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Land snail diversity in the monsoon tropics of Northern Australia: revision of the genus *Exiligada* Iredale, 1939 (Mollusca: Pulmonata: Camaenidae), with description of 13 new species

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Vast parts of the monsoon tropics of Australia feature semi-arid habitats, which are generally thought to harbour a depauperate land snail fauna as compared to the mesic continental fringes, in particular the Australian wet tropics. However, our knowledge of land snails inhabiting these often remote environments is still very patchy. In order to improve the understanding of land snail diversity in the monsoon tropics, we revised the camaenid land snail genus *Exiligada* based on comprehensive collections, undertaken by use of helicopters on remote limestone outcrops in the Northern Territory and in Western Australia. Based on comparative analyses of shell and genital morphology and patterns of molecular differentiation, we recognize 15 species within *Exiligada*, 13 of which are newly described. In addition, we suggest a revised delimitation of the type species *Exiligada negriensis*, as compared to the latest available revision, by removing *Exiligada qualis* from its synonymy and recognizing it as a distinct species. A key for species identification is also provided. Molecular phylogenetic analyses strongly supported the monophyly of *Exiligada* with respect to other confamilial genera known to occur in the same geographical region. Most *Exiligada* species are narrowly endemic to restricted limestone outcrops that cover areas with a diameter of about 20 to 150 km. Within the distributional range of *Exiligada*, the ranges of up to seven species overlap but we never found more than three species to occur in sympatry at a given sampling site. We propose that species originated by allopatric differentiation, followed by secondary range expansion, leading to sympatric distributions. Our study confirms that less complex rock habitats in more xeric environments support no more than three sympatric species, this being likely to be a result of ecological exclusion.

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ADDITIONAL KEYWORDS: anatomy – Helicoidea – limestone – phylogeny – Western Australia.

INTRODUCTION

Land snails of the family Camaenidae are a diverse element of the invertebrate fauna of rainforests in the mesic zone along the eastern coast of the Australian continent (Stanisic *et al*., 2010; Hugall & Stanisic, 2011) as well as in more humid regions of the Kimberley region in the far north-west of Western Australia (e.g. Solem, 1991; Köhler, 2010b, 2011b, c). Camaenid species numbers in Australian rainforests range between about 30 and 45 per 5° grid within the eastern mesic zone, whereas in the wetter parts of the Kimberley, an area of similar size, about 200 species are known to occur (Hugall & Stanisic, 2011: fig. 1). These patterns of species richness are governed by a combination of moderate to high alpha-diversity (two to a maximum of 13 sympatric species per site in the Kimberley) and considerable beta-diversity (high species turn-over along spatial gradients because of narrow-range endemism; Gibson & Köhler, 2012).

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However, vast parts of Australia feature more xeric habitats, which are characterized through the absence of rainforests, and which are generally thought to represent marginal land snail habitats with depauperate land snail faunas as compared to the mesic continental fringes, and in particular to the Australian Wet Tropics and Kimberley regions. The relative paucity of species in more arid regions has been attributed to a reduced complexity of habitats, which therefore provide fewer opportunities to realise ecological niches. This factor results in lower species richness of areas and wider distributions of single species (reduced levels of alpha- and beta-diversity) (Cameron, 1992; Slatyer *et al*., 2007). The surprisingly diverse land snail fauna in the arid centre of the continent, which consists of about 65 species, has generally been seen as a notable exception to this general phenomenon (Solem, 1993). Here, the increased species richness is correlated with the occurrence of sharp topographical reliefs in the MacDonnell Ranges (Slatyer *et al*., 2007). As vast landscapes throughout the monsoonal tropics of Western Australia, the Northern Territory, and Queensland remain poorly studied, it is unclear whether land snail faunas in more arid regions are indeed depauperate or, alternatively, just poorly documented. Whereas regional land snail faunas were comprehensively studied along the eastern and western coastlines of the continent (Solem, 1981a, b, 1984, 1985, 1992, 1997; Stanisic *et al*., 2010; Köhler, 2010a, b, 2011a, 2012; Köhler & Shea, 2012), vast areas in the interiors of the Northern Territory, Western Australia, and Queensland remained unstudied. The present knowledge of land snails in the Northern Territory, for instance, rests on late 20th century revisions that are based on anecdotal historical accounts and collections undertaken along major roads that cover only a small fraction of the Territory's surface (Solem, 1984, 1985, 1993). Within this vast and remote region, limestone outcrops and their associated monsoon vine thickets (dry rainforest) comprise a distinctive but poorly known ecological community (Braby *et al*., 2012). Although limestone outcrops in general are known as important refuges for land snails (Schilthuizen *et al*., 2003; Clements *et al*., 2006, 2008); limestone-associated land snails in the Northern Territory are very little known because of the inaccessibility of most areas. Where studied, however, limestone outcrops in the Northern Territory have been found to support multiple, mostly narrowly endemic species (Willan *et al*., 2009). This finding on a small scale indicated that limestone areas in xeric habitats across Australia might support diverse but widely unknown land snail communities, similar to what has been documented for the topographically complex MacDonnell and Flinders Ranges in the arid centre of Australia (Slatyer *et al*., 2007).

Here we study the diversity of one camaenid taxon, the genus *Exiligada* Iredale, 1939, on limestone outcrops in remote areas of the Northern Territory (Daly River and Victoria River Districts) and adjacent parts of the East Kimberley in Western Australia. The present work is based on the first ever helicopter-based, comprehensive survey of remote limestone surfaces in the Northern Territory. During this survey we collected land snail samples at more than 100 sites that had never been surveyed before. Based on these new field collections and available museum samples, we revised the taxonomy of *Exiligada* Iredale, 1939, which represents the first named genus-group taxon from this area. The latest revision by Solem (1984) recognized only one extant species, the type *Exiligada negriensis* Iredale, 1939. The present work was based on analyses of mtDNA sequences and anatomical features of many new samples from the study area. This study has resulted in a considerably increased knowledge of *Exiligada*, unearthing a large number of previously unknown species. This improvement of documentation may serve as a yardstick to estimate how complete our knowledge of the land snail fauna of vast areas in the Australian monsoonal tropics in particular and the invertebrate fauna in general really is.

MATERIAL AND METHODS

Material

This study was based on ethanol-preserved samples and dry shells collected during field surveys in 2009 and 2010 and supplementary material, including types, from the Malacology Collection of the Australian Museum. Newly collected samples and types have been deposited with the Western Australian Museum, Perth (WAM) and the Australian Museum, Sydney (AM).

Field work

Snail samples were collected between 2009 and 2010. Otherwise inaccessible sites in remote areas were visited by helicopter and aestivating snails were taken from their hiding places under rocks, in crevices, or under leaf litter and spinifex grass tussocks (*Triodia* spp.) during comparatively short stays of about 30 min per site. The collecting sites were selected prior to field work by use of satellite imagery (Google Earth; www.google.com/earth) and geological maps; priority was given to rocky limestone outcrops that were considered as particularly suitable habitats for the snails.

Morphological studies

Samples from each collection site were initially sorted into morphotypes based on external shell morphology (sculpture, shape, size) and coloration. Adult shell characters (adults were recognized by a complete apertural lip) were measured with a calliper precise to 0.1 mm. Characters measured were shell height (H = maximum dimension parallel to axis of coiling, including lip), shell diameter (D = maximum dimension perpendicular to H, including lip), and width of umbilicus (U = diameter at half of total depth). The number of whorls (N), including protoconch, was counted precise to 0.1 as shown in Köhler (2010b: fig. 2).

Statistical analyses (pairwise ANOVAs) of the morphometric characters H, D, U, N, and H/D were employed to test whether morphotypes varied in their morphometry with statistical significance. Representatives of each local population of each morphotype were dissected in order to study the genital anatomy by use of a Leica M8 stereo microscope with drawing mirror. Whenever the number of available specimens allowed, the anatomy was studied in two (in small series) to five specimens per sample in order to confirm that morphological features are consistently found amongst conspecific specimens. Anatomical features are reported in the generic diagnosis and the species descriptions below; the terminology used is the same as in Köhler (2011b).

A key is provided based on shell colour pattern and features of the genitalia to assist future workers with the identification of species.

Molecular studies

Up to five specimens from each sampling site and each recognizable morph were selected for sequencing with precedence to dissected individuals. DNA was extracted from small pieces of foot muscle by use of a QIAGEN DNA extraction kit for animal tissue following the standard procedure in the manual. Fragments of the mitochondrial 16S rRNA (16S) and of the cytochrome *c* oxidase subunit 1 (COI) genes were amplified by PCR using the primer pairs: 16Scs1 (Chiba, 1999) and 16Sbd1 (Sutcharit, Asami & Panha, 2007), and L1490 and H2198 (Folmer *et al.*, 1994), respectively. Reactions were performed under standard conditions with an annealing step of 90 s at 55 °C for 16S and of 60 s at 50 °C for COI. Both strands of purified PCR fragments were cycle sequenced by use of the PCR primers. Electropherograms were manually corrected for misreads, if necessary, and forward and reverse strands were merged into one sequence file using CodonCode Aligner v. 3.6.1 (CodonCode Corporation, Dedham, MA, USA). Sequences have been deposited in GenBank (Table S1).

Sequence alignments were generated using MUSCLE as implemented in MEGA 5 (Tamura *et al.*, 2011). For each mtDNA fragment, we checked for saturation using tests implemented in DAMBE (Xia & Xie, 2001). Uncorrected pairwise genetic distances were calculated using MEGA 5 under the option 'pairwise deletion of gaps'. For phylogenetic analyses, sequences were concatenated into one partitioned data set. Prior to the model-based phylogenetic analyses, the best-fit model of nucleotide substitution was identified for each gene partition separately using the model proposal function of MEGA 5. To infer phylogenetic relationships, we performed Bayesian inference (BI) and maximum likelihood (ML) methods. The ML analysis was performed using MEGA 5 with nearest-neighbour-interchange as the heuristic method and automatic generation of the initial tree. Two hundred ML bootstrap replicates were performed to assess the topology support.

Bayesian posterior probabilities of phylogenetic trees were estimated by running a 10^7 generations Metropolis-coupled Markov chain Monte Carlo (two runs each with four chains, of which one was heated) as implemented by MrBayes v. 3.1.2 (Ronquist & Huelsenbeck, 2003). A data partition was applied that allowed parameters to be estimated separately for each gene fragment and each codon position of the COI gene. Sampling rate of the trees was 1000 generations. Generations sampled before the chain reached stationarity were discarded as burn-in. Stationarity was considered to be reached when the average standard deviation of split frequencies shown in MrBayes was less than 0.01 (Ronquist & Huelsenbeck, 2003) and the log likelihood of sampled trees reached a stationary distribution.

Species concept and delimitation of species-taxa

Following the biological species concept (Mayr, 1942), we consider species as 'groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups'. As we are unable to test for reproductive isolation in the wild, we need to rely on analyses of morphological and genetic characteristics to formulate hypotheses on the identity of species-taxa and their delimitation. We postulate that populations are reproductively isolated from each other when (1) they differ in morphological features while intermediate morphs are absent and phenotypic divergence is considered to be under genetic control and (2) the presence of well-individualized and mutually monophyletic mtDNA lineages indicates separate lineage evolution over a considerable period of time. Such 'species hypotheses' (i.e. circumscribed species-taxa) receive corroboration when the species so delimited maintain their identity also in sympatry.

Species-taxa were delimited through a step-wise evaluation of the mitochondrial and morphological variation ('reciprocal corroboration') employing the following criteria to infer a distinct species status: (1) mtDNA sequences form a clade, (2) clade is well differentiated from other such clades, (3) consistent morphology within clade, (4) morphology differs from sister clades in at least one characteristic, which is considered to be under genetic control.

Abbreviations

alp, apical longitudinal pilaster(s); AM, Australian Museum, Sydney; ap, apical pad; at, atrium (genital pore); atu, apical tubercles; bc, bursa copulatrix; bf, basal folds; blp, basal longitudinal pilaster(s); D, shell diameter; dry, number of dry shells; e, epiphallus; EK, East Kimberley; el, epiphallus length; fo, free oviduct; H, shell height; H/D, shell height diameter ratio; lp, longitudinal pilasters; N, number of shell whorls; nlp, nodulose longitudinal pilasters; NT, Northern Territory; oe, epiphallus opening; ol, free oviduct length; p, penis; pl, penis length; rm, retractor muscle; sh, penial sheet; U, umbilicus diameter; vd, vas deferens; vg, vagina; vl, vagina length; VRD, Victoria River District; WA, Western Australia; WAM, Western Australia Museum, Perth; wet, number of ethanol-preserved specimen(s).

RESULTS

Morphological analyses

The delimitation and identification of species by means of shell morphology alone proved to be error-prone because of the usually little variation in shell characters and the overlap of the morphospace of different species (Table 1; Fig. 2). Statistical analyses of shell height and diameter by means of pairwise ANOVAs revealed no significant variation for almost all pairwise species comparisons (Fig. 3). Exceptionally, *Exiligada limbunya* differed significantly from all other species in shell height whereas only two species pairs (*E. limbunya* – *Exiligada gregoriana*, *Exiligada rivifontis* – *Exiligada monochroma*) differed significantly in both shell characters. In addition, a few species differed from one another in either H or D.

Four distinct coloration patterns were found amongst *Exiligada* species with no intermediates. Shells can either be (1) monochrome (i.e. unbanded) or may have (2) one peripheral continuous spiral band, (3) several continuous spiral bands, or (4) several interrupted (i.e. dashed) spiral bands (Figs 1, 4–6).

The taxonomically most informative characteristics of the genital anatomy encompassed (1) absolute and relative length of epiphallus and penis, (2) attachment of retractor muscle to penis, (3) coiling of penis, and (4) sculpture of the inner penial wall. The considerably different penial anatomy of several species permitted their identification (e.g. *Exiligada nodulicauda*, *Exiligada longicauda*). In other species, the penial anatomy revealed comparatively little variation, which by itself would have not permitted the unambiguous identification of species.

Molecular analyses

The final concatenated data set of COI and 16S had a total length of 1541 bp (16S: 886 bp, COI: 655 bp) containing sequences from 95 specimens of *Exiligada* spp. and 42 sequences that represented various camaenid taxa from north-western Australia (*Mesodontrachia* spp., *Prototrachia* spp., *Ordtrachia* spp., *Westraltrachia* spp.) that were used as the outgroup to root the tree. Owing to problems with PCR amplification, for nine individuals only the COI fragment was available and for three individuals only the 16S fragment. In these cases, the missing sequence in the concatenated data was coded as unknown. However, for all but one species (*Exiligada qualis*, only COI available) complete sequence data were available from additional specimens. In general, specimens represented by only one sequence in the data set clustered together with conspecific individuals represented by complete sequence data. Specimens with identical COI and 16S sequences (nine sequence pairs) were represented by one haplotype in the analysed data set. Tests indicated no or little saturation in both mitochondrial fragments. The hierarchical likelihood test revealed the Tamura-three-parameter model (Tamura, 1992) as the best-fit model of sequence evolution for both genes. A discrete gamma distribution was used to model evolutionary rate differences amongst sites [five categories (+G, parameter = 1.0354)]. The rate variation model allowed for some sites to be evolutionarily invariable [(+I), 42.0316% sites]. Parameters of the ML and BI analyses were adjusted accordingly.

The ML and BI analyses resulted in largely identical phylogenies that differed only in minor details as outlined below. Therefore, only the Bayesian tree is shown herein (Fig. 1). Both phylogenies strongly supported the monophyly of *Exiligada* with respect to the outgroup, which represented all other shell-wise somewhat similar camaenid genera known to occur in the study region and surroundings (*Torresitrachia*, *Setobaudinia*, and *Xanthomelon* were not included because of their very different shell). The ML tree differed from the BI phylogeny depicted here in showing *E. monochroma* in a position basal to *Exiligada montejinni* instead of suggesting a sister-group relationship

Table 1. Shell dimensions (mm) and whorl counts of *Exiligada* species recognized in the present work

Species	S	H	D	H/D	U	N
Exiligada negriensis	28	10.9–13.5 (12.4 ± 0.7)	18.6–22.8 (20.3 ± 0.9)	0.6–0.7 (0.6 ± 0.0)	1.7–3.5 (2.7 ± 0.3)	4.2–4.6 (4.4 ± 0.1)
Exiligada brabyi	8	10.3–12.6 (11.3 ± 0.8)	17.2–19.8 (18.3 ± 0.7	0.6–0.7 (0.6 ± 0.0)	2.0–3.0 (2.5 ± 0.3)	4.3–5.0 (4.6 ± 0.2)
Exiligada calciphila	23	11.5–14.5 (12.9 ± 0.8)	18.1–20.9 (19.8 ± 0.8)	0.6–0.7 (0.7 ± 0.0)	2.3–3.4 (2.9 ± 0.3)	4.4–5.0 (4.7 ± 0.1)
Exiligada floraevallis	23	11.1–13.3 (12.2 ± 0.6)	17.7–20.0 (18.8 ± 0.7)	0.6–0.7 (0.6 ± 0.0)	2.2–3.5 (3.0 ± 0.3)	4.1–4.5 (4.3 ± 0.1)
Exiligada gregoriana	20	10.6–12.6 (11.7 ± 0.6)	17.7–19.7 (18.5 ± 0.5)	0.6–0.7 (0.6 ± 0.0)	2.5–3.5 (3.0 ± 0.3)	4.3–5.0 (4.7 ± 0.2)
Exiligada limbunya	23	5.9–7.2 (6.5 ± 0.3)	12.2–15.6 (14.1 ± 0.8)	0.4–0.5 (0.5 ± 0.0)	2.1–2.8 (2.4 ± 0.2)	3.6–4.2 (3.8 ± 0.1)
Exiligada longicauda	1	12.2–12.2 (12.2 ± 0.0)	17.8–17.8 (17.8 ± 0.0)	0.7–0.7 (0.7 ± 0.0)	2.8–2.8 (2.8 ± 0.0)	5.0–5.0 (5.0 ± 0.0)
Exiligada monochroma	18	10.3–12.0 (11.1 ± 0.5)	18.0–20.0 (19.1 ± 0.6)	0.5–0.6 (0.6 ± 0.0)	3.0–3.7 (3.2 ± 0.2)	4.2–4.7 (4.4 ± 0.1)
Exiligada montejinni	14	12.2–14.2 (13.4 ± 0.6)	18.8–21.7 (19.9 ± 0.7)	0.6–0.7 (0.7 ± 0.0)	2.4–3.0 (2.7 ± 0.2)	4.3–5.1 (4.6 ± 0.2)
Exiligada nodulicauda	24	8.9–12.0 (10.1 ± 0.8)	16.3–19.2 (18.0 ± 0.8)	0.5–0.6 (0.6 ± 0.0)	1.6–2.9 (2.3 ± 0.4)	4.3–4.8 (4.6 ± 0.1)
Exiligada pallida	27	10.7–13.2 (12.0 ± 0.6)	18.6–22.0 (20.3 ± 2.3)	0.5–1.3 (0.6 ± 0.1)	1.9–3.7 (3.1 ± 0.5)	4.3–4.7 (4.5 ± 0.1)
Exiligada punctata	16	10.8–14.0 (12.3 ± 0.8)	18.1–21.6 (19.8 ± 0.8)	0.5–0.7 (0.6 ± 0.0)	2.0–3.1 (2.6 ± 0.3)	4.3–4.7 (4.5 ± 0.1)
Exiligada qualis	10	10.7–12.8 (11.6 ± 0.7)	17.7–19.9 (18.8 ± 0.7)	0.6–0.6 (0.6 ± 0.0)	1.7–2.5 (2.1 ± 0.3)	4.3–5.2 (4.7 ± 0.3)
Exiligada rivifontis	9	12.0–16.2 (14.5 ± 1.2)	19.0–22.5 (20.8 ± 1.0)	0.6–0.8 (0.7 ± 0.0)	2.0–3.0 (2.3 ± 0.3)	4.2–4.9 (4.6 ± 0.2)
Exiligada unistriata	27	10.5–14.2 (12.1 ± 0.9)	18.7–22.0 (20.2 ± 0.7)	0.5–0.7 (0.6 ± 0.0)	2.7–9.2 (3.6 ± 1.2)	4.2–4.7 (4.4 ± 0.1)
Genus	271	6.5–14.5 (11.7 ± 0.7)	14.1–20.8 (19.1 ± 0.8)	0.5–0.7 (0.6 ± 0.0)	2.1–3.6 (2.8 ± 0.4)	3.8–4.7 (4.5 ± 0.2)

Values given are minimum–maximum (average ± SD).
S, number of measured shells; H, height, D, diameter, U, diameter of umbilicus, N, number of whorls.

