

The Leopard Mantis Shrimp, *Ankersquilla pardus*, a New Genus and Species of Eurysquillid from Indo-West Pacific Coral Reefs

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ABSTRACT. The mantis shrimp superfamily Eurysquilloidea Manning, 1977, with the single family Eurysquillidae Manning, 1977, contains six genera and 32 species, the majority of which occur in the Indo-West Pacific. Here, we describe a new species of eurysquillid, *Ankersquilla pardus*, from the central and western Pacific that cannot be assigned to any recognized genera, and, accordingly, propose a new genus for its reception. *Ankersquilla pardus* is unique in Eurysquilloidea in bearing three teeth on the dactylus of the raptorial claw. Similar raptorial claw armature is otherwise known only in the Parasquilloidea and Pseudosquillidae (Gonodactyloidea). All other eurysquillids have four or more teeth on the dactylus of the raptorial claw. The most unusual aspect of *Ankersquilla pardus*, however, is the finely spinose posterior abdomen and telson, which resembles members of the Coronidae (Lysiosquilloidea). Although superficially similar to some coronid lysiosquillids, the ovate maxilliped 3–4 propodi, ventrally arising intermediate and lateral denticles of the telson, and form of the male pleopod 1 endopod show *Ankersquilla pardus* to be a eurysquillid.

Introduction

The mantis shrimp superfamily Eurysquilloidea Manning, 1977, with the single family Eurysquillidae Manning, 1977, contains six genera and 32 species, the majority of which occur in the Indo-West Pacific (Ahyong, 2001, Ahyong, 2010; Lucatelli *et al.*, 2013). Eurysquillidae was originally assigned to the Gonodactyloidea Giesbrecht, 1910, based on the ovate maxilliped 3–5 propodi and possession of one or two intermediate denticles on the telson (Manning, 1980; Ahyong, 1997a), but was shown to be outside of the gonodactyloids and instead formed a clade together with the

Parasquilloidea Manning, 1995 (also initially thought to be gonodactyloids) and the Squilloidea Latreille, 1802 (Ahyong & Harling, 2000; Van Der Wal *et al.*, 2017). Although highly diverse in telson and uropod ornamentation, eurysquillids are united by the combination of ovate maxilliped 3–4 propodi and position of the intermediate and lateral denticles of the telson, which arising submarginally on the ventral surface, rather than on the posterior margin (Ahyong & Harling, 2000). Here, we describe a new species of eurysquillid from the western Pacific that cannot be assigned to any currently recognized genera, and, accordingly, propose a new genus for its reception.

Keywords: Crustacea; Stomatopoda; Eurysquilloidea; Eurysquillidae; French Polynesia; Indonesia

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Materials and methods

Morphological terminology and size descriptors generally follow Ah Yong (2001, 2012). Specimens are measured in millimetres (mm). Total length (TL) is measured along the dorsal midline, from the apex of the rostral plate to the apices of the submedian teeth of the telson. Carapace length (CL) is measured along the dorsal midline and excludes the rostral plate. The corneal index (CI) is given as 100CL/corneal width. The propodal index (PI) is given as 100CL/propodus length. Specimens are deposited in the collections of the Australian Museum (AM) and Florida Museum of Natural History, University of Florida, Gainesville (UF).

