Zoological Studies **61**:12 (2022)
doi:10.6620/ZS.2022.61-12

Zoological Studies

Open Access

Phylogenetic Appraisal of Lysiosquillidae Giesbrecht, 1910, and a New Species of *Lysiosquilloides* Manning, 1977, from Taiwan (Crustacea: Stomatopoda: Lysiosquilloidea)

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Received 15 October 2021 / Accepted 4 February 2022 / Published 5 May 2022
Communicated by Benny K.K. Chan

The mantis shrimp family Lysiosquillidae includes the largest known stomatopods and presently includes three genera: *Lysiosquilla* Dana, 1852, *Lysiosquillina* Manning, 1995, and *Lysiosquilloides* Manning, 1977. Since 1995, new species assigned to all three lysiosquilloid genera have been recognised: *Lysiosquilla manningi* Boyko, 2000, *Lysiosquillina lisa* Ahyong & Randall, 2001, *Lysiosquilla colemani* Ahyong, 2001, *Lysiosquilla suthersi* Ahyong, 2001, and *Lysiosquilloides mapia* Erdmann & Boyer, 2003, and *Lysiosquilla isos* Ahyong, 2004. *Lysiosquillina lisa*, *Lysiosquilla campechiensis* Manning, 1962 and *Lysiosquilla suthersi*, however, proved problematical to assign to genera owing to the possession of characters intermediate between *Lysiosquilla* sensu stricto and *Lysiosquillina* sensu stricto. In particular, species that are transitional between *Lysiosquilla* and *Lysiosquillina* challenge the validity of the latter genus. Here, we reassess the status and composition of the lysiosquillid genera by cladistic analysis of all known species in the family. *Lysiosquillina* is synonymized with *Lysiosquilla* and a new species of *Lysiosquilloides* is described from Taiwan. A key to the species of *Lysiosquilloides* is provided.

Key words: Mantis shrimp, Indo-West Pacific, Phylogeny, Systematics, Taxonomy, Coral reef.

BACKGROUND

The mantis shrimp superfamily Lysiosquilloidea presently comprises Lysiosquillidae Giesbrecht, 1910; Coronididae Manning, 1980; Nannosquillidae Manning, 1980; and Tetrasquillidae Manning & Camp, 1993, united by the subquadrate propodi of maxillipeds 3 and 4, absence of a distinct median carina on the telson, and the antizoeal early larva (Ahyong and Harling 2000; Ahyong et al. 2014). Lysiosquilloids typically occupy deep vertical burrows in soft substrates but unlike members of most other stomatopod groups, they seldom leave their burrows, instead ambushing prey from the burrow mouth. As in callianassoid axiideans (Decapoda), lysiosquilloid morphology is commensurate with the cryptic, infaunal lifestyle: the body is dorsoventrally flattened, weakly calcified and generally loosely articulated, permitting great flexibility within the confines of the burrow. Lysiosquillidae includes some of the largest known stomatopods (exceeding total length 380 mm), most of which are boldly marked with light and dark transverse bands (Ahyong 2001). Within Lysiosquilloidea, synapomorphies of Lysiosquillidae include the absence of posterolateral spines on

Citation: Ahyong ST, Lin CW. 2022. Phylogenetic appraisal of Lysiosquillidae Giesbrecht, 1910, and a new species of *Lysiosquilloides* Manning, 1977, from Taiwan (Crustacea: Stomatopoda: Lysiosquilloidea). Zool Stud **61**:12. doi:10.6620/ZS.2022.61-12.

abdominal somite 6, an unfolded proximodorsal margin on the uropodal endopod, intermediate and lateral primary teeth fused into the telson margin, and low, rounded intermediate denticles on the telson (Ahyong and Harling 2000; Ahyong 2001).

Until 1995, two genera, *Lysiosquilla* Dana, 1852, and *Lysiosquilloides* Manning, 1977, were recognized in Lysiosquillidae. *Lysiosquilloides* was distinguished from *Lysiosquilla* primarily on the basis of the articulated apices of the submedian teeth of the telson and the low and blunt, instead of spinous dorsal processes of the antennular somite. Manning (1995) further divided *Lysiosquilla* based on antennal characters, erecting *Lysiosquillina* for three species with a broad, ovate antennal scale (length about 2.5 × width) and absence of the dorsomesial spine on the antennal protopod (Fig. 1A), and restricting *Lysiosquilla* to species having a mesiodorsal spine on the antennal protopod and a slender antennal scale (length ≥ 3.0 × width) (Fig. 1D). Thus, Lysiosquillidae presently includes three genera: *Lysiosquilla*, *Lysiosquillina* and *Lysiosquilloides* (see Manning 1995; Ahyong 2001). Since 1995, new species assigned to all three lysiosquilloid genera have been recognised: *Lysiosquilla manningi* Boyko, 2000, *Lysiosquillina lisa* Ahyong & Randall, 2001, *Lysiosquilla colemani* Ahyong, 2001, *Lysiosquilla suthersi* Ahyong, 2001, and *Lysiosquilloides mapia* Erdmann & Boyer, 2003, and *Lysiosquilla isos* Ahyong, 2004. *Lysiosquillina lisa*, *Lysiosquilla campechiensis* Manning, 1962, and *Lysiosquilla suthersi*, however, proved problematical to assign to genera owing to the possession of features intermediate between *Lysiosquilla* sensu stricto and *Lysiosquillina* sensu stricto (see Ahyong and Randall 2001; Ahyong 2001; Fig. 1B, C). The presence of species transitional between *Lysiosquilla* and *Lysiosquillina* challenges the validity of the present generic system. In the present study, the status and composition of the lysiosquillid genera are tested by cladistic analysis of all known species of the family, and a new species of *Lysiosquilloides* is described from Taiwan.

MATERIALS AND METHODS

Taxonomy

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.

