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ORIGINAL ARTICLE

First zoeal stage of Processidae (Decapoda, Caridea): review and new descriptions of *Ambidexter symmetricus* Manning and Chace 1971 and *Processa fimbriata* Manning and Chace 1971

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Abstract This study reviews the morphology of the first zoeal stage of the pantropical and subtropical marine shrimps of the family Processidae. We present the first descriptions of the zoea I of *Ambidexter symmetricus* and *Processa fimbriata* and compare them with available published descriptions, in order to detect patterns to differentiate the genera. Among the species of Processidae, the zoea I of *Ambidexter* can be differentiated by the presence of a rostrum, and the resemblance to *Nikoides* and *Processa*, previously reported for adults, is now confirmed for the larval morphology. Based on the new descriptions, *A. symmetricus* and *A. panamensis* can be easily separated by four independent larval characters: anterior tubercle on the carapace (present in *A. panamensis* and absent in *A. symmetricus*), the antennal scale (segmented distally in *A. panamensis* and unsegmented in *A. symmetricus*), and the anal spine and second pereiopod (absent in *A. panamensis* and present in *A. symmetricus*). *P. fimbriata* can be separated from the other 11 species of *Processa* by means of two larval characters: 4 aesthetascs on the exopod of the antennules, and the presence of an anal spine.

Keywords Larval · *Processa* · *Ambidexter* · Processidae

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Introduction

The family Processidae Ortmann 1896 comprises 68 recognized species, in five genera (De Grave and Fransen 2011): *Ambidexter* Manning and Chace 1971 (3 species), *Clytomanningus* Chace 1997 (2), *Hayashidonus* Chace 1997 (1), *Nikoides* Paul'son 1875 (10), and *Processa* Leach 1815 (52). Shrimps of this family are small, nocturnal, and abundant in marine shallow-water habitats, primarily on grass flats and in tide pools in pantropical and subtropical regions; some are components of the offshore fauna (Manning and Chace 1971; Chace 1997).

This family is represented in Brazil by seven species (Christoffersen 1998): *Ambidexter symmetricus* Manning and Chace 1971, *Processa bermudensis* (Rankin 1900), *P. brasiliensis* Christoffersen 1979, *P. fimbriata* Manning and Chace 1971, *P. guyanae* Holthuis 1959, *P. hemphilli* Manning and Chace 1971, and *P. profunda* Manning and Chace 1971. The morphology of the first zoeal stage is known only for *P. bermudensis*, described by Gurney (1936) from larvae from Bermuda.

Here, we describe the zoea I of *Ambidexter symmetricus* and *Processa fimbriata.* We also review the morphology of the first zoeal stage of the family Processidae, using all descriptions available in the literature, in order to detect patterns to differentiate the genera.

Materials and methods

An ovigerous female of *Ambidexter symmetricus* was collected in June 2006 at Araçá Beach (São Sebastião, State of São Paulo, Brazil, 23°48′S, 45°24′W) by hand in a rocky intertidal area. An ovigerous female of *Processa fimbriata* was collected on November 2002 on the infralittoral rocky

shores of East Beach, Anchieta Island (Ubatuba, State of São Paulo, Brazil, 23°33′S, 45°05′W) by SCUBA diving.

Both females were maintained in containers with natural sea water until the zoeae hatched. Actively swimming larvae were conserved in 4 % formaldehyde. For each species, the number of hatches was counted, and 10 larvae were measured and drawn. The carapace length (CL) of the larvae and ovigerous females was measured as the maximum length from the posterior margin of the ocular orbit to the posterior margin of the carapace. Appendages were dissected under a Zeiss Stemi SV6 stereomicroscope, and drawings and measurements were taken using a Leica DM1000 microscope equipped with a camera lucida. Larval descriptions and setal counts follow the method proposed by Clark et al. (1998), and we use the setal terminology suggested by Landeira et al. (2009). In Fig. 2d–f, the setae are drawn truncated, because they are the same as the setae in Fig. 2a–c. 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, accession numbers: 3495 for *A. symmetricus* and 3501 for *P. fimbriata*).