The phylogenetic framework from Porter *et al.* (2010) was used to place the newly described species within known stomatopod taxonomic diversity. New sequences (GenBank accession nos: MT062514–MT062516, MT062837–MT062843) for the complete 18S rDNA (c. 2000 bp) and partial 28S rDNA (expansion segments D2–D7b and D9–D10, c. 2800 bp) nuclear genes, and partial 16S (c. 460 bp) and cytochrome oxidase I (COI, c. 650 bp) mitochondrial genes were generated for two specimens of *A. pardus* (AM P102286, P104060) as well as the eurysquilloid species *Manningia pilaensis* De Man, 1902 (AM P100682, Singapore). DNA was extracted from tissues using the NucleoSpin Tissue XS DNA isolation kit (Macherey-Nagel). Polymerase chain reaction (PCR) products for the complete 18S rDNA (c. 2000 bp) and partial 28S rDNA (expansion segments D2–D7b and D9–D10, c. 2800 bp) nuclear genes, and partial 16S (c. 460 bp) and cytochrome oxidase I (COI, c. 650 bp) mitochondrial genes were amplified using one or more sets of general primers as in Porter *et al.* (2010) and Feller *et al.* (2013). Standard PCR conditions (final concentrations in 25 µl: 1 × buffer, 200 nmol l⁻¹ of each primer, 200 µmol l⁻¹ dNTPs and 1 U HotMaster taq from Eppendorf, Hauppauge, NY, USA) were used on a BioRad C1000 Touch Thermal Cycler, with the following cycling parameters: initial denaturation at 96°C for 2 min, followed by 40 cycles of 96°C for 1 min, 46°C for 1 min and 72°C for 1 min, followed by a final chain extension at 72°C for 10 min. PCR products were visualized by agarose gel electrophoresis and purified using the NucleoSpin Extract II kit (Machery Nagel) or ExoSAP-IT (Affymetrix). Sequences were generated in both directions on an ABI PRISM 3500 Automated Capillary Genetic Analyzer (Applied Biosystems, Foster City, CA, USA) using the ABI BigDye Ready-Reaction kit using 1/16th of the suggested reaction volume. Based on the results of Ah Yong & Jarman (2009), Porter *et al.* (2010) and Van Der Wal (2017), which inferred Hemisquillidae (Gonodactyloidea) to be the sister group to the remaining extant stomatopods, we rooted the analysis to *Hemisquilla australiensis* Stephenson, 1967 and *H. californiensis* Stephenson, 1967. Nucleotide sequences of the 16S, 18S and 28S genes were aligned with the online MAFFT server using the E-INS-I strategy (<http://mafft.cbrc.jp/alignment/server/>) (Katoh *et al.*, 2002; Katoh *et al.*, 2005). The COI sequences were inspected for evidence of pseudogenes (e.g., stop codons, indels not contiguous with codons) and then manually aligned using the translated amino acid sequences. Phylogenetic analyses of combined datasets can reveal hidden support for relationships in conflict among analyses of individual markers (Gatesy *et al.*, 1999); therefore, the four gene regions were concatenated, and highly divergent and/or ambiguous regions of the entire alignment were removed using the program GBlocks (Castresana, 2000). The phylogeny was reconstructed using RaxML (Stamatakis *et al.* 2005; Stamatakis *et al.* 2008; Pfeiffer & Stamatakis 2010) as implemented in the CIPRES portal (Miller *et al.* 2010).

Systematics

Stomatopoda

Eurysquilloidea Manning, 1977

Eurysquillidae Manning, 1977

Ankersquilla gen. nov.

<http://zoobank.org/NomenclaturalActs/3724004A-0FF7-41CC-8CB3-6A213641E825>

Type species. *Ankersquilla pardus* sp. nov.

Diagnosis. Cornea bilobed, set transversely on stalk, with 6 mid-band rows of ommatidia. Rostral plate simple, apex rounded. Antennular somite not elongated, shorter than twice length of rostral plate. Raptorial claw dactylus with 3 teeth on occlusal margin; propodus occlusal margin fully pectinate; carpus with single dorsal spine. Pleopod 1 endopod with lateral lobe on distal ‘endite’. Body dorsoventrally flattened. Abdominal somites 5–6, telson and proximal surface of uropodal protopod densely spinose, obscuring dorsal sculpture. Telson transversely ovate, wider than long, primary spines short, acute, dorsal outline obscured by dorsal spination of telson; submedian denticles absent; intermediate and lateral denticles without dorsal lobe. Uropodal protopod inner primary spine longer than outer; inner margin spinose.

Etymology. Named after Arthur Anker, our friend and colleague who collected the type material. Gender: feminine.

Ankersquilla pardus sp. nov.

