Revision of the larval morphology (Zoea I) of the family Hippolytidae Bate (Caridea), with a description of the first stage of the shrimp *Hippolyte obliquimanus* Dana, 1852

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Abstract

The aim of this study was to describe the first zoeal stage of *H. obliquimanus* from two geographically distinct populations, Caribbean and Brazilian, and to summarize the available data on larval morphology of the first zoea of the family Hippolytidae. Ovigerous females of *Hippolyte obliquimanus* were collected at Ubatuba (São Paulo, Brazil) and at Cahuita (Limón, Costa Rica). All morphological characters observed in the first zoeal stage of *H. obliquimanus* are shared with others species of the family Hippolytidae. Intraspecific variability in *Hippolyte obliquimanus* was detected in one morphological aspect: the first zoea had four denticles on the ventral margin of the carapace in the Brazilian population, while specimens from the Costa Rican population had three. We compiled the published descriptions of all hippolytids Zoea I (63 spp., 20%), and all zoeae share several characteristics; however, these morphological features cannot be used to distinguish the first zoeae of Hippolytidae from other caridean larvae. Historically, the presence of an exopodal seta at the maxillule and the absence of the anal spine/papilla have been considered as characteristic for the Zoea I of the genus *Hippolyte*. The results of our revision, however, did not support these conclusions: although *H. obliquimanus* showed an exopodal seta at the maxillule, and four congeners did not bear such structure; moreover, *H. obliquimanus* as well as one other congener have an anal spine/papilla.

Keywords: Crustacea, caridean shrimp, Decapoda, larval development, Western Atlantic

Introduction

The family Hippolytidae Bate is distributed worldwide (Bauer 2004) and consists of 318 species divided in 36 genera (De Grave *et al.* 2009). The genus *Hippolyte* Leach comprises 31 species (De Grave *et al.* 2009) occurring all around the world except in extremely cold waters (Udekem d´Acoz 1996). The larval morphology of the family Hippolytidae or some hippolytid

genera has been reviewed by several authors (Lebour 1932; Gurney 1937; Gurney 1942; Haynes 1985).

The genus *Hippolyte* is represented in America by eight species (Udekem d´Acoz 2007): three species occur along the Pacific coast (*H. californiensis* Holmes, *H. williamsi* Schmitt and *H. clarkii* Chace), and five species have been reported from the Atlantic coast (*H. coerulescens* (Fabricius), *H. pleuracanthus* (Stimpson), *H. zostericola* (Smith), *H. obliquimanus* Dana and *H. nicholsoni* Chace). The first zoeal stage was studied in five of these species: *H. clarkii* (by Needler 1934 as *Hippolyte californiensis)*, *H. coerulescens* (by Gurney 1936 as *H. acuminata*), *H. pleuracanthus* (by Shield 1978), *H. williamsi* (by Albornoz & Wehrtmann 1997) and *H. zostericola* (by Negreiros-Fransozo *et al.* 1996). However, except for *H. pleuracanthus*, the other descriptions of the first zoeal stage were incomplete, since many structures were not cited or described in detail. Concerning the hippolytid species reported so far for the Americas (8 spp.: Udekem d´Acoz 2007), the larval morphology of *H. californiensis*, *H. nicholsoni* and *H. obliquimanus*, has not been described yet.

Based only on adult morphology, Udekem d'Acoz (1997) postulated that *Hippolyte curacaoensis* Schmitt from Curaçao is a junior synonym of *H. obliquimanus* from Brazilian waters. Recent genetic studies, using the mithocondrial 16S and COI genes, have corroborated this hypothesis (Terossi & Mantelatto unpubl. data). Thus, *H. obliquimanus* is endemic to the Western Atlantic coast, and is restricted to shallow waters of the Caribbean and off Brazil from Ceará to Santa Catarina (Fausto-Filho 1975; Udekem d' Acoz 1997; Young 1998).

The aim of this study was to review the larval morphology (Zoea I) of the family Hippolytidae and to describe the first zoeal stage of *H. obliquimanus* provided from two geographically distinct populations from the Caribbean (Cahuita Beach, Limón, Caribbean coast of Costa Rica) and from Brazil (Ubatuba, State of São Paulo) in order to document interspecific and possible intraspecific

morphological variability. ~~Moreover, we compiled and compared available descriptions of the first zoeal stage from hippolytid shrimps.~~

Material and Methods

Ovigerous females of *Hippolyte obliquimanus* were collected at Cahuita Beach (Limón, Costa Rica, 09º39′304″N, 82º45′163″W) on February 2009 and May 2010 and at Itaguá Beach (Ubatuba, State of São Paulo, Brazil, 23º27′414″S, 45º03′047″W) on May 2009 and February 2010. Detailed information regarding site and method of sampling can be checked at Terossi *et al.* (in press). These females were maintained in containers with natural sea water until hatching. Recently-hatched larvae were obtained from ten females (carapace length: 2.09 ± 0.47 mm) from the Brazilian population and four females (carapace length: 2.43 ± 0.40 mm) from Costa Rican. Hatching larvae with active natatory behavior were fixed in 4% formaldehyde and 80% ethanol. The carapace length (CL) of the larvae was measured as maximum length from the posterior margin of the ocular orbit to the posterior margin of the carapace. Appendages were dissected under a Leica Wild MZ8 binocular microscope, and drawings and measurements were made using a Zeiss Axioskop 50 microscope equipped with *camera lucida*. All drawings and measurements were based on 20 larvae (10 from each locality). Larval description and setal counts followed the method proposed by Clark *et al*. (1998), and we used the setal terminology as suggested by Landeira *et al*. (2009). Some freshly hatched larvae from both populations with active natatory behavior were maintained frozen (-20 ºC) in glycerine for observation of the chromatophore pattern (Darryl L. Felder, pers. comm.). Voucher maternal specimens and larvae were deposited at the Crustacean Collection of the Biology Department of FFCLRP, University of São Paulo, Brazil (CCDB/FFCLRP/USP, access numbers: 2710 and 2711).

Results

Hippolyte obliquimanus Dana, 1852

Zoea I

Carapace length: Brazil: 0.31 ± 0.02 mm (n = 10); Costa Rica: 0.31 ± 0.02 (n = 10)

Carapace (Figures 1A,B): with a median tubercle, supraorbital spines absent, pterygostomian spine present; anteroventral margin with 3 (Costa Rica) or 4 (Brazil) denticles. Rostrum slender, without teeth and long, overreaching the extremity of the antennular peduncle.

Antennule (Figure 2A): peduncle unsegmented with an outer spiny projection near the exopod; endopod as a long plumose seta; exopod with 3 terminal aesthetacs, 1 terminal spatulate seta, and 1 inner terminal minute spine.

Antenna (Figures 2B): peduncle with a inner spiny projection near the endopod; endopod unsegmented, wider proximally, and with two equal rows of spines in the mediodistal region; exopod (antennal scale) 4-segmented distally with 10 plumose setae, plus 1 short simple seta on the distal segment (5, 1, 1, 3+1).

Mandible: with an incisor and molar processes well developed, without palp.