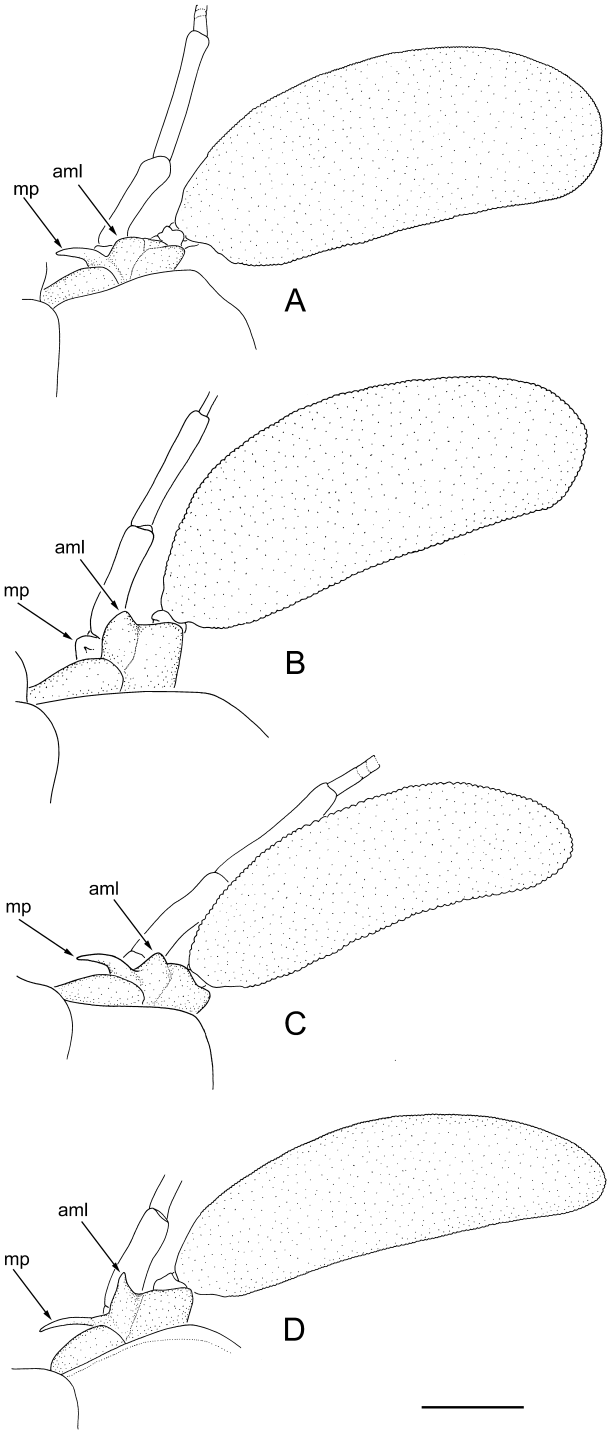

Fig. 1. Right antenna. A, *Lysiosquilla maculata* (Fabricius, 1793) (formerly *Lysiosquillina*), male, TL 162 mm, Queensland, Australia, AM P14919; B, *Lysiosquilla lisa* (Ahyong & Randall, 2001) comb. nov. (formerly *Lysiosquillina*), male holotype, TL 295 mm, Bali, Indonesia, MZB Cru1444; C, *Lysiosquilla suthersi* Ahyong, 2001, male holotype, TL 150 mm, Queensland, Australia, QM W24225; D, *Lysiosquilla scabricauda* (Lamarck, 1818), male TL 210 mm, Key West Florida, AM P45739. Scale: A = 7.0 mm, B = 3.5 mm, C = 12.0 mm, D = 5.0 mm. Abbreviations: mesial papilla (mp), anteromesial lobe (aml).

The corneal index (CI) is given as 100CL/corneal width. The propodal index (PI) of the raptorial claw is given as 100CL/propodus length. The genus names, *Lysiosquilla*, *Lyiosquillina* and *Lysiosquilloides* are abbreviated *L*., *Ln*., and *Ls*., respectively. The holotype of *Lysiosquilloides taiwanica* sp. nov. is deposited in the National Museum of Marine Biology and Aquarium, Kenting, Taiwan (NMMBA).

Phylogenetic analysis

All 20 recognised lysiosquillid species (including *Lysiosquilloides taiwanica* sp. nov.) were included as terminals. Although Lysiosquilloidea and Erythrosquilloidea are accepted as sister-groups, the phylogenetic position of Lysiosquillidae with the superfamily is currently unresolved. Phylogenetic analyses variously recover lysiosquillids as the sister group to Nannosquillidae or as sister to the remaining lysiosquilloids (Ahyong 1997; Ahyong and Harling 2000; Porter et al. 2010; Van Der Wal et al. 2017). Therefore, the analysis was rooted to *Erythrosquilla megalops* Manning & Bruce, 1984, but with a representative nannosquillid (*Acanthosquilla multifasciata* (Wood-Mason, 1895)) and tetrasquillid (*Heterosquilla platensis* (Berg, 1900)) included in the in-group. Character states of other ingroup species were scored from specimens in the collections of the Australian Museum, Sydney (AM) (*Lysiosquilla colemani* Ahyong, 2001, *Lysiosquilla isos* Ahyong, 2004, *Lysiosquillina lisa* Ahyong & Randall, 2001, *Lysiosquillina maculata* (Fabricius, 1793), *Lysiosquilla scabricauda* (Lamarck, 1818), *Lysiosquilloides siamensis* (Naiyanetr, 1980), *Lysiosquillina sulcata* (Manning, 1978), *Lysiosquilla sulcirostris* Kemp, 1911, *Lysiosquilla tredecimdentata* (Holthuis, 1941)); Macleay Museum, University of Sydney (MM) (*Lysiosquilla capensis* Hansen, 1895); Muséum National d'Histoire Naturelle, Paris (MNHN) (*Lysiosquilla hoevenii* Herklots, 1851, *Lysiosquilla monodi* Manning, 1977); Museum Zoologicum Bogoriense, Indonesia (MZB) (*Lysiosquillina lisa* Ahyong & Randall, 2001, *Lysiosquilloides mapia* Erdmann & Boyer, 2003); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM) (*Lysiosquilla campechiensis* Manning, 1961, *Lysiosquillina glabriuscula* (Lamarck, 1818), *Lysiosquilla manningi* Boyko, 2000, *Lysiosquilla panamica* Manning, 1971); Naturalis Biodiversity Centre, Leiden (*Lysiosquilloides aulacorhynchus* (Cadenat, 1957)); Queensland Museum, Brisbane (QM) (*Lysiosquilla suthersi* Ahyong, 2001).

The data matrix, constructed in MacClade 4.0 (Maddison and Maddison 2000), includes 23 terminals and 37 characters (Appendix 1). Characters were unordered (non-additive) and equally weighted, and polymorphisms were scored as such rather than assuming a plesiomorphic state. Trees were generated in PAUP 4.0b2a (Swofford 2002) under the heuristic search (MULPARS, tree-bisection-reconnection, 1000 replications with random input order). Relative stability of clades was assessed using jackknifing (30% character deletion; 1000 pseudoreplicates).

Morphological characters

Eyes, antennules and antennae

Character 1. Cornea mesial lobe: normal (0); conical (1). The mesial lobe in stomatopods with a broadened, bilobed eye, is typically rounded and somewhat hemispherical, but in most species of *Lysiosquilloides*, conical and distally pointed.

Character 2. Antennular somite dorsal process apices: directed anteriorly (0); directed anterolaterally (1). The apices of the antennular somite dorsal processes are directed anteriorly in the outgroups and most ingroup species, but are directed anterolaterally in *Lysiosquilla isos*, *L. monodi* and *L. sulcirostris*.

Character 3. Antennular somite dorsal processes: low, reduced (0); prominent, well-developed (1).

The dorsal processes of the antennular somite are prominent and well developed in erythrosquilloids and most lysiosquilloids, but low and reduced in *Lysiosquilloides*. The apices of the dorsal processes are directed anteriorly in most lysiosquilloids, anterolaterally directed in *Lysiosquilla isos*, *L. monodi* and *L. sulcirostris* (see Ahyong 2004).

Character 4. Antennular peduncle flanges: absent (0); present (1). The antennular peduncle of species of *Lysiosquilloides* have lateral flange on articles 1 and 2. The flange on article 1 is prominent, with the disto- and proximolateral corner almost a right-angle; that of article 2 is weakly cristate. Other lysiosquilloids lack these distinct flanges, instead having at most a narrow crista.

Character 5. Antennal protopod anteromesial projection: forming a spine (0); papillate (1); a low blunt lobe (2); absent (3). The anteromesial margin of the antennal protopod is armed in most species of *Lysiosquilla*, unarmed in most species assigned to *Lysiosquillina,* and with a low blunt lobe in *Lysiosquilla campechiensis*, *L. suthersi*, and *Lysiosquillina lisa*. In *Lysiosquilloides*, anteromesial projection forms a prominent papilla.

