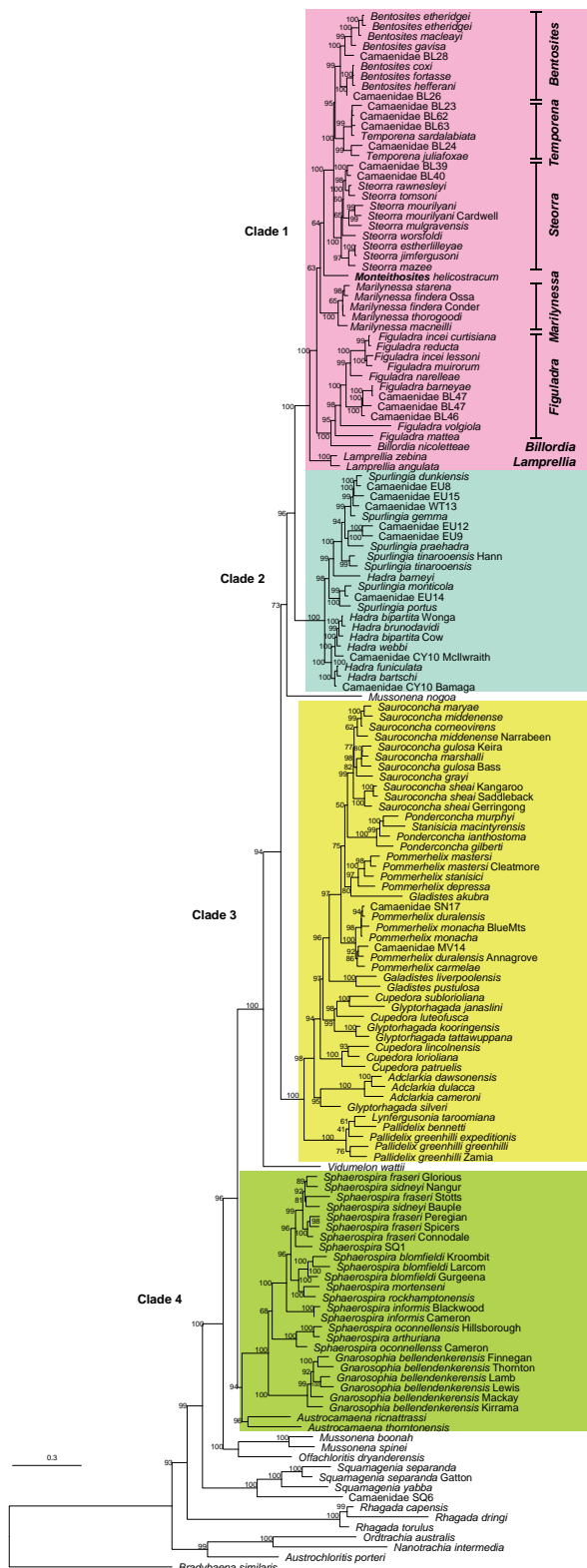
Fig. 1. Maximum Likelihood tree based on analysis of GenBank sequences representing the clades 1 to 4 in the tree depicted by Hugall and Stanisic (2011, fig. 7) showing a reconstruction of the phylogenetic relationships among the Eastern Australian hadroid snails. Species names have been updated in accordance with the current taxonomy proposed by Stanisic *et al.* (2010). Phylogeny courtesy of Andrew Hugall.

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Abbreviations used

General: SEM, scanning electron microscopy; SC, spirit collection; RC, dry collection.

Institutions: AMS, Australian Museum, Sydney; QM, Queensland Museum, Brisbane.

Geography: BL, Brigalow Lands; Ck, Creek; I, Island; MEQ, mid-eastern Queensland; Mt, Mount; NP, National Park; NQ, North Queensland; NSW, New South Wales; R, River; Ra, Range; SCQ, southern-central Queensland; SEQ, south-eastern Queensland; SF, State Forest, WA, Western Australia; WT, Wet Tropics.

Molecular phylogenetics: *16S*, *16S* rRNA gene; BI: Bayesian Inference; *COI*, cytochrome *c* oxidase subunit I gene; ML, Maximum Likelihood.

Shell features: D, shell diameter; H, shell height; H/D, ratio of shell height to shell diameter; W, number of whorls.

Genital anatomy: BC, bursa copulatrix; DG, prostate; E, epiphallus; EF, epiphallic flagellum; EP, epiphallic pore; GD, hermaphroditic duct; GG, albumen gland; P, penis; PPL, penial pilasters; PRM, penial retractor muscle; PS, penial sheath; PV, penial verge; UT, uterus; UV, free oviduct; V, vagina; VD, vas deferens; Y, atrium.

Materials and methods

Specimens and sampling

This work is based on examinations of dry shells and ethanol preserved samples deposited in the Queensland Museum, Brisbane and the Australian Museum, Sydney. This includes material collected recently during field trips in eastern Queensland. Live specimens were transported from the field to the laboratory, euthanased by immersing in water, usually overnight, fixed in 95% ethanol and subsequently stored in 70% ethanol for use in anatomical and molecular studies. All newly collected specimens have been lodged in the Queensland Museum (Supplementary Table S1).

Molecular phylogenetics

Genomic DNA was extracted from small pieces of foot muscle using the QIAGEN DNeasy tissue kit following the Spin Column protocol. Fragments of two partial mitochondrial genes (*16S* and *COI*) were amplified by PCR using the primers 16SCS1 (Chiba 1999) and 16SBD1 (Sutcharit *et al.* 2007) for *16S* and LCO1490 and HCO2198 (Folmer *et al.* 1991) for *COI*. Standard M13F and M13R primer sequences were appended to the *COI* primers to assist sequencing. PCR reactions (Supplementary Table S2) were performed under the following conditions: initial denaturation at 98°C for 2 min, followed by 35 cycles of 98°C for 30 s, 48°C for 30 s and 72°C for 30 s, with a final elongation step at 72°C for 5 min for *16S*; initial denaturation at 94°C for 2 min, followed by 45 cycles of 95°C for 60 s, 50°C for 60 s and 72°C for 60 s, with a final elongation step at 68°C for 10 min for

COI. The size of the PCR products was checked using UV transillumination after gel electrophoresis in a 1.5% agarose gel and TAE buffer solution. The PCR products were purified and sequenced at Macrogen Inc. (South Korea).

Sequences generated (from 34 individuals) have been deposited in GenBank under the accession numbers OL753690–OL753711 (*COI*) and OL839880–OL839914 (*16S*). Using the camaenid phylogeny of eastern Australia published by Hugall and Stanisic (2011) as a guide, several additional camaenid sequences were downloaded from GenBank and included in our analysis. Clades 1–4 from Hugall and Stanisic (2011) were defined as the hadroid clades and we have used this framework to anchor our study (Fig. 1). Accordingly, we included species shown to be more closely related to *Figuladra* (Clade 1 of the tree from Hugall and Stanisic 2011) and species that often occur in sympatry with *Figuladra* species considered to belong to a distantly related clade (Clade 4 of the tree from Hugall and Stanisic 2011). Sequences of the Western Australian camaenid *Rhagada dampierana* and *Austrochloritis porteri* from SEQ (Clade 9 from Hugall and Stanisic 2011) were used to root the tree. Details of the sequences used in the analysis can be found in Table 1.

The mtDNA sequences were aligned using the MAFFT (ver. 7.308, see https://mafft.cbrc.jp/alignment/software/; Katoh and Standley 2013) plug-in within Geneious (ver. 9.1.8, see https://www.geneious.com/; Kearse *et al.* 2012), with default settings. We used Guidance2 (ver. 2.02, see http://guidance.tau.ac.il/; Sela *et al.* 2015) to identify and remove unreliably aligned regions in the *16S* alignment by employing default settings. *COI* sequences were translated into amino acid sequences to ensure that possible pseudogenes were not included. For phylogenetic analyses, *16S* and *COI* nucleotide sequences were concatenated into one partitioned dataset. Four partitions were designated, one for each of the three codon positions of the *COI* and one for the *16S* gene fragment.

Phylogenetic relationships were estimated by employing a Maximum Likelihood-based method of tree reconstruction and Bayesian Inference. A Maximum Likelihood (ML) phylogeny was reconstructed by using the software IQ-TREE (ver. 1.6, see http://iqtree.cibiv.univie.ac.at/; Nguyen *et al.* 2015). We used the integrated modellfinder under the option 'merge' to identify the best-fit model of sequence evolution and merge partitions with similar models before the analysis (Kalyaanamoorthy *et al.* 2017). Nodal support of the best ML tree was estimated by performing 1000 ultra-fast bootstrap replicates. Bayesian posterior probabilities were estimated by running a 10 000 000 generation Metropolis-coupled Markov chain Monte Carlo (four chains, one heated, sampling rate 1000 generations) with a burn-in of 100 000 as implemented by the MrBayes (ver. 2.2.4, see https://github.com/NBISweden/MrBayes/; Ronquist and Huelsenbeck 2003) plug-in in Geneious (ver. 9.1.8).

Mean genetic *p*-distances within and among groups were calculated using MEGA6 (ver. 10.2.6, see www.megasoftware.net; Tamura *et al.* 2013).

Comparative morpho-anatomy

Details of the samples used for analysis of morpho-anatomy are provided in Supplementary Table S1. Characters investigated included shell shape, size (height and diameter), whorl count and colour patterns of both shell and mantle tissue (shell secreting organ). Standard definitions for conchological characters were used (Solem and van Bruggen 1984). Shell dimensions (height, diameter, whorl count) were measured using callipers with a precision of 0.1 mm. Differences in shell size (diameter) are indicated in the diagnoses using the following terms: medium (10–20 mm), large (21–40 mm), very large (> 40 mm). Whorls were counted to the nearest 1/8 whorl following Clark (2009). The microsculpture of the teleoconch was examined using a TM-1000 Tabletop Scanning Electron Microscope in topo image mode. For SEM, shells were cleaned by gently brushing in warm soapy water followed by ultrasound treatment. Samples were mounted on sticky tabs, sputter-coated with gold, and imaged under high vacuum.

Bodies were removed from the shells and dissected to extract the reproductive system that was submerged in a shallow container of 75% ethanol and pinned to a black latex base using very fine 'Austerlitz' entomological pins. Photographs of the reproductive system were taken using a NIKON Coolpix 4500 camera mounted on a WILD M5 stereo microscope.

Radulae and jaws were extracted from preserved specimens and cleaned by soaking in 10% KOH solution overnight followed by rinsing in water and ethanol. Specimens were mounted on aluminium stubs, coated with gold and studied under scanning electron microscopy.

High resolution images of shells and penial anatomy (260–600 MB) were obtained using a Visionary Digital BK-Plus laboratory system camera set-up located in the Queensland Museum's Digital Imaging Unit.

Results

Molecular phylogeny

We analysed two different datasets. First, we used Hugall and Stanisic's (2011) original sequences and re-calculated relationships among the hadroid forest snails (Clade 1) but updated the taxa following the classification of Stanisic *et al.* (2010). We did this because Hugall and Stanisic (2011) used many placeholder names that cannot be translated to currently accepted taxonomy without expert knowledge.

We analysed a restricted sequence dataset containing new and previously reported (GenBank) sequences of *Figuladra* and some more closely related taxa to resolve the relationships of *Figuladra* in more detail. Phylogenetic analyses were based on 25 newly produced *COI* and 34 new *16S* sequences of Queensland camaenids, and several GenBank sequences (2 for *COI* and 18 for *16S*). These sequences

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Table 1.   Specimens, nomenclature and GenBank accessions used in the mtDNA analyses.

Taxon	Voucher ID	GenBank 16S	ID COI	Sampling location	Source
Camaenid BL47	QMMO87456	OL839881	OL753690	Seaforth	Present study
Camaenid SQ17	QMMO87079	OL839882	OL753691	Bagara SEQ	Present study
Figuladra appendiculata	QMMO86833	OL839884	OL753693	Mount Archer SEQ	Present study
F. barneyae	QMMO87127	OL839885	OL753694	Connors Hump MEQ	Present study
F. barneyae	QMMO87435	OL839886	OL753695	Saint Lawrence, MEQ	Present study
F. bayensis	QMMO86659	OL839887	OL753696	Mount Biggenden SEQ	Present study
F. bayensis	QMMO86928	OL839888	OL753697	Mount Mudlo SEQ	Present study
F. challisi	QMMO86828	OL839889	OL753698	Keswick Island	Present study
F. challisi	QMMO86829	OL839890	OL753699	Saint Bees Island	Present study
F. incei	QMMO87064	OL839891	OL753700	Percy Island MEQ	Present study
F. incei	QMMO87064	OL839891	OL753701	Percy Island MEQ	Present study
F. incei	QMMO87064	OL839891	OL753702	Percy Island MEQ	Present study
F. incei	QMMO87084	OL839892	NA	Percy Island MEQ	Present study
F. lessoni	QMMO87105	OL839893	OL753691	Tannum Sands, SEQ	Present study
F. mattea		GQ851106	NA	Taroom, SCQ	Hugall and Stanisic (2011)
F. mattea	QMMO86643	OL839894	NA	Injune, SCQ	Present study
F. mattea	QMMO86640	OL839895	NA	South Bend, SCQ	Present study
F. mattea	QMMO87243	OL839896	NA	Dan Dan Scrub, SEQ	Present study
F. mattea	QMMO86799	OL839897	OL753705	Targinnie SEQ	Present study
F. mattea	QMMO86812	OL839898	OL753706	Dulacca SCQ	Present study
F. mattea	QMMO86908	OL839899	OL753707	Isla Gorge SCQ	Present study
F. mattea	QMMO86916	OL839900	NA	Henickes Road, SEQ	Present study
F. mattea	QMMO87090	OL839901	OL753708	Moura SEQ	Present study
F. mattea	QMMO87138	OL839902	NA	Horrigans Road, SEQ	Present study
F. mattea	QMMO87140	OL839903	OL753709	Fire Creek, SEQ	Present study
F. mattea	QMMO87234	OL839901	NA	Pointy Vernon, SEQ	Present study
F. mattea	QMMO87640	OL839902	NA	Arcadia Valley SCQ	Present study
F. muirorum	QMMO87137	OL839904	NA	Marlborough SEQ	Present study
F. narelleae	QMMO86831	OL839905	OL753703	Bouldercombe Gorge SEQ	Present study
F. reducta	QMMO86815	OL839906	NA	Mount Perry SEQ	Present study
F. volgiola		GQ851328	NA	Broadsound Range, SEQ	Hugall and Stanisic (2011)
F. volgiola	QMMO78118	OL839910	OL753710	Peak Range, SCQ	Present study
F. volgiola	QMMO78170	OL839907	NA	Mount McDonald, SCQ	Present study
F. volgiola	QMMO78170	OL839911	NA	Mount McDonald, SCQ (2)	Present study
F. volgiola	QMMO87092	OL839908	NA	Duaringa, SCQ	Present study
F. volgiola	QMMO87092	OL839912	NA	Duaringa, SCQ	Present study
F. volgiola	QMMO87096	OL839913	OL753711	Duaringa, SCQ	Present study
F. volgiola	QMMO87135	OL839909	NA	Langdale Hill, MEQ	Present study