<http://zoobank.org/nomenclaturalActs/0BD75B46-0194-43AD-A2E9-049982C56C18>

Figs 1–4

Holotype: UF23346, ♂ (TL 52 mm), Moorea [French Polynesia], NW side of Cook Bay, off Gump station, 17°29.406'S 149°49.578'W, back-reef, sandy reef flat with massive coral blocks and rubble, 1 m, deep in sand under large piece of rubble, fcn BMOO-6054, sta BIZ 5, coll. A. Anker, 17 October 2009. **Paratype:** AM P102286, ♀ (TL 53 mm), Moorea, SW coast, lagoon off Nihimaru estuary, 17°31.998'S 149°54.306'W, back-reef, sandy reef flat with massive corals, algae and rubble, deep under large algae-covered piece of rubble, 1.5 m, fcn BMOO-4918, sta MIB 167, coll. A. Anker, 29 October 2008.

Other material examined. AM P104060, 1 female (TL 82 mm), Indonesia (probably Bali), purchased, aquarium trade, July 2006.

Description. Eye subtriangular, extending almost to end of or slightly beyond antennular peduncle article 1; cornea strongly bilobed, set transversely on stalk, with 6 mid-band rows of ommatidia; CI 419–501. Ophthalmic somite anterior margin transverse; ventral surface with blunt spine arising proximally and minute distomedian granule. Ocular scales triangular, separate, anterior margins concave, apices directed laterally.

Antennular peduncle 0.58–0.71CL. Antennular somite dorsal processes directed anterolaterally, apices blunt. Antennal protopod dorsally unarmed; with small ventrodorsal spine and 1 ventral papilla. Antennal scale length 0.58–0.61CL.

