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DNA Barcoding Identifies the Final Pelagic Larval Stage of the Mantis Shrimp *Lysiosquilloides taiwanicus* Ahyong & Lin, 2022 (Crustacea, Stomatopoda, Lysiosquilloidea) from Taiwan and Japan

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Understanding the occurrence and developmental stages of larvae is essential for ecological studies and the effective resource management of stomatopods. However, reliable species identification of stomatopod larvae remains limited, even for species of commercial interest. During a scuba diving survey off Okinawa Island, a larva exhibiting a distinctive carapace shape was collected. DNA barcoding identified the specimen as *Lysiosquilloides taiwanicus* Ahyong & Lin, 2022, representing the first confirmed record of the pelagic larval stage of this species. This Japanese larval specimen is also morphologically identical to a larva of this species recently collected off southeastern Taiwan. The morphological characteristics of the larva are described and illustrated herein. One of the most remarkable characteristics of this larva is the shape of the carapace: almost triangular in dorsal view; armed with a long rostrum, a long median spine, and a pair of posterolateral spines; posterolateral spines extending laterally. The uropodal protopod is forked, with the inner fork longer than the outer, as observed in other lysiosquillid larvae. Both the Japanese and Taiwanese specimens represent the final pelagic larval stage, there is a high possibility that adult *L. taiwanicus* also occurs in Japanese waters. Morphological comparisons with previously described larvae tentatively assigned to the family Lysiosquillidae demonstrate that these specimens represent the first documented larval form of *L. taiwanicus* worldwide.

Keywords: Carapace morphology, Lysioerichthus, Pelagic larva, Taxonomy, Uropod

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BACKGROUND

Stomatopods or mantis shrimps are crustaceans belonging to the order Stomatopoda in the class Malacostraca. They are ecologically important animals (Antony et al. 2010; Schram et al. 2013; Ng et al. 2026) as well as important fisheries resources particularly in the Asian and Mediterranean regions (Ahyong et al. 2017). In Asia, the Japanese mantis shrimp *Oratosquilla oratoria* (de Haan, 1844) is the most commercially harvested species, followed by large stomatopods, such as the members of the genus *Harpiosquilla* Holthuis, 1964 and the family Lysiosquillidae Giesbrecht, 1910 including the zebra mantis shrimp *Lysiosquilla maculata* (Fabricius, 1793) (Hamano 2005; Arshad et al. 2015).

As with many other aquatic animals, information on larval occurrence and developmental stages is essential for understanding the ecology, assessing biodiversity, and managing fishery resources of stomatopods (Shanbhogue 1973; Hamano 2005; Ahyong et al. 2014). Achieving these objectives requires accurate species identification of stomatopod larvae. The second maxilliped is well-developed from the mid-larval stages onward, making the stomatopod larvae relatively easy to distinguish from other planktonic crustaceans captured by plankton nets or other fishing gear. Furthermore, larvae can be identified to the superfamily level based on the morphology of the carapace, uropods, and telson (Ahyong et al. 2014). However, reliable diagnostic information for identification at lower taxonomic levels remains extremely limited. Although morphological classifications schemes for stomatopod larvae have been proposed, they are still very fragmentary and often rely on assumptions based on the known distribution of adults (*e.g.*, Komai and Tung 1929; Alikunhi 1952; Veena and Kaladharan 2010). Given that stomatopod larvae may disperse over wide areas during their prolonged planktonic phase, the collection locality of larvae does not necessarily correspond to the distribution of adults. Currently, DNA barcoding offers an effective approach to reduce uncertainty in larval species identification and complement morphology-based classifications of crustaceans including stomatopods (Feller et al. 2013; Palecanda et al. 2020; Steck et al. 2020; Wong et al. 2021; Hidaka et al. 2022; Jiang et al. 2024; Fujita et al. 2025).