(Continued on next page)

Table 1. *(Continued)*

Taxon	Voucher ID	GenBank 16S	ID COI	Sampling location	Source
Outgroups					
Rhagada dampierana	AMSC470227	KP085081.1	KP085399.1	Rosemary Island WA	Criscione and Köhler (2014b)
Austrochloritis porteri		MN526441.1	MN512679.1	Lamington NP SEQ	Köhler et al. (2020)
Clade 1					
Bentosites etheridgei	QMMO87460	OL839880	NA	Seaforth MEQ	Hugall and Stanisic (2011)
Billordia nicoletteae	QMMO78854	GQ851018.1	NA	Lotus Creek MEQ	Hugall and Stanisic (2011)
Denhamiana laetifica	QMMO85422	OL839883	OL753692	Hazelwood Gorge MEQ	Present study
Lamprellia zebina		GQ851049.1	NA	Rishton Scrub WT	Hugall and Stanisic (2011)
Monteithosites heliostracum		GQ851007.1	NA	Bakers Blue Mountain NEQ	Hugall and Stanisic (2011)
Clade 4					
Austrocamaena ricnattrassi	QMMO21426	AY151082.1	NA	Cape York	Hugall et al. (2002)
Austrocamaena thortoniana		AY151065.1	NA	Wet Tropics	Hugall et al. (2002)
Gnarosophia bellendenkerensis		AY151070	NA	Mount Bellenden Kerr NQ	Hugall et al. (2002)
Sphaerospira arthuriana	QMMO86846	OL839914	NA	Saint Bees Island MEQ	Present study
S. bencarlessi		AY151066.1	NA	Bobby Range SEQ	Hugall et al. (2002)
S. blomfieldi		AY151064.1	NA	SEQ	Hugall et al. (2002)
S. fraseri	QMMO56695	AY151080.1	NA	SEQ	Hugall et al. (2002)
S. informis		AY151068.1	NA	MEQ	Hugall et al. (2002)
S. mortenseni	QMMO54521	AY151078.1	NA	Parnassus Range SEQ	Hugall et al. (2002)
S. oconnellensis	QMMO35787	AY151081.1	NA	MEQ	Hugall et al. (2002)
S. rockhamptonensis		AY151077.1	NA	Mount Archer SEQ	Hugall et al. (2002)

MEQ, mid-eastern Queensland; NA, not available; NQ, North Queensland; SCQ, southern-central Queensland; SEQ, south-eastern Queensland; WA, Western Australia; WT, Wet Tropics.

represented 33 species from 11 genera (Table 1). We found that the topology of our tree was consistent with the one of Hugall and Stanisic (Fig. 2). However, we note that many of the key nodes had posterior probability/ultrafast bootstrap values below 95 and are thus only moderately supported. According to this tree, *Figuladra* is most closely related to *Lamprellia, Monteithosites, Marilynessa* and members of a clade containing *Steorra, Temporena* and *Bentosites* all from Clade 1 as first identified by Hugall and Stanisic (2011). *Billordia* is nested within the *Figuladra* clade. The *Figuladra* clade contained three major lineages, *Figuladra mattea, Figuladra volgiola* and a lineage including three subclades with a geographical structuring – one lineage from MEQ, another from the coastal area of SEQ and a third from the montane areas of the Boyne Range, Mount Biggenden and Mount Mudlo.

This dataset contained sequences of 48 individuals. All *COI* sequences had a length of 655 bp after pruning of the primer sites, whereas the multiple *16S* sequence alignment had a length of 770 bp after trimming of ends and removing ambiguously aligned sections. For the phylogenetic analysis,

a data partition was applied that allowed parameters for each codon position of the *COI* fragment and the *16S* fragment to be modelled independently. The model test implemented in IQ-Tree identified the following models of sequence evolution as the best-fit models for the different partitions by means of the Bayesian information criterion: TIM2 + F + I + G4 for *16S*, TN + F + I + G4 for the 1st and 2nd and TPM3 + F + I for 3rd codon positions in *COI*. These models were applied in the partitioned Maximum Likelihood analysis. The concatenated alignment had 1425 columns, of which 546 were parsimony-informative, 136 were singleton sites and 743 were constant sites.

The best Maximum Likelihood tree (Fig. 2a) was generally consistent with the phylogeny produced by Hugall and Stanisic (2011) placing *Figuladra* within 'Clade 1' and separate from the *Sphaerospira* species in Clade 4. The bootstrap consensus tree of the ML analysis confirmed all species of *Figuladra* formed a clade that also contained *Billordia nicoletteae*. Nodal support was high for three major clades within *Figuladra*, however support for higher-level relationships was moderate. The Bayesian consensus phylogram (Fig. 2b)
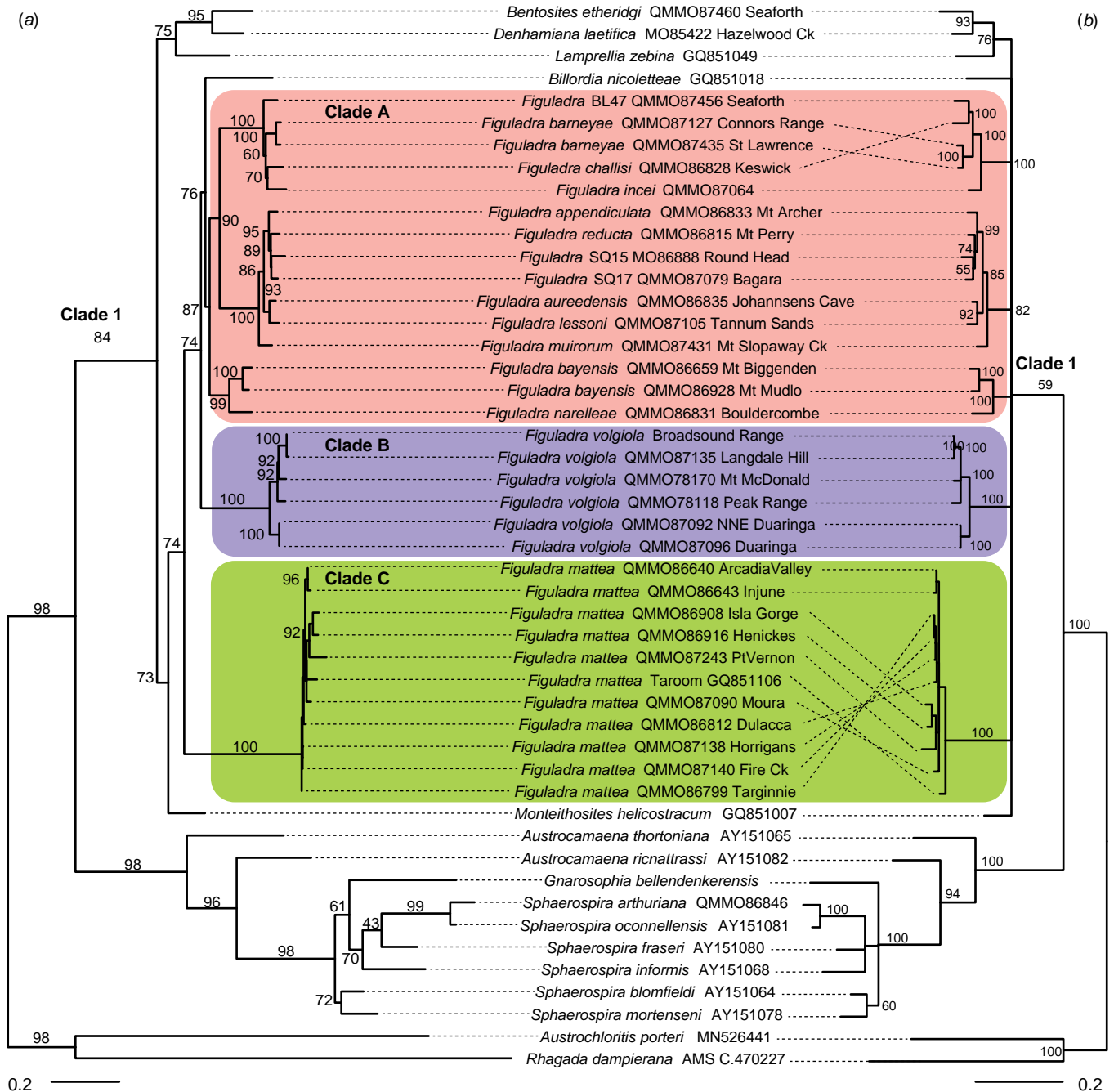
Fig. 2. Reconstructions of phylogenetic relationships of *Figuladra* and related hadroid genera from eastern Queensland based on phylogenetic analyses of concatenated *16S* and *COI* sequences. (*a*) Maximum Likelihood phylogram. (*b*) Bayesian consensus phylogram. Numbers on branches report ML ultrafast bootstrap values and Bayesian posterior probabilities respectively.

exhibited a largely identical topology with the exception of the placement of *Billordia* and the *Sphaerospira* clade that was shown to be unresolved with respect to the seven species included in the tree.

We recognise three major clades within the *Figuladra* lineage (Fig. 2). The first major clade, Clade A, comprised several *Figuladra* species. The clade revealed a bifurcation between two sub-clades that contained the MEQ (*F. incei*

incei, *F. challisi*, *F. barneyae* and Camaenid BL47) and SEQ species respectively. A third sub-clade contained two species occupying upland habitats, *F. narelleae* (Bouldercombe Gorge, Boyne Range and related drainage lines) and *F. bayensis* (Mount Mudlo and Mount Biggenden). The second major clade, Clade B, corresponded to *F. volgiola* from MEQ and SCQ. Branches within this clade corresponded to geographically isolated sub-populations of *F. volgiola* in the

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Table 2. Mean *p*-distances (%) between sequences from different clades.

		Clade 1	Clade A	Clade B	Clade C	*Billordia*
Clade 1 (Hugall & Stanisic) species	*16S*				*16S* mean	18.7
	COI				*COI* mean	13.1
Clade A *Figuladra*	*16S*	18.5				
	COI	12.7				
Clade B *F. volgiola*	*16S*	18.4	16.2			
	COI	12.1	11.4			
Clade C *F. mattea*	*16S*	19.0	18.9	16.5		
	COI	14.1	13.8	14.5		
Billordia	*16S*	23.0	23.6	11.71	10.0	–

Peak Range, Broadsound Range and Expedition Range respectively. Clade C corresponded to *Figuladra mattea*, a species with a broad SEQ and SCQ distribution.

Genetic distances

p-distances within clades ranged from 0.1 to 32.6% for *16S* and from 0.4 to 26.1% for *COI* (Supplementary Table S3). The interspecific distances within *F. mattea* were below 5.4% across the entire range in SEQ and SCQ for both genes. *F. volgiola* showed low divergence within *16S* (0.25–0.43%) and higher divergence within *COI* (7.8%).

Intraspecific *p*-distances ranged from 1.3 to 19.8% in Clade A, from 0.2 to 7.8% in Clade B and from 0.1 to 3.6% in Clade C (Supplementary Table S3). These intraspecific distances were considerably lower than the mean interclade *p*-distances ranging from 10.0 to 23.6%. Although the *p*-distance within species was low, the *p*-distance over sequence pairs among groups suggested by the ML and BL tree topology averaged 13% for the *COI* gene and 19% for the *16S* gene (Table 2). Differences among genera ranged between 10% (Clade C and *Billordia*) and 23.6% (Clade A and *Billordia*).

Morphological variation

Genital morphology

A total of 39 specimens of *Figuladra mattea* (Clade B) and *F. volgiola* (Clade C) from SEQ, MEQ and SCQ and 6 specimens of *Billordia* species were dissected. Although 202 specimens of *Figuladra* (Clade A) have been dissected for comparison, only 3 representative specimens of *Figuladra* from this set are featured herein. Other specimens from Clade 1 were dissected for genital anatomical comparison (see Supplementary Table S1). There was a clear distinction between the genital anatomies of *Figuladra mattea*, *F. volgiola* and all other species of *Figuladra*. *Billordia* Stanisic, 2010, *Denhamiana* Stanisic, 2016 and *Bentosites* Iredale, 1933 were also noticeably dissimilar in gross anatomical structure (Fig. 3). A shorter, thicker epiphallus and bands

of muscular tissue at the epiphallic-penial junction are characteristics of all species of Clade A (= *Figuladra sensu* stricto; Fig. 3*b*). This muscular tissue connecting the apical portion of the penis with the epiphallus is lacking in both *F. mattea*, *F. volgiola* and *Billordia* (Fig. 4). Furthermore, the long, twisted and looped epiphallus of *F. volgiola* (Clade B), the long, coiled descending arm of the epiphallus of *F. mattea* (Clade C) and the knotted epiphallus of *Billordia* are distinguishing characters from all other *Figuladra* species (Clade A; Fig. 4). The ratio between the length of the penis and the length of the vagina is much lower in *F. mattea* (mean 1.6) and *F. volgiola* (mean 1.7) than in *Figuladra s.s.* (mean 2.4) (Supplementary Table S4).

The penial interior of *F. volgiola* (Clade B) was characterised by one fleshy longitudinal pilaster running the full length of the penis descending into the atrium, and an apical region with basal ridges forming thin, chevron-like thickenings for one-third of the penial length (Fig. 5). This pattern was consistent across *F. volgiola* specimens from different localities including the Peak, Expedition, Boomer and Broadsound Ranges. All had chevron pilasters in the apical region and the penial-length longitudinal plaster (Supplementary Fig. S1).