Results

The parental females of *Ambidexter symmetricus* and *Processa fimbriata* collected measured 5.7 and 4.6 mm in CL, respectively, and the number of hatched larvae was 127 and 93, respectively.

Morphological description

Ambidexter symmetricus Manning and Chace 1971
Zoea I

Carapace length: 0.35 ± 0.02 mm ($n = 10$).

Cephalothorax (Fig. 1a): Supraorbital spines absent, pterygostomian spine present; 4 denticles on anteroventral margin; rostrum slender, without teeth, and short, not overreaching the extremity of the antennular peduncle.

Antennule (Fig. 1b): Peduncle unsegmented; endopod as a long plumose seta; exopod with 4 terminal aesthetascs and 1 plumose inner terminal seta.

Antenna (Fig. 1c): Peduncle with an inner spiny projection near the endopod; endopod unsegmented, wider proximally and with two equal rows of spines in the mediodistal region; exopod (antennal scale) unsegmented, with 12 setae arranged as 9 plumose setae + 1 simple seta + 2 plumose setae.

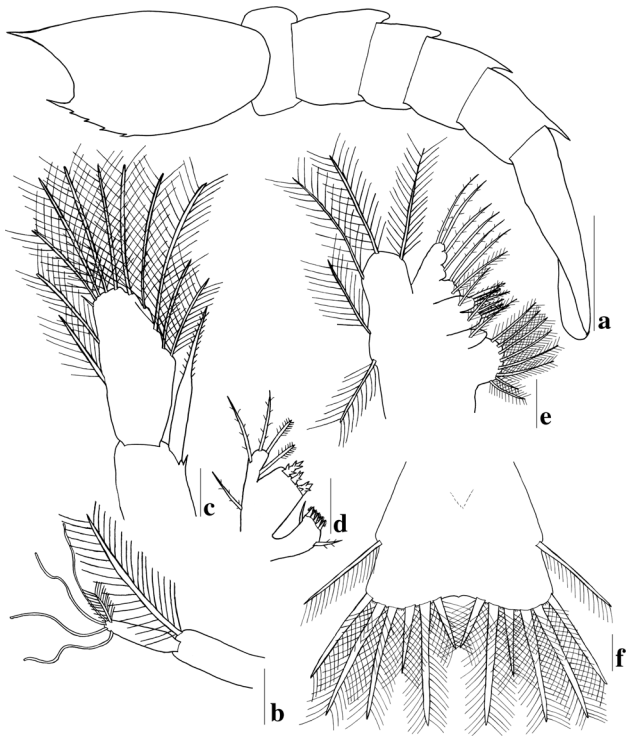

Fig. 1 *Ambidexter symmetricus*. Zoea I. (*a*) Lateral view; (*b*) antennule; (*c*) antenna; (*d*) maxillule; (*e*) maxilla; and (*f*) telson. *Scale bars* (*a*) 0.2 mm, (*b–f*) 0.05 mm

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

Maxillule (Fig. 1d): Coxal endite with 7 setae (1 sparsely plumose, 5 sparsely hardy plumose and 1 simple); basial endite with 3 plumodenticulate cuspidate setae; endopod unsegmented, with 3 terminal setae (2 sparsely plumose and 1 sparsely hardy plumose) and 1 sparsely hardy plumose lateral seta; exopodal seta present.

Maxilla (Fig. 1e): Coxal endite bilobed, with 8 plumose marginal setae on proximal lobe and 1 plumose marginal seta on distal lobe; basial endite bilobed, with 4 setae (3 sparsely hardy plumose marginal and 1 plumose submarginal) on each lobe; endopod with 4 lobes with 3 (1 plumose and 2 sparsely plumose), 1 (sparsely plumose), 1 (sparsely plumose), and 2 (sparsely plumose) setae, respectively; exopod (scaphognathite) with 5 plumose marginal setae.