Lysiosquilloides taiwanicus Ahyong and Lin, 2022 (originally spelled *taiwanica* but corrected here to *taiwanicus* following the masculine gender of *Lysiosquilloides* Manning, 1977) was described from Taiwan as the fourth known species of the genus *Lysiosquilloides* (here after as *L.*). This discovery has significantly advanced the systematic revision and taxonomic understanding of the family Lysiosquillidae (Ahyong and Lin 2022). In contrast to the progress made in the taxonomy of adult forms, taxonomic assignment of larval forms remains poorly developed. To date, larval stages have been described for four species of the genus *Lysiosquilla* (here after as *Ly.*) (Alikunhi 1952; Townsley 1953; Michel 1970; Diaz and Manning 1998; Steck et al. 2022), whereas no larval forms have been previously identified in any species of *Lysiosquilloides*. Amongst the stomatopod larvae recently collected off Japan and Taiwan, there are specimens identifiable as *Lysiosquilloides taiwanicus* through DNA barcoding. This result is reported herein and being the first account of the larval morphology of *Lysiosquilloides* as well as representing the first description of the larval form of *L. taiwanicus*.

MATERIALS AND METHODS

A stomatopod larva (NSMT-Cr 33382) was collected during a scuba diving survey conducted at night off Kyan (approximately 5 km west of the coast, ca. 10 m), Itoman, Okinawa Prefecture on November 12, 2024. The sampling method for the scuba diving survey followed Wakabayashi et al. (2020). Another larva (NTOU_CHYS321) was collected from southeastern Taiwan (station SK3, 21°47.64'N 121°37.67'E, 107–958 m) by ORI plankton net on July 1, 2025. Both larvae were preserved in 99.5% ethanol.

DNA sequences for barcoding were determined following the method described by Fujita et al. (2025) with minor modifications. Left pleopods 1 and 2 were removed from the stomatopod larvae for genomic DNA extraction. A partial sequence of the mitochondrial 16S ribosomal RNA

(16S) gene was amplified using the primer set of 16S1471/16S1472 (Crandall and Fitzpatrick 1996) and the purified PCR product was used for sequencing. The determined nucleotide sequence was confirmed using Chromas 2.6.6v (Technelysium Pty Ltd, South Brisbane) and the sequence similarity was searched using BLASTN (National Center for Biotechnology Information, Bethesda, MD, USA).

The measurements were obtained from the larval specimens as follows: total length (TL) from the distal end of rostrum to posterior end of telson including posterior spine, carapace length (CL) from the base of rostrum to posterior end of carapace midline excluding median spine, carapace width (CW) as the maximum distance across the carapace, carapace height (CH) as the height of carapace from the ventral margin to the base of median spine, and pleon width (PW) as the maximum distance across the pleon. Body observations and illustrations were conducted under a stereomicroscope (SZX-7, Olympus, Tokyo) and compound microscope (BX-51, Olympus, Tokyo) with the aid of a camera lucida attachment (U-DA, Olympus, Tokyo). The illustrations were digitally edited using drawing software MediBang Paint Pro (MediBang, Tokyo). The Japanese specimen (NSMT-Cr 33382) was dissected in preparation for the Description. Terminology and developmental stage assessments followed Ahyong and Lin (2022) and Fujita et al. (2025). The specimens used in this study were deposited in crustacean collections of the National Museum of Nature and Science, Tsukuba (NSMT) and National Taiwan Ocean University, Keelung (NTOU).

RESULTS

Identification of the stomatopod larva

The partial 16S rRNA gene sequences obtained from the larvae were deposited in GenBank (PZ710570.1, PZ710571.1). The nucleotide pairwise differences were 0.54% (PZ710570.1) and 0.19% (PZ710571.1) with *L. taiwanicus* (PV188212.1) which sequence was determined from the holotype (NMMBA CD5609). The next closest sequence matching was *Lysiosquilloides siamensis* (Naiyanetr, 1980) (ON490887.1) with 4.84% (PZ710570.1) and 4.79% (PZ710571.1) divergence. The sequence differences ranged 9.38–11.58% with species of *Lysiosquilla*. The present larvae can be positively identified as *L. taiwanicus* based on high (*i.e.*, 99.46–99.81%) molecular similarity (Tang et al. 2010).