The penial interior of *F. mattea* (Clade C) is characterised by an upper penial chamber with numerous irregular pustules giving rise to a chevron-like pattern of pustules; a single longitudinal pilaster in the upper penial chamber; and several regular longitudinal thickenings that descend into the atrium (Fig. 6). This pattern of pilasters in the penial chamber architecture of all *F. mattea* specimens examined from within the broad range in SEQ and SCQ was consistent, with only minimal variations in the number of pilasters in the atrium (Supplementary Fig. S2).

Billordia bridgettae has a double longitudinal thickening descending into the atrium and an apical region with basal ridges forming thin, chevron-like thickenings for more than one-half of the penial length (Fig. 7*a*). Typical *Figuladra* species (Clade A) have a single or double longitudinal thickening in the apical region that also has rugose, crenelated or spade-like pilasters in various combinations generally for

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one-third of the penial length and bifurcating before descending into the atrium (Fig. 7b–d).

Shell morphology

In total, 635 shells of *F. mattea* and *F. volgiola*, and 34 shells of *Billordia nicoletteae* and *B. bridgettae* were examined and measured (Supplementary Table S1). Variation in shape, colour patterns and shell morphometry (shell parameters H, D, H/D, W) was minimal within *F. mattea* and *F. volgiola*. Shells of *F. volgiola* (Clade B) and *F. mattea* (Clade C) were similar in size and whorl count (Fig. 8, Table 3) compared to other *Figuladra* species. *F. volgiola* differed from all other species by having a fully closed umbilicus (Fig. 9). With the exception of *F. volgiola* with a closed umbilicus, the shells of all *Figuladra* species exhibit only minor differences among species. Both *Billordia* species were smaller and flatter than any *Figuladra* species in Clade A, B and C and have a significantly lower H/D ratio and whorl count. The sub-discoidal shell shape with a more open umbilicus in *Billordia* species differed from the depressedly globose to trochoidally globose shell shape of Clades A, B and C (see Fig. 12e). We observed variations in lip colour and suffusion: *F. mattea*, *F. volgiola*, *B. nicoletteae* and *B. bridgettae* had white lips with no suffusion behind the lip unlike all other *Figuladra* species that d varying levels of brown suffusion behind the lip. All *Figuladra* species exhibited a variety of colour forms ranging from solid dark to banded. One species, *F. pallida*, also exhibited a 'blond' form. *Figuladra volgiola* was always banded (Fig. 9). Shells of *F. mattea* were generally banded but the species also encompassed a heavily banded, darker form in Dulacca, SCQ and a 'blond' form in Ipswich, SEQ (Fig. 10). Neither *F. mattea*, *F. volgiola* nor *Billordia* species had solid dark, unbanded shells.

SEM investigation of teleoconch microsculpture revealed similarities among all specimens. Shell sculpture consisted of fine, irregularly disposed microradical, periostrical threads. The exception was *Billordia* with *B. bridgettae* and *B. nicollettae*, both having a pustulose teleoconch microsculpture (Fig. 11).

Mantle colour

Differences were observed in the colour of the mantle (Fig. 12a–d, f). The orange mantle of *Figuladra volgiola* was similar to the mantle colour in *Bentosites,* but differed from that of *Figuladra* species in Clade A, that had a strong pink mantle colour (Stanisic *et al.* 2010). The mantle of *F. mattea* was consistently orange–pink across the species' entire range. This feature distinguished these groups from the *Sphaerospira* clade that had a black mantle and other genera belonging to Clade 1 (Table 4).

Jaw and radula

No significant differences in jaw and radular morphology were detected among any of the examined species (Fig. 13).

The radulae were typically camaenid with a unicuspid central tooth, laterals gradually becoming bicuspid and multicuspid marginals (Solem 1973).

Discussion

Phylogenetic relationships

Current knowledge of the phylogenetic relationships of the eastern Australian Camaenidae essentially rests on the phylogenetic study of Hugall and Stanisic (2011). This study presented a mitochondrial phylogeny based on the analysis of three partial mitochondrial genes (*12S, 16S, COI*), in which species now placed in *Figuladra* were shown as members of Clade 1 (labelled as the *mattea, volgiola*, BL4 and *appendiculata* lineages).

Our new phylogeny included samples from the Hugall and Stanisic's original tree. This phylogeny is consistent with Hugall and Stanisic (2011) in the placement of *Bentosites, Steorra, Monteithosites, Marilynessa, Figuladra, Billordia* and *Lamprellia* in Clade 1 and the grouping of *Sphaerospira, Austrocamaena* and *Gnarosophia*, all Queensland hadroid snails, in a separate clade (Clade 4). However, the placement of *Billordia nicoletteae* within the *Figuladra* clade differed from the Hugall and Stanisic's (2011) phylogeny. The implication is that *Figuladra* as circumscribed by Stanisic *et al.* (2010) is not monophyletic. To maintain monophyletic taxa, the following options exist: synonymising *Billordia* with *Figuladra*, with *Billordia* as the older name having priority, or alternatively, describing new monotypic genera for *F. mattea* and *F. volgiola* thus maintaining *Billordia* and *Figuladra* as distinct genera. As the placement of *Billordia nicolettaea* had very low support within the maximum likelihood analysis, and was unresolved by the Bayesian analysis, a taxonomic decision as to how best to delineate genera requires an evaluation of comparative morpho-anatomy in addition to the phylogenetic inference.

Genetic distances

Davison *et al.* (2009) found a large overlap between intra- and interspecific divergence in mitochondrial DNA in stylommatophoran land snails with intraspecific distances sometimes extreme, reaching 20–30%. In Asian camaenids, Kameda *et al.* (2007) reported uncorrected pairwise sequence divergences of 0–7.3% within and 0.3–20.5% among traditionally circumscribed species. In our study, the observed *p*-distances among clades A, B and C (Table 2) are comparable with the genetic divergence observed among genera in other studies of Australian camaenids (Köhler and Johnson 2012; Taylor *et al.* 2015). Similar genetic distances are observed among genera of other taxa. Oba *et al.* (2015) in their study of 275 click beetles, stated an average *p*-distance among genera using the *COI* gene as 11.6%. In the study of sea snails

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(Neogastropoda), Zou *et al.* (2011) established that the mean pairwise divergence among specimens of different sea snail genera using both the *16S* and *COI* genes was 18.4% (range 6.3–24.8%). However, although no such benchmark is available for delimitation of land snail genera, sea snails do show very similar generic *p*-distances to those observed here within the hadroid camaenids.

Morphological variation

Using *COI* and *16S* genes, Köhler and Johnson (2012) showed an association between a genetic distance greater than 6% and the presence of distinct genital morphology in snails. With all comparative *p*-distances greater than 10% for both *16S* and *COI* genes among *F. mattea*, *F. volgiola*, *Billordia* and *Figuladra s.s.* lineages, this substantial mitochondrial differentiation is not unexpectedly complemented by a significant difference in penial anatomy (Fig. 3, Table 2). Solem (1997) proposed that the gross genital anatomy of adult camaenids is informative for delimitation of genera and as such, this anatomical feature is an important aspect of this study. The separation of *F. mattea* and *F. volgiola* from *Billordia* and *Figuladra s.s.* is reinforced by differences in gross genital features. The genital anatomy of *Billordia* has a knotted epiphallus and lacks the uncoiled epiphallus of *Figuladra* in Clade A, and the coiled, looped and twisted epiphalluses of *F. mattea* (Clade B) and *F. volgiola* (Clade C) respectively. The muscular tissue at the penial–epiphallic junction that characterises *Figuladra* species is absent in *Billordia*, *F. mattea* and *F. volgiola*. The penial–vagina ratio is significantly different among *Figuladra s.s.*, *F. mattea* and *F. volgiola*.

Radulae and jaws have previously been shown to be of little use in generic or species delimitation in camaenids (Solem 1984; Köhler 2010*b*) and this study reveals similar results. However, comparisons of the mantle tissue that generally extends to the foot and body in hadroid snails, shows a difference from the pink mantle and pinkish grey animal of *Figuladra s.s.* to pinkish-orange to orange forms in both *F. mattea* and *F. volgiola* respectively. This difference in colour pattern is consistent with the differences among other hadroid genera (see Table 4).

Shell characters have been shown to typically offer little value to the delimitation of these genera. All the hadroid species in Clade 1 and 4 display banding patterns in various combinations. However, the lack of umbilicus in *Figuladra volgiola* is a shell character separating this species from *Billordia* species and any species in *Figuladra s.s.* Unlike *Figuladra* species that have sub-globose to globose shells, *Billordia* is typified by a subdiscoidal shell with a low spire (Fig. 12*e*) and is distinguished from *Figuladra* species by the pustulose microsculpture on the teleoconch. *Bentosites*, *Monteithosites*, *Denhamiana* and *Figuladra* species all have a relatively smooth teleoconch with a microsculpture of fine periostracal microradial threads.

New genera

We have taken a multidisciplinary approach and have considered not only the phylogenetic evidence and genetic distances but also morphological evidence. As most of the key nodes from the molecular phylogenetic analysis had posterior probability/ultrafast bootstrap values below 95, our proposed classification rests predominantly on our morphological analysis. We note that the molecular phylogenetic analysis is congruent with our proposed classification. The use of additional markers may improve support values in future studies. From our assessment of the observable differences, we consider the best option to be to not to subsume Clades A to C within the genus *Billordia* given the extent of anatomical and morphological differentiation but to recognise the *mattea* and *volgiola* lineages as distinct genera as these represent evolutionarily distinct lineages that are characterised by unique anatomical features. Accordingly, we support Clades A, B, C and *Billordia* as separate lineages within the Queensland hadroid group. Two new monotypic genera, *Euryladra*, gen. nov. (Clade B, the *mattea* lineage) and *Brigaladra* gen. nov. (Clade C, the *volgiola* lineage), are therefore diagnosed by the combination of shell and penial morphology supported by phylogenetic data. Updated diagnoses of *Figuladra* and *Billordia* are therefore included.

These phylogenetic reconstructions indicate that *Euryladra* and *Brigaladra* are both monophyletic and monotypic. Although highly unusual for single camaenid species to persist across such a vast region as SEQ, SCQ and MEQ, there is no evidence to support multiple species within these two lineages. Monotypic genera in land snails are not unknown with 50 monotypic camaenid genera in Australia including 23 from Queensland (Köhler 2010*a*, 2010*b*; Stanisic *et al.* 2010, 2018; Stanisic 2016). This scenario is reflective of the complex history of land snail evolution in eastern Australia whereby mesic communities have undergone a long history of climate-induced fragmentation and isolation.

Biogeography: diversification across habitats in Clade 1 camaenid land snails

Land snails are dependent on mesic conditions for activity and many groups have retained a preference for rainforest or other environments that are at least seasonally mesic (Solem and van Bruggen 1984; Stanisic 1994; Stanisic *et al.* 2007). Land snails also show an excellent capacity to persist in relatively localised areas, especially in association with limestone outcrops or other rocky ranges that provide microrefugia from key potential threats such as fire and aridity (Couper and Hoskin 2008). Accordingly, land snails are potentially an excellent group for understanding biotic patterns in response to broadscale climatic change, such as the ongoing and increasing aridification of the Australian continent (Byrne *et al.* 2008, 2011).

Unlike some other lineages of eastern Australian camaenids that have distributions centred on wet evergreen

rainforests (for example: Hugall *et al.* 2003), Clade 1 land snails are strongly associated with relatively drier closed forest (Stanisic *et al.* 2010; Hugall 2011), referred to in Australia as vine-thickets and scrub, but on a global scale consistent with what is referred to as dry seasonal tropical forests or subtropical dry forest (Webb and Tracey 1981; Neldner *et al.* 2019). Six of the nine genera recognised in Clade 1 have distributions centred on these vine-thicket habitats and three have diversified into other habitats in addition to vine thicket (see Table 5). This diversity in dry closed forest habitats suggests that this clade adapted to these habitats early in the evolutionary history and has subsequently undergone ecological and evolutionary diversification. One putative driver of this diversification may have been the spread of open grassy and fire-affected woodland or savannah habitats that are generally depauperate in land snails (Stanisic 1994; Stanisic and Ponder 2004). Reflecting this trend, within Clade 1 only two lineages (*Lamprellia* and the newly recognised *Euryladra*) regularly occur in more open woodland habitats, despite these habitats covering vast areas of eastern Australia.

Within this broader evolutionary and paleo-environmental context the four focal genera for study show contrasting contemporary distributions that likely reflect differences in habitat and ecology. *Figuladra s.s.* is the only clade among these four genera that is restricted to an area east of the Great Dividing Range. This genus is distributed in near-coastal dry vine thickets with nine species now distributed from north of the Mary River, Gympie, SEQ to slightly south of the O'Connell River, south of Proserpine, MEQ (Stanisic *et al.* 2010). Records from both QM and AM, and our observations from field work show that species appear to be primarily vine thicket dwellers, but can occur in gallery forests along adjacent or emanating drainage lines.

Brigaladra also appears to be an obligate vine thicket occupant that is represented by a single species, *B. volgiola*. Although this species occurs west of the Great Dividing Range, records have only been made in ranges (Peak, Broadsound, Boomer and Expedition Ranges) living in vine thickets on rocky scree. Within these ranges *B. volgiola* is closely associated with vine thickets, although the species also occasionally occurs in woodland along emanating drainage lines, for example in Charlevue Creek, Expedition Range, SCQ; in Roper Creek, Peak Range, MEQ; and in Apis Creek, Boomer Range, MEQ (Fig. 14, 15*a, b*). These ranges are located on either side of the Isaac-Comet Downs Bioprovince that has been largely cleared for farming. The Isaac-Comet Downs, a lowland region of brigalow and open savannah woodland, is home to camaenids such as *Pallidelix potteri* Stanisic, 2018. Museum records (AM and QM) show that no *B. volgiola* were found in this lowland area in early collections made before much of the subsequent land clearing. The apparent disjunct distribution of the *B. volgiola* populations in scattered vine thickets of rock-strewn ranges

appears to mirror the fragmented contemporary distribution of these vine thickets.