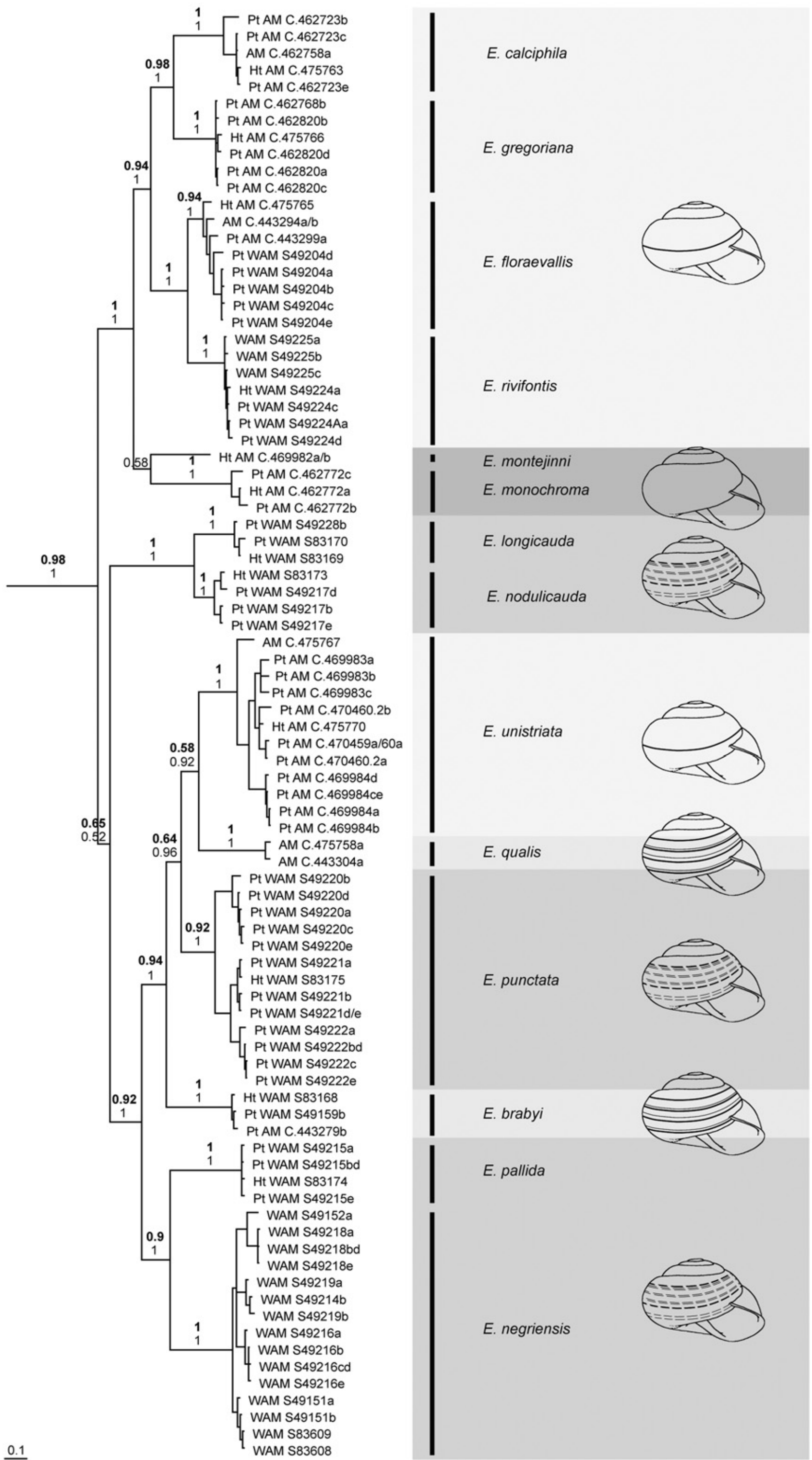

Figure 1. Bayesian consensus phylogram for *Exiligada* based on the combined COI and 16S sequence data set (out–group pruned from tree). Nodal support is indicated by mapping Bayesian posterior probabilities and ML bootstrap values (in bold) onto branches. Terminal tips are labelled with voucher numbers of analysed samples.

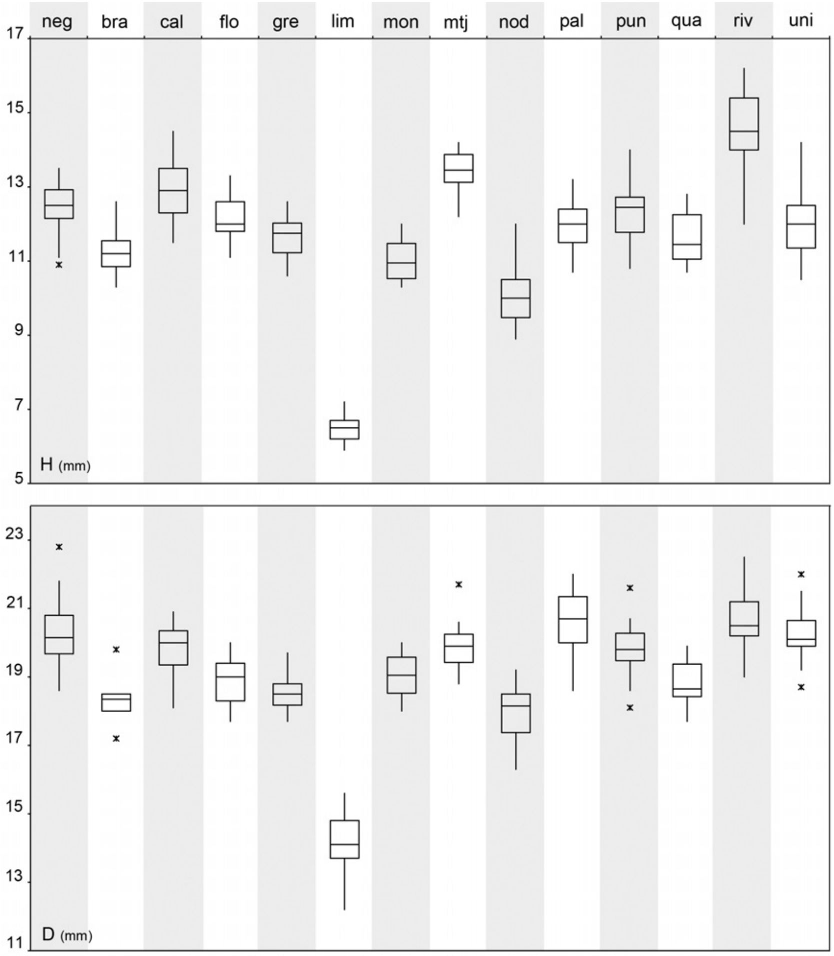

Figure 2. Comparison of specimens of *Exiligada* species by means of box and whisker plots for shell parameters H and D.

between the two species. However, both topologies were only weakly supported. Consistently, both trees revealed the presence of several well-supported clades, which were employed as operational units to assess species status by means of their morphology.

SYSTEMATICS

Gastropoda

Heterobranchia

Stylommatophora

Camaenidae Pilsbry, 1895

Exiligada Iredale, 1939: 68. Solem, 1984: 670

Generic diagnosis: Shell (Figs 4–6): moderately large, subglobose, periphery slightly angulated to rounded, spire weakly to moderately elevated, thin to moderately thick; umbilicus narrowly winding, open to almost completely concealed by columellar reflection; protoconch and teleoconch with moderately fine radial growth lines, fine micropustulations or microdepressions sometimes present. Last whorl moderate to wide in cross-section, periphery uniformly rounded. Apertural lip reflected, moderately expanded, parietal wall thin; no internal lip nodes. Shell colour variable, background whitish, yellowish or brownish horn, without or with one to several moderately wide to thin brown-reddish spiral bands, sometimes randomly to regularly dashed, with or without dark grey punctuations.

Genitalia: typically camaenid with prostate and uterus being fused forming spermoviduct and lacking diverticulum and stimulatory organs; development of gonads depending on seasonal activity and maturity. Penial sheath well developed, extending entire length, usually thickened distally. Epiphallus forming a tube surrounded by thick layers of muscle, well separated from penis, distally connected to penis through a narrow duct in a zigzag configuration; epiphallus variable in length, three times shorter to two times longer than penis. Penial retractor muscle inserting on vas-epiphallic junction, with fibres

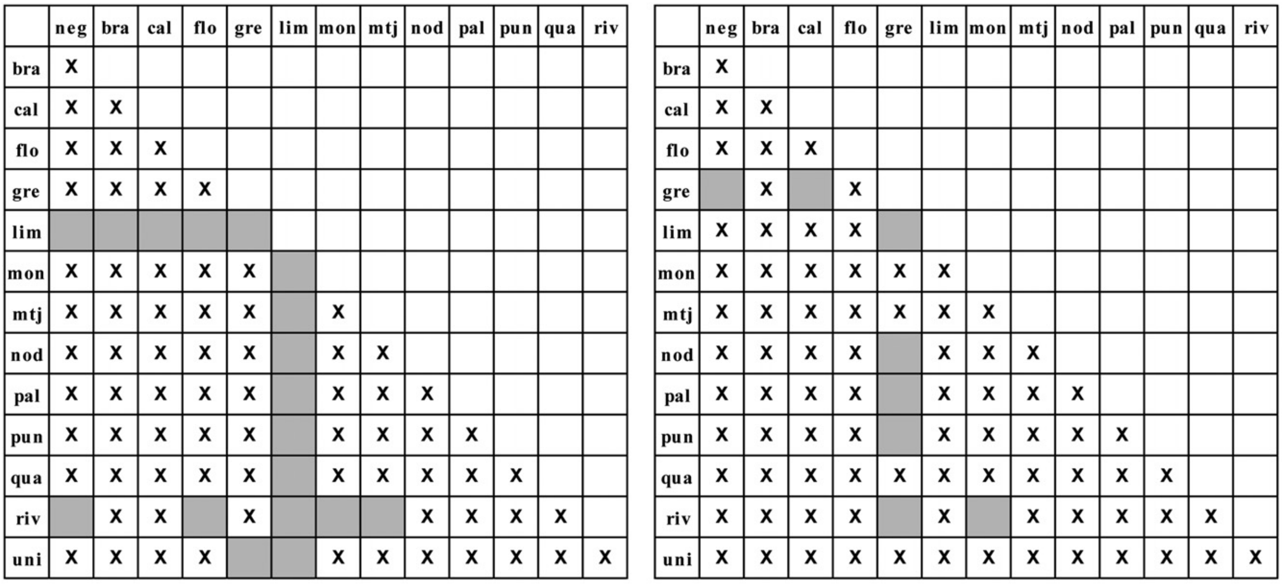

Figure 3. Diagrammatic representation of pair–wise comparisons of shell parameters in *Exiligada* species by means of pair-wise one–way ANOVA (H, left; D, right). Full squares: null hypothesis that group means are equal rejected with statistical significance (P < 0.05). Crosses: null hypothesis not rejected (P > 0.05).

continuing along epiphallus, and attached to apical part of penis. Vas deferens entering penial sheath basally to almost halfway up, continuing apically within sheath until reflexing into epiphallus. Penis ten to three times longer than wide, not coiled or coiled inside sheath, with moderately thick wall; inner penial wall structure variable, usually consisting of several irregularly shaped, often corrugated, wide longitudinal pilasters or of fewer regularly shaped, smooth, narrower ones. Pilaster often running along entire wall length, but sometimes interrupted. In some species finer sculptures, such as irregular tubercles or regular nodules, can be present. Sculptures of posterior part of wall often different from that of anterior part. Vagina four times shorter to slightly longer than penis, usually three times shorter to as long as free oviduct, but up to more than two times longer in some species; bursa copulatrix relatively simple, usually as long as free oviduct and sometimes slightly shorter, reaching anterior end of spermoviduct, with or without well-differentiated end. Albumen gland large. Talon embedded in albumen gland within proximal portion. Hermaphroditic duct tightly undulating.

Aestivating strategy: Aestivating as 'free sealers'.

Remarks: If not stated otherwise, holotypes are dissected wet specimens, whose shell was cracked to permit access to soft tissues. References to size are intended as relative to other congeneric species.

Typical combination of features separating *Exiligada* from other camaenids are shell shape of the 'chloritid type', presence of dashed shell bands (where present), and in particular shape and zigzag configuration of epiphallus. Amongst other camaenid genera occurring in EK and NT, *Mesodontrachia* is most similar in shell shape and size but differs by slightly lower spire and by whorls being never angulated as in some but not all *Exiligada* species; shell very different from all other genera by larger size and much higher spire, narrower umbilicus with greater extent of cover by columellar reflection; protoconch microsculpture similar to *Prototrachia* and some *Ordtrachia* species; teleoconch sculpture similar to *Mesodontrachia* but differing from remaining genera by absence of radial ribs and spiral keels; shell colour usually lighter; colour pattern very distinct from all other genera by presence of spiral bands, but species with no banding most similar to *Mesodontrachia*. Bursa copulatrix similar to that of *Mesodontrachia* and *Ordtrachia* but much shorter than in *Torresitrachia*; penis differing from that of *Mesodontrachia* by presence of epiphallus; epiphallus differing from *Torresitrachia* in shape, thickness of wall, and by absence of flagellum; penial wall differing by presence of main stimulatory pilaster in some *Exiligada* species.

EXILIGADA NEGRIENSIS IREDALE, 1939

(FIGS 4A, 5A, 7A–C, 8)

Exiligada negriensis Iredale, 1939: 69, plate V, figure 4.

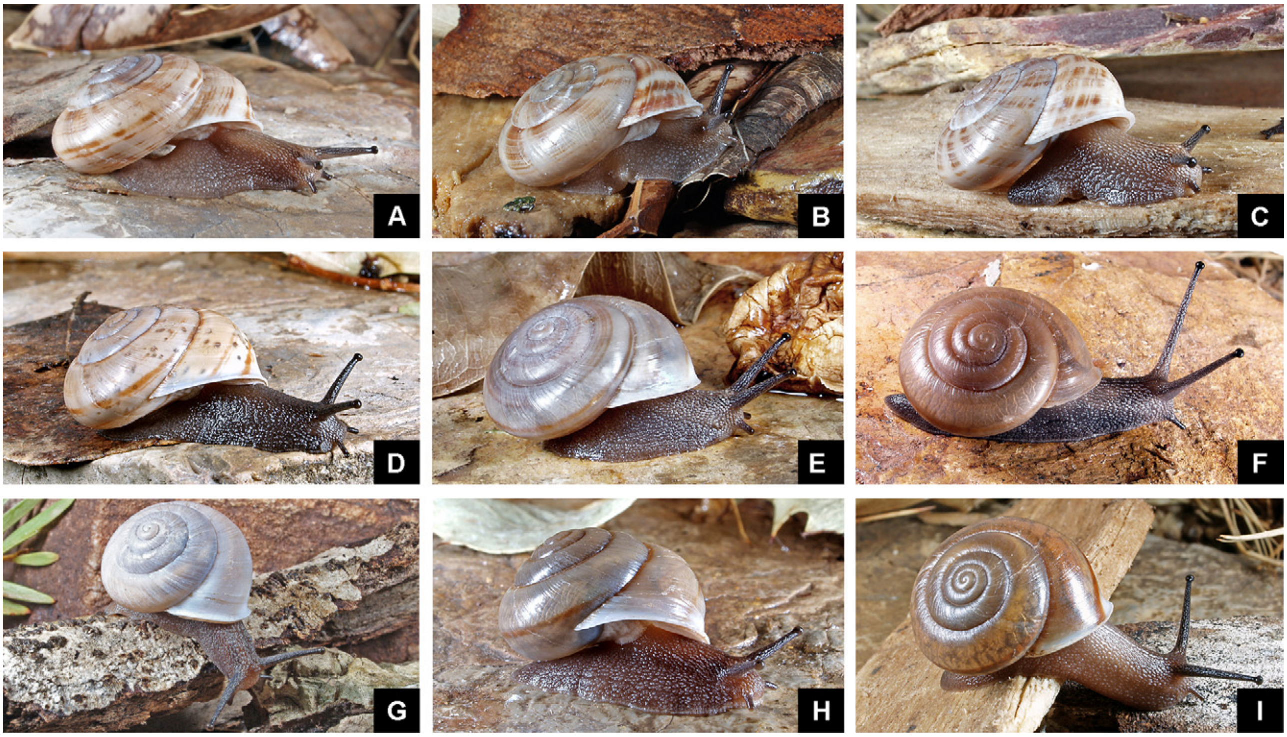

Figure 4. Photographs of living specimens of *Exiligada* species (courtesy Vince Kessner, Adelaide River). A, *E. negriensis* Iredale, 1939. B, ***E. pallida* sp. nov.** C, ***E. nodulicaudata* sp. nov.** D, ***E. punctata* sp. nov.** E, *E. qualis* Iredale, 1939. F, ***E. monochroma* sp. nov.** G, ***E. unistriata* sp. nov.** H, ***E. floraevallis* sp. nov.** I, ***E. rivifontis* sp. nov.**

Exiligada negriensis – Solem, 1984: 673–677, fig. 174 (a–c) (in part).

