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An Integrated Taxonomy Approach Identified the Final Stage of Giant Phyllosoma of *Parribacus antarcticus* (Lund, 1793) (Crustacea: Decapoda: Scyllaridae) from Taiwan Waters

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A bizarre marine planktonic organism giant phyllosoma with a body length of 79 mm was collected off Taiwanese waters for the first time. The specimen is positively identified as *Parribacus antarcticus* (Lund, 1793) by DNA barcoding, representing the largest and the first final stage giant phyllosoma with identification confirmed. The characteristics of the phyllosoma from Taiwan is described and illustrated in detail. As morphometric ratios previously proposed for identifying phyllosomae of *Parribacus* failed to assign correctly the species of the Taiwanese specimen, there is still no reliable morphological character for separating these giant phyllosomae. A key to the different phyllosoma stages of *P. antarcticus* is provided.

Key words: Lobsters, Larvae, New record, DNA barcoding

BACKGROUND

The extremely thin and leaf-like larvae of spiny and slipper lobsters are one of the amazing larval forms of marine creatures. These special larval forms are called "phyllosoma". Even more extraordinary is the phyllosoma of the slipper lobsters in the genus *Parribacus* Dana, 1852, which has a very large body with a size as large as a human adult hand (Fig. 1) and amongst the largest larvae known for marine invertebrates (Palero et al. 2014). Although these peculiar giant phyllosoma have been known for two centuries (Guérin-Méneville 1833), their identifications down to species have only been recently confirmed by DNA barcoding technique (Palero et al. 2014; Chow et al. 2022) because larval rearing of *Parribacus* is still unsuccessful due to their very long larval stages that have more than 11 stages and last for about nine months (Booth et al. 2005). Nevertheless, the phyllosomae of the six known species in *Parribacus* (Holthuis 1985 1991; Chan 2010 2019) are still very difficult to distinguish by morphology (Coutures 2001; Palero et al. 2014; Chow et al. 2022) and there is still no final stage giant phyllosoma which has its species confirmed.

The large size of these giant phyllosomae, however, do not make them common amongst plankton collection even though they have been collected from world-wide tropical and subtropical seas (see Yoneyama and Takeda 1998; Palero et al. 2014; Chow et al. 2022). There are two species of *Parribacus* slipper lobsters, namely *P. japonicus* Holthuis, 1960 and *P. antarcticus* (Lund, 1793), in Taiwan and they are rather common in

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rocky reef areas sustaining a small fishery (Chan and Yu 1989 1993). *Parribacus japonicus* is distributed only in Japan and Taiwan while *P. antarcticus* has a world-wide circumtropical distribution (Holthuis 1985 1991). Nevertheless, no giant phyllosoma had been known off the waters of Taiwan. Recently, a giant phyllosoma was collected off northeastern Taiwan with a size almost the largest known for phyllosomae. Although it has been proposed that some morphometric ratios may be able to separate the phyllosomae of *P. japonicus* and *P. antarcticus* (Yoneyama and Takeda 1998; Chow et al. 2022), the Taiwanese specimen cannot be satisfactory identified using these ratios. On the other hand, DNA barcoding is now generally used to identify unknown larvae including lobster phyllosoma (*e.g.*, Palero et al. 2014; Ueda et al. 2021; Chow et al. 2022; Hidaka et al. 2022; Genis-Armero et al. 2023). Using DNA barcoding, the present phyllosoma can be positively identified as *P. antarcticus*. This work reports the first record of giant phyllosoma from Taiwan, with its characteristics fully described and illustrated. According to Palero et al. (2014) and Chow et al. (2022), the Taiwanese phyllosoma is at the final stage of larval development. This is also the first report of final stage giant phyllosoma with identification confirmed. A key to the different phyllosoma stages of *P. antarcticus* is herein provided.

MATERIALS AND METHODS

The giant phyllosoma specimen was collected by commercial fishing trawler with a fishing ground off the northeastern coast of Taiwan. The specimen is deposited at the National Taiwan Ocean University (NTOU). The specimen was dissected under a stereomicroscope (ZEISS Stemi SV-6) using dissecting needles, with descriptions and terminology follow Higa and Shokita (2004) and Palero et al. (2014). Measurements follow Chow et al. (2022) and they are: Body Length (BL)- from anterior margin of cephalic shield between eyes to posterior margin of telson; Cephalic Length (CL)- from anterior to posterior margins of cephalic shield; Cephalic Width (CW)- widest part of cephalic shield; Thorax Width (TW)- widest part of thorax.