Like *Brigaladra*, *Billordia* is also associated with vine thickets in the drier ranges (Peak, Broadsound) west of the Great Dividing Range on either side of the Isaac-Comet Downs. The two species, *B. bridgettae* and *B. nicoletteae* live among vine thicket on rocky scree and, unlike *Brigaladra*, have not been found in vine thickets on other substrates. The former has been found sympatrically with *Brigaladra* in the Peak Range, MEQ, but museum records show that each occur within different vine thickets in the same locality. *B. nicoletteae* occurs in the vicinity of Lotus Creek at the southern end of the Connors Range, MEQ. *Billordia* species have a flattened shell and correlated open umbilicus (see Fig. 12*e*). These features are hypothesised to be adaptations to living among rocky scree where more globose shell shapes impede access to movement in these refugia (Criscione and Köhler 2013; Hamilton 2021). The pustulose teleoconch and sharply reflected lip represent a marked divergence from the shells of the other members of Clade 1. Given the very limited wet material available in QM, molecular data from both *Billordia* species would enhance future comparative study.

Euryladra is represented by a single species, *E. mattea*, that has a very wide distribution in the eucalypt woodland east and west of the Great Dividing Range (Fig. 15*c, d*). Occasionally, but relatively infrequently, *E. mattea* occupies semi-deciduous vine thicket. *Euryladra* appears to be one of only two lineages in Clade 1 that can persist in the evolving drier eucalypt-dominated landscape. The physiological, behavioural or morphological adaptations that have enabled this taxon to occur across a vast area outside of vine thickets remain unknown, but could be an interesting area for further investigation.

Systematics

<div align="center">

Class **GASTROPODA**

Order **EUPULMONATA**

Superfamily **HELICOIDEA**

Family **CAMAENIDAE**

Brigaladra L. Stanisic, gen. nov.

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Type species: *Varohadra volgiola* Iredale, 1933, p. 46 [nom. nov. for *Helix andersoni* Cox, 1872]. – Iredale (1937, p. 33).

Etymology

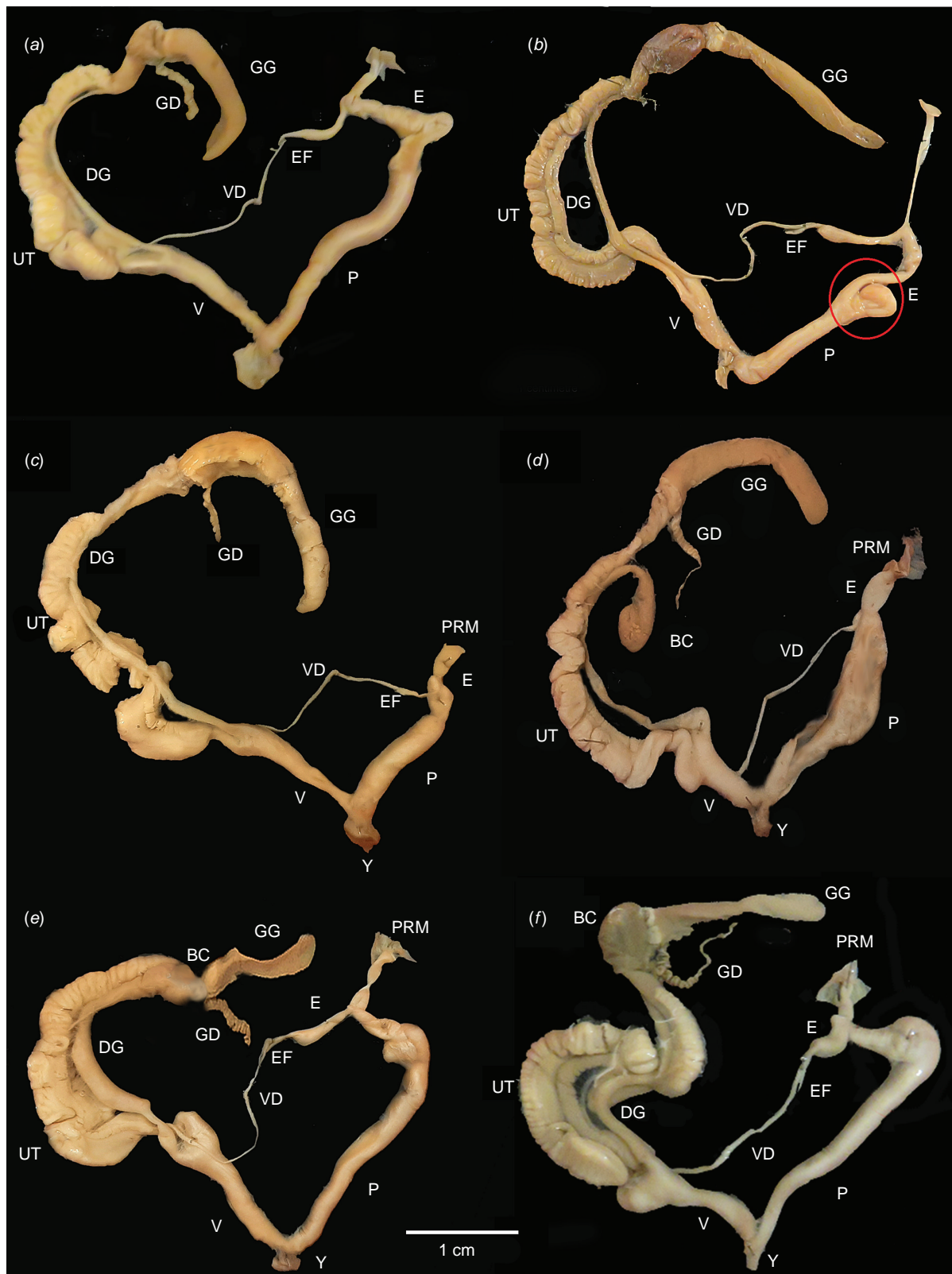Named for the brigalow lands and a contraction of *Figuladra*.

Fig. 3. Anatomy of terminal genitalia (*a*) *Figuladra volgiola* QMMO46238, Boomer Range, SCQ. (*b*) *Figuladra mattea* QMMO86814, Mount Perry, SEQ with the penial–epiphallic junction circled in red. (*c*) *Bentosites macleayi* (Iredale, 1933), QMMO52114, Hook I, MEQ. (*d*) *Denhamiana laetifica* (Stanisic, 2013), QMMO54313, Denham Range, MEQ. (*e*) *Billordia bridgettae* Stanisic, 2010, QMMO78106, Lords Table, SCQ. (*f*) *Figuladra reducta*, QMMO85417, Goodnight Scrub, SEQ. Scale bar: 1 cm.
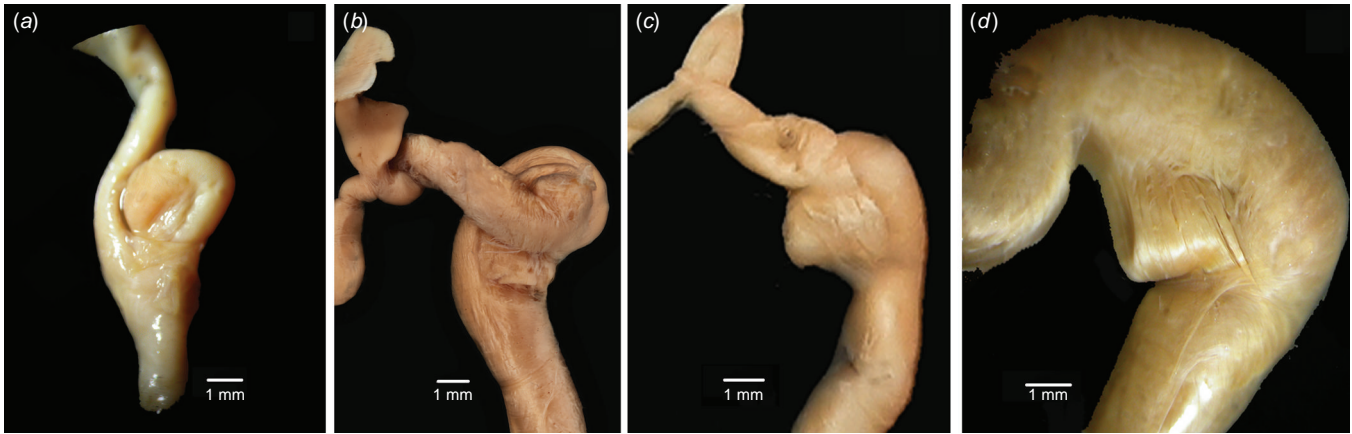
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Fig. 4. Close up of muscular tissue at the epiphallus–penis junction (*a*) *Euryladra mattea* QMMO86814, Mount Perry, SEQ (*b*) *Brigaladra volgiola* QMMO78066, Peak Range, SCQ. (*c*) *Billordia bridgettae* QMMO78106, Lords Table, SCQ. (*d*) *Figuladra narelleae* QMMO21496, Mount Morgan Dee Range, SEQ. Image B: Geoff Thompson, QM. Scale bars: 1 mm.

Diagnosis

Shell large, sutures weakly impressed; protoconch with weak, crowded radial ridges, teleoconch smooth, microsculpture of fine microradial periostracal threads; lip reflected, umbilicus closed. Shell yellowish with white suffusion behind lip, white with brown banding continuing onto the lip; brown circum-umbilical patch. Animal orange–grey with an orange mantle. Reproductive system with long epiphallus looped and twisted bound in connective tissue; penis approximately the same length as the vagina.

Range

Boomer Range and Broadsound Range, SEQ; Expedition Range and Peak Range, SCQ.

Remarks

Brigaladra is distinguished from *Billordia*, *Figuladra* and *Euryladra* by having a fully closed umbilicus and a long twisted epiphallus. *Figuladra* has a shorter, thicker epiphallus and muscular tissue at the epiphallic–penial junction. *Billordia* has a knotted epiphallus and *Euryladra* has a coiled epiphallus encased in connective tissue at the epiphallic–penial junction.

Brigaladra volgiola (Iredale, 1933), comb. nov.

(Fig. 3*a*, 4*b*, 5, 8, 10, 11*b*, 13*d–f*, 14, 15*a,b*, Tables 1–4)

Helix andersoni Cox, 1872, p. 644, pl. 52, fig. 4 [non *Helix andersoni* Blandford, 1869].

Fig. 5. *Brigaladra volgiola* QMMO44110, Charlevue Creek, Blackdown Tableland, SCQ. Penial architecture showing the rugose pilasters in the apical chamber and multiple longitudinal pilasters. Scale bar: 5 mm. Image: Geoff Thompson, QM.

Varohadra volgiola Iredale, 1933, p. 46 [nom. nov. for *Helix andersoni* Cox, 1872]. – Iredale (1937, p. 33).

Sphaerospira volgiola. – Smith (1992, p. 159).

Figuladra volgiola. – Stanisic *et al.* (2010, p. 474, sp. 755, figure in text).

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Fig. 6. *Euryladra mattea*, QMMO86814, Mount Perry, SEQ. Penial architecture showing the numerous irregular pustules giving rise to a chevron-like pattern of pustules and several regular longitudinal thickenings that descend into the atrium. Scale bar: 5 mm.

Common name

Boomer Range Banded Snail.

Material examined

Lectotype. NHMUK 1880.12.11.14 [N end of Expedition Range. W of Rockhampton. Height of shell 22.64 mm, diameter 30.62 mm, H/D 0.739, whorls 5.875].

Paralectotypes. AMSC107629 [6RC, N end Expedition Range, W of Rockhampton, 23°42′S, 148°59′E, 1872, J.C. Cox collection]; AMSC107630 [6RC, N end Expedition Range, W of Rockhampton, 23°42′S, 148°59′E, 1872, J.C. Cox collection].

Other material. (All SCQ and MEQ) Boomer Range. QMMO46286, 9SC/RC; QMMO23495, 3SC/RC; QMMO44110, 13SC; QMMO47961, 4RC; Broadsound Range, MEQ. AMSC107641, 4RC; AMSC386835, 1RC, QMMO45967, 77SC/RC; QMMO45973, 18SC/RC; QMMO46282, 27SCRC; Expedition Range, SCQ: AMSC5579, 1RC; AMSC471624, 2RC; QMMO46300, 1 RC; QMMO87091, 6SC; QMMO87092, 6SC; QMMO87093, 12SC; QMMO87094, 12SC; QMMO87095, 12SC; QMMO87096, 11SC; Peak Range. QMMO78066, 85SC/RC; QMMO78080, 3RC, QMMO78082, 6RC, QMMO78113, 12SC/RC; QMMO78117, 3SC/RC; QMMO78118, 22SC; QMMO78123, 10SC; QMMO78133, 18 RC; QMMO78134, 25SC/RC; QMMO78145, 1RC; QMMO78148, 2RC; QMMO78155, 4 RC; QMMO78170, 10SC/RC.

Taxonomic note

When Cox (1872) described *Helix andersoni*, a holotype was not explicitly nominated and mention was made that the shell was one of 'many fine specimens that Mr Anderson had collected' (p. 654). This demonstrates the existence of a type series. Smith (1992) labelled a specimen 1880.12.11.4 as a holotype and listed the two paratype lots but did not acknowledge the set as part of a type series. The NHMUK has the collection log showing 14 'species' (1800.12.11.5–21) presented to the museum by Dr Cox. This set includes the single specimen of *H. andersoni* considered to be part of this series. Two paratype lots, each with 6 specimens labelled as being from Cox's collection, are considered to be part of this type series and are located in the Australian Museum. Consultation with the NHMUK proved that Smith's voucher number was printed incorrectly (J. Ablett, pers.obs.). To correct this error, the specimen with registration number NHMUK1880.12.11.14 is redesignated as a lectotype, and AMSC107629 and AMSC107630 are redesignated as paralectotypes.

Diagnosis

As for genus.

Description

Shell large, diameter 26.91–34.13 mm (mean 30.33 mm), height 19.64–26.96 mm (mean 23.25 mm), H/D ratio 0.716–0.841 (mean 0.766), whorls 5.750–6.250 (mean 6.000); subglobose with a moderately elevated spire; whorls rounded, sutures impressed; protoconch with weak crowded radial ridges, teleoconch smooth, microsculpture of fine periostracal microradial threads; shell yellow with numerous narrow brown spiral bands; lip reflected, white with brown banding continuing onto the lip and clearly visible in the aperture; umbilicus closed with brown circum-umbilical patch; animal orange–grey with an orange mantle. Based on 211 measured adult specimens (see Supplementary Table S1).

