Recognizing two new *Hippolyte* species (Decapoda, Caridea, Hippolytidae) ~~form~~ from the South China Sea based on integrative taxonomy

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Abstract

~~Shrimps of~~ *Hippolyte* shrimps exhibit abundant biological diversity and display great ecological~~ly~~ ~~significant~~ significance in ~~the ecosystem of~~ seaweed bed ecosystems. Dozens of *Hippolyte* specimens were collected from Hainan Island and the Xisha Islands in the South China Sea. Detailed examination indicates that ~~they~~some of these specimens represent ~~some~~ new *Hippolyte* species ~~to the genus~~. Based on morphological, genetic, and ecological data, ~~*Hippolyte*~~ *H. chacei* sp. nov. and ~~*Hippolyte*~~ *H. nanhaiensis* sp. nov. are described. ~~*Hippolyte*~~ *H. chacei* sp. nov. was collected from the biotope of *Sargassum* sp. in Hainan Island~~, it~~ and is ~~distinguishes~~ distinguished from ~~the~~ its congeners by ~~its~~ the unique mandible and ~~particular~~ dactyli of the third to fifth pereiopods, which ~~corresponding~~ corresponds to its basal position in the Indo-West ~~pacific~~ Pacific species clade of the phylogenetic tree. ~~*Hippolyte*~~ *H. nanhaiensis* sp. nov. was collected from the biotopes of *Galaxaura* sp. and *Halimeda* sp. in the Xisha Islands., ~~it~~ This new species differs from ~~the~~ its congeners ~~by the combined~~based on a combination of features of the rostrum, scaphocerite, antennular peduncle, and ~~the~~ spines ~~in~~ on the dactyli of the third to fifth pereiopods~~,~~; ~~and~~ additionally, it is~~forms~~ sister ~~group with~~to ~~*Hippolyte*~~ *H. australiensis* in the phylogenetic tree. An identification key to mature female *Hippolyte* of the Indo-West Pacific and neighboring seas is provided.

~~**Key words:** Caridea, *Hippolyte*, Integrative taxonomy, Marine biodiversity, New species, South China Sea~~

Introduction

Shrimps ~~belonging to~~of the genus *Hippolyte* Leach, 1814, which display ~~incredible~~high diversity in morphology, coloration, and ecological habits, ~~are~~ mainly occur in tropical and temperate oceans, but can also occur in the polar region. For example, *H. varians* Leach, 1814 were recorded from the Arctic Circle in Norway (d'Udekem d'Acoz, 2007). Most *Hippolyte* species ~~commonly perching~~ inhabit ~~in the~~ seaweed of the euphotic layer ~~of tropical and subtropical oceans around the planet~~, and a few are obligatory or facultative symbionts of other organisms, such as gorgonians, and crinoids (d'Udekem d'Acoz, 2007; Marin et al., 2011). ~~and display wondrously bio-diverse in morphology, coloration, and ecological habit.~~ In the last decade, the taxonomy, phylogeny, and biology of *Hippolyte*~~genus~~ ~~has~~ have attracted considerable attention ~~in the research of taxonomy, phylogeny and biology~~ (Manjón-Cabeza et al., 2011; Marin et al., 2011; Terossi & Mantelatto, 2012; Liasko et al., 2015; Duarte & Flores, 2017; Duarte et al., 2017; Gan & Li, 2017a; 2017b; Liasko et al., 2017; Terossi et al., 2017). Currently, a total of 35 valid species are recognized worldwide (d'Udekem d'Acoz, 1996; 2007; De Grave & Fransen, 2011; Marin et al., 2011; Gan & Li, 2017a; 2017b; Terossi et al., 2017). Among these species, ~~no more than half of them~~fewer than half (~~about~~ approximately 12 species) ~~are~~ occur~~ring~~ in the Indo-West Pacific region. ~~In the meantime~~Moreover, some unnamed ~~species or~~and cryptic species ~~are~~ were also documented in ~~the~~ previous publications (Hayashi, 1986; d'Udekem d'Acoz, 1996; 2007; Terossi et al., 2017) waiting to be revised.

Because of its extensive morphological diversity and ~~morphic~~ overlap, as well as complex information described in previously published literature~~as well as the confusions appeared in the literatures~~, the taxonomic~~al~~ research of *Hippolyte* ~~is~~ has always been considered ~~to be~~ difficult based ~~on the morphological method~~morphology (d'Udekem d'Acoz, 1996; Gan & Li, 2017a). The situation is even more ~~serious referring to~~complicated for the '~~*Hippolyte*~~ *H. ventricosa* H. Milne Edwards, 1837' species complex, which includes *H. acuta* (Stimpson, 1860), *H. australiensis* (Stimpson, 1860), *H. ngi* Gan & Li, 2017, *H. singaporensis* Gan & Li, 2017, *H. ventricosa* H. Milne Edwards, 1837, *Hippolyte* sp. A from Australia, *Hippolyte* sp. B from Hawaii, *Hippolyte* sp. C from the Malay Archipelago, and *Hippolyte* sp. D from Madagascar (d'Udekem d'Acoz, 1996; Gan & Li, 2017a; 2017b). More recently, Terossi et al. (2017) further recognized four cryptic or pseudocryptic species (*H. ventricosa* group-sp. 1 and sp. 2 from Indonesia, *H. ventricosa* group-sp. 3 from Fiji, and *H. ventricosa* group-sp. 4 from Taiwan) based on genetic analysis, ~~but~~ however, their morphological features are ~~greatly~~ very similar to those of *H. ventricosa*.

During recent biodiversity surveys of islands (2014–2018) of the South China Sea, dozens of *Hippolyte* specimens were collected from Hainan Island and the Xisha Islands by snorkeling. After detailed examination and multiple ~~analysis~~analyses, we described two new species of the

Comentário [AdS1]: Rephrase this sentence. E.g. inhabit the euphotic layer on seaweed beds?