First maxilliped (Fig. 2a): Coxa with 3 marginal setae (1 short simple, 1 sparsely plumose, and 1 plumose) arranged as (2 + 1); basis with 12 setae arranged in 4 groups, the proximal group with 1 plumose marginal seta, the next groups with 4 (1 short simple submarginal and 3 sparsely plumose marginal), and 3 (1 short simple submarginal and 2 sparsely plumose marginal) setae, and the distal one with 3 (1 short simple submarginal, 1 simple marginal, and 1 sparsely plumose marginal) setae; endopod 4-segmented,

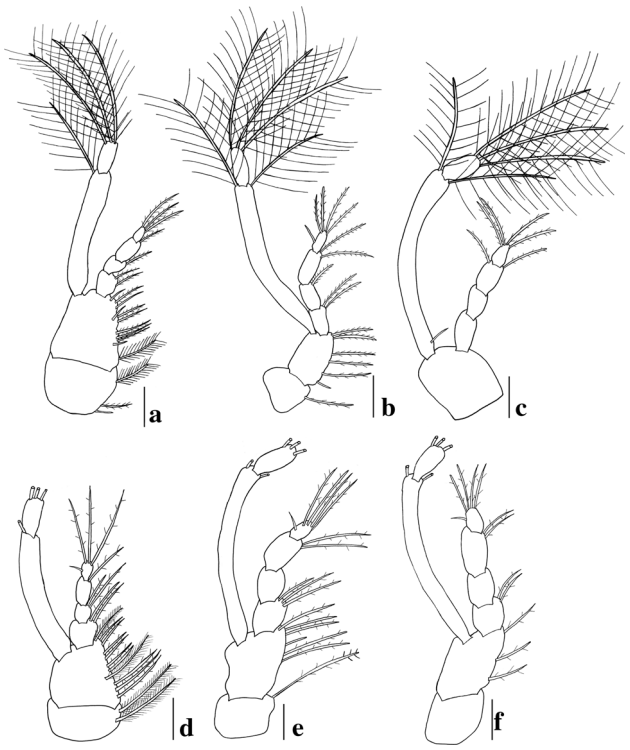

Fig. 2 Zoea I. *a*, *b*, *c Ambidexter symmetricus*. *d*, *e*, *f Processa fimbriata*. (*a*, *d*) First maxilliped; (*b*, *e*) second maxilliped; and (*c*, *f*) third maxilliped. *Scale bars* 0.05 mm. Plumose natatory setae of *P. fimbriata* are as those in *A. symmetricus*