Character 6. Antennal papillae size: short, squat (0); elongated, prominent (1). The antennal papillae are slender and elongated in lysiosquillids and *Acanthosquilla*, short and squat in other taxa.

Character 7. Antennal mesial papilla: absent (0); present (1) (Ahyong and Harling 2000; Ahyong 2001).

Character 8. Antennal scale proportions: slender, length 3.0 × width or greater (0); broad, length about 2.5 × width (1) (Manning 1995; Ahyong 2001; Ahyong and Randall 2001).

Character 9. Antennal scale outline: pale (0); darkly pigmented (1) (Manning 1978; Ahyong 2001).

Character 10. Antennal scale median pigment patch: absent (0); present (1) (Manning 1978; Ahyong 2001).

Character 11. Ocular scales: short, blunt (0); slender, spiniform (1) (Ahyong 2001, 2004).

Rostral plate

Shape (Characters 12, 15, 16) and surface ornamentation (Characters 13, 14) of the rostral plate is informative for species and genera. The rostral plate is triangular or cordiform-ovate in most terminal taxa, but polygonal in *Acanthosquilla*. A median carina or median sulcus is usually present in lysiosquillids, but in several species, a flanking sulcus lateral to the midline may also be present.

Character 12. Rostral plate general shape: triangular (0); cordiform-ovate (1); polygonal (2).

Character 13. Rostral plate midline: smooth (0); carinate (1); sulcate (2).

Character 14. Rostral plate surface lateral to midline: smooth (0); sulcate (1).

Character 15. Rostral plate widest point: basally (0); proximally, slightly in advance of base (1); at midlength (2).

Character 16. Rostral plate proximal margin: straight to slightly convex (0); concave (1). The lateral margin in the proximal half of the rostral plate is concave in *Lysiosquilla campechiensis* and *L. suthersi*, straight to convex in other terminal taxa.

Thoracic somites and appendages

Character 17. Thoracic sternite 8 keel shape: rounded (0); quadrate (1); triangular (2). (Ahyong 2001).

Character 18. Thoracic sternite 8 apex: blunt (0); angular (1); sharply pointed (2). (Ahyong 2001).

Character 19. Pereopod 1 endopod shape: oval-elongate (0); liguliform (1). (Ahyong 1997; Ahyong and Harling 2000).

Character 20. Raptorial claw dactylus teeth: five (0); six (1); seven (2); eight (3); nine (4); ten or more (5).

Abdominal somites and appendages

Character 21. Abdominal somite 5 posterior margin spinules: absent (0); present (1). (Manning 1969, 1977).

Character 22. Abdominal somite 6 dorsal surface irregular, scabrous ornamentation: absent (0); present (1). Irregular, scabrous ornamentation on abdominal somite 6 is present in several species of

Lysiosquilla

Character 23. Abdominal somite 6 margin and surface spinulation: absent (0); present (1). Several lysiosquillids have small spinules on the margins and surface of abdominal somite 6.

Character 24. Abdominal somite 6 posterolateral spine: present (0); absent (1). The posterolateral angle of the abdominal somite 6 is unarmed in lysiosquillids, but produced to a spine in the remaining terminals.

Character 25. Uropodal protopod dorsal spinules: absent (0); present (1). The dorsal surface of the uropodal protopod may be spinulose adjacent to the dorsal spine above the exopod articulation.

Character 26. Uropodal protopod tubercle or spine at base of endopod articulation: present (0); absent (1).

Character 27. Uropodal endopod shape: reniform (0); spatulate (1). The uropodal endopod is reniform in two outgoups (*Heterosquilla* and *Erythrosquilla*), and spatulate in other terminal taxa.

Character 28. Uropodal protopod inner primary spine length: shorter than outer spine (0); longer than outer spine(1).

Character 29. Uropodal protopod terminal spines shape: broad, dorsoventrally flattened (0); slender (1). The terminal spines of the uropodal protopod are dorsoventrally flattened in erythrosquilloids and many lysiosquilloids, but slender and spiniform in lysiosquillids.

Telson

Character 30. Telson surface: smooth (0); tuberculate, spinular (1). The dorsal surface the telson is tuberculate and minutely spinular in adults of *Lysiosquilla hoevenii*, *L. manningi* and *L. scabricauda*.

Character 31. Telson outline in adults: polygonal (0); subrectangular (1); semi-ovate (2). The telson outline is subrectangular or semi-ovate in most ingroup species, and polygonal in *Heterosquilla* and the outgroup, *Erythrosquilla*.

Character 32. Telson median boss or carina posterior spine or lobe: present (0); absent (1).

Character 33. Telson lateral margin armature: absent (0); present (1). The lateral margin of the telson is lined with short spines or serrations in adults of *Lysiosquilla hoevenii* and *L. scabricauda*.

Character 34. Telson submedian teeth: movable (0); fixed (1) (Ahyong and Harling 2000).

Character 35. Telson submedian denticles: present (0); absent (0) (Ahyong and Harling 2000).

Character 36. Telson intermediate denticles: spiniform (0); rounded (1) (Ahyong and Harling 2000).

Character 37. Telson intermediate and lateral teeth: well-developed, spiniform (0); stout, fused into telson margin (1) (Ahyong and Harling 2000).

RESULTS

The phylogenetic analysis resulted in a single most parsimonious cladogram (length 78, consistency index 0.6154, retention index 0.8077; Fig. 2). Unambiguous character state changes are given in table 1. Lysiosquillidae comprises two reciprocally monophyletic clades, one corresponding to *Lysiosquilloides* (100% jackknife support) and the other containing the remaining lysiosquilloids (94% jackknife support), comprising species assigned to *Lysiosquilla* and *Lysiosquillina*. Within *Lysiosquilloides*, the Indo-West Pacific species form a clade as sister to the eastern Atlantic *Ls. aulacorhynchus*. *Lysiosquillina* is monophyletic but nested within *Lysiosquilla*, rendering the latter paraphyletic. The three species with features that are intermediate between *Lysiosquilla* and *Lysiosquillina*, namely *L. campechiensis*, *L. suthersi* and *Ln. lisa*, form a grade leading to *Lysiosquillina* sensu stricto. The remaining species of *Lysiosquilla* comprised two reciprocally monophyletic clades, one containing species having a rugose, tuberculate telson surface (*L. scabricauda*, *L. hoevenii* and *L. manningi*) and the other containing species with a relatively smooth, non-tuberculate telson surface.

SYSTEMATICS

Stomatopoda
Lysiosquilloidea Giesbrecht, 1910
Lysiosquillidae Giesbrecht, 1910

Lysiosquilla Dana, 1852

Lysiosquilla Dana, 1852: 615. Type species *Lysiosquilla inornata* Dana, 1852 [a junior subjective synonym of *Lysiosquilla scabricauda* (Lamarck, 1818)], by subsequent designation by Fowler (1912: 539). Name on Official List of International Commission on Zoological Nomenclature. Gender feminine.