Genitalia. Penis long and tapered with slightly expanded apical bulb, penial sheath present; penial chamber with one fleshy longitudinal pilaster descending into the atrium, apical region with basal ridges forming thin chevron-like
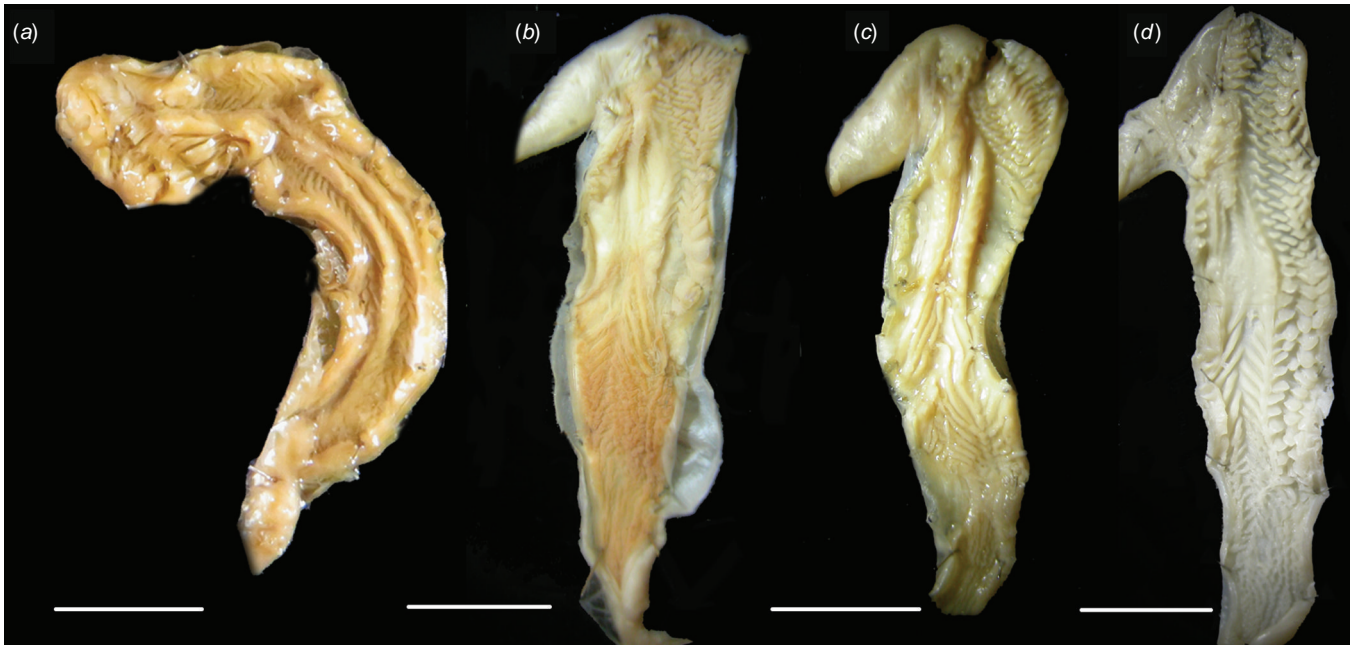
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Fig. 7. Penial anatomy of (*a*) *Billordia bridgettae* QMMO78169, Lords Table, MEQ, showing the longitudinal pilaster the length of the penis. (*b*) Clade A (MEQ example), *Figuladra challisi*, QMMO86829, St Bees I showing crenelated pilasters descending to larger spade like pilasters in the apical chamber and a single longitudinal pilaster bifurcating into the atrium. (*c*) Clade A (SEQ example), *Figuladra incei curtisiana*, QMMO86791, Bororen, showing rugose pilasters in the apical chamber and a double longitudinal pilaster bifurcating into the atrium. (*d*) Clade A (*bayensis–narelleae* example), *Figuladra narelleae*, QMMO86831, Bouldercombe Gorge showing spaded like pilasters in most of the penis. Scale bars: 5 mm.

thickenings for one-third of the penial length; penial retractor muscle inserted at the junction of the two arms of the epiphallus; epiphallus with short, thin muscular ascending arm, descending arm relatively longer, more expanded; epiphallus entering penis through a simple pore; vas deferens thin and attached to penial sheath with connective tissue; short, vestigial epiphallic flagellum present at the epiphallus–vas deferens junction, tightly bound to the vas deferens; vagina short but more than half the length of the penis, PVR 1.052–2.051 (mean 1.709); free oviduct shorter than vagina; bursa copulatrix situated at the base of the albumen gland, with a slender stalk; atrium simple. Prostate, uterus and hermaphroditic duct without unusual features. Based on 19 dissected adult specimens (see Supplementary Tables S1, S4).

Distribution and habitat

Boomer Range, Broadsound Range, SEQ; Expedition Range, Peak Range, SCQ; semi-evergreen vine thicket to adjoining dry woodland, living under rocks and inside logs.

Euryladra L. Stanisic, gen. nov.

Type species: *Varohadra incei mattea* (Iredale, 1933)

Etymology

From the New Latin prefix *eurys*, which means widespread and a contraction of *Figuladra*.

Diagnosis

Shell large, sutures weakly impressed; protoconch with weak crowded radial ridges, teleoconch smooth, microsculpture of extremely fine periostracal microradial threads; lip expanded and moderately flared; umbilicus open. Shell yellowish with white suffusion behind lip and dark brown circum-umbilical patch; animal pinkish-orange–grey with a pinkish-orange mantle. Reproductive system with long, coiled epiphallus entwined in connective tissue at the epiphallic-penial junction; penis approximately the same length as the vagina.

Range

From Tweed River, NE NSW to Rockhampton, SEQ and inland as far west as Carnarvon NP, SCQ.

Remarks

Euryladra differs from *Brigaladra*, *Billordia* and *Figuladra* by genital characteristics such as a strongly coiled epiphallus
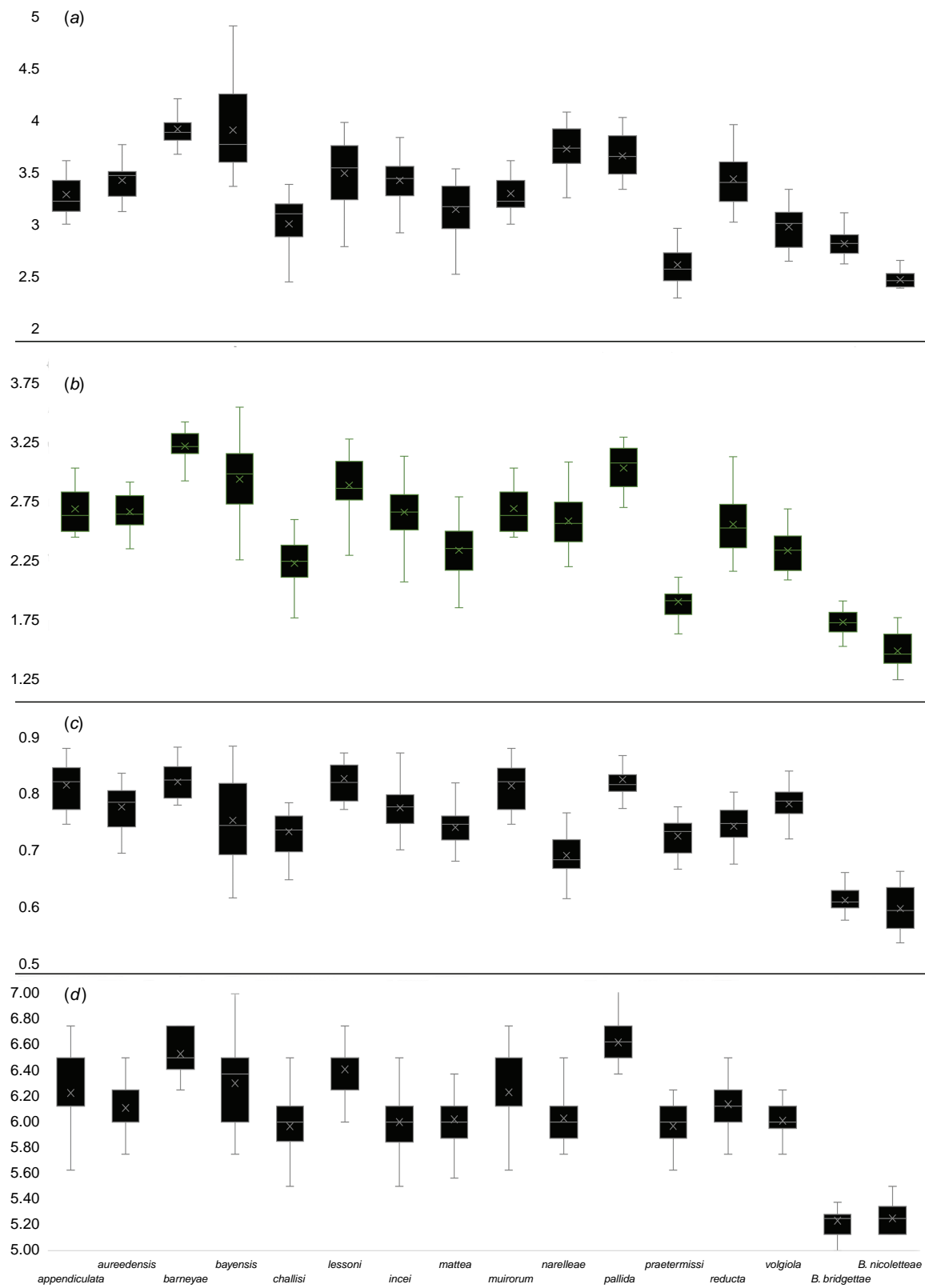
Fig. 8. Box and whisker plots show comparison among shell features of species in the *Figuladra* clade. (*a*) Shell diameter. (*b*) Shell height. (*c*) Height/diameter ratio. (*d*) Whorl count. Image (*a*, *b*) measurements in centimetres.

Table 3. Shell measurements for *Figuladra mattea*, *F. volgiola*, *Billordia nicoletteae* and *B. bridgettae*.

Taxon	*n*	Height (mm)	Diameter (mm)	Whorls	H/D ratio
Figuladra mattea SEQ, SCQ	494	18.50–27.47	26.05–34.48	5.750–6.750	0.710–0.788
Mean		22.74	30.29	6.000	0.750
s.d.		±2.00	±2.28	±0.191	±0.025
Figuladra volgiola MEQ, SCQ	141	21.46–26.96	27.47–34.19	5.875–6.125	0.721–0.841
Mean		23.58	30.63	6.000	0.770
s.d.		±1.452	±1.680	±0.119	±0.025
Billordia nicoletteae SCQ	12	13.78–17.67	21.43–26.61	5.125–5.375	0.538–0.664
Mean		14.85	24.76	5.250	0.598
s.d.		±0.170	±0.145	±0.141	±0.073
Billordia bridgettae SCQ	22	15.24–19.07	26.28–31.16	4.50–5.675	0.544–0.662
Mean		17.28	28.21	5.250	0.613
s.d.		±0.097	±0.123	±0.212	±0.027
Figuladra s.s. MEQ	387	25.15	32.43	6.146	0.781
Figuladra s.s. SEQ	353	27.53	34.83	6.220	0.792

MEQ, mid-eastern Queensland; SCQ, southern-central Queensland; SEQ, south-eastern Queensland.

and the configuration of the penial pilasters. *Euryladra* lacks the muscular tissue connecting the penis to the epiphallus that is present in *Figuladra*. The single longitudinal pilaster in the upper penial chamber of *Euryladra* differs from the longitudinal thickenings in *Brigaladra*, *Billordia* and *Figuladra*.

Euryladra mattea (Iredale, 1933), comb. nov.

(Fig. 3*b*, 6, 8, 10, 11*a*, 12*c,d*, 13*a–c*, 14, 15*c,d*, 16, Tables 1–4)

Varohadra incei mattea Iredale, 1933, p. 46. – Smith (1992, p. 154 [in synonymy]).

Varohadra mattea Iredale, 1937, p. 33, pl. 3, fig. 12.

Figuladra mattea. – Stanisic *et al.* (2010, p. 470, sp. 746, figure in text).

Common name

Pale Banded Snail.

Material examined

Holotype. AMSC100642 [Rockhampton, SEQ, 23°22′S, 152° 32′E, coll. H. Bernhard, ii. 1932. Diameter 2.04 mm, height 2.92 mm, H/D 0.699, number of whorls 6].