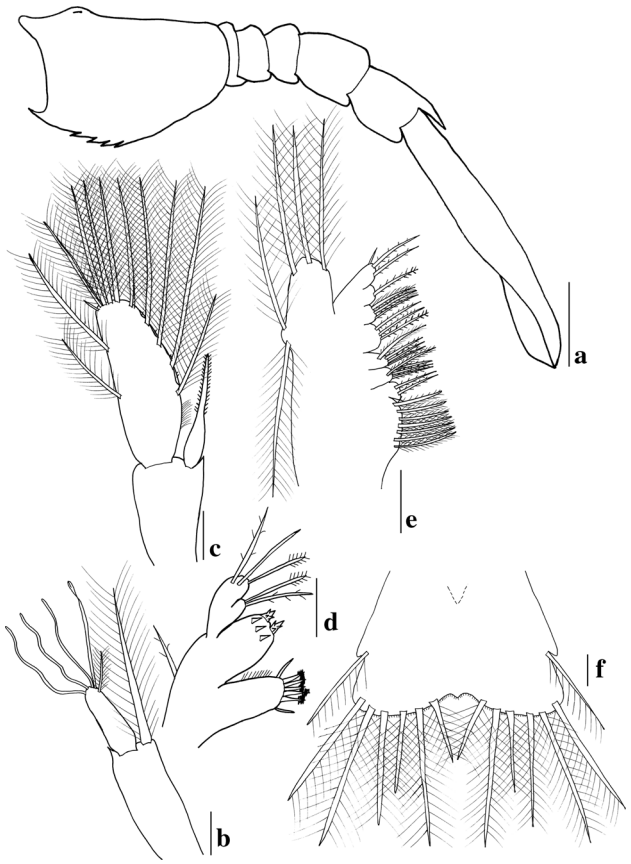

Fig. 3 *Processa fimbriata*. Zoea I. (*a*) Lateral view; (*b*) antennule; (*c*) antenna; (*d*) maxillule; (*e*) maxilla; and (*f*) telson. *Scale bars* (*a*) 0.2 mm, (*b–f*) 0.05 mm

with 2 (1 marginal and 1 terminal), 1 (terminal), 1 (terminal), and 3 (terminal) sparsely plumose setae, respectively; exopod 2-segmented with 1, 3 plumose terminal natatory setae.

Second maxilliped (Fig. 2b): Coxa with 1 marginal sparsely plumose seta; basis with 1 short simple marginal seta and 5 sparsely plumose marginal setae (1 + 1+1 + 2); endopod 4-segmented, with 2 (sparsely plumose terminal), 1 (sparsely plumose terminal), 2 (sparsely plumose terminal), and 5 (4 sparsely plumose terminal and 1 simple marginal) setae, respectively; exopod 2-segmented, with 2, 3 plumose natatory setae.

Third maxilliped (Fig. 2c): Coxa and basis without setae; endopod 4-segmented, with 0, 0, 2, 4 sparsely plumose terminal setae, respectively; exopod 2-segmented, with 2, 3 plumose natatory setae.

Pereiopods: Buds of first and second pereiopods present.

Abdomen (Figs. 1a, 4a): With 5 somites without setae, pair of posterodorsal spines on somites 4 and 5; anal spine present (Fig. 1f).

Pleopods and uropods: Absent.

Telson (Figs. 1f, 4a): Broad at posterior margin, with 7 + 7 setae (inner 5 plumose, outer 2 laterally plumose setae), outer pair of setae subterminal; one row of spinules on distal margin and around bases of the 6 + 6 inner setae.

Processa fimbriata Manning and Chace 1971
Zoea I

Carapace length: 0.42 ± 0.01 mm ($n = 10$)

Cephalothorax (Fig. 3a): With an anterior tubercle, supraorbital spines absent, pterygostomian spine present; anteroventral margin with 4 denticles. Without rostrum.

Antennule (Fig. 3b): Peduncle unsegmented, with outer spiny projection near exopod; endopod as a long plumose seta; exopod with 4 terminal aesthetascs and 1 plumose inner terminal seta.

Antenna (Fig. 3c): Peduncle with inner spiny projection near endopod; endopod unsegmented, wider proximally and with two equal rows of spines in mediodistal region; exopod (antennal scale) unsegmented, with 12 setae, arranged as 9 plumose setae + 1 simple seta + 2 plumose setae.

Mandible: With incisor and well-developed molar processes, without palp.

Maxillule (Fig. 3d): Coxal endite with 7 setae (1 simple, 5 sparsely hardy plumose, and 1 simple) and microtrichia; basial endite with 2 plumodenticulate cuspidate setae and 3 spiniform setae; endopod bilobed, with 2 terminal (1 sparsely plumose and 1 sparsely hardy plumose) setae on proximal lobe and 3 (2 subterminal, 1 simple, and 1 sparsely plumose; and 1 terminal sparsely hardy plumose) setae on distal lobe; exopodal seta present.