Material examined: AUSTRALIA, NT, VRD: holotype from 40 km north of Ord River Station, Negri outstation (coll. R. Helms, 1896), dry (AM C.64865); ten paratypes (same data as for holotype) (AM C.64916); 6 km south-west of Lissadell Station homestead (H/S), limestone outcrops with slabs on upper slopes, spinifex, patches of vine thicket, in talus, under boulders, 16°43′16″S, 128°31′23″E, (coll. V. Kessner, R. Hokkanen, 28.viii.2009; WA-57/09) two wet (WAM S49214), 12 dry (WAM S49145); 9.5 km south-east of Lissadell Station H/S, limestone ridge east of Ord River, dissected limestone area with small vine thicket patches on the slopes, exposed on the top, under talus, 16°43′07″S, 128°37′51″E (coll. V. Kessner, R. Hokkanen, 28.vii.2009; WA-58/09), 18 dry (WAM S49146); south-east of Lake Argyle, 15.5 km south-west of Behn River crossing, large limestone mass with karst formations, vine thicket patches, native grasses, under slabs, 16°37′20″S, 128°48′47″E (coll. V. Kessner, R. Hokkanen, 28.viii.2009; WA-59/09), 32 dry (WAM S49147); 29.8 km north of Spring Creek Station H/S, East Kimberley limestone gully along a seasonal stream with vine thicket patches, under large slabs, 16°43′40″S, 128°52′25″E (coll. V. Kessner, R. Hokkanen, 28.viii.2009; WA-60/09), 16 dry (WAM S49148); 1 km south of Negri River junction, east bank of Ord River, narrow and open limestone ridge, very dry, dead in crevices, 17°04′38″S, 128°53′48″E (coll. V. Kessner, R. Hokkanen, 29.viii.2009; WA-65/09), 13 dry (WAM S49149); 30.4 km east-south-east of Spring Creek Station H/S, limestone gully along a stream, cliffs 8–10 m high, base of limestone cliffs along a seasonal stream, talus, spinifex and native grass, 17°02′04″S, 129°08′35″E (coll. V. Kessner, R. Hokkanen, 30.viii.2009; WA-67/09) one wet (WAM S83171), 130 dry, two wet (WAM S49151); 39.6 km south-east of Spring Creek Station H/S, low limestone cliffs over sandstone base south of Stirling Creek, spinifex and native grass, in talus, 17°11′20″S, 129°10′35″E (coll. V. Kessner, R. Hokkanen, 30.viii.2009; WA-68/09), 1 wet, 53 dry (WAM S49152); low exposed limestone hills in Nelson Creek drainage, Limbunya Station, limestone layer over sedimentary rocks, spinifex, in rock piles, under spinifex, 17°18′23″S, 129°12′29″E (coll. V. Kessner, R. Hokkanen, 30.viii.2009; WA-69/09), eight wet (WAM S49216), 29 dry (WAM S49153); 30.2 km north-east of Kirkimbie Station (Stn) H/S, karst limestone formation in open woodland, spinifex, 17°29′23″S, 129°22′46″E (coll. V. Kessner, R. Hokkanen, 2.ix.2009; WA-82/09) one wet (WAM S83172); 21.6 km north of

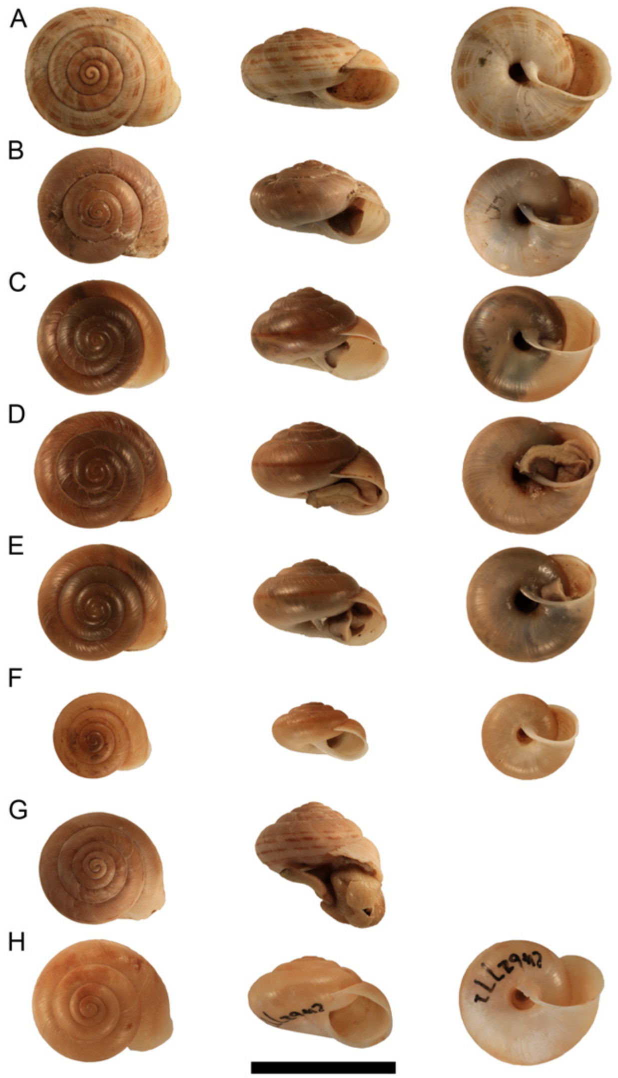

Figure 5. Shells of *Exiligada* species. A, *E. negriensis* (holotype AM C.64865). B, ***E. brabyi* sp. nov.** (paratype C.443279). C, ***E. calciphila* sp. nov.** (paratype C.462723). D, ***E. floraevallis* sp. nov.** (paratype WAM S49204). E, ***E. gregoriana* sp. nov.** (paratype AM C.462820). F, ***E. limbunya* sp. nov.** (paratype AM C.470205). G, ***E. longicauda* sp. nov.** (paratype WAM S49228). H, ***E. monochroma* sp. nov.** (paratype AM C.469772).

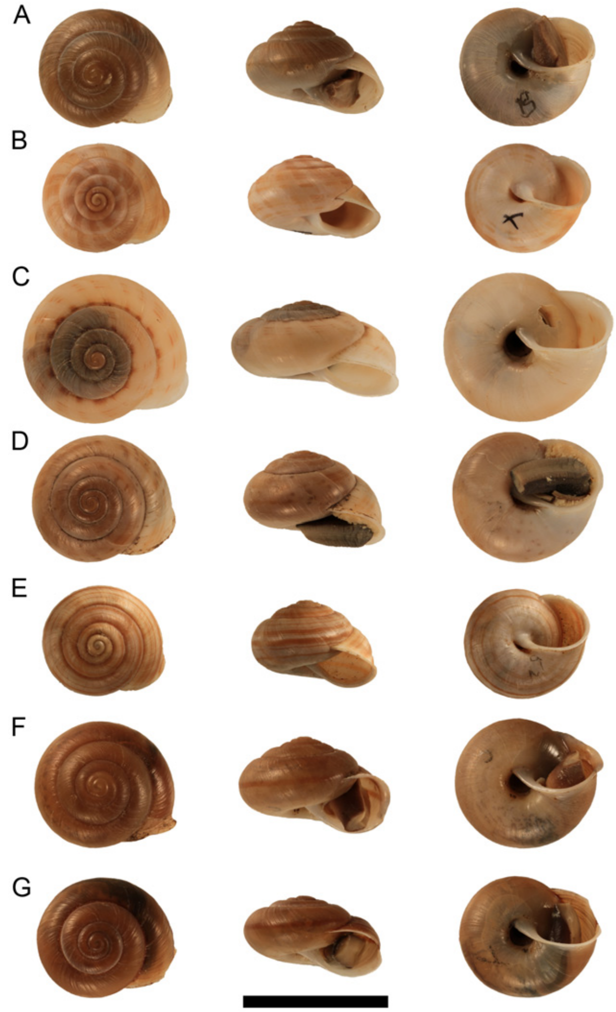

Figure 6. Shells of *Exiligada* species. A, ***E. montejinni* sp. nov.** (paratype AM C.469982). B, ***E. nodulicauda* sp. nov.** (paratype WAM S49160). C, ***E. pallida* sp. nov.** (paratype WAM S49215). D, ***E. punctata* sp. nov.** (paratype WAM S49221). E, *E. qualis* Iredale, 1939 (holotype AM C.64866). F, ***E. rivifontis* sp. nov.** (WAM S49225). G, ***E. unistriata* sp. nov.** (paratype AM C.470460). Scale bar = 2 mm. Note that foot produces from some shells.

Kirkimbie Station H/S, narrow limestone ridge, steep open slopes, well-developed spinifex on upper slopes, in talus, under spinifex, 17°32′20″S, 129°16′03″E (coll. V. Kessner, R. Hokkanen, 2.ix.2009; WA-83/09), six wet (WAM S49218), 20 dry (WAM S49161); west of Duncan Highway (Hwy), Spring Creek Station, limestone area east of Mud Spring Creek, open limestone slopes, well-developed spinifex, dead under slabs, 16°41′20″S, 128°54′55″E (coll. V. Kessner, R. Hokkanen, 3.ix.2009; WA-85/09), one dry (WAM S49162); 5.4 km south-west of Lissadell Stn H/S, low limestone ridge, base of the cliffs, small pockets of vine thicket, under rocks in loose soil, 16°42′31″S, 128°30′58″E (coll. V. Kessner, K. Carnes 6.ix.2009; WA-97/09), two dry (WAM S49166); 6.7 km south-west of Lissadell Stn H/S, narrow limestone ridge, base of the cliffs, small pockets of vine thicket, spinifex, under rocks, 16°43′17″S, 128°30′46″E (coll. V. Kessner, K. Carnes, 6.ix.2009; WA-98/09), two dry (WAM S49219), nine dry (WAM S49163); 12 km south-west of Lissadell Stn H/S, low limestone exposed hill with karst limestone, few shady trees, spinifex and tussock grass, in talus, 16°46′16″S, 128°30′09″E (coll. V. Kessner, K. Carnes, 6.ix.2009; WA-99/09), 16 dry (WAM S49164).

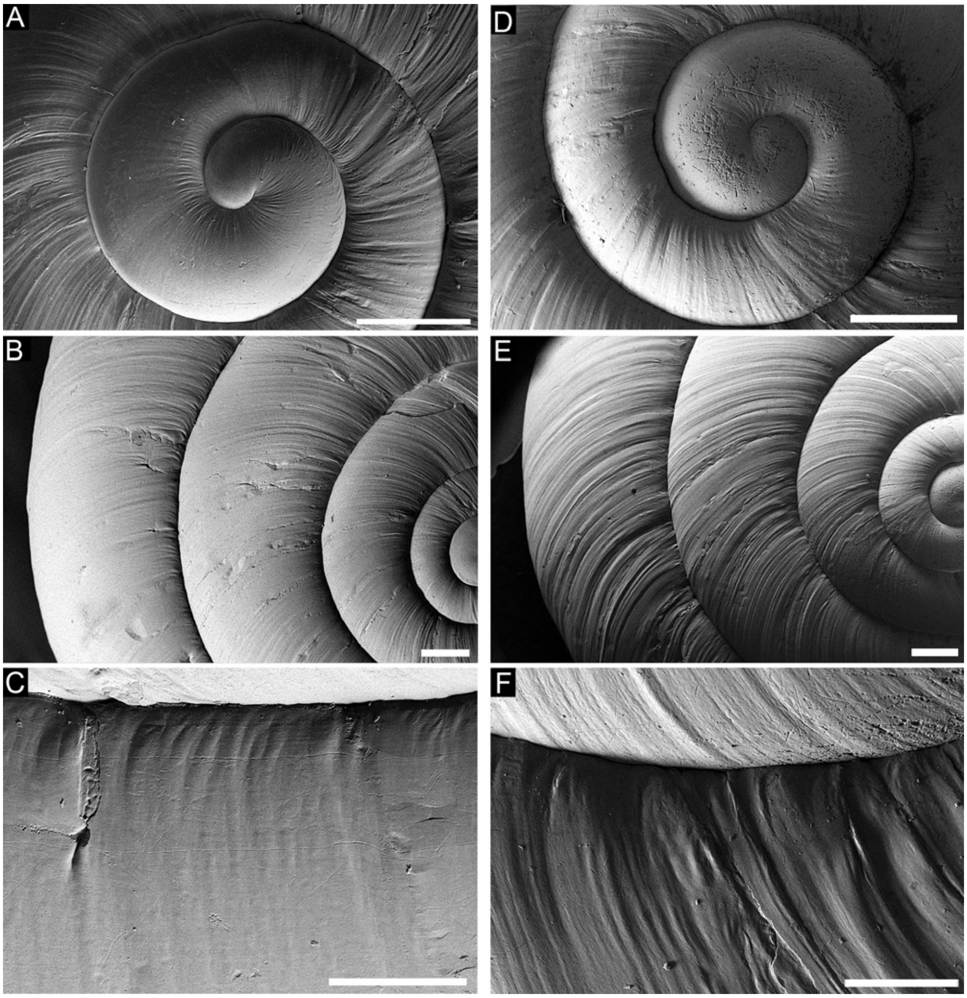

Figure 7. SEM micrographs of *Exiligada* shells. A-C, *E. negriensis* Iredale, 1939 (WAM S49152). A, Apical view showing protoconch and first whorl. B, Close-up from above of sculpture across entire shell. C, Microsculpture on teleoconch whorl. D-F. ***E. brabyi* sp. nov.** (paratype WAM S49159). D, Apical view showing protoconch and first whorl. E, Close-up from above of sculpture across entire shell. F, Microsculpture on teleoconch whorl. Scale bars: A-B, D-E = 1 mm, C, F = 0.5 mm.

Description: Shell (Figs 4A, 5A, 7A–C). Large, moderately elevated, moderately thick; micropustulations absent; background colour yellowish horn fading to whitish towards shell base, with several conspicuous to faint brown-reddish spiral bands, equally conspicuous on entire shell, often present on base, often interrupted radially; no maculations.

Genitalia (Fig. 8). Epiphallus as long as penis. Vas deferens entering penial sheath halfway up. Penis five times longer than wide, not coiled inside sheath, inner penial wall with weak, irregular longitudinal pilasters restricted to anterior half, posteriorly with thick, cone-shaped pad. Vagina half as long as penis, a third of length of free oviduct, bursa copulatrix with elongated, pointed well-differentiated end.

Remarks: The species is delimited here differently as compared to the latest revision of Solem (1984). Originally, amongst a single set of mostly eroded shells from the same locality, Iredale (1939: 69) recognized two *Exiligada* species based on shell morphology and coloration: *E. negriensis*, which he designated as the type species of the genus *Exiligada*, and *E. qualis*. The type locality as originally cited by Iredale (1939) ('Negri Outstation') could not be specified subsequently (Solem, 1984). However, based on the information provided by Iredale [25 miles (= 40 km) north of Ord River Station, near Negri River], the type locality is herein restricted to an area close to the Negri River between the point where the Negri River flows into the Ord River in WA (17°04′11″S,

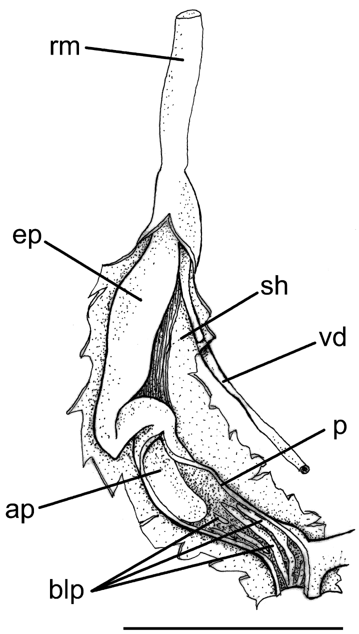

Figure 8. Penial anatomy of *E. negriensis* Iredale, 1939 (WAM S49216). Scale bar = 5 mm.

128°53′10″E) and the Duncan Highway bridge over the Negri River near the WA/NT border (17°04′32″S, 129°00′10″E). Solem (1984: 672–673) considered the differences between the type series of *E. negriensis* and *E. qualis* as not significant and synonymized the two species names. Based on comparative study of additional material, we found that the area including the type locality is inhabited by three *Exiligada* species. Differences between two of these species as delimited herein are consistent with the original delimitation of *E. negriensis* and *E. qualis* by Iredale (1939), refuting Solem's (1984) proposal that both were identical (see also below under *E. qualis*). To complicate matters even further, Solem (1984: 676) used specimens from 'Duncan Hwy, 37.2 km N of Nicholson River' (about 60–70 km south of the type locality) to describe the genital anatomy of what he considered to be *E. negriensis.* We studied material from sites much closer to the type locality and found that *E. negriensis* differs from Solem's (1984: 676, fig. 175) anatomical description. Based on shell colour patterns, we found that he used specimens from a different species, named herein *Exiligada brabyi* further below, to illustrate the genital anatomy of *E. negriensis*. Hence, Solem's (1984) description of '*E. negriensis*' is based on mixed material from three species (*E. negriensis*, *E. qualis*, *E. brabyi*). His description and figure of genital features is here attributed to *E. brabyi* (see below). *Exiligada negriensis* as restricted here is defined by the presence of dashed spiral bands on shells as opposed to *E. qualis* and *E. brabyi* both having shells with continuous spiral bands.

Exiligada negriensis differs from *Exiligada pallida* in absence of micropustulations on the shell. Its shell colour pattern is similar to that of four other *Exiligada* species, which are distinguished by a lower number of spiral bands (*E. longicauda*), by bands being more regularly interrupted (*E. nodulicauda*), by lighter background (*E. pallida*), and presence of maculations (*E. punctata*). Its penis length relative to width (pl/pw) is smaller than average, almost as large as in *E. pallida*; epiphallus length relative to penis (el/pl) is average, as large as in *E. pallida*. Inner penial wall sculpture is very similar to *E. pallida* and *E. punctata*, differing by wider posterior pad and shorter longitudinal pilasters of the penial wall never extending to posterior part of wall. Vagina length relative to penis and free oviduct (vl/pl, vl/ol) is the smallest amongst congeners.

EXILIGADA BRABYI SP. NOV.

(FIGS 5B, 7D–E)

Exiligada negriensis – Solem, 1984: 673, plate 57F; figure 175 (a–c) (in part).

Holotype: AUSTRALIA, NT, VRD, east of Duncan Hwy, 37.7 km north-west of Kirkimbie Station H/S, large, open, and very rugged limestone formation, in talus, under spinifex, 17°26′59″S, 129°03′20″E (coll. V. Kessner, R. Hokkanen 2.ix.2009), wet (WA – 81/09, WAM S83168).

Paratypes: Same data as for holotype, 27 dry, two wet (WAM S49159); Duncan Rd, old Ord River homestead, Forrest Creek (Ck), 70 km north of Nicholson homestead, under limestone rocks and concrete of old structures, 17°23′56″S, 128°52′01″E (coll. R. Crookshanks, 29.i.2005), four dry, two wet (AM C.443279).

Etymology: In honour of Michael Braby, for his most valuable help with fieldwork in the Victoria River District, noun in genitive case.

Description: Shell (Figs 5B, 7D, E). Moderately large, moderately elevated, moderately thick; micropustulations absent; background colour yellowish horn fading to whitish towards shell base, with one faint to conspicuous, continuous, brown-reddish peripheral band, and few regularly spaced, narrower spiral bands, more conspicuous on body whorl, absent on shell base; no maculations.