Morphological descriptions

Order Stomatopoda Latreille, 1817

Suborder Unipeltata Latreille, 1825

Superfamily Lysiosquilloidea Giesbrecht, 1910

Family Lysiosquillidae Giesbrecht, 1910

***Lysiosquilloides taiwanicus* Ahyong & Lin, 2022**

(New Japanese standard name: Shojo-Nokoba-Torafu-Shako)

Final pelagic stage larva

(Fig. 1)

Material examined: JAPAN • 1 larva, TL 16.3 mm, CL 7.6 mm, CW 8.1 mm, CH 5.8 mm, PW 3.4 mm; Okinawa, Itoman, off Kyan; ca. 10 m; 12 Nov. 2024; Shota Ishino and Aiko Kayama leg.; scuba diving; NSMT-Cr 33382; GenBank: PZ710570.1. TAIWAN • 1 larva, TL 13.7 mm, CL 6.2 mm, CW 6.8 mm, CH 5.3 mm, PW 2.9 mm; R/V "New Ocean Researcher 1" station SK3, 21°47.64'N, 121°37.67'E, off southeastern coast; 107–958 m; 1 Jul. 2025; Chien-Hui Yang leg.; ORI plankton net; NTOU_CHYS321 GenBank: PZ710571.1.

Etymology of Japanese name: The new Japanese name refers to *Shōjō*, the Japanese name for an imaginary creature originating from traditional Chinese literature (*Xingxing* in Chinese), which is commonly described as having red or yellow fur that recalls the coloration of adult *L. taiwanicus* (Ahyong and Lin 2022: fig. 4).

