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Molecular phylogenetics and complementary geographical distributions of species of the Western Australian land snail genera *Plectorhagada* Iredale, 1933 and *Strepsitaurus* Solem, 1997 (Gastropoda: Camaenidae)

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The Western Australian camaenid genera *Plectorhagada* and *Strepsitaurus* have morphological similarities and mutually exclusive ranges near Cape Range. Sequences of ctyochrome *c* oxidase subunit I (*COI*) and *16S* mitochondrial DNA (mtDNA) genes confirmed that the two genera are genetically close sister clades. Targeted sampling showed that *Strepsitaurus*, which is confined to Cape Range, lies within a hole in the distribution of the more broadly distributed *Plectorhagada* that occurs on the coastal strip surrounding Cape Range. Species of the two genera meet at the transition between the rocky Cape Range and the sandier coastal areas, providing a rare example of the close replacement of genera. Within each genus, mtDNA sequences confirmed the monophyly and genetic distinctness of species, with few exceptions that show the need for additional work, and with the addition of three new species in the Cape Range area. As is typical of Australian camaenids, distributions of congeneric species are mutually exclusive, but in some cases close proximity is associated with contrasting habitats, such as gorge endemics versus the species on top of Cape Range. In sympatry, *Strepsitaurus rugus* (Cotton, 1951) and *Strepsitaurus williami* Solem, 1997 are separated by microhabitat. These local associations with habitat indicate that ecological differences, and not simply allopatric divergence, contribute to the lack of sympatry between closely related Australian camaenids.

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ADDITIONAL KEYWORDS: Cape Range – *COI* – barcoding – habitat – mtDNA – parapatry.

INTRODUCTION

The Camaenidae are taxonomically the dominant group of land snails in northern Australia. Although diverse in terms of numbers of species, a remarkable feature of this group is that sympatry of congeneric species is rare. Instead, species in the same genus have geographically exclusive ranges, although sympatry of species from different genera is common (Solem, 1988, 1997; Solem & McKenzie, 1991; Cameron, Pokryszko & Wells, 2005; Hugall & Stanisic, 2011; Gibson & Köhler, 2012). The scarcity of congeneric sympatry raises questions about the origins and maintenance of the geographical replacements, and means that direct tests of biological species are usually impossible. In both contexts, searches for contact zones are important. In the Western Australian genus *Rhagada* Albers, 1860, for example, sharp clines between distinct morphospecies are the result of selection between contrasting habitats in the Dampier Archipelago, with free interbreeding in the intermediate zone (Stankowski, 2011, 2013). In contrast, on the adjacent Pilbara mainland, there is hybridization in a narrow zone of secondary contact between the widely distributed coastal species *Rhagada*

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convicta (Cox, 1870) and a genetically divergent, undescribed inland form (Hamilton & Johnson, 2015). Although the spatial scales are very different, in both of these cases the different forms are associated with contrasting environments, suggesting that allopatric divergence alone does not explain their complementary distributions.

In this context, the Western Australian genera *Plectorhagada* Iredale, 1933 and *Strepsitaurus* Solem, 1997 are of special interest. *Strepsitaurus* is a possible exception to the absence of sympatry of congeneric species, as Solem (1997) recorded the co-occurrence of *Strepsitaurus rugus* (Cotton, 1951) and the smaller *Strepsitaurus williami* Solem, 1997 on the eastern side of the Cape Range, although this report included only shells of dead *S. williami*. The entire genus, comprising four described extant species, is found only in the Cape Range, including its southern extension into Ningaloo Station, so detailed sampling could reveal further contacts.

In addition, the relationships of the genera *Strepsitaurus* and *Plectorhagada* need testing with genetic comparisons. *Plectorhagada* has a much larger distribution, spanning about 500 km from the vicinity of Cape Range to southern Shark Bay, and from the coast to 160 km inland (Solem, 1997). Its four described species have disjunct geographical ranges. In the vicinity of Cape Range there is an apparent complementarity of the distribution of the two genera, with *Strepsitaurus* on Cape Range and *Plectorhagada scolythra* Solem, 1997 on the coastal strip adjacent to Cape Range (Fig. 1). Despite this proximity, species of the two genera have not been found in sympatry, a pattern more typical of species within genera. In addition to their complementary geographical distributions, species of both genera share several features. They are rock-sealing aestivators, with individuals of *Strepsitaurus* sealing themselves solely to rock faces, and with individuals of *Plectorhagada* sealing themselves to both rocks and other individuals. Despite anatomical differences between the genera, they share more similarities relative to other genera (Solem, 1997). In addition, shells of both genera have distinct crenulations of varying degrees. These are more pronounced and extensive in *Stepsitaurus*, but the shells of *Plectorhagada meilgana* Solem, 1997 are especially similar to *Strepsitaurus* in sculpture and angularity of the body whorl. Solem (1997) lacked live specimens of *P. meilgana*, so its placement within *Plectorhagada* is based only on shell features. The geographical relationships and morphological similarities between the two genera thus point to a need for molecular examination.

In this study, we combine more detailed geographical sampling with molecular genetic analysis to re-examine taxonomic and geographical relationships within and between *Plectorhagada* and *Strepsitaurus*, to answer questions at three levels. First, what are the relationships of the two genera? Are they phylogenetically distinct, or is *Stepsitaurus* simply a part of the more widely distributed *Plectorhagada*? Preliminary DNA sequencing indicated that the genera are very similar sister groups, but this was based on a few individuals and did not include all species (O'Neill *et al*., 2014). Second, are the morphologically described species distinct genetic and phylogenetic groups, and are there additional species? Third, do the distributions of the species meet, and if so, what is the nature of the contact zone? We also describe three new species from the Cape Range area.

MATERIAL AND METHODS

Samples

Samples of *Plectorhagada* (16 sites) and *Strepsitaurus* (28 sites) were collected between 2002 and 2010 (Fig. 1; Table 1). The samples include all described extant species. Sampling was more concentrated in the Cape Range area, in order to search for possible contacts between species. Most collections in the Cape Range were made during wet periods, when the snails were active. At each site, snails were collected in an area with a diameter of no more than 20 m. The collections included three sites where species were sympatric (where different labels were used for each species): site SRG/SWB for *S. rugus* and *S. williami*; sites PSH/SRN and PSI/SRO for *P. scolythra* and *Strepsitaurus ningaloo* Solem, 1997. For use as out-groups, samples were also obtained of all but one of the other camaenid genera in the region, as well as the more southern genus *Sinumelon* (Table 1). The missing genus is the rare, monotypic *Caperantrum polygyrum* Solem, 1997, an endemic of the Cape Range. Except for *C. polygyrum*, the out-group includes all described Western Australian genera of the subfamily Sinumeloninae, which includes *Plectorhagada* and *Strepsitaurus* (Solem, 1997; Hugall & Stanisic, 2011; O'Neill *et al*., 2014). All specimens were held at −80 °C prior to DNA extraction.

Molecular analysis

DNA was extracted from foot tissue using the QIAGEN DNeasy blood and tissue extraction kit protocol. Where possible, two specimens from each sampling site were used (54 snails from 28 sites for *Strepsitaurus* and 19 snails from 13 sites for *Plectorhagda*). Polymerase chain reaction (PCR) was used to amplify partial sequences of the mitochondrial genes cytochrome *c* oxidase subunit I (*COI*) and *16S* rRNA, using the primers LCO1490 and HCO2198 of Folmer *et al*. (1994) for *COI*, and the primers of Palumbi *et al*. (1991) for *16S*. PCR reactions were performed in 25-μL volumes: 10 μL (for *16S*; 9 μL for *COI*) of sterile distilled water, 5 μL of