Maxilla (Fig. 3e): Coxal endite bilobed, with 7 plumose marginal setae on proximal lobe and 2 sparsely plumose marginal setae on distal lobe; basial endite bilobed, with 4 setae (3 sparsely hardy plumose marginal and 1 plumose submarginal) on each lobe; endopod with 4 lobes, with 3 (2 sparsely plumose and 1 sparsely hardy plumose), 3 (2 plumose and 1 sparsely plumose), 1 (sparsely hardy plumose), and 3 (2 sparsely plumose and 1 simple) marginal setae, respectively; exopod (scaphognathite) with 5 plumose marginal setae.

First maxilliped (Fig. 2d): Coxa with 2 plumose marginal setae; basis with 11 setae arranged in 4 groups, proximalmost group with 3 sparsely plumose marginal setae, next 2 groups with 3 (1 plumose submarginal and 2 sparsely plumose marginal) and 2 sparsely plumose marginal setae, and distalmost group with 3 (2 sparsely plumose marginal and 1 plumose marginal) setae; endopod 4-segmented, with 2 (sparsely plumose terminal), 2 (sparsely plumose terminal), 1 (sparsely plumose terminal), and 4 (3 sparsely plumose terminal and 1 short simple marginal) setae, respectively; exopod 2-segmented, with 1, 3 plumose terminal natatory setae.

Second maxilliped (Fig. 2e): Coxa with 1 sparsely plumose marginal seta; basis with 1 short simple marginal seta and 5 sparsely plumose marginal setae (arranged as 2 + 1 simple + 3); endopod 4-segmented, with 3 (sparsely plumose terminal), 0, 2 (sparsely plumose terminal), and 5 (4 sparsely plumose terminal and 1 simple marginal) setae, respectively; exopod 2-segmented, with 2, 3 plumose natatory setae.

Third maxilliped (Fig. 2f): Coxa without setae; basis with 3 sparsely plumose marginal setae; endopod 4-segmented, with 2 (sparsely plumose terminal), 0, 2 (sparsely plumose terminal), and 5 (4 sparsely plumose terminal and 1 simple marginal) setae, respectively; exopod 2-segmented, with 2, 3 plumose natatory setae.

Pereiopods: Buds of first pereiopod present.

Abdomen (Figs. 3a, 4b): With 5 somites without setae, pair of posterodorsal spines on somite 5; anal spine present (Fig. 3f).

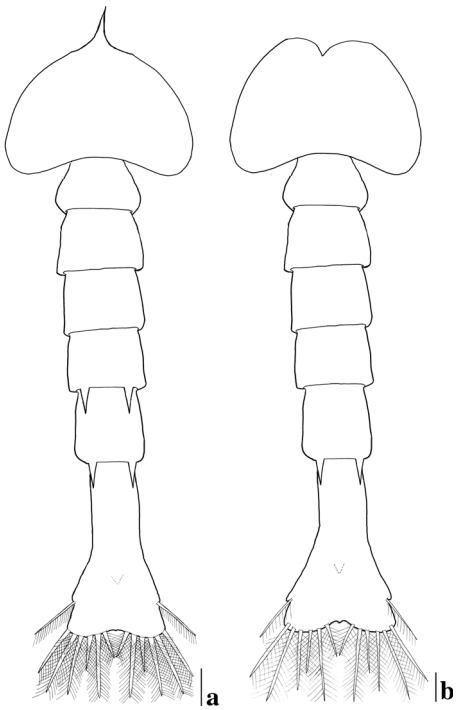

Fig. 4 Zoea I. dorsal view. *a Ambidexter symmetricus*. *b Processa fimbriata*. *Scale bars* 0.10 mm

Pleopods and uropods: Absent.

Telson (Figs. 3f, 4b): Broad at posterior margin, with 7 + 7 setae (inner 5 plumose, outer 2 laterally plumose), the 2 outermost setae subterminal; one row of spinules on distal margin and around bases of the 6 + 6 inner setae.