Other Material. (All SEQ and SCQ) Ambrose limestone quarry: QMMO8158; Archookoora Forest Stn, via Kingaroy: QMMO4262; Auburn R NP, via Mundubbera: QMMO64432; Ban Springs, QMMO21151; Banana Ra, QMMO50489, QMMO50640, QMMO50657, QMMO50658; Baralaba, MO23499; Bauhinia Downs Stn: QMMO35820, QMMO5858; Beaudesert: QMMO68572; Big Woody I: QMMO65483; Biggenden: QMMO47478, QMMO47483, AMSC136406, AMSC434601; Biloela: QMMO76378, QMMO76379, QMMO76380, QMMO80514, AMSC158652; Blackwater: QMMO67777, AMSC444386; Boomer Ra: QMMO47963, QMMO50487, QMMO50488; Bouldercombe: QMMO29869, QMMO31296: Boyne Range: QMMO80364; Bracewell: QMMO72175, QMMO79346, QMMO8135; Bribie Is: QMMO32359, QMMO9822; Brisbane: QMMO75436, QMMO76682, QMMO77887, AMSC158527, AMSC434606, SAMAD14513, MCZ315889; Broadsound Ra: QMMO45979, QMMO47847; Builyan Railway Stn: QMMO20317; Bundaberg: QMMO6775, AMSC92299; Burnett R: QMMO31420, AMSC136724; Burrum Heads: QMMO52122, AMSC467373; Byfield: AMSC471706; Calliope: QMMO72201, QMMO72203, QMMO72204, QMMO72285, QMMO72316, QMMO72331, AMSC444295; Cania Gorge: QMMO23133, QMMO35092; Cannindah: MO24559; Carnarvon NP: QMMO56643; Clifton Ra: QMMO22384, QMMO22994; Comet: QMMO44100, AMSC400913; Cooloola SF: QMMO5106, QMMO5254, QMMO5857; Coomba Falls: QMMO5002, QMMO5003; Coringa: QMMO24180; Cracow: QMMO79549, QMMO79555, QMMO79560; Curtis Island: QMMO4222, QMMO4267, QMMO4907; Dallarnil: QMMO35093; Dan Scrub: QMMO80301; Dawes Ra: QMMO22640, AMSC136769; Dawson Ra: QMMO44136, AMSC137865; Dingo: QMMO46309, QMMO55291; Dulacca: QMMO86812; Dululu: QMMO45532; Eidsvold: QMMO49081, QMMO55229, AMSC31654, AMSC80633; Emerald: QMMO57096; Emu Park: QMMO6801; Esk: QMMO6783, QMMO77842; Gayndah: QMMO76041, QMMO76062, QMMO76125, AMSC137799; Gin: QMMO38277, AMSC471651; Gladstone: QMMO72181, QMMO72215, QMMO72255, AMSC444319; Glastonbury SF, QMMO21591; Gogango Ra: QMMO49020, QMMO60906; Goodnight Scrub: QMMO21800, QMMO23439; Goomeri: QMMO51966, QMMO52024, AMSC434603; Goondiwindi: QMMO76043,
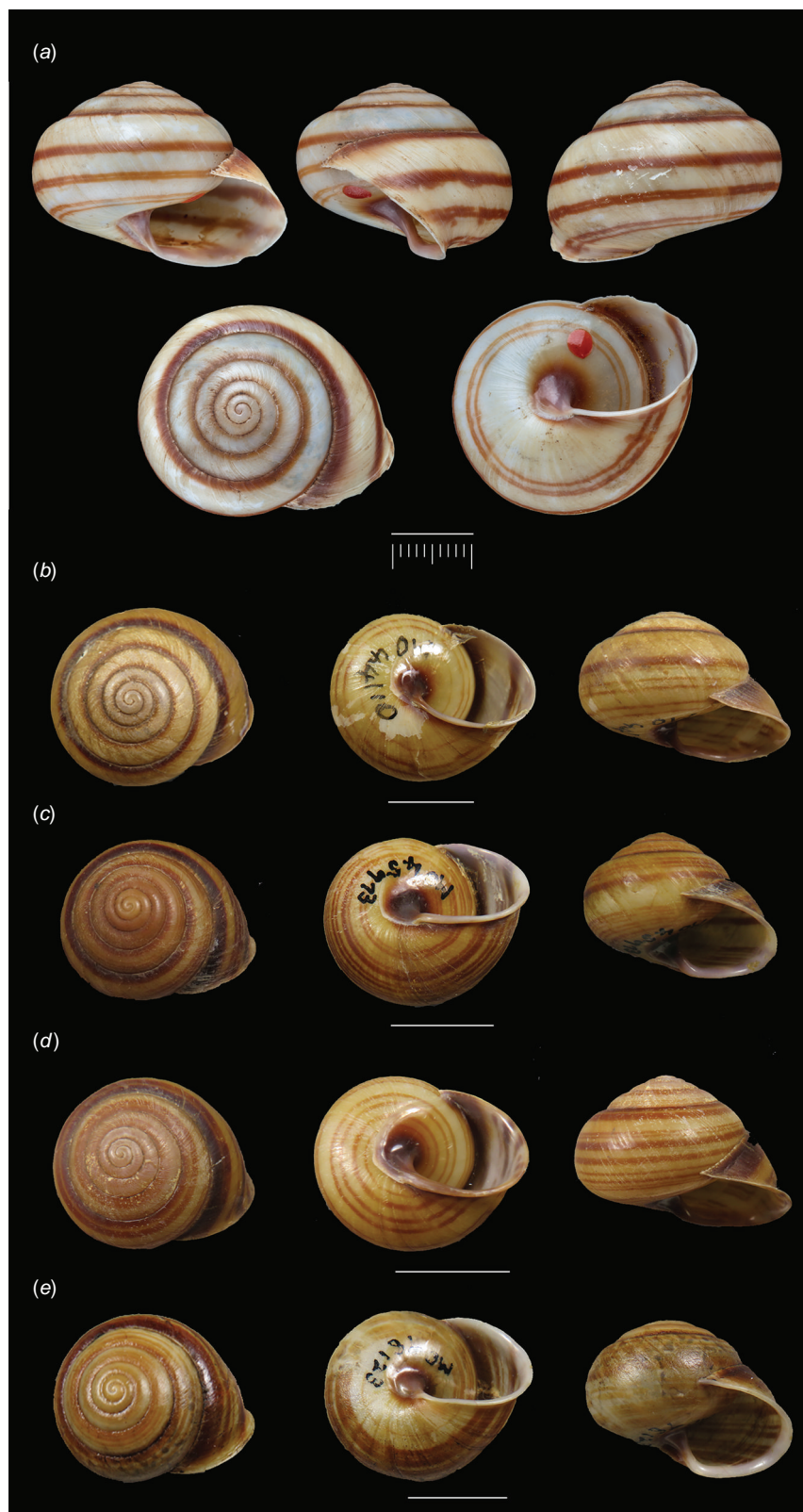
Fig. 9. Representative shells. (*a*) *Varohadra volgiola*, holotype in NHMUK 1880.12.11.14. (*b*) *Brigaladra volgiola*, QMMO44110, Charlevue Creek, Blackdown Tableland, SCQ, type locality. (*c*) *B. volgiola*, QMMO45973, Broadsound Range, SEQ. (*d*) *B. volgiola*, QMMO46286, Boomer Range, SEQ. (*e*) *B. volgiola*, QMMO78123, Peak Range, SCQ. Image (*a*) Jon Ablett, NHMUK. Scale bars: 10 mm.

QMMO76067, QMMO76068; Granite Ck: QMMO43549; Gumdale: QMMO62313; Gympie: QMMO51937, QMMO55771; Henickes Hill: QMMO86916; Horrigan Ck: MO23558; Injune: QMMO79093, QMMO86640, QMMO86643, AMSC478030; Ipswich: QMMO55362, QMMO62694, QMMO6774, QMMO77877, AMSC113806, AMSC444317; Isla Gorge NP: QMMO73099, QMMO76050, QMMO86908; Kalpowar SF:

Fig. 10. Colour variations of *Euryladra mattea*. (*a*) Holotype, AMSC100642, Rockhampton, SEQ. (*b*) Rare blonde form QMMO4252, North Ipswich, SEQ; (*c*) dark form, QMMO86812, Dulacca, SCQ. (*d*) Common form from the type locality, QMMO15091, Rockhampton, SEQ. (*e*) Variation in banding, QMMO86647, Banana, SCQ. Scale bar: 10 mm.
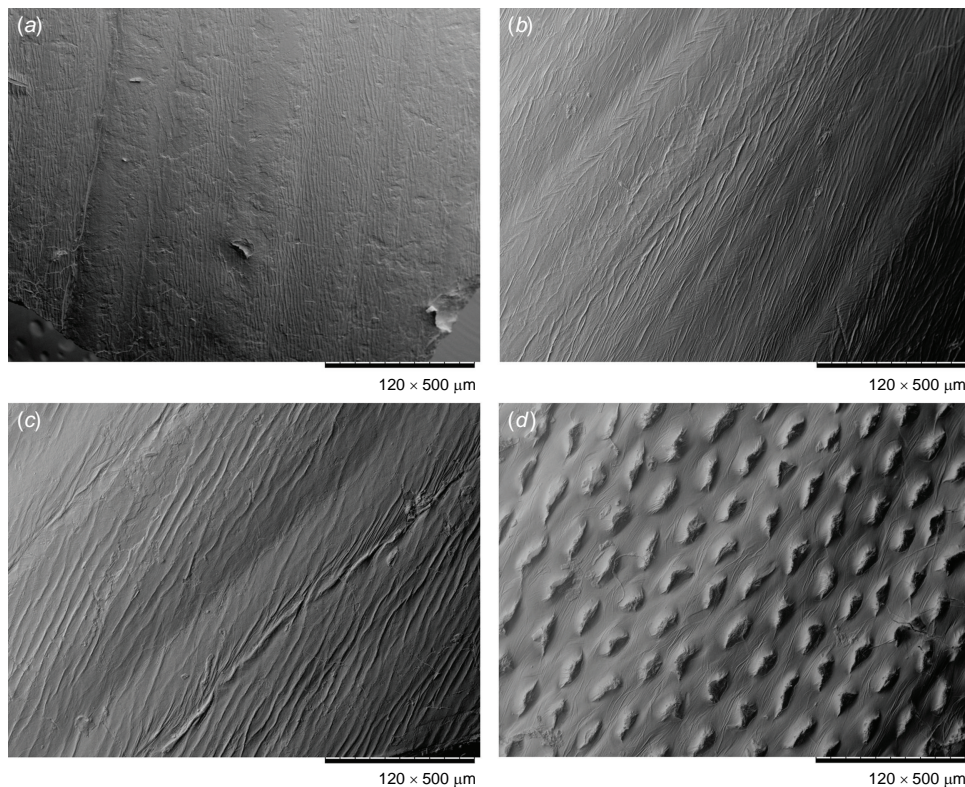
Fig. 11. Scanning electron micrographs showing microsculpture on body whorl. (*a*) *Figuladra mattea* QMMO14788, Rockhampton, SEQ. (*b*) *Figuladra volgiola* QMMO87118, Peak Range, SCQ. (*c*) *Figuladra incei curtisiana* QMMO72207, Farmers Point, SEQ. (*d*) *Billordia bridgettae* QMMO78169, Lords Table, SCQ. Scale bars: 500 μm.

QMMO21069; Keppel Bay: AMSC434528; Kilcoy: QMMO70157; Kilkivan: QMMO86935; Kroombit Tops: QMMO80556, QMMO80564, QMMO80592, AMSC434529, AMSC468221; Laidley: QMMO77848; Lake Weyba: QMMO6788; Lawgi Hall: QMMO80578, QMMO80585; Limestone Ck: QMMO5114; Many Peaks: QMMO66635, QMMO67031, QMMO6782; Marlborough: QMMO34413, QMMO46280; Maryborough: QMMO4879, QMMO6778, QMMO6787, AMSC136495, AMSC444349, AMSC444364; Miriam Vale: QMMO64065; Monto: QMMO79759, QMMO79779, QMMO79827, AMSC101254, AMSC434599; Montville: QMMO6784, AMSC137863; Morganville: DM13834941; Morinish: QMMO5123; Moura: QMMO76124, QMMO76400, QMMO76402, QMMO76681, QMMO76781, AMSC79101; Mt Aldis: QMMO79420; Mt Gayndah: MO20171; Mt Kelly: MO24547; Mt Larcom: QMMO72178, QMMO72212, QMMO79341, QMMO79348, QMMO80406, AMSC444335; Mt Misery: QMMO26439, QMMO74666; Mt Morgan: QMMO29770, QMMO21498, MO23484, QMMO4618, QMMO61898, AMSC157846, AMSC444318, AMSC467372; Mt Ox: QMMO79356; Mt Perry: QMMO86814, QMMO86836; Mt Scoria: QMMO80448, QMMO80461; Mt Tamborine: QMMO3967; Mt Walsh NP: QMMO66840, QMMO71480; Mt Woowoonga: QMMO22440, QMMO86675, AMSC136717; Mudlo Gap: QMMO22990, QMMO39435; Mulgildie Plateau: QMMO70171; Mundubbera: QMMO75425, QMMO76436; Murgon: QMMO22988; N Stradbroke I: QMMO66654; Nambour: QMMO56696; Nanango: QMMO70503; Noosa: QMMO62242; Noosa, QMMO64296; Noosa, QMMO71569; Nuga Nuga NP: QMMO79448, QMMO85015; Oakey Ck: QMMO35104; Palmgrove NP: QMMO79416; Pialba: AMSC79125; Planet Downs: QMMO35829, QMMO44123; Port Curtis: AMSC17593, AMSC79083; Raglan: QMMO21483, QMMO72172, QMMO7294; Redcliffe: QMMO37947; Ridgelands: QMMO5130, AMSC444329; Rockhampton: QMMO15091, QMMO77035, QMMO78027, QMMO78061, QMMO78090, QMMO78100, AMSC158986, AMSC434605, AMSC444308; Somerset Dam: QMMO62243; Springsure: QMMO79964, QMMO85045; St Helena I:, QMMO67338, QMMO69417, AMSC172702; Targinnie: QMMO72332, QMMO86799; Taroom: QMMO79553, QMMO79569, QMMO86895; Thangool: MO28447; Theodore: QMMO60849, QMMO60851, QMMO64382, AMSC444457; Toogoom: QMMO39448; Warwick:, QMMO64531; Weyba NP: QMMO47501; Woodgate NP: QMMO63797; Woody I: QMMO5856; Woolooga: QMMO71212, QMMO74836; Wowan: QMMO54777, QMMO60709, AMSC471659, AMSC75111. (Other records are available from the Australian and Queensland Museums).

Diagnosis

As for genus.

Description

Shell large, diameter of shell 18.50–27.47 mm (mean 22.68 mm), height 25.28–34.48 mm (mean 30.23 mm), H/D 0.683–0.820 (mean 0.749); evenly coiled, depressedly globose with a low domed spire; whorls rounded 5.750–6.750 (mean 6.00); sutures weakly impressed; protoconch with weak crowded radial ridges, teleoconch smooth, microsculpture of extremely fine periostracal microradial threads; shell yellowish with prominent broad subsutural and peripheral bands and numerous narrower dark brown spiral lines and bands; dark brown circum-umbilical patch; lip white, expanded and moderately flared, reflected over umbilicus and partially occluding this; umbilicus narrowly open to almost closed, excavate. Animal pinkish-orange–grey with pinkish-orange mantle. Based on 434 measured adult specimens (see Supplementary Table S1).

Fig. 12. Colouration of living animals. (*a*) *Brigaladra volgiola*, Ropers Creek, Peak Range, SCQ. (*b*) Orange mantle of *Brigaladra volgiola*, Ropers Creek, Peak Range, SCQ. (*c*) *Euryladra mattea*. Brandts Road, Mount Woowoonga, SEQ. (*d*) Pinkish-orange mantle of *Euryladra mattea*, Henickes Road, Ambrose, SEQ. (*e*) *Billordia bridgettae*, Lord's Table, SCQ, (*f*) Pink mantle of *Figuladra incei curtisiana*, Targinnie, SEQ.