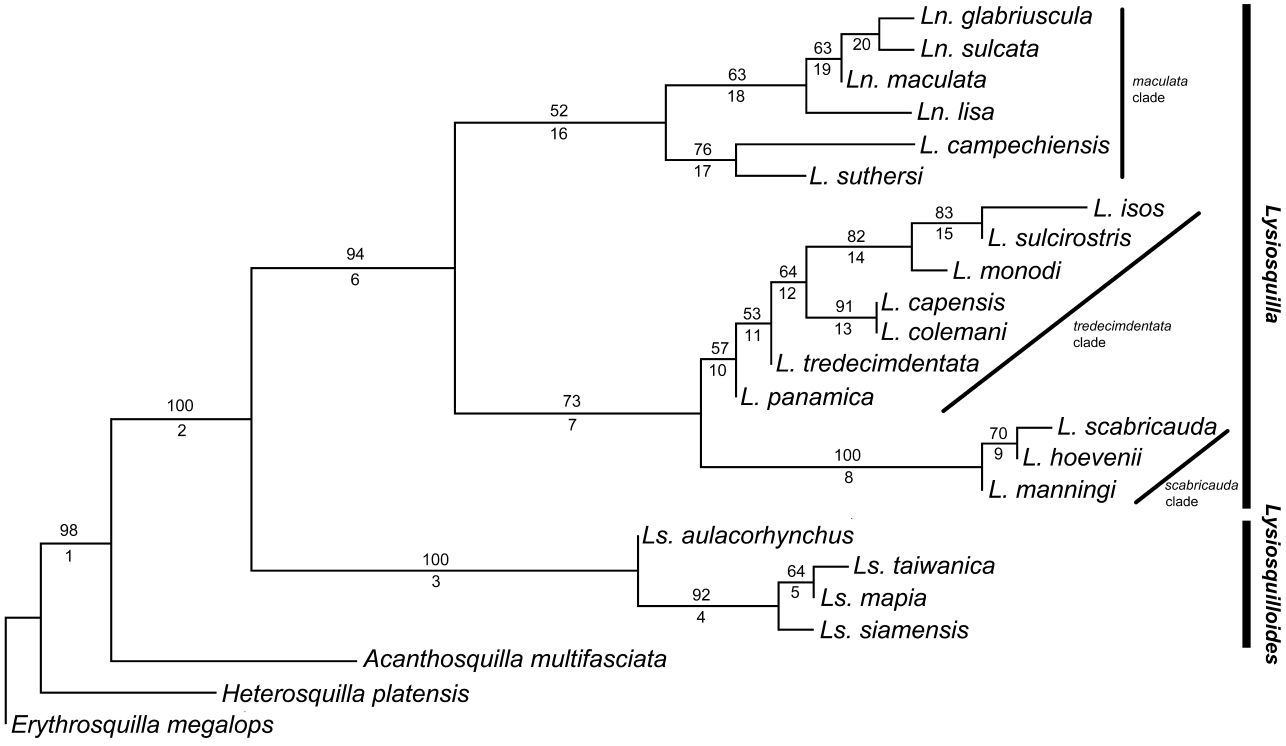

Fig. 2. Phylogeny of Lysiosquillidae. Single most parsimonious cladogram, length 78, consistency index 0.6154, retention index 0.8077. Numbers on nodes indicate jackknife support values (above) and node number (below) with unambiguous character state changes listed in table 1.

Lysiosquillina Manning, 1995: 133. Type species *Squilla maculata* Fabricius, 1793, by original designation. Gender feminine. [New synonymy]

Diagnosis: Rostral plate anteriorly smooth or with low median carina, without median sulcus. Eye large, T-shaped; cornea strongly bilobed, mesial lobe rounded. Dorsal processes of antennular somite well-developed, with anterolateral spine. Antennular peduncle article 1 weakly cristate laterally; article 2 subcylindrical. Antennal protopod mesially unarmed, with short blunt lobe or short anteromesial spine anterior to mesial papilla. Mandibular palp present or absent. Telson submedian teeth with fixed apices in adults; submedian denticles absent adults; median boss without posterior spine or lobe.

Composition: *Lysiosquilla campechiensis* Manning, 1962; *L. capensis* Hansen, 1895; *L. colemani* Ahyong, 2001; *L. glabriuscula* (Lamarck, 1818); *L. hoevenii* (Herklots, 1851); *L. isos* Ahyong, 2004; *L. lisa* (Ahyong & Randall, 2001) comb. nov.; *L. maculata* (Fabricius, 1793); *L. manningi* Boyko, 2000; *L. monodi* Manning, 1977; *L. panamica* Manning, 1971; *L. scabricauda* (Lamarck, 1818); *L. sulcata* Manning, 1978; *L. sulcirostris* Kemp, 1913; *L. suthersi* Ahyong, 2001; and *L. tredecimdentata* Holthuis, 1941.

Remarks: Given the synonymization of *Lysiosquillina* and *Lysiosquilla*, the two remaining genera of Lysiosquillidae are rediagnosed herein. *Lysiosquilla* now includes 16 species including the four species previous assigned to *Lysiosquillina*. Distinctions between *Lysiosquilla* and *Lysiosquilloides* are discussed in the Remarks of the latter. All species of *Lysiosquilla* exceed TL 100 mm in maximum size (usually > TL 150 mm), with *L. maculata* from the Indo-West Pacific, the largest known stomatopod, reaching TL 385 mm (Roxas and Estampador 1930).

Lysiosquilloides Manning, 1977

Lysiosquilloides Manning, 1977: 84–85. Type species *Lysiosquilla aulacorhynchus* Cadenat, 1957, by original designation and monotypy. Gender masculine.

Diagnosis: Rostral plate anteriorly with median sulcus. Eye large, T-shaped, cornea strongly bilobed, mesial lobe distinctly conical (less pronounced in *Ls. siamensis*). Dorsal processes of antennular somite low, blunt, without anterolateral spine. Antennular peduncle article 1 with prominent lateral crista, disto- and proximolateral corner almost a right-angle; article 2 lateral margin weakly cristate. Antennal protopod margin anterior to mesial papilla with prominent, anteromesial projection, distally uncalcified, papillate, apex soft, pointed. Mandibular palp present. Telson submedian teeth with movable apices; submedian denticles present adults; median boss with posterior spine or blunt lobe.

Composition: *Lysiosquilloides aulacorhynchus* (Cadenat, 1957); *Ls. mapia* Erdmann & Boyer, 2003; *Ls. siamensis* (Naiyanetr, 1980), *Ls. taiwanica* sp. nov.

Remarks: *Lysiosquilloides* is most easily

Table 1. Unambiguous character state reconstructions for single most parsimonious cladogram (length 78, consistency index 0.6154, retention index 0.8077) for nodes as indicated in figure 2

Node 1. 6: 0→1; 27: 0→1; 28: 0→1; 29: 0→1
Node 2. 7: 0→1; 19: 0→1; 24: 0→1; 36: 0→1; 37: 0→1
Node 3. 1: 0→1; 3: 1→0; 4: 0→1; 5: 0→1; 17: 0→1
Node 4. 8: 0→1; 11: 0→1; 15: 1→2
Node 5. 17: 1→2
Node 6. 32: 0→1; 34: 0→1; 35: 0→1
Node 7. 9: 0→1; 17: 0→2
Node 8. 18: 0→1; 21: 0→1; 22: 0→1; 23: 0→1; 25: 0→1; 30: 0→1; 31: 1→2
Node 9. 33: 0→1
Node 10. 19: 1→0
Node 11. 18: 0→2
Node 12. 2: 0→1
Node 13. 11: 0→1; 13: 1→0
Node 14. 12: 1→0; 14: 0→1
Node 15. 15: 1→0; 26: 0→1
Node 16. 5: 0→2
Node 17. 15: 1→2; 16: 0→1; 20: 5→2
Node 18. 10: 0→1
Node 19. 5: 2→3
Node 20. 20: 5→2

distinguished from *Lysiosquilla* by the movable (versus fixed) submedian teeth on the telson, presence of submedian denticles in adults, conical mesial lobe of the cornea (most prominent in *Ls. mapia* and *Ls. taiwanica*), the median boss of the telson having a short posterior spine or lobe (unarmed in *Lysiosquilla*), the low, unarmed dorsal processes of the antennular somite and the large, papillate dorsomesial projection on the antennal protopod. A new distinguishing feature of *Lysiosquilloides* identified here is in the ornamentation of the lateral margin of antennular peduncle articles 1–2: a distinct lateral crista on article 1 and weakly cristate margin on article 2. In *Lysiosquilla*, antennular peduncle article 1 is weakly cristate, and article 2 is subcylindrical and smooth, without a lateral crista.