Rostral plate linguiform to subtriangular, slightly

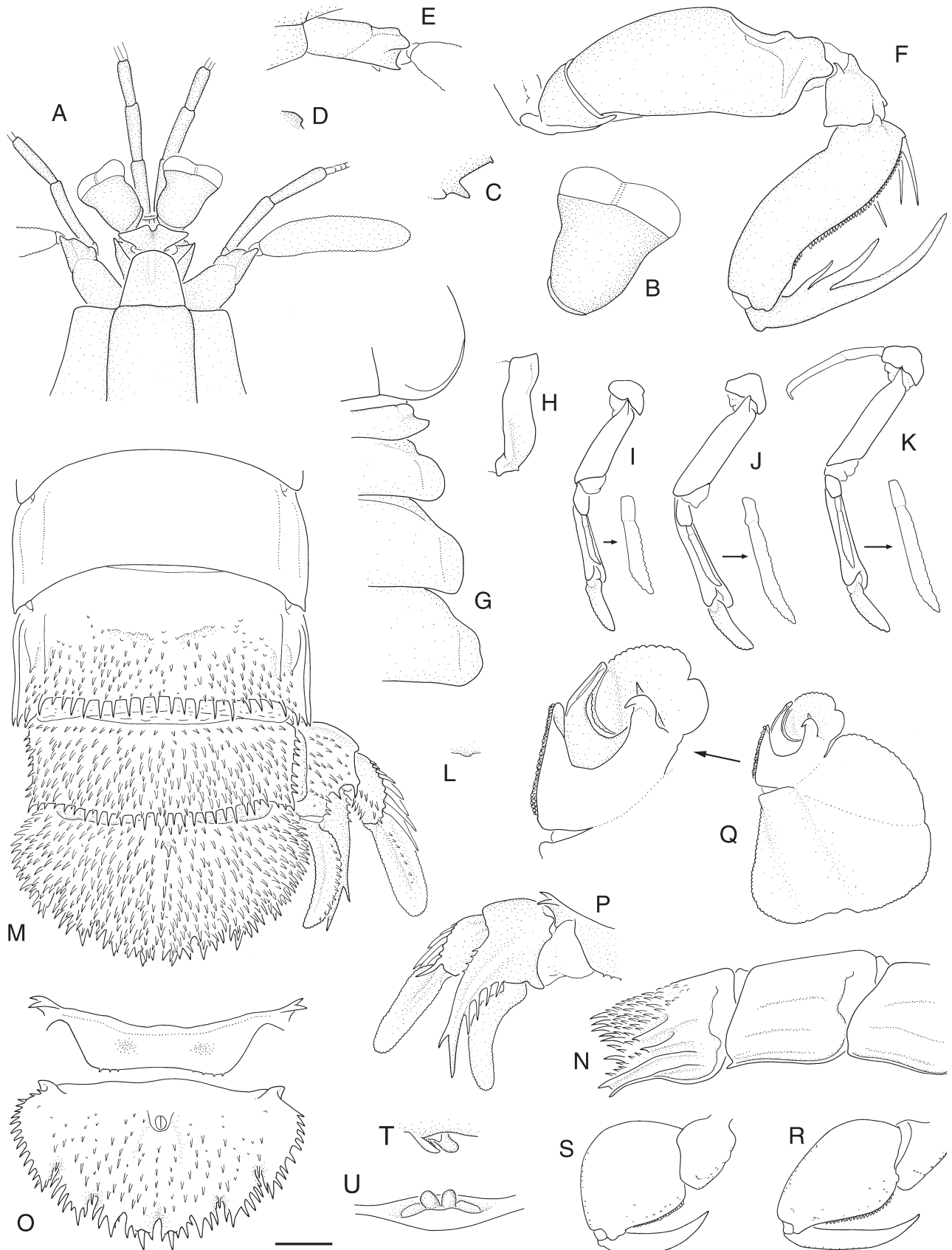


Figure 1. *Ankersquilla pardus* gen. et sp. nov. (A–S) male holotype, TL 52 mm, Moorea, UF23346. (T–U) female paratype, TL 53 mm, Moorea, AM P102286. (A) anterior cephalothorax, dorsal view; (B) right eye, dorsal view; (C) ventral spine and ventral margin of ophthalmic somite, right lateral view; (D) right dorsal process of antennular somite, lateral view; (E) right antennal protopod; (F) right raptorial claw; (G) posterolateral portion of carapace and thoracic somites 5–8, right dorsal view; (H) thoracic somite 5, right lateral view; (I–K) right pereopods 1–3, posterior view; (L) thoracic somite 8, sternal ‘keel’; (M) abdominal somites 4–6, telson and right uropod, dorsal view; (N) abdominal somites 3–5, right lateral view; (O) abdominal somite 6 and telson, ventral view; (P) right uropod, ventral view; (Q) right pleopod 1 endopod; (R, S) right maxillipeds 3–4 dactylus–carpus; (T, U) female gonopore, right lateral view and ventral view. Setae omitted. Scale = A, C–K, M–P = 2.0 mm; B, L, Q, R–U = 1.0 mm.



Figure 2. *Ankersquilla pardus* gen. et sp. nov. (A–C) female, TL 82 mm, Indonesia, AM P104060: eye, telson and right lateral habitus, respectively. (D) female paratype, TL 53 mm, Moorea, AM P102286; (E) male holotype, TL 52 mm, Moorea, UF23346. (Photos: A–C, R. Caldwell; D–E, A. Anker).

wider than long, widest basally, lateral margins straight, convergent, apex rounded; low, indistinct median carina. Carapace anterolateral angles bluntly angular, anterior margins straight; carinae absent except for marginal carina, indicated posterolaterally.

Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod. Maxillipeds 3–4 propodi ovate, rounded, without distoventral ribbing. Maxilliped 5 basal article without ventrally directed spine.

Raptorial claw dactylus with 3 teeth; outer margin very weakly sinuous on proximal half, curving distally, with distinct basal notch. Propodus with 3 movable spines proximally, distal margin unarmed; distal margin unarmed;

propodus shorter than carapace, when folded, not extending posterior beyond merus; PI 105 (male), 109–120 (female). Carpus dorsal margin terminating in short, ventrally directed spine. Merus inferodistal margin rounded, unarmed. Ischium shorter than one-fourth merus length. Basis lateral surface with 2 or 3 short denticles.

