

Larval development of *Scyra acutifrons* (Crustacea: Decapoda: Epialtidae) with a key from the northern Pacific

Seong Mi Oh and Hyun Sook Ko*

Department of Biological Science, Silla University, Busan 617-736, Korea

(Received 23 June 2010; received in revised form 28 July 2010; accepted 2 August 2010)

The larvae of *Scyra acutifrons* are described and illustrated for the first time. The larval stage consists of two zoeal and a megalopal stages. The zoea of *S. acutifrons* is compared with those of other known species of the Epialtidae from the northern Pacific. The zoea of *Scyra acutifrons* can be easily distinguished from that of *S. compressipes* by having a longer rostral carapace spine and an endopod of maxillule with three setae. It is found that the genus *Scyra* (Pisinae) shows a great similarity to *Pisoides bidentatus* (Pisinae) and the genus *Pugettia* (Epialtinae) in the family Epialtidae; especially, *S. acutidens* coincides well with two *Pugettia* species (*Pugettia incisa* and *P. gracilis*) in the characteristics of the zoeal mouthpart appendages. To facilitate the study of plankton-collected material, a provisional key to the known zoeae of the Epialtidae from the northern Pacific is provided.

Keywords: Epialtidae; larva; *Scyra acutifrons*; *Pugettia*; zoeal morphology; key; northern Pacific

Introduction

The majoid family Epialtidae contains four subfamilies; Epialtinae, Pisinae, Pliosomatinae, and Tychinae (see Ng et al. 2008). The larval descriptions have been known for 16 species of the subfamilies Epialtinae and Pisinae from the northern Pacific (Table 1). The pisinid genus *Scyra* Dana, 1852, includes three species (Griffin and Tranter 1986): *Scyra acutifrons* Dana, 1852, *Scyra compressipes* Stimpson, 1857, and *Scyra tuberculata* Yokoya, 1933. Of these, the sharpnose crab, *S. acutifrons*, is found in the northeastern Pacific of America from Alaska to California (Jensen 1995). *S. compressipes* and *S. tuberculata* are known to occur in the northwestern Pacific of Korea and Japan (Kim 1973; Sakai 1976).

The larval development of *S. compressipes* has been reported by Kim and Hong (1999), but no larval stages of *S. acutifrons* have been described yet. Therefore, the aims of this paper are to describe the larval stage of *S. acutifrons*, compare its morphology to previously described larvae of the family, and provide a key to the known zoeae of the Epialtidae from the northern Pacific.

Materials and methods

Ovigerous females of *Scyra acutifrons* were collected by trawl in the Burrow Bay (48°28'N, 122°40'W), Anacortes, WA, USA, on 2 February 2004. On 12 April the zoeae hatched in the laboratory. They were reared

individually at a water temperature of $15 \pm 1^\circ$ and salinity of $29.7 \pm 0.6\text{‰}$. Each of the individually reared zoeae was held in a plastic well containing 5–6 ml of seawater for the first and second stages. From the megalopal stage, they were transferred to a larger well containing 15–16 ml of seawater. The water was changed daily and each larva was provided with newly hatched *Artemia* nauplii once per day. The mass culture consisted of three dishes, each containing 150 zoeae in 200 ml of seawater, which was also changed daily. Both individual and mass cultures were checked daily for exuviae and dead through the megalopal stage. Molts and dead larvae were fixed and preserved in 10% buffered formalin for later examination. Dissected appendages were examined and drawn using a Leitz Laborlux S Microscope with camera lucida. Setal counts on appendages and measurements were based on the mean of ten specimens per larval stage. The sequence of the larval description is based on the malacostracan somite plan and described from anterior to posterior (Clark et al. 1998). Setal armature on appendages is described from proximal to distal segments and in order of endopod to exopod. The long plumose natatory setae of the first and second maxillipeds were drawn truncated. A micrometer was used for measurements: CL (carapace length) was measured from base of the rostral spine to the most posterior carapace margin and SL (spine to spine length) was from tip of the rostral to tip of the dorsal spine. The classification follows that of Ng et al. (2008). The

*Corresponding author. Email: hsko@silla.ac.kr

Table 1. Species, stages and sources of known larval descriptions of the family Epiplatidae from the northern Pacific (Z and M = zoeal and megalopal stages; * = brief description).

Species	Larval stages	Sources
PISINAE		
<i>Doclea ovis</i>	ZI, ZII, M	Terada 1983; Mohan and Kannupandi 1985
<i>Hyastenus diacanthus</i>	ZI, ZII, M*	Kurata 1969
<i>Hyastenus elongatus</i>	ZI, ZII, M; ZI	Terada 1983; Ko 1997
<i>Pisoides bidentatus</i>	ZI, ZII, M	Kornienko and Korn 2007
<i>Pisoides ortmanni</i>	ZI, ZII, M*; ZI, ZII	Kurata 1969; Terada 1983
<i>Phalangipus hystrix</i>	ZI, ZII	Terada 1983
<i>Scyra compressipes</i>	ZI, ZII, M	Kim and Hong 1999
EPIALTIINAE		
<i>Goniopugettia sagamiensis</i>	ZI, ZII, M	Taishaku and Konishi 2001
<i>Huenia proteus</i>	ZI*; ZI, ZII*	Aikawa 1937; Kurata 1969; Terada 1981
<i>Menaethius monoceros</i>	ZI, ZII; ZI, ZII, M	Terada 1981; Gohar and Al-Kholy 1957
<i>Pugettia gracilis</i>	ZI	Oh and Ko 2007
<i>Pugettia incisa</i>	ZI, ZII, M*; ZI, ZII	Kurata 1969; Terada 1981
<i>Pugettia intermedia</i>	ZI, ZII; M	Ko 1998; Ko and Hwang 1997
<i>Pugettia marissinica</i>	ZI, ZII; M	Ko 1998; Ko and Hwang 1997
<i>Pugettia quadridens</i>	ZI; ZI, ZII; ZI, ZII, M*; M	Aikawa 1929; Ko 1998; Kurata 1969; Terada 1981; Ko and Hwang 1997
<i>Pugettia similis</i>	ZI, ZII	Terada 1981

larvae and the spent females were deposited in Silla University, Korea (SUZCr103258).

Results

First zoea (Figure 1)

Size. CL 0.83 ± 0.05 mm. SL 1.95 ± 0.13 mm.

Carapace (Figure 1A, E). Dorsal spine spinulate, slightly curved, slightly longer than rostral spine; rostral spine spinulate, approximately equal in length to antennal protopod; lateral spine absent; pair of posterodorsal setae present; each ventral

margin with one plumose anterior and four posterior setae; eyes stalked.

Antennule (Figure 1B). Uniramous; endopod absent; exopod with two long, stout aesthetascs, one shorter, thinner aesthetasc, and one long and one shorter setae, all terminal.

Antenna (Figure 1C). Endopod bud present; protopod spinulate; exopod about 3/4 length of protopod, with two subterminal setae, bearing minute spinules distally.

Mandibles (Figure 1D). Asymmetrical; right molar process with two teeth and left molar process with one tooth, confluent with incisor processes; endopod palp absent.

Maxillule (Figure 1F). Coxal endite with seven plumodenticulate setae; basal endite with seven plumodenticulate setae; endopod 2-segmented, proximal segment with one plumose seta, distal segment with four terminal plumose setae.

Maxilla (Figure 1G). Coxal endite bilobed, with 4 + 4 plumose setae; basal endite bilobed, with 5 + 5 plumose setae; endopod with 3 plumose setae; exopod (scaphognathite) margin with 10 plumose setae and one distal stout plumose process.

First maxilliped (Figure 1H). Coxa without seta; basis with nine plumose setae arranged 2 + 2 + 2 + 3 (9); endopod 5-segmented with 3, 2, 1, 2, 5 (one strong subterminal spinous seta + four terminal plumose setae) setation; exopod 2-segmented, distal segment with four terminal plumose natatory setae.

Second maxilliped (Figure 1I). Coxa unarmed; basis with 1 + 1 + 1 (3) plumose setae; endopod 3-segmented, with 0, 1, 4 (two subterminal plumose setae + two terminal plumose setae) setation; exopod 2-segmented, distal segment with four terminal plumose natatory setae.

Third maxilliped (Figure 1J). Biramous.

Pereopods (Figure 1K). Present, cheliped bilobed.

Abdomen (Figure 1A, L). With five somites; somite 1 with two dorsomedial setae; somite 2 with pair of lateral processes, somites 2–5 each with pair of posterodorsal setae, somites 3–5 with posterolateral processes; pleopod buds present as buds.

Telson (Figure 1L). Posterior margin with three serrated setae. Each fork long, distally spinulate, with one lateral spine.

Second zoea (Figure 2)

Size. CL 1.03 ± 0.06 mm. SL 2.30 ± 0.09 mm.

Carapace (Figure 2A, E). Each ventral margin with one plumose anterior and six posterior setae.

Antennule (Figure 2B). Exopod with six long aesthetascs and two setae, all terminal.

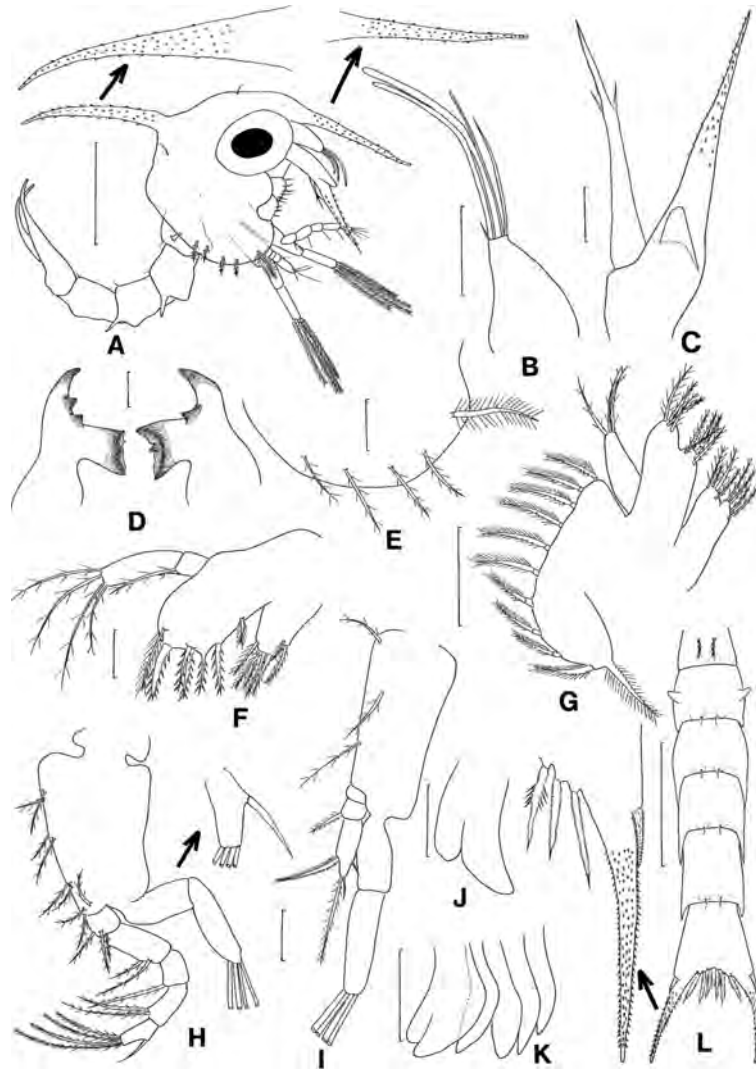


Figure 1. *Scyra acutifrons*, first zoeal stage. A, lateral view; B, antennule; C, antenna; D, mandibles; E, lateral expansion of carapace; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped; K, chela and pereopods; L, dorsal view of abdomen and telson. Scale bars = 0.5 mm (A, L), 0.1 mm (B, C, E, G–I, K) and 0.05 mm (D, F, J).

Antenna (Figure 2C). Endopod bud about 1/2 length of exopod.

Mandibles (Figure 2D). Palps present.

Maxillule (Figure 2F). Epipod with plumose seta; coxal endite with seven setae; basal endite with five plumodenticulate and five plumose setae.

Maxilla (Figure 2G). Coxal endite with 4 + 4 plumose setae; basal endite with 5 + 5 plumose setae; exopod (scaphognathite) margin with 21 plumose setae.

First maxilliped (Figure 2H). Exopod 2-segmented, distal segment with six terminal plumose natatory setae.

Second maxilliped (Figure 2I). Exopod 2-segmented, distal segment with six terminal plumose natatory setae.

Third maxilliped (Figure 2J). More developed.

Pereopods (Figure 2K). More developed, segments differentiated.

Abdomen (Figure 2A, L). With six somites; pleopod buds more developed, those on somites 2–5 biramous; pair of dorsomedial setae now present on somites 2, 3.

Telson (Figure 2L). Unchanged.

Megalopa (Figures 3, 4)

Size. Carapace width 0.95 ± 0.04 mm. Carapace length 1.48 ± 0.08 mm.

Carapace (Figure 3A). Subquadrate, longer than wide, with one short rostral process, pair of processes anterior to eye stalks.

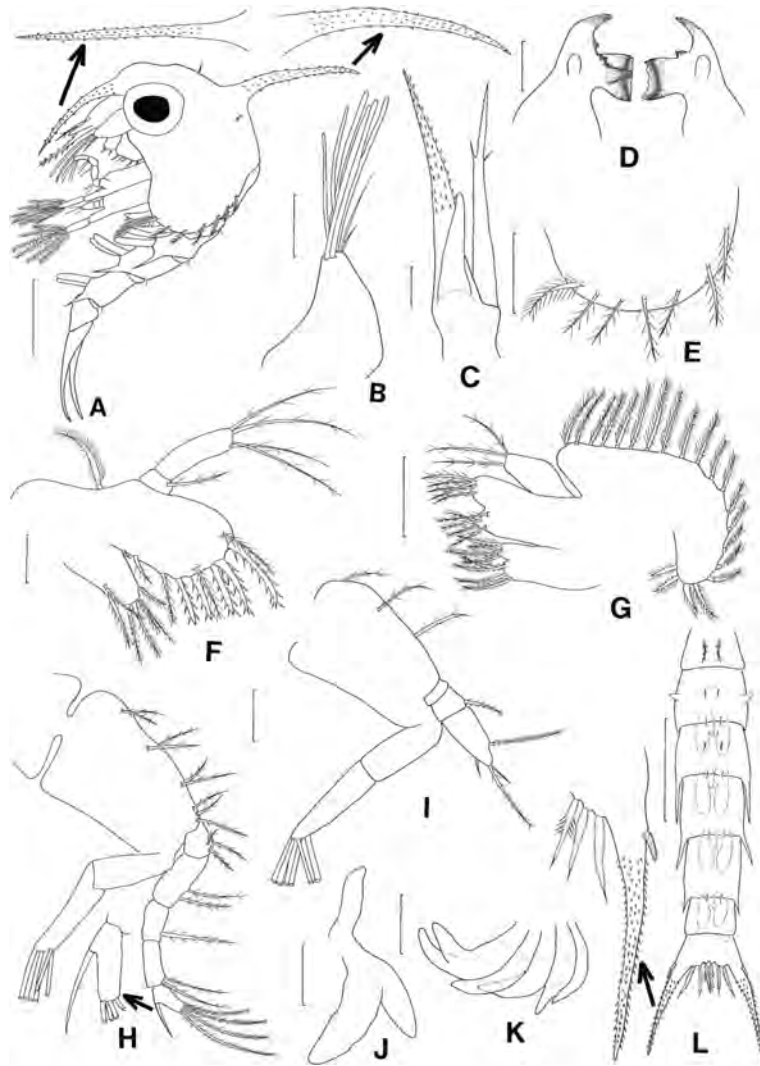


Figure 2. *Scyra acutifrons*, second zoeal stage. A, lateral view; B, antennule; C, antenna; D, mandibles; E, lateral expansion of carapace; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped; K, chela and pereopods; L, dorsal view of abdomen and telson. Scale bars = 0.5 mm (A, L), 0.25 mm (E, K), 0.1 mm (B–D, G–J) and 0.05 mm (F).

Antennule (Figure 3B). Peduncle 3-segmented, segments

2, 3 each with one seta; endopod 2-segmented, with one subterminal and two terminal setae; exopod 3-segmented, segment one with five aesthetascs and one short seta, segment 2 with four aesthetascs, segment 3 with one subterminal aesthetasc.

Antenna (Figure 3C). Seven-segmented, each with 1, 2, 3, 0, 0, 4, and 4 setae.

Mandible (Figure 3D). Endopod palp 2-segmented, distal segment with five marginal plumose setae.

Maxillule (Figure 3E). Coxal endite with nine plumose setae; basal endite with 11 plumodenticulate and four plumose setae; endopod 2-segmented, proximal with one plumose seta, distal with four terminal plumose setae.

Maxilla (Figure 3F). Coxal endite bilobed, with 6 + 4 plumose setae; basal endite bilobed, with 6 + 7

plumose setae; endopod with one terminal simple seta; exopod (scaphognathite) with 39 marginal plumose setae and three surface simple setae.

First maxilliped (Figure 3G). Epipod with eight long simple setae; coxal and basal endites each with six and 10 plumose setae; endopod with four terminal simple setae; exopod 2-segmented, proximal segment with one distal plumose setae, distal segment with four long terminal plumose and one simple setae.

Second maxilliped (Figure 3H). Epipod unarmed; coxa and basis not differentiated; endopod 4-segmented, with 0, 1, 4, 5 setation; exopod 2-segmented, proximal segment without seta, distal segment with four long terminal plumose setae.

Third maxilliped (Figure 3I). Epipod with six long simple setae and nine proximal plumose setae; coxa

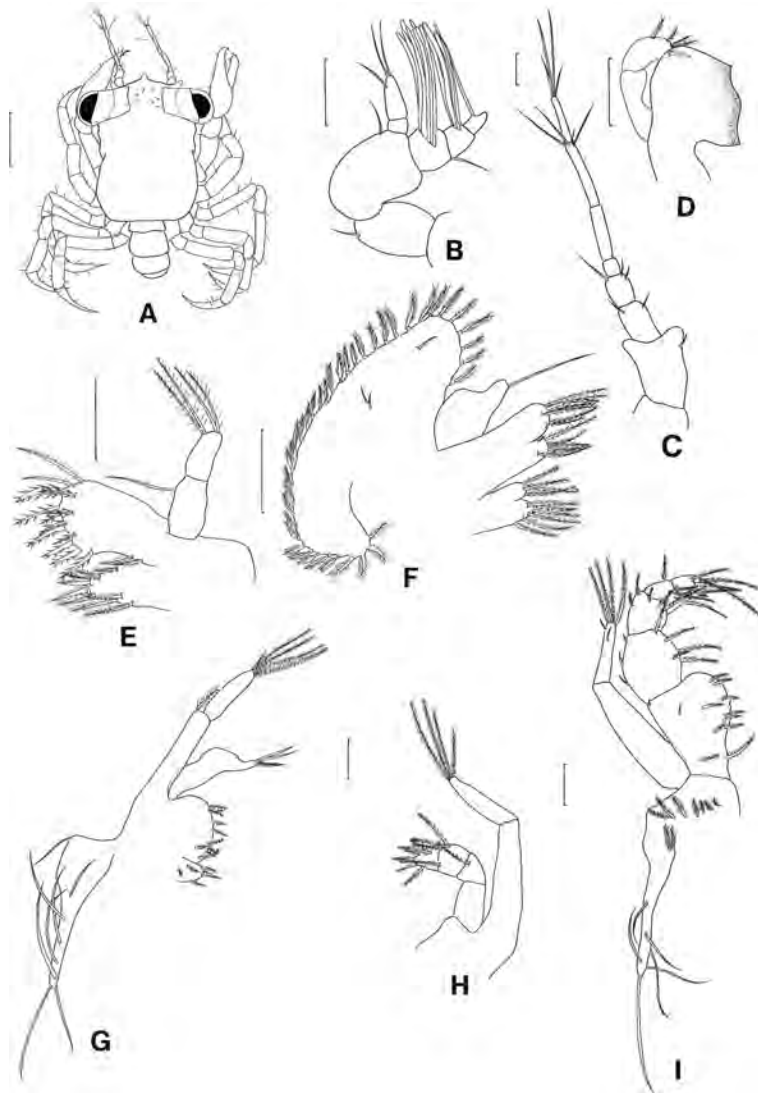


Figure 3. *Scyra acutifrons*, megalopal stage. A, dorsal view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped. Scale bars = 0.5 mm (A) and 0.1 mm (B–I).

and basis not differentiated; endopod 5-segmented, with 12, 8, 5, 6, 4 setation; exopod 2-segmented, proximal segment without seta, distal segment with four long terminal plumose and two short subterminal simple setae.

Chela (Figure 4J). All segments with a few short setae; outer surface of finger with a few granules, tip slightly hooked.

Pereopods 1–4 (Figure 4K–N). All segments well differentiated and sparsely armed with setae; only pereopod 1 with distinct ischial spine; dactylus with three spines on inner margin, tip spinulate, with a few granules on inner margin, sharp pointed.

Pleopods (Figure 4O–Q). Endopod with two hooks except in pleopod 5; pleopods 1–5 with 12, 12, 12, 9, 5 plumose setae on distal segment.

Abdomen and telson (Figure 4R). Abdomen 6-segmented; somites 1–6 with 4, 8, 8, 10, 10, 2 setae on dorsal surface; broad, rounded telson with two dorsomedial setae.

Discussion

The morphological differences between the larvae of *Scyra acutifrons* and those of *S. compressipes* described by Kim and Hong (1999) are shown in Table 2. The first and second zoeae of *S. acutifrons* are larger in size, the length of the rostral carapace spine being approximately equal to that of the antennal protopod, an endopod of the maxilla has three setae, and a distal segment of an endopod of the first maxilliped has a strong spinous subterminal seta; whereas those of *S. compressipes* are smaller in size, the length of the

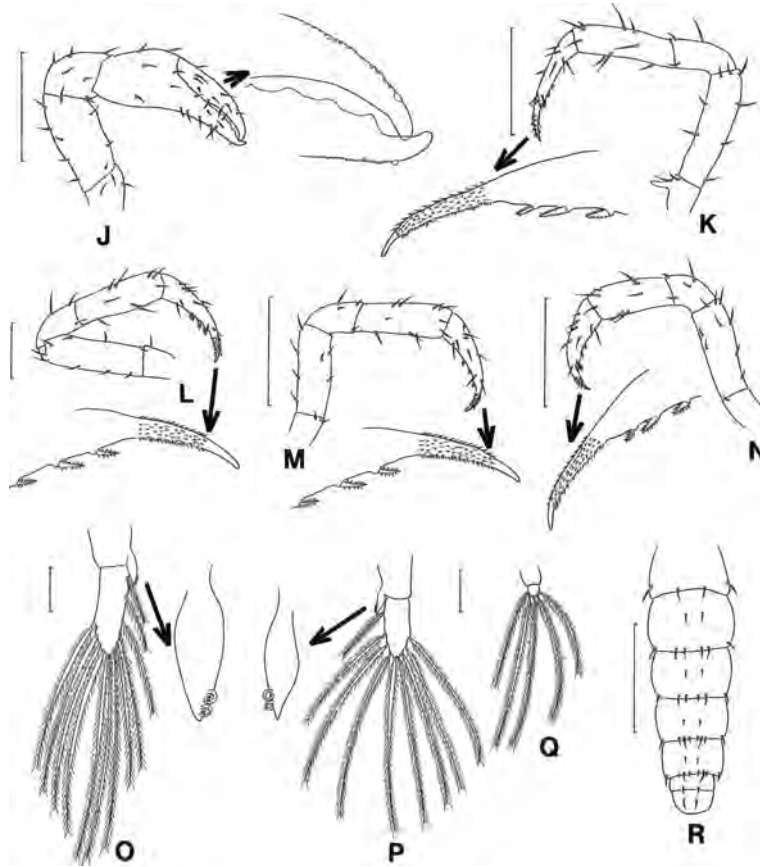


Figure 4. *Scyra acutifrons*, megalopal stage. J, chela; K–N, pereopods 1–4; O, pleopod 2; P, pereopod 4; Q, pereopod 5; R, dorsal view of abdomen and telson. Scale bars = 0.5 mm (J, K, M, N, R), 0.25 mm (L) and 0.1 mm (O–Q).

rostral carapace spine being approximately half that of the antennal protopod, an endopod of the maxilla has four setae, and a distal segment of an endopod of the first maxilliped has a plumose subterminal seta. In megalopa *S. acutifrons* is larger in size and has more setae or aesthetascs on the appendages except in a coxal endite of the maxillule.

Santana et al. (2004) stated there was no apparent larval character that differentiated pisinid larvae after reviewing larvae of 28 pisinid species. According to Table 3, the family Epialtidae must be heterogeneous based on characteristics of the zoeal mouthpart appendages. Based on the adult morphology, Griffin and Tranter (1986) reported that the *Scyra* could be separated from a subfamily Pisininae because of a truncate male first pleopod with widely flared tip. Kornienko and Korn (2007) reported that zoeae of *Pisoides bidentatus* and *Pugettia quadridens* were identical, so they should be assigned to one genus. As shown in Table 3, zoeae of *Scyra acutifrons* (Pisininae) coincide well with those of *Pugettia gracilis* and *P. incisa* (Epialtinae) in having an endopod of the maxilla with three setae. Hence, it is found that a distinct group including the genera *Pisoides*, *Scyra*, and *Pugettia* exists in the Epialtidae. This group

possesses common characteristics such as endopods of the maxillule and the maxilla with 1, 4 and 3 or 4 setae, a basis of the first maxilliped with 2 + 2 + 2 + 3 (9) setae, and an endopod of the second maxilliped with 0, 1, 4 setation. Therefore, it is suggested that the taxonomic status of the genera *Pisoides*, *Scyra*, and *Pugettia* should be re-examined in the family Epialtidae.

Rice (1980) provided a key to the brachyuran families based on the zoeal characters. Using his key, the majoid zoeae could be distinguished from most other brachyurans in having no lateral carapace spine, no lateral process on the third abdominal somite, and a telson fork with a single lateral spine. Also, Ko (1998) summarized zoeal characteristics for zoeae of the subfamily Epialtinae as follows: lateral carapace spines absent, an exopod of the antenna nearly equal to the protopodal process with two unequal subterminal setae; a proximal segment of the endopod of the maxillule with or without a seta; setations of the endopod and basis of the first maxilliped as 3, 2, 1, 2, 5 and 2 + 2 + 2 (rarely 3) + 3; setations of the endopod and basis of the second maxilliped as 0, 1, 4 and 1 + 1 + 1; the first abdominal somite with one pair of dorsomedial setae; a lateral process present on the second abdominal somite; each

Table 2. Differences in the larval characteristics between *Scyra compressipes* described by Kim and Hong (1999) and *Scyra acutifrons* in the present study.

	<i>Scyra compressipes</i>	<i>Scyra acutifrons</i>
ZOEAI		
Carapace		
length	0.69 mm	0.83 mm
rostral spine	<1/2 antennal protopod length	<antennal protopod length
lateral margin	6 setae	5 setae
Antennule	5 aesthetascs +1 seta	3 aesthetascs +2 setae
Maxilla		
endopod	4 setae	3 setae
Maxilliped I		
distal segment of endopod	1 plumose seta subterminally	1 spinous seta subterminally
ZOEAI		
Carapace		
length	0.81 mm	1.03 mm
rostral spine	<1/2 antennal protopod length	<antennal protopod length
lateral margin	6 setae	7 setae
Antennule	8 aesthetascs + 2 setae	6 aesthetascs +2 setae
Maxilla		
endopod	4 setae	3 setae
scaphognathite	16 setae	21 setae
Maxilliped I		
distal segment of endopod	1 plumose seta subterminally	1 spinous seta subterminally
MEGALOPA		
Carapace		
length	1.04 mm	1.48 mm
Antennule		
distal segment of endopod	2 setae	3 setae
exopod	10 aesthetascs + 1 seta	14 aesthetascs + 1 seta
Antenna	0, 2, 3, 0, 0, 3, 4 setation	1, 2, 3, 0, 0, 4, 4 setation
Maxillule		
endopod	1, 1 setae	1, 4 setae
basial endite	15 setae	15 setae
coxal endite	10 setae	9 setae
Maxilla		
endopod	no seta	1 seta
coxal endite	6 + 2 setae	6 + 4 setae
Scaphognathite	33-34 setae	42 setae
Maxillipeds I-III		
exopods	4, 4, 4 setae	5, 4, 6 setae
Pleopods I-V		
exopods	11, 11, 11, 8, 4 setae	12, 12, 12, 9, 5 setae

fork of telson spinulate, with a lateral spine. For the identification of the known zoeae in the family Epialtidae the following provisional key is provided from the northern Pacific. The characteristics employed are usually consistent during the zoeal development.

A key to zoeae of 17 known epialtid species from northern Pacific

1. Proximal segment of endopod of maxillule without seta 2
- Proximal segment of endopod of maxillule with 1 seta 4

2. Dorsal carapace spine present..... 3
- Dorsal carapace spine absent.....
.....*Menaethius monoceros*
3. Distal segment of endopod of maxillule with 2 setae.....*Goniopugettia sagamiensis*
- Distal segment of endopod of maxillule with 1+4 setae.....*Huenia proteus*
4. Endopod of maxillule with 1, 4 setae 5
- Endopod of maxillule with 1, 5 or 6 setae 13
5. Endopod of maxilla with 3 setae 6
- Endopod of maxilla with 4 setae 8

Table 3. Comparisons of the setations of the mouthpart appendages in the known zoeae of the subfamilies Epialtinae and Pisinae (Epialtidae) from the northern Pacific.

Species	Maxillule endopod	Maxilla endopod	Maxilliped I basis	Maxilliped II endopod	Authors
PISINAE					
<i>Hyastenus</i>					
<i>H. elongatus</i>	1, 2 + 4	2 + 3	2 + 2 + 3 + 3	0, 1, 5	Ko 1997
<i>H. diacanthus</i>	1, 5	2 + 3	no data	0, 1, 4(5)	Kurata 1969
<i>Doclea</i>					
<i>D. ovis</i>	1, 2 + 4	5	2 + 2 + 3 + 3	0, 1, 4	Terada 1983
<i>Phalangipus</i>					
<i>P. hystrix</i>	1, 2 + 4	4(5)	2 + 2 + 3 + 3	0, 1, 4	Terada 1983
<i>Pisoides</i>					
<i>P. ortmanni</i>	1, 4	4	2 + 2 + 2 + 3	0, 1, 4	Terada 1983
<i>P. bidentatus</i>	1, 4	4	2 + 2 + 2 + 3	0, 1, 4	Kornienko and Korn 2007
<i>Scyra</i>					
<i>S. compressipes</i>	1, 4	4	2 + 2 + 2 + 3	0, 1, 4	Kim and Hong 1999
<i>S. acutifrons</i>	1, 4	3	2 + 2 + 2 + 3	0, 1, 4	Present study
EPIALTINAE					
<i>Pugettia</i>					
<i>P. marissinica</i>	1, 4	4	2 + 2 + 2 + 3	0, 1, 4	Ko 1998
<i>P. intermedia</i>	1, 4	4	2 + 2 + 2 + 3	0, 1, 4	Ko 1998
<i>P. quadridens</i>	1, 4	4	2 + 2 + 2 + 3	0, 1, 4	Ko 1998
<i>P. similis</i>	1, 4	4	2 + 2 + 2 + 3	0, 1, 4	Terada 1981
<i>P. incisa</i>	1, 4	3	2 + 2 + 2 + 3	0, 1, 4	Terada 1981
<i>P. gracilis</i>	1, 4	3	2 + 2 + 2 + 3	0, 1, 4	Oh and Ko 2007
<i>Menaethius</i>					
<i>M. monoceros</i>	0, 1 + 4	5	2 + 2 + 2 + 3	0, 1, 4	Terada 1981
<i>Huenia</i>					
<i>H. proteus</i>	0, 1 + 4	4	2 + 2 + 2 + 3	0, 1, 4	Terada 1981
<i>Goniopugettia</i>					
<i>G. sagamiensis</i>	2	4	2 + 2 + 3 + 3	0, 1, 4	Taishaku and Konishi 2001

- 6. Subterminal seta on distal segment of endopod of maxilliped I spinous..... 7
- Subterminal seta on distal segment of endopod of maxilliped I plumose*Pugettia gracilis*
- 7. Rostral carapace spine $\leq 1/2$ length to antennal protopod *Pugettia incisa*
- Rostral carapace spine equal length to antennal protopod*Scyra acutifrons*
- 8. Subterminal seta on distal segment of endopod of maxilliped I spinous..... 9
- Subterminal seta on distal segment of endopod of maxilliped I plumose *Scyra compressipes*
- 9. Dorsal carapace spine > carapace length *Pisoides ortmanni*
- Dorsal carapace spine < carapace length..... 10
- 10. Anterior base of dorsal carapace spine with chromatophore..... 11
- Anterior base of dorsal carapace spine without chromatophore *Pugettia marissinica*
- 11. Middle of dorsal carapace spine without chromatophore 12

- Middle of dorsal carapace spine with chromatophore *Pugettia quadridens*
- 12. Lateral to eye with chromatophore..... *Pugettia intermedia*
- Lateral to eye without chromatophore..... *Pugettia similis, Pisoides bidentatus*
- 13. Endopod of maxillule with 1, 6 setae..... 14
- Endopod of maxillule with 1, 5 setae..... *Hyastenus diacanthus*
- 14. Endopod of maxilliped 2 with 0, 1, 5 setae *Hyastenus elongatus*
- Endopod of maxilliped 2 with 0, 1, 4 setae 15
- 15. Rostral carapace spine $1/5$ length to antennal protopod..... *Doclea ovis*
- Rostral carapace spine $\leq 1/2$ length to antennal protopod *Phalangipus hystrix*

Acknowledgements

H.S.K. gratefully acknowledges Dr Stephen Sulkin for an invitation as a visiting researcher to Shannon Point Marine

Center, USA, from 2003 to 2004. The authors wish to thank Mrs Se Jin Ok for help with drawings.

References

- Aikawa H. 1929. On larval forms of some Brachyura. Rec Oceanogr Wks Japan. 2:17–55.
- Aikawa H. 1937. Further notes on brachyuran larvae. Rec Oceanogr Wks Japan. 9:87–162.
- Clark PF, Calazans DK, Pohle GW. 1998. Accuracy and standardization of brachyuran larval descriptions. Invert Reprod Develop. 33:127–144.
- Gohar HAF, Al-Kholy AA. 1957. The larvae of four Decapod Crustacea (from the Red Sea). Publ mar boil Sta Al Ghardaqa Egypt. 9:177–202.
- Griffin DJG, Tranter HA. 1986. The Decapoda Brachyura of the Siboga Expedition. Part VIII. Majidae. Leiden: Siboga-Expeditie (Monograph) 39, C4, Livraison. p. 1–335.
- Jensen GC. 1995. Pacific coast crabs and shrimps. Sea Challengers Publication. p. 1–87, figs 1–163.
- Kim HS. 1973. Anomura, Brachyura. Illustrated encyclopedia of fauna and flora of Korea. The Ministry of Education, Korea (in Korean). p. 458–506.
- Kim ND, Hong SY. 1999. Larval development of *Scyra compressipes* (Decapoda: Brachyura: Majidae: Pisinae) reared in the laboratory. J Crust Biol. 19:782–791.
- Ko HS. 1997. The first zoeal stage of *Hyastenus elongatus* (Ortmann, 1893) (Decapoda, Brachyura, Majidae). Korean J Syst Zool. 13:1–8.
- Ko HS. 1998. Zoeal development of three species of *Pugettia* (Decapoda: Majidae), with a key to the known zoeas of the subfamily Epialtinae. J Crust Biol. 18:499–510.
- Ko HS, Hwang SG. 1997. The megalopal stages of three *Pugettia* species (Crustacea: Decapoda: Majidae) reared in the laboratory. Korean J Syst Zool. 13:261–270.
- Kornienko ES, Korn OM. 2007. The larvae of the spider crab *Pisoides bidentatus* (A. Milne-Edwards, 1873) (Decapoda: Majoidea: Pisinae) reared under laboratory conditions. J Plankton Res. 29:605–617.
- Kurata H. 1969. Larvae of decapod Brachyura of Arasaki, Sagami Bay. IV. Majidae. Bull Tokai Reg Fish Res Lab. 57:81–127.
- Mohan R, Kannupandi T. 1985. Life history of laboratory reared spider crab *Doclea ovis* (Herbst). Indian J Mar Sci. 14:24–30.
- Ng PKL, Guinot DL, Davie PJF. 2008. Systema Brachyurorum: Part 1. An annotated checklist of extant brachyuran crabs of the world. Raffles Bull Zool. 17:1–286.
- Oh SM, Ko HS. 2007. First zoea of *Pugettia gracilis* (Crustacea: Decapoda: Majidae) reared in the laboratory. Integrative Biosci. 11:51–54.
- Rice AL. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. Trans Zool Soc London. 25:271–424.
- Sakai T. 1976. Crabs of Japan and the adjacent seas. Tokyo: Kodansha. p. 1–773, pls 1–251.
- Santana W, Pohle G, Marques F. 2004. Larval development of *Apiomithrax violaceus* (A. Milne Edwards, 1868) (Decapoda: Brachyura: Majoidea: Pisidae) reared in laboratory conditions, and a review of larval characters of Pisidae. J Nat Hist. 38:1773–1797.
- Taishaku H, Konishi K. 2001. Lecithotrophic larval development of the spider crab *Goniopugettia sagamiensis* (Gordon, 1931) (Decapoda: Brachyura: Majidae) collected from the continental shelf break. J Crust Biol. 21:748–759.
- Terada M. 1981. Zoeal development of six species of crabs in the subfamily Acanthonychinae. Res Crust. 11:77–85.
- Terada M. 1983. Larval development of four Japanese spider crabs (Brachyura, Majidae, Pisinae). Proc Jap Soc Syst Zool Tokyo. 25:18–30.