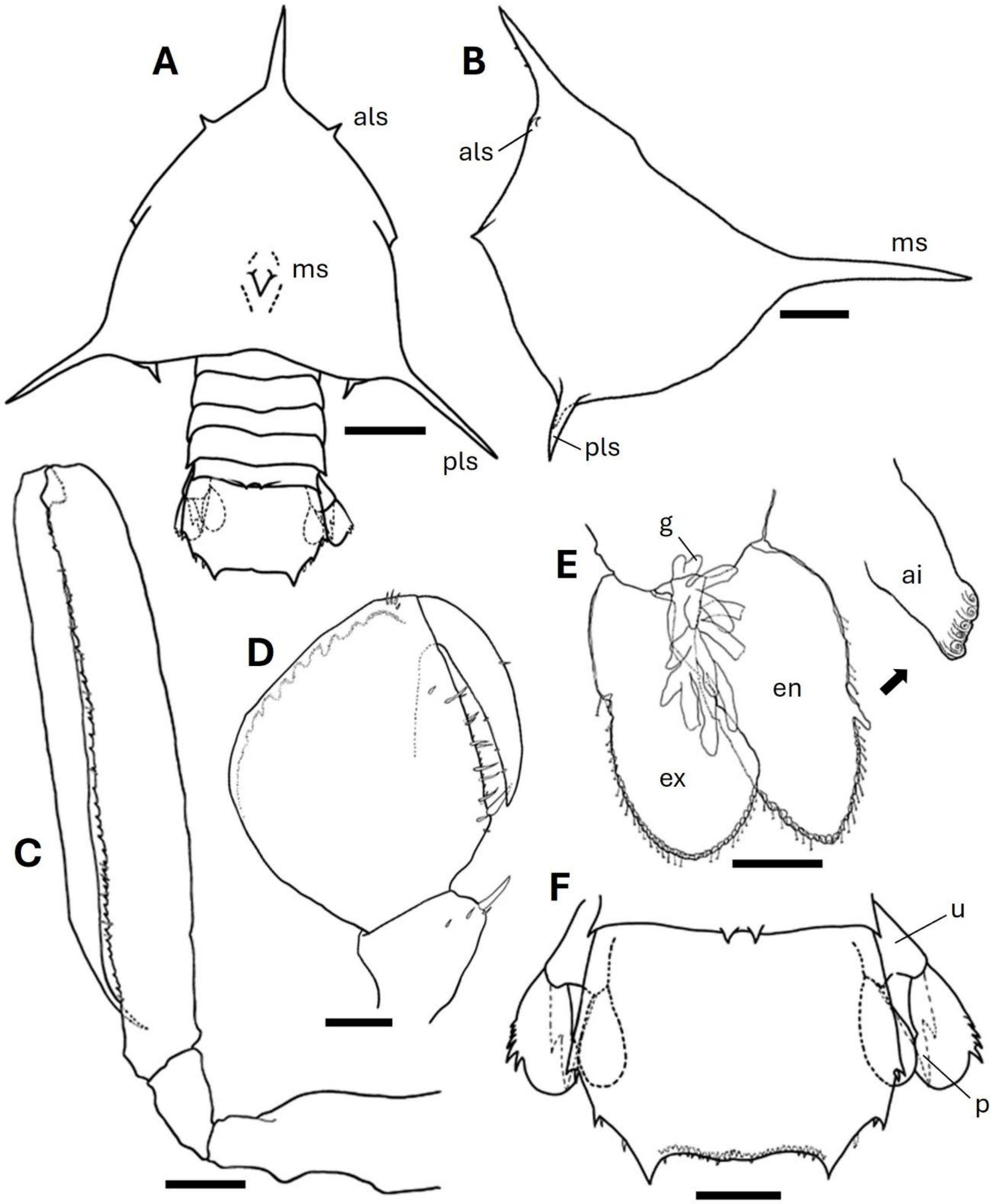

Fig. 1. *Lysiosquilloides taiwanicus* Ahyong and Lin, 2022, larva, final pelagic stage (NSMT-Cr 33382). A. Habitus, dorsal view; B. Carapace, lateral view; C. Distal end of second maxilliped, right, medial view; D. Distal end of fourth maxilliped, right, lateral view; E. First pleopod, right, anterior view; F. Uropods and telson, dorsal view. ai: appendix interna, als: anterolateral spine, en: endopod, ex: exopod, g: gill bud, ms: median spine, p: protopod, pls: posterolateral spine, u: uropod. Scale bars: 2 mm (A, B), 1 mm (F), 0.5 mm (C, E), 0.2 mm (D).

*Description***:** (based on NSMT-Cr 33382) Carapace (Fig. 1A, 1B) almost triangular in dorsal view, armed with pair of short anterolateral spines, pair of long posterolateral spines directed laterally, pair of short posterior spines, and 1 long median spine on posterior margin; rostrum armed with 2 small denticles ventrally; posterior margin of carapace reaching pleomere 2. Antennule with

