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 eurysquilloids 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 Coronididae (Lysiosquilloidea). Although superficially similar to some coronidid lysiosquilloids, 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 eurysquilloid.

**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, 1910; 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, eurysquilloids 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.
Materials and methods

Morphological terminology and size descriptors generally follow Ahyong (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 25μl: 1 x buffer, 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 (Macherey 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 Big dye Ready- Reaction kit using 1/16th of the suggested reaction volume. Based on the results of Ahyong & 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 (Stamatkis et al. 2005; Stamatakis et al. 2008; Pfeiffer & Stamatakis 2010) as implemented in the CIPRES portal (Miller et al. 2010).
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.
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 subtruncated; 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 posteroventral 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 disoventral 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.

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.

**Colour in life** (Figs 2, 3). Overall pale 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 Euryzouilloidea in having three teeth on the dactylus of the raptorial claw; all other euryzouillids have four (*Manningia* Seréne, 1962; *Coronidopsis* Hansen, 1926) or more dactylar teeth (*Euryzouilla* Manning, 1963; *Euryzouilloides* Manning, 1963; *Raysouilla* Ahyong, 2000; *Sinouzouilla* Liu & Wang, 1978) (*Ahyong, 1997b, 2001*). Three spear-like teeth on the dactylus of the raptorial claw are otherwise present only in members of the Parasquillioidea 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 euryzouillids except for *Euryzouilloides* Manning, 1963 (*Ahyong & Harling, 2000; Ahyong, 2001*). Perhaps the
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 coronidid 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 euryssquilloid-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 euryssquiloids. Thus, *Neocoronida* could instead prove to be a euryssquilloid 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 euryssquilloid 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 eury squilloid-lysiosquilliod 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 articu lated body form shared by most members of Eury squilloidea and Lysiosquilloidea could be synapomorphic rather than convergent.

Most eury squilloids 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 eury squilloids, is instead indicated only by a longitudinal row of spines of similar size to the surrounding telson spines. Among eury squilloids, 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 eury squilloids 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 specimens 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 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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References