Comentário [AdS2]: This sentence should be revised. It is not clear what H. ventricosa are you exactly mentioning in the end.

'*H. ventricosa* H. Milne Edwards, 1837' species complex based on integrative methods, namely, the validity of the new species is supported by the morphological, genetic and ecological data.

Materials & Methods

Sample collection and morphological examination. All the specimens were collected by a handheld net when snorkeling among the seaweed. After photographing, the specimens were preserved in 95% ethanol. Dissection and illustrations were made using a stereomicroscope (Nikon SMZ 1500, Japan) and a microscope (Nikon AZ100, Japan). Measurements and length ratios were calculated according to the method proposed by d'Udekem d'Acoz (1996). All the specimens are ~~depositing~~ deposited in the Marine Biological Museum of Chinese Academy of Sciences (MBM) in the Institute of Oceanology of Chinese Academy of Sciences, Qingdao, China (IOCAS)

Comentário [AdS3]: Provide more information on the Island biodiversity surveys, here.

Molecular data and analysis. Total genomic DNA was extracted from the pleopods of the specimens using the QIAamp DNA Mini Kit (QIAGEN, Germany) following the manufacturer's instructions. The extracted DNA was eluted in 100 µl of double-distilled H_2O (ddH_2O). Partial sequences of the 16S rRNA genes were amplified from the diluted DNA via the polymerase chain reaction (PCR). The reactions were carried out in a 50-µl volume containing the following reagents: 25 µl Premix Taq (TaKaRa Taq™ Version 2.0 plus dye, Japan), 1 µl forward and reverse primers (10 µM) respectively, 3 µl DNA template, and 20 µl ddH2O. The primers 16S-AR/1472, 5′-CGCCTGTTTATCAAAAACAT-3′/5′-AGATAGAAACCAACCTGG-3′, were used (Crandall & Fitzpatrick, 1996). The PCR profile was as follows: 3 min at 94 °C for initial denaturation, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 40 s and elongation at 72 °C for 50 s, with a final extension at 72 °C for 10 min. The PCR products were purified using the QIAquick Gel Extraction Kit (QIAGEN, Germany), and then bidirectionally sequenced using the same primers with an ABI 3730xl Analyzer (Applied Biosystems, USA). The obtained sequences were checked and proofread by ContigExpress 6.0 (a component of the Vector NTI Suite 6.0).

~~Besides of~~In addition to the sequences obtained by PCR (Table 1, Dataset S1), we ~~also~~ downloaded some ~~other sequences of~~ *Hippolyte* sequences ~~species~~ from Genbank ~~with caution~~, including the previously reported cryptic or pseudocryptic species, namely *H. ventricosa* group-sp. 1 (KX588914), *H. ventricosa* group-sp. 2 (KX588915), *H. ventricosa* group-sp. 3 (KX588915), and *H. ventricosa* group-sp. 4 (KX588915) reported by Terossi et al. (2017) and *H. ventricosa* group-sp. 5 (KF023090) reported by De Grave et al. (2014). The molecular data, including 37 sequences of 16S rRNA genes, were aligned using MUSCLE 3.8 (Edgar, 2004). The highly divergent and poorly aligned sites were omitted from the alignment according to GBlocks 0.91b (Castresana, 2000). The best-fitting nucleotide base substitution model (GTR+I+G) for the alignment data was determined by ModelTest 3.7 (Posada & Crandall, 1998). Then this model was subsequently applied to phylogenetic analysis using the maximum likelihood (ML) method by PhyML 3.1 (Guindon & Gascuel, 2003) with 1000 bootstrap reiterations. The Bayesian inference (BI) tree was constructed using MrBayes 3.2 (Huelsenbeck

& Ronquist, 2001), the Markov chains were run for 2000000 generations, with sampling every 2000 generations, after the first 25% trees were discarded as burn-in, the remaining trees were used to construct the 50% majority-rule consensus tree and to estimate posterior probabilities. The genetic distances were calculated under the Kimura 2-parameter (K2P) model in MEGA 7.0 (Kumar et al., 2016).

Ecological data. When the shrimp specimens were captured, their biotopes (mainly the algal colony ~~where~~ in which the shrimp liv~~ing in~~ed) were documented.

The following abbreviations are used: CL, carapace length, the length from the posterior orbital margin to the posterior dorsal border of the carapace; Coll., collector (s).

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Results

Taxonomy

Order Decapoda Latreille, 1802

Family Hippolytidae Spence Bate, 1888

Genus *Hippolyte* Leach, 1814

***Hippolyte chacei* sp. nov.**

(Figs. 1–~~5~~4, ~~10A~~5A)

Material examined. ***Holotype***: MBM285015, non-ovigerous female, 3.3 mm CL, Hongtang bay, Hainan Island, northern South China Sea, 1–3 m, Coll. Z B, Gan, 25 March 2018 (GenBank accession number of 16S rRNA gene: MK231007). ***Paratypes***: MBM285016, 1 male, 2.3 mm CL, same collection data as holotype (GenBank accession number of 16S rRNA gene: MK231008); MBM285017, 2 non-ovigerous female, 2.7–3.0 mm CL, Houhai bay, Hainan Island, northern South China Sea, 2–3 m, Coll. Z B. Gan, 22 March 2018.

Description. ~~Large sized shrimp of *Hippolyte*, o~~Outline robust (Fig. 1~~,2~~). Ratio lateral length/height of carapace 1.56–1.72. Rostrum long, slightly shorter than carapace, distinctly overreaching antennular peduncle, nearly reaching to the end of scaphocerite~~,~~ ; without lateral carina, superior border slightly concave, unarmed in the female specimens (Fig. ~~3A~~2A,B) and armed with only one proximal tooth in the male specimen (Fig. ~~3C~~2C), inferior border slightly convex, armed with 4 teeth in the distal half length. Carapace smooth and glabrous, with robust supraorbital~~ spine~~, antennal ~~spine~~ and hepatic spines (Fig. ~~3A~~2A,B). Base of supraorbital spine posterior to the posterior orbital margin. Tip of antennal spine slightly overreaching inferior orbital angle. Tip of hepatic spine falling short of anterior edge of carapace. Inferior orbital angle strongly produced, knob-like (Fig. ~~3B~~2B,D). Branchiostegal margin with a distinct notch. Pterygostomian region rounded, strongly produced (Fig. 1,~~3B~~2B).