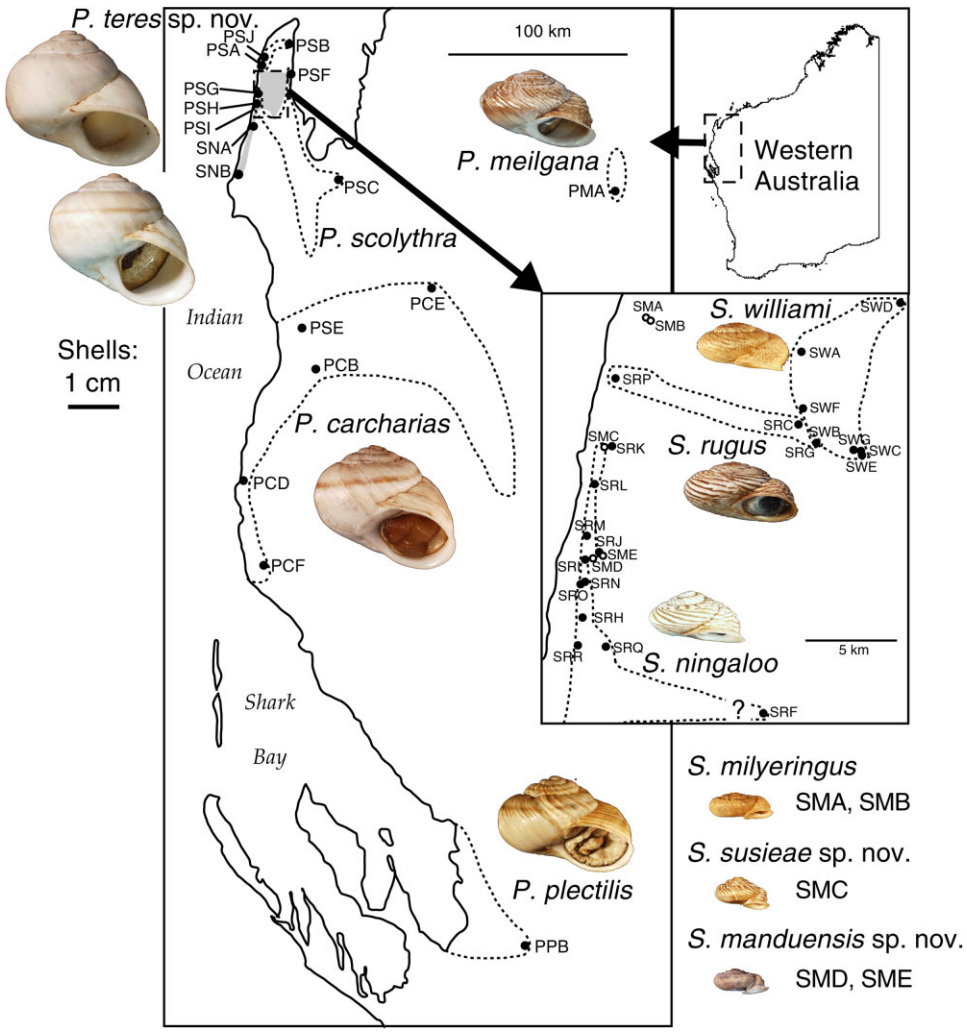

Figure 1. Sample sites for *Plectorhagada* and *Strepsitaurus*. Large map (between North West Cape and Cape Range in the north and Shark Bay in the south) shows sites for *Plectorhagada* and southernmost sample sites of *Strepsitaurus ningaloo* (SNA, SNB). The shaded area is the known distribution of *Strepsitaurus.* The expanded map shows central Cape Range, with the sample sites of *Strepsiaurus.* Dotted lines indicate recorded distributions of species, based on Solem (1997). Open circles indicate sites for species restricted to gorges on the western side of the Cape Range, the shells of which are shown in the lower right corner. Site codes as described in Table 1.

5× PCR buffer, 1.3 μL (for *16S*; 2.3 μL for *COI*) of 50 mM magnesium chloride, 3.75 μL of 2 μM primer, 0.2 μL of *Taq* polymerase, and 1 μL of DNA. PCR included an initial denaturation step of 94 °C for 2 min, a denaturation step of 94 °C for 30 s, an annealing step of 51 °C for 45 s, an extension step of 72 °C for 1 min, and a final extension step of 72 °C for 5 min. All steps except the initial denaturation and final extension were run for 40 cycles. Sequencing was performed by the Sanger method using Big Dye chemistry, using an ABI3730 96-capillary sequencing machine at the State Agricultural Biotechnology Centre, Murdoch University, Western Australia. Sequences were edited and aligned using SEQUENCHER 4.6 (Gene Codes Corporation). Sequences not previously reported by O'Neill *et al*. (2014) have been deposited in GenBank (accession numbers KP182177–KP182345).

Phylogenetic analysis was based on concatenated sequences of *COI* (484 bp) and *16S* (353 bp), using both maximum-likelihood (ML) and Bayesian methods. The appropriate model of evolution was the Tamura three-parameter model, as determined in MEGA 5 (Tamura *et al*., 2011), and this was used in calculation of genetic p-distances and in phylogenetic analyses. The ML tree was calculated in MEGA 5, with 1000 bootstrap pseudoreplicates to measure nodal support. Bayesian analysis was conducted using MrBayes 3.2.0 (Ronquist & Huelsenbeck, 2003).

Table 1. Site information for samples of *Plectorhagada* (*P.*), *Strepsitaurus* (*S.*), and the out-groups *Falspleuroxia* (*F*), *Pleuroxia* (*Pl.*), *Promonturconchum* (*Pr.*), *Sinumelon* (*Si.*), *Quistrachia* (*Q.*), and *Rhagada* (*R.*)

Code	Species	Latitude, S	Longitude, E
PCF	*P. carcharias*	24°25′56.8″	113°29′49.3″
PCB	*P. carcharias*	23°32′04.5″	113°57′49.7″
PCD	*P. carcharias*	23°27′55.8″	113°47′31.5″
PSE	*P. carcharias*	23°19′16.3″	113°55′56.2″
PCE	*P. carcharias*	23°14′52.1″	114°27′34.6″
PMA	*P. meilgana*	22°55′59.0″	115°42′26.4″
PPB	*P. plectilis*	26°30′08.9″	114°29′51.6″
PSC	*P. scolythra*	22°37′55.4″	114°15′38.5″
PSD	*P. scolythra*	22°34′33.0″	114°10′07.0″
PSH	*P. scolythra*	22°09′42.7″	113°52′45.4″
PSI	*P. scolythra*	22°09′39.4″	113°52′54.2″
PSG	*P. scolythra*	22°06′50.5″	113°53′35.3″
PSF	*P. scolythra*	22°03′51.1″	114°06′13.8″
PSA	***P. teres* sp. nov.**	21°59′18.6″	113°57′13.1″
PSJ	***P. teres* sp. nov.**	21°58′16.6″	113°57′11.1″
PSB	***P. teres* sp. nov.**	21°54′42.7″	114°07′12.0″
SMD	***S. manduensis* sp. nov.**	22°08′59.7″	113°53′14.7″
SME	***S. manduensis* sp. nov.**	22°08′54.6″	113°53′33.4″
SMB	*S. milyeringus*	22°02′13.0″	113°56′07.0″
SMA	*S. milyeringus*	22°02′06.5″	113°56′00.0″
SRM	*S. ningaloo*	22°08′18.6″	113°53′09.0″
SRI	*S. ningaloo*	22°09′01.5″	113°52′59.7″
SRR	*S. ningaloo*	22°11′31.7″	113°52′22.9″
SRJ	*S. ningaloo*	22°08′51.8″	113°53′30.1″
SNB	*S. ningaloo*	22°32′51.6″	113°42′57.2″
SRL	*S. ningaloo*	22°06′49.2″	113°53′37.2″
SRK	*S. ningaloo*	22°05′44.6″	113°54′06.9″
SNA	*S. ningaloo*	22°19′44.5″	113°49′23.3″
SRH	*S. ningaloo*	22°10′43.4″	113°52′40.0″
SRN	*S. ningaloo*	22°09′42.7″	113°52′45.4″
SRO	*S. ningaloo*	22°09′39.4″	113°52′54.2″
SRQ	*S. ningaloo*	22°11′40.0″	113°52′18.4″
SRF	*S. ningaloo*?	22°14′16.1″	113°58′01.3″
SRG	*S. rugus*	22°06′31.8″	114°00′52.1
SRC	*S. rugus*	22°05′55.1″	114°00′22.7″
SRP	*S. rugus*	22°03′46.5″	113°54′45.6″
SMC	***S. susieae* sp. nov.**	22°05′46.7″	113°54′19.6″
SWE	*S. williami*	22°07′01.3″	114°02′26.0″
SWB	*S. williami*	22°06′31.8″	114°00′52.1
SWF	*S. williami*	22°05′27.2″	114°00′35.8″
SWC	*S. williami*	22°06′52.8″	114°02′01.4″
SWA	*S. williami*	22°03′45.9″	114°00′47.0″
SWD	*S. williami*	22°02′40.9″	114°04′09.5″
SWG	*S. williami*	22°06′57.0″	114°02′15.2″
FOA	*F. overlanderensis*	26°30′08.9″	114°29′51.6″
FOB	*F. overlanderensis*	26°24′36.8″	114°27′52.8″
PlEB	*Pl. elfina*	32°07′36.4″	126°20′32.7″
PlEA	*Pl. elfina*	31°57′57.6″	125°55′02.6″
PrSB	*Pr. superbum*	22°10′43.4″	113°52′40.0″
PrSC	*Pr. superbum*	22°09′01.5″	113°52′59.7″
PrSA	*Pr. superbum*	22°05′55.1″	114°00′22.7″
Qu503	*Q. herberti*	21°19′35.8″	117°12′55.9″
Qu512	*Q. montebelloensis*	20°57′57.2″	115°20′00.6″
Qu518	*Q. montebelloensis*	20°20′31.6″	115°31′55.6″
PCA1	*Q. warroorana*	24°01′21.1″	113°27′34.9″
R427	*R. convicta*	20°41″34.0″	116°53′40.0″
PSD1	*R. convicta*	22°34′40.8″	114°10′07.0″
SiNA	*Si. nullarboricum*	33°03′10.0″	123°23′00.7″
SiVA	*Si. vagente*	29°18′00.0″	116°41′00.0″
SiVB	*Si. vagente*	29°11′48.0″	116°30′53.0″

Species listed alphabetically within genera; sites listed fromnorth to south within species.

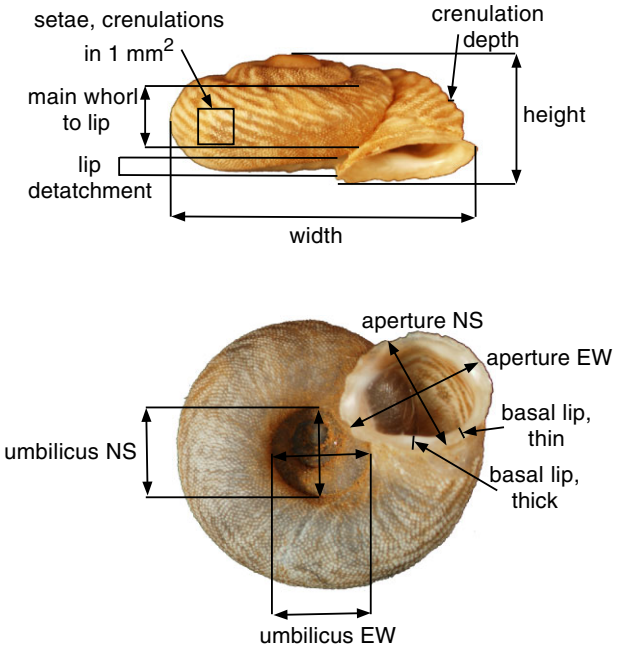

Figure 2. Frontal and basal views of a specimen of *Strepsitaurus milyeringus*, showing shell measurements. Whorls were counted in apical view (not shown).