Pereopods 1–3 proximal-most article with outer ventrolaterally directed triangular lobe; inner margin unarmed. Endopod distal article slender, liguliform, tapering distally; outer and inner distal margins setose.

Thoracic somite 5 lateral process obsolete, with small ventrally directed spine. Thoracic somites 6–8 lateral process rounded to subtruncate; faintly indicated lateral carina.

Thoracic somite 6 female gonopore with bilobed median papillae flanked by lower lateral papilla. Thoracic somite 8 sternal keel low, rounded.

Male pleopod 1 endopod with lateral lobe on distal 'endite'.

Abdominal somites loosely articulated; somites 1–4 smooth dorsally; posterior margin unarmed; 3 shallow grooves laterally (upper two corresponding to intermediate and lateral carina) and marginal carina; somites 1–3 posterolaterally unarmed; somite 4 with posterolateral spine; ventral pleural margin straight to faintly concave. Abdominal somite 5 with posterior half to two-thirds covered with short posteriorly directed spines; posterior margin lined with posteriorly directed spines; laterally with 3 posteriorly armed carinae (first and third corresponding to intermediate and lateral carinae) and posteriorly armed marginal carina; ventral pleural margin distinctly concave. Abdominal somite 6 surface entirely covered with short posteriorly directed spines; posterior margin lined with posteriorly directed spines; lateral carina indicated, lined with spines; 2 triangular spines anterior to uropodal articulation, apices simple or bifid (in largest specimen); sternum posterior margin unarmed medially, with 3–10 small spines on each posterolateral margin.

Telson length half width, dorsal outline evenly curved; dorsal surface and posterior margin densely covered with short, curved spines; median carina indicated by longitudinal row of short, curved spines of similar size to adjacent spines on telson surface; submedian teeth short, margins spinose, movable apices conical, curved, separated by narrow, U-shaped cleft; submedian denticles absent; with single spiniform submarginal intermediate and lateral denticles, dorsal lobe absent. Intermediate and lateral teeth short, stout, spinose, not produced beyond general posterior telson outline. Ventral surface covered with short spines; postanal carina absent.

Uropodal protopod dorsal surface covered with short spines; anterior margin convex, unarmed; inner primary spine ventrally carinate, distinctly longer than outer spine; inner margin with 3–5 graded spines; outer margin with 4–11 short spines, unarmed anterior to endopod articulation. Uropodal exopod proximal segment dorsal surface with patch of short spines on inner half; inner margin concave, unarmed; slender, curved distoventral spine; outer margin with 7 or 8 graded movable spines, distalmost not reaching beyond midlength of distal segment. Exopod distal segment longer than proximal segment; dorsal midrib with 7–11 short spines; ventral midrib with 0–3 minute spines. Endopod elongate, reniform, apex bluntly rounded; length 4.57–4.67 × width; dorsolateral surface with row of 10–15 short spines.

Colour in life (Figs 2, 3). Overall pale yellowish-tan with diffuse whitish mottling and numerous black or black-brown spots over cephalothorax, abdomen, tailfan and pereopods, forming leopard-spotted pattern. Eyes pale yellow-tan; cornea silver. Antennular and antennal peduncles with diffuse white speckling; antennular articles distally yellow-brown. Antennal protopod pale with black-brown spots; scale speckled white with dark, irregular patch slightly proximal to midlength and at distal end. Raptorial claw propodus and carpus translucent white and diffuse irregular brown mottling and diffuse blue-green highlights; movable propodal spines translucent white overall (TL 52–53 mm) to black-green on proximal two-thirds (TL 82 mm); dactylus translucent white teeth margined with orange-brown; ischiomerus pale



Figure 3. *Ankersquilla pardus* gen. et sp. nov., lagoon patch of *Halimeda* algae on sand in about 8 m of water at Kwajalein Atoll, Marshall Islands, 27 August 2012. Photo: S. Johnson. Specimen not collected.

yellowish-tan with diffuse white mottling and several dark diffuse spots, distal margin diffuse blue-green. Uropodal exopod distal article and endopod distal half dark-brown; marginal setae dull-pink.