Discussion

The first zoeal stage of shrimps of the family Processidae is presently known for only 15 species, including the two studied here (Table 1). There are no data on the first zoeal stages of the genera *Clytomanningus* and *Hayashidonus.*

Based on the few descriptions then available, Gurney (1937, 1942) listed generic characteristics of zoea I of the family Processidae: carapace without rostrum; anterior margin of carapace serrated; antennal scale unsegmented; maxillule with exopodal seta; and abdominal segment 5, and sometimes also segment 4, with a pair of posterodorsal spines. Some of these characters can no longer be considered as diagnostic (Table 1), because zoea I of *Ambidexter* has the rostrum present, and four taxa (*A. panamensis*, *P. modica modica*, *P. modica carolii,* and *P. nouveli holthuisi*) have the antennal scale segmented.

Some authors (Gurney 1923; Lebour 1936; Ortega et al. 2005) have suggested that larvae of Processidae resemble those of the family Hippolytidae Bate 1888. According to

Table 1 Morphological characters of the first zoeal stage described for species of the family Processidae

Characters	A_pa	A_sy	N_da	P_ae	P_be	P_ca	P_co	P_ec	P_ee	P_fr	P_ma	P_mm	P_mc	P_nh	P_nn
Reference	1	2	3	3	4	5	6	7	8	2	9	10	10	10	11
Number of larval stages	8	?	9	9	8	9	10	?	?	?	9	7	9	9	9
Rostrum	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−
Anterior tubercle on carapace	+	−	?	?	?	+	+	+	+	+	+	+	+	+	+
Denticles on anteroventral margin of carapace	3–6	4	2–3	2–3	?	?	3	2	?	4	3–4	4	4	3–4	3–6
Aesthetascs on exopod of antennule	3–4	4	?	?	?	3	3	3	3	4	3	3	3	3	3
Antennal scale	s	u	u	U	u	u	u	u	u	u	u	s	s	s	s
Plumose setae on antennal scale	11	11	12	12	11	11	11	12	11	11	11	11	11	11	11
Exopodal seta on maxillule	+	+	?	?	+	?	+	+	+	+	+	?	+	+	+
Setae on distal segments of exopod of Mxlp1	4	4	4	4	?	5	5	4	?	4	4	4	4	4	4
Dorsal spine on abdominal segment 3	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−
Abdominal segment with pair of posterodorsal spines	4, 5	4, 5	5	5	5	4, 5	5	5	5	5	5	5	5	5	5
Anal spine	−	+	?	?	?	?	?	?	?	+	?	?	?	−	−
Pereiopod buds	1	1, 2	1	1	1	?	1, 2	1, 2	?	1	1	1	1	?	?
Setae on telson	a	b	?	?	a	b	a	b	b	b	b	a	a	a	a

Codes used for species: A_pa—*Ambidexter panamensis* Abele 1972; A_sy—*Ambidexter symmetricus* Manning and Chace 1971; N_da—*Nikoides danae* Paul'son 1875; P_ae—*Processa aequimana* (Paul'son 1875); P_be—*Processa bermudensis* (Rankin 1900); P_ca—*Processa canaliculata* Leach 1815; P_co—*Processa compacta* Crosnier 1971; P_ec—*Processa edulis crassipes* Nouvel and Holthuis 1957; P_ee—*Processa edulis edulis* (Risso 1816); P_fr—*Processa fimbriata* Manning and Chace 1971; P_ma—*Processa macrodactyla* Holthuis 1952; P_mm—*Processa modica modica* Williamson in Williamson and Rochanaburanon 1979; P_mc—*Processa modica carolii* Williamson in Williamson and Rochanaburanon 1979; P_nh—*Processa nouveli holthuisi* Al-Adhub and Williamson 1975; P_nn—*Processa nouveli nouveli* Al-Adhub and Williamson 1975. References: 1—Williamson 1980; 2—present study; 3—Gurney 1937; 4—Gurney 1936; 5—Lebour 1936; 6—Jagadisha and Sankolli 1977 (as *P. barnardi*); 7—Gurney 1923 (as *P. canaliculata*); 8—Gurney 1942; 9—González-Gordillo and Rodríguez 2000, Ortega et al. 2005; 10—Williamson and Rochanaburanon 1979; 11—according to Santos 1999 (we did not have access to the original description: Barnich 1996). Characters: +, present; −, absent; ?, data not available; s, segmented; u, unsegmented; a, 7 + 7; b, (2 laterally plumose setae + 5 plumose setae) + (2 laterally plumose setae + 5 plumose setae)