Genitalia. Epiphallus as long as penis. Vas deferens entering penial sheath within anterior third. Penis five times longer than wide, not coiled inside sheath, with thick wall, inner penial wall with thick, regularly shaped, sometimes interrupted main longitudinal pilaster restricted to posterior half, with several thin longitudinal folds anteriorly. Vagina half as long as penis, as long as free oviduct. Bursa copulatrix with no well-differentiated end (Solem, 1984: fig. 175, '*E. negriensis*').

Remarks: Shell colour pattern not readily distinguishable from that of *E. qualis*. Solem's (1984: 676, fig. 175) description of genital anatomy of '*E. negriensis*' is here attributed to *E. brabyi*. Penis length relative to width (pl/pw) average, epiphallus length relative to penis (el/pl) half of average. Inner penial wall sculpture very similar to that of *E. qualis* and *Exiligada unistriata*, from which it can be distinguished by the posteriorly situated, main longitudinal pilaster being interrupted and by a larger number of anterior folds. Vagina length relative to penis and free oviduct (vl/pl, vl/ol) shorter than average.

EXILIGADA CALCIPHILA SP. NOV.

(FIGS 5C, 9A–C, 10)

Holotype: AUSTRALIA, NT, VRD, Humber River Station, isolated limestone, hill 39 km south-east of Bullita, 16°23′59″S, 130°39′14″E (coll. V. Kessner, 14.vii.2008), (AM C.475763).

Paratypes: Same data as for holotype, 51 dry, four wet (AM C.462723).

Other material: AUSTRALIA, NT, VRD, limestone hill 9.5 km south-west of VRD Station H/S, 16°27′35″S, 130°56′56″E (coll. V. Kessner, 15.vii.2008), four dry, one wet (AM C.462758).

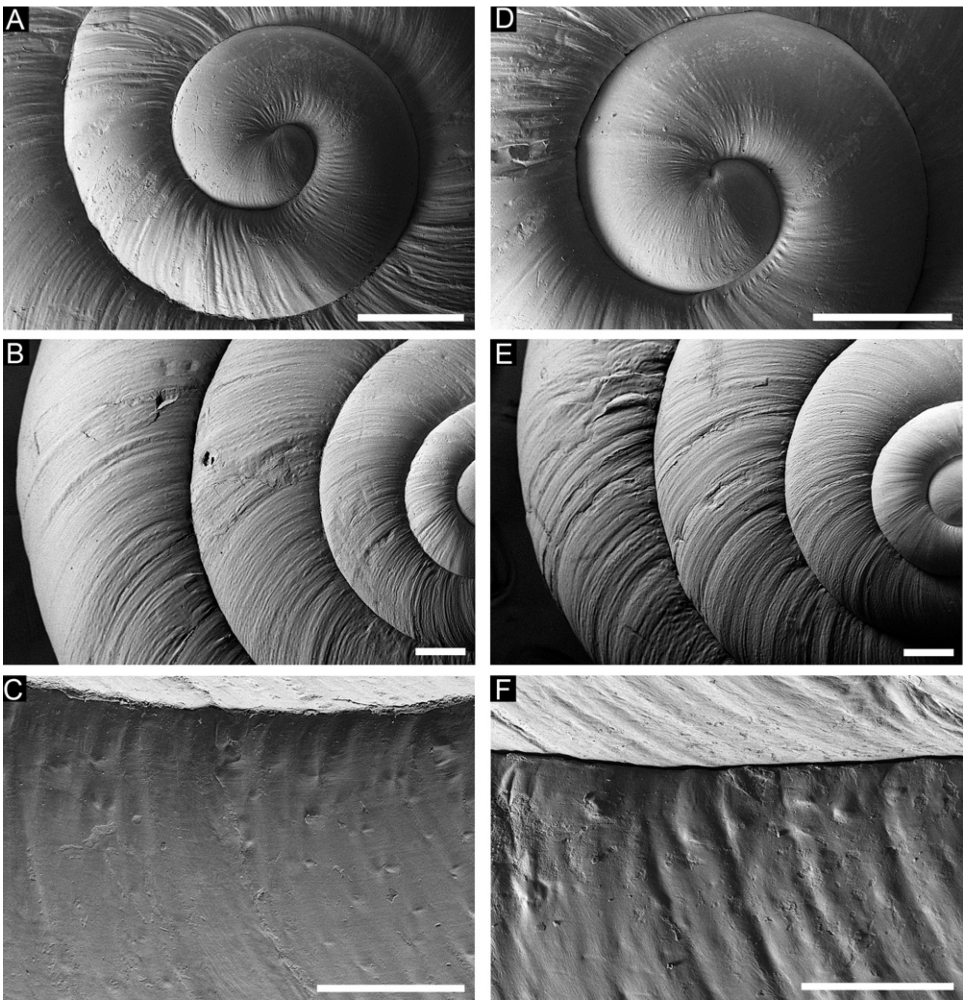

Figure 9. SEM micrographs of *Exiligada* shells. A-C, ***E. calciphila* sp. nov.** (paratype AM C.462723). A, Apical view showing protoconch and first whorl. B, Close-up from above of sculpture across entire shell. C, Microsculpture on teleoconch whorl. D-F, ***E. floraevallis* sp. nov.** (WAM S49136). D, Apical view showing protoconch and first whorl. B, Close-up from above of sculpture across entire shell. C, Microsculpture on teleoconch whorl. Scale bars: A-B, D-E = 1 mm, C, F = 0.5 mm.

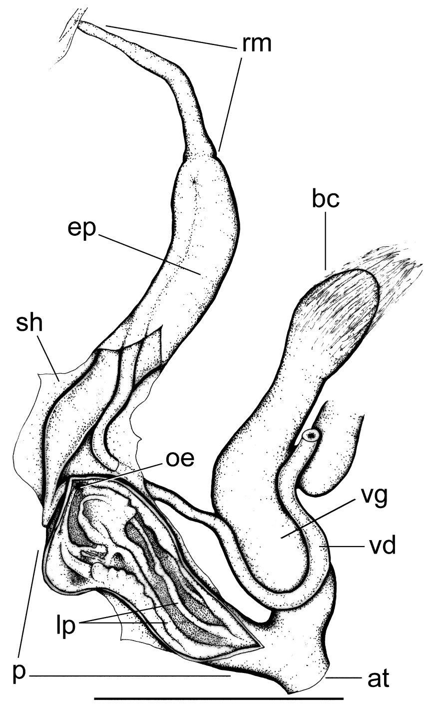

Figure 10. Penial anatomy of ***E. calciphila* sp. nov.** (holotype AM C.475763). Scale bar = 5 mm.

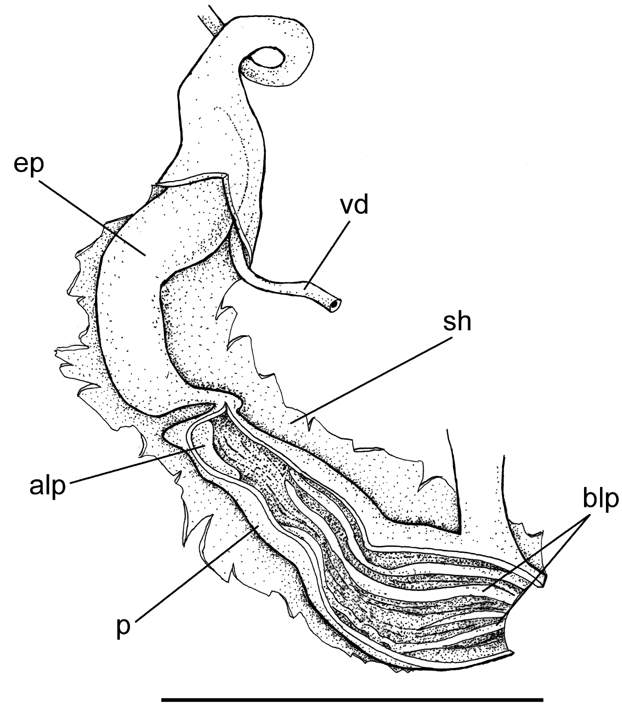

Figure 11. Penial anatomy of ***E. floraevallis* sp. nov.** (holotype AM C.475765). Scale bar = 5 mm.

Etymology: In reference to limestone habitat preferred by the species, derived from 'calx' (Latin = limestone) and 'philos' (Greek = affectionate), adjective of feminine gender.

Description: Shell (Figs 5C, 9A–C). Moderately large, moderately elevated, thin; micropustulations present; background colour brown horn fading to whitish towards shell base, with one faint to conspicuous, continuous, narrow brown-reddish peripheral band; no maculations.

Genitalia (Fig. 10). Epiphallus two times longer than penis. Vas deferens entering penial sheath halfway up. Penis six times longer than wide, not coiled inside sheath; inner penial wall with complex sculpture formed by five irregularly shaped longitudinal pilasters running along entire wall length, two of which with corrugations. Vagina half as long as penis, as long as free oviduct. Bursa copulatrix with short, rounded, well-differentiated end.

Remarks: Along with *E. gregoriana* and *E. rivifontis*, largest number of shell whorls. Teleoconch microsculpture differing from that of *E. gregoriana* by presence of micropustulations. Colour pattern of shell very similar to *Exiligada floraevallis*, *E. gregoriana*, *E. limbunya*, *E. rivifontis*, and *E. unistriata*. Penis length relative to width (pl/pw) average but longer than in *E. gregoriana*. Epiphallus length relative to penis (el/pl) two times the average and as large as in *E. gregoriana*. Penial inner wall sculpture almost identical to *E. gregoriana*, but having fewer pilasters with reduced corrugation. Vagina length relative to penis (vl/pl) average, smaller than in *E. gregoriana*. Vagina length relative to free oviduct (vl/ol) average and longer than in *E. gregoriana*.

Exiligada floraevallis sp. nov.

(Figs 4E, 5D, 9D–F, 11)

Holotype: AUSTRALIA, WA, EK, 58 km north-north-west of Nicholson H/S, disused racecourse near Linnekar Yard on Linnekar Ck, under debris of old structures, woodland, 17°32′28″S, 128°42′37″E (coll. R. Crookshanks, 29.i.2005) (AM C.475765).

Paratypes: AUSTRALIA, WA, EK, same data as for holotype, 11 dry, four wet (AM C.443299); Halls Creek District, isolated limestone area south-east of Flora Valley, limestone gully with patches of vine thicket, open slopes, under spinifex, in talus, 18°18′11″S, 128°07′08″E (coll. V. Kessner, R. Hokkanen, 1.ix.2009; WA-74/09), 51 dry, seven wet (WAM S49204); Springvale-Lansdowne Rd, Little Gold River drainage, 93 km north-west of Halls Creek, on and in soil between rocks of roadside scree under palm, 17°31′10″S, 127°11′52″E (coll. R. Crookshanks, 31.i.2005), five dry, two wet (AM C.443294).

Other material: AUSTRALIA, WA, EK, Halls Creek District, isolated limestone area south-east of Flora Valley, limestone gully with patches of vine thicket, open slopes, under spinifex, in talus, 18°18′11″S, 128°07′08″E (coll. V. Kessner, R. Hokkanen, 1.ix.2009), 51 dry (WA-74/09, WAM S49136).

Etymology: In reference to the type locality, Latinized and derived from 'flora' and 'vallis' (Latin = valley), nouns of female gender in genitive case.

Description: Shell (Figs 4E, 5D, 9D–F). Moderately large, moderately elevated, thin; micropustulations present; background colour brownish horn fading to whitish towards shell base, with one conspicuous, continuous, relatively wide, brown-reddish peripheral band; no maculations.

Genitalia (Fig. 11). Epiphallus as long as penis. Vas deferens entering penial sheath halfway up. Penis four times longer than wide, not coiled inside sheath, with inner wall supporting several irregularly shaped, partly interrupted or corrugated longitudinal pilasters, tapering in prominence posteriorly. Vagina about half as long as penis and two times shorter than free oviduct. Bursa copulatrix with long, pointed well-differentiated end.

Remarks: Micropustulation much finer than in *E. rivifontis*. Shell colour pattern very similar to *E. calciphila*, *E. gregoriana*, *E. limbunya*, *E. rivifontis*, and *E. unistriata*. Penis length relative to width (pl/pw) smaller than average and *E. rivifontis*; epiphallus length relative to penis (el/pl) 1.5 times the average and as long as in *E. rivifontis*. Penial inner wall sculpture very similar to *E. rivifontis*. Vagina length relative to penis (vl/pl) average and larger than in *E. rivifontis*, vagina length relative to free oviduct (vl/ol) larger than average and *E. rivifontis*.

***EXILIGADA GREGORIANA* SP. NOV.**

(FIGS 5E, 12A–C, 13)

Holotype: AUSTRALIA, NT, VRD, Gregory NP, 41.5 km south-south-east of Bullita O/S, 16°28′47″S, 130°32′11″E (coll. V. Kessner, 14.vii.2008) (AM C.475766).

Paratypes: AUSTRALIA, NT, VRD, same data as for holotype, 23 dry, one wet (AM C.462768); 30 km south-south-west of Timber Creek, NT, 15°46′16″S, 130°13′41″E (coll. V. Kessner, S. Roberts, 12.vii.2008), four wet (AM C.462820).

Etymology: Name chosen for similarity with *Adansonia gregorii*, the baob tree under which snails were found, and the name of Gregory National Park, derived from 'gregorianus' (Latin), adjective of feminine gender.

Description: Shell (Figs 5E, 12A–C). Moderately large, moderately elevated, moderately thin; micropustulations absent; background colour brownish horn fading to whitish towards shell base, without band or with one conspicuous to faint, continuous, relatively wide, brown-reddish peripheral band; no maculations.

Genitalia (Fig. 13). Epiphallus two times longer than penis. Vas deferens entering penial sheath within anterior third. Penis four times longer than wide, not coiled inside sheath, inner penial wall with highly complex sculpture formed by several crowded, irregularly shaped, corrugated longitudinal pilasters running along entire wall length, giving rise to pad-like thickenings. Vagina one quarter shorter than penis and free oviduct, bursa copulatrix with short, rounded, well-differentiated end.

Remarks: Along with *E. calciphila* and *E. rivifontis*, largest number of shell whorls. Teleoconch microsculpture differing from that of *E. calciphila* by presence of micropustulations. Shell colour pattern very similar to *E. floraevallis*, *E. calciphila*, *E. limbunya*, *E. rivifontis*, and *E. unistriata*. Penis length relative to width (pl/pw) average and longer than in *E. calciphila*. Epiphallus length relative to penis (el/pl) two times the average and as long as in *E. calciphila*. Penial inner wall sculpture almost identical to *E. calciphila*, but having more pilasters with increased corrugation. Vagina length relative to penis (vl/pl) larger than average and *E. calciphila*. Vagina length relative to free oviduct (vl/ol) shorter than average and *E. calciphila*.

***EXILIGADA LIMBUNYA* SP. NOV.**

(FIGS 5F, 12D–F)

Holotype: AUSTRALIA, NT, VRD, 27 km south-west of Limbunya Station, limestone outcrop with small vine thicket patches, in talus, 17°28′27.0″S, 129°53′14.0″E (coll. T. Parkin, 23.vii.2010), dry (AM C.475866).

Paratypes: AUSTRALIA, NT, VRD, same data as for holotype, 30 dry (AM C.470205).

Other material: AUSTRALIA, NT, VRD, 27.2 km south-west of Limbunya Station, small limestone outcrops with very small vine thicket patches, in talus, 55 dry (AM C.470200).

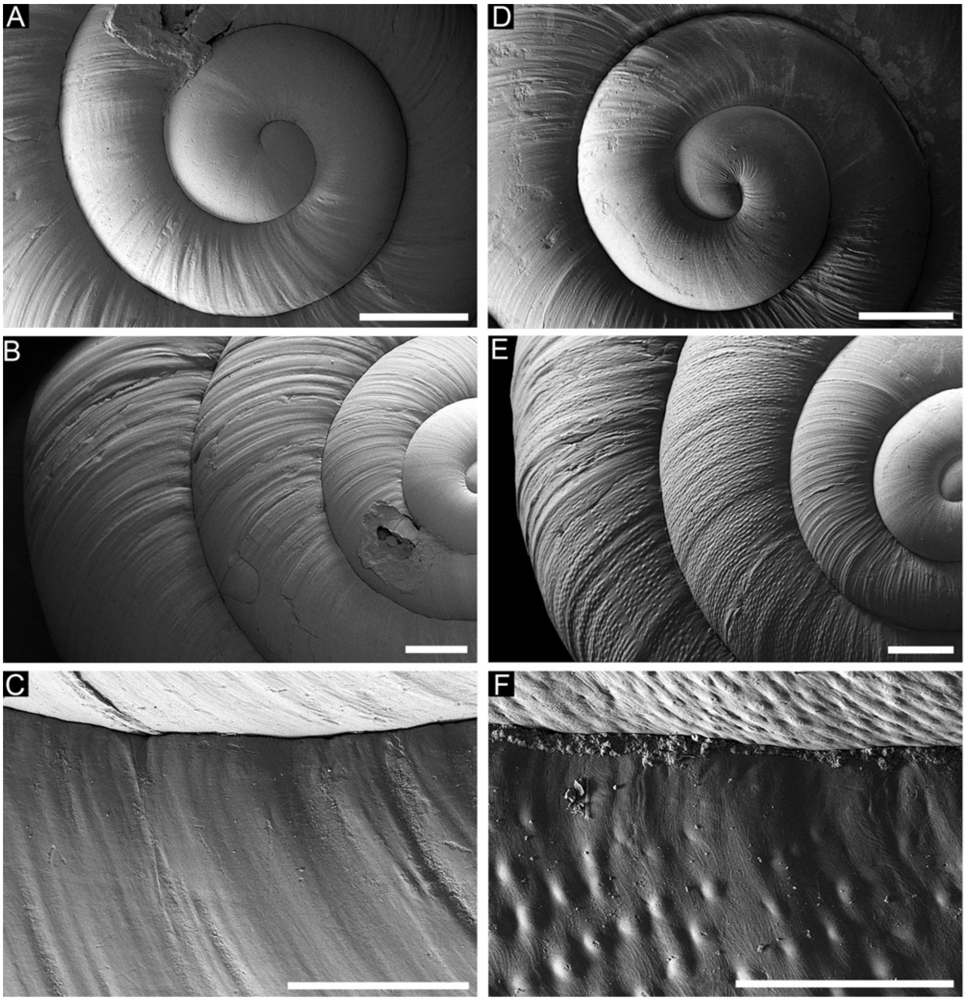

Figure 12. SEM micrographs of *Exiligada* shells. A-C, ***E. gregoriana* sp. nov.** (paratype AM C.462768). A, Apical view showing protoconch and first whorl. B, Close-up from above of sculpture across entire shell. C, Microsculpture on teleoconch whorl. D-F, ***E. limbunya* sp. nov.** (holotype C.475866). D, Apical view showing protoconch and first whorl. E, Close-up from above of sculpture across entire shell. F, Microsculpture on teleoconch whorl. Scale bars: A-B, D-E = 1 mm, C, F = 0.5 mm.

Etymology: In reference to the type locality, Limbunya Station, noun in apposition.

Description: Shell (Figs 5F, 12D–F). Small, weakly elevated, thin; micropustulations present; background colour brownish horn fading to whitish towards shell base, with one faint to very conspicuous, brown-reddish peripheral band; no maculations.