In parallel with *Lysiosquilla* as revised herein, *Lysiosquilloides* includes species with slender through broad antennal scales. The antennal scale is most slender in *Ls. aulacorhynchus* (length 2.9–3.1 × width), broadest in *Ls. mapia* and *Ls. taiwanica* sp. nov. (~2.5) and somewhat intermediate in *Ls. siamensis* (2.4–2.7) (Manning 1977; Ahyong 2001; Erdmann and Boyer 2003).

Lysiosquilloides taiwanica sp. nov.

(Figs. 3, 4)

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Type material: NMMBA CD5609, male holotype (TL 145 mm), Hojie, Pingtung County, Taiwan, 26–28 m, from burrow in sandy bottom close to coral reef, coll. C.-W. Lin, 18 February 2017.

Diagnosis: Cornea mesial lobe distinctly conical, apex bluntly pointed. Antennal scale broad, length 2.50 × width. Rostral plate ovate, slightly longer than wide, widest at midlength; apex deflexed; with short median sulcus anteriorly. Raptorial claw dactylus with 7 teeth. Thoracic somite 8 sternal keel blunt, angular. Telson length 0.70 × width; with median boss terminating in small spine. Uropodal protopod with small ventral spine anterior to endopod articulation; endopod extending posteriorly slightly beyond telson posterior margin.

Description: Eye large, cornea set slightly obliquely on stalk, extending to end of antennular peduncle article 2 (Fig. 3A); cornea mesial lobe distinctly conical, apex bluntly pointed; CI 347. Ophthalmic somite anterior margin obtusely angular, unarmed; ventral margin with bluntly rounded median keel (Fig. 3D). Ocular scales produced as slender spines, directed anterodorsally (Fig. 3C).

Antennular peduncle length 0.46CL; articles 1–2 lateral margin with straight, narrow crista, widest on article 1 (Fig. 3E). Antennular somite dorsal processes low, broad, subquadrate, apices short, acute directed anteriorly (Fig. 3A).

Antennal protopod with 1 mesial and 2 ventral papillae; anteromesial margin with prominent, elongate lobe, basally sclerotised, distally papilliform, larger and longer than mesial papilla, apex inclined anteriorly (Fig. 3A, F). Antennal scale length 2.50 × width; 0.51CL; entire margin setose (Fig. 3A).

Rostral plate ovate; slightly longer than wide; widest at midlength; margins convex, almost straight in proximal one-third; apex slightly deflexed, rounded; dorsal surface with median sulcus anteriorly; ventral surface smooth (Fig. 3A, B). Carapace anterolateral angles rounded; posterior margin concave.

Raptorial claw (Fig. 3G) dactylus with 7 graded teeth, outer margin broadly convex along distal half, almost straight along proximal half, with shallow basal notch. Propodus longer than carapace, distal margin unarmed; occlusal margin pectinate, with 4 movable spines proximally; PI 73. Carpus dorsal margin terminating in short stout spine, directed ventrally when claw folded. Merus unarmed. Ischium length one-third merus length.

Mandibular palp 3-segmented. Maxilliped 5 basal segment unarmed; merus with broad

flange on inner margin, distally truncate (Fig. 3H). Maxilliped 1–5 each with epipod.

Thoracic somite 5 lateral process obsolete. Thoracic somites 6–8 lateral process broadly rounded (Fig. 3I). Thoracic somite 8 sternal keel angular, blunt (Fig. 3J).

Pereopods 1–3 proximal article unarmed; endopod slender, flattened, liguliform (Fig. 3K–M).

Pleopod 1 endopod without posterior ‘endite’ (Fig. 3Q).

Abdominal somites 1–5 with rounded posterolateral angles. Somite 5 smooth medially and laterally; posterior margin unarmed. Abdominal somite 6 (Fig. 3N) smooth medially; with low, smooth lateral boss flanked mesially by shallow groove; with acute, triangular ventrolateral projection anterior to uropodal articulation; sternum posterior margin unarmed.

Telson (Fig. 3N) subquadrate, wider than long, length 0.70 × width; surface smooth, with few, broad, shallow pits flanking low median and submedian bosses; median boss posterior spine well developed, slightly overreaching posterior telson margin (Fig. 3O); margin carina distinct; lateral margins weakly convex, unarmed; articulated submedian teeth slender, conical; 13–16 submedian denticles either side of midline; intermediate and lateral teeth short, slender; intermediate and lateral denticles rounded, each with minute spiniform apex; ventral surface unarmed.