3-articulated peduncle, 2 flagella on distal end; inner flagellum 6-segmented (18 segments visible internally for next stage); outer flagellum bilobed; inner lobe 6-segmented (18 segments visible internally for next stage); outer lobe with 20 aesthetascs arranged in 3-3-3-3-3-3-2 on inner margin. Antennal scale with 64 plumose setae; flagellum of antenna divided into 7 segments. Maxillule with basal endite bearing 1 sharp spine and 2 setae, 1 thin seta on anterior margin; coxal endite bearing 15 marginal spines; apex with 4 setae. Maxilla 3-segmented, proximal incompletely segmented; bearing 23, 6, and 6 marginal setae on proximal, second, distal segments, respectively. Maxilliped 1 6-articled with dactylus bearing 4 long and 3 short setae on outer and inner margins; propodus with 10 teeth on anterior margin, numerous setae on inner margin; carpus with numerous setae on inner margin; merus bearing 3 long and 1 short distal setae. Maxilliped 2 (Fig. 1C) 6-articled, with dactylus lacking tooth on occlusal margin; propodus with 35 denticles and 14 small setae on the inner margin. Maxillipeds 3–5 6-articled; dactylus bearing 2 or 3 short setae; propodus with 5–10 long setae and 5–11 short denticles. Maxillipeds 4 (Fig. 1D) and 5 with propodus having strong seta on posteromedial margin. Maxillipeds 3 and 4 with carpus bearing 1 strong and 1 small setae distally. Maxilliped 5 carpus with 3 small setae. Pereopods 1–3 unequally biramous; endopod unsegmented, shorter than exopod; exopod 2-articled. Pleopods 1–5 (Fig. 1E) biramous; endopod with 25–28 plumose setae, appendix interna with 4–5 cincinnuli; exopod with 36–42 plumose setae; gill buds well developed. Uropod (Fig. 1F) biramous with forked protopod, inner fork longer than outer; endopod with 30 plumose setae on distal margin, extending over lateral tooth of telson; exopod unsegmented and extending beyond outer fork of protopod, with 45 plumose setae on distal margin, 4 spines on outer margin. Telson (Fig. 1F) well-developed with 1 lateral, 1 intermediate, 1 submedian teeth on each side; 16 (left) –17 (right) submedian denticles, 2 intermediate denticles, 1 lateral denticle present.

Coloration: Entire body transparent in life, with no visible chromatophores. Specimen white after preservation in ethanol.

DISCUSSION

The present study confirmed the identity of the two larvae collected from Okinawa and Taiwan as *L. taiwanicus*. These two specimens are morphologically almost identical except that the Taiwanese larva has a shorter total length. This also represents the first known record of the larval stage of *L. taiwanicus* and the first record of any life stage of this species in Japanese waters. Although *L. siamensis* has previously been reported from the Ryukyu Archipelago, Okinawa, Japan

(Nakajima et al. 2022), the present study clearly demonstrates that the larva is genetically distinct from *L. siamensis*. To date, four species of Lysiosquillidae (*Ly. maculata*, *Ly. sulcirostris* Kemp, 1913, *Ly. tredecimdentata* Holthuis, 1941, and *L. taiwanicus*) have been recorded from Taiwan (Ahyong et al. 2008; Ahyong and Lin 2022; Chang et al. 2025), of which two species (*Ly. maculata* and *Ly. sulcirostris*) have also been reported in Japan (Hamano 2005). Both larvae were determined to be at the final pelagic stage based on its well-developed gills on the pleopods and the uropodal exopod extending beyond the outer fork of protopod (Fujita et al. 2025). The number of internally visible segments on both the antennule and antenna has tripled, supporting this determination. Considering the developmental stage of the larvae, the relatively recent recognition of *L. taiwanicus* in Taiwan, and the generally wide distribution of most lysiosquillid stomatopods, the occurrence of a final stage larva of *L. taiwanicus* in Okinawa strongly suggests that this species inhabits Japanese waters, including the Ryukyu Archipelago, rather than representing accidental migration resulting from planktonic dispersal from Taiwan. Ahyong and Lin (2022) also suggested that *L. taiwanicus* probably occurs more widely in the Indo-West Pacific on the basis of underwater photographs of what appear to be the species from Papua New Guinea and the Philippines.