Genitalia. Penis with thin sheath, long, cylindrical; walls of upper penial chamber with numerous irregular pustules giving rise to a chevron-like pattern of pustules; a single longitudinal pilaster in the upper penial chamber and several regular longitudinal thickenings that descend into the atrium. Epiphallus with a muscular ascending arm partially coiled and entwined in connective tissue at the epiphallic–penial junction, when unravelled, 2–3 times the length of a thinner descending arm; epiphallus entering penis through a simple pore. Penial retractor muscle

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inserted at the junction of two arms of the epiphallus. Vas deferens attached to penial sheath with connective tissue; vestigial epiphallic flagellum situated at epiphallus–vas deferens junction, tightly bound to vas deferens; vagina short almost the same length as the penis, PVR 1.293–1.958 (mean 1.616); free oviduct much shorter than vagina,

swollen at the junction to the vagina; bursa copulatrix with a slender stalk and clavate head located at the base of the albumen gland. Ovotestis and albumen gland, hermaphroditic duct typical. Based on 20 dissected adult specimens (see Supplementary Tables S1, S4).

Distribution and habitat

From Tweed River, NE NSW to Rockhampton, SEQ and inland as far west as Carnarvon NP, SCQ; open woodland and dry vine thicket living under rocks and logs.

Remarks

Euryladra mattea exhibits a range of banding patterns and colour suffusions. Specimens from Taroom, Dulacca and Planet Downs, SCQ have a darker shell than most *E. mattea* from the extensive range. A very rare 'blonde' form with no banding occurs at Bergins Hill near Ipswich, SEQ. All forms however, have a pale base. Flattening of the shell in some forms also results in a wider umbilicus (Fig. 10). In the past, *E. mattea* has been confused with *Figuladra challisi* (Cox 1873). *E. mattea* species are only found south of Rockhampton whereas *F. challisi* is a species described from Keswick I, MEQ. The true *F. challisi* lacks the excavated umbilical area of *E. mattea* and has a much more solid, porcelain-like shell (Stanisic *et al.* 2010; Stanisic and Stanisic 2020).
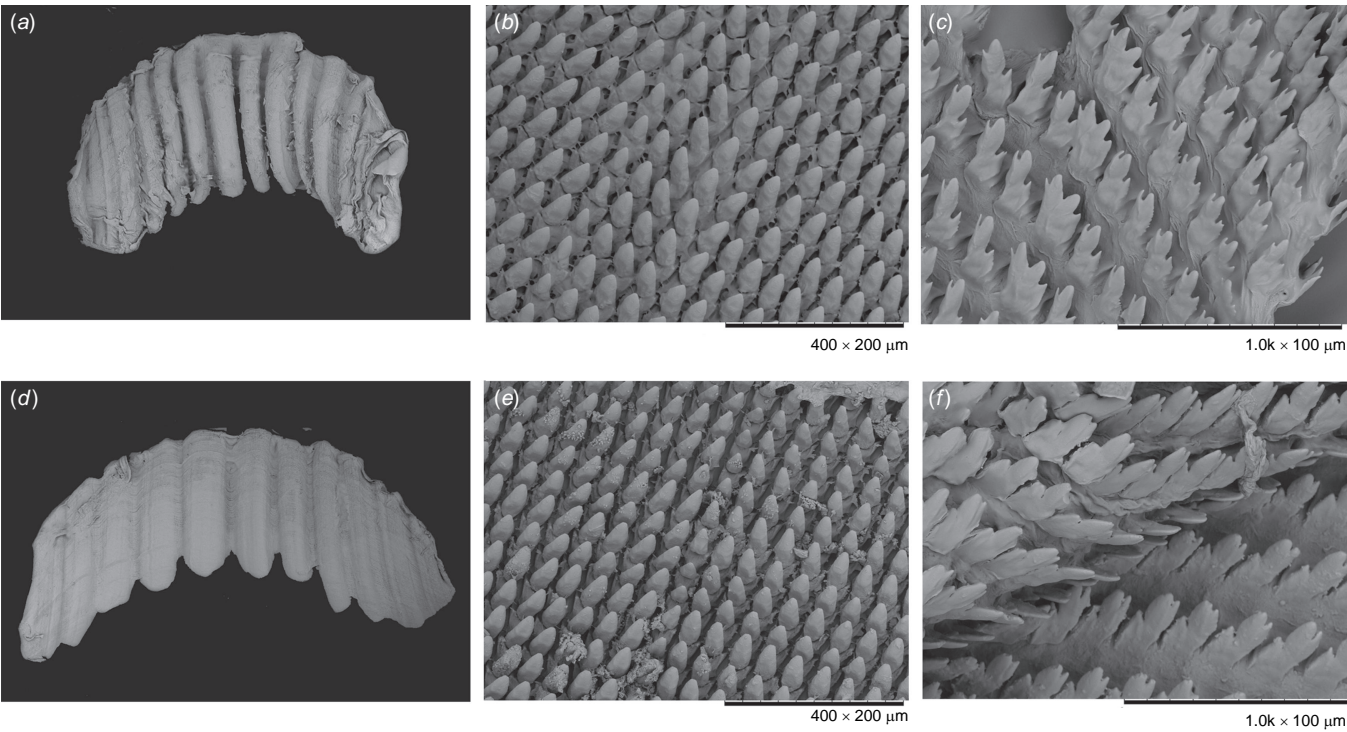
Table 4. Mantle colours in hadroid land snails from eastern Queensland.

Hadroid snail genus	Locality	Mantle colour
Clade 1: red mantle lineages		
Bentosites (Iredale, 1933)	MEQ	Orange
Billordia Stanisic 2010	MEQ	Reddish
Figuladra Köhler & Bouchet, 2020	SEQ, MEQ, SCQ	Pink
Lamprellia Stanisic, 2010	NQ	Red
Marilynessa Stanisic, 2010	MEQ	Orange–red
Monteithosites Stanisic, 1996	NQ	Orange–red
Steorra Stanisic, 2010	WT, NQ	Orange–red
Temporena Iredale, 1933	MEQ	Orange–red
Clade 4: black mantle lineages		
Sphaerospira Mörch, 1867	NE NSW to MEQ	Black
Gnarosophia Iredale, 1933	WT	Black

Fig. 13. Scanning electron micrographs showing jaws, central and lateral parts of radula. (*a–c*) *Euryladra mattea* QMMO86640, Arcadia Valley, (*d–f*) *Brigaladra volgiola* QMMO87134, Peak Range, SCQ. Scale bars: 500 μm.

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Table 5.   Clade I camaenids and preferred habitats.

Genus	Locality	Preferred habitat	Biome
Bentosites	MEQ	Vine thicket	Subtropical dry forest
Billordia	SCQ	Vine thicket on rocky scree	Subtropical dry forest
Brigaladra (Clade C)	MEQ, SCQ	Vine thicket on rocky slopes	Subtropical dry forest
Euryladra (Clade B)	SEQ, SCQ	Open woodland and the edges of vine thickets	Woodland and savannah
Figuladra (Clade A)	MEQ, SEQ	Vine thicket and dry rainforest	Subtropical dry forest
Lamprellia	NQ	Open woodland and vine thicket	Woodland
Marilynessa	MEQ	Vine thicket and dry rainforest	Subtropical dry forest
Steorra	WT	Rainforest and adjacent woodland; vine thicket	Tropical rainforest
Temporena	MEQ	Vine thicket on rocky outcrops, Casuarina forest	Subtropical dry forest

MEQ, mid-eastern Queensland; NQ, North Queensland; SCQ, southern-central Queensland; SEQ, south-eastern Queensland; WT, Wet Tropics.
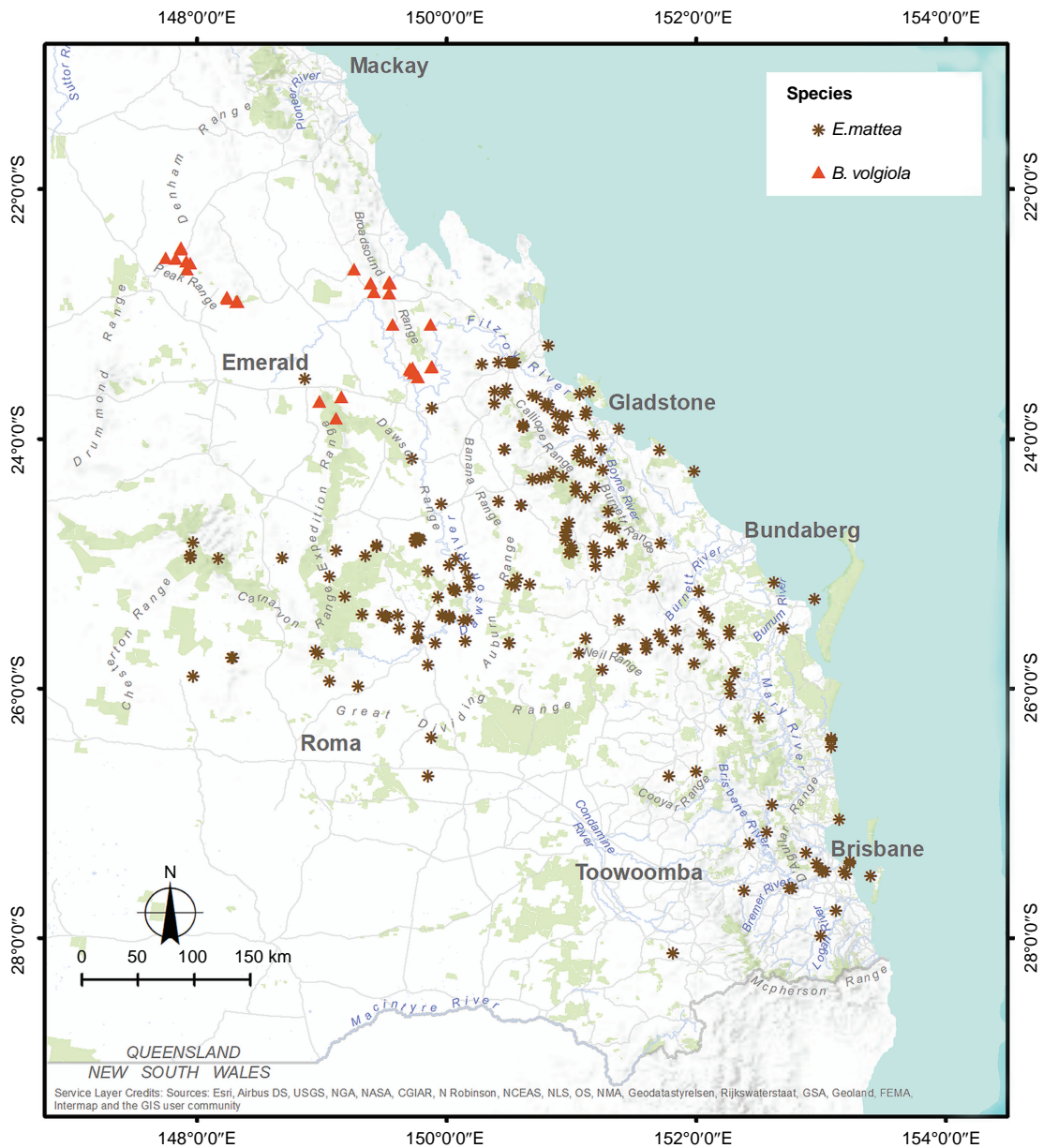

Fig. 14.   Distribution of *Brigaladra volgiola* and *Euryladra mattea* in Queensland. Map: Kim Maxwell.

Figuladra Köhler & Bouchet, 2020

Varohadra Iredale, 1933, p. 45.

Figuladra Iredale, 1933, p. 45 (*nomen nudum*).

Figuladra Köhler & Bouchet, 2020, p. 4.

Type species: *Helix curtisiana* L. Pfeiffer, 1864 – by original designation.

Diagnosis

Shell large to very large (diameter 20–41 mm, height 20–34 mm), loosely to tightly coiled; depressedly globose to trochoidally globose with a dome-shaped spire; whorls rounded and often laterally compressed with weakly impressed sutures; protoconch features weak crowded radial ridges, teleoconch has a smooth microsculpture of extremely fine periostracal microradial threads; lip is reflected, white with a dark brown suffusion behind this and at the top of the columella; umbilicus narrowly open; yellow to dark brown circum-umbilical patch; shell colour variable even within species from dark brown with few to numerous brown spiral bands to monochrome brown or yellow; animal dark grey with a pinkish tinge and a pinkish-red mantle. Reproductive system with a sheath of muscular tissue connecting the epiphallus to the top of the penis; vas deferens thin and attached to penial sheath with connective tissue; short, thin epiphallic flagellum is present, situated near the epiphallus–vas deferens junction, tightly bound to the vas deferens; vagina short, generally less than half the length of the penis; atrium is simple; free oviduct is shorter than vagina; bursa copulatrix simple with a slender stalk, situated at the base of the albumen gland; prostate, uterus and hermaphroditic duct without unusual features.

Range

Eastern Queensland from Maryborough to St Helen's Beach, on off-lying islands from the South Cumberland Island group to Fraser Island, and west to the Great Dividing Range.

Fig. 15. Habitat images (*a*) *Brigaladra volgiola*: semi-evergreen vine thicket on rocky scree, Lords Table, Peak Range, SCQ. (*b*) *Brigaladra volgiola*: semi-evergreen vine thicket, Langdale Hill, MEQ. (*c*) *Euryladra mattea*: Open woodland, Taroom, SCQ. (*d*) *Euryladra mattea*: edge of vine thicket, Bagara, SEQ.

Fig. 16. *Euryladra mattea* living under a eucalypt tree (overlying large timber removed), Horrigans Road, Raglan, SEQ.

Remarks

Among eastern Australian camaenids, *Figuladra* is distinguished by the almost smooth microsculpture and pinkish mantle. Genital anatomy separates *Figuladra* from other hadroid snail genera by having a band of muscular tissue connecting the penis and epiphallus. This feature is not present in any other hadroid genus. *Figuladra* is also separated from *Euryladra* and *Brigaladra* by the penial–vaginal ratio in which the vagina is considerably shorter than the penis.

Billordia Stanisic, 2010

Type species: *Billordia nicoletteae* Stanisic, 2010.

Diagnosis

Shell medium to large (diameter 15–26 mm), subdiscoidal with a low spire; whorls rounded (average 5.250), sutures weakly impressed; protoconch with weak radial ridges, teleoconch sculpture of minute scattered pustules overlain by crowded periostracal scales; lip sharply reflected; umbilicus open, partly covered by the reflected columella. Colour yellowish-brown with numerous prominent brown spiral bands of varying widths, with or without a brown circum-umbilical patch, and a white lip. Reproductive system with long, knotted epiphallus entwined in connective tissue at the epiphallic–penial junction; penis approximately twice the length of the vagina.

Range

Western foothills of the southern Connors Range and Peak Range, SCQ and MEQ (inland).