Morphological analysis

The variation of shell morphology was examined to determine the distinctiveness of groups detected by the molecular analyses, with particular attention paid to relationships between undescribed forms. When available, five shells per site were photographed in three views using an Olympus SZ61 dissecting microscope: frontal, perpendicular to the columella, with the aperture facing the camera, including maximum width of the shell; apical, with the apex facing the camera; and basal, with the umbilicus facing the camera. Only adult shells were included, recognized by the presence of a reflected lip.

Images of snails were measured using ImageJ 1.43u (Abramoff, Magelhaes & Ram, 2004) for characters used previously to allocate species groups, and which best encompass the observed variation (Fig. 2): (1) height, the distance from the top of the apex to the bottom of the aperture, parallel with the columella; (2) main whorl to lip, the distance between the top of the main body whorl to the insertion of the aperture lip to the main body whorl; (3) lip detachment, the distance from the aperture lip to the main body whorl in cases where there is no fusion of the aperture lip onto the rest of the shell; (4) band thickness, the thickness of any distinct pigmented spiral band present on the main body whorl; (5) setae, the number of setae present within a 1-mm^2 area on the body whorl; (6) degree of crenulation, the number of distinct crenulations present within

a 1-mm^2 area; (7) crenulation depth, the distance between the top and bottom of a crenulation; (8) width, the maximum diameter of the shell; (9) whorl count, with the protoconch included as the first whorl; (10) umbilicus EW and (11) umbilicus NS, the distance across the umbilicus from left to right, and from top to bottom, respectively (see Fig. 2); (12) aperture EW, the distance across the aperture from the basal lip to the opposite lip; (13) aperture NS, the distance across the aperture from the cessation of the parietal lip to the opposite lip; and (14) basal lip ratio, calculated by dividing the thickest part of the basal lip by the thinnest part. All distance measures were taken in mm.

To summarize patterns of variation without prior assignment to groups, shell measurements were subjected to principal component analysis with the program XLSTAT (Addinsoft). To determine the level and pattern of distinctiveness of species, discriminant analysis of these quantitative traits was carried out using XLSTAT. To test the effectiveness of discriminant classifications, a group of specimens was omitted from the calculation of the discriminant functions, forming a test group. The test group included one individual from each site with at least three specimens. In addition to these quantitative analyses, the qualitative traits used in Solem's (1997) classification were examined.

RESULTS

Molecular comparisons

The combined sequences of *COI* and *16S* revealed 66 haplotypes among the 74 individuals examined from *Plectorhagada* and *Strepsitaurus*. Of the 837 bp sequenced 215 were variable, 190 of which were parsimony informative. Both ML and Bayesian phylogenetic analyses with the out-groups confirmed *Plectorhagada* and *Strepsitaurus* as closely related sister groups within the Sinumeloninae, with the divergence between the two genera being less than that among some species within the genus *Quistrachia* (Fig. 3).

With few exceptions, the haplotypes of each of the currently recognized species formed monophyletic groups, but our samples also included new, highly distinct lineages. Within *Plectorhagada*, a partial exception to monophyletic species was between *Plectorhagada carcharias* (Pfeiffer, 1864) and *P. scolythra*. Most specimens indicated two closely related sister species, but the specimen of *P. carcharias* from the inland site PCE lay outside the pair, making *P. scolythra* paraphyletic (Fig. 3). More importantly, the most distinctive lineage within *Plectorhagada* included sites PSA, PSB, and PSJ, indicating a new species at the previously unsampled northern end of Cape Range.

New species were also evident in *Strepsitaurus*, where undescribed, highly divergent lineages were found in two gorges on the western side of Cape Range: (1) site SMC in a small gorge south of Tulki Gorge; (2) sites SMD and SME in Mandu Mandu Gorge. These two forms were not closely related to *Strepsitaurus milyeringus* Solem, 1997, the described species known only from the more northern Milyering Gorge. Instead, *S. milyeringus* was a sister species to *S. williami*, from the eastern side of Cape Range. A parallel relationship was seen in the other northern species, *S. rugus*, in which the eastern and western populations were as distinct as *S. williami* and *S. milyeringus*. The more widespread southern and western species, *S. ningaloo*, formed a monophyletic group. The only ambiguous relationships were those of site SRF, from the south-central region of Cape Range.

Pairwise genetic distances were calculated separately for *COI* and *16S*, with a correlation of 0.828 between the two genes. The slope of the regression of *16S* distance on *COI* distance was 0.315, indicating the greater sensitivity of *COI*. The frequency distribution of *COI* p-distances showed distinct valleys at about 3.5 and 11% (Fig. 4). Distances exceeded 12% in all comparisons between *Plectorhagada* and *Strepsitaurus*, but differences that large were also common between congeneric species. These large congeneric distances involved *P. meilgana* and the newly discovered species in both genera. For the remaining species, there was a clear bimodality of congeneric genetic distances, corresponding almost completely with comparisons within or between species. All distances within species were less than 4%, except those involving the western (site SRP) and eastern (sites SRC and SRG) samples of *S. rugus*. The few interspecific comparisons with distances <4% involved *P. carcharias* with *P. scolythra*, as well as comparisons between *S. ningaloo* and the phylogenetically ambiguous specimens from site SRF.

Morphological comparisons

Principal component analyses were performed separately for the two genera, which the mitochondrial DNA (mtDNA) analysis had shown to be monophyletic groups. In *Plectorhagada*, four axes had eigenvalues greater than 1, accounting for 83% of the total variation (Table 2). The first component (PC1, 45.1% of total variation) had moderate to strong loadings by most traits, representing primarily size, but with moderate negative loadings by the degree of sculpturing and the size of the umbilicus. The combination of PC1 with PC2 (18.8%), which also represented the extent of crenulation (negative) and size of the umbilicus (positive), illustrated substantial variation within *P. carcharias* and *P. scolythra*, but with little overlap of these species or *P. meilgana* and *Plectorhagada plectilis* (Benson, 1853) (Fig. 5). Despite its large genetic distance, the new species, *Plectorhagada teres* sp. nov., was morphologically within

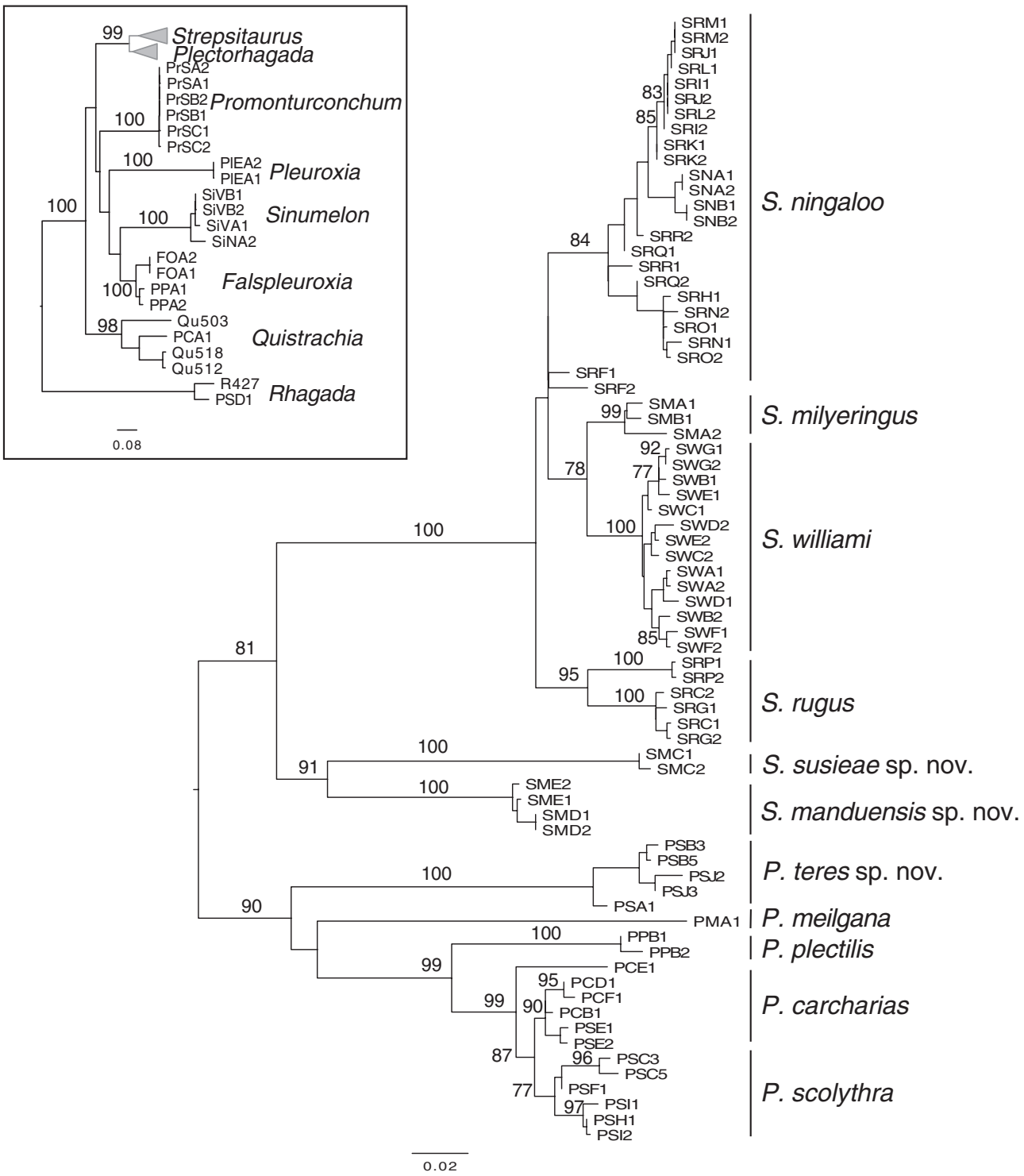

Figure 3. Maximum-likelihood (ML) tree for *Plectorhagada* and *Strepsitaurus* based on concatenated sequences of *COI* and *16S*. Inset shows relationships with the out-groups. Numbers indicate bootstrap support for the ML tree, all of which were less than or equal to the posterior probabilities from the Bayesian analysis.