Etymology. Derived from the formal name of the Leopard, *Panthera pardus* (Linnaeus, 1758), for the distinctive, leopard-spotted colour pattern of the new species; used as a noun in apposition.

Measurements. Male (n = 1) TL 52 mm; female (n = 2) TL 53–82 mm. Other measurements of holotype: CL 9.0 mm, antennular peduncle length 6.4 mm, antennal scale 5.2 mm, propodus length 8.3 mm, abdominal somite 5 width 10.3 mm.

Habitat. The French Polynesian specimens were collected from shallow (1–1.5 m) sandy back-reef sites with rubble and algae; both were burrowed beneath coral boulders. The Marshall Islands individual was photographed at 8 m depth at Kwajalein Atoll in a lagoon patch of *Halimeda* sp. on sand. The precise collecting locality of the TL 82 mm Indonesian specimen is not known, but in 2000, RLC and Mark Erdmann observed but failed to capture another Indonesian individual in Tolitoli Bay, Sulawesi, dwelling in a large worm tube in massive coral head at 2 m depth.

Distribution. Central to western Pacific, from French Polynesia, the Marshall Islands and Indonesia.

Discussion

Ankersquilla gen. nov., represented by *A. pardus* sp. nov., is unique in Eurysquilloidea in having three teeth on the dactylus of the raptorial claw; all other eurysquillids have four (*Manningia* Serène, 1962; *Coronidopsis* Hansen, 1926) or more dactylar teeth (*Eurysquilla* Manning, 1963; *Eurysquilloides* Manning, 1963; *Raysquilla* Ahyong, 2000; *Sinosquilla* Liu & Wang, 1978) (Ahyong, 1997b, 2001). Three spearing teeth on the dactylus of the raptorial claw are otherwise present only in members of the Parasquilloidea and in Pseudosquillidae Manning, 1977 (Gonodactyloidea). Another unusual feature of *Ankersquilla* is the absence of upright rounded lobes associated with the intermediate and lateral denticles of the telson; these lobes are present in all other eurysquillids except for *Eurysquilloides* Manning, 1963 (Ahyong & Harling, 2000; Ahyong, 2001). Perhaps the