Uropodal protopod (Fig. 3N, P) unarmed dorsally

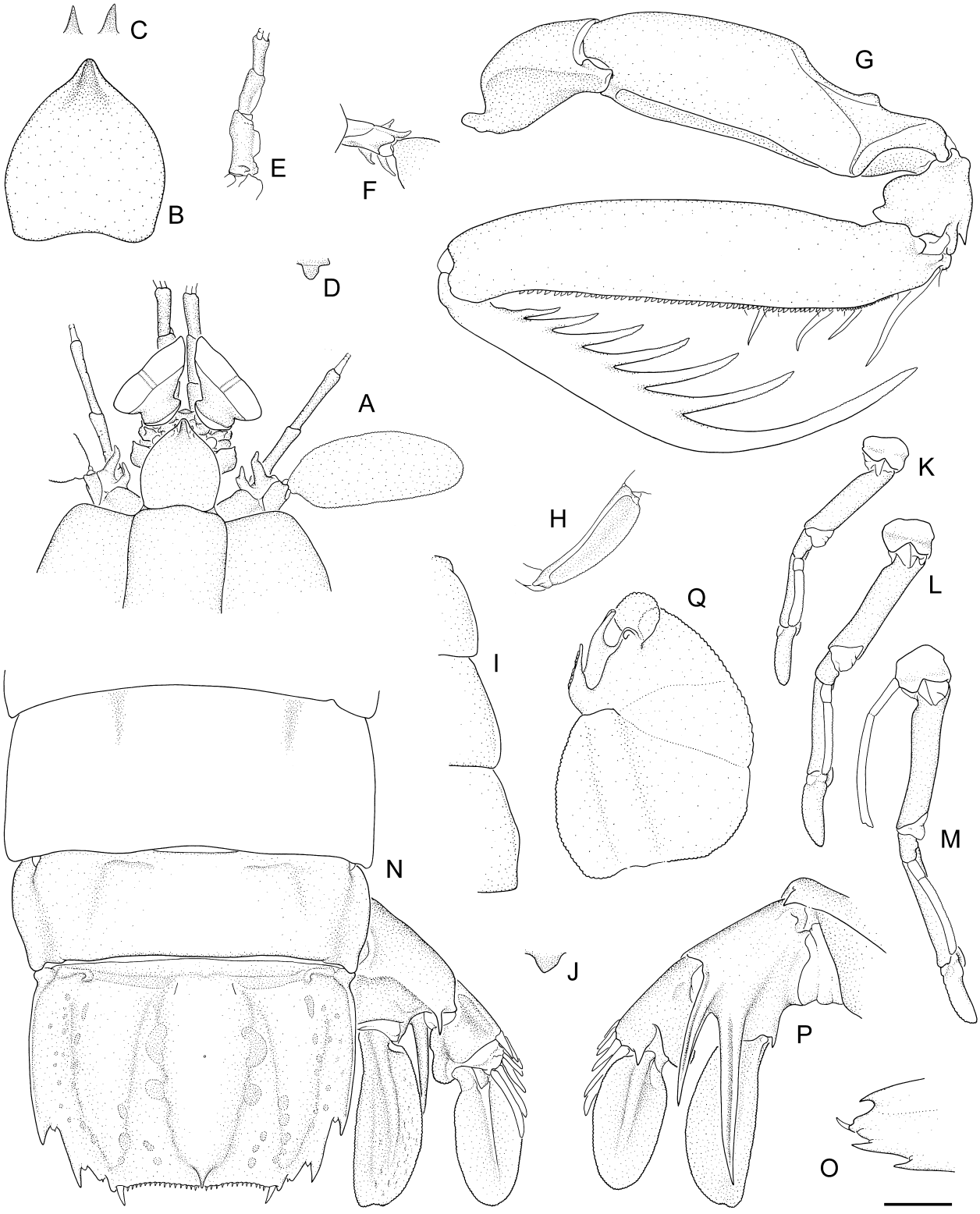

Fig. 3. *Lysiosquilloides taiwanica* sp. nov., male holotype, TL 145 mm, Hojie, Taiwan, NMMBA CD5609: A, anterior cephalothorax, dorsal view; B, rostral plate, dorsal view; C, ocular scales, dorsal view; D, ophthalmic somite ventral keel, right lateral view; E, right antennular peduncle, dorsal view; F, right antenna, lateral view; G, right raptorial claw, lateral view; H, right maxilliped 5 merus; I, right thoracic somites 6–8, dorsal view; J, thoracic somite 8 sternal keel, right lateral view; K–M, right pereopods 1–3, posterior view; N, posterior abdomen and right uropod, dorsal view; O, posterior telson, right lateral view; P, right uropod, ventral view; Q, right pleopod 1 endopod, anterior view. Scale: A, D–P = 5 mm; B, C, Q = 2.5 mm.

except for spine above proximal exopod articulation; with small ventral spine anterior to endopod articulation. Uropodal exopod proximal segment unarmed dorsally; inner distal margin with broad, round lobe; outer margin with 7 movable, distally flattened spines, distalmost spine reaching midlength of distal segment; distal margin with stout ventral spine. Exopod distal segment ovate, length twice width, longer than proximal segment, with dorsal and ventral median carina. Endopod elongate, length 2.45 × width, extending posteriorly slightly beyond telson posterior margin.

Colour in life: (Fig. 4). Carapace and antennal scale transversely banded with pale cream-yellow and dark maroon; maroon bands diffuse, mottled, on anterior

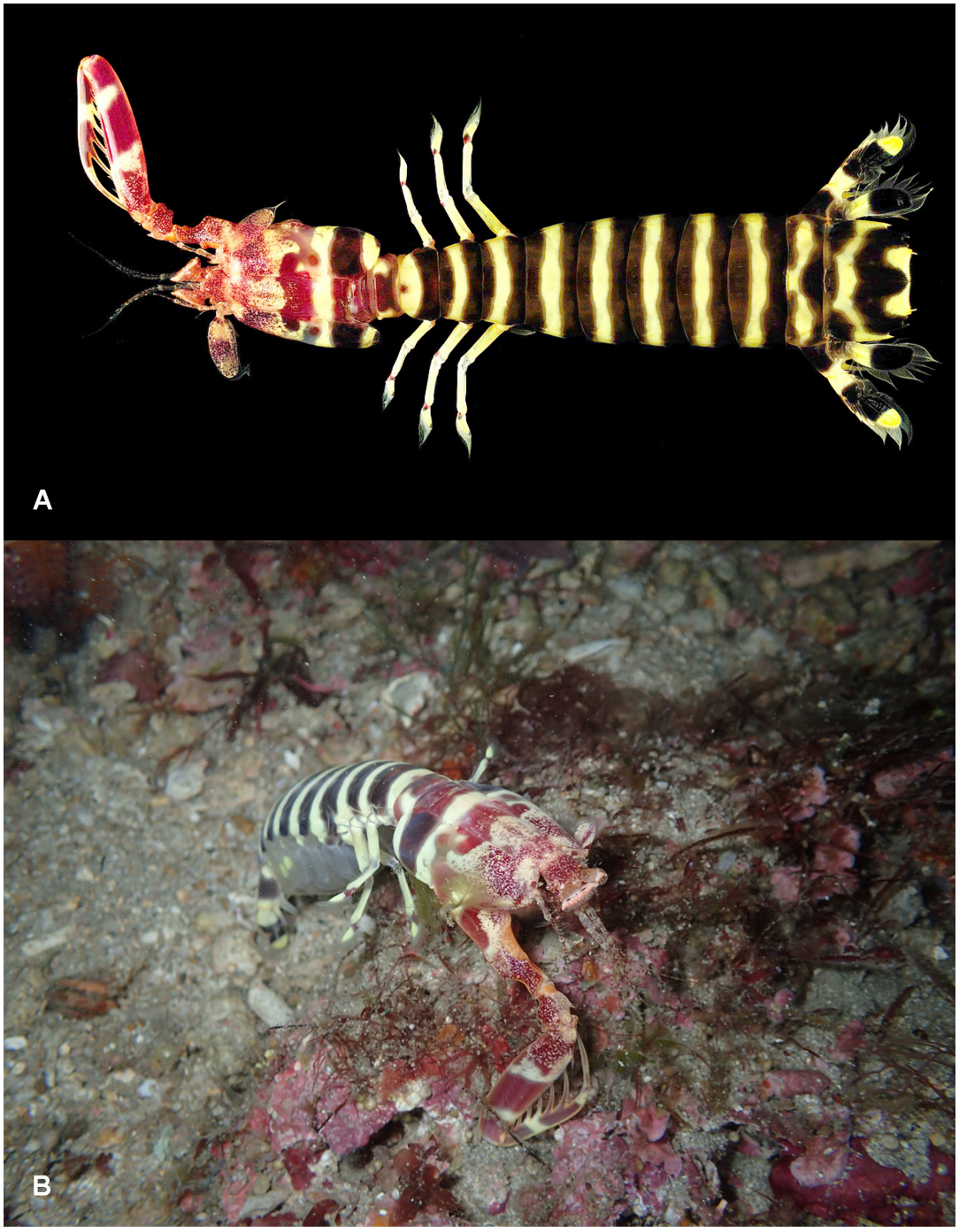

Fig. 4. *Lysiosquilloides taiwanica* sp. nov., male holotype, TL 145 mm (left raptorial claw missing), Hojie, Taiwan, NMMBA CD5609, colour in life. A, dorsal habitus; B, in habitat.

half of carapace, solid medially on posterior half, with posterior band black-brown laterally. Raptorial claw dactylus to ischiomerus banded pale yellow and dark maroon. Pereopods proximally yellow, distally translucent white with maroon proximal spot on distal exopod article. Thorax and abdomen transversely banded with pale yellow and black-brown across somite articulations; bands on abdominal somite 6 and telson becoming irregular, blotchy, posterior dark band on telson W-shaped. Uropodal protopod black-brown proximally, pale yellow distally; exopod pale yellow with broad black-brown band across articulation of distal and proximal articles; endopod pale yellow proximally, black-brown distally.