Maxillule (Figures 2C,D): coxal endite with 7 setae (1 plumose, 2 simple and 4 sparsely plumose) and microtrichia; basial endite with 3 short spines and 2 spines with apical crown of spinules (Figure 2D); endopod with 5 terminal setae (1 sparsely plumose, 2 sparsely hardy plumose and 2 simple); exopodal plumose setae present.

Maxilla (Figure 2E): coxal endite bilobed with 9 terminal setae (7 sparsely plumose and 2 plumose) on proximal lobe and 4 setae (2 terminal sparsely plumose and 2 subterminal plumose) on distal lobe; basial endite bilobed with 4 setae (3 terminal, 2 sparsely plumose + 1 simple, and 1 subterminal plumose) on each lobe; endopod with 4 lobes with 4 (3 sparsely plumose and 1 sparsely hardy plumose), 2 (1 sparsely plumose and 1 sparsely hardy plumose), 1 (sparsely hardy plumose), and 2 (1 sparsely plumose and 1 sparsely hardy plumose) setae, respectively, and microtrichia; exopod (scaphognathite) with 5 marginal plumose setae and microtrichia.

First maxilliped (Figure 3A): coxa with 5 plumose seta (2+1+2); basis with 12 setae arranged (3+3+3+3), the proximal one with 2 terminal plumose and 1 subterminal sparsely plumose setae, and the three distal groups with 3 sparsely plumose (2 terminal and 1 subterminal) setae each; endopod 4-segmented with 3 (2 terminal and 1 subterminal), 1 (terminal), 2 (terminal), and 4 (3 terminal and 1 subterminal) sparsely plumose setae, respectively; exopod 4-segmented with 0, 0, 1, 3, plumose natatory setae.

Second maxilliped (Figure 3B): coxa with 1 terminal sparsely plumose seta; basis with 8 sparsely plumose setae (1+1+3+3); endopod 4-segmented with 3 (sparsely plumose, 2 terminal and 1 subterminal), 1 (terminal sparsely plumose), 2 (terminal sparsely plumose), and 5 (4 terminal sparsely plumose and 1 subterminal simple) setae respectively; exopod 4-segmented with 0, 0, 2, 3, plumose natatory setae.

Third maxilliped (Figure 3C): coxa without setae; basis with 1 terminal sparsely plumose seta; endopod 4- segmented with 1 (terminal sparsely plumose), 1 (subterminal simple), 3 (terminal, 2 sparsely plumose and 1 simple), 3 (terminal sparsely plumose) respectively; exopod 4-segmented with 0, 0, 2, 3 plumose natatory setae.

Pereiopods: absent

Abdomen (Figures 1A, 4): with 5 somites without setae, pair of posterolateral spines on somite 5; somite 6 fused with the telson; pleopods and uropods absent, anal spine present.

Telson (Figure 4B): broad in the posterior margin, with 7+7 setae (inner 5 plumose, outer 2 laterally plumose setae), the outer pair is subterminal; one row of spinules on distal margin and around base of the 6+6 inner setae.

Chromatophores pattern (Table 3): all chromatophores observed in the zoea I from both populations are erythrophores (dark red) with the following arrangement; one at the base of rostrum (Figure 1C); one each side between antennular peduncle and the base of the eye (Figure 1C); one each side anterior carapace margin, near of the base of the eye (Figure 1C); one posterolaterally each

side on carapace (Figure 1C); two on the basis of antennule (Figure 2A); two on the basis of antenna (Figure 2B); one on the protopod of the maxilla (Figure 2E); one on the coxa of the first maxilliped (Figure 3A); one on the basis of the second maxilliped (Figure 3B); one each side of the posterior margin of third abdominal segment (Figure 4A); one each side of the fifth segment abdominal, near the posterolateral spine (Figure 4A); and two on the fused sixth abdominal segment-telson (Figure 4A).

Discussion

The larvae of the family Hippolytidae exhibit an immense diversity in larval forms, which makes it impossible to define any larval characters typical for the entire family (Gurney 1942; Gilchrist *et al.* 1983; Yang *et al.* 2001). This family consists of 318 recognized species, encompassing 36 genera (De Grave *et al.* 2009), but the first zoeal stage is known only for 63 species (20%) of 15 genera (41.6 %) (see Table 1), and for many species the description of this stage is poorly described or incomplete. We detected a critical scenario regarding the overall knowledge of the morphology of hatching larvae in Hippolytidae: in genera with more than 10 species, on average, 77% have not been described yet (Figure 5), which make a detailed comparison within and among genera extremely difficult.

Despite these limitations considering the descriptions available, all newly-hatched zoeae of Hippolytidae have the following characters in common: eye sessile, endopod of the antennules as a seta, rostrum without teeth, unsegmented peduncle of the antennules, pleopods and uropods absent, sixth abdominal segment fused with telson. However these characteristics cannot be used to distinguish hippolytids first zoeae from other caridean larvae. Table 2 summarizes the morphological characters of the first zoeal of all species so far described and indicates morphological variability between species and genera.

There are some characters that allow differentiating some genera from the rest of Hippolytidae, for example (Table 2): the absence of dorsal tubercle on carapace in two species of *Caridion,* the presence of more than 25 setae on the scaphognathite and more than 7 pairs of setae on telson of two species of *Lebbeus.*

The larval phase of hippolytid species with an unabbreviated development consists of six to nine stages (Pike & Williamson 1961; Haynes 1985; Yang *et al.* 2001), while species with an abbreviated development, like in the genus *Lebbeus*, have three or four larval stages (Haynes 1985). This kind of abbreviated development leads to some morphological differences in the first zoeal stage hatched (Table 2), with more than 7 pairs of setae on telson, more than 25 setae in the scaphognathite, and pereiopods developed with a small lobe like an exopodite (Haynes 1981).

Based on the published data concerning the larvae of 12 species of the genus *Hippolyte* (39% of the species described), the following characters can be found in all first zoeal stage of this genus: never with rudimentary pereiopod 3 to 5, and the presence of a posterolateral spine on the abdominal segment 5 (no data indicated in the description for *H. acuta,* Yokoya 1957).

The first zoea of *H. obliquimanus* bears 10 plumose setae on the antennal scale, and this characteristic is shared with three species congeners (Table 2). For the genus, the number of plumose setae can vary between 9 and 10. Negreiros Fransozo *et al.* (1996) described the antennal scale of the first zoea of *H. zostericola* as bearing 10 setae, however, the figure is indicating only 9 setae. We considered that the figure is correct, because it is more common that authors made a mistake in the descriptive part than in the figure.

The first zoeal stage of *H. obliquimanus* bears an exopodal seta at the basis of the maxillule, a morphological characteristic shared by the following four congeneric species: *H. bifidirostris* (Packer 1985), *H. multicolorata* (Packer 1985) *H. prideauxiana* (Lebour 1931) and *H. varians* (Lebour 1931). Historically, the presence of this characteristic was considered as a unique character of the genus *Hippolyte* (Lebour 1931; Gurney 1937; Lebour 1940; Williamson 1957). Nevertheless,

more recent studies of first zoeal stage of this genus revealed that four species (*H. acuta*, *H. pleuracanthus*, *H. williamsi* and *H. zostericola*) did not show this seta (Yokoya 1957; Shield 1978; Albornoz & Wehrtmann 1997; Negreiros-Fransozo *et al.* 1996; respectively). The presence of this exopodal seta in the maxillule of Zoea I has been reported also from other members of the family Hippolytidae: *Alope spinifrons* (Packer 1985), *Thor novaezealandiae* (Packer 1985) and species from the genus *Nauticaris* (Packer 1985; Wehrtmann & Albornoz 1998) as well as from other caridean shrimps (Gurney 1942; Haynes 1985) Therefore, this character cannot be used to separate the first zoeal stage of representatives of *Hippolyte* from those of other hippolytid and caridean shrimps.