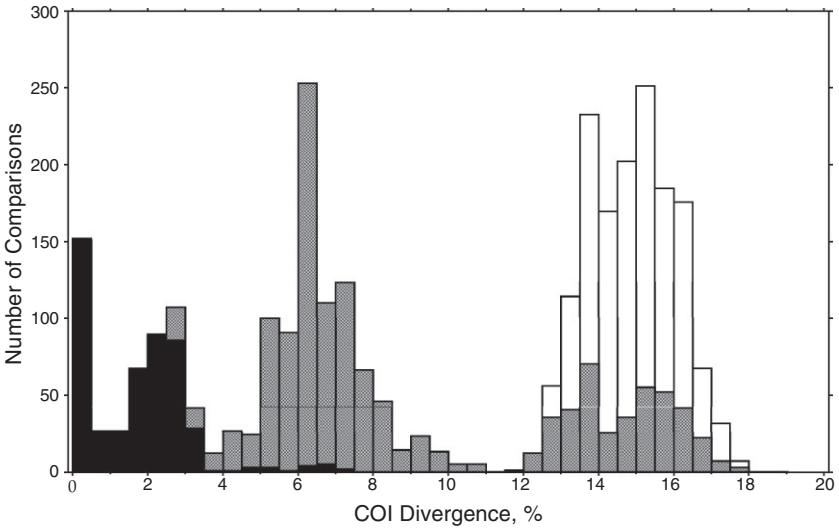

Figure 4. Frequency distribution of genetic p-distances for *COI* in *Plectorhagada* and *Strepsitaurus*; white, comparisons between genera; grey, comparisons between congeneric species; black, comparisons within species.

Table 2. Correlations of shell variables with principal components in *Plectorhagada*

Trait	PC1 (45.1%)	PC2 (18.8%)	F3 (10.0%)	F4 (9.9%)
Height	0.725	0.378	−0.314	0.361
Whorl to lip	0.883	−0.109	0.142	−0.267
Band thickness	−0.007	0.221	0.744	0.555
Crenulation degree	−0.437	−0.634	0.125	0.393
Crenulation depth	−0.619	−0.574	0.032	−0.114
Width	0.842	−0.158	0.204	−0.299
Whorl count	0.664	0.133	0.331	0.012
Umbilicus EW	−0.612	0.637	0.249	−0.241
Umbilicus NS	−0.657	0.603	0.199	−0.303
Aperture EW	0.698	−0.411	0.344	−0.259
Aperture NS	0.795	0.388	−0.210	0.197

Numbers in brackets indicate percent of total variance represented by each component.

the range of *P. scolythra*, although their separation was greater with the inclusion of PC3 (10.0%), representing mainly the size of the shell band (Fig. 5). PC4 did not help to resolve the species.

To clarify differences of the new species from *P. carcharias* and *P. scolythra*, discriminant analysis was performed on just these three species (Fig. 6; Table 3). For each species, one individual from each of three sites was excluded from the calculation of the discriminant functions, and these specimens were used to test the classifications. The species were largely separated on the basis of size and the degree of banding, but there was still some overlap between *P. scolythra* and *P. teres* sp. nov. The discriminant functions correctly classified all 17 *P. carcharias* and all 15 *P. teres* sp. nov.; however, four of 18 *P. scolythra* were identified by their shells as *P. teres* sp. nov. These included three specimens used in the calculation of the discriminant functions, highlighting the morphological similarity of these genetically highly divergent forms.

In the analysis of shells of *Strepsitaurus*, three principal components had eigenvalues greater than 1 (Table 4). The first two components separated the species into two distinct groups. Despite their large genetic distances, the three small endemics of gorges on the western side of Cape Range formed a relatively tight group, based on their small shells with detached lips and large umbilici, whereas the three larger, more broadly distributed species formed a more variable group (Fig. 7). PC1, representing 51.2% of the total variation, was a general size factor, but with strong negative loadings of the size of the umbilicus and lip detachment, and was the major separator of the two groups of species. Within each of these groups, there

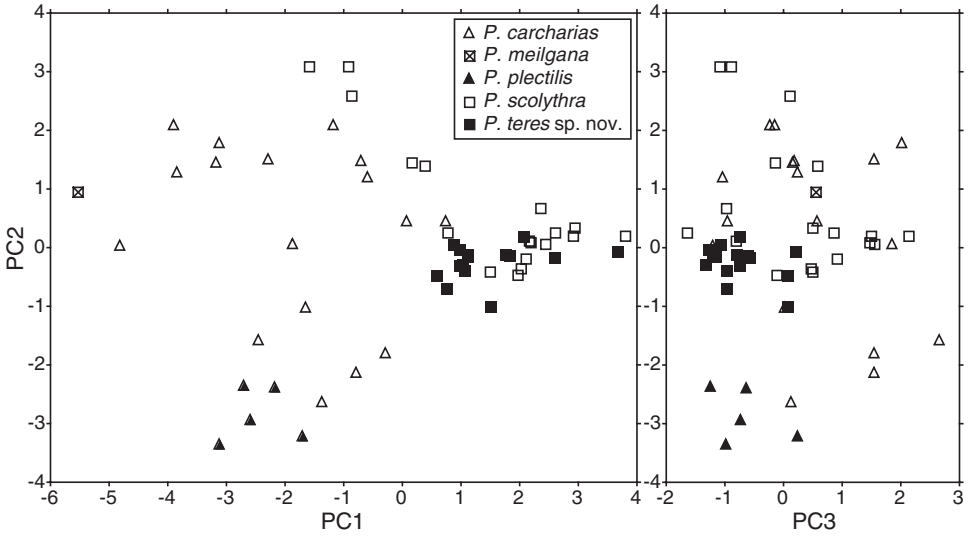

Figure 5. Scores on the first three principal components for shell morphology in *Plectorhagada*.

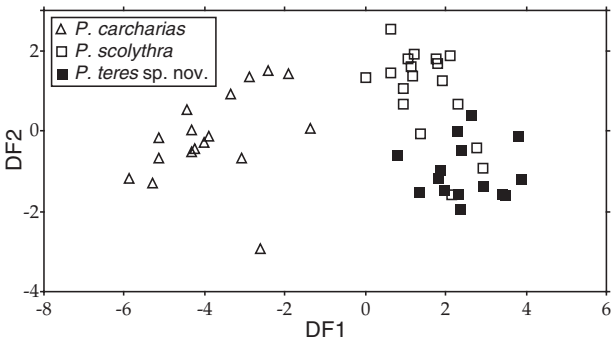

Figure 6. Scores on discriminant functions of shell traits among *Plectorhagada carcharias*, *Plectorhagada scolythra*, and ***Plectorhagada teres* sp. nov.**

Table 3. Correlations of shell variables with discriminant functions among *Plectorhagada carcharias*, *Plectorhagada scolythra*, and ***Plectorhagada teres* sp. nov.**

	DF1	DF2
Height	0.603	0.402
Whorl to lip	0.747	0.080
Band thickness	−0.527	0.576
Crenulation degree	−0.482	−0.160
Crenulation depth	−0.613	−0.094
Width	0.760	0.082
Whorl count	0.254	0.445
Umbilicus EW	−0.436	0.312
Umbilicus NS	−0.438	0.261
Aperture EW	0.491	0.190
Aperture NS	0.756	0.402

Table 4. Correlations of shell variables with principal components in *Strepsitaurus*

Trait	PC1 (51.2%)	PC2 (13.9%)	PC3 (11.1%)
Height	0.690	0.078	−0.518
Whorl to lip	0.901	0.032	0.245
Setae	0.066	0.777	−0.363
Crenulation degree	0.312	−0.323	0.235
Crenulation depth	0.610	−0.649	0.187
Width	0.893	0.168	0.290
Whorl count	0.723	0.328	0.391
Umbilicus EW	−0.835	0.374	0.166
Umbilicus NS	−0.829	0.298	0.280
Aperture EW	0.915	0.019	0.234
Aperture NS	0.893	0.162	−0.306
Basal lip ratio	−0.151	0.426	0.634
Lip detachment	−0.730	−0.599	0.060

Numbers in brackets indicate percent of total variance represented by each component.