Remarks

Billordia is distinguished from *Figuladra*, *Euryladra* and *Brigaladra* by the subdiscoidal shell with pustulose

microsculpture on the teleoconch, shell coiling pattern and knotted epiphallus in the genitalia.

Supplementary material

Supplementary material is available online.

References

Bishop MJ (1978) A revision of the genus *Thersites* Pfeiffer (Pulmonata: Camaenidae). *Journal of the Malacological Society of Australia* **4**(1–2), 9–21. doi:10.1080/00852988.1978.10673904

Byrne M, Yeates D, Joseph L, Kearney M, Bowler J, Williams M, Cooper S, Donnellan S, Keogh J, Leys R (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology* **17**(20), 4398. 4417. doi:10.1111/j.1365-294X.2008.03899.x

Byrne M, Steane DA, Joseph L, Yeates DK, Jordan GJ, Crayn D, Aplin K, Cantrill DJ, Cook LG, Crisp MD, Keogh JS, Melville J, Moritz C, Porch N, Sniderman JMK, Sunnucks P, Weston PH (2011) Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *Journal of Biogeography* **38**(9), 1635–1656. doi:10.1111/j.1365-2699.2011.02535.x

Chiba S (1999) Accelerated evolution of land snails *Mandarina* in the oceanic Bonin Islands: evidence from mitochondrial DNA sequences. *Evolution* **53**(2), 460–471. doi:10.1111/j.1558-5646.1999.tb03781.x

Clark SA (2009) A review of the land snail genus *Meridolum* (Gastropoda: Camaenidae) from central New South Wales, Australia. *Molluscan Research* **29**(2), 61–120.

Couper PJ, Hoskin CJ (2008) Litho-refugia: the importance of rock landscapes for the long-term persistence of Australian rainforest fauna. *Australian Zoologist* **34**(4), 554–560.

Cox JC (1872) Description of a new volute and twelve new species of land-shells from Australia and the Solomon Islands. *Proceedings of the Zoological Society of London* **1871**, 643–647.

Cox JC (1873) Descriptions of new species of land and marine shells from Australia and the Solomon and Louisiade Islands. *Proceedings of the Zoological Society of London* **1873**, 564–569.

Criscione F, Köhler F (2013) Conserved shell disguises diversity in *Mesodontrachia* land snails from the Australian Monsoon Tropics (Gastropoda: Camaenidae). *Zoologica Scripta* **42**(4), 389–405. doi:10.1111/zsc.12011

Criscione F, Köhler F (2014a) Molecular phylogenetics and comparative anatomy of *Kimberleytrachia* Köhler, 2011 – a genus of land snail endemic to the coastal Kimberley, Western Australia with description of new taxa (Gastropoda, Camaenidae). *Contributions to Zoology* **83**(4), 245–267. doi:10.1163/18759866-08304003

Criscione F, Köhler F (2014b) *Cardiotrachia* and *Rachita* – two new land snail genera from the East Kimberley, Western Australia (Eupulmonata: Camaenidae) *Systematics and Biodiversity* **12**(1), 55–64. doi:10.1080/14772000.2013.877998

Davison A, Blackie RLE, Scothern GP (2009) DNA barcoding of stylommatophoran land snails: a test of existing sequences. *Molecular Ecology Resources* **9**, 1092–1101. doi:10.1111/j.1755-0998.2009.02559.x

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1991) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**(5), 294–299.

Hamilton ZR (2021) Repeated evolution of an undescribed morphotype of *Rhagada* (Gastropoda: Camaenidae) from the inland Pilbara, Western Australia. *Invertebrate Systematics* **35**(2), 203–215. doi:10.1071/IS20038

Hugall A, Moritz C, Moussalli A, Stanisic J (2002) Reconciling paleo-distribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosophia bellendenkerensis* (Brazier 1875). *Proceedings of the National Academy of Sciences of the United States of America* **99**(9), 6112–6117. doi:10.1073/pnas.092538699

Hugall A, Stanisic J, Moritz C (2003) Phylogeography of terrestrial gastropods: the case of the Sphaerospira lineage and history of

Queensland rainforests. In 'Molecular systematics and phylogeography of Mollusks'. (Eds L Lydeard C, R David) pp. 270–301. (Smithsonian Institution Press: Washington, DC, USA)

Hugall AF (2011) Phylogeny and biogeography of the camaenid land snails of eastern Australia. PhD dissertation, University of Adelaide. Available at https://hdl.handle.net/2440/119079

Hugall AF, Stanisic J (2011) Beyond the prolegomenon: a molecular phylogeny of the Australian camaenid land snail radiation. *Zoological Journal of the Linnean Society* **161**(3), 531–572. doi:10.1111/j.1096-3642.2010.00644.x

International Trust for Zoological Nomenclature (2012) 'International Code of Zoological Nomenclature', 4th edn. (ICZN: London, UK) Available at https://www.iczn.org/the-code/the-code-online/ [Verified 17 August 2021]

Iredale T (1933) Systematic notes on Australian land shells. *Records of the Australian Museum* **19**(1), 37–59. doi:10.3853/j.0067-1975.19.1933.690

Iredale T (1937) A basic list of the land Mollusca of Australia. Part II. *Australian Zoologist* **9**, 1–39.

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* **14**(6), 587–589. doi:10.1038/nmeth.4285

Kameda Y, Kawakita A, Kato M (2007) Cryptic genetic divergence and associated morphological differentiation in the arboreal land snail *Satsuma* (*Luchuhadra*) *largillierti* (Camaenidae) endemic to the Ryukyu Archipelago, Japan. *Molecular Phylogenetics and Evolution* **45**, 519–533. doi:10.1016/j.ympev.2007.03.021

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**(4), 772–780. doi:10.1093/molbev/mst010

Kearse M, Moir R, Wilson A, *et al.* (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**(12), 1647–1649. doi:10.1093/bioinformatics/bts199

Köhler F (2010a) Three new species and two new genera of land snails from the Bonaparte Archipelago in the Kimberley, Western Australia (Pulmonata, Camaenidae). *Molluscan Research* **30**(1), 1–16.

Köhler F (2010b) Uncovering local endemism in the Kimberley, Western Australia: description of new species of the genus *Amplirhagada* Iredale, 1933 (Pulmonata, Camaenidae). *Records of the Australian Museum* **62**, 217–284. doi:10.3853/j.0067-1975.62.2010.1554

Köhler F (2011a) The camaenid species of the Kimberley Islands, Western Australia (Stylommatophora: Helicoidea). *Malacologia* **54**, 203–406. doi:10.4002/040.054.0108

Köhler F (2011b) *Australocosmica*, a new genus of land snails from the Kimberley, Western Australia (Eupulmonata, Camaenidae). *Malacologia* **53**, 199–216. doi:10.4002/040.053.0201

Köhler F, Bouchet P (2020) On unavailable genus-group names introduced by Tom Iredale for Australian non-marine gastropods: nomenclatural clarifications and descriptions of new genera. *Molluscan Research* **40**(2), 150–159. doi:10.1080/13235818.2020.1724603

Köhler F, Criscione F (2015) A molecular phylogeny of camaenid land snails from north-western Australia unravels widespread homoplasy in morphological characters (Gastropoda, Helicoidea). *Molecular Phylogenetics and Evolution* **83**, 44–55. doi:10.1016/j.ympev.2014.11.009

Köhler F, Johnson MS (2012) Species limits in molecular phylogenies: a cautionary tale from Australian land snails (Camaenidae: *Amplirhagada* Iredale, 1933). *Zoological Journal of the Linnean Society* **165**(2), 337–362. doi:10.1111/j.1096-3642.2011.00810.x

Köhler F, Criscione F, Shea M (2020) A mitochondrial phylogeny uncovers taxonomic ambiguity and complex phylogeographic patterns in the eastern Australian land snail *Austrochloritis* (Stylommatophora, Camaenidae). *Journal of Zoological Systematics and Evolutionary Research* **58**, 1005–1020. doi:10.1111/jzs.12366

Neldner VJ, Butler DW, Guymer GP (2019) 'Queensland's regional ecosystems: building a maintaining a biodiversity inventory, planning framework and information system for Queensland. Version 2.1.' (Queensland Herbarium, Department of Environment and Science: Brisbane, Qld, Australia)

Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating Maximum Likelihood phylogenies. *Molecular Biology and Evolution* **32**, 268–274. doi:10.1093/molbev/msu300

Oba Y, Ôhira H, Murase Y, Moriyama A, Kumazawa Y (2015) DNA barcoding of Japanese click beetles (Coleoptera, Elateridae). *PLoS One* **10**, e0116612. doi:10.1371/journal.pone.0116612

Parkyn J, Newell DA (2013) Australian land snails: a review of ecological research and conservation approaches. *Molluscan Research* **33**(2), 116–129. doi:10.1080/13235818.2013.782793

Perez KE, Defreitas N, Slapcinsky J, Minton RL, Anderson FE, Pearce TA (2014) Molecular phylogeny, evolution of shell shape, and DNA barcoding in Polygyridae (Gastropoda: Pulmonata), an endemic North American clade of land snails. *American Malacological Bulletin* **32**(1), 1–31. doi:10.4003/006.032.0103

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**(12), 1572–1574. doi:10.1093/bioinformatics/btg180

Sela I, Ashkenazy H, Katoh K, Pupko T (2015) GUIDANCE2: accurate detection of unreliable alignment regions accounting for the uncertainty of multiple parameters. *Nucleic Acids Research* **43**(W1), W7–W14. doi:10.1093/nar/gkv318

Smith BJ (1992) Non-marine Mollusca. In 'Zoological Catalogue of Australia'. (Ed. WWK Houston) Vol. 8, p. 405. (Australian Government Publishing Service)

Solem A (1973) Convergence in pulmonate radulae. *The Veliger* **15**, 165–170.

Solem A (1979) A theory of land snail biogeographic patterns through time. In 'Pathways in Malacology'. (Eds S Van der Spoel, AC Van Bruggen, J Lever) pp. 225–249. (Scheltema & Holkema: Utrecht, Netherlands)

Solem A (1984) Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). IV. Taxa from the Kimberley, *Westraltrachia* Iredale, 1933 and related genera. *Records of the Western Australian Museum Supplements* **17**, 427–705.

Solem A (1985) Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). V. Remaining Kimberley genera and addenda to the Kimberley. *Records of the Western Australian Museum Supplements* **20**, 707–981.

Solem A (1992) Camaenid land snails from Southern and eastern South Australia, excluding Kangaroo Island. Records of the South Australian Museum. *Monograph Series* **2**, 1–338.

Solem A (1997) Camaenid land snails from western and central Australia (Mollusca: Camaenidae). VII. Taxa from Dampierland through the Nullarbor. *Records of the Western Australian Museum* **50**, 1461–1906.

Solem A, van Bruggen AC (1984) World-wide snails: biogeographical studies on non-marine Mollusca. In 'Biogeographical Studies on Non-marine Mollusca'. (Eds A Solem, AC van Bruggen) pp. 6–22. (E.J. Brill/W. Backhuys: Leiden, Netherlands)

Stanisic J (1994) The distribution and patterns of species diversity of land snails in eastern Australia. *Memoirs of the Queensland Museum* **36**(1), 207–214.

Stanisic J (1996) A new camaenid land snail from the Wet Tropics Biogeographic Region, northeastern Queensland (Eupulmonata, Camaenidae). *Memoirs of the Queensland Museum* **39**, 355–363.

Stanisic J (2013) A new genus, *Denhamiana* gen. nov., and two new species of land snail from inland central Queensland (Eupulmonata, Camaenidae). *Memoirs of the Queensland Museum* **58**(1), 367–374.

Stanisic J (2016) A new genus and two new species of land snail from geographically remote lithorefugial habitats in Queensland including a remarkable range extension for *Quistrachia* Iredale, 1939 (Gastropoda: Eupulmonata: Camaenidae). *Memoirs of the Queensland Museum, Nature* **60**, 43–51. doi:10.17082/j.2204-1478.60.2016.2016-12

Stanisic J, Ponder WF (2004) Forest snails in eastern Australia – one aspect of the other 99%. In 'Conservation of Australia's Forest Fauna'. (Ed. D Lunney) pp. 127–149. (Royal Zoological Society of New South Wales)

Stanisic L, Stanisic J (2020) Reconciling nomenclature and type localities of some Queensland hadroid camaenids: a prelude to a revision of *Figuladra* Köhler & Bouchet, 2020 (Gastropoda: Eupulmonata: Camaenidae). *Memoirs of the Queensland Museum, Nature* **62**, 1–24.

Stanisic J, Cameron RAD, Pokryszko BM, Nekola JC (2007) Forest snail faunas from S.E. Queensland and N.E. New South Wales (Australia): patterns of local and regional richness and differentiation. *Malacologia* **49**(2), 445–462. doi:10.4002/0076-2997-49.2.445

Stanisic J, Shea M, Potter D, Griffiths O (2010) 'Australian land snails. Volume 1. A field guide to eastern Australian species.' (Bioculture Press: Mauritius)

Stanisic J, Shea M, Potter D, Griffiths O (2018) 'Australian land snails. Volume 2. A field guide to southern, central and western Australian species.' (Bioculture Press: Singapore)

Sutcharit C, Asami T, Panha S (2007) Evolution of whole-body enantiomorphy in the tree snail genus *Amphidromus*. *Journal of Evolutionary Biology* **20**(2), 661–672. doi:10.1111/j.1420-9101.2006.01246.x

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* **30**(12), 2725–2729. doi:10.1093/molbev/mst197

Taylor JPA, Johnson MS, Stankowski S (2015) Molecular phylogenetics and complementary geographical distributions of species of the Western Australian land snail genera *Plectorhagada* Iredale, 1933 and *Strepsitaurus* Solem, 1997 (Gastropoda: Camaenidae). *Zoological Journal of the Linnean Society* **174**(2), 305–321. doi:10.1111/zoj.12238

Webb LJ, Tracey JG (1981) Australian rainforests: patterns and change. In 'Ecological Biogeography of Australia'. (Ed. A Keast) pp. 605–694. (W. Junk: The Hague, Netherlands)

Zou S, Li Q, Kong L, Yu H, Zheng X (2011) Comparing the usefulness of distance, monophyly and character-based DNA barcoding methods in species identification: a case study of neogastropoda. *PLoS One* **6**(10), e26619. doi:10.1371/journal.pone.0026619

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