The first zoea of *Hippolyte obliquimanus* has two spines with an apical crown of spinules at the basis of maxillule (Figure 2D), one with a strong central spinule and other one with two strong central spinules. Based upon the currently available descriptions of the first larval stage in *Hippolyte*, this might be a character that could be used to differentiate this species from other hippolytid species. The spines at the maxillule of *H. futilirostris* (Yang & Kim 2005, Figure 1E) are similar, but not identical compared to those found in *H. obliquimanus* (Figure 2D), being these stronger than those described for *H. futilirostris*.

All published descriptions of the Zoea I in *Hippolyte* mention a posterolateral spine on the abdominal segment 5 (no data indicated in the description for *H. acuta*, Yokoya 1957). However, such a spine it is not exclusive for *Hippolyte* and can be found also in other genera (Table 2).

The first zoeal stage of *H. obliquimanus* bears an anal spine/papilla (Figures 1A, 4), which has been described also for *H. pleuracanthus* (Shield 1978). On the other hand, the anal spine/papilla is absent in two species congeners (*H. clarki* and *H. williansi*, Table 2). The absence of such a spine was considered as characteristic of first zoeal stage of the genera *Caridion*, *Hippolyte*, *Lysmata*, *Tozeuma*, *Saron* (Gurney 1937; Haynes 1985); however, our results do not support this conclusion.

The first zoeal stage of six species of *Hippolyte* presents the two outer pairs of spines on the telson feathered only on their inner side (Table 2), now also including *H. obliquimanus* (Figure 4B). However, in *H. zostericola* all setae of the telson have plumose setae on both sides (Negreiros-Fransozo *et al*. 1996), while the telson of the first zoea of *H. williamsi* has only the outer pair of setae bearing plumose setae on its inner side (Albornoz & Wehrtmann 1997). For the other four species of this genus indicated in the Table 2 detailed information about these setae on the telson is not available.

All morphological characters observed in the first zoeal stage of *H. obliquimanus* are shared with others species of the family Hippolytidae. The external morphology of *Hippolyte obliquimanus* showed little variation between the two populations studied by us: the first zoea from the Brazilian population has four denticles on the ventral margin of the carapace, while specimens from the Costa Rican population present only three denticles. This can be considered as an intraspecific variation, already described for other species (Table 2), including the congeners *H. bifidirostris*, *H. multicolorata*, *H. prideauxiana* and *H. zostericola* (Packer 1985; Lebour 1931; Negreiros Fransozo *et al.* 1996; respectively). Despite the fact that freshly-extruded eggs of *H. obliquimanus* were larger in the Brazilian population compared to those produced in the Costa Rican population (Terossi *et al.* in press), the hatching larvae from both populations were identical in size.

The chromatophores are recognizable in the embryo and are specifically constant in number and position (Gurney 1942). According this author, the chromatophores are so constant that species otherwise almost undistinguishable may be easily identified by their chromatophores. In the present description, we found that both populations presented identical pattern of chromatophores. In this sense, more studies based on freshly-collected larvae are necessary to complete the description of chromatophore patterns in most caridean shrimps and to validate the use of this character as distinctive feature for species identification (Table 3).

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Legends

Figure 1: *Hippolyte obliquimanus*. Zoea I. (A) Lateral view, Brazilian specimen; (B) Carapace, lateral view, Costa Rican specimen; (C) Dorsal view, with chromatophore pattern. Scale bars: 0.1 mm.

Figure 2: *Hippolyte obliquimanus*. Zoea I. (A) Antennule; (B) Antenna; (C) Maxillule; (D) Detail of the spines crowned of spinules of the maxillule basial endite; (E) Maxilla. Position of chromatophores is indicated. Scale bars: (A, B, C, E) 0.1mm; (D) 0.01 mm.

Figure 3: *Hippolyte obliquimanus*. Zoea I. (A) First maxilliped; (B) Second maxilliped; (C) Third maxilliped. Position of chromatophores is indicated. Scale bars: 0.1 mm.

Figure 4: *Hippolyte obliquimanus*. Zoea I. (A) Abdomen, dorsal view; (B) Telson. Position of chromatophores is indicated. Scale bars: 0.1 mm.

Figure 5: Hippolytidae species for which zoea I have been described. The numbers on the right side correspond to the total number of species of each genus (left side).

Table 1: Hippolytidae species for which zoea I have been described.

Code	Species	Reference
Al_sp	*Alope spinifrons* (H. Milne-Edwards)	Packer 1985
Ca_go	*Caridion gordoni* (Bate)	Lebour 1930
Ca_st	*Caridion steveni* Lebour	Lebour 1930
Ch_an	*Chorismus antarcticus* (Pfeffer)	Gurney 1937
Ch_tu	*Chorismus tuberculatus* Bate	Thatje & Bacardit 2000
Eu_ba	*Eualus barbatus* (Rathbun)	Ivanov 1971; Haynes 1985
Eu_do	*Eualus dozei* (A. Milne Edwards)	Albornoz & Wehrtmann 1997
Eu_fa	*Eualus fabricii* (Krøyer)	Haynes 1981
Eu_ga	*Eualus gaimardii* (Milne Edwards)	Pike & Williamson 1961; Squires 1993
Eu_he	*Eualus herdmani* (Walker)	Needler 1934 as *Spirontocaris herdmani*
Eu_le	*Eualus leptognathus* (Stimpson)	Yamashita & Hayashi 1984
Eu_ma	*Eualus macilentus* (Krøyer)	Ivanov 1971; Haynes 1985
Eu_oc	*Eualus occultus* (Lebour)	Pike & Williamson 1961
Eu_pu	*Eualus pusiolus* (Krøyer)	Pike & Williamson 1961
Eu_si	*Eualus sinensis* (Yu)	Kurata 1968a as *E. gracilirostris*, Yang *et al*. 2001
Eu_su	*Eualus suckleyi* (Stimpson)	Haynes 1981
He_br	*Heptacarpus brevirostris* (Dana)	Needler 1934 as *Spirontocaris brevirostris*
He_ca	*Heptacarpus camtschaticus* (Stimpson)	Haynes 1981
He_fu	*Heptacarpus futilirostris* (Bate)	Kurata 1968b; Yang & Kim 2005
He_ge	*Heptacarpus geniculatus* (Stimpson)	Kurata, 1968c Yamashita & Hayashi 1980
He_pa	*Heptacarpus paludicola* Holmes	Needler 1934 as *Spirontocaris paludicola*
He_pn	*Heptacarpus pandaloides* (Stimpson)	Yamashita & Hayashi 1980
He_re	*Heptacarpus rectirostris* (Stimpson)	Yamashita & Hayashi 1979; Yang & Ko 2002
He_tr	*Heptacarpus tridens* (Rathbun)	Needler 1934 as *Spirontocaris tridens*
Hi_ac	*Hippolyte acuta* (Stimpson)	Yokoya 1957
Hi_bi	*Hippolyte bifidirostris* (Miers)	Packer 1985
Hi_cl	*Hippolyte clarki* Chace	Needler 1934 as *Hippolyte californiensis*
Hi_co	*Hippolyte coerulescens* (Fabricius)	Gurney 1936 as *H. acuminata*
Hi_mu	*Hippolyte multicolorata* Yaldwyn	Packer 1985
Hi_ob	*Hippolyte obliquimanus* Dana	Present study
Hi_pl	*Hippolyte pleuracanthus* (Stimpson)	Shield 1978
Hi_pr	*Hippolyte prideauxiana* Leach	Lebour 1931
Hi_va	*Hippolyte varians* Leach	Lebour 1931
Hi_ve	*Hippolyte ventricosa* H. Milne Edwards	Gurney 1927 *as H. orientalis*
Hi_wi	*Hippolyte williamsi* Schmitt	Albornoz & Wehrtmann 1997
Hi_zo	*Hippolyte zostericola* (Smith)	Negreiros-Fransozo *et al*. 1996
La_ac	*Latreutes acicularis* Ortmann	Yang 2007
La_an	*Latreutes anoplonyx* Kemp	Yang 2005