was a negative association between PC1 and PC2, with the latter having a strong correlation with the number of setae and negative loadings from crenulation depth and lip detachment (Fig. 7; Table 4). Whereas the three small gorge-endemics were distinguishable on the basis of PC1 and PC2, the species in the other group showed overlap. Variation in *S. ningaloo* was substantial, overlapping that of *S. williami* and totally encompassing that of *S. rugus*. The phylogenetically ambiguous sample from site SRF was in the middle range of variation in *S. ningaloo*. Despite some overlap between *S. rugus* and *S. williami*, the two species were well separated

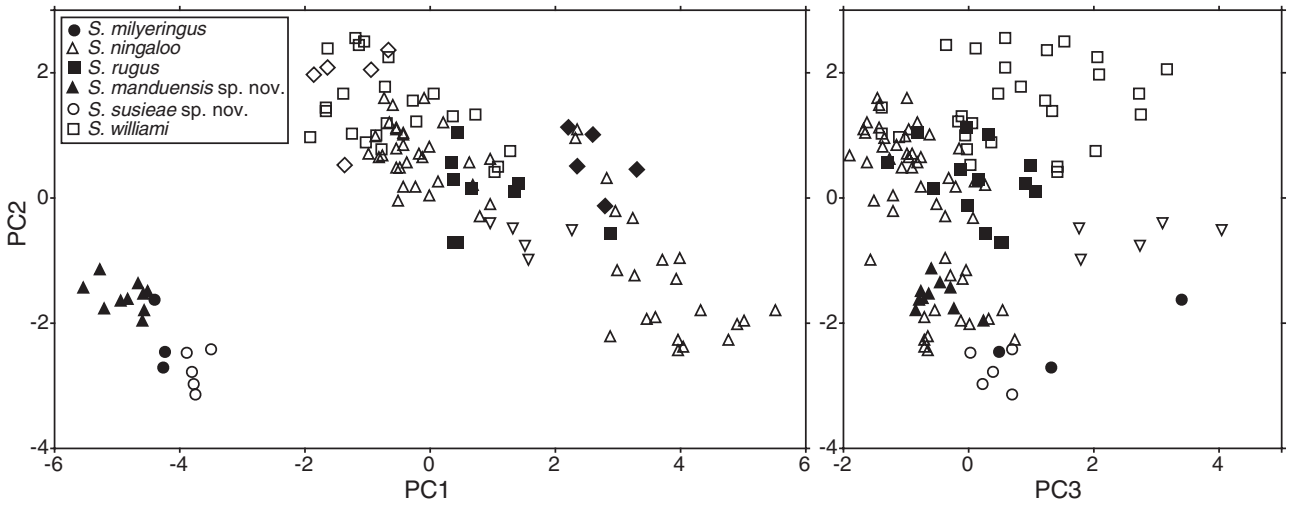

Figure 7. Scores on the first three principal components for shell morphology in *Strepsitaurus*. Putative *Strepsitaurus ningaloo* from site SNF are indicated by inverted triangles. In the left-hand plot, symbols of sympatric *Strepsitaurus rugus* and *Strepsitaurus williami* (site SRG/SWB) are rotated by 45° to highlight the distinctiveness of the two species.

Table 5. Correlations of shell variables with discriminant functions among *Strepsitaurus ningaloo*, *Strepsitaurus rugus*, and *Strepsitaurus williami*

	DF1	DF2
Height	0.409	0.521
Whorl to lip	0.272	–0.175
Setae	–0.163	–0.342
Crenulation degree	0.516	–0.278
Crenulation depth	0.427	0.179
Width	0.413	–0.277
Whorl count	–0.188	–0.303
Umbilicus EW	–0.606	–0.045
Umbilicus NS	–0.624	0.108
Aperture EW	0.499	–0.183
Aperture NS	0.659	0.290
Basal lip ratio	–0.781	0.020

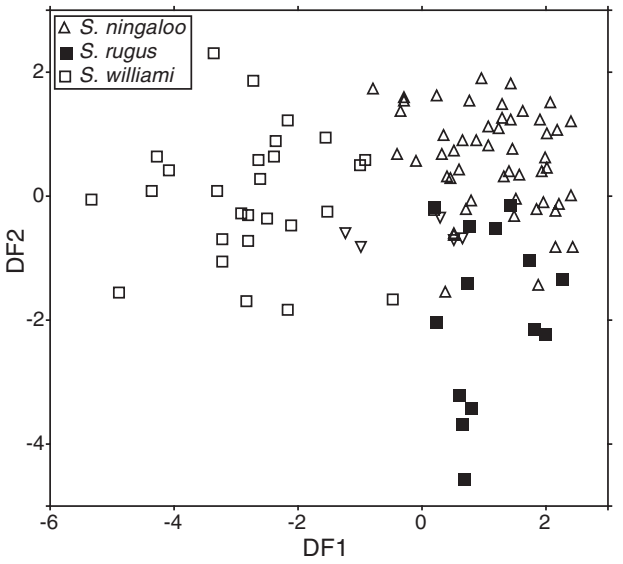

Figure 8. Scores on discriminant functions of shell traits among *Strepsitaurus ningaloo*, *Strepsitaurus rugus*, and *Strepsitaurus williami*. Putative *S. ningaloo* from site SNF are indicated by inverted triangles.

morphologically at the sympatric site SRG/SWB, showing no evidence of interbreeding (Fig. 7). The inclusion of PC3 illustrated the distinctiveness of *S. williami*, with its relatively flat shells, but did not further separate *S. rugus* and *S. ningaloo* (Fig. 7; Table 4). PC3 also separated the sample from site SRF from both *S. ningaloo* and *S. rugus*.

To examine more closely possible differences amongst the three larger species, we performed discriminant analysis within that group, excluding the already clearly defined small gorge-endemics (Fig. 8; Table 5). For this analysis, the five specimens from site SNF, plus one specimen from each other site with at least three individuals (ten *S. ningaloo*, three *S. rugus*, and five *S. williami*) were excluded from the calculation of discriminant functions, and were used to test the effectiveness of classification. All 74 specimens used directly in the discriminant analysis were correctly assigned to species, as were the tested specimens of *S. ningaloo*, including those from site SNF; however, one of five tested *S. williami* was misclassified as *S. ningaloo*, and all three of the tested *S. rugus* were misclassified, two as *S. ningaloo* and one as *S. williami*.

DISCUSSION

Taxonomic relationships

The molecular analyses presented here largely corroborate Solem's (1997) morphological taxonomy of *Plectorhagada* and *Strepsitaurus*, while also revealing three new species and expanding our geographical understanding of each genus. The mtDNA sequences confirm the monophyly of each genus. Although the two genera are phylogenetically distinct, they are very similar sister taxa, with low *COI* difference compared with other pairs of genera of Western Australian camaenids (Criscione & Köhler, 2013; O'Neill *et al*., 2014). Indeed, the p-distances between *Plectorhagada* and *Strepsitaurus* lie within the range seen between congeneric species of *Quistrachia* and *Rhagada* (Johnson *et al*., 2012; O'Neill *et al*., 2014) in the Pilbara region, and *Amplirhagada*, *Exiligada*, and *Nanotrachia* in the Kimberley (Criscione, Law & Köhler, 2012; Köhler & Johnson, 2012; Köhler & Criscione, 2013). Even within *Plectorhagada* and *Strepsitaurus*, some p-distances between congeneric species are as high as those between the two genera, highlighting the close relationship of these genera.

Within genera, the mtDNA sequences indicate that Solem's (1997) species are generally monophyletic, but with some complications. In *Plectorhagada*, the reciprocal monophyly of the similar *P. carcharias* and *P. scolythra* is incomplete, as the most inland specimen of *P. carcharias* examined lies outside the otherwise pair of sister species. The relatively large geographical distribution of the morphologically variable *P. carcharias*, combined with this genetic outlier, raises the possibility that further sampling inland might reveal a species complex. Indeed, Solem (1997) recognized this possibility, but the general lack of live specimens from the inland areas makes testing difficult. In *Strepsitaurus*, the phylogenetically unresolved issue is the placement of specimens from the top of Cape Range at site SRF, an area considered by Solem (1997) to include *S. rugus*.

Supporting the phylogenetic evidence, the distribution of p-distances for *COI* shows a clear gap between the described species at about 3.5%, with few exceptions. This quantitative correspondence with Solem's (1997) morphologically defined species indicates the usefulness of barcoding for identifying likely new species in these genera. The distribution of genetic distances in *Plectorhagada* and *Strepsitaurus* also highlights that species thresholds vary among the Western Australian genera of camaenids. The gap at 3.5% is in the range seen in *Exiligada* in the north-east Kimberley region (Criscione *et al*., 2012), and lower than the *COI* threshold of about 6% corresponding with distinctive genitalia in *Amplirhagada* from western Kimberley islands (Köhler & Johnson, 2012). Higher still is the gap at about 10% between morphologically defined species of *Quistrachia* (O'Neill *et al*., 2014). Such levels of variation are typical among genera of land snails (Davison, Blackie & Scothern, 2009). Thus, although useful barcoding thresholds may apply within genera, the actual levels cannot be extrapolated across genera.