Crude genomic DNA was extracted from the remaining segment of the broken pereiopod III in the right side using the Chelex-resin method (Palero et

Fig. 1. First giant phyllosoma found off Taiwanese waters.

al. 2010). Common animal DNA barcoding gene, the mitochondrial cytochrome *c* oxidase I, was selected as the molecular marker for assisting the identification (Hebert et al. 2003; Hajibabaei et al. 2007) and the universal primer was used for PCR amplification (LCO1490/HCO2198, 657 bp, Folmer et al. 1994). PCR reactions, cycling profiles, products checking and sequencing procedures followed those used in Yang et al. (2012), but the PCR volumes adjusted into 25 µl containing with 25–75 ng of the DNA templates, 2.5 µl of 10X polymerase buffer, 15 mM magnesium chloride ($MgCl_2$), 2.5 mM of deoxyribonucleotide triphosphate mix (dNTPs), 5 µM of each primer, and 1 unit of Taq polymerase (5 units/µl Super-Therm; TaKaRa, Otsu, Japan). After the successful sequencing work, the output sequences were edited for contig assembly by SeqMan Pro™ (Lasergene®; DNASTAR, Madison, WI, USA), then blasted on GenBank (NCBI) for checking if any potential contamination. EditSeq (Lasergene®; DNASTAR) was used to translate into the corresponding amino acid sequences to avoid inclusion of pseudogenes for *COI* dataset (Song et al. 2008).

Five out of the six known species in *Parribacus* are with *COI* sequences in the GenBank. All *COI* sequences from adults of these five species in GenBank were downloaded for species matching analysis: *P. antarcticus* (JN701666-Taiwan, MW278747-Hawaii, KF009638-Philippines, MF490044-Brazil), *P. caledonicus* Holthuis, 1960 (KJ150683, New Caledonia), *P. holthuisi* Forest, 1954 (KC706776, French Polynesia), *P. japonicus* (KJ150684, Taiwan), and *P. perlatus* Holthuis, 1967 (KJ150685, Easter Island). However, the sequence of *P. holthuisi* is too short (311 bp) and produced many gaps during alignment. Therefore, we replaced it with a new sequence from a specimen of *P. holthuisi* (NTOU M02623, PQ484180, Tuamotu). The remaining species *P. scarlatinus* Holthuis, 1960 (MNHN [Muséum national d'Histoire naturelle, Paris] IU-2013-6920, PQ484181, Archipel des Marquises) was also sequenced in order to construct a complete dataset for all the known species in *Parribacus*. All phyllosoma identified as *P. antarcticus* and with *COI* sequences in the GenBank were also included in the analysis. Sequence alignment and calculation of nucleotide pairwise distance based on Kimura 2-parameter model (K2P, Kimura 1980) were conducted by MEGA v.11 (Tamura et al. 2021). The maximum-likelihood (ML) tree was constructed based on the *COI* dataset using MEGA v.11 by 1000 bootstrap replicates.

RESULTS

DNA barcoding identification

Genetic analysis (Fig. 3) revealed that the Taiwanese giant phyllosoma is with 99.8% *COI* sequence similarity (657 bp) with an adult *P. antarcticus* from Taiwan (NTOU M00975). On the other hand, there are 13.4 to 17.6% pairwise divergences on the *COI* dataset (594–657 bp) between the Taiwanese giant phyllosoma and the other five species of *Parribacus* (*i.e.*, *P. japonicus* 13.4%, *P. scarlatinus* 14.0%, *P. perlatus* 15.4%, *P. holthuisi* 17.4%, and *P. caledonicus* 17.6%). Therefore, such a high *COI* sequence similarity (99.8%) positively matches (see Palero et al. 2014; Ueda et al. 2021; Genis-Armero et al. 2022; Hidaka et al. 2022) the Taiwanese giant phyllosoma with *P. antarcticus*. Moreover, within *P. antarcticus* there are only 1.4–2.1% divergence between phyllosomae from the Atlantic and West Pacific, while materials from different localities in the West Pacific have 0–1.0% divergences in the *COI* dataset.

TAXONOMY

Order DECAPODA Latreille, 1802
Family SCYLLARIDAE Latreille, 1825
Genus *Parribacus* Dana, 1852

Parribacus antarcticus (Lund, 1793)
(Figs. 1–2, 4–5)

Material examined: 1 specimen, Dasi fishing port, Yilan County, commercial trawler, 20 September 2023 (NTOU M02622). BL = 79 mm, CL = 56 mm, CW = 47 mm, TW = 40 mm.

Description: Cephalic shield (Fig. 4A, B): Subrectangular, 1.2 times longer than wider, anterior margin slightly concave.

Antennule (Fig. 4C): 3-segmented, outer flagellum slightly shorter than inner flagellum.

Antenna (Fig. 4C): Segmentation indistinct, broadened at base, lateral triangular process developed, slightly longer than antennule.