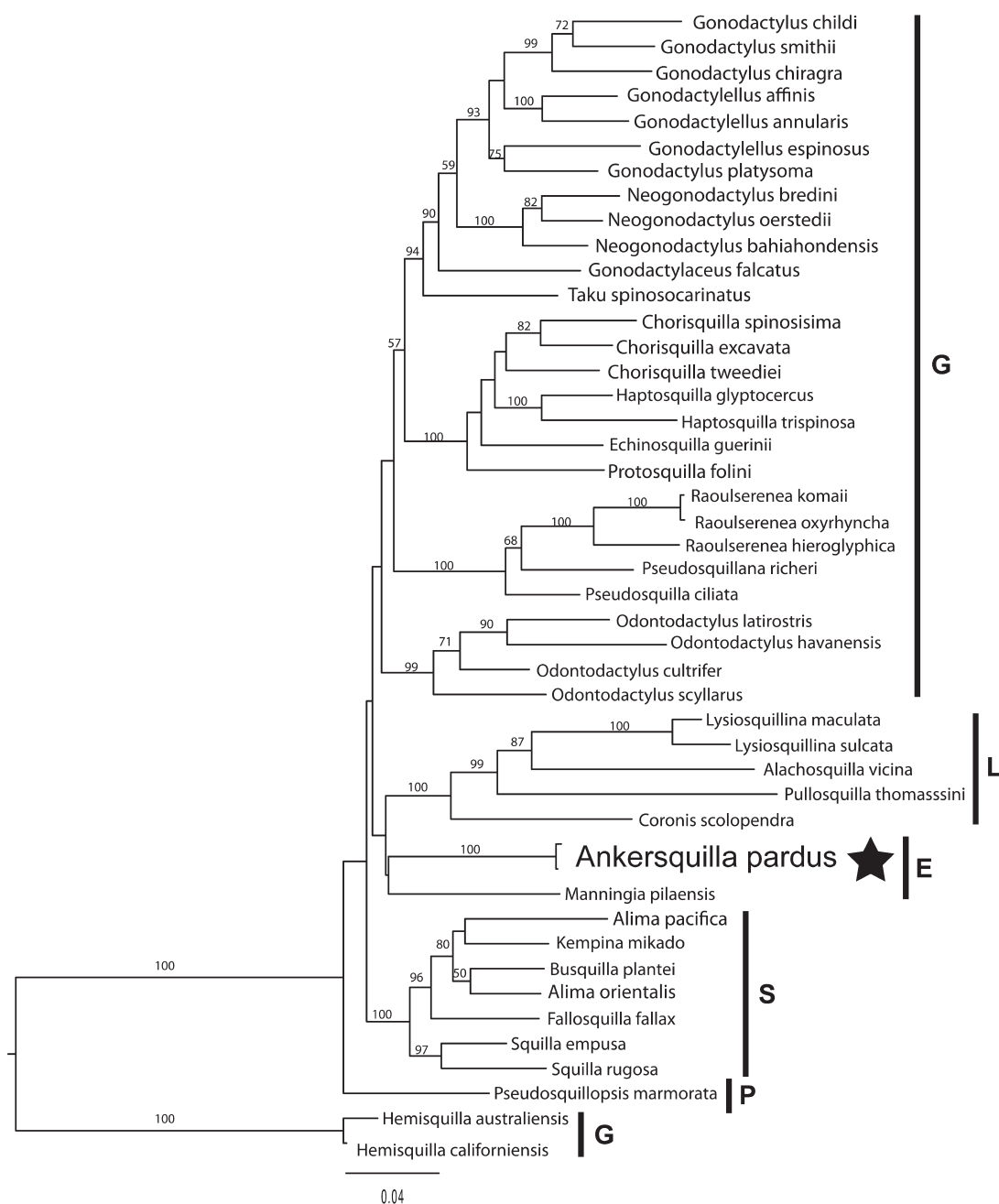


Figure 4. Phylogenetic position of *Ankersquilla pardus* gen. et sp. nov. based on maximum likelihood analysis of concatenated 18S, 28S, 16S, COI sequences using RaXML. Log likelihood -31189.005. Bootstrap support indicated on branches. Superfamily abbreviations: Eurysquilloidea (E), Gonodactyloidea (G), Lysiosquilloidea (L), Parasquilloidea (P), Squilloidea (S).

most remarkable aspect of *Ankersquilla* is its resemblance to some members of the Coronididae Manning, 1980, in the superfamily Lysiosquilloidea Giesbrecht, 1910. The uniformly and densely spinose surface of abdominal somite 6 and the telson of *Ankersquilla*, with a wide, semi-circular telson having short primary teeth resemble the condition in the coronid genus, *Neocoronida* Manning, 1976. This resemblance between the two genera is further accentuated by the simple, unarmed rostral plate, wide ocular scales, subtriangular eyes and strikingly similar uropod structure (compare Fig. 1M, P with Manning, 1972: fig. 1e, g). Although *Ankersquilla* is clearly not a lysiosquilloid, as indicated by the simple and ovate, rather than ribbed,

quadrate propodi of maxillipeds 3–4, and eurysquilloid-form male pleopod 1 endopod (Ahyong & Harling, 2000), it should not be assumed that the similarities to *Neocoronida* are the result of convergence. The maxilliped 3–4 propodi of *Neocoronida* also lack ventral ribbing (Manning, 1976; Adkison *et al.*, 1983) and the intermediate and lateral denticles of the telson are ventrally recessed, as in eurysquilloids. Thus, *Neocoronida* could instead prove to be a eurysquilloid rather than lysiosquilloid, but further assessment of other members of the Coronididae are required prior to making formal changes to the classification. Also, of possible phylogenetic significance is that the two eurysquilloid exemplars form a clade that is placed closer