Ortega et al. (2005), the larvae of these families can be differentiated by two main characters: (1) The distance between the bases of the antennules is greater than the width of each antennule in Processidae and (2) the presence of an anal spine in the first zoea in Hippolytidae. However, here, we report the presence of an anal spine in *A. symmetricus* and *P. fimbriata*, both members of Processidae, and many species of Hippolytidae do not have an anal spine (Terossi et al. 2010).

Except for the first character noted by Ortega et al. (2005), a comparison of these two families (Table 2) reveals no additional characters that can distinguish their larvae. The larvae of Hippolytidae show a wide range of variation (see review by Terossi et al. 2010), which encompasses the variation shown by larvae of Processidae (Table 2). There are two feasible explanations for this: (1) The family Hippolytidae is more diverse and has almost five times the number of recognized species as Processidae; (2) some species of Hippolytidae have abbreviated development, which usually leads to some morphological differences in the first zoeal stage, such as having more than seven pairs of setae on the telson, more than five setae on the scaphognathite, and more pereiopod buds (see review by Terossi et al. 2010).

The number of larval stages ranges from seven to ten in the family Processidae (Table 1), which indicates extended development. The only species with an unknown number of larval stages are *A. symmetricus* and *P. fimbriata*; however, considering their larval morphology (zoea I), they probably show extended development.

Based on the present review, it is possible to form conjectures about the zoeal morphology for genera of Processidae. Adults of the genus *Ambidexter* have a peculiar character, whereas other members of the family Processidae have only one pereiopod 1 chelate (usually the right) and the other with a simple dactyl, the species of *Ambidexter* have both pereiopods 1 symmetrically chelate (Chace 1997). This may well represent the ancestral condition in the Processidae (Williamson 1980). We also observed an

Table 2 Comparison of some characters of Zoea I from families Processidae and Hippolytidae

Characters	Processidae	Hippolytidae
Number of recognized species	68	318
Number of species with first zoeal stage known	15	66[a]
Dorsal tubercles on carapace	Absent or 1	Absent, 1 or 2
Distance between bases of antennules in relation to width of each antennule[b]	Longer	Shorter
Plumose setae on antennal scale	11 or 12	9–14
Plumose setae on scaphognathite	5	3–35
Abdominal segments with dorsolateral spines	4 and 5, or only 5	Absent, 4 and 5, or only 5
Pereiopod buds	1 or 2	Absent or 1–5
Pairs of setae on telson	7	7–10
Abbreviated development	Not reported	Present

Data for latter family from Terossi et al. (2010), [a] until 2010; [b] according to Ortega et al. (2005). Number of recognized species according to De Grave and Fransen (2011)

exclusive character (presence of a rostrum) for the first zoeal stage of species of *Ambidexter* (Table 1).

There are three recognized species of the genus *Ambidexter* (De Grave and Fransen 2011): *A. panamensis, A. swifti* Abele 1972, and *A. symmetricus*. At present, only the morphology of zoea I of *A. swifti* remains unknown (Table 1). The other two species show some differences in the morphology of the first zoea (Table 1), in the anterior tubercle on the carapace (present in *A. panamensis* and absent in *A. symmetricus*), the antennal scale (segmented distally in *A. panamensis* and unsegmented in *A. symmetricus*), and the anal spine and second pereiopod (absent in *A. panamensis* and present in *A. symmetricus*).