Mandible (Fig. 5A): Left incisor process with 5 short strong teeth and 24 setae between incisor and molar processes; right incisor process with 3 strong teeth and 14 setae between incisor and molar processes.

Maxillule (Fig. 5B): Palp absent; coxal endites with 15 setae (2 long, strong terminal setae); basial endite with 8 setae (3 long, strong terminal cuspidate setae) and 1 short seta near posterior margin.

Maxilla (Fig. 5C): Scaphognathite with anterior

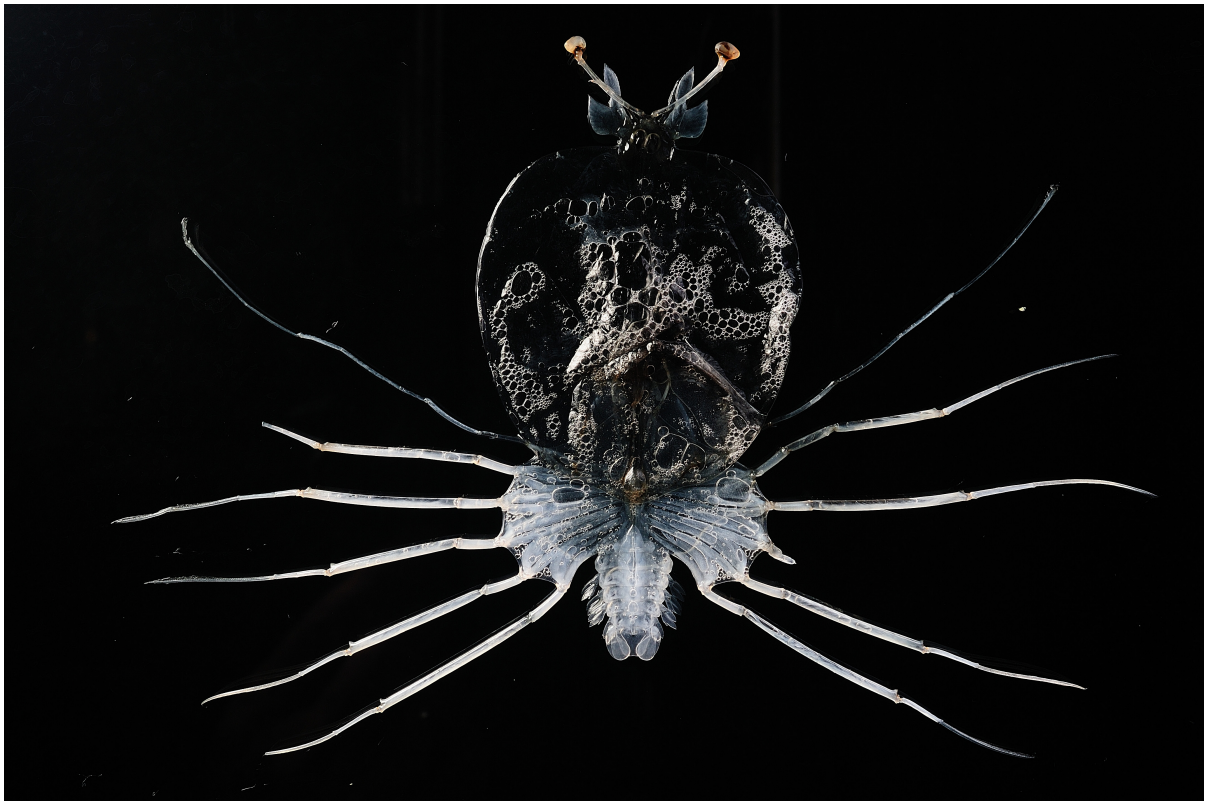

Fig. 2. Final phyllosoma stage of *Parribacus antarcticus* (Lund, 1793), BL 79 mm, Dasi fishing port, Yilan County, commercial trawler, 20 September 2023 (NTOU M02622), dorsal view.