La_at	*Latreutes antiborealis* Holthuis	Albornoz & Wehrtmann 1997
La_la	*Latreutes laminirostris* Ortmann	Kim & Hong 1999
Le_gr	*Lebbeus groenlandicus* (Fabricius)	Ivanov 1971; Haynes 1978; Squires 1993
Le_po	*Lebbeus polaris* (Sabine)	Haynes 1981
Ly_an	*Lysmata anchisteus* Chace	Knowlton & Alavi 1995
Ly_se	*Lysmata seticaudata* (Risso)	Calado *et al.* 2004
Me_rh	*Merguia rhizophorae* (Rathbun)	Gilchrist *et al.* 1983
Na_ma	*Nauticaris magellanica* (A. Milne Edwards)	Wehrtmann & Albornoz 1998
Na_mr	*Nauticaris marionis* Bate	Packer 1985
Sa_ma	*Saron marmoratus* (Olivier)	Gurney 1937
Sp_ar	*Spirontocaris arcuata* Rathbun	Haynes 1981
Sp_cr	*Spirontocaris cranchii* (Leach)	Lebour 1932, 1936
Sp_ga	*Spirontocaris gaimardi* (H. Milne-Edwards)	Lebour 1940
Sp_ge	*Spirontocaris geniculata* (Stimpson)	Yokoya 1957
Sp_mu	*Spirontocaris murdochi* Rathbun	Haynes 1984
Sp_oc	*Spirontocaris ochotensis* (Brandt)	Haynes 1981
Sp_pa	*Spirontocaris pandaloides* (Stimpson)	Yokoya 1957
Sp_ph	*Spirontocaris phippsii* (Krøyer)	Haynes 1985; Squires 1993
Sp_re	*Spirontocaris rectirostris* (Stimpson)	Yokoya 1957
Sp_sp	*Spirontocaris spinus* (Sowerby)	Pike & Williamson 1961; Squires 1993
Sp_si	*Spirontocaris spinus* var. *lilljeborgi* (Danielssen)	Lebour 1937
Th_am	*Thor amboinensis* de Man	Yang & Okuno 2004
Th_fl	*Thor floridanus* Kingsley	Broad 1957; Dobkin 1968
To_ca	*Tozeuma carolinense* Kingsley	Gurney 1937; Ewald 1969
To_no	*Tozeuma novaezealandiae* Borradaile	Packer 1985

Table 2: Morphological characters of the first zoeal stage described for species of the family Hippolytidae. Abbreviations: Mxlp, maxilliped; P, pereiopods; L, laterally plumose seta; p, plumose seta. (*uncertain, see the discussion for explanation). Codes used for species identification according to Table I; in bold code numbers that refer to *Hippolyte* species, and underlined *H. obliquimanus*. Many species do not have information about some characters.

Characters			**Species**	**Genera**
Carapace	*Supraorbital spine*	*absent*	Eu_ba, Eu_fa, Eu_ga, Eu_he, Eu_le, Eu_ma, Eu_su, **Hi_ac, <u>Hi_ob</u>,** La_ac, La_an, Na_ma, Sp_ar, Sp_ge, Sp_mu, Th_am, To_ca	Ca, He, Le
		present	Sp_oc, Sp_ph, Sp_sp	
	Pterygostomian spine	*absent*	Eu_si, He_ca, He_ge, He_pn	Ca
		present	Eu_do, Eu_fa, Eu_ga, Eu_he, Eu_le, Eu_oc, Eu_pu, Eu_su, He_fu, He_pa, He_re, **Hi_cl, Hi_co, <u>Hi_ob</u>, Hi_ve, Hi_wi,** La_ac, La_at, Ly_an, Me_rh, Na_ma, Sa_ma, Sp_ar, Sp_cr, Sp_ga, Sp_mu, Sp_oc, Sp_ph, Sp_sp, Sp_si, Th_fl, To_ca	Ch, Le
	Number of denticles margin anteroventral	*absent*	Eu_ba, Eu_fa, Eu_si, He_br, He_ca, He_ge, He_pn, He_tr, La_la, Le_po, Me_rh, Sp_mu, Sp_sp, Sp_si, To_ca	Ca
		present	Al_sp, **Hi_co, Hi_va, Hi_ve,** La_ac, La_an, Na_mr, Th_am	
		2	Eu_le, Eu_oc, He_fu, He_pa, He_re, **Hi_pl,** Sa_ma	
		3	Ch_tu, Eu_do, Eu_he, Eu_pu, Sp_cr, Sp_ga, Th_fl	
		3-4	Eu_ga, Eu_su, **<u>Hi_ob</u>**	
		4	Eu_ma, **Hi_cl, Hi_wi**	
		others	*1* (La_at, Sp_oc); *2-3* (Le_gr, Sp_ar); *3-5* (**Hi_bi, Hi_mu**), *4-5* (**Hi_pr, Hi_zo**); *6* (Ly_se)	
	Dorsal tubercle	*absent*		Ca
		Present median	Ch_an, Eu_ga, **Hi_co, <u>Hi_ob</u>, Hi_pr, Hi_va,** La_la, Me_rh, Sp_ge, Sp_ph,	