In the present study, the maintenance of the distinctness of *S. rugus* and *S. williami* in sympatry provides direct evidence for reproductive isolation, although their average p-distance of 6.9% is well above the apparent species threshold of 3.5%. Interspecific distances below this threshold are the smallest values between *P. carcharias* and *P. scolythra*, which have an average p-distance for *COI* of 3.8%. Although the disjunct distributions of these species preclude direct evidence of reproductive isolation, the two species are distinct in their shells and penial anatomies. Also within this lower range of genetic divergence are the comparisons between *S. ningaloo* and the phylogenetically unresolved specimens from site SRF, at Central Hill. Solem (1997) included snails from this area in *S. rugus*, but also suggested that *S. rugus* might include a complex of species. Our specimens from site SRF have an average *COI* p-distance of 6.4% from *S. rugus*, and only 3.4% from *S. ningaloo*, favouring the provisional inclusion of the SRF population with *S. ningaloo*. More extensive sampling in this area is needed to resolve this issue with confidence. The other question arising from our findings comes from relatively high intraspecific p-distances between the western and eastern populations of *S. rugus*. It may well be that these represent sister species, as both the average p-distances and the phylogeny parallel the split between *S. milyeringus* (west) and *S. williami* (east); however, we take the conservative approach of provisionally including the western population (site SRP) within *S. rugus*. The resolution of this issue will require sampling in the 8-km gap separating these populations, but the relatively inaccessible and rough terrain across the Cape Range area makes sampling difficult.

Geographical relationships

Our increased sampling in the Cape Range area highlights the replacement of species both geographically and at a local level. The complementarity of distributions of *Plectorhagada* and *Strepsitaurus* is closer than was recognized by Solem (1997), who lacked samples from the western and northern sides of the range. The finding of *P. scolythra* on the western edge and *P. teres* sp. nov. in the north shows that the distribution of *Strepsitaurus* is completely encircled by that of *Plectorhagada*. On its western side, the Cape Range descends as a series of uplifted marine terraces, towards the sandy coastal strip (Wyrwoll, Kendrick & Long, 1993). *Stepsitaurus* is associated with the rocky Cape Range, including gorges and terraces, whereas

Plectorhagada is associated with mixed sandy and rocky habitats, which are largely restricted here to the coastal margins. The two genera meet on the western side, where the rocky terraces give way to the sandier habitat. We found sympatric populations along this boundary area (sites PSN/SRN and PSI/SRO), but not broad overlap. Indeed, the association with habitat was highlighted by sites PSG (west of the terrace, with *P. scolythra* only) and SRL (on the terrace, with *S. ningaloo* only), which are only 50 m apart. This contrast is associated with differences in aestivation behaviour. Species of *Plectorhagada* typically aestivate attached to other shells, forming chains that lie loose in the litter or rubble, whereas species of *Strepsitaurus* aestivate attached to rocks (Solem, 1997).

Although geographical replacements are the norm for congeneric species of camaenids in northern Australia, we know of no other examples of such close geographical replacement of genera. The extremely close relationship of the two genera may well make their geographical relationships more akin to those within other genera. For example, in *Rhagada*, the most species-rich camaenid genus in the Pilbara region, there are few exceptions to lack of sympatric species, but the three known zones of overlap involve highly divergent species. Two of these are on the Burrup Peninsula, where the distribution of an undescribed local endemic species overlaps slightly with *R. convicta* in the south and with *R. angulata* in the north, without hybridization (Stankowski & Johnson, 2014). The third example is between mainland *R. convicta* and an undescribed species, which have an overlap zone of 1–4 km, with some hybridization (Hamilton & Johnson, 2015). In these three cases, average *COI* p-distances are 17–19%, higher than that between *Plectorhagada* and *Strepsitaurus*.

It is not clear whether the overlapping species of *Rhagada* are segregated by microhabitat where they co-occur, but such segregation is evident in *Strepsitaurus*. Our samples included one site (SRG/SWB) spanning 15 m, with both *S. rugus* and *S. williami*; however, the two species were not syntopic, but were separated by microhabitat. The site includes a steep-sided ravine, and all ten *S. williami* were found on a vertical rock face of 2 m in height, whereas one *S. rugus* was found on the floor of the ravine and the other 21 were found on the adjacent, relatively flat area above the ravine. This local separation parallels the broader contrasts between these species, whereby *S. rugus* is associated with the top of the Cape Range and *S. williami* is associated with the canyons. Although not seen on such a fine scale, a similar association occurs on the western side of the range, where the three small species *S. milyeringus*, *Strepsitaurus susieae* sp. nov., and *Strepsitaurus manduensis* sp. nov. are known only from the south-facing walls of steep-sided gorges, whereas *S. rugus* in the north and *S. ningaloo* in the south are found on the top of the range or on the terraces. At Mandu Mandu Gorge, our samples of *S. ningaloo* above the gorge were 920 m apart, and our samples of *S. manduensis* sp. nov. on the vertical face of the gorge were 560 m apart, but samples of the two species were within 130 m of each other. The consistent small size, low spire, and detached lip of *S. milyeringus*, *S. susieae* sp. nov., and *S. manduensis* sp. nov. indicate specialization to the rock-face habitat, and each of these species is known from a single gorge. There are numerous isolated gorges on the western face of the Cape Range, and it may well be that other gorge-endemics remain to be found.

The general inference that can be made from the complementary distributions in the Cape Range is that they are not simply the result of allopatric divergence without subsequent contact. The strictly allopatric scenario is presumably the basis of the many geographically disjunct species (Solem, 1997; Stanisic *et al*., 2010; O'Neill *et al*., 2014), and fits the broader geographical replacement of disjunct species of *Plectorhagada*. It does not apply to the species of *Plectorhagada* and *Strepsitaurus* in the Cape Range area, however, where the proximity of species is close, so isolation cannot explain the scarcity of sympatry. Instead, there are clear associations with habitat, indicating predominantly ecological mechanisms. This parallels two examples of contact zones between morphologically divergent forms of *Rhagada*. In the Dampier Archipelago, sharp changes between the most divergent morphotypes in the genus are the direct result of selection associated with steep gradients between rocky and sandy habitats (Stankowski, 2011, 2013), whereas on a broader scale the widespread *R. convicta* of the sandy coastal plain has a narrow hybrid zone with an undescribed species from the rockier interior (Hamilton & Johnson, 2015). Whether the lack of expansion of distributions partly results from competitive exclusion is uncertain, and would require experimental testing. Nevertheless, our findings for *Plectorhagada* and *Strepsitaurus* add to the few examples in *Rhagada*, in showing that the lack of congeneric sympatry in Western Australian camaenids is not simply the result of geographical isolation.

SYSTEMATICS

GASTROPODA

STYLOMMATOPHORA

CAMAENIDAE

PILSBRY, 1965

PLECTORHAGADA IREDALE, 1933

Plectorhagada Iredale, 1933: 52; 1938: 113; 1939: 69–71; Burch, 1976: 136; Solem, 1997: 1575–1611.

Type species
Helix plectilis Benson, 1853, by original description.

Diagnosis
Shell medium sized, variable (adult diameter, *D* = 10.9–22.0 mm; height, *H* = 4.9–18.3 mm), between 3 3/4 and 5 7/8 whorls. Spire very low to very high (*H/D* = 0.45–0.99). Apical sculpture with dense to scattered, often elongated micropustules, sometimes arranged in radial rows. At least the upper spire with prominent crenulated ridges (except *P. teres* sp. nov.). Body whorl rounded (except angulated in *P. meilgana*). Umbilicus closed or a narrow lateral crack in the most globose species (*P. carcharias*, *P. plectilis*, *P. scolythra*, and *P. teres* sp. nov.), narrowly open in *Plectorhagada rovina* Iredale, 1939 and *P. meilgana*, widely open in *Plectorhagada gascoynensis* (Smith, 1894). Palatal and basal lips narrowly to moderately reflected and expanded, columellar lip usually wider. Parietal wall callus varying from thin to thick and elevated, lip edge always appressed to parietal wall if thickened. Where known, shell colour light brownish or yellowish suffusion, often with a narrow reddish brown spiral supraperipheral band. Lip white. Genitalia with slightly to greatly enlarged albumen gland. Vagina short to very short, free oviduct and shaft of spermatheca twisted around each other, head of spermatheca reaching just above base of prostate–uterus. Epiphallic caecum either absent or a small knob. Vas deferens very slender, entering directly into slightly expanded head of epiphallus. Epiphallus not circling penial retractor muscle, which inserts in an arc at the point where the epiphallus enters the penis through a simple pore. Penis globular to somewhat elongated, without an identifiable sheath.

Distribution
Species of *Plectorhagada* range from near the southern tip of Shark Bay, north to the northern edge of the Cape Range along the coast, and up to 160 km inland, as far north as Meilga and Glen Florrie Stations, Western Australia.

PLECTORHAGADA TERES SP. NOV.

FIGURES 1, 3, 5. 6, 9, 10, 11

Type locality
Western Australia, Cape Range (21°59′18.6″S, 113°57′13.1″E)

Material examined
Holotype: WAM S67364. Paratypes: WAM S67365, S67366, and S67367.

Etymology
Latin '*teres*', meaning polished, smooth, referring to the lack of sculpturing on the shell, in contrast with other members of the genus.

Description
Holotype: shell 19.3 mm wide, 15.7 mm high, *H/D* ratio 0.81, with 4.4 whorls, and fully closed umbilicus. Based on 15 measured adults, shell relatively large, adult diameter 18.54–21.75 mm (mean 19.70 mm, SD 0.96 mm), with 4.125–4.500 (mean 4.33, SD 0.18) whorls (Fig. 9). Apex and spire moderately and evenly elevated, shell height 14.16–16.94 mm (mean 15.69 mm, SD 0.91 mm), *H/D* ratio 0.640–0.870 (mean 0.799, SD 0.075). Body whorl evenly rounded, without trace of angulation, whorls of spire relatively flat. Early spire with very fine pustules. Spire lacking crenulations (Fig. 10). Body whorl descending sharply just behind lip. Palatal and basal lips reflected and narrowly expanded, columellar lip covering most of umbilicus. Umbilicus closed or with a narrow lateral crack. Parietal wall with thin to medium thick callus, its edge not raised. Colour very light yellow above (almost white), lighter on shell base, sometimes with a faint narrow reddish brown spiral supraperipheral band. Based on six dissected adults, genitalia (Fig. 11) with medium to large albumen gland, shortened prostate, about half the length of the uterus. Spermatheca short to medium in length, with a thick shaft. Vagina shorter than penis, widest at the centre. Epiphalus relatively long, tapering into a long slender vas deferens. Epiphalic caecum absent. Large, kidney-shaped penis without accessory ridges. U-pilaster thin, running the length of the penis.