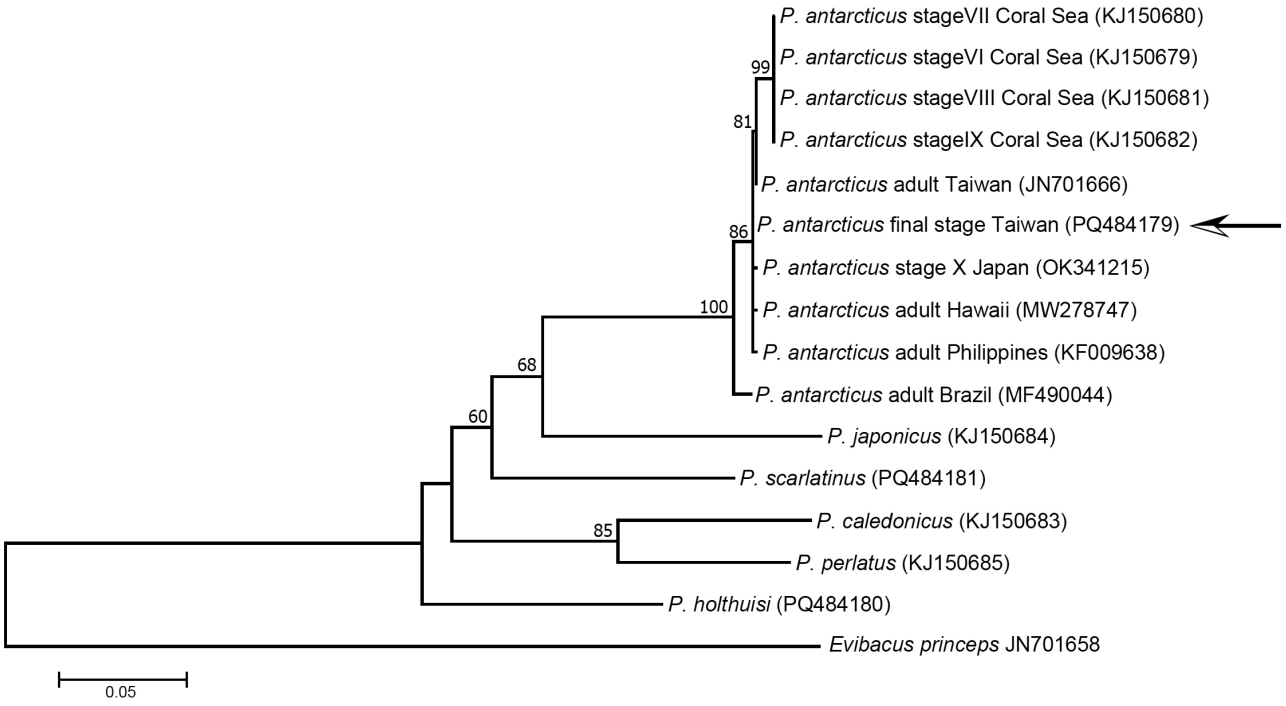

Fig. 3. Maximum likelihood phylogenetic tree for all the six species of *Parribacus* as well as phyllosomae of *P. antarticus* based on a mitochondrial *COI* gene (594–657 bp) dataset available in the GenBank plus the present giant phyllosoma from Taiwan. *Evibacus princeps* Smith, 1869 was chosen as outgroup. Bootstrap values less than 50 are not shown.