Abdominal segments smooth (Fig. 1). Third abdominal segment geniculately curved. Ratio dorsal length/height of the sixth abdominal segment 1.95–2.10. Telson (Fig. ~~3E~~2E) longer than the sixth abdominal segment~~;~~, posterior margin rounded, armed with eight strong spines, outer spines smallest, medial two longest, without intermediate spinule~~s~~ or seta~~.~~; ~~Dorsal~~ dorsal surface armed with two pairs of spines situated on distal 0.31–0.35 and 0.59–0.63 telson length.

Eye (Fig. ~~3A~~2A) well developed~~;~~, tip of cornea nearly reaching to the end of first segment of antennular peduncle when extended forward; unpigmented part of eyestalk longer than broad; cornea semispherical, distinctly shorter than unpigmented part of eyestalk.

Antennular peduncle (Fig. ~~3F~~2F) slightly overreaching mid~~dle~~-length of scaphocerite. First segment of antennular peduncle with one well developed distolateral tooth~~,~~; inner ventral tooth (Fig. ~~3G~~2G) ~~on~~ 0.47–050 of first segment (excluding distolateral tooth). Stylocerite large, reaching 0.56–0.62 (distolateral tooth included), or 0.69–0.75 (distolateral tooth excluded) of first segment. Second segment of antennular peduncle 0.81–0.86 times as long as broad in dorsal view, approximately 0.86–0.98 times as long as third segment in dorsal view. Outer antennular flagellum shorter than inner ~~flagellum~~ one and proximal 6–8 segments thicker than ~~orthers~~~~others~~distal ones. Scaphocerite (Fig. ~~2H~~2H) 3.06–3.18 times as long as wide, distolateral spine of scaphocerite far from reaching distal margin of blade, distolateral spine and blade separated by a distinct notch.

Mandible (Fig. ~~4A~~3A,B) without palp, incisor process ~~unique in the genus *Hippolyte*,~~ with 15–17 acute teeth. Maxillula (Fig. ~~4C~~3C) with broad curved palp, distal margin of upper lacinia armed with 14–18 spines and scattered simple long setae. Maxilla (Fig. ~~4D~~3D) with short palp~~;~~, scaphognathite broad and long, lateral border nearly straight; inner lacinia bilobed, distal margin furnished with row of spines and long plumose setae; proximal endite round, with long setae on distal margin. Epipod of first maxilliped (Fig. ~~4E~~3E) slightly bilobed, endopod broad with distal long setae, exopod~~ with~~ well-developed, caridean lobe broad. Second maxilliped (Fig. ~~4F~~3F) with well-developed exopod, flagelliform; endopod normal, dactylar segment oval, terminal margin furnished with simple and spinous setae; propodal segment with anteromedial margin round, bearing simple setae; carpus broader than long, and shorter than merus; ischium and basis fused. Third maxilliped (Fig. ~~4G~~3G) reaching to 0.32–0.39 of the scaphocerite when extended forward~~.~~, ~~Exopod~~ exopod relatively short, only reaching to the mid-length of antepenultimate segment~~.~~ of endopod; ~~Ultimate~~ ultimate segment (excluding apical spine) of endopod 1.23–1.32 times as long as penultimate segment, distal half armed with 7–9 strong spines; antepenultimate segment nearly equal length to the last two segments combined.

First pereiopod (Fig. ~~5A~~4A) shortest among pereiopods, robust and oblique, reaching to the end of basicerite when extended forward. Ventral margin of ischium, merus and carpus furnished

Comentário [AdS4]: This sentence is difficult to understand. Revise it, please.

Comentário [AdS5]: Is this word needed here?

Comentário [AdS6]: Length?

with long simple setae. Terminal margin of carpus cotyloid. Cutting edges of chela non-denticulate, with tiny setula and long simple distal setae; tip of fingers armed with 3 acute spines respectively (Fig. ~~5B~~4B).

Second pereiopod (Fig. ~~5C~~4C) slightly overreaching the end of third maxilliped when extended forward. Carpus with three subsegments, first subsegment 1.70–1.85 times as long as second subsegment, third subsegment slightly longer than or subequal to first subsegment; first subsegment 2.45–2.56 times as long as wide, second subsegment 1.08–1.12 times as long as wide, third subsegment 2.06–2.12 times as long as wide. Cutting edges of chela not denticulate, with tiny setula and long simple setae; tip of fixed finger and dactylus armed with 3 acute spines respectively (Fig. ~~5D~~4D).

Comentário [AdS7]: Where are this in the figure?