The final-stage larva of *Ly. maculata* recently collected from the Lizard Island reef, Australia (Steck et al. 2022, fig. 2) shows close similarity to what reported under the name *Ly. maculata* by Alikunhi (1952, fig. 17), but exhibits slight differences from that illustrated by Townsley (1953, fig. 25e), notably in the absence of a projection on the lateral margin of the carapace. Michel (1970) pointed out that *Ly. maculata* larva observed by Alikunhi was probably *Ly. tredecimdentata* judging from the morphology of post-larvae and juveniles that he raised. Alikunhi (1952, fig. 18) also illustrated the carapace and telson of the final-stage larva of *Ly. sulcirostris* and highlighted the morphological differences between this species and *Ly. maculata*. A final-stage larva collected in Miami, Florida was identified as *Ly. scabricauda* (Lamarck, 1818) after being reared to the juvenile stage (Diaz and Manning 1998). Although the carapace and telson of this larva are morphologically similar to those of *Ly. maculata* and *Ly. sulcirostris*, the larva of *Ly. scabricauda* can be distinguished by the presence of ventral denticles on the rostrum, which are absent in the other two species. All the larvae listed above possess an uropodal protopod with the inner fork longer than the outer fork, a common trait in adult lysiosquillid stomatopods. This characteristic is also observed in the larvae of *L. taiwanicus*, supporting the usefulness of the uropodal protopod as a diagnostic feature of lysiosquillid larvae (Fujita et al. 2025). Nevertheless, a distinct difference is found in the posterolateral spine of the carapace between the larvae of *L. taiwanicus* and the larvae of the other two genera. The posterolateral spine is directed outward in *L. taiwanicus*, whereas it extends posteriorly in the species of the other genera. This difference suggests that the orientation of the posterolateral spine may represent a useful diagnostic character in distinguishing larvae of *Lysiosquilloides* from *Lysiosquilla*.

Larvae of lysiosquillid stomatopods were formerly classified under the suppressed generic names Erichthus and Lysioerichthus (here after as *Lys.*) (Brooks 1886; Shanbhogue 1975). These larvae are similar to each other in having a large, wide, and thick carapace that is more or less curved ventrally. *Lysioerichthus tectus* (Milne-Edwards, 1837) (Foxon 1932, fig. 4) closely resembles the larvae of *L. taiwanicus* but can be distinguished by the posterior margin of the carapace (covering the third pleonite in *Lys. tectus* but the second pleonite in *L. taiwanicus*). *Lysioerichthus* A (Shanbhogue 1975, fig. 3e–g) also seems to be a lysiosquillid larva with a pair of posterolateral spines directed outwards, but can be distinguished from the larvae of *L. taiwanicus* by the presence of a long spine on the lateral margin of the carapace. *Lysioerichthus duvaucellii* (Guérin-Méneville, 1844) (Brooks 1886, pl. x, fig. 7 & pl. xi, fig. 4; Shanbhogue 1975, fig. 3a–d), *Lys. edwardsi* (Eydoux and Souleyet, 1841) (Eydoux and Souleyet 1841, pl. 5, figs 39–54; Hansen 1895, pl. 7, fig. 4), *Lys. latreilli* (Guérin-Méneville, 1830) (Claus 1871, fig. 18; Gurney 1946, fig. 11E), *Lys. pulcher* Hansen, 1895 (Jurich 1904, pl. V, fig. 2; Gurney 1946, fig. 11A–D), *Lys. vitreus* (*sensu* Latreille, 1817) (Eydoux and Souleyet 1841, pl. 5, figs 18–23), *Erichthus guerinii* Eydoux and Souleyet, 1841 (Eydoux and Souleyet 1841, pl. 5, figs 32–38; Claus 1871, fig. 17), *E. leachii* Eydoux and Souleyet, 1841 (Eydoux and Souleyet 1841, pl. 5, figs 26–31), and *E. palliatus* Dana, 1852 (Dana 1852; Dana 1855, pl. 41, fig. 6) are probably larvae belonging to Lysiosquillidae, because their inner spine of the forked uropodal protopods is longer than the outer spines. In fact, *Lys. duvaucellii* has been considered the larva of either *Ly. maculata* or *Ly. sulcirostris* (Brooks 1886; Hansen 1895; Alikunhi 1952; Shanbhogue 1975; Steck et al. 2022), *Lys. edwardsii* considered the larva of *Ly. glabriuscula* (Hansen 1895), and *Lys. pulcher* considered the larva of *Ly. capensis* (Hansen 1895). However, the carapace morphology of these larvae does not agree with that of *L. taiwanicus*, as their posterolateral spines are directed posteriorly. *Lysioerichthus duvaucellii* (Claus 1871, fig. 13), *Lys. minutus* (Brooks, 1886) (Brooks 1886, pl. 7, fig. 4 & pl. 8, figs 1–8, 11; Hansen 1895, pl. 8, fig. 2), *Lys. ophthalmicus* Hansen, 1895 (Hansen 1895, pl. 7, fig 7 & pl. 8, fig. 1), *Lys. triangularis* (Milne-Edwards, 1837) (Komai and Tung 1929, pl. 8, figs 20–24 & pl. 9, figs 1–8), *Lys.* A (Tattersall 1906, figs 30–34), *Lys.* B (Tattersall 1906, figs 35–40), *Lys*. sp. (Komai and Tung 1929, pl. 9, figs 9–12; Gamô 1979, figs 1–2), *E. armatus* (Leach, 1818) (Eydoux and Souleyet 1841, pl. 5, figs 12–17; Claus 1871, fig. 15), *E. epineux* Eydoux and Souleyet, 1841 (Eydoux and Souleyet 1841, pl. 5, figs 6–11), *E. narwal* Guérin-Méneville, 1830 (Guérin-Méneville 1830, pl. 3, figs 2–4), and *E. spiniger* Dana, 1852 (Dana 1852; Dana 1855, pl. 42, fig. 1) are highly unlikely to belong to Lysiosquillidae, as the inner spine of the uropodal protopod is equal to or shorter than the outer spine. The actual identities of *Lys. duvaucellii* (Guérin-Méneville 1844, pl. 24, fig. 3), *Lys. edwardsi* (Claus 1871, fig. 7–8, 10–11; Jurich 1904, pl. 4, fig. 7), *Lys. latreilli* (Guérin-Méneville 1830, pl. 3, fig. 5–7), *Lys. rostratus* (Foxon 1939, fig. 3), and *E. vestitus* Dana, 1852 (Dana 1852; Dana 1855, pl. 41, fig. 7) could not be determined because the uropods are either insufficiently developed or inadequately illustrated.