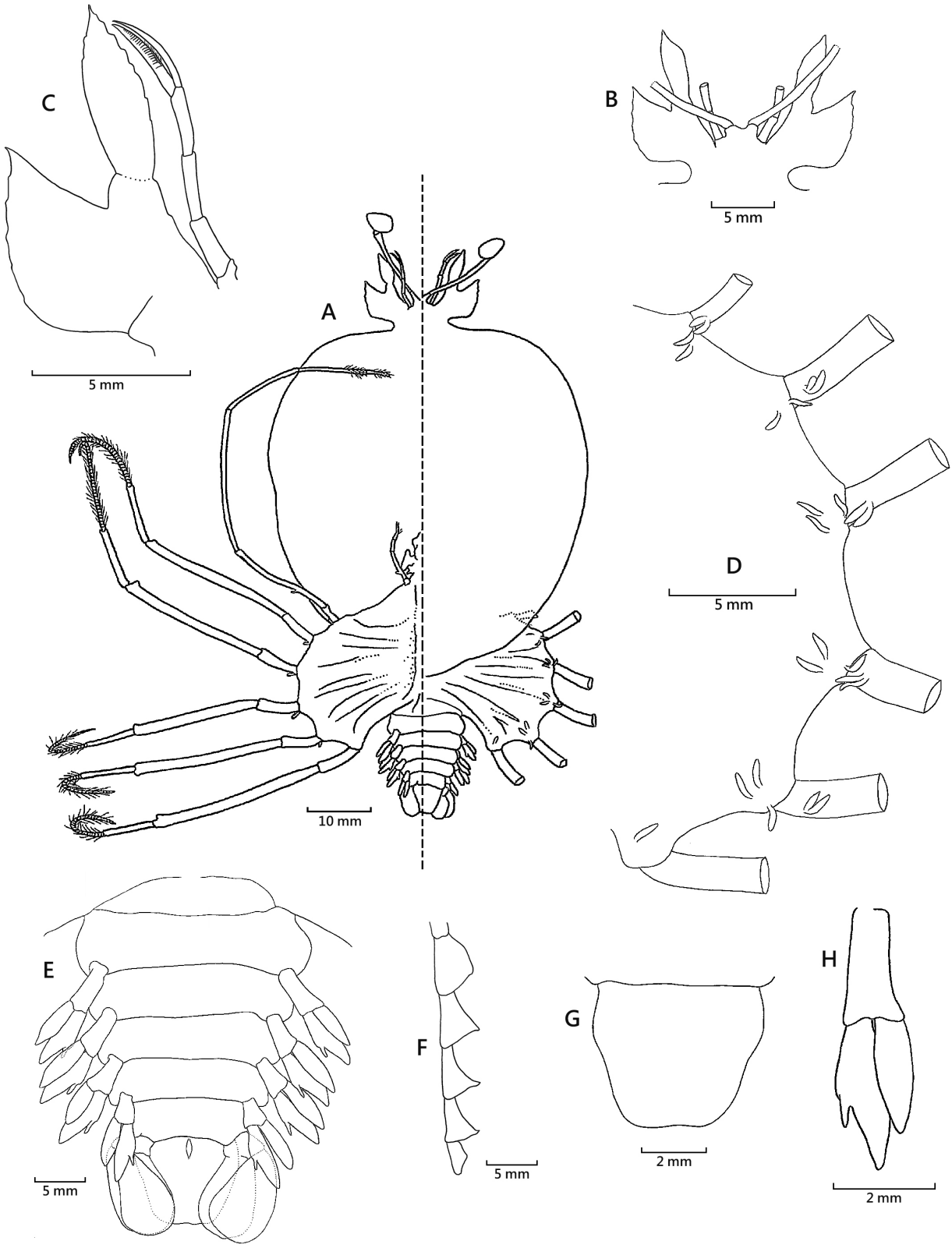

Fig. 4. Final phyllosoma stage of *Parribacus antarcticus* (Lund, 1793), Taiwan (NTOU M02622). A, left and right, ventral and dorsal views, pereiopod III with right side originally incomplete and redrawn after left side; B, frontal details, dorsal; C, right antennule and antenna; D, dorsal view of thorax details, with bases of third maxilliped and pereiopods I–V; E, ventral view of pleon; F, lateral view of pleon; G, telson, dorsal; H, left pleopod I, anterior.