The larval development of *A. panamensis* was described by Williamson (1980), who stated that no other potentially unique generic-level larval character had been discovered, besides the relatively large exopodal seta on the maxillule in the late zoeal stages. We propose that among the first zoea larvae of Processidae, the presence of a rostrum is exclusive to the genus *Ambidexter*.

The presence of posterodorsal spines on abdominal segment 4 of the first zoea was reported for the genus *Ambidexter*, and curiously also for *P. canaliculata* (Table 1). In her description of the first zoeal stage of *P. canaliculata*, Lebour (1936) provided an illustration of these spines, which leaves no doubt as to their existence. Probably, this structure is present in other unknown larvae of the genus *Processa*. Gurney (1923) also reported the larval stages of *P. canaliculata*; however, the zoea that he described was actually the larvae of two species, the early stages of *P. edulis crassipes* and the later stages of *P. nouveli holthuisi* (Fincham and Williamson 1978; Williamson and Rochanaburanon 1979).

The zoea I stages of *Nikoides* and *Processa* share the lack of a rostrum (Table 1). According to our observations, these genera cannot be separated based on their larval morphology (Table 1). In addition, the adults are extremely similar and can be differentiated only by the absence (*Processa*) or presence (*Nikoides*) of exopods in pereiopod 1 (Manning and Chace 1971; Chace 1997). Despite the morphological resemblance of both adults and larvae in *Processa* and *Nikoides*, the molecular phylogeny of Caridea proposed by Bracken et al. (2009) showed *Processa* as a sister group of *Ambidexter*, and *Nikoides* fell outside this group. In order to clarify the relationships between the genera of Processidae, further studies on the morphology (adults and larvae) and genetic data of these species, also including the genera *Clytomanningus* and *Hayashidonus*, will be needed.

For the genus *Nikoides*, the first zoea is known for only one species (Table 1). Among the described species, *N. danae* shares more characters with *P. aequimana* and *P. edulis crassipes* than with the other species (Table 1): 2-3 denticles on the anteroventral margin of the carapace (2 in *P. edulis crassipes*), antennal scale unsegmented, and 12 plumose setae on the margin of the antennal scale. This similarity is not associated with the geographic distribution, because *N. danae* and *P. aequimana* were both collected in the Red Sea, and *P. edulis crassipes* was collected in the English channel.

The first zoeal stage of *Processa* shows extensive variation, and four species have characters that are not shared by the other species of this genus (Table 1): *P. compacta* and *P. canaliculata* have 5 setae on the distal segments of the exopod of maxilliped 1, and the other species have 4; *P. aequimana* has a small dorsal spine on abdominal segment 3, and the others lack dorsal spines at this location; *P. edulis crassipes* and *P. compacta* have buds of pereiopod 2 present, and the others have buds only of pereiopod 1. Here, we compared the first stage of the development in the family Processidae; for comparisons among other stages of the development of the genus *Processa*, see Ortega et al. (2005).

The first zoeal stage of *P. fimbriata* described here can be separated from the other eight species of *Processa* (Table 1) by means of two characters (Table 2): the presence of 4 aesthetascs on the exopod of the antennules and the presence of the anal spine. The zoea I of *P. fimbriata* is closer to *P. canaliculata*, *P. compacta*, *P. edulis edulis*, *P. macrodactyla*, *P. modica modica*, *P. modica carolii,* and *P. nouveli holthuisi*; these species share the presence of an anterior tubercle on the carapace, and 11 plumose setae on the margin of the antennal scale.

To date, there are no exclusive characters in the first zoeal stage of Processidae. Among the species of this family, the zoea I of *Ambidexter* can be differentiated by the presence of a rostrum, and the resemblance of *Nikoides* and *Processa,* previously reported for adults, is now confirmed for the larval morphology.

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