Classification systems for stomatopod larvae have been proposed based on morphological characteristics, and the most recent framework consists of a three-level hierarchy: Level 1—type based on overall body shape (i.e. Alima or Erichthus); Level 2—subtypes within each larval type based on unique defensive features (i.e. Flying Saucer, Spiny Balloon, or Gnome-Hat); and Level 3—morphotypes within each subtype based on family- or species-level characteristics (Haug et al. 2016; Steck et al. 2022). According to this system, the larvae of *L. taiwanicus* can be identified as the “Tank” subtype, which is defined by a dorsally smooth carapace that is thickened entirely compared with those of other Erichthus-type larvae (Steck et al. 2022). Although larvae assigned to the Tank subtype have been suggested to belong to Lysiosquillidae (Steck et al. 2022), which is supported by the present study, larvae possessing such carapace morphology may also be assignable to other families or superfamilies, as noted above. Therefore, knowledge from the larvae of more species is necessary to modify the definitions of larval morphological features at each hierarchical level in order to ensure reliable and widespread application of this classification system.

CONCLUSIONS

This study provides the first description of the final pelagic larval stage of *L. taiwanicus* which identity was confirmed using an integrative approach combining DNA barcoding and detailed morphology. Larvae collected from Okinawa and southeastern Taiwan were shown to be morphologically identical with a slight difference in body size. Diagnostic features, particularly carapace shape and uropodal protopod structure, distinguish this larva from other lysiosquillid taxa. The finding represents the first record of *L. taiwanicus* from Japanese waters and highlights the value of molecular tools for resolving long-standing uncertainties in stomatopod larval taxonomy and biogeography.

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Conflict of interests: The authors have declared that no competing interests exist.

Availability of data and materials: Specimens examined were deposited in National Museum of Nature and Science, Tsukuba, Japan and National Taiwan Ocean University, Keelung, Taiwan. DNA sequences determined in this study were deposited in GenBank. Other data that support the findings of this study are available upon request.

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Ethics approval consent to participate: Not applicable.

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