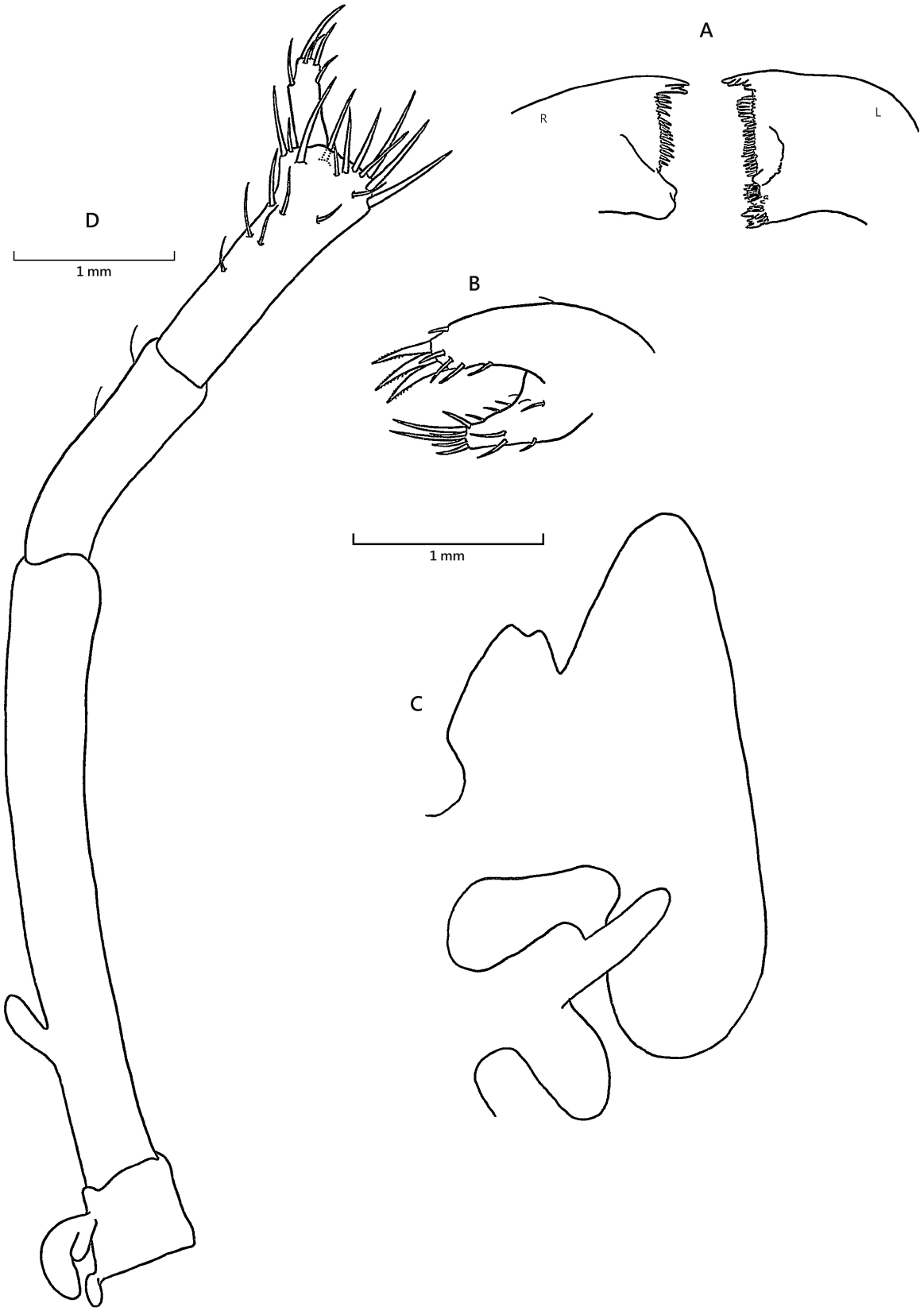

Fig. 5. Final phyllosoma stage of *Parribacus antarcticus* (Lund, 1793), Taiwan (NTOU M02622). A, left and right mandibles, ventral; B, left maxillule, ventral; C, left maxilla and first maxilliped, ventral; D, left second maxilliped, dorsal.

and posterior parts significantly expanded.

First maxilliped (Fig. 5C): Lobe-like, undeveloped bud.

Second maxilliped (Fig. 5D): 5-segmented, with 0, 0, 2, 18, 5 setae; exopod bud present, coxa with 1 arthrobranch, epipod and podobranch.

Third maxilliped (Fig. 4A): 6-segmented with small exopod bud, gill buds present, with 1 pleurobranch, 1 arthrobranch and epipod with podobranch.

Pereiopods and gills (Fig. 4A, D): Endopod of all pereiopods missing. Exopods flagellated distally and each with about 65 annulations; pereiopods I with 1 pleurobranch, 1 arthrobranch and 2 podobranchs; pereiopods II–IV with 2 pleurobranchs, 1 arthrobranch, 2 podobranchs. Pereiopods V with 1 pleurobranch.

Pleon (Fig. 4A, E–H): With 6 somites plus telson, without setae, somites III–V with posterolateral spinous processes; pleopods biramous, endopod with appendix interna; uropod well developed, posterior margin extends beyond tip of telson; posterior margin of telson nearly rectangular.

DISCUSSION

The present phyllosoma has the endopods of all pereiopods lost, and the exopods of the left pereiopod I and right pereiopod III incomplete (Figs. 1–2). DNA barcoding results positively identified this giant phyllosoma with *P. antarcticus*. Molecular identification by DNA barcoding using *COI* gene is now very common and reliable for decapod crustaceans and their larvae (Marco-Herrero et al. 2021; Varela and Bracken-Grissom 2021; Xu et al. 2022). *Parribacus antarcticus* is one of those few decapod crustacean species with a nearly circumtropical distribution from the Indo-West Pacific and western Atlantic (Holthuis 1991). Although there is no population study yet for *P. antarcticus*, the present *COI* sequence analysis shows that materials of this species from the Indo-West Pacific and Atlantic formed a very robust clade (bootstrap value = 100) and there are more than 97.9% sequence similarities between materials from the disjuncted West Atlantic and Indo-West Pacific. Such low genetic divergence suggested that there may be no separate populations in this widely distributed species (Alam et al. 2017; Lee et al. 2019; Chan et al. 2019), with the prolong planktonic larval stages of *P. antarcticus* likely facilitate the gene flow amongst different localities.

The Taiwanese phyllosoma has a very large size and bears distinct gill buds at the bases of pereiopods (Fig. 4A, D) showing that it is at the final stage according to the different larval developmental stages defined by Yoneyama and Takeda (1998), Palero et al. (2014), and Chow et al. (2022). The largest giant phyllosoma reported can reach a body length of 83 mm (see Chow et al. 2022) collected from the South Pacific (Michel 1971) but with unknown species identification. As species identification of giant phyllosoma is still difficult to determine by morphology, the largest size of giant phyllosoma with identification confirmed by DNA barcoding only has a body length of 70.9 mm at the subfinal stage and belongs to *P. japonicus* (Chow et al. 2022). Moreover, no final stage giant phyllosoma had its identification confirmed by DNA barcoding. Thus, the present Taiwanese specimen (BL 79 mm) represents the largest as well as the first final stage giant phyllosoma with confirmed identification. For *P. antarcticus*, the largest phyllosoma reported before with identification confirmed by DNA barcoding was BL 50.7 mm at stage X (Chow et al. 2022, with stage X of Chow et al. 2022 = stage XI of Palero et al. 2014).