Comparative remarks
Shells of *Plectorhagada teres* sp. nov. are most similar to those of *P. scolythra*, its geographically closest congener (Fig. 9). They are slightly larger, but with substantial overlap. The most consistent difference is the lack of crenulations on the upper spire of *Plectorhagada teres* sp. nov. (Fig. 10). The supraperipheral band is also typically fainter than in *P. scolythra*. Based on shells alone, however, distinguishing between the two species is difficult. The reproductive system of *Plectorhagada teres* sp. nov. shares common characteristics with other species of *Plectorhagada*, including a relatively short prostate, uterus, and vagina, and an epiphalus that tapers into a slender vas deferens. There are, however, some clear differences. *Plectorhagada teres* sp. nov. can be distinguished from *P. scolythra* (see Solem, 1997) by the lack of an epiphallic caecum, which is present in *P. scolythra*, and the absence of accessory ridges on the anterior penial wall, which are greatly enlarged in *P. scolythra*. The species can be distinguished from

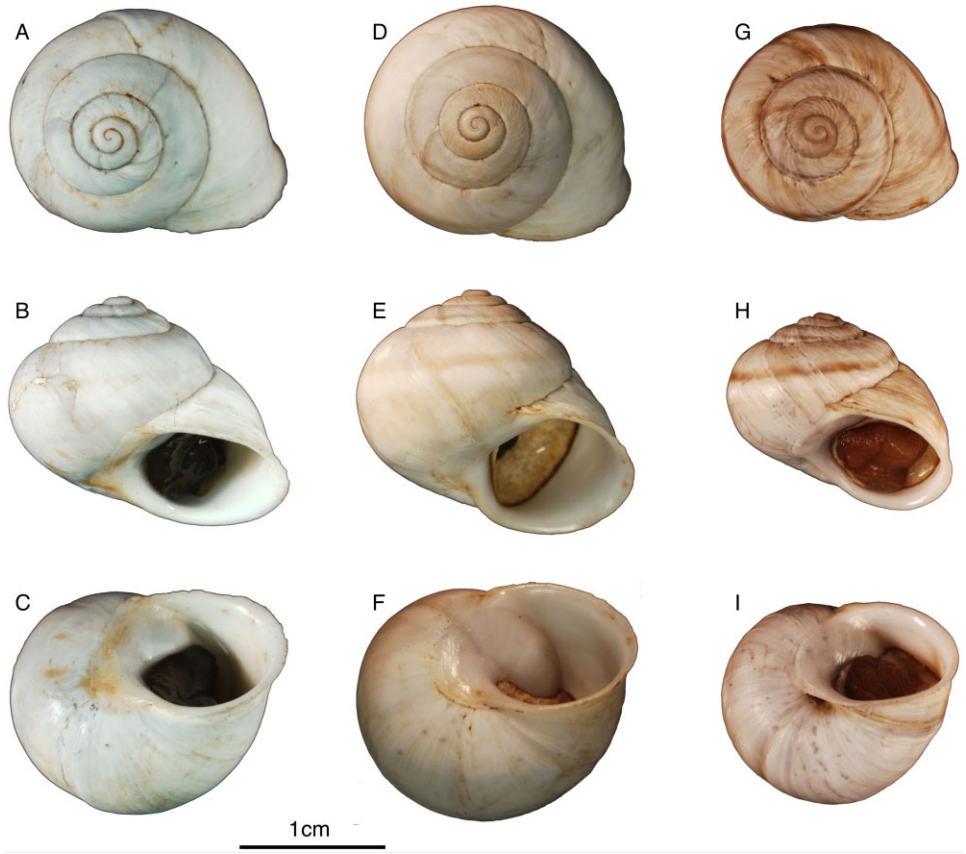

Figure 9. Shells of holotype of ***Plectorhagada teres* sp. nov.** (A–C), compared with *Plectorhagada scolythra* from site PSI (D–F) and *Plectorhagada carcharias* from site PCD (G–I).

P. plectilis based on the size of the albumen gland, which is enormous in *P. plectilis* and only slightly enlarged in *P. teres* sp. nov. Also, accessory ridges on the internal penial wall are very small in *P. plectilis* and are absent in *Plectorhagada teres* sp. nov. *Plectorhagada carcharias* has a very similar reproductive system to *P. teres* sp. nov., but has prominent accessory ridges on the interior penial wall, which are absent in *P. teres* sp. nov.

Distribution

This species is known only from the periphery of the northern end of Cape Range, from near Mangrove Bay on the west side to near Exmouth on the east side. This distribution spans 19 km, and complements that of *P. scolythra*, which is on the periphery of Cape Range further south. The gap between the known distributions of the two species is 15 km on the west side and 17 km on the east.

STREPSITAURUS SOLEM, 1997

Strepsitaurus Solem, 1997: 1611–1647.

Type species

Pleuroxia ruga Cotton, 1953, by original description.

Diagnosis

Shell small to medium sized (adult D = 6.8–18.7 mm, H = 3.0–11.1 mm), between 3 1/3 and 5 3/8 whorls. Spire low to strongly elevated (H/D = 0.38–0.76). Apical sculpture of dense, often elongated micropustules, usually arranged in radial rows, sometimes coalescing to form wavy radial ridges. Spire and body whorl with crenulated ridges, prominence variable from low to very large, plus large micropustules; setae in some species. Body whorl rounded to obtusely angulated, descending moderately to sharply behind lip. Umbilicus variable among species, including open, narrow, or closed. Palatal and basal lips reflected and moderately to broadly expanded, columellar lip wider. Parietal wall with a thick callus or a free lip edge. Shell colour white on rib tops, redish to purplish brown in areas between ribs. Lip white or with slight brownish tone. Where known, genitalia with normal sized albumen gland. Talon and hermaphroditic gland typical. Prostate and uterus slightly shortened. Free oviduct very short. Spermatheca with short

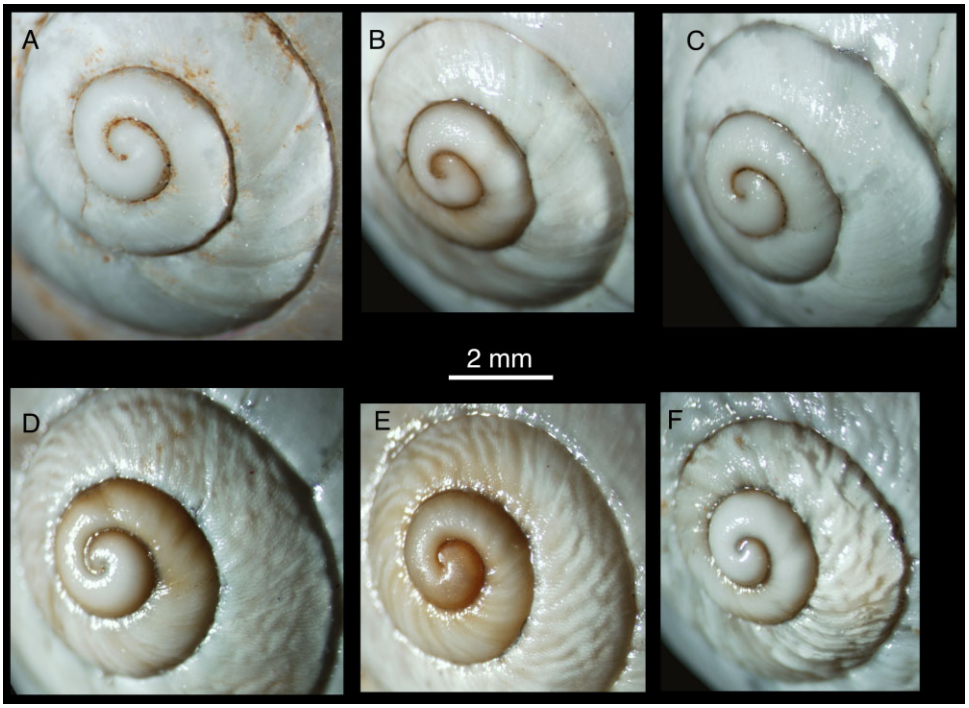

Figure 10. Upper spire of holotype (A) and paratypes (B, site PSB; C, site PSJ) of ***Plectorhagada teres* sp. nov.**, illustrating its lack of sculpture compared with *Plectorhagada scolythra* (D, site PSH; E, site PSF) and *Plectorhagada carcharias* (F, site PCF).