Remarks: Species only known from dry shells, which differ significantly from all other congeners permitting recognition as a distinct species. Smallest shell of the genus, with lowest number of whorls and lowest height, diameter and H/D ratio. Micropustulation as fine as in *E. calciphila*, *E. floraevallis*, and *E. unistriata*. Shell colour pattern similar to *E. calciphila*, *E. floraevallis*, *E. gregoriana*, *E. rivifontis*, and *E. unistriata*. This species co-occurs with its putative sister species *E. unistriata* and shares the same shell coloration.

EXILIGADA LONGICAUDA SP. NOV.

(FIGS 5G, 14A–C, 15)

Holotype: AUSTRALIA, NT, VRD, 7 km east of Kirkimbie Station H/S, top of the cliffs along the stream, well-developed spinifex, 17°43′34″S, 129°18′36″E (coll. V. Kessner, 2.ix.2009; WA-84/09) (WAM S83169).

Paratypes: AUSTRALIA, NT, VRD, same data as for holotype, one wet (WAM S49228); east of Duncan Hwy, 37.7 km north-west of Kirkimbie Station H/S,

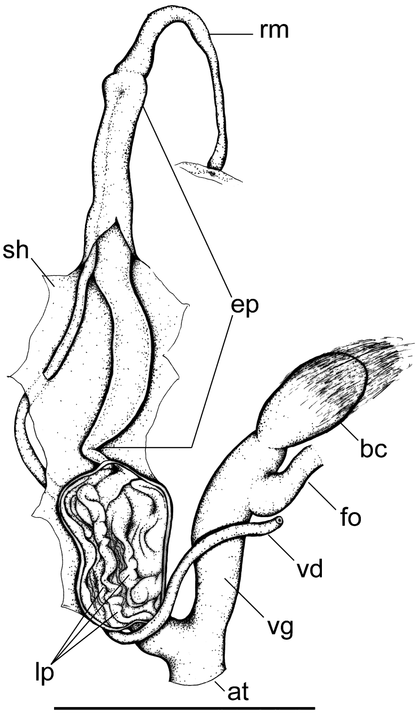

Figure 13. Penial anatomy of ***E. gregoriana* sp. nov.** (holotype AM C.475766). Scale bar = 5 mm.

large, open and very rugged limestone formation, open limestone formation, in talus, under spinifex (coll. V. Kessner, R. Hokkanen, 2.ix.2009), one wet (WAM S83170).

Etymology: In reference to the remarkable length of the penis, derived from 'longus' (Latin = long) and 'cauda' (Latin = tail, penis), adjective of feminine gender.

Description: Shell (Figs 5G, 14A–C). Large, moderately elevated, moderately thick; protoconch and teleoconch whorls moderately strong radial growth lines, micropustulations absent. Shell background colour yellowish horn fading to whitish towards shell base, with few brown-reddish spiral bands, equally conspicuous on entire shell, covering whorl periphery to shell base, often interrupted radially; no maculations.

Genitalia (Fig. 15). Epiphallus one third as long as penis. Vas deferens entering penial sheath halfway up. Penis 12 times longer than wide, heavily coiled inside sheath, posterior part of inner wall supporting many irregular tubercles; anterior part with narrow, regularly shaped and spaced longitudinal pilasters. Vagina almost as long as penis and more than two times as long as free oviduct. Bursa copulatrix with short, rounded, well-differentiated end.

Remarks: Only two shells examined. Shell colour pattern very similar to shells of four congeners; to be distinguished from *E. nodulicauda* and *E. negriensis* by reduced number of spiral bands, from *E. pallida* by darker background, and from *E. punctata* by absence of maculations. Along with *E. nodulicauda*, only species with a coiled penis.

Penis length relative to width (pl/pw) almost two times the average and largest amongst congeners; epiphallus length relative to penis (el/pl) one third of average and smallest amongst congeners. Inner penial wall sculpture unique by consisting exclusively of tubercles. Vagina length relative to penis (vl/pl) larger than average and almost as large as in *E. nodulicauda*; vagina length relative to free oviduct (vl/ol) largest amongst congeners.

EXILIGADA MONOCHROMA SP. NOV.

(FIGS 4F, 5H, 14D–F, 16)

Holotype: AUSTRALIA, NT, VRD, 46 km south-west of VRD Station H/S, limestone outcrop, 16°41′22″S, 130°42′12″E (coll. V. Kessner, 16.vii.2008) (AM C.475768).

Paratypes: AUSTRALIA, NT, VRD, same data as for holotype, 31 dry, two wet (AM C.462772).

Etymology: In reference to the coloration, derived from 'monos' (Greek = unique) and 'chroma' (Greek = colour), adjective of feminine gender.

Description: Shell (Figs 4F, 5H, 14D–F). Moderately large, moderately elevated, thin; micropustulations absent. Shell colour brown horn fading to whitish towards shell base; no maculations.

Genitalia (Fig. 16). Epiphallus as long as penis. Vas deferens entering penial sheath halfway up. Penis five times longer than wide, not coiled inside sheath, with inner wall supporting three moderately large, regularly spaced longitudinal pilasters running along its entire length. Vagina slightly longer than penis and one and a half times longer than free oviduct, bursa copulatrix with short, rounded well-differentiated end.

Remarks: Teleoconch microsculpture differing from that of *E. montejinni* by absence of micropustulations. Spiral bands almost always absent; readily distinguished from *E. montejinni* by its darker brownish horn background colour.

Penis length relative to width (pl/pw) average, longer than in *E. montejinni*; epiphallus length relative to penis (el/pl) average and equal to *E. montejinni*. Inner penial wall sculpture similar to that of *E. montejinni*, but with more organized pattern. Vagina length relative to penis (vl/pl) and vagina

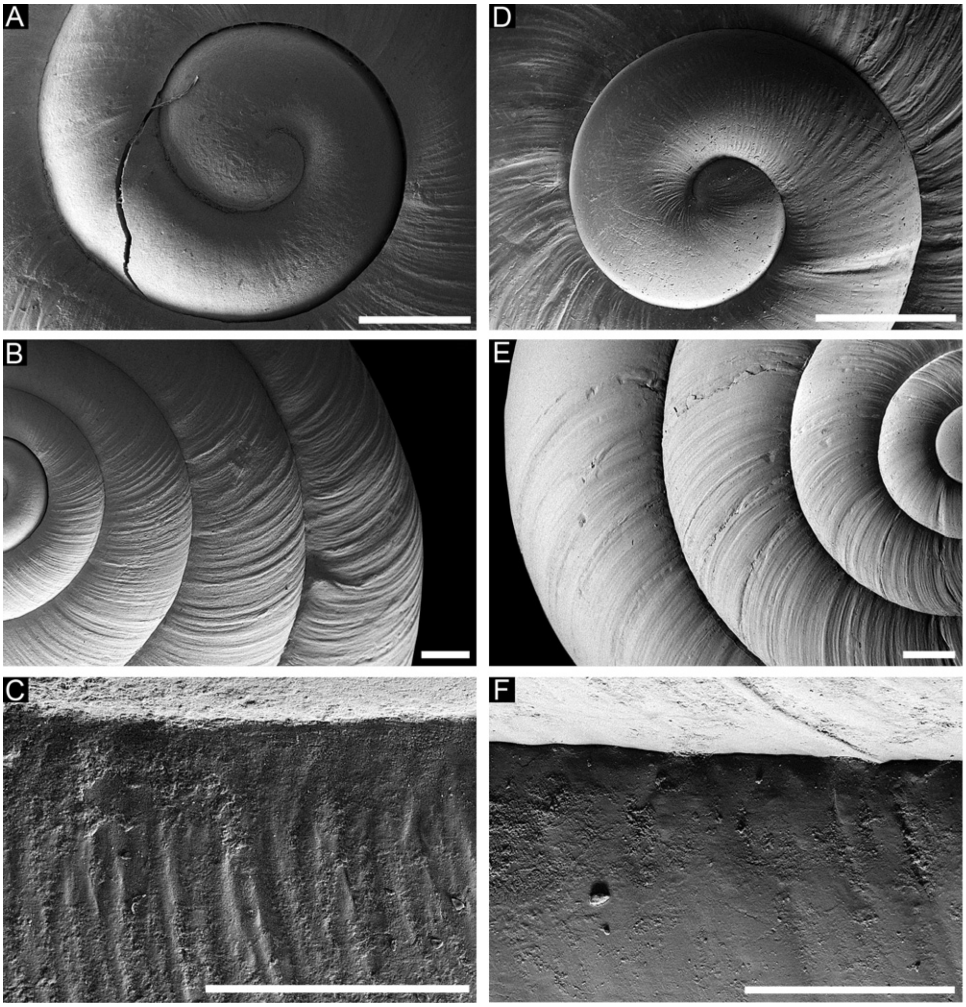

Figure 14. SEM micrographs of *Exiligada* shells. A-C, ***E. longicauda* sp. nov.** (paratype WAM S 49228). A, Apical view showing protoconch and first whorl. B, Close-up from above of sculpture across entire shell. C, Microsculpture on teleoconch whorl. D-F, ***E. monochroma* sp. nov.** (paratype AM C.462772). D, Apical view showing protoconch and first whorl. E, Close-up from above of sculpture across entire shell. F, Microsculpture on teleoconch whorl. Scale bars: A-B, D-E = 1 mm, C, F = 0.5 mm.

length relative to free oviduct (vl/ol) larger than average and *E. montejinni*.

EXILIGADA MONTEJINNI SP. NOV.

(FIGS 6A, 17A–C, 18)

Holotype: AUSTRALIA, NT, VRD, 15.5 km west-south-west of Montejinni Stn H/S, 16°42′22″S, 131°37′28″E (coll. V. Kessner, M. Braby, T. Parkin, 29.vii.2010) (AM C.475769).

Paratypes: AUSTRALIA, NT, VRD, same data as for holotype, 20 dry, two wet (AM C.469982).

Etymology: In reference to the type locality, Montejinni Station; noun in apposition.

Description: Shell (Figs 6A, 17A–C). Moderately large, moderately elevated, thin; protoconch and teleoconch whorls with fine radial growth lines, micropustulations present. Shell background colour entirely yellowish horn and fading to whitish towards the base, sometimes with a darker subsutural area, never resembling a band.

Genitalia (Fig. 18). Epiphallus as long as penis. Vas deferens entering penial sheath from one third up. Penis four times longer than wide, not coiled inside sheath, with inner wall supporting few longitudinal pilasters, some of which merging anteriorly into a single structure, some others running independently along wall. Vagina slightly shorter than penis and free oviduct, bursa copulatrix with short, rounded, well-differentiated end.

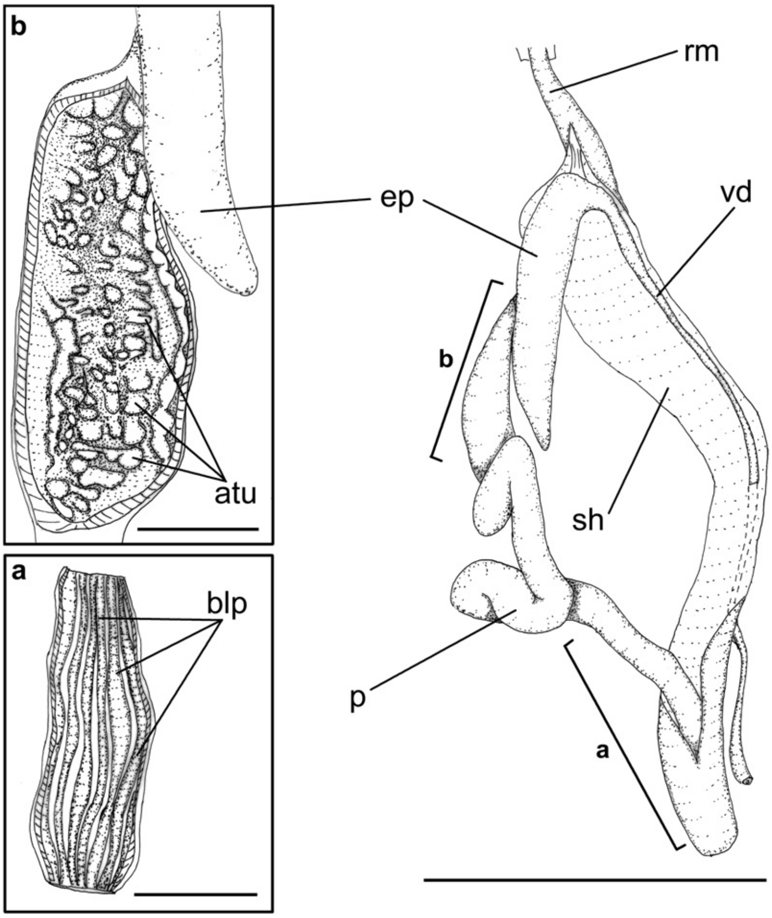

Figure 15. Penial anatomy of ***E. longicauda* sp. nov.** (holotype WAM S83169). A. Detail of apical portion of inner penial wall. B. Detail of basal portion of inner penial wall. Scale bars: 5 mm; A, B = 1 mm.

Remarks: Teleoconch microsculpture differing from that of *E. monochroma* by presence of micropustulations. Together with *E. unistriata* widest umbilicus of genus. Spiral bands always absent; readily distinguished from *E. monochroma* by its lighter yellowish horn shell background colour. Penis length relative to width (pl/pw) smaller than average and *E. monochroma*; epiphallus length relative to penis (el/pl) average. Inner penial wall sculpture similar to that of *E. montejinni* but with less organized pattern. Vagina length relative to penis (vl/pl) larger than average and smaller than *E. monochroma*; vagina length relative to free oviduct (vl/ol) smaller than average and two times smaller than in *E. monochroma*.

Exiligada nodulicauda sp. nov.

(Figs 4C, 6B, 17D–F, 19)

Holotype: AUSTRALIA, NT, VRD, 30.2 km north-east of Kirkimbie Station H/S, karst limestone formation in open woodland, open limestone formation, spinifex, 17°29′23″S, 129°22′46″E (coll. V. Kessner, R. Hokkanen, 2.ix.2009), (WAM S83173).

Paratypes: AUSTRALIA, NT, VRD, same data as for holotype, four wet (WAM S49217); 161 dry (WAM S49160).

Etymology: In reference to the regular pattern of nodules typical of the inner penial wall, derived from ‘nodulus’ (Latin = noduled) and ‘cauda’ (Latin = tail or penis), adjective of feminine gender.

Description: Shell (Figs 4C, 6B, 17D–F). Moderately large, weakly elevated, moderately thick; micropustulations absent. Shell background colour yellowish horn fading to whitish towards shell base, with numerous and dense brown-reddish spiral bands, equally conspicuous on entire shell, often present on shell base, often regularly interrupted radially and giving the appearance of a regular radial bandage; maculations absent.

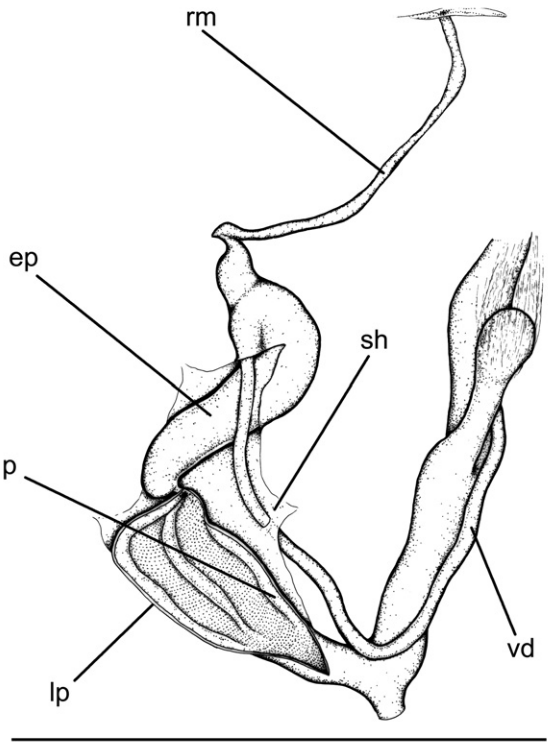

Figure 16. Penial anatomy of ***E. monochroma* sp. nov.** (holotype AM C.475768). Scale bar = 5 mm.

Genitalia (Fig. 19). Epiphallus length two thirds that of penis. Vas deferens entering penial sheath from one third up. Penis seven times longer than wide, coiled inside sheath, with posterior part of inner wall supporting three regularly nodulose, longitudinal pilasters fading into three irregularly shaped folds not reaching the genital pore. Vagina as long as penis, two times longer than free oviduct, bursa copulatrix with long, rounded well-differentiated end.

Remarks: Together with *E. qualis* narrowest umbilicus of genus. Shell colour pattern very similar to shells of four congeners; to be distinguished from *E. longicauda* by larger number of spiral bands, from *E. negriensis* by more regularly interrupted bands, from *E. pallida* by darker background, and from *E. punctata* by absence of maculations. Along with *E. longicauda*, only species in genus with a coiled penis. Penis length relative to width (pl/pw) larger than average and smaller than *E. longicauda*; epiphallus length relative to penis (el/pl) smaller than average and two times that of *E. longicauda*. Inner penial wall sculpture unique, in consisting of longitudinal pilasters sculptured by regularly spaced and shaped nodules. Vagina length relative to penis (vl/pl) larger than average and almost as large as in *E. longicauda*; vagina length relative to free oviduct (vl/ol) slightly smaller than in *E. longicauda* and largest amongst remaining congeners.

EXILIGADA PALLIDA SP. NOV.

(FIGS 4B, 6C, 20A–C, 21)

Holotype: AUSTRALIA, NT, VRD, 28.2 km east of Spring Creek Station H/S, base of limestone cliffs along a seasonal stream bed, 15–20 m or more high, large overhangs, talus and boulders, under rocks, 17°00′44″S, 129°07′35″E (coll. V. Kessner, R. Hokkanen, 30.viii.2009; WA-66/09) (WAM S83174).

Paratypes: AUSTRALIA, NT, VRD, same data as for holotype, 22 wet (WAM S49215), 106 dry (WAM S49150).

Etymology: In reference to the pale shell background colour, derived from 'pallidus' (Latin = pale); adjective of feminine gender.

Description: Shell (Figs 4B, 6C, 20A–C). Large, moderately elevated, moderately thick; micropustulations present. Shell background colour pale horn fading to whitish towards shell base, with several conspicuous to faint brown-reddish spiral bands, equally conspicuous on entire shell, often present on shell base, often regularly interrupted radially and giving the appearance of a regular radial bandage; maculations absent.

Genitalia (Fig. 21). Epiphallus as long as penis. Vas deferens entering penial sheath from halfway up. Penis six times longer than wide, not coiled inside sheath, with inner wall supporting a posterior cone-shaped pad and five longitudinal pilasters, two arising close to posterior part of pad and reaching genital pore, three from posterior end of penis, only two of which reaching genital pore. Vagina one third shorter than penis length and as long as free oviduct, bursa copulatrix with long, pointed well-differentiated end.

Remarks: Teleoconch microsculpture differing from that of *E. negriensis* by presence of micropustulations.