Only three giant phyllosomae recorded before are bigger than the present Taiwanese specimen. They are reported as *P. antarcticus* from the Indian Ocean (Prasad et al. 1975), *P. japonicus* from Japan (Yoneyama and Takeda 1998), and *P.* sp. from the South Pacific (Michel 1971). All were at the final developmental stage and without genetic data supported their identification. The giant phyllosoma, BL 80 mm, from the Indian Ocean highly likely belongs to *P. antarcticus* as it is the only species of the genus occurring in the Indian Ocean (see Holthuis 1985 1991) and the figures provided by Prasad et al. (1975: fig. 4C) are generally similar to the present final stage phyllosoma. The giant phyllosoma from Japan, also with BL 80 mm, has its identification questionable because both *P. antarcticus* and *P. japonicus* occur in Japanese waters like in Taiwan (see Holthuis 1985 1991; Nomura and Sekiguchi 1995). The one from the South Pacific is the largest phyllosoma ever recorded with BL 83 mm and reported as *Parribacus* sp. (Michel 1971). As there are five species of *Parribacus* distributed in the South Pacific (Holthuis 1985 1991), the exact identity of this largest known phyllosoma is still unknown.

Yoneyama and Takeda (1998) and Palero et al. (2014) suggested that some morphometric ratios may be useful in separating *Parribacus* phyllosomae. Chow et al. (2022) further elaborated this hypothesis using phyllosomae with identification confirmed by DNA barcoding and argued that CW/TW ratio against BL can be used to distinguish between the phyllosomae of *P. antarcticus* and *P. japonicus*. However, the CW/TW ratio (47 mm/ 40 mm = 1.18) against BL (79 mm) of the present *P. antarcticus* final stage phyllosoma falls out far away from both regression lines proposed for *P. antarcticus* and *P. japonicus* by Chow et al. (2022)

(Fig. 6). Moreover, the similar size giant phyllosoma, BL 80 mm, reported as *P. japonicus* by Yoneyama and Takeda (1998) from Japan also has a CW/TW ratio (about 1.22; Yoneyama and Takeda 1998: fig. 8, point 13) very close to that of the present Taiwanese specimen identified as *P. antarcticus.* As mentioned above, only adults of *P. antarcticus* and *P. japonicus* are found in Japan but Yoneyama and Takeda's (1998) Japanese final stage phyllosoma with a CW/TW ratio does not fit in both the regression lines proposed for *P. antarcticus* and *P. japonicus* by Chow et al. (2022) as well. Thus, there is still no reliable morphological character or morphometric ratios found to separate phyllosomae of the genus *Parribacus*.

With the present confirmation of the final phyllosoma stage for *P. antarcticus*, only three of the 12 larval development stages still cannot be traced back to adults. The characteristics of the first three phyllosoma stages of *P. antarcticus* were reported from laboratory rearing experiment by Saisho (1962) though there are possibilities that the ovigerous female hatched the larvae may actually be *P. japonicus*. Palero et al. (2014) and Chow et al. (2022) recently discussed in details the late phyllosoma stages (*i.e.*, stages VI–XII) of *Parribacus* and identified the stages VI–X of *P. antarcticus* by DNA barcoding matching with adults. Nevertheless, they defined differently the two stages before the final stage. Palero et al. (2014) lacked stage X and their stage XI and subfinal stage are essentially equal to the stages X and XI of Chow et al. (2022), respectively. Early phyllosoma stages of *Parribacus* had been reported by various earlier workers (Aikawa and Isobe 1955; Saisho 1962; Sims 1965; Johnson 1971; Prasad et al. 1975; Coutures 2001) and there are also in discrepancies amongst them. For example, the budding of pereiopod V is defined as stage III by Saisho (1962) and Prasad et al. (1975) but as stage IV by Sims (1965). Moreover, the pereiopod V was defined as segmented in stage IX by Sims (1965) but the stage VI defined by Palero et al. (2014) already had the pereiopod V segmented. Only the work of Saisho (1962) was based on laboratory rearing experiment to stage III. Therefore, the characteristics of the first three stages in *Parribacus* phyllosomae are referred to Saisho (1962). As the larval stages defined by Sims (1965) somewhat differed from Saisho (1962), the characteristics of stages IV and V are here mainly referred to Johnson (1971) and Prasad et al. (1975). The following is a key to the different stages of the phyllosoma in *P. antarcticus*. This key could be equally used in the other species of *Parribacus* as no distinct difference have been found yet to separate their phyllosomae.