Measurements: TL 145 mm, CL 25.3 mm, cornea width 7.3 mm, antennular peduncle length 11.7 mm, antennal scale length 12.9 mm, raptorial claw propodus length 36.2 mm.

Etymology: Named *taiwanica*, after the region of the type locality.

Remarks: Like its Indo-West Pacific congeners, *Ls. taiwanica* has a cordiform-ovate rostral plate (Fig. 3A, B) (versus triangular in the West African *Ls. aulacorhynchus*), a relatively broad antennal scale (length about 2.5 × width versus 2.9–3.1 in *Ls. aulacorhynchus*) and a posterior spine on the median boss of the telson (Fig. 3N, O) (blunt, dorsoventrally flattened lobe in *Ls. aulacorhynchus*). As in other species of *Lysiosquilloides*, the apex of the rostral plate is rounded, but also deflexed, and because of the anterior median sulcus on the dorsal surface, the apex can appear to be notched if observed in oblique dorsal view. The new species most closely resembles *Ls. mapia* in sharing the prominently conical mesial lobe of the cornea with bluntly pointed apex (Fig. 3A) (versus conical with rounded apex in *Ls. siamensis* and *Ls. aulacorhynchus*) and angular thoracic somite 8 sternal keel (Fig. 3J) (versus quadrate in *Ls. aulacorhynchus* and *Ls. siamensis*). *Lysiosquilloides taiwanica* and *Ls. mapia* differ subtly morphologically: the telson is slightly shorter proportionally in *Ls. taiwanica* (length 0.70 × width versus 0.74) and when the uropod is extended, the endopod extends slightly beyond (versus not reaching) the posterior margin of the telson (Fig. 3N). The most striking difference between *Ls. taiwanica* and *Ls. mapia*, however, is the live colouration (Fig. 4; Erdmann and Boyer 2003: figs 2, 3). The raptorial claws and anterior half of the cephalothorax are almost uniformly bright orange in *Ls. mapia*, compared to mottled maroon with diffuse cream banding in *Ls. taiwanica*. In-situ, *Ls. mapia* at its burrow mouth is unlikely to be mistaken for other lysiosquillids because of its bright orange cephalothorax, but *Ls. taiwanica* at its burrow may be overlooked as *L. lisa* because of often similar mottled cream and maroon colouration. Additionally, the thorax and abdomen are transversely banded with black-brown and yellow in *Ls. taiwanica* or with black-brown, yellow and orange in *Ls. mapia*.

Although *Ls. taiwanica* is confirmed only from Taiwan based on a specimen, underwater photographs of individuals from Milne Bay, Papua New Guinea (https://www.inaturalist.org/observations/19753630) and the Philippines (Moalboal, 7 m: https://www.inaturalist.org/observations/7792398; Leyte Gulf, 24 m: https://www.poppe-images.com/index.php/product/lysiosquillina-lisa-6/) suggest the species has a wide range in the western Pacific.

Habitat: Burrowing in sandy bottom close to coral reef; with small pieces of coral rubble scattered around the burrow mouth; 7–28 m.

Distribution: Presently known with certainty only from Taiwan but probably wide ranging in the western Pacific.

Key to species of *Lysiosquilloides*

1. Rostral plate triangular. Antennal scale slender, length ≥ 2.9 × width. Telson median boss terminating in blunt, medially emarginated lobe. Distribution: West Africa ..... *Ls. aulacorhynchus*
– Rostral plate cordiform. Antennal scale broad, length 2.4–2.7 × width. Telson median boss terminating in acute spine. Distribution: Indo-West Pacific 2
2 Cornea mesial lobe rounded. Thoracic somite 8 sternal keel quadrate ..... *Ls. siamensis*
– Cornea mesial lobe distinctly conical. Thoracic somite 8 sternal keel angular 3
3 Cephalothorax anterior half and raptorial claw uniformly bright orange in life. Telson length 0.74 × width. Uropod, when extended, with endopod not extending posteriorly to posterior margin of telson ..... *Ls. mapia*
– Cephalothorax anterior half and raptorial claw with cream banding and mottled maroon in life. Telson length 0.70 × width. Uropod, when extended, with endopod extending posteriorly beyond posterior margin of telson ..... *Ls. taiwanica*

DISCUSSION

Consistent synapomorphies of *Lysiosquilloides* identified here are the presence of low, unarmed dorsal processes of the antennular somite (Character 3:0; Fig. 3A), the presence of lateral cristae on the antennular peduncle (Char. 4:1; Fig. 3E), and the large, papillate dorsomesial projection on the antennal protopod (Char. 5:1; Fig. 3A, E). The distinctly conical cornea is also a derived feature (Char. 1: 1; Fig. 3A), although being less pronounced in *Ls. siamensis.* The presence of eight teeth on the dactylus of the raptorial claw is a ground-pattern state in *Lysiosquilloides* but the number varies in *Ls. siamensis* and *Ls. mapia*. The most taxonomically

distinctive features of *Lysiosquilloides*, the movable apices of the submedian teeth of the telson and presence of submedian denticles in adults (Fig. 3M), are plesiomorphies, present in most lysiosquilloids (Ahyong and Harling 2000).

The monophyletic origin of the Indo-West Pacific species of *Lysiosquilloides* with respect to *Ls. aulacorhynchus* from West Africa suggests possible differentiation following the formation of the Atlantic and Pacific oceans during the Mesozoic. The Indo-West Pacific species of *Lysiosquilloides* all occur in the western Pacific between New Caledonia, Australia and the South China Sea (Ahyong 2001; Erdmann and Boyer 2003; Laboute and Richer de Forges 2004); the genus is yet to be recorded from the Indian Ocean.

Manning (1995) diagnosed *Lysiosquillina* with a broad antennal scale with length of about 2.5× width and an unarmed antennal protopod, and restricted *Lysiosquilla* to species with a slender antennal scale (length 3.0× width or greater) and dorsomesial spine on the antennal protopod. The position of *Lysiosquillina* as nested within *Lysiosquilla*, together with the polarization of characters 5 and 8 indicates that the broad antennal scale and absence of the anteromesial spine on the antennal peduncle are derived states in Lysiosquillidae. Although *Lysiosquillina* is itself monophyletic, its nested position within *Lysiosquilla* causes paraphyly of the latter. Moreover, three species with features intermediate between *Lysiosquillina* and *Lysiosquilla* sensu Manning (1995), namely *L. campechiensis*, *L. suthersi* and *Ln. lisa*, form a grade leading to *Lysiosquillina* sensu stricto (Fig. 1). The antennal protopod in these three 'aberrant' species is neither unadorned mesially (as in *Lysiosquillina* sensu stricto; Fig. 1A) nor spined (as in *Lysiosquilla* sensu stricto; Fig. 1D), but presents an intermediate condition in a short, blunt mesiodorsal lobe (Fig. 1B, C). Their generic placement, then, relies solely on the proportions of the antennal scale: slender in *Lysiosquilla suthersi* and *Lysiosquilla campechiensis* and relatively broad in *Lysiosquillina lisa* (although the antennal scale is proportionally narrower than in other species of *Lysiosquillina* at 2.6–3.0; Ahyong & Randall, 2001). The transitional features in *L. suthersi*, *L. campechiensis* and *Ln. lisa* invalidate the morphological distinctions between *Lysiosquilla* and *Lysiosquillina* proposed by Manning (1995). Therefore, given the paraphyly of *Lysiosquilla* caused by *Lysiosquillina*, and the lack of effective distinguishing characters, synonymization of the two genera is justified.