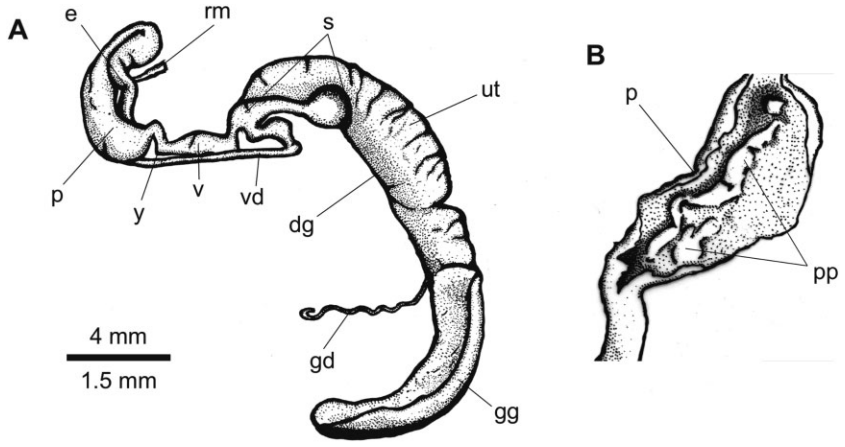

Figure 11. Reproductive system (A) and penial anatomy (B) of ***Plectorhagada teres* sp. nov.** Abbreviations: dg, prostate; e, epiphalus caecum; gd, hermaphroditic duct; gg, albumen gland; p, penis; pp, U-shaped pilaster; rm, retractor muscle; s, spermatheca; ut, uterus; uv, oviduct; v, vagina; vd, vas deferens; y, atrium. All notations follow Solem (1997).

to very short shaft, expanded head at base of prostate–uterus, extending a little way upwards. Vagina short to medium in length, thicker than free oviduct. Vas deferens typical, entering directly into enlarged head of epiphallus. No epiphallic caecum. Epiphallus very thin-walled, internally with longitudinal pilasters. Penial retractor muscle variable in length, inserting in an arc on middle of epiphallus. Penis short, thick-walled, internally with massive pilaster occupying upper two-thirds of chamber. Pilaster with central groove and cross corrugations. Lower portion of penis chamber with simple longitudinal pilasters.

Distribution

Extant species of *Strepsitaurus* are restricted to the Cape Range, Western Australia, whereas *Strepsitaurus*

cardabius Solem, 1997, known only from subfossils in coastal dunes, extends the distribution southwards, from near Ningaloo Homestead to Gnaraloo (22°42′S).

STREPSITAURUS MANDUENSIS SP. NOV.

FIGURES 1, 3, 7, 12

Type locality

Western Australia, Cape Range, Mandu Mandu Gorge (22°08′59.7″S, 113°53′14.7″E).

Material examined

Holotype WAM S67369. Paratypes WAM S67370, S67371.

Etymology

Refers to Mandu Mandu Gorge.

Description

Holotype: shell 7.4 mm wide, 3.3 mm high, *H/D* ratio 0.45, with 3.5 whorls. Based on ten measured adults, shell small, adult diameter 6.8–7.6 mm (mean 7.19 mm, SD 0.26 mm), with 3.33–3.63 (mean 3.5) whorls. Apex and spire evenly elevated, shell height 3.0–3.5 mm (mean 3.23, SD 0.13 mm), *H/D* ratio 0.407–0.479 (mean 0.449, SD 0.020). Body whorl rounded, without trace of angulation. Protoconch densely pustulose. Early spire with prominent pustules but only weak axial ridges. Lower spire and body whorl with faint, deeply pustulose diagonal ridges above periphery, ridges becoming even less prominent on shell base. Umbilicus wide, regularly decoiling, slightly narrowed by columellar lip, width 1.5–1.9 mm (mean 1.67 mm, SD 0.15 mm). Body whorl descending sharply behind aperture. Palatal and basal lips sharply reflected and broadly expanded, and columellar lip wide, parietal lip free of wall and strongly elevated. Basal lip without knob on top of lip. Shell colour white on top of ridges, reddish to purplish brown in interstices.

Comparative remarks

Strepsitaurus manduensis sp. nov. is similar to *S. milyeringus* and *S. susieae* sp. nov., with these three species differing from *S. ningaloo*, *S. rugus*, and *S. williami* by their smaller size, lower whorl count, lips distinctly detached from the body whorl, and lack of setae on the shell. They also lack the prominent knob on the basal lip, which characterizes *S. williami* (Solem, 1997). *Strepsitaurus manduensis* sp. nov. is distinguished largely from *S. milyeringus* and completely from *S. susieae* sp. nov. by its relatively low spire [mean *H/D* 0.449 (0.407–0.479), compared with 0.484 (0.443–0.548) and 0.575 (0.544–0.597)], and its less developed ridges.

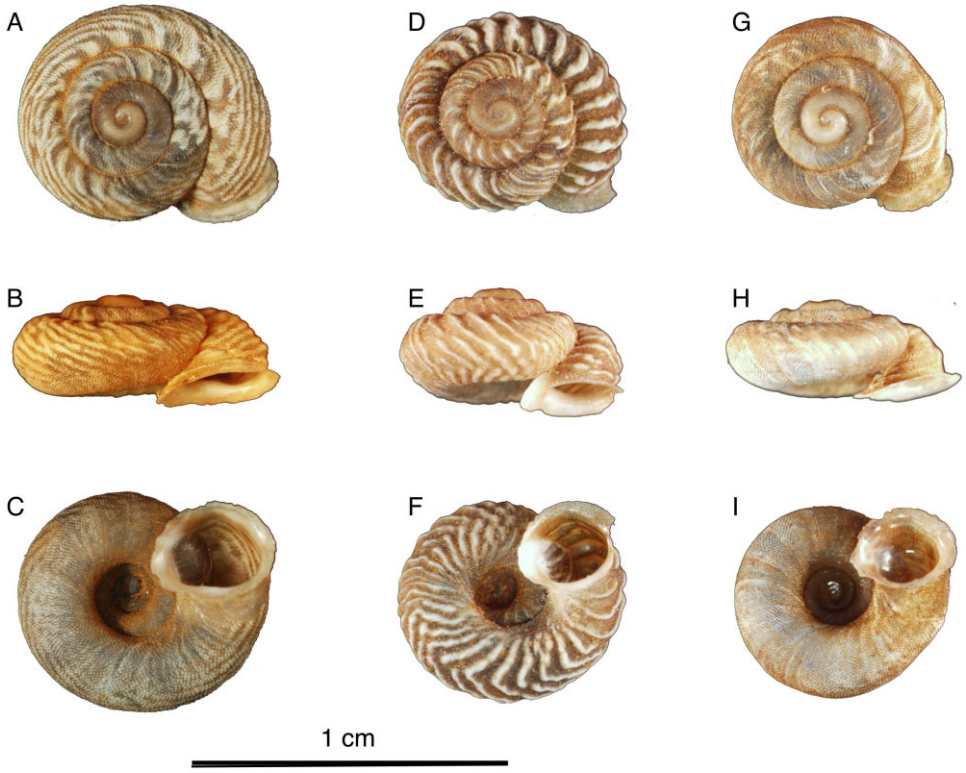

Figure 12. Shells of *Strepsitaurus milyeringus* (A–C), and holotypes of ***Strepsitaurus susieae* sp. nov.** (D–F) and ***Strepsitaurus manduensis* sp. nov.** (G–I).

Distribution
This species is known only from Mandu Mandu Gorge, on the western side of Cape Range, where it was found on vertical rock faces on the north side of the gorge, at two sites 560 m apart. It was not found above the gorge, where the larger *S. ningaloo* occurs.

STREPSITAURUS SUSIEAE SP. NOV.

FIGURES 1, 3, 7, 12

Type locality
Western Australia, Cape Range, in small gorge south of Tulki Gorge (22°05′46.7″S, 113°54′19.6″E).

Material examined
Holotype: WAM S67368. Paratypes: WAM S59657.

Etymology
Refers to Susie Johnson, who has assisted extensively with collections of Western Australian camaenids, including the discovery of this species.

Description
Holotype: shell 7.1 mm wide, 4.1 mm high, *H/D* ratio 0.57, with 3.6 whorls. Based on five measured adults, shell small, diameter 7.1–7.5 mm (mean 7.33 mm, SD 0.35 mm), with 3.63–3.75 (mean 3.5, SD 0.12) whorls. Apex and spire evenly elevated, shell height 4.1–4.3 mm (mean 4.22, SD 0.09 mm), *H/D* ratio 0.544–0.597 (mean 0.575, SD 0.019). Body whorl rounded, without trace of angulation. Protoconch densely pustulose. Early spire with prominent ridges and pustules. Lower spire and body whorl with very prominent, deeply pustulose diagonal ridges, both above and below periphery. Umbilicus wide, regularly decoiling, slightly narrowed by columellar lip, width 1.5–1.9 mm (mean 1.72 mm, SD 0.11 mm). Body whorl descending sharply behind aperture. Palatal and basal lips sharply reflected and broadly expanded, and columellar lip wide, parietal lip free of wall and strongly elevated. Basal lip with or without weak knob on top of lip. Shell colour white on top of ridges, reddish brown in interstices.

Comparative remarks
Strepsitaurus susieae sp. nov. is similar to *S. milyeringus* and *S. manduensis* sp. nov., with these three species differing from *S. ningaloo*, *S. rugus*, and *S. williami* by their small size, low whorl count, lips distinctly detached from the body whorl, and lack of setae on the shell. They also lack the prominent knob on the basal lip, which characterizes *S. williami* (Solem, 1997). *Strepsitarus susieae* sp. nov. is distinguished from *S. milyeringus* and *S. manduensis* sp. nov. by its relatively higher spire [mean H/D 0.575 (0.544–0.597), compared with 0.484 (0.443–0.548) and 0.449 (0.407–0.479)], and its very prominent ridges both above and below the periphery of the body whorl.

Distribution
This species has been found only in an unnamed small gorge (~1.2 km long), south of Tulki Gorge, on the west side of Cape Range. All specimens were found on or at the base of the vertical north wall of the gorge during wet weather.

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