Key to the phyllosoma stages of *Parribacus antarcticus*:

1. Eyes unstalked ..... Stage I**
- Eyes stalked 2
2. Pereiopod IV as small bud ..... Stage II**
- Pereiopod IV at least as a long bud 3
3. Pereiopod IV with exopod as a bud ..... Stage III**

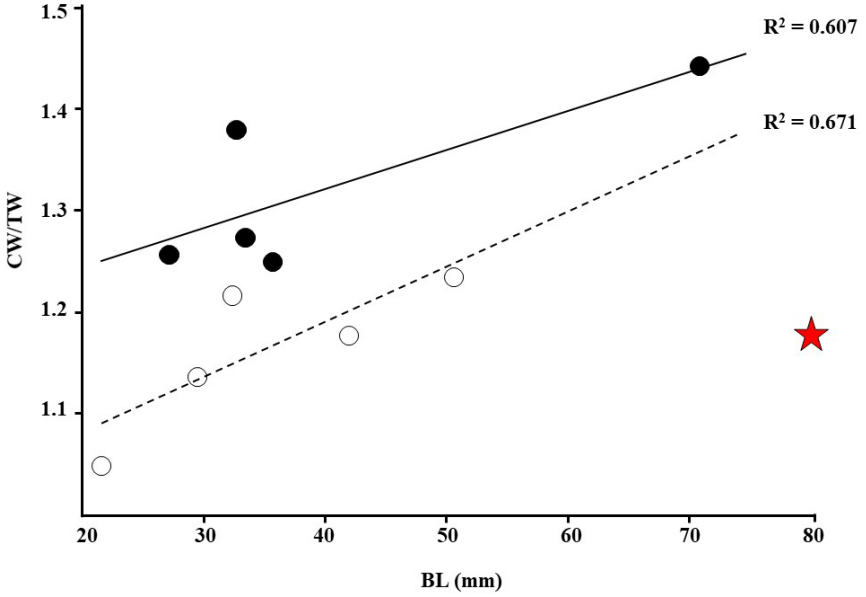

Fig. 6. Ratio of cephalic shied width to thorax width (CW/TW) against body length (BL) of *Parribacus antarcticus* (Lund, 1793) and *P. japonicus* Holthuis, 1960 with identification confirmed through DNA barcoding by Chow et al. (2022) and the present study. Solid circle: *P. antarcticus* from Chow et al. (2022), open circles: *P. japonicus* from Chow et al. (2022), star: Taiwan *P. antarcticus* in this study. Regression lines after Chow et al. (2022).

- Pereiopod IV exopod setose 4
4. Pereiopod V without exopod bud ..... Stage IV
- Pereiopod V with exopod at least as a bud 5
5. Pereiopod V unsegmented ..... Stage V
- Pereiopod V segmented 6
6. Antenna extending to middle of first antennule segment .... Stage VI*
- Antenna overreaching first antennule segment 7
7. Pleopod lacking ..... Stage VII*
- Pleopods at least as buds 8
8. Pleopods and uropods as buds ..... Stage VIII*
- Pleopods and uropods bilobed 9
9. Antenna with lateral process rudimentary, uropod extending to middle of telson ..... Stage IX*
- Antenna with lateral process distinct, uropods almost reaching posterior margin of telson 10
10. Uropod not overreaching telson ..... Stage X*#
- Uropod overreaching telson 11
11. Gill bud absent ..... Stage XI##
- Gill bud present ..... Final or Stage XII*

*identification confirmed by DNA barcoding.
**identification of ovigerous female used in laboratory rearing experiment, but may actually represent *P. japonicus* in Saisho (1962).
= Stage XI in Palero et al. 2014.
= Subfinal stage in Palero et al. 2014.

Although *P. antarcticus* is a common inhabitant of the rocky and coral reefs around Taiwan (Chan and Yu 1989 1993), no phyllosoma of this species had been collected before. Slipper lobsters of the genus *Parribacus* have prolong larval stages and known to be able to drift with currents far away from shores (Booth et al. 2005). As the present phyllosoma was collected by a commercial trawler with fishing ground not far from shore (Wang et al. 2013), it is not unexpected that this phyllosoma was at the final developmental stage near to settle to a rocky reef off northeastern Taiwan.

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Authors' contributions: GCJ drafted the manuscript and drawings, CHY preformed molecular analysis, KW gathered related references and finalized the manuscript, TYC prepare the photographs, drafted and finalized the manuscript.

Competing interests: There is no competing interests.

Availability of data and materials: Can be found in the manuscript, GenBank and collection at the National Taiwan Ocean University and Muséum national d'Histoire naturelle, Paris.

Consent for publication: There is no consent for publication.

Ethics approval consent to participate: There is no ethic issue in this manuscript.

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