Third to fifth pereiopods long and robust. Third pereiopod (Fig. ~~5E~~4E) ~~of female specimen~~ reaching to the distolateral spine of scaphocerite when extended forward~~. ~~; ~~Dactylus~~ dactylus ~~of third pereiopod~~ with 13–16 spines, the last 2–3 subdorsal spines distinctly shorter than the other terminal spines (Fig. ~~5F~~4F~~).~~); ~~Propodus~~ propodus 5.56–5.62 times as long as wide, armed with 6–7 pairs of spines on ventral margin~~.~~; ~~Carpus~~ carpus 2.66–2.73 times as long as wide, armed with one proximal lateral spine~~.~~; ~~Merus~~ merus 5.58–5.62 times as long as wide, armed with 3 lateral spines. Ratio length of third pereiopod dactylus with longest apical spine/length of propodus 0.45–0.49; ratio length of third pereiopod dactylus with longest apical spine/length of carpus 0.79–0.83; ratio length of dactylus without spines/breadth of dactylus without spines 2.61–2.69; ratio length of dactylus with longest spines/breadth of dactylus without spines 2.95–3.10; ratio length of longest spine of dactylus/breadth of dactylus without spines 0.62–0.71; ratio length of longest spine of dactylus/length of dactylus without spines 0.22–0.28. Third pereiopod (Fig. ~~5G~~4G,H) of male specimen with propodus and dactylus forming a prehensile apparatus. Fourth and fifth pereiopods (Fig. ~~5I~~4I,J,K,L) similar in shape to third pereiopod of female specimen, but slightly decreasing in size. Merus of fourth pereiopod armed with 2 lateral spine; merus of fifth pereiopod without lateral spine.

First pleopod (Fig. ~~5M~~4M) of female specimen normal, endopod about 0.54–0.62 times as long as exopod. First pleopod (Fig. ~~5N~~4N) of male specimen with endopod about 0.41–0.46 times as long as exopod. Second pleopod (Fig. ~~5O~~4O) of male specimen with endopod about 0.81–0.89 times as long as exopod, appendix masculina with 9 apical setae, about 0.39–0.43 times as long as appendix interna (Fig. ~~5P~~4P).

Coloration. Generally light brown over body (Fig. ~~2~~5A), with few tawny stripes on carapace~~,~~ and ~~with~~ faint~~pindling~~ tawny spots on abdomen.

Biotope. All specimens were captured among gulfweed (*Sargassum* sp.) ~~under the~~at depths of 1–3 m. Plenty of *Hippolyte* cf. *ventricosa* were ~~co-~~captured ~~at the same time~~simultaneously~~, the ratio of prisal nearly reached to 1:8~~.

Distribution. Hongtang bay and Houhai bay, Hainan Island, northern South China Sea~~;~~ ~~–~~. ~~presumably~~Presumably, also distribute in Malayan Archipelago and Madagascar (see discussion).

Comentário [AdS8]: Occurs? Revise the sentence.

Etymology. The new species is named after Dr. Fenner A. Chace, Jr. in recognition of his great contribution to the crustacean taxonomy.

Hippolyte nanhaiensis **sp. nov.**

(Figs. 6–9, ~~10B~~5B–E)

Material examined. ***Holotype:*** MBM285018, ovigerous female, 1.6 mm CL, Ganquan Island, Xisha Islands, the South China Sea, 1–3 m, Coll. Z B, Gan, 15 May 2015 (GenBank accession number of 16S rRNA gene: MK231005). ***Paratypes:*** MBM285019, 1 male, 1.1 mm CL, same collection data as holotype (GenBank accession number of 16S rRNA gene: MK231006); MBM189210, 4 ovigerous female, 1.3–1.6 mm CL, 2 female, 1.2–1.3 mm CL, 2 male, 0.9–1.1 mm CL, 1 juvenile 0.6 mm CL, same collection data as holotype; MBM189211, 19 ovigerous female, 1.3–1.9 mm CL, 6 female, 1.0–1.4 mm CL, 5 male, 0.8–1.1 mm CL, 5 juvenile 0.6-0.8 mm CL, Bei Island, Xisha Islands, the South China Sea, 1–3 m, Coll. Z B. Gan, 13 May 2015.

Description. ~~Middle sized shrimp of *Hippolyte*, o~~Outline stout~~soft~~ (Fig. 6~~, 10B–E~~). Ratio lateral length/height of carapace 1.49–1.58. Rostrum distinctly shorter than carapace, reaching to or slightly overreaching the end of antennular peduncle, without lateral carina; superior border straight, armed with 1–2 tooth in proximal position (Fig. 7A–D); inferior border armed with 1 subdistal tooth~~distal teeth~~ in female specimens (Fig. 7C), and unarmed or only with 1 tiny distal notch in male specimens (Fig. 7D). Carapace smooth and glabrous, with supraorbital~~ spine~~, antennal ~~spine~~ and hepatic spines (Fig. 7B,C). Base of supraorbital spine posterior to posterior orbital margin. Antennal spine small, slightly overreaching inferior orbital angle. Hepatic spine reaching to or slightly overreaching anterior edge of carapace. Inferior orbital angle produced, knob-like (Fig. 7B,C). Branchiostegal margin sinuous. Pterygostomian region rounded, strongly produced (Fig. 7C).

Abdominal segments smooth (Fig. 6), without or with few long plumose setae on tergum. Third abdominal segment geniculately curved. Ratio dorsal length/height of the sixth abdominal segment 1.91–2.08. Telson (Fig. 7E) longer than sixth abdominal segment~~;~~, posterior margin rounded, armed with eight strong spines, outer spines smallest, medial two longest, without or with two intermediate long plumose setae~~.~~; ~~Dorsal~~ dorsal surface armed with two pairs of spines situated on distal 0.21–0.26 and 0.43–0.49 telson length.

Eye (Fig. 7A) well developed, tip of cornea falling short of the first segment of antennular peduncle when extended forward~~,~~; unpigmented part of eyestalk slightly longer than broad~~,~~; cornea semispherical, slightly shorter than unpigmented part of eyestalk.

Antennular peduncle (Fig. 7F) distinctly overreaching mid-~~dle~~length of scaphocerite. First segment of antennular peduncle with one distolateral tooth~~,~~; inner ventral tooth (Fig. 7G) on 0.59–0.66 of first segment (excluding distolateral tooth), small~~samll~~. Stylocerite large, reaching 0.86–0.92 (distolateral tooth included), or 0.76–0.81 (distolateral tooth excluded) of first segment. Second segment of antennular peduncle 0.88–0.96 times as long as broad in dorsal view, 0.83–0.95 times as long as third segment. Outer antennular flagellum shorter than inner flagellum and proximal 7–9 segments thicker than ~~orthers~~~~others~~distal ones. Scaphocerite (Fig.