to the lysiosquilloids (Fig. 4) than to the squilloids and parasquilloids as indicated by previous analyses (Ahyong & Harling, 2000; Van Der Wal *et al.*, 2017). Nodal support for the euryrsquilloid-lysiosquilloid affinity is low (as are the relationships between other superfamilies), but such a relationship, if corroborated, would indicate that the dorsoventrally flattened and generally loosely articulated body form shared by most members of Euryrsquilloidea and Lysiosquilloidea could be synapomorphic rather than convergent.

Most euryrsquilloids have variously spinose posterior abdominal somites and telson, but the surface sculpture and telson outline is not usually obscured as it is in *Ankersquilla*. Also, the median carina of the telson in *Ankersquilla*, which is distinct in most euryrsquilloids, is instead indicated only by a longitudinal row of spines of similar size to the surrounding telson spines. Among euryrsquilloids, similarly unusual abdominal and telson ornamentation is approached only in *Sinosquilla*. Both species of *Sinosquilla* have dense dorsal spination on abdominal somite 6 and the telson, which largely obscures surface sculpture (Ahyong, 2001: fig. 16; 2010: fig. 1C, D). In *Sinosquilla sinica* Liu & Wang, 1978, the median carina of the telson is distinct and unbroken, but in *S. hispida* Liu & Wang, 1978, the overall dorsal spination is more uniform (albeit more pronounced) and the median carina of the telson is indicated by a row of spines, much like that of *A. pardus*. *Ankersquilla* and *Sinosquilla*, however, are otherwise dissimilar and probably not closely related, being readily separated by numerous features including: three teeth on the dactylus of the raptorial claw in *Ankersquilla* (eight or more in *Sinosquilla*); a short, rounded rostral plate in *Ankersquilla* (long, spiniform in *Sinosquilla*); intermediate and lateral telson denticles without upright lobes in *Ankersquilla* (lobes present in *Sinosquilla*); and short, spiniform intermediate and lateral primary telson teeth that in *Ankersquilla* do not extend beyond the general dorsal outline (prominent, lobe-like in *Sinosquilla*). The phylogenetic position of *Ankersquilla* within the euryrsquilloids is presently unclear and awaits comprehensive revision and analysis of all genera (currently underway).

The Indonesian specimen of *A. pardus* (TL 82 mm; AM P104060; Fig. 2A,C) survived in captivity for approximately six and one half years during which it regularly moulted but remained essentially the same size, suggesting that it had already attained maximum length. In captivity this animal fed on shrimp and crabs, but did not break open snails and hermit crabs. Despite their wide geographic separation, the Indonesian specimen of *A. pardus* agrees closely with the smaller French Polynesian type specimens (TL 52–53 mm), differing chiefly in the more tapering rostral plate, blunter dorsal telson and abdominal spines, more numerous short spines overall (most notably those of abdominal somite 5 covering the posterior two-thirds instead of half), and slightly greater spination along the lateral margin of the uropodal protopod (11 versus 4–8) and posterolateral margins of the abdominal sternite 6 (7–10 versus 3–5). These differences are probably a function of the much larger size of the Indonesian specimen (TL 82 mm versus TL 52–53 mm). Evidently, *A. pardus* has strong dispersal capabilities given the low (1%) COI sequence divergence between Indonesian and French Polynesian specimens.

The distinctive coloration of *A. pardus* is consistent in all of the specimens examined, including the individual observed but not captured in Tolitoli Bay, Indonesia (see Habitat above). We identify an individual from the Marshall Islands (photographed but not captured; Fig. 3) as *A. pardus* based on the visible morphology and the distinctive colour pattern. Although common names are seldom used for stomatopods, we here propose Leopard Mantis Shrimp for *A. pardus*, given its distinctive colour pattern.

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