				Th_fl	
			median and posterior	Ch_tu, Eu_do, Eu_fa, Eu_le, Eu_oc, Eu_pu, Eu_si, Eu_su, He_fu, He_re, **Hi_wi,** La_ac, La_an, La_at, Na_ma, Sa_ma, Sp_ar, Sp_cr, Sp_mu, Sp_oc, Th_am, To_ca	Le
Antenna	*Scale*		*unsegmented*	He_tr, **Hi_cl, Hi_zo,** Sp_si	
			segmented distally	Al_sp, He_br, He_ca, He_fu, He_ge, He_pa, He_re, **Hi_ac, Hi_bi, Hi_co, Hi_mu, Hi_ob, Hi_pl, Hi_pr, Hi_va, Hi_ve, Hi_wi,** Me_rh, Sa_ma, Sp_ar, Sp_cr, Sp_ga, Sp_ge, Sp_mu, Sp_oc, Sp_pa, Sp_re, Sp_sp	Ca, Ch, Eu, La, Le, Ly, Na, Th, To
	Plumose setae on scale		*9*	Ch_an, **Hi_zo***, Na_ma	
			10	He_re, He_tr, **Hi_ac, Hi_ob, Hi_ve,** Sp_mu, Sp_pa, Sp_sp, Sp_si, To_ca	
			11	Ch_tu, Eu_su, He_ca, La_ac, La_an, La_la, Le_po, Th_am	
			12	Eu_oc, Eu_pu, Eu_si, He_fu, Me_rh, Sa_ma, Sp_ar, Sp_oc	Ly
			others	*9-10* (**Hi_pl**); *10-11* (Eu_ga, Le_gr); *13* (Eu_fa); *11-14* (Th_fl)	
Maxillule	*Exopod seta on the basis*		*absent*	Ch_tu, Eu_ba, Eu_do, Eu_fa, Eu_ga, Eu_he, Eu_le, Eu_ma, Eu_su, He_pa, He_re, **Hi_ac, Hi_pl, Hi_wi, Hi_zo,** La_ac, La_la, Sa_ma, Sp_ar, Sp_cr, Sp_ge, Sp_mu, Sp_oc, Sp_pa, Sp_re, Sp_sp, Th_fl, To_ca	Ca, Le, Ly
			present	Al_sp, **Hi_bi, Hi_mu, Hi_ob, Hi_pr, Hi_va,** To_no	Na
Maxila	*Number of endites (coxal and basial)*		*4*	Ch_tu, Eu_fa, Eu_he, Eu_le, Eu_si, Eu_su, He_br, He_fu, He_pa, He_re, **Hi_ac, Hi_cl, Hi_ob, Hi_pl, Hi_pr, Hi_va, Hi_zo,** La_ac, La_an, La_la, Me_rh, Na_ma, Sp_ar, Sp_mu, Sp_oc	Ca, Le, Ly, Th, To
	Setae on the scaphognathite		*4*	Eu_su, Sp_ar, Sp_ge, Sp_pa, Sp_re	
			5	Ch_tu, Eu_ba, Eu_he, Eu_le, Eu_ma, Eu_si, He_br, He_fu, He_pa, He_re, **Hi_ac, Hi_cl, Hi_co, Hi_ob, Hi_pl, Hi_zo,** La_ac, La_an, La_la, Na_ma, Sa_ma, Sp_mu, To_ca	Ly, Th
			others	*3* (Me_rh); *7-8* (Sp_oc); >20 (Ch_an); *25* (Le_po); *33-35* (Le_gr)	
Maxillipeds	*Number of setae on distal*	*Mxlp1*	*(1 + 3)*	Ca_st, Ch_tu, Eu_fa, Eu_ga, Eu_he, Eu_le, Eu_oc, Eu_pu, Eu_si, Eu_su, He_br, He_fu, He_pa, He_re, **Hi_cl, Hi_co, Hi_ob, Hi_zo,** Me_rh, Na_ma,	Le, Ly, Th

	segments of the exopod (penultime segment + ultime segment)		Sp_ar, Sp_ga, Sp_ge, Sp_mu, Sp_oc, Sp_re, To_ca	
			(1 + 4)	**Hi_pl,** La_ac, La_la
		Mxlp2	*(1 + 3)*	To_ca
			(2 + 3)	Ca_st, Ch_tu, Eu_ba, Eu_fa, Eu_ga, Eu_he, Eu_le, Eu_ma, Eu_oc, Eu_pu, Eu_si, Eu_su, He_br, He_fu, He_pa, He_re, **Hi_cl, Hi_co, Hi_ob, Hi_pl,** Ly_an, Me_rh, Na_ma, Sp_ar, Sp_ga, Sp_ge, Sp_mu, Sp_oc, Sp_re, Sp_si	Le, Th
			(2 + 4)	La_ac, La_la, Ly_se, Sa_ma
		Mxlp3	*(2 + 3)*	Ch_tu, Eu_ba, Eu_fa, Eu_ga, Eu_he, Eu_le, Eu_ma, Eu_oc, Eu_pu, Eu_si, Eu_su, He_br, He_fu, He_pa, He_re, **Hi_cl, Hi_co, Hi_ob, Hi_pl,** Ly_an, Me_rh, Na_ma, Sp_ar, Sp_ga, Sp_ge, Sp_mu, Sp_oc, Sp_re, Sp_si, To_ca	Le, Th
			(2 + 4)	La_ac, La_la, Ly_se, Sa_ma
	Pereiopods	*absent*		Eu_ba, Eu_he, Eu_ma, Eu_oc, Eu_pu, Eu_si, He_br, He_fu, He_pa, He_tr, **Hi_co, Hi_ob, Hi_pl, Hi_zo,** La_ac, La_an, La_la, To_ca
		rudimentary P1		**Hi_cl,** Ly_se,Th_am
		rudimentary P1 - P2		He_ge, He_re, **Hi_bi, Hi_mu, Hi_pr, Hi_va, Hi_ve, Hi_wi,** La_at, Na_ma, Sa_ma, Sp_cr	Ca
		rudimentary P1 - P3		Eu_do
		rudimentary P1 - P4		Eu_ga, Sp_ga
		rudimentary P1 - P5		Ch_an, Eu_fa, Eu_su, He_ca, He_pn, Sp_ar, Sp_oc, Sp_ph, Sp_sp, Sp_si, Th_fl	Le
Abdomen	*Segment with dorsolateral spines*	*absent*		Al_sp, Eu_ba, Eu_do, Eu_he, Eu_le, Eu_ma, Eu_oc, Eu_pu, Eu_si, He_br, He_ca, He_ge, He_pa, He_pn, He_re, He_tr	Ch, Th
		4 and 5		Eu_fa, He_fu, La_ac, La_an, La_la, Me_rh, Sp_ar, Sp_mu, Sp_oc, Sp_ph, Sp_sp	Le
		5		Ch_tu, Eu_ga, Eu_su, **Hi_bi, Hi_cl, Hi_co, Hi_mu, Hi_ob, Hi_pl, Hi_pr, Hi_va, Hi_ve, Hi_wi, Hi_zo,** La_at, Na_mr, Sp_cr, Sp_ga, Sp_si	Ca, To
	Anal papilla/spine	*absent*		**Hi_cl, Hi_wi,** La_ac, La_an, To_ca	

			present	He_br, He_ca, He_fu, He_ge, He_pa, He_tr, **Hi_ob, Hi_pl,** La_at, Sp_ar, Sp_cr, Sp_ga, Sp_mu, Sp_oc, Sp_ph, Sp_sp, Sp_si, Th_am	Eu, Le
Telson	*Setae*	*9 + 9*		Le_po	
		9 or 10 + 10 or 11		Le_gr	
		7 + 7	*7p + 7p*	Eu_fa, Eu_fa, Eu_si, Eu_su, He_ca, He_pa, **Hi_zo,** Ly_an, Me_rh, Sp_ar, Sp_mu, Sp_oc	
			(1L + 6p) + (6p + 1L)	**Hi_wi**	
			(2L + 5p) + (5p + 2L)	Ca_st, He_fu, He_re, **Hi_ac, Hi_co, Hi_ob, Hi_pl, Hi_va, Hi_ve,** Ly_se, To_ca	La, Th

Table 3: Chromatophore pattern of the first zoeal stage of species of the genus *Hippolyte*. Abbreviations: (-) absent, (+) present, but number of chromatophores and position not defined.