Shell colour pattern similar to that of four other *Exiligada* species; to be distinguished from *E. longicauda* and *E. nodulicauda* by its lighter background colour and from *E. punctata* by absence of maculations.

Penis length relative to width (pl/pw) average and larger than in sister species *E. negriensis*; epiphallus length relative to penis (el/pl) as long as average and as *E. negriensis*. Inner penial wall sculpture similar to *E. negriensis* and *E. punctata*, to be distinguished from these species by narrower posterior pad and longer longitudinal pilasters, always reaching the posterior part of the wall, and by

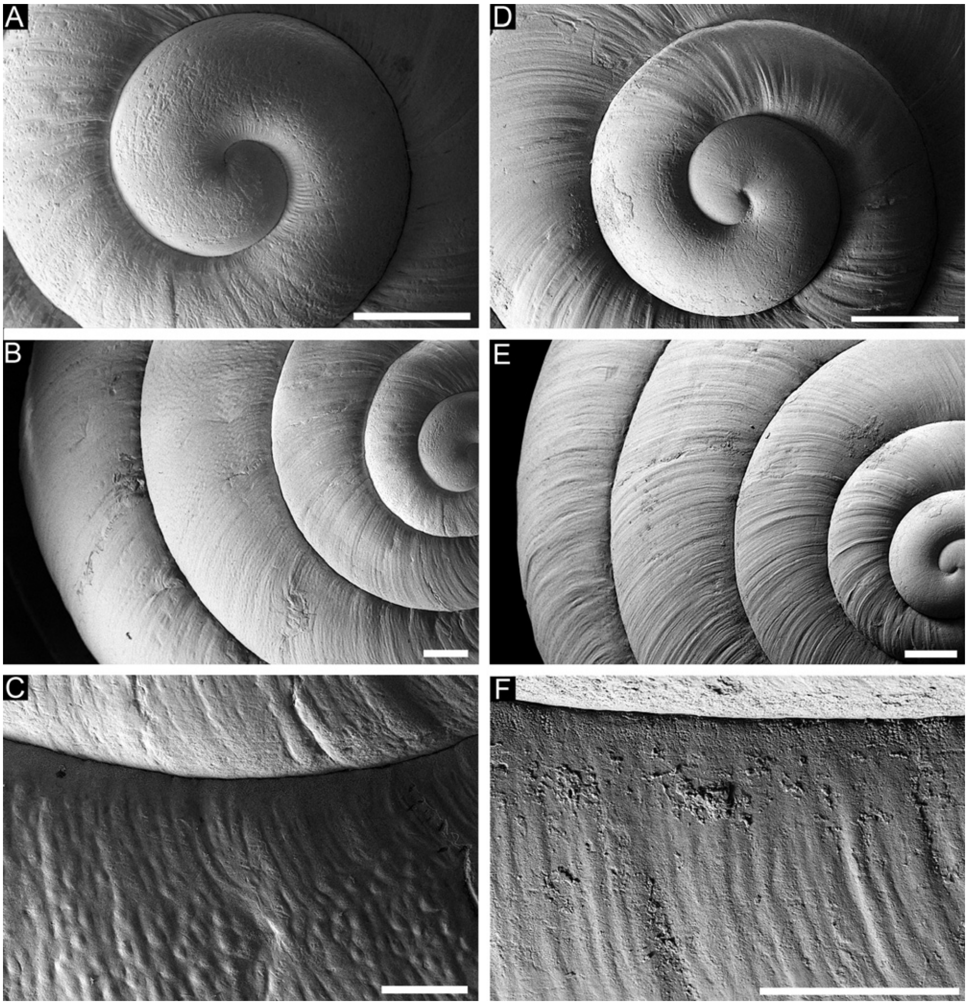

Figure 17. SEM micrographs of *Exiligada* shells. A-C, ***E. montejinni* sp. nov.** (paratype AM C.469982). A, Apical view showing protoconch and first whorl. B, Close-up from above of sculpture across entire shell. C, Microsculpture on teleoconch whorl. D-F, ***E. nodulicauda* sp. nov.** (paratype WAM S49160). A, Apical view showing protoconch and first whorl. B, Close-up from above of sculpture across entire shell. C, Microsculpture on teleoconch whorl. Scale bars: A-B, D-E = 1 mm, C, F = 0.5 mm.

noncorrugated posterior pad. Vagina length relative to penis (vl/pl) and relative to free oviduct (vl/ol) average.

***Exiligada punctata* sp. nov.**

(Figs 4D, 6D, 20D–F, 22)

Holotype: AUSTRALIA, WA, EK, Halls Creek District, south of Panton River, low and open limestone area, numerous gullies, under well-developed spinifex, in talus, 17°49′23″S, 128°14′58″E (coll. V. Kessner, R. Hokkanen, 1.ix.2009; WA-76/09) (WAM S 83175).

Paratypes: AUSTRALIA, WA, EK, same data as for holotype, ten wet (WAM S49221); Halls Creek District, 57 km east of Nicholson Station H/S, very open limestone area, well-developed spinifex, talus, under spinifex and slabs, 17°58′43″S, 128°21′34″E (coll. V. Kessner, R. Hokkanen, 1.ix.2009; WA-75/09), 15 wet, > 24 dry (WAM S49220); Halls Creek District, large rather open limestone area, 4.5 km north of Panton River, numerous gullies, under spinifex, in talus, 17°46′47″S, 128°13′59″E (coll. V. Kessner, R. Hokkanen, 1.ix.2009; WA-77/09), seven wet (WAM S49222), 22 dry (WAM S49139).

Other material: AUSTRALIA, WA, EK, Halls Creek District, 57 km east of Nicholson Station H/S, very open limestone area, well-developed spinifex, talus, under spinifex and slabs, 17°58′43″S, 128°21′34″E (coll. V. Kessner, R. Hokkanen, 1.ix.2009; WA-75/09), 30 dry (WAM S49137); Halls Creek District, south of

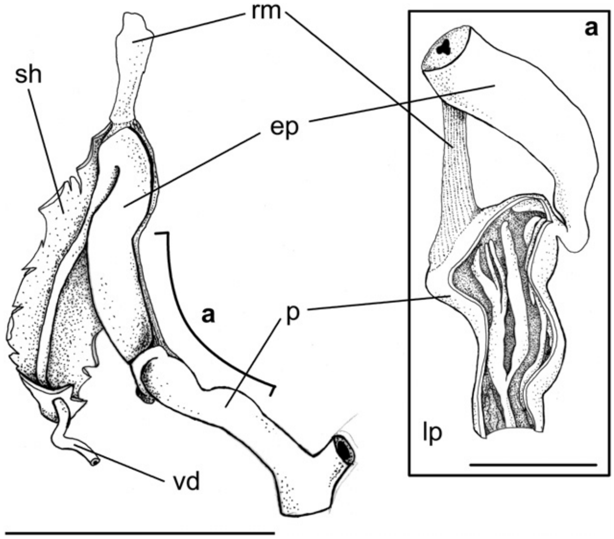

Figure 18. Penial anatomy of ***E. montejinni* sp. nov.** (holotype C.475769). A. External anatomy of penial complex, penial sheath removed. B. Anatomy of inner penial wall and detail of epiphallus–penis junction. Scale bar = 5 mm; a = 1 mm.

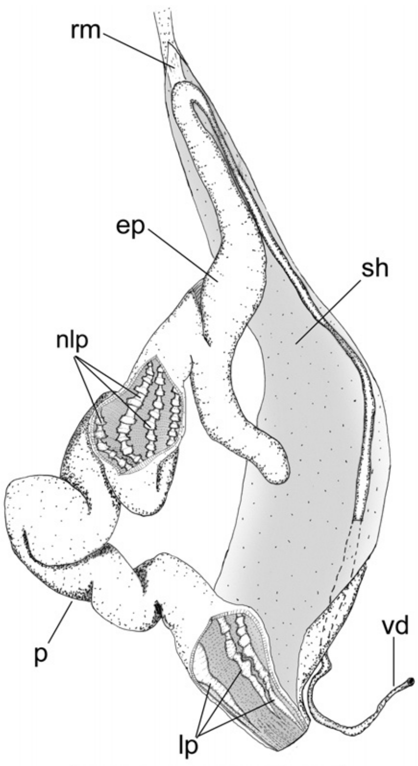

Figure 19. Penial anatomy of ***E. nodulicauda* sp. nov.** (holotype WAM S83173). Scale bar = 5 mm.

Panton River, low and open limestone area, numerous gullies, under well-developed spinifex, in talus, 17°49′23″S, 128°14′58″E (coll. V. Kessner, R. Hokkanen, 1.ix.2009; WA-76/09), 17 dry (WAM S49138); Halls Creek District, south of Panton River, low and open limestone area, numerous gullies, under well-developed spinifex, in talus, 17°49′23″S, 128°14′58″E (coll. V. Kessner, R. Hokkanen, 1.ix.2009; WA-76/09), four dry (WAM S49144).

Etymology: In reference to the peculiar colour pattern, formed by fine maculations, derived from 'punctatus' (Latin = dotted), adjective of feminine gender.

Description: Shell (Figs 4D, 6D, 20D–F). Large, moderately elevated, moderately thick; micropustulations absent. Shell background colour yellowish horn fading to whitish towards shell base, with several brown-reddish spiral bands, most conspicuous on body whorl, never present on shell base, often interrupted radially; sparse brown maculations in radial clusters present on whole spire and increasing in number on last whorls.

Genitalia (Fig. 22). Epiphallus one third of penis. Vas deferens entering penial sheath from one third up. Penis five times longer than wide, not coiled inside sheath, with inner wall supporting a large apical corrugated pad and six narrow, regularly shaped longitudinal pilasters, five of which interrupted posteriorly and one running along entire wall length. Vagina one third shorter than penis and as long as free oviduct, bursa copulatrix shape variable, without well-differentiated end or with a short to long rounded end.

Remarks: Shell colour pattern similar to *E. pallida*, *E. longicauda*, *E. nodulicauda*, and *E. negriensis*, but easily distinguishable by presence of maculations. Penis length relative to width (pl/pw) and epiphallus length relative to penis (el pl^{-1}) smaller than average. Inner penial wall sculpture similar to *E. negriensis* and *E. pallida*, to be distinguished from these species by narrower posterior pad and longer longitudinal pilasters, always reaching the posterior part of the wall, and by latter by posterior pad being corrugated. Vagina length relative to penis (vl/pl) and relative to free oviduct (vl/ol) average.

Exiligada qualis Iredale, 1939

(Figs 4E, 6E, 23A–C, 24)

Exiligada qualis Iredale, 1939: 69, plate V, figure 2.
Exiligada negriensis – Solem, 1984: 673–677, figure 174 (d–f) (in part).

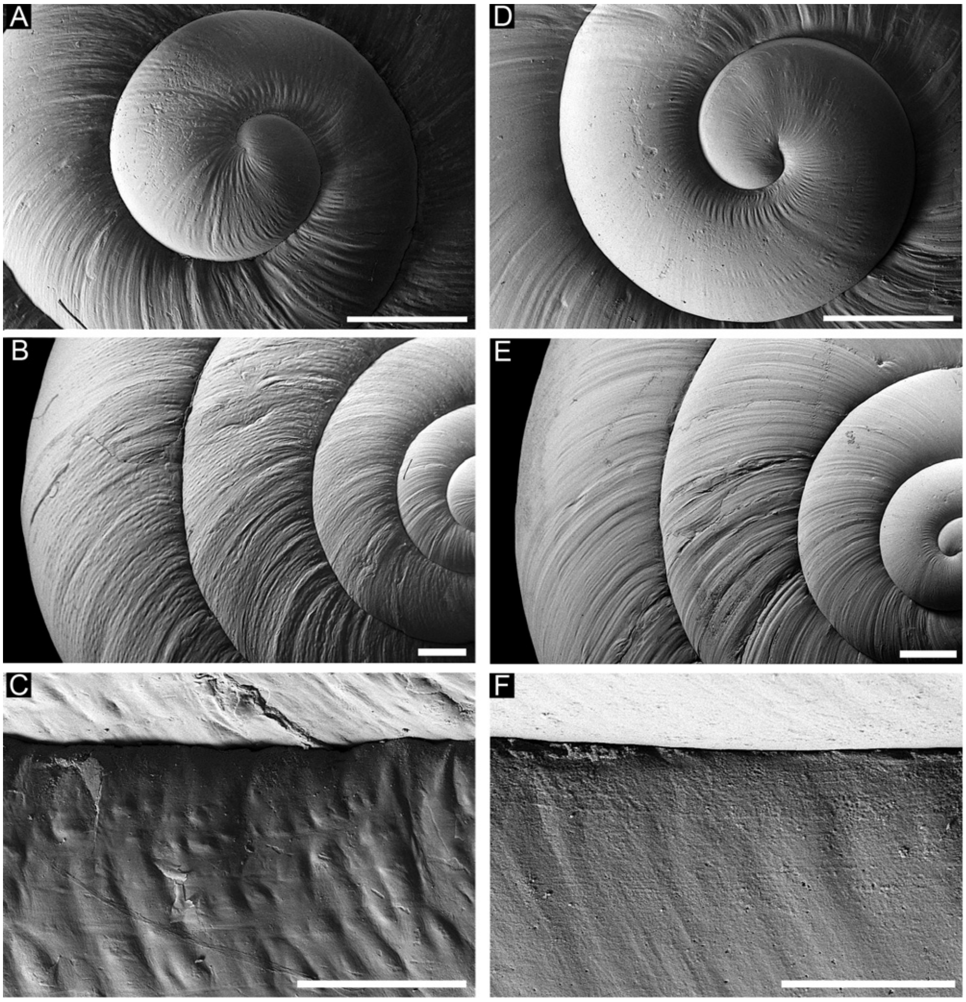

Figure 20. SEM micrographs of *Exiligada* shells. A-C, ***E. pallida* sp. nov.** (paratype WAM S49150). A, Apical view showing protoconch and first whorl. B, Close-up from above of sculpture across entire shell. C, Microsculpture on teleoconch whorl. D-F, ***E. punctata* sp. nov.** (paratype WAMS49139). D, Apical view showing protoconch and first whorl. E, Close-up from above of sculpture across entire shell. F, Microsculpture on teleoconch whorl. Scale bars: A-B, D-E = 1 mm, C, F = 0.5 mm.

Material examined: AUSTRALIA, NT, VRD, holotype from 25 miles north of Ord River Station, Negri outstation (coll. R. Helms, 1896), dry (AM C.64866), 43 paratypes (same data as for holotype) (AM C.64915); 35 km north of Nicholson H/S, Duncan Rd, limestone cliffs, 500 m west of road, under rocks at dripline of cave overhang, 17°42′45″S, 128°50′10″E (coll. R. Crookshanks, 28.i.2005), three dry, one wet (AMS C.443304).

Duncan Rd, old Ord River homestead, Forrest Ck, 70 km north of Nicholson homestead, under limestone rocks and concrete of old structures, 17°23′56″S, 128°52′01″E (coll. R. Crookshanks, 29.i.2005), one wet (AM C.475758).

Description: Shell (Figs 4E, 6E, 23A–C). Moderately large, moderately elevated, moderately thin; teleoconch with short regularly alternate microdepressions. Shell background colour yellowish horn fading to whitish towards shell base, with few conspicuous to moderately faint continuous brown-reddish spiral bands; maculations absent.

Genitalia (Fig. 24). Epiphallus as long as penis. Vas deferens entering penial sheath from halfway up. Penis six times longer than wide, not coiled inside sheath, with inner wall supporting a large apical stimulatory pilaster and (several) basal pilasters. Vagina two thirds of penis and free oviduct, bursa copulatrix with no well-differentiated end.

Remarks: The type locality is identical to that of *E. negriensis* and as such also restricted to an area close to the Negri River between the point where the Negri River flows into the Ord River in WA (17°04′11″S, 128°53′10″E) and the Duncan Highway bridge over the Negri River near the WA/NT border

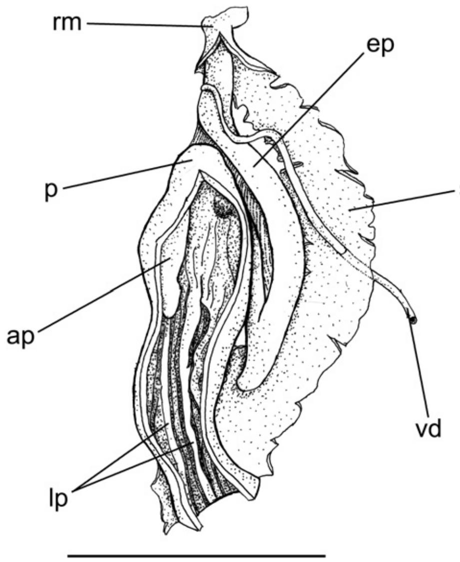

Figure 21. Penial anatomy of ***E. pallida*** **sp. nov.** (holotype WAM S83174). Scale bar = 5 mm.

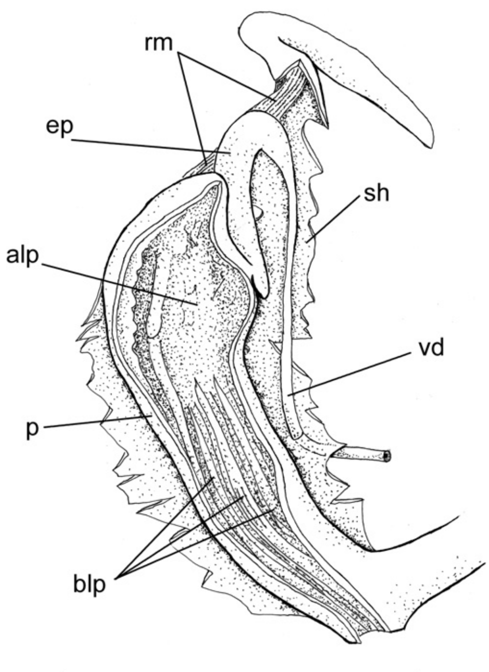

Figure 22. Penial anatomy of ***E. punctata*** **sp. nov.** (holotype WAM S83175). Scale bar = 5 mm.

(17°04′32″S, 129°00′10″E). The species is removed from the synonymy of *E. negriensis*. Together with *E. nodulicauda* it has the narrowest umbilicus in the genus. Teleoconch microsculpture is unique in being composed of regularly arranged microdepressions rather than micropustulations. Shell colour pattern not easily distinguished from *E. brabyi*. Penis length relative to width (pl/pw) and epiphallus length relative to penis (el/pl) average. Inner penial wall sculpture similar to those of *E. brabyi*, to be distinguished by posterior pilaster being continuous. Vagina length relative to penis (vl/pl) average and vagina length relative to free oviduct (vl/ol) half the average.

EXILIGADA RIVIFONTIS SP. NOV.

(FIGS 4I, 6F, 23D–E, 25)

Holotype: AUSTRALIA, NT, VRD, 30.4 km east-south-east of Spring Creek Station H/S, limestone gully along a stream, cliffs 8–10 m high, base of limestone cliffs along a seasonal stream, talus, spinifex and native grass, in talus. 17°02′04″S, 129°08′35″E (coll. V. Kessner, R. Hokkanen, 30.viii.2009; WA-67/09) (WAM S83176).