Three major clades are evident in *Lysiosquilla* as redefined here: a clade in which the broadened antennal scale is derived (Char. 8:1) and in which the anteromesial antennal spine is lost (Char. 5:2), containing species previously referred to *Lysiosquillina* and allies (here referred to as the *maculata* clade); a clade containing species in which the telson, abdominal somite 6 and uropods are dorsally spinulate and scabrous in adults (Chars. 22:1, 23:1, 25: 1, 29:1, 30:2) (including the type species of the genus, *L. scabricauda*; the *scabricauda* clade); and a clade containing the remaining non-dorsally spinose species of the genus (the *tredecimdentata* clade), united by the elongate-ovate pereopod 1 endopods (Char. 19:1). Members of the *scabricauda* clade are restricted to the Atlanto-East Pacific, but other groups within the genus are represented in both the Atlanto-East Pacific and Indo-West Pacific. For instance, in the *maculata* clade, the Indo-West Pacific *L. suthersi* and *L. sulcata* are most closely related to *L. campechiensis* and *L. glabriuscula*, respectively, from the Western Atlantic. Most species of the *tredecimdentata* clade occur in the Indo-West Pacific, except for *L. monodi* from the eastern Atlantic (as sister to *L. sulcirostris* + *L. isos*) and *L. panamica* from the eastern Pacific (as sister to the remaining members of the *tredecimdentata* clade). *Lysiosquilla colemani* (southeastern Australia) and *L. capensis* (South Africa), both from southern hemisphere temperate waters, are sister species. Although regional differentiation has occurred in *Lysiosquilla*, the presence of sister lineages that span the Indo-West Pacific and Atlanto-East Pacific is consistent with a Tethyan origin hypothesized for the group (Reaka and Manning 1987).

Synapomorphies of *Lysiosquilla* as reconstituted here are the absence of the posterior spine on the median boss of the telson (Char. 32: 1), fixed apices of the submedian teeth (Char. 34: 1), and absence of submedian denticles (Char. 35: 1). The corresponding condition for each of these features is evident in *Lysiosquilloides* as moveable apices of the submedian telson teeth, a short posterior spine on the median boss of the telson, and presence of submedian denticles in adults. In addition, *Lysiosquilloides* also shares the presence of lateral cristae on antennular peduncle articles 1–2 and the papillate anteromesial projection on the antennal protopod, which finds its homologue in the mesial spine or lobe of most species of *Lysiosquilla*.

Prior to the present study 31 genera and 68 species of stomatopod were known from Taiwan, on the basis of adult specimens (Ahyong et al. 2008; Yeh and Hsueh 2010; Wang and Chiou 2017; Ahyong and Lin 2020). Subsequently, Wong et al. (2021) added three species and two genera to the known Taiwanese stomatopod inventory by associating captured larvae with known adult DNA sequences. The discovery of *Ls. taiwanica* sp. nov. confirms an additional genus and species from Taiwan. Notable among the findings of Wong et al. (2021) were several nannosquillid lysiosquilloid

larvae of the "*Acanthosquilla* group" that could not yet be matched to known sequences. Although *Ls. taiwanica* sp. nov. belongs to a different family than the unidentified larvae of Wong et al. (2021), the present discovery further highlights the underestimated stomatopod diversity in Taiwanese waters. The known Taiwanese stomatopod fauna now stands at 33 genera and 72 species.

CONCLUSIONS

Phylogenetic analysis of all species of the cosmopolitan mantis shrimp family Lysiosquillidae, previously comprising three genera, corroborated the validity of *Lysiosquilloides* but demonstrated that *Lysiosquillina* is deeply nested within *Lysiosquilla*. Moreover, the presence of species whose morphology is transitional between *Lysiosquilla* and *Lysiosquillina* confounds reliable separation of the two genera. Therefore, *Lysiosquillina* is synonymized with *Lysiosquilla*, leaving two genera in family. Discovery of a *Lysiosquilloides mapia* sp. nov. expands the Taiwanese stomatopod fauna to 33 genera and 72 species.

Acknowledgments: This work and the new species name were registered with ZooBank under urn:lsid:zoobank.org:pub:B93DDB43-07B7-4632-924E-CB43337C8CE6. We wish to thank Rafael Lemaitre and Karen Reed for their hospitality during visits to the National Museum of Natural History, Smithsonian Institution. Karen Van Dorp (Naturalis Biodiversity Centre), Peter Davie (Queensland Museum), and Laure Corbari (Muséum national d'Histoire naturelle, Paris) are gratefully acknowledged for the loan of specimens. We also thank three anonymous reviewers for their constructive comments on the manuscript.

Authors' contributions: STA conducted analyses and conceived the study. CWL collected and photographed specimens. Both authors drafted, read and approved the final manuscript.

Competing interests: The authors declare no competing interests.

Availability of data and materials: Not applicable.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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Supplementary materials

Appendix 1. Data matrix. Polymorphic characters coded as follows: 0&1 = A, 1&2 = B, 2&3 = C, 3&4&5 = D. *Lysiosquilla* (*L.*), *Lysiosquillina* (*Ln.*), *Lysiosquilloides* (*Ls.*), *Heterosquilla* (*H.*), *Acanthosquilla* (*A.*), *Erythrosquilla* (*E.*)

	000000000011111111122222222233333333 **12345678901234567890123456789012345678**
L.campechiensis	00102110100110210012010100111011011111
L.capensis	01100110101100102205000100111011011111
L.colemani	01100110101100102205000100111011011111
L.hoevenii	00100110100110102115111110111121111111
L.isos	01100110010011002000B00010111011011111
L.manningi	00100110100110102115111110111121011111
L.monodi	01100110100011102204000100111011011111
L.panamica	00100110100110102005000100111011011111
L.scabricauda	0010011010011010211D11111111112111111
L.sulcirostris	01100110100011002200C00010111011011111
L.suthersi	00102110000110210012000101111011011111
L.tredecimdentata	00100110100110102205000100111011011111
Ln.glabriuscula	00103111010110100000B00010111011011111
Ln.lisa	0010211A0101110000150001011110110111
Ln.maculata	00103111010110100015000101111011011111
Ln.sulcata	0010311101012010001C00010111011011111
Ls.aulacorhynchus	10011110000020101013000100111010000011
Ls.mapia	10011111001120202013000100111010000011
Ls.siamensis	1001111100112020101C00010011101000011
Ls.taiwanica	10011111001120202012000100111010000011
H.platensis	00100000100100100005000000000000000000
A.multifasciata	00103100000200100000A00000111102000000
E.megalops	00000000000000000000000000000000000000