	Hippolyte coerulescens	***Hippolyte obliquimanus***	***Hippolyte pleuracanthus***	***Hippolyte prideauxiana***	***Hippolyte varians***	***Hippolyte zostericola***
Color	almost colourless, greenish-brown	dark red	Red	yellowish with dark brown	yellowish to orange	Dark olive-brown
Base of the rostrum	(-)	1	1	(-)	(-)	(-)
Between antennular peduncle and base of the eye	(-)	1 each side	1 each side	1 each side	1 each side	1 each side
Anterior carapace margin, near base of the eye (postocular)	2	1 each side	1 each side	1 each side	(+)	(+)
Dorsal transverse midline of carapace	(-)	(-)	2	1 each side	(+)	2
Posterolaterally on carapace	(-)	1 each side	2	1 each side	(+)	2
Basis of antennula	(-)	2	(-)	(-)	(+)	(-)
Basis of antenna	2	2	(-)	(-)	(+)	(-)
Near mouth	(-)	(-)	1	(-)	(-)	(-)
Maxilla	(+)	1	(-)	(-)	(-)	(-)
First maxilliped	(-)	1 (coxa)	(-)	(-)	(-)	(-)
Second maxilliped	(-)	1 (basis)	(-)	(-)	(-)	1 (basis)

Third maxilliped	(-)	(-)	(-)	(+)	(-)	(-)
Dorsal midline of first and second abdominal segments	(-)	(-)	1 each side	1	(+)	(-)
Posterior margin of third abdominal segment	(-)	1 each side	2	2	(+)	2
Fourth abdominal segment	(-)	(-)	(-)	(+)	(-)	(-)
Fifth abdominal segment, near the spine posterolateral	(-)	1 each side	(-)	(+)	1 each side	1 each side
Fused sixth abdominal segment-telson	1	2	1	3	3	1
Reference	Gurney 1936 as *H. acuminata*	Present study	Shield 1978	Lebour 1931	Lebour 1931	Gurney 1936 as *H. pleuracantha bermudensis*