Paratypes: Same data as for holotype, four wet (WAM S49224).

Other material: AUSTRALIA, NT, VRD, 28.2 km east of Spring Creek Station H/S, base of limestone cliffs 15–20 m or higher, large overhangs, in talus and under boulders, 17°00′44″S, 129°07′35″E (coll. V. Kessner, R. Hokkanen, 30.viii.2009; WA-66/09), three wet (WAM S49225); 30.4 km east-south-east of Spring Creek Station H/S, limestone gully along a stream, cliffs 8–10 m high, base of limestone cliffs along a seasonal stream, spinifex and native grass, in talus, 17°02′04″S, 129°08′35″E (coll. V. Kessner, R. Hokkanen, 30.viii.2009; WA-67/09), three dry (WAM S94141); AUSTRALIA, WA, EK, 1.7 km south of Behn River crossing, limestone ridge west of Duncan Hwy, east large open limestone ridge, very small vine thicket patches, dead in rock piles, 16°35′48″S, 128°57′10″E (coll. V. Kessner, R. Hokkanen, 27.viii.2009; WA-54/09), five dry (WAM S49140); 12.3 km east of Spring Creek Station H/S, low exposed hills with small 2–3-m-high limestone cliffs east of Duncan Hwy, spinifex, few fig trees, dead under talus, 16°59′57″S, 128°58′34″E (coll. V. Kessner, R. Hokkanen, 30.viii.2009; WA-70/09), one dry (WAM S49142); Halls Creek District, 57 km east of Nicholson Station H/S, very open limestone area, well-developed spinifex, talus under spinifex, 17°58′43″S, 128°21′34″E (coll. V. Kessner, R. Hokkanen 1.ix.2009; WA-75/09), two dry (WAM S49143).

Etymology: In reference to Spring Creek, close to type locality, Latinized and derived from ‘rivus’ (Latin = creek) and ‘fons’ (Latin = spring), nouns of respectively masculine and feminine gender in genitive case.

Description: Shell (Figs 4I, 6F, 23D, E). Large, strongly elevated, moderately thin; micropustulations

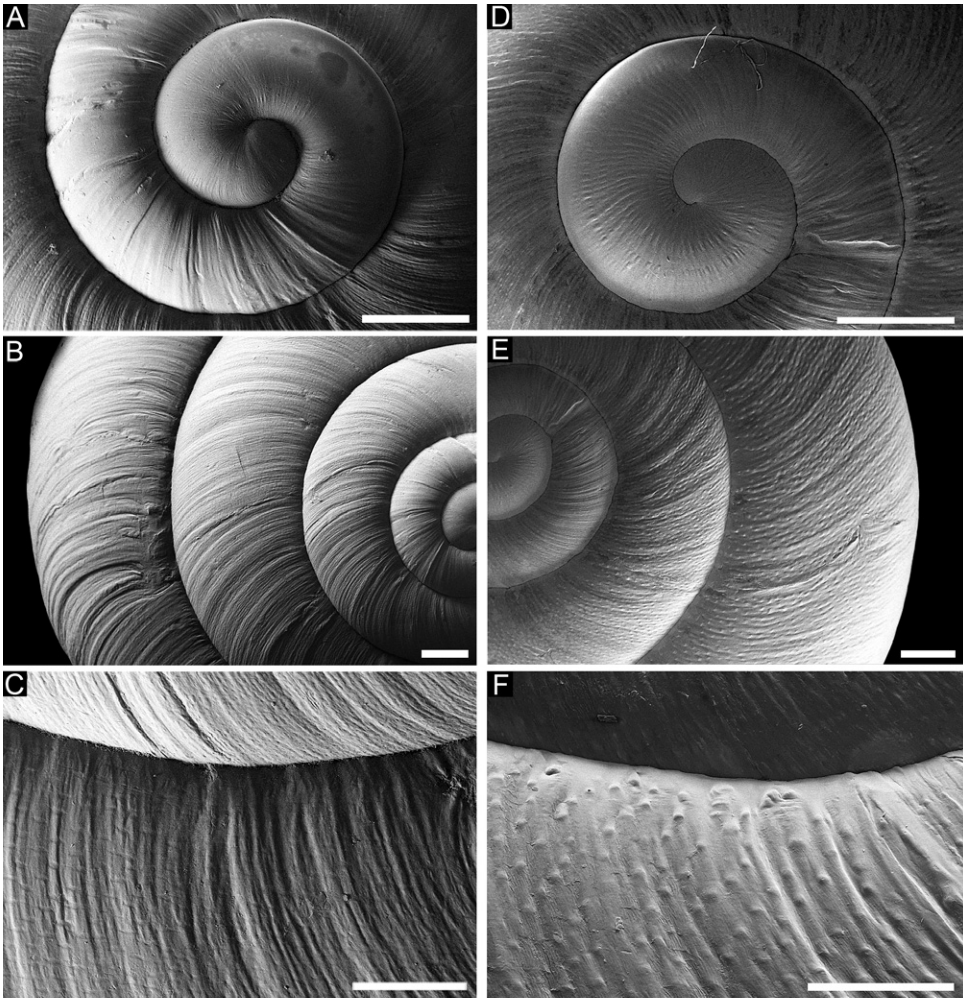

Figure 23. SEM micrographs of *Exiligada* shells. A-C, *E. qualis* Iredale, 1939 (paratype AM C.64915). A, Apical view showing protoconch and first whorl. B, Close-up from above of sculpture across entire shell. C, Microsculpture on teleoconch whorl. D-F, ***E.rivifontis* sp. nov.** (WAM S49141). D, Apical view showing protoconch and first whorl. E, Close-up from above of sculpture across entire shell. F, Microsculpture on teleoconch whorl. Scale bars: A-B, D-E = 1 mm, C, F = 0.5 mm.

present. Shell background colour brown horn fading to whitish towards shell base, with one faint to conspicuous continuous narrow brown-reddish spiral band on whorl periphery; maculations absent.

Genitalia (Fig. 25). Epiphallus two times longer than penis. Vas deferens entering penial sheath from one third up. Penis three times longer than wide, not coiled inside sheath, with inner wall supporting several moderately large, irregularly shaped longitudinal pilasters, often not running along entire wall length. Vagina two times shorter than penis and free oviduct, bursa copulatrix with short, rounded well-differentiated end.

Remarks: Highest shell, largest shell diameter, and largest number of shell whorls (together with *E. gregoriana* and *E. rivifontis*) within genus. Colour pattern very similar to *E. calciphila*, *E. floraevallis*, *E. gregoriana*, *E. limbunya*, and *E. unistriata*. Penis length relative to width (pl/pw) smaller than the average and *E. rivifontis*; epiphallus length relative to penis (el/pl) 1.5 times the average and as large as in *E. floraevallis*. Penial inner wall sculpture very similar to *E. floraevallis* and not easily distinguishable. Vagina length relative to penis (vl/pl) average and as large as in *E. floraevallis*, vagina length relative to free oviduct (vl/ol) smaller than average and *E. floraevallis*.

EXILIGADA UNISTRIATA SP. NOV.

(FIGS 4G, 6G, 26, 27)

Holotype: AUSTRALIA, NT, VRD, 14.5 km south-west of Limbunya Stn H/S, large limestone hills with cliffs and karst formations in open woodland, small patches

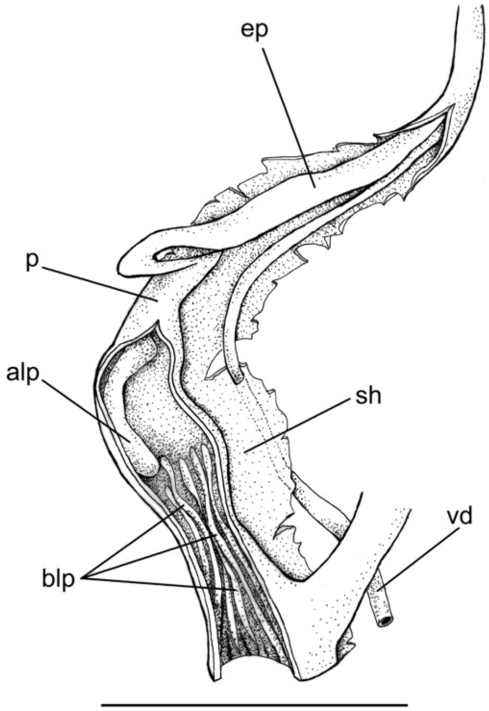

Figure 24. Penial anatomy of *E. qualis* Iredale, 1939 (AM C.475758). Scale bar = 5 mm.

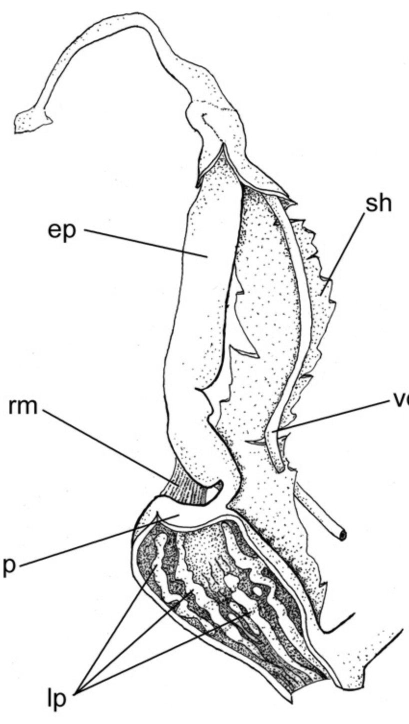

Figure 25. Penial anatomy of ***E. rivifontis* sp. nov.** (holotype WAM S83176). Scale bar = 5 mm.

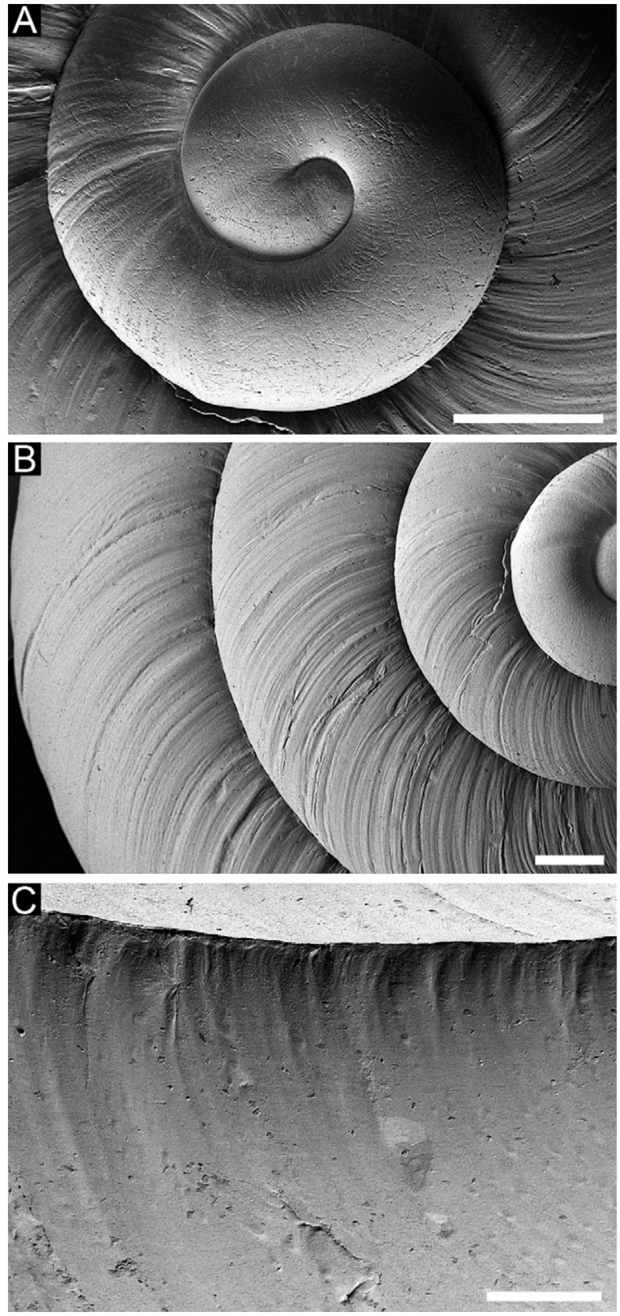

Figure 26. SEM micrographs of shell of ***E. unistriata* sp. nov.** (paratype AM C.469983). A, Apical view showing protoconch and first whorl. B, Close-up from above of sculpture across entire shell. C, Microsculpture on teleoconch whorl. Scale bars: A-B = 1 mm, C = 0.5 mm.

of vine thicket, spinifex, 17°18′20.6″S, 129°46′38.6″E (coll. T. Parkin, M. Braby, 24.vii.2010; NT-15/10) (AM C.475770).

Paratypes: Same data as for holotype, ten dry, nine wet (AM C.470460); 14.2 km south-west of Limbunya Stn H/S, large limestone hills with cliffs and karst

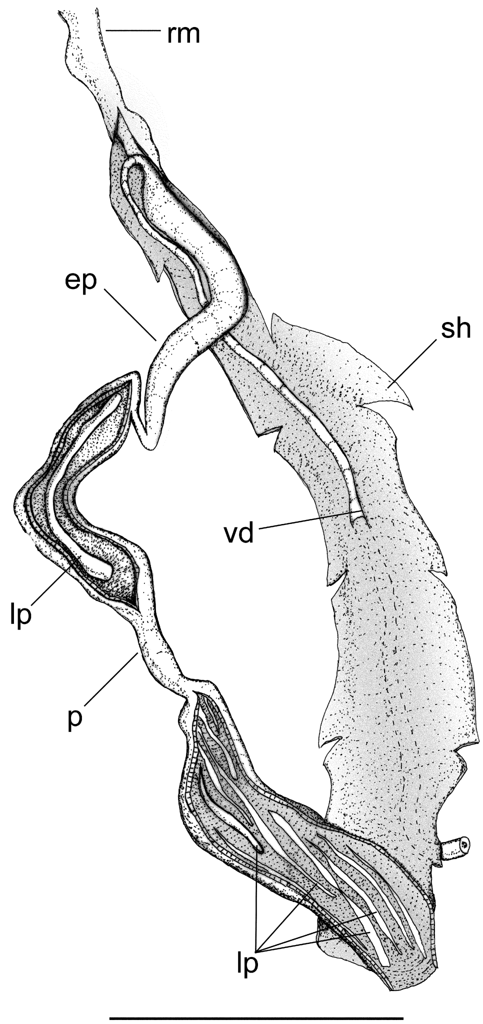

Figure 27. Penial anatomy of ***E. unistriata* sp. nov.** (holotype AM C.475770). Scale bar = 5 mm.

formations in open woodland, small patches of vine thicket, spinifex, in talus, 17°18′27.3″S, 129°46′51.5″E (coll. V. Kessner, M. Braby, T. Parkin, 24.vii.2010; NT-14/10), four wet (AM C.470459); 17.5 km south-west of Limbunya Station, upper Stirling Creek drainage system, low limestone hills in open woodland beside seasonal stream, small pockets of vine thicket, spinifex, in talus, free sealer. 17°21′46.0″S, 129°47′55.0″E (coll. V. Kessner, M. Braby, T. Parkin, 23.vii.2010; NT-8/10), 20 dry, five wet (AM C.469984), 20 dry (AM C.469985); 26.6 km south-west of Limbunya Stn H/S, open limestone slopes, few shady bushes, in deep talus, 17°24′22.2″S, 129°44′03.9″E (coll. V. Kessner, M. Braby, T. Parkin, 24.vii.2010; NT-16/10), 20 dry, two wet (AM C.469983).

Other material: AUSTRALIA, NT, VRD, limestone hill 9.5 km south-west of VRD Station H/S, 16°27′35″S, 130°56′56″E (coll. V. Kessner, 15.vii.2008), four dry, one wet (AM C.462758); 27 km south-west of Limbunya Station, limestone outcrop with small vine thicket patches, in talus; 17°28′27.0″S, 129°53′14.0″E (coll. T. Parkin, 23.vii.2010), one wet (AM C.475767).

Etymology: In reference to the shell colour pattern, derived from 'unus' (Latin = one) and 'striatus' (Latin = striped), adjective of feminine gender.

Description: Shell (Figs 4G, 6G, 26). Large, moderately elevated, thin; micropustulations absent. Shell background colour brown horn fading to whitish towards shell base, with one faint to very conspicuous brown-reddish spiral band on whorl periphery; maculations absent.

Genitalia (Fig. 27). Epiphallus half of penis. Vas deferens entering penial sheath from halfway up. Penis eight times longer than wide, not coiled inside sheath, with inner wall supporting one posterior large longitudinal pilaster and several short basal pilasters, arising from different point of wall and often reaching genital pore. Vagina slightly shorter than penis and slightly longer than free oviduct, bursa copulatrix with long, rounded well-differentiated end.

Remarks: Widest umbilicus of genus together with *E. montejinni*. Shell colour pattern very similar to *E. calciphila*, *E. floraevallis*, *E. gregoriana*, *E. limbunya*, and *E. rivifontis*. Penis length relative to width (pl/pw) larger than the average, epiphallus length relative to penis (el/pl) half average. Penial inner wall sculpture very similar to *E. brabyi*, to be distinguished by posterior longitudinal pilaster being continuous and smaller number of anterior folds. Vagina length relative to penis (vl/pl) and vagina length relative to free oviduct (vl/ol) larger than average.

DISCUSSION

Taxonomy and systematics

The delimitation of taxa within the Australian Camaenidae still relies almost entirely on morphological revisions, which emphasize characters of the shell (shape, size, and sculpture) and genitalia, in particular penial anatomy. Molecular studies remain rare and are usually restricted to analyses of congeneric species. However, where available, such studies have largely supported the morphology-based taxonomy (Köhler, 2010b, 2011a, b; Köhler & Johnson, 2012).