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Comentário [AdS9]: I question if this is the right place for this word. Please, revise the sentence.

Comentário [AdS10]: Revise this sentence to clarify the meaning.

Comentário [AdS11]: ?

7H) 2.19–2.38 times as long as wide, distolateral spine of scaphocerite far from reaching distal margin of blade, distolateral spine and blade separated by a notch.

Mouthparts typical for genus. Mandible (Fig. 8A) without palp, incisor process with 5 acute teeth. Maxillula (Fig. 8B) with curved palp, distal margin of upper lacinia armed with 8–10 spines and two long plumose setae. Maxilla (Fig. 8C) with ~~pudgy~~ short palp; scaphognathite broad in upper half and narrow in lower half, lateral border nearly straight; inner lacinia bilobed, distal margin furnished with spinous setae; proximal endite round, with long plumose setae on distal margin. Endopod of first maxilliped (Fig. 8D) slender, with long plumose setae; exopod with feeble caridean lobe on base. Second maxilliped (Fig. 8E) with well-developed exopod, flagelliform; endopod normal, dactylar segment arched, terminal margin armed with row of long spines; propodal segment bearing few long plumose setae; carpus longer than broad, shorter than merus. Third maxilliped (Fig. 8F) reaching to mid-~~lenght~~length of the scaphocerite when extended forward; exopod reaching to 0.72–0.79 of antepenultimate segment; ultimate segment (excluding apical spine) of endopod 1.61–1.78 times as long as penultimate segment, distal half armed with 6–9 strong spines; antepenultimate segment slightly shorter than the last two segments combined.

First pereiopod (Fig. 9A) shortest among pereiopods, oblique, nearly reaching to mid-~~lenght~~length of the scaphocerite when extended forward. Ventral margin of basis, ischium, and merus furnished with long plumose setae. Terminal margin of carpus cotyloid. Cutting edges of chela non-denticulate, with tiny setula and long simple setae; tip of fixed finger with 3 acute spines, tip of dactylus with 4 acute spines (Fig. 9B).

Second pereiopod (Fig. 9C) slightly overreaching~~reaching to~~ the distolateral spine of scaphocerite when extended forward. Carpus with three subsegments, first subsegment 2.13–2.26 times as long as second subsegment, third subsegment slightly shorter than first subsegment; first subsegment 2.65–2.76 times as long as wide, second subsegment 1.08–1.16 times as long as wide, third subsegment 1.76–1.83 times as long as wide. Cutting edges of chela not denticulate, with ~~tiny setula and~~ long ~~simple~~ distal setae. Tip of fixed finger with 3 acute spines, tip of dactylus with 4 acute spines (Fig. 9D).

Third to fifth pereiopods long and robust. Third pereiopod (Fig. 9E) ~~of female specimen~~ reaching beyond terminal blade of scaphocerite by dactylus when extended forward~~.~~; ~~Dactylus~~ dactylus ~~of third pereiopod~~ with 8–10 spines, all spines in ventral and apical positions (none in dorsal or subdorsal positions), with two ~~large~~ apical spines larger than others (the ultimate longer but thinner than the penultimate) (Fig. 9F~~).~~); ~~Propodus~~ propodus 6.98–7.12 times as long as wide, armed with 4–6 pairs of spines on ventral margin~~.~~; ~~Carpus~~ carpus 2.96–3.14 times as long as wide, armed with one proximal lateral spine~~.~~; ~~Merus~~ merus 6.45–6.63 times as long as wide, armed with 2 lateral spines. Ratio length of third pereiopod dactylus with longest apical spine/length of propodus 0.42–0.46; ratio length of third pereiopod dactylus with longest apical spine/length of carpus 0.86–0.92; ratio length of dactylus without spines/breadth of dactylus without spines 2.86–2.93; ratio length of dactylus with longest spines/breadth of dactylus without spines 4.35–4.43; ratio length of longest spine of dactylus/breadth of dactylus without spines

1.50–1.55; ratio length of longest spine of dactylus/length of dactylus without spines 0.53–0.58. Third pereiopod ~~(Fig. 9G,H)~~ of male specimen with propodus and dactylus forming a prehensile apparatus (Fig. 9G,H). Fourth and fifth pereiopods (Fig. 9I,J) similar in shape to third pereiopod of female specimen, but slightly decreasing in size. Merus of fourth pereiopod armed with 0–1 lateral spine~~;~~, merus of fifth pereiopod without lateral spine.

First pleopod (Fig. 9K) of female specimen normal, endopod about 0.72–0.78 times as long as exopod. First pleopod (Fig. 9L) of male specimen with endopod about 0.25–0.29 times as long as exopod. Second pleopod (Fig. 9M) of male specimen with endopod about 0.79–0.86 times as long as exopod~~,~~; appendix masculina with 8 apical setae, about 0.41–0.47 times as long as appendix interna (Fig. 9N).

Coloration and Biotopes. The specimens collected ~~in~~ from different biotopes ~~exhibiting~~ exhibited different body ~~colours~~colors. Specimens (Fig. ~~10B~~5B,C) captured among *Galaxaura* sp. are generally pink over the body with numerous white spots; specimens (Fig. ~~10D~~5D,E) captured among *Halimeda* sp. are generally light green over the body with white or pink stains on the carapace, abdomen, and telson. All specimens were captured ~~under the~~at depths of 1–3 m~~, without other *Hippolyte* spp. was co-captured~~.

Distribution. Xisha Islands, the South China Sea~~;~~. ~~presumably~~Presumably, also distribute in Taiwan Island~~s~~ (see discussion).

Etymology. ‘Nanhai’ means the South China Sea; the new species is named after its type locality.

Discussion

Hippolyte chacei sp. nov. can be distinguished from all ~~of the~~ valid *Hippolyte* species ~~of *Hippolyte*~~ by ~~its~~ the ~~particular~~ unique dactyli of the third to fifth pereiopods. This kind of dactyli was seldom recorded ~~from~~ in previous literatures~~,~~ ;~~and~~ all ~~the~~ specimens with this kind of dactyli were ~~under the name~~previously considered as *H. ventricosa* ~~once upon a time~~, ~~namely~~ such as specimens ~~the~~ recorded from Malayan Archipelago (~~of~~ Holthuis ~~(~~, 1947) ~~from Malayan Archipelago~~, ~~the record of Ledoyer (1970) from~~ Madagascar (Ledoyer, 1970), and ~~also the record of Hayashi (1981) from~~ Hawai (Hayashi, 1981). ~~d’Udekem~~ D’Udekem d’Acoz (1996) considered that all these ~~specimens~~ previous descriptions were not real *H. ventricosa*~~,~~ and might represent some undescribed species~~.~~; ~~The~~ the present work, based on molecular data, ~~-~~confirmed ~~the~~ this suspicion~~judgment of d’Udekem d’Acoz (1996) based on molecular data~~. In the 16S rRNA phylogenetic tree (Fig. ~~11~~10) ~~of 16S rRNA gene segments~~, *H. chacei* sp. nov. (two specimens) formed an ~~lonely~~ isolated branch clustered in the subbasal position of the Indo-West ~~pacific~~ Pacific clade (Terossi et al., 2017~~), ~~). ~~and~~ Additionally, the average genetic divergence between *H. chacei* sp. nov. and other *Hippolyte* spp. ~~is~~ was 20.8%, which is slightly larger than the average interspecific genetic divergence, 20.5% (calculated from the 30 *Hippolyte* species ~~of *Hippolyte*~~ in th~~e present~~is study). ~~According to~~Based on the oversimplified and ~~inadequacy~~ inadequate descriptions ~~of~~ by Holthuis (1947) and Ledoyer (1970), their specimens are ~~were~~ morphologically very similar to *H. chacei* sp. nov.~~ in morphology, ~~. ~~so~~ Therefore, ~~it is~~we speculate~~d~~ that the~~ir~~ specimens may belong to *H. chacei* sp. nov~~.,~~ .; however, ~~the validation~~

~~should be support~~this should be tested by ~~a~~ further detailed examination of the ~~specimens of~~ Holthuis (1947) and Ledoyer (1970) specimens. Hayashi (1981) stated that the mouthparts of ~~his~~ Hawaiian specimens were similar to those of *H. edmondsoni* and *H. jarvisensis*, ~~and~~ but ~~this kind of~~the~~se~~ir mouthparts ~~is we~~are distinctly different from ~~that~~ those of *H. chacei* sp. nov~~., ~~.; ~~and the difference is also shown in~~moreover, differences were also observed in the position of hepatic spine. Presumably, the specimens recorded by Hayashi (1981) may represent a different species from *H. chacei* sp. nov..

~~Our specimens of *Hippolyte chacei* sp. nov. were captured among *Sargassum* sp. together with *Hippolyte cf ventricosa*. This may indicate that the two species occupy similar ecological niche, but the ratio of prisal nearly reached to 1:8. We speculate that *H. chacei* sp. nov. probably remain a predicament in the interspecific competition.~~

~~In morphology~~Morphologically, ~~*Hippolyte*~~ *H. nanhaiensis* sp. nov. is closely related to *H. acuta*, *H. australiensis*, *H. ngi*~~;~~, *H. singaporensis*, and *H. ventricosa* (redescribed by d'Udekem d'Acoz, 1999~~.~~); ~~They~~ they all have the ~~features of~~ first article of the antennular peduncle with one distolateral tooth, fifth pleonite without dorsolateral ~~tooth~~teeth, and third to fifth pereiopods with normal dactyli. *H. nanhaiensis* sp. nov. differs from *H. acuta*, *H. australiensis*, and *H. ngi* by ~~the~~ its shorter rostrum (reaching to or slightly overreaching the end of the antennular peduncle *vs.* distinctly overreaching the end of the antennular peduncle). Furthermore, *H. acuta* is distinguished from *H. nanhaiensis* sp. nov. ~~also~~ by ~~a~~ its particularly long eyestalk (Stimpson, 1860; Hayashi & Miyake, 1968; Yanagawa & Watanabe, 1988; d'Udekem d'Acoz, 1996)~~, and~~. *H. australiensis* is distinguished from *H. nanhaiensis* sp. nov. by ~~the~~ its rostrum, ~~with~~ which has a sharp lateral carina, and ~~the~~ also by its dactyli of the third to fifth pereiopods, which ~~with~~ have 4 large apical spines (d'Udekem d'Acoz, 2001). *H. ngi* differs from *H. nanhaiensis* sp. nov. by ~~the~~ its hepatic, which overreaches the anterior edge of carapace by distal ~~half of hepatic spine overreaches the anterior edge of carapace~~ half length, and also by its ~~the~~ dactyli of the third to fifth pereiopods ~~with~~, which have 3 large apical spines (Gan & Li, 2017b).

According to the *H. ventricosa* redescription ~~of *Hippolyte ventricosa*~~ by d'Udekem d'Acoz (1999) based on type specimens, *H. ventricosa* and *H. nanhaiensis* sp. nov. both have 2 large apical spines on the dactyli of the third to fifth pereiopods ~~with 2 large apical spines, ~~. ~~however~~However, the latter has more long~~er~~ apical spines. The ratio ~~length~~ of the longest spine of the dactylus/length of the dactylus without spines is 0.53–0.58 in *H. nanhaiensis* sp. nov., but ~~it~~ is only 0.35 in *H. ventricosa*. The ~~rostrum of~~ *H. ventricosa* rostrum distinctly overreaches the end of the antennular peduncle, but ~~it~~ only reaches to or slightly overreaches the end of the antennular peduncle in *H. nanhaiensis* sp. nov.. The ~~scaphocerite of~~ *H. ventricosa* scaphocerite is 3.10 times as long as wide, ~~while it~~but is 2.19–2.38 times as long as wide in *H. nanhaiensis* sp. nov.. According to d'Udekem d'Acoz (1999), the total length ~~of syntype~~ of the *H. ventricosa* syntypes is up to 17 mm, which is nearly two times larger than the largest ~~specimen of~~ *H. nanhaiensis* sp. nov. specimen. Furthermore, the two species ~~take up~~inhabit different ecological niches~~,~~; *H. ventricosa* ~~living~~ lives among *Zostera* sp. and *Padina* sp., ~~maybe~~ and may also be found among *Sargassum* sp. ~~etc~~and other organisms. Nevertheless, *H. nanhaiensis* sp. nov. was

Comentário [AdS12]: What kind of organism? Please specify.

not found from any of these biotopes~~,~~; it was only captured from *Galaxaura* sp. and *Halimeda* sp., ~~among~~ which are currently found in higher temperatures ~~at present~~, and ~~no other species of *Hippolyte* were co-captured~~ no congeneric species were found from these biotopes either. ~~As d~~Different species ~~possibly present~~may have different ecological requirements~~,~~ and prefer different biotopes ~~(d'Udekem d'Acoz, 1996)~~.

In the 16S rRNA phylogenetic tree (Fig. ~~11~~10) ~~of 16S rRNA gene segments~~, ~~*Hippolyte*~~ *H. nanhaiensis* sp. nov. (two specimens)~~,~~ formed a clade ~~together~~ with *H. ventricosa* group~~–~~-sp. 4 (Terossi et al., 2017), ~~form a monophyletic clade being sister group with~~and this clade is sister to *H. australiensis*. The average genetic divergence between *H. nanhaiensis* sp. nov. and other *Hippolyte* spp. is 22.5%, which is larger than the average interspecific genetic divergence~~,~~ (20.5%) ~~(calculated from the 30 species of *Hippolyte* in the present study)~~. The result of 16S rRNA sequence~~s~~ alignment ~~of 16S rRNA gene segments shows~~showed that the *H. nanhaiensis* sp. nov. sequences were ~~of *H. nanhaiensis* sp. nov. is~~ identical ~~with~~to, or only ~~has~~ had one nucleotide base ~~different~~ difference from, that of *H. ventricosa* group~~–~~-sp. 4 (KX588916). ~~In this case~~Therefore, *H. ventricosa* group~~–~~-sp. 4 and *H. nanhaiensis* sp. nov. may represent the same species.

During the biodiversity surveys (Hainai Island biodiversity surveys were conducted in 2014, 2015, 2016, 2017, and 2018, the Xisha Islands biodiversity surveys were conducted in 2015, 2016), dozens of ~~*Hippolyte*~~ *H.* cf. *ventricosa* (GenBank accession number of 16S rRNA gene: MK231003, MK231004, MK231009) were collected among biotopes of *Sargassum* sp. and *Thalassia* sp. from the nearshore waters of ~~Hannai~~ Hainan Island (no specimens were found from the Xisha Islands). These specimens ~~have~~ had the following features: (1) first article of the antennular peduncle ~~has~~ with one distolateral tooth, and fifth pleonite ~~has~~ no dorsolateral tooth; (2) carapace length of mature females ~~is~~ among 1.8–3.3 mm, and total length among~~is~~ 13–24 mm; (3) rostrum distinctly ~~overreaches~~ overreaching the end of the antennular peduncle but falling short of scaphocerite apex, superior border with 1–2 ~~tooth~~ teeth and inferior border with 1-5 ~~tooth~~teeth; (4) incisor process of mandible with 5–6 teeth; (5) scaphocerite 2.79–3.38 times as long as wide; (~~4~~6) ~~the~~ dactyli of the third to fifth pereiopods with 2 large apical spines, but the longest apical spine~~s~~ never exceeding the half-length of dactyli properly, the ratio ~~length~~ of the longest spine of dactylus/length of dactylus without spines ~~is~~ among 0.33–0.41; (~~5~~7) ~~the~~ specimens displaying various colorations (Fig. ~~10F~~5F–G). All of these features differed from ~~that~~ those of *H. acuta*, *H. australiensis*, *H. ngi*~~;~~, *H. singaporensis*, and *H. nanhaiensis* sp. nov., but ~~indicate these specimens belong to~~are similar to those of *H. ventricosa* (based on the redescription by d'Udekem d'Acoz, 1999). ~~However~~Recently, more than four cryptic or pseudocryptic species ~~of *H. ventricosa*~~ were detected ~~through~~ with molecular data ~~(De Grave et al., 2014; Terossi et al., 2017)~~, ~~although d'Udekem d'Acoz (1999) detailedly redescribed *H. ventricosa* based on type specimens~~which were also morphologically very similar to *H. ventricosa* (De Grave et al., 2014; Terossi et al., 2017). Therefore, ~~It~~ it is currently unclear which specimens represent ~~confused to determine which one is~~ true *H. ventricosa*~~,~~; ~~the~~ 16S rRNA ~~gene~~

Comentário [AdS13]: Praries?

Comentário [AdS14]: Specify the temperatures you are meaning here.

Comentário [AdS15]: Delete this.

Comentário [AdS16]: The information on the islands biodiversity surveys, including the exact dates of occurrence should be placed on the Mat&Met section. Remove it from here. A small description of each biotope (Hanai Island and Xisha Island should be included.

Comentário [AdS17]: This information should be added to the Results section and here it should be only discussed.

~~segment~~ or other genetic data derived from the *H. ventricosa* topotype ~~of *H. ventricosa* is expected~~are expected to clarify this issue.

Conclusions

As ~~pointed~~ noted by d'Udekem d'Acoz (1999; 2001), the systematics of the Indo-West ~~pacific~~ Pacific genus *Hippolyte* is extremely ~~hysteretic~~complicated, ~~despite~~ even though this region ~~was~~ is considered ~~to be~~ the origin center of the genus (Terossi et al., 2017). The taxonomic ~~troubles~~ confusion ~~come from~~results from both the lack of knowledge on several species, such as *H. proteus*, *H. kraussiana*, and *H. acuta*, ~~the poorly known species~~ and the vast continuous variation of morphological character~~istic~~s. Our ~~research indicate~~study revealed that the proportion of the rostrum, ~~the scale of~~ scaphocerite scale, ~~the~~ position of the hepatic spine, and ~~the~~ features of the dactyli of the third to fifth pereiopods are ~~more significant~~extremely important in *Hippolyte* morphological taxonomy ~~of *Hippolyte*~~. ~~And in the future, a new taxon established based on integrative datum, eg morphological data, genetic data, and ecological data and so on, will be more valuable and credible.~~ A preliminary key ~~to~~for the identification of mature female of the genus *Hippolyte* of the Indo-West Pacific and neighboring seas is provided. This key only contains the valid species listed in WoRMS (http://www.marinespecies.org), and the cryptic or pseudocryptic species of *H. ventricosa* are temporarily pooled together as '*H. ventricosa*' *sensu lato*.

Key to mature female of *Hippolyte* ~~of~~for the Indo-West Pacific and neighboring seas

1-First segment of antennular peduncle without distolateral tooth……………………..………..….2

1-First segment of antennular peduncle with one distolateral tooth……………………...……….3

2-Merus of third pereiopod with no more than one lateral spine, scaphocerite about 2.8 times as long as wide………………………………………………………….….…………*H. proteus*

2-Merus of third pereiopod with 3–5 lateral spines, scaphocerite about 3.5 times as long as wide……………………………………………………………………….….*H. kraussiana*

3-Dactyli of third to fifth pereiopods single-unguiculate, lacking or with tiny ventral spines, mainly associated with ~~a~~Alcyonacean corals………………..………………………..…………..4

3-Dactyli of third to fifth pereiopods with obvious ventral or subdorsal spines, mainly inhabited among seaweeds……………………………………………………………………..……….5

4-Carapace with dorsal surface fabulously gibbous…………………………..……….. *H. dossena*

4-Carapace with dorsal surface normal, not gibbous……………..……………….…*H. commensalis*

5-Rostrum subequal to or shorter than carapace, not exceeding the end of antennular penduncle obviously………………...……………………………………………………...……….6

5-Rostrum subequal to or longer than carapace, distinctly overreaching the end of antennular penduncle……………………………………..…………………………...….…..….……..11

6-Rostrum less than half length of carapace, reaching to the end of first segment of antennular peduncle at most………………………………………………………………*H. edmondsoni*

Comentário [AdS18]: Relatively to exactly what?

Comentário [AdS19]: What exactly are the relevant morphological features of the scaphocerite? And it is the scaphocerite scale is exactly?

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Comentário [AdS20]: Modify the numbering, e.g. 1a and 1b, etc. to make it clear.

Comentário [AdS21]: What this means exactly?

Comentário [AdS22]: Please replace this word with a more scientific one, clarifying what you mean here.

Comentário [AdS23]: What is a normal surface.

Comentário [AdS24]: When the rostrum is subequal to the carapace it is not possible to clearly distinguish the 2 taxa. Please revise this to make it clear.

6-Rostrum longer than the half length of carapace, reaching to the end of antennular peduncle..……………………………………………………………………..………………...7

7-Rostrum without dorsal tooth, base of hepatic spine nearly situating at anterior edge of carapace……………………………………………………………………….…. *H.singaporensis*

7-Rostrum with 1-2 dorsal teeth, base of hepatic spine situating at posterior to the anterior edge of carapace………………..…………………………………...………………..……………8

8-Dactyli of third to fifth pereiopods with three long terminal teeth, distal half of hepatic spine overreaching anterior edge of carapace…………………...…………………………....…*H. ngi*

8-Dactyli of third to fifth pereiopods with two terminal teeth, hepatic spine slightly overreaching anterior edge of carapace…...............……………………………………………...….……9

9-Distal spine of dactylus of third pereiopod longer than the half length of dactylus proper (excluding spines)…………………………..…………………...………………………..………10

9-Distal spine of dactylus of third pereiopod shorter than the half length of dactylus proper (excluding spines)……………………………………..……………………………..…. *H. jarvinensis*

10-Rostrum with postrostral spine, situating at just above the orbit……………….…..…*H.caradina*

10-Rostrum without postrostral spine, all dorsal spines situating at prior to the orbit……………………………………………………………….…..…*H. nanhaiensis* sp. nov.

11-Incisor process of mandible with no more than 8 acute teeth……………………………….12

11-Incisor process of mandible with 15–17 acute teeth, dactyli of third to fifth pereiopods with 2–3 subdorsal spines………………..……………………………………………*H. chacei* sp. nov.

12-Unpigmented part of eyestalk 3 times as long as cornea…………………...…..…... *H. acuta*

12-Unpigmented part of eyestalk no more than 3 times as long as cornea……………...…..……13

13-Rostrum without dorsal spine…………………………………………………...…………..14

13-Rostrum with dorsal spine………………………………………………………..…………..15

14-Apex of the rRostrum with trifid apex………………..…………………………………..…*H. multicolorata*

14-Apex of rostrum normal, non-trifidsimple……………………………………......……*H. australiensis*

15-Apex of the Rrostrum with bifid apex………………………………………….……..*H. bifidirostris*

15-Apex of rostrum normal, non-bifidsimple…………….………………….…*H. ventricosa sensu lato*

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