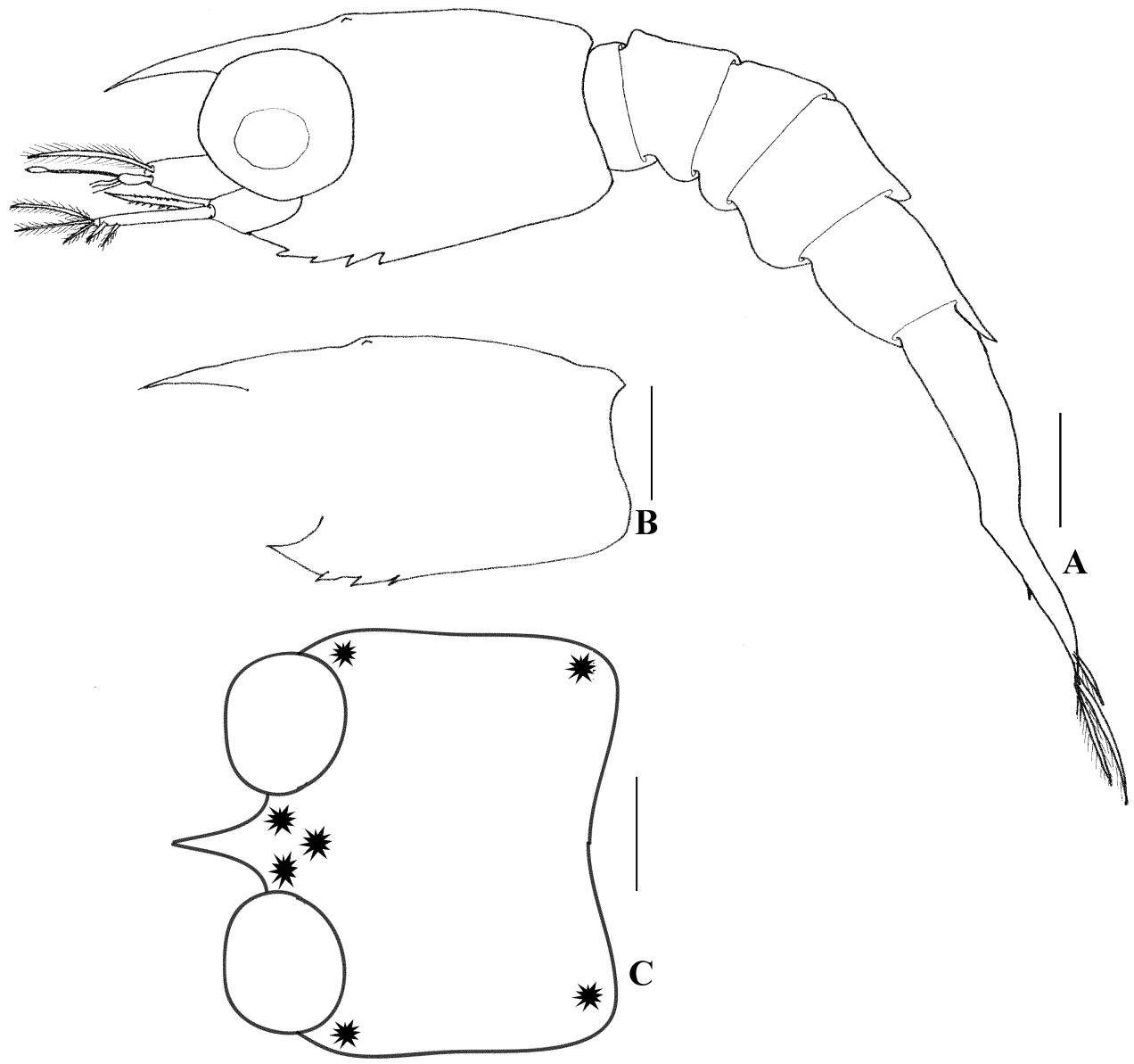


Figure 1

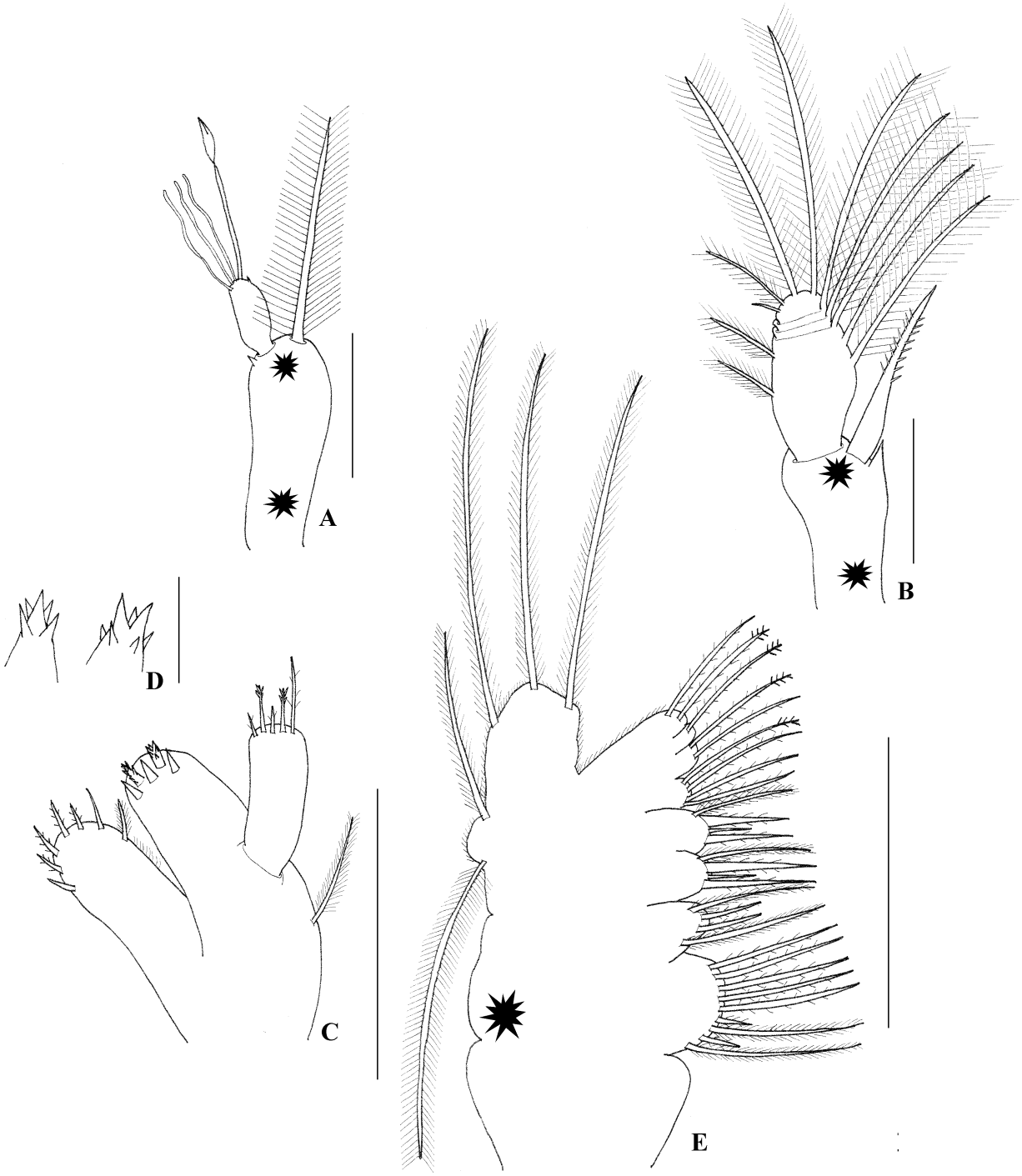


Figure 2

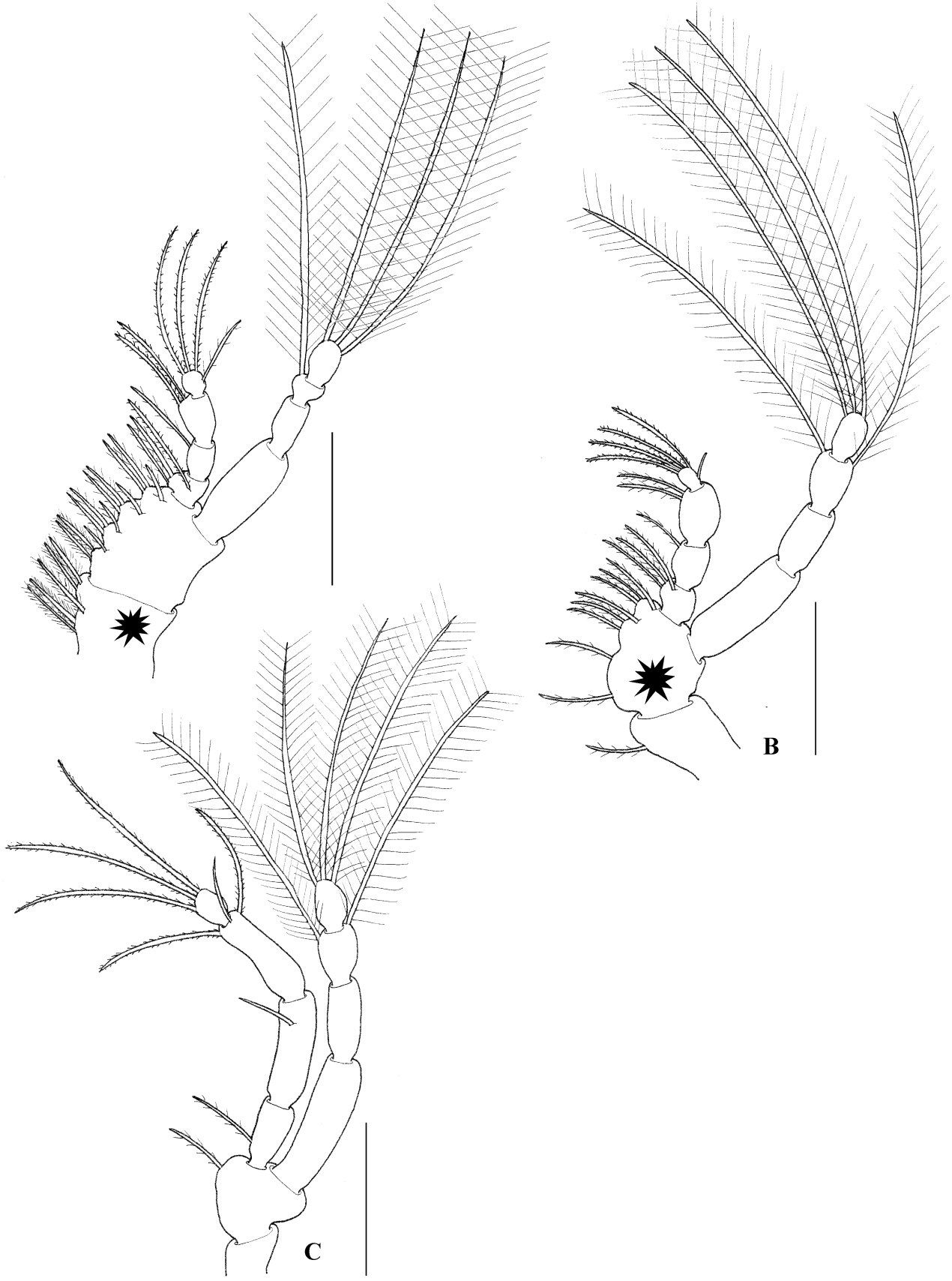


Figure 3

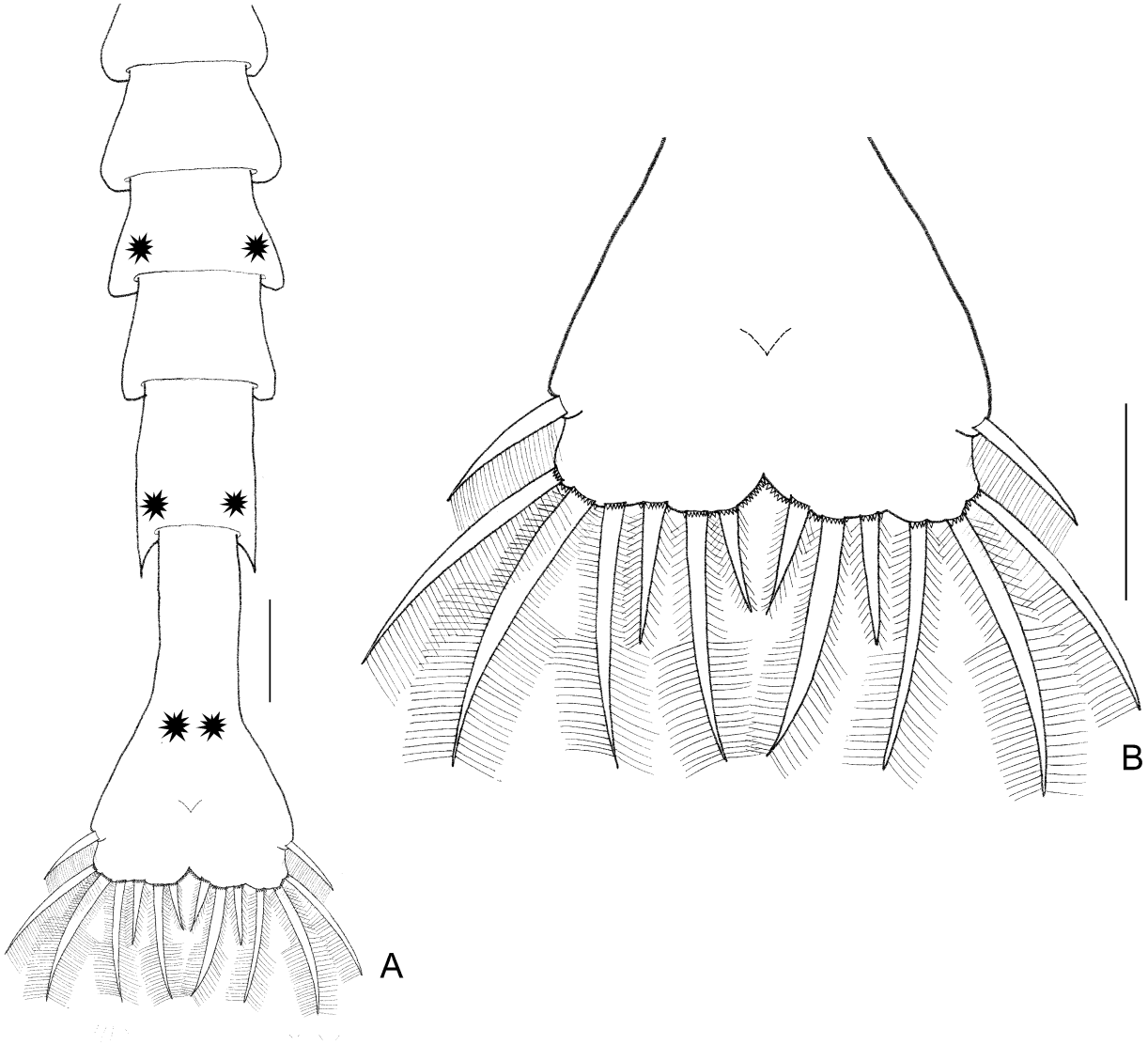
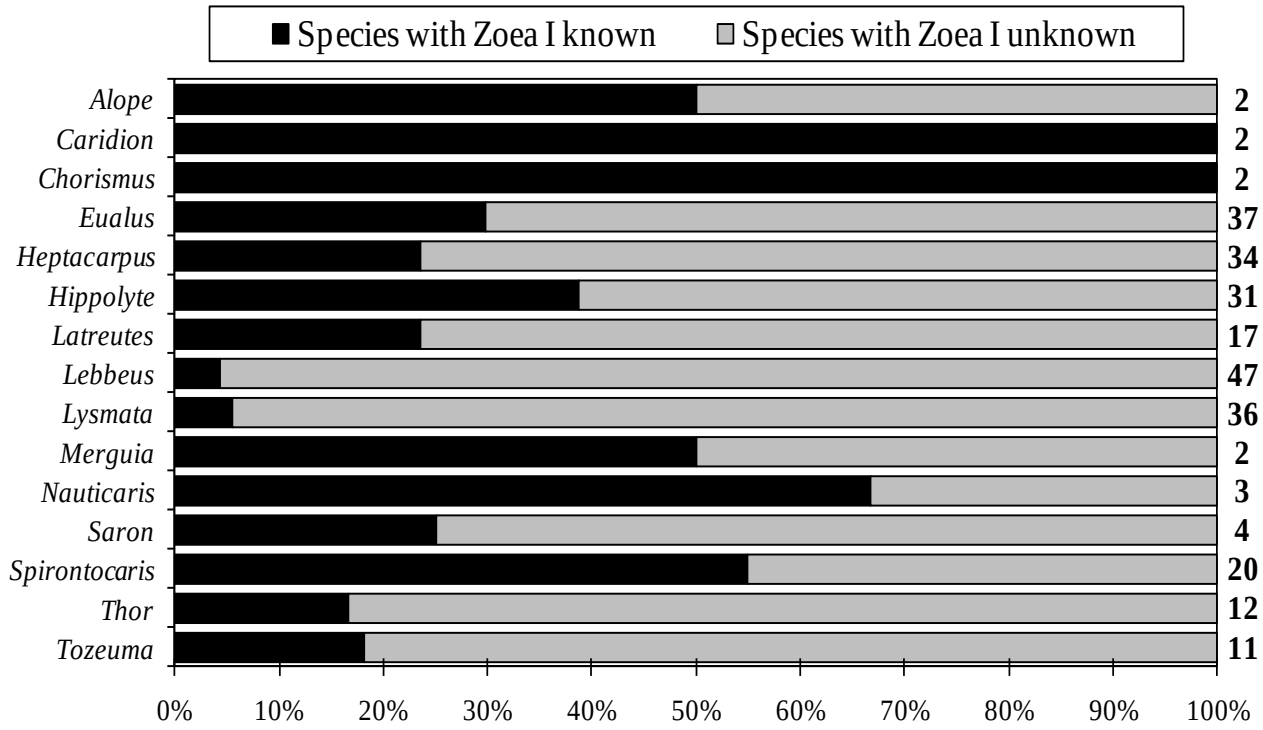


Figure 4


Species with Zoea I known
Species with Zoea I unknown
Alope
Caridion
Chorismus
Eualus
Heptacarpus
Hippolyte
Latreutes
Lebbeus
Lysmata
Merguia
Nauticaris
Saron
Spirontocaris
Thor
Tozeuma
2
2
2
37
34
31
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60%
70%
80%
90%
100%

Figure 5