Previous to the present study, *Exiligada* contained only one recognized species (Solem, 1984) and therefore the monophyly of the genus was previously not of concern. Our study revealed that *Exiligada* comprises

KEY TO THE SPECIES OF *EXILIGADA*

1.	Shell with brown-reddish spiral bands	2
–.	Shell without bands	3
2.	Bands interrupted	4
–.	Bands continuous	5
3.	Shell background colour yellowish horn	*Exiligada montejinni*
–.	Shell background colour brownish horn	*Exiligada monochroma*
4.	Maculations present	*Exiligada punctata*
–.	Maculations absent	6
5.	One spiral band present	9
–.	More than one spiral band present	10
6.	Penis coiled	7
–.	Penis not coiled	8
7.	Penis shorter than epiphallus	*Exiligada nodulicauda*
–.	Penis longer than epiphallus	*Exiligada longicauda*
8.	Shell background whitish horn, thin (body visible by transparency)	*Exiligada pallida*
–.	Shell background yellowish horn, thin (body visible by transparency)	*Exiligada negriensis*
9.	Shell small (H < 8 mm, D < 17 mm)	*Exiligada limbunya*
–.	Shell larger than that (H > 8 mm, D > 17 mm)	11
10.	Penis as long as epiphallus	*Exiligada qualis*
–.	Penis longer than epiphallus	*Exiligada brabyi*
11.	Penis longer than epiphallus	*Exiligada unistriata*
–.	Penis as long as epiphallus	12
–.	Penis shorter than epiphallus	13
12.	Inner penial wall with pilasters running along entire wall length	*Exiligada rivifontis*
–.	Inner penial wall with pilasters limited to median and anterior part of wall	*Exiligada floraevallis*
13.	Pilasters of inner penial wall always corrugated	*Exiligada gregoriana*
–.	Pilasters of inner penial wall partly without corrugations	*Exiligada calciphila*

more species than previously recognized and our phylogenetic analysis of mtDNA sequences confirmed the monophyly of *Exiligada*. This analysis included representatives of all camaenid genera known from the region, which are not readily distinguishable by their shell (i.e. *Turgenitubulus* Solem, 1981b, *Ningbingia* Solem, 1981b, *Mesodontrachia* Solem, 1985, *Ordtrachia* Solem, 1984, *Prototrachia* Solem, 1984). It firmly placed all *Exiligada* species within a monophyletic ingroup (Fig. 2; outgroup pruned from the tree). The generic diagnosis of *Exiligada* has accordingly been formulated to capture the whole known morphological range of this group. Based on the mitochondrial phylogeny, we were able to evaluate the systematic significance of genital and shell characters to assign species to *Exiligada*. Most prominently, *Exiligada* species differ from most other camaenids from Western Australia and the Northern Territory in their peculiar epiphallus–penis–penial retractor configuration. Only *Ordtrachia* and *Prototrachia* exhibit a similar epiphallus–penis configuration, but these groups differ clearly in their penial wall and shell sculpture (Solem, 1984). For a comparison of morphological characteristics in camaenids from the Kimberley see Köhler (2011b), in the newly described genus *Youwanjela* see Köhler & Shea (2012), in *Parglogenia* and *Arnemelassa* from Arnhemland see Köhler (2012), and in Northern Territory camaenids, such as *Turgenitubulus*, *Ningbingia*, and *Mesodontrachia*, see Solem (1981a, b, 1985).

The central finding of the present study is that only a combination of morphological and genetic evidence allows a reliable assessment of species boundaries within *Exiligada*, with the data sets only of limited utility when considered separately. When delineating species by their morphology, the shape and size of shells are of little value, with only a single species (*E. limbunya*) being readily recognizable by its small and flat shell (Figs 2, 3). Likewise, shell coloration can be reliably used as an identification tool in a few cases (e.g. *E. punctata* and *E. monochroma*). A more intriguing aspect is however revealed when features of shell coloration (i.e. shell banding) are combined with other characters in order to differentiate species of *Exiligada*. Banding patterns are readily recognizable in living specimens but may be more difficult to detect in dead collected shells, which are often bleached. Variation in banding patterns has already been noted by Solem (1984), but their taxonomic significance has remained unrecognized because of the fact that Solem (1984) examined shells from mixed lots of sympatric species with varying banding patterns. Here, the molecular framework and anatomical data enabled us to untangle confounded species identifications based on the shell only, while also confirming the consistency of colour patterns within single species (Fig. 1). Indeed, shell coloration can be used as a first pass approach to identify species or species groups (see key). Shells of *E. unistriata* and of the clade comprising *E. calciphila* + *E. gregoriana* + *E. floraevallis* + *E. rivifontis* have a single band, whereas shells of *E. punctata* and of the two sister pairs *E. longicauda* + *E. nodulicauda* and *E. negriensis* + *E. pallida* have dashed bands. Uniquely, *E. monochroma* + *E. montejinni* have no bands. However, their sister-group relationship is only weakly supported in the molecular tree (Fig. 1). Therefore, none of the above-mentioned colour patterns can be confidently attributed to only one clade. To the contrary, similar banding patterns are found amongst unrelated species or species groups, suggesting their convergent or plesiomorphic origin in different clades. The tree is inconclusive as to which of the colour patterns is plesiomorphic within *Exiligada*. Uniformly coloured and continuously banded shells are found in many Australian camaenids, including taxa from north-western Australia (Köhler, 2011b). Only the presence of dashed spiral lines is characteristic for *Exiligada*.

Against the background of widespread polymorphism of shell banding in various other stylommatophoran land snails, the taxonomic utility of this trait in *Exiligada* may appear questionable. In several stylommatophorans shell colour patterns are controlled by dominant/recessive Mendelian genetic inheritance plus selection by predation or climatic factors (e.g. Murray & Clarke, 1976; Jones, Leith & Rawlings, 1977; Clarke *et al*., 1978). It has been demonstrated that the frequency of certain phenotypes may be extremely low because of strong selection in extreme environments (Johnson, 1981, 2011; Ożgo, 2005). Although we did not find polymorphic populations in *Exiligada*, one could therefore argue that colour patterns only appear to be fixed because of the low frequency of divergent phenotypes that are under strong negative selection and that these phenotypes were overlooked as a consequence of the small sample sizes in our study.

However, all the available evidence suggests that there is no banding polymorphism in *Exiligada*, but that banding patterns are indeed species-specific: differences in shell banding between spatially isolated populations cannot be attributed to strong divergent selection because of the similarity of habitats and life styles of these populations or species. Secondly, there is a strict correlation between shell banding and phylogenetic relationships (Fig. 2). Individuals with different shell banding are always genetically well differentiated whereas in turn individuals of the same phylogenetic cluster always share the same banding phenotype. Thus, we consider banding patterns to be a reliable taxonomic marker in *Exiligada*.

The features of the penial wall vary little within populations, but show diagnostic differences amongst different mitochondrial lineages, with consistent differences in development and configuration of penial wall sculpture and also, in part considerably, in the relative length of penis, epiphallus, vagina, and free oviduct. Consistent observations were made also in camaenids from the Kimberley (Köhler, 2010a, b, 2011a, b, c) and Northern Territory (Solem, 1984, 1985). In general, penial morphology in stylommatophorans is extremely varied, whereas morphological details frequently are species-specific (Barker, 2001). It has been suggested that the diagnostic value of penial features relates to the penis' function as the prime species recognition character during mating and copulation (Gómez, 2001). Although precopulatory behaviour might also be relevant, character displacement of penial characteristics in sympatric Asian camaenids, such as *Mandarina* (Chiba, 1996) and *Satsuma* (Kameda, Kawakita & Kato, 2009), underlines their significance for mate recognition and speciation.

In *Exiligada*, this correspondence between distinct penial morphotypes and mitochondrial clades is good evidence that these groups are separate species, and is the basis for our taxonomic revision. Indeed, patterns of inner penial wall sculpture were consistent not only with the branching patterns in the phylogenetic tree but also with the above-described patterns of shell coloration. The inner penial wall of *E. calciphila*, *E. gregoriana*, *E. floraevallis*, and *E. rivifontis*, forming a clade, has a rather complex and irregular sculpture, composed of interrupted pilasters and folds. No marked differences are exhibited at the posterior vs. anterior part of the penial wall. By contrast, species of a second clade, *E. longicauda* + *E. nodulicauda* and *E. negriensis* + *E. pallida*, consistently exhibit clear differences in the sculpture of the anterior vs. posterior parts of the penial wall, with a relatively simple and well-organized sculpture of regular patterns posteriorly and more irregular folds or pilasters anteriorly.

Species were found to be differentiated by on average about 12% uncorrected p-distance in both mitochondrial markers and we found no overlap between intraspecific and interspecific genetic distances, with the highest intraspecific distances amounting to about 3% and the lowest interspecific to about 6% (Table 2). This contrasts findings from other stylommatophorans where interspecific and intraspecific distances overlapped (e.g. Davison, Blackie & Scothern, 2009)

Table 2. Intraspecific and interspecific genetic differentiation amongst *Exiligada* species by means of p-distances

		neg	cal	flo	gre	uni	lon	mot	mon	bra	nod	pal	pun	qua	riv
neg	COI	**0.018**													
	16S	**0.026**													
cal	COI	0.119	**0.016**												
	16S	0.151	**0.011**												
flo	COI	0.114	0.104	**0.018**											
	16S	0.138	0.092	**0.015**											
gre	COI	0.107	0.080	0.102	**0.004**										
	16S	0.136	0.078	0.088	**0.003**										
uni	COI	0.103	0.127	0.129	0.128	**0.033**									
	16S	0.128	0.166	0.140	0.144	**0.020**									
lon	COI	0.123	0.141	0.138	0.135	0.125	**0.003**								
	16S	0.148	0.142	0.134	0.133	0.143	**0.012**								
mot	COI	0.105	0.100	0.096	0.094	0.124	0.123	**0.000**							
	16S	0.141	0.113	0.091	0.099	0.140	0.143	**0.000**							
mon	COI	0.106	0.102	0.104	0.095	0.115	0.120	0.083	**0.009**						
	16S	0.138	0.123	0.115	0.120	0.155	0.148	0.105	**0.022**						
bra	COI	0.107	0.118	0.119	0.126	0.102	0.142	0.123	0.120	**0.001**					
	16S	0.115	0.142	0.118	0.131	0.102	0.138	0.129	0.141	**0.008**					
nod	COI	0.125	0.135	0.139	0.139	0.128	0.067	0.130	0.117	0.142	**0.010**				
	16S	0.133	0.137	0.129	0.127	0.136	0.060	0.133	0.136	0.127	**0.017**				
pal	COI	0.089	0.121	0.124	0.112	0.105	0.128	0.125	0.104	0.109	0.129	**0.001**			
	16S	0.106	0.158	0.131	0.146	0.122	0.142	0.144	0.145	0.116	0.131	**0.009**			
pun	COI	0.112	0.130	0.133	0.124	0.103	0.140	0.125	0.117	0.104	0.134	0.107	**0.030**		
	16S	0.117	0.147	0.129	0.135	0.085	0.130	0.131	0.133	0.090	0.120	0.111	**0.027**		
qua	COI	0.116	0.134	0.141	0.144	0.096	0.138	0.129	0.126	0.110	0.147	0.120	0.106	**0.008**	
	16S	–	–	–	–	–	–	–	–	–	–	–	–	–	
riv	COI	0.122	0.109	0.061	0.114	0.138	0.149	0.116	0.120	0.129	0.153	0.142	0.143	1.144	**0.006**
	16S	0.144	0.096	0.063	0.087	0.143	0.134	0.085	0.123	0.121	0.130	0.133	0.131	–	**0.003**

		Min.	Max.	Mean
COI	within	0.000	0.033	0.011
	between	0.061	0.153	0.119
16S	within	0.000	0.027	0.013
	between	0.060	0.166	0.125

Bold numbers: intraspecific distances; rows on top: cytochrome oxidase subunit I (COI) distances; rows below: 16S distances; inset: minimum, maximum and average intraspecific and interspecific p-distances amongst *Exiligada* species neg, *Exiligada negriensis*; cal, *Exiligada calciphila*; flo, *Exiligada floraevallis*; gre, *Exiligada gregoriana*; uni, *Exiligada unistriata*; lon, *Exiligada longicauda*; mot, *Exiligada montejinni*; mon, *Exiligada monochroma*; bra, *Exiligada brabyi*; nod, *Exiligada nodulicauda*; pal, *Exiligada pallida*; pun, *Exiligada punctata*; qua, *Exiligada qualis*; riv, *Exiligada rivifontis*.

but replicates patterns found in other Australian camaenids, such as *Amplirhagada* (Köhler & Johnson, 2012) and *Rhagada* (Johnson *et al*., 2012). Hence, mitochondrial differentiation might also serve as a first pass to delimit species in *Exiligada* confirming findings in *Amplirhagada*, a camaenid from the Western Australian Kimberley, where the species threshold was at about 6% sequence divergence in 16S and COI (Johnson, O'Brien & Fitzpatrick, 2010; Köhler & Johnson, 2012). This apparent threshold of 6% in north-western Australian camaenids exceeds the best average of about 4% found across a broad range of stylommatophoran land snails (Davison *et al*., 2009).

By combining evidence from shell characters (coloration, size), penial wall anatomy, and patterns of mitochondrial differentiation, here we were able to delimit 15 species of *Exiligada*, which represents a significant increase from the previously only accepted species *E. negriensis*. Most of our species descriptions are based on newly collected material, but a few have also been recognized amongst material previously assigned to *E. negriensis* as a result of a refined approach to species delimitation. We demonstrate that in the latest revision, Solem (1984) subsumed material under one name, *E. negriensis*, which is here attributed to three distinct species, *E. negriensis*,

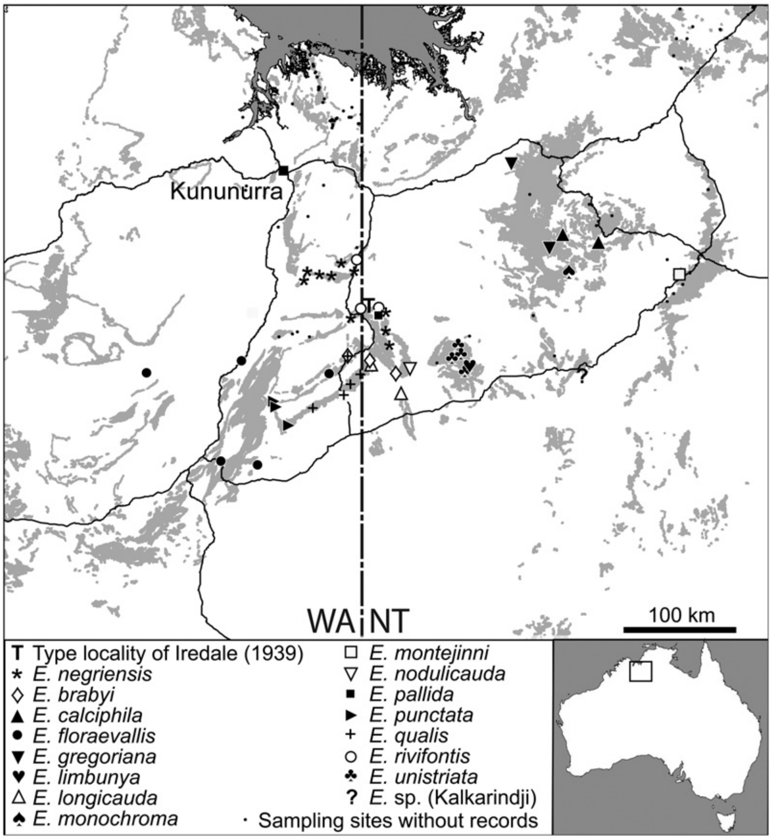

Figure 28. Map showing distributions of *Exiligada* species treated herein in the Daly and Victoria River Districts (NT) and the East Kimberley (WA). Occurrence and extent of limestone outcrops (in grey) based on available GIS information of distribution of carbonates in geological surface layers.

E. qualis, and *E. brabyi*. His notion that differences between the types of two nominal taxa described by Iredale (1939), *E. negriensis* and *E. qualis*, were not significant is refuted here based on our combined evidence. Therefore, *E. qualis* is removed from the synonymy of *E. negriensis* and recognized as a proper species.

Distributional patterns and the significance of limestone areas

Limestone areas have been identified as local hotspots of land snail diversity around the world (Solem, 1985; Stanisic, 1999; Schilthuizen & Rutjes, 2001; Schilthuizen *et al*., 2003; Schilthuizen, 2004; Örstan, Pearce & Welter–Schultes, 2005; Willan *et al*., 2009; Ketmaier *et al*., 2010), hence why limestone outcrops were specifically targeted in our field survey. In the Australian monsoonal topics, limestone outcrops occur sporadically and in a fragmented manner mainly in the drier inland areas but their importance as snail habitat is poorly studied (Slatyer *et al*., 2007). Population genetic studies in other land snails have demonstrated that abundances of snails on noncarbonate bed rocks surrounding the limestone areas are usually considerably lower, restricting gene flow between limestone areas (Schilthuizen & Lombaerts, 1994; Schilthuizen & Scott, 2004). In *Exiligada* the species ranges often extend across narrower stretches of a few kilometres of noncarbonated bed rock in between limestone outcrops but only twice do they span gaps larger than 25 km (*E. floraevallis*, *E. rivifontis*; Fig. 28). Throughout Australia, camaenids distributions are generally characterized by allopatry and microendemism (Solem, 1998; Köhler, 2010b; Hugall & Stanisic, 2011); only the extent of species ranges varies amongst taxa and regions. Our study provides the best available estimate for the size of species ranges within *Exiligada*, which can be compared with those of other camaenids from different regions. On the Kimberley mainland the average range of camaenid species is small, stated to be on average 20 km in diameter (Solem, 1991). Based on observations on offshore islands in the Kimberley it has been suggested that species ranges may even be smaller than that (Köhler, 2011b). In the

Kimberley, many species are obligate inhabitants of rainforests (including vine thickets), and their distributions are therefore governed by the distribution and size of suitable patches of habitat. In *Exiligada* species, ranges are consistently larger than the 20 km diameter given for the Kimberley camaenids. If species found at one locality only are disregarded, maximum linear distances between different collection sites in *Exiligada* range from a minimum of more than 20 km to well above 150 km (in *E. floraevallis*). These comparatively large ranges are attributed to the larger extent of suitable habitat, limestone outcrops, and the ability of species to live in a more open landscape. *Exiligada* species also differ from other known camaenids in the extent of sympatry. In most Australian camaenids, sympatric species predominantly belong to different genera, with each genus displaying unique adaptations with respect to aestivation behaviour, body size, and/or shell shape, indicating that species coexistence is related to niche differentiation (Solem, 1985; Gibson & Köhler, 2012). We found that the ranges of up to seven *Exiligada* overlap in parts of the study area (Fig. 28). However, the number of species found at the same sampling site rarely exceeded two and never three species per site even when species from other camaenid genera are taken into account: two species of *Ordtrachia* were found in the study area and where they occurred, the maximum number of sympatric camaenid species was still three or fewer.

For the narrowly endemic and predominantly allopatric distribution of most Australian camaenids, spatial separation has been postulated as the main factor driving speciation (Johnson *et al*., 2010; Köhler, 2011b). Habitat contractions and expansions as well as mutual ecological exclusion of species have played a role in maintaining or modifying these allopatric patterns (Cameron, 1992; Hugall *et al*., 2002). Our observations in *Exiligada* are consistent with these findings. Allopatric speciation is considered as the most likely mode of speciation in *Exiligada* because of their highly similar ecology (aestivation, foraging, shell-shape adaptation). Sympatry of species is probably secondary because of range expansions. Eventually, ecological exclusion may explain why only a limited number of species are found to co-occur at given sites even though the ranges of more species overlap in larger areas. This scenario is in agreement with what has been suggested for other mainland camaenids (Cameron, 1992).

In summary, our study confirms the existence of a large number of undiscovered species in a poorly studied part of the Australian monsoon tropics. Similar discoveries can be expected in other poorly surveyed areas. Our study confirms that xeric habitats support a lower alpha-diversity (in general up to three sympatric species) as compared to wetter areas, which may support up to 13 sympatric species from many different genera (Cameron, 1992; Gibson & Köhler, 2012). This general correlation between species richness and precipitation may be explained by the increased complexity of forest habitats in mesic zones of Australia, which provide more opportunities to realise ecological niches than less complex rock habitats.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Species identifications, museum registration numbers, type status, locality data and GenBank accession numbers of examined samples.