# Larval development of *Capitulum mitella* (Cirripedia: Pedunculata) reared in the laboratory

Chu Lee, Jeong Min Shim and Chang Hyun Kim\*

Aquaculture Division, East Sea Fisheries Research Institute, National Fisheries Research and Development Institute, no. 8–6 Dongduck-ri, Yeongok-myon, Kangnung 210–860, Korea. E-mail: ascidian@chollian.net \*Department of Biology, College of Natural Sciences, Pusan National University, Pusan 609–735, Korea

Larval development of Capitulum mitella (Cirripedia: Pedunculata) comprises six nauplius stages and a cyprid. Unilobed labrum, a larval trait of pedunculate and chthamalid barnacles, bears two groups of slender hairs and two pairs of strong teeth on the distal labral margin, and a pair of teeth on the lateral labral margin. Frontolateral horns extended under the anterior cephalic shield margin are diagnostic features through all nauplius stages. The posterior border of the cephalic shield bears a pair of distal cephalic shield spines in nauplius stages II and III, and a pair of long posterior shield spines in nauplius stages IV, V and VI. A hispid seta is consistently found at the fourth group of the antennal endopodite through stages II–VI. The dorsal thoracic spine, abdominal process and the paired posterior shield spines have numerous small spines. Morphological features such as the cephalic shield, labrum, abdominal process, antennules, antennae and mandibles in all nauplius and cyprid stages are illustrated and described. In this species, the numerical setations of the antennule are found to be beneficial for intraspecific identification of barnacle nauplius stages without the need for dissection.

## INTRODUCTION

Capitulum mitella Linnaeus, 1758, formerly assigned to the genus Pollicipes Leach, 1817, is a predominant species attached to the intertidal rocks shaded from sunlight. It ranges from Korea through India to the West Pacific Ocean (Darwin, 1851; Nilsson-Cantell, 1927; Kim, 1985, 1998). Larval descriptions of pedunculate barnacles are rare and generally incomplete. Early workers failed to rear the pedunculate larvae from hatching through the nauplius to the cyprid stage (Groom, 1894; Coker, 1902; Hoek, 1913). Lang (1979) reared the larvae of Lepas anserifera Linnaeus, 1767 to stage III and those of L. pectinata (Spengler, 1793) to stage V. The larvae of following species have been completely described and illustrated: Calantica spinosa (Quoy & Gaimard, 1834) from New Zealand (Batham, 1945); Ibla idiotica Batham, 1945 from New Zealand (Batham, 1945); Ibla quadrivalvis Cuvier, 1817 from Australia (Anderson, 1965); Scalpellum scalpellum Linnaeus, 1767, from Sweden (Kaufman, 1965); Ibla cumingii Darwin, 1851, from India (Karande, 1974); Pollicipes polymerus Sowerby, 1833, from North America (Lewis, 1975); Octolasmis mülleri (Coker, 1958), from North America (Lang, 1976); Conchoderma auritum Linnaeus, 1767, from England (Dalley, 1984); Lepas anatifera Linnaeus, 1767, and L. pectinata from England (Moyse, 1987); and Lithotrya dorsalis Ellis & Solander, 1786, from North America (Dineen, 1987). Larval development of Capitulum mitella is known only through Yasugi (1937) who only described the outline shape of five nauplius, a metanauplius and cyprid larvae, and did not draw the correct setal morphologies of appendages. Therefore, complete larval descriptions and setal formulas are needed for each of the antennules, antennae, mandibles, thoraco-abdominal process and

labrum by dissection. It is the purpose of the present study to describe the detailed morphology of the nauplius and the cyprid stages of *C. mitella* and to compare them with other pedunculate larvae within pedunculata.

# MATERIALS AND METHODS

Capitulum mitella was collected from the rocks of the intertidal zone near Pusan, Korea. The barnacles were placed in an aquarium containing filtered seawater. They were fed daily on Brachionus sp. and newly hatched Artemia nauplii. The hatched nauplii concentrated near the light source were removed with a Pasteur pipette and transferred into several six-well tissue culture plates to examine the developmental process. The basic culture method was derived from that of Lee & Kim (1991) and Lee et al. (1999). Preserved larvae and exuviae were dissected under a stereomicroscope using fine tungsten needles in a mixture of glycerin and alcohol. Drawings were made with the aid of a camera lucida. At least ten specimens at each stage were examined. Measurements were made with an ocular micrometer. Total length was measured from the frontal margin of the cephalic shield to the end of the dorsal thoracic spine. Shield width was measured at its widest point and shield length from the front of the cephalic shield to the end of the posterior shield spine.

## RESULTS

The larvae cultured in the laboratory pass through six nauplius stages and one cyprid stage before metamorphosis to the juvenile. The nauplius consists of a cephalic shield, frontolateral horns, labrum, appendages, abdominal

Journal of the Marine Biological Association of the United Kingdom (2000)

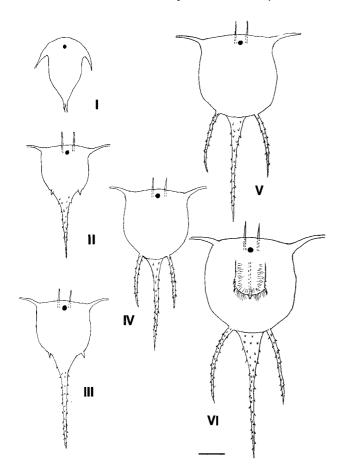
**Table 1.** Total length and shield width of larval stage of Capitulum mitella Linnaeus, 1758 (N=10).

	Total length $(\mu m)$		Shield width( $\mu$ m)		
Larval stage	Mean ±SD	Range	Mean ±SD	Range	
I II III IV V VI	$308 \pm 19$ $510 \pm 21$ $610 \pm 15$ $680 \pm 16$ $730 \pm 18$ $810 \pm 15$	289–327 490–531 595–625 664–696 712–748 795–825	$   \begin{array}{c}     164 \pm 17 \\     235 \pm 19 \\     252 \pm 21 \\     312 \pm 15 \\     387 \pm 23 \\     432 \pm 15   \end{array} $	147–181 216–254 231–273 297–327 364–410 417–447	
Cyprid	$790 \pm 27$	763-817	$312 \pm 23$	289-335	

processes from nauplius stages I–VI and prominent posterior shield spines at stages IV, V and VI. The mean size of each stage is given in Table 1. Descriptive drawings at each stage are given in Figures 1–6. In addition to the drawing of the appendages, an alphabetical setation formula proposed by Newman (1965) and modified by Sandison (1967) is given in Table 4. Details of the morphological characteristics at each stage are as follows:

#### Nauplius I

The frontal margin of these larvae is evenly rounded when compared with those of later stages. The cephalic shield is more or less elliptical and very slender.



**Figure 1.** Outline drawing of six nauplius stages of *Capitulum mitella* Scale bar:  $100 \, \mu \text{m}$ .

Journal of the Marine Biological Association of the United Kingdom (2000)

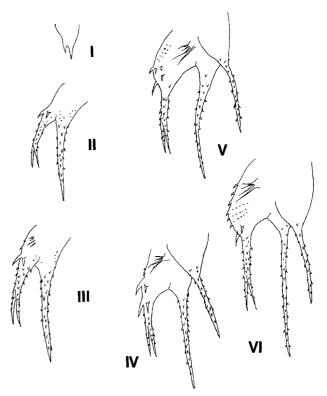
Fronto-lateral horns project backward along the side of the shield. Frontal filaments are not found. The thoracoabdominal process and dorsal thoracic spine are short and poorly developed. A medial nauplius eye is present in this and all subsequent stages. The setae of each appendage bear no setules. The unilobed labrum has small teeth on the frontal side.

#### Nauplius II

The fronto-lateral horns are swollen and oriented perpendicular to the body axis. The cephalic shield has a pair of distal shield spines on each side of the cephalic shield spine. The abdominal process and cephalic shield spine bear numerous fine elongated spinules (Figure 8B). The frontal filaments are present and remain without change in all the subsequent stages. The labrum is unilobed, with slender hairs through all subsequent stages. A pair of abdominal spines appears on the proximal portion of the thoraco-abdominal process. There are 10–12 irregular small thoracic spines on the abdominal spines. Some setae of the appendages bear minute setules. There is a hispid seta at the fourth group of the antennal endopodite.

## Nauplius III

The size of the larvae is increased in total length and width when compared with that of stage II. The frontal margin is flatter than that of stage II. The cephalic shield itself bears a specific distal shield spine, which appears around the cephalic shield spine. The thoraco-abdominal process bears a pair of abdominal spines. Irregular small thoracic spines of stage II are replaced with two transverse



**Figure 2.** Outline drawing of lateral view of six nauplius stages of *Capitulum mitella* Scale bar:  $100 \, \mu \text{m}$ .

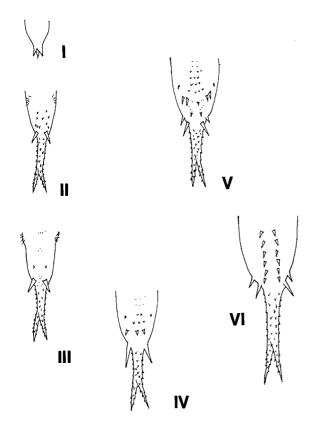


Figure 3. Outline drawing of abdominal process of six nauplius stages of Capitulum mitella. Scale bar:  $100 \, \mu \text{m}$ .

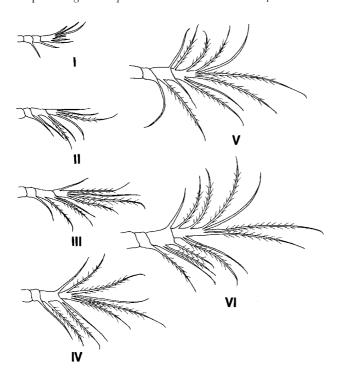


Figure 4. Antennules of six nauplius stages of Capitulum mitella. Scale bar:  $100 \, \mu \text{m}$ .

small thoracic spines in the median region on the abdominal spines. A preaxial seta is present on the antennules as a diagnostic feature of this nauplius. There is a hispid seta at the fourth group of the antennal endopodite through all subsequent stages.

Journal of the Marine Biological Association of the United Kingdom (2000)

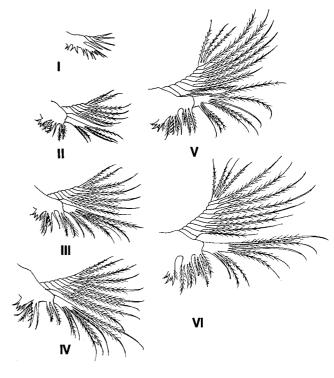


Figure 5. Antennae of six nauplius stages of Capitulum mitella. Scale bar:  $100 \, \mu \text{m}$ .

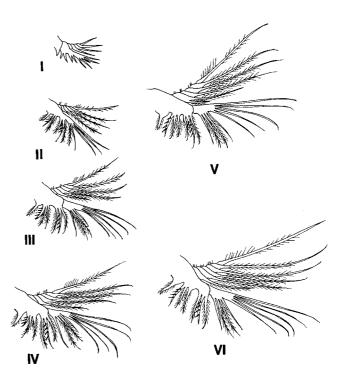
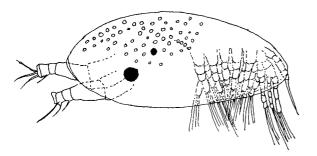


Figure 6. Mandibles of six nauplius stages of Capitulum mitella. Scale bar:  $100 \, \mu \text{m}$ .

## Nauplius IV

There is a pair of long posterior shield spines at this stage. A pair of long spines marks the posterior edge. There are two rows of seven thoracic spines and three transverse thoracic spines on the abdominal spines. Several rows of minute spinules are present on the surface



**Figure 7.** Cyprid of Capitulum mitella. Scale bar:  $100 \, \mu \text{m}$ .

of the abdominal process. Two preaxial setae are present on the antennules as a diagnostic feature of this nauplius stage.

## Nauplius V

The cephalic shield bears long posterior shield spines as in nauplius IV except for its enlargement. The dorsal thoracic spine becomes shorter than that of stage IV. There are two small thoracic spines on the abdominal spines and an open circle of seven thoracic spines on them. Several rows of fine spinules are present on the thoracic spines. The abdominal process bears two pairs of abdominal spines and the distal pair is relatively longer than the proximal pair. Three preaxial setae and five postaxial setae are present on the antennules as a diagnostic feature of this nauplius stage.

#### Nauplius VI

Six pairs of thoracic spines are present under the thorax and the primordia of the cyprid thoracic appendages can be seen within the exoskeleton of the thoracic spines (Figure 8D). Three preaxial setae and six postaxial setae are present on antennules as a diagnostic feature of this nauplius stage. Paired compound eyes appear in the later period of this stage but are not figured.

#### Cyprid

Six pairs of thoracic appendages are present on thoracic region. The anterior end is packed with oil cells. The segments of the antennule are reduced when compared with those of nauplius VI (Figure 7).

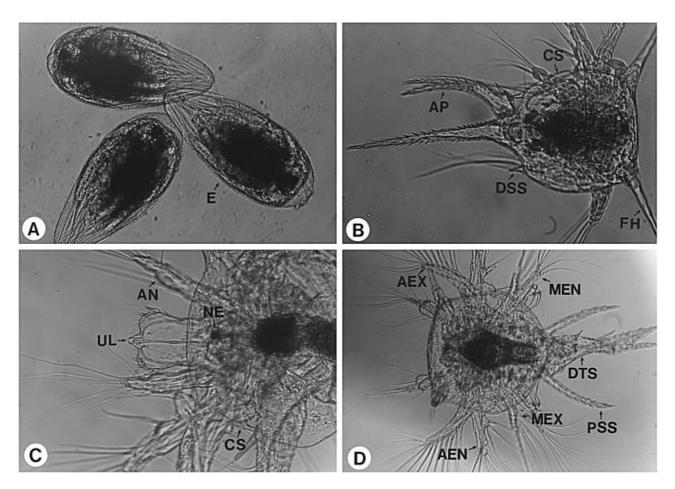


Figure 8. Microscopic view of eggs, nauplii of Capitulum mitella. (A) Eggs surrounded with egg membrane immediately before hatching to nauplius I. (B) Cephalic shield with species-specific distal shield spines of nauplius II. (C) A unilobed labrum observed in nauplius II. (D) Nauplius VI with species-specific elongated posterior shield spines. AEN, antennal endopodite; AEX, antennal exopodite; AN, antennule; AP, abdominal process; CS, cephalic shield; DSS, distal shield spine; E, egg; FH, frontolateral horn; MEN, mandibular endopodite; MEX, mandibular exopodite; NE, nauplius eye; PSS, posterior shield spine; UL, unilobed labrum.

Journal of the Marine Biological Association of the United Kingdom (2000)

Table 2. Comparison of morphological features between the larvae of Capitulum mitella Linnaeus, 1758, in the present study and those of Pollicipes polymerus Sowerby, 1833, described by Lewis (1975).

Morphological features	Capitulum mitella	Pollicipes polymerus
Cephalic shield in stages II–III	Short paired distal shield spines	None
Posterior shield spine in stages IV–VI	Paired elongated posterior shield spines	None
Shape of labrum	Unilobed, median protuberance, two lateral teeth	Unilobed, dorsal row of fine hairs and minute ventral teeth
Shape of cephalic shield	Inverted triangle	Globoid, dorsal surface approximates a semicircle
Thoraco-abdominal process	Slender, elongate	Stout and stubby
Dorsal thoracic spine	Elongated	Stout and barbed
Total length in stages IV–VI	$680-810  \mu \text{m}$	$392-542  \mu \mathrm{m}$
Setal type in antenna	Plumo-denticulate, hispid setae in antennal endopodite	Feathery, hispid setae in antennal endopodite
Length of posterior shield spine in stages IV–VI	$250-350  \mu \mathrm{m}$	$120-160  \mu \text{m}$

**Table 3.** Morphological characteristics of larvae depending on larval stage.

Stage	Species	TL (µm)	SW (µm)	LB	SS	ST
	- Престей	. ,	. ,			
I	CA	278	173	Quadrate	CSS	Simple
I	LA	470	230	Quadrate	CSS	Simple
I	OM	_	_	Elliptical	CSS	Simple
I	$\mathbf{C}\mathbf{M}$	308	164	Quadrate	CSS	Simple
I	PP	207	114	Quadrate	CSS	Simple
I	LD	362	186	Quadrate	CSS	Simple
H	CA	843	190	Quadrate	CSS	Feathered
II	LA	520	252	Quadrate	CSS	Hispid
II	OM	814	107	Elliptical	CSS	Cuspidate
II	$\mathbf{C}\mathbf{M}$	510	235	Quadrate	CSS+DSS	Hispid
II	PP	315	185	Quadrate	CSS	Hispid
II	LD	546	238	Quadrate	CSS	Feathered
III	CA	969	255	Quadrate	CSS	Feathered
III	LA	468	228	Quadrate	CSS	Cuspidate
III	OM	1004	125	Elliptical	CSS	Cuspidate
III	$\mathbf{C}\mathbf{M}$	610	252	Quadrate	CSS+DSS	Hispid
III	PP	350	222	Quadrate	CSS	Hispid
III	LD	749	258	Quadrate	CSS	Feathered
IV	CA	2376	416	Quadrate	PSS	Feathered
IV	LA	400	200	Quadrate	PSS	Cuspidate
IV	OM	1270	173	Elliptical	PSS	Cuspidate
IV	$\mathbf{C}\mathbf{M}$	680	312	Quadrate	PSS	Hispid
IV	PP	392	270	Quadrate	NPSS	Hispid
IV	LD	899	323	Quadrate	PSS	Feathered
V	CA	4351	661	Quadrate	PSS	Feathered
V	LA	591	324	Quadrate	PSS	Cuspidate
V	OM	1735	247	Elliptical	PSS	Cuspidate
V	$\mathbf{C}\mathbf{M}$	730	387	Quadrate	PSS	Hispid
V	PP	465	326	Quadrate	NPSS	Hispid
V	LD	1035	409	Quadrate	PSS	Feathered
VI	CA	-	1812	Quadrate	PSS	Feathered
VI	LA	638	398	Quadrate	PSS	Hispid
VI	OM	2659	378	Elliptical	PSS	Cuspidate
VI	$\mathbf{C}\mathbf{M}$	810	432	Quadrate	PSS	Hispid
VI	PP	542	390	Quadrate	NPSS	Hispid
VI	LD	1141	464	Quadrate	PSS	Feathered

TL, total length; SW, shield width; LB, shape of unilobed labrum; SS, shape of shield spine; CSS, cephalic shield spine; DSS, distal shield spine; ST, specific setal type observed in 3rd and 4th segment of antennal endopodite; PSS, posterior shield spine; NPSS, no posterior shield spine. CA, Conchoderma auritum; LA, Lepas anatifera; OM, Octolasmis mülleri; CM, Capitulum mitella; PP, Pollicipes polymerus; LD, Lithotrya dorsalis.

**Table 4.** Alphabetical setal formulas of larval appendages of six pedunculate barnacle species.

Stage	Species	Antennule	Antenna	Mandible
I	CA	_	_	_
I	LA	4S:2S:S:S	S:4S-3S:2S:2S:2S:G	S:3S-3S:2S:2S:2S:G
I	OM	4S:S:S	2S:3S-3S:S:S:G	2S:2S-3S:2S:G
I	$\mathbf{C}\mathbf{M}$	4S:2S:S:S	S:4S-3S:2S:2S:2S:G	S:3S-3S:2S:2S:2S:G
I	PP	4S:2S:S:S	S:4S-3S:2S:2S:2S:G	S:3S-3S:2S:2S:2S:G
I	LD	4S:2S:S:S	S:4S-3S:2S:2S:2S:G	S:3S-3S:2S:2S:2S:G
II	$\mathbf{C}\mathbf{A}$	2SPS:P:P:S	SP:4PS-2PS:2S:2F:SFC:G	P:3PS-3S:SP:3P:2P:G
II	LA	S:PS2P::SP:P:S	2P:5P-2PSP:PS:PD:SPCS:G	P:4P-5S:S2PS:PCP:2PC:G
II	OM	SP2S:P:P	SP:4PS-2P2S:S:S:C:G	2S:3S-C2P:2P:G
II	$\mathbf{C}\mathbf{M}$	SP2S:SP:S:S	2P:4PS-2PS:PS:PD:SHP:G	P:3PS-3S:SP:PCP:PC:G
II	PP	4S:SP:P:S	SP:P3PS-P2S:2S:2F:SFH:G	P:3PS-3S:SP:PCP:2P:G
II	LD	2SPS:SP:P:S	SP:4PS-P2S:SP:2F:SPC:G	P:3PS-3S:PS:PCP:2P:G
III	$\mathbf{C}\mathbf{A}$	P:BS2S:SB:B:S	2P:3S2P-3P:P:2F:2PSC:G	P:3PS-3S:SPS:DPC:DPC:G
III	LA	S:PS2P:2S:P:S	2P:5P-3P:SP:PD:PSC:G	P:3PS-3S:SPS:PDP:PC:G
III	OM	P:SP2S:P:P	2P:5P-3P:P:S:S:C:G	2S:3S-C2P:3P:G
III	$\mathbf{C}\mathbf{M}$	P:PS2P:SP:P:S	2P:5P-2PSP:PS:PD:SHCS:G	P:4P-5S:S2PS:PCP:2PC:G
III	PP	S:P3S:SP:P:S	2P:5P-2PSP:2S:2F:SFSH:G	P:3PS-4S:SPS:PCP:3P:G
III	LD	S:PSPS:SP:P:S	2P:5P-3P:SP:2F:2PSC:G	P:3PS-3S:P2S:PCP:3P:G
IV	CA	P:P:B3S:SB:B:S	PS:3S4P-3PS:P2S:FSF:3PC:G	P:3PS-4S:SP:PS3P:3P:G
IV	LA	S:S:PS2P:PS:P:S	3P:5PS-3P2S:SPS:PD:S2PC:G	P:3PS-4S:S2P:DSPC:DPC:G
IV	OM	P:P:SP2S:P:P	2P:5P2S-3PSPS:S:2SC:G	2S:3S-C2P:3P:G
IV	$^{\mathrm{CM}}$	S:P:PS2P:SP:P:S	2P:7P-2PSPS:SPS:PD:SHCS:G	P:4P-5S:S2PS:PCP:PCP:G
IV	PP	S:P:2P2S:SP:P:S	2P:7P-2PSPS:3S:FSF:SFPH:G	P:4P-5S:S2P:SPCP:3P:G
IV	LD	S:P:PSPS:SP:P:S	2P:7P-2PSPS:2SP:FSF:PFSC:G	P:4P-4S:PSP:PSCP:3P:G
V	CA	P:P:B3S:PB:S:S:B:S	2PS:3S4PF-2PS2P:2P:3F:3PC:G	P:5P-4S:SPSP:S3P:3P:G
V	LA	S:S:P:PS2P:2P:P:S:S	3P:7P-2PS2P:SPS:PD:PC2S:G	P:4PS-4S:S2PS:SPDP:PCP:G
V	OM	P:P:SP2S:P:S:S:P	2PS:7P-4P:2P:S:2SC:G	3S:3S-C2P:3P:G
V	$\mathbf{C}\mathbf{M}$	S:S:P:2P2S:SP:S:P:S	3P:7PS-2PS2P:2PS:PDP:SFHP:G	P:5P-5S:S2PS:PCP:PCP:G
V	PP	S:P:P:PS2P:SP:P:PS:P	3P:8P-5P:3S:SFPF:SFPH:G	P:5P-5S:S2PS:PCP:PCP:G
V	LD	S:S:P:PSPS:SP:S:P:S	3P:7PS-2PSPS:2SP:FSPF:PFSC:G	P:5P-5S:PSPS:PSCP:3P:G
VI	CA	P:P:B3S:PB:S:B:BS:S	2P2S:2S5PF-2PS2P:PSP:S3F:PSPC:G	P:5P-5S:SPSP:S3P:3P:G
VI	LA	S:P:P:2PSP:SP:P:2S:P	3P:8P-5P:2SPS:SPDSP:SCPH:G	P:5P-2SPSP:S3PS:PDP:PCP:G
VI	OM	P:P:SP2S:P:S:P:P	3PS:7P-4P:2P:S:2SC:G	3S:3S-C2P:3P:G
VI	$\mathbf{C}\mathbf{M}$	S:P:P:PS2P:SP:P:PS:P	4P:8P-2PS2P:2PS:PDP:SFHP:G	P:5P-5S:S2PS:PCP:PCP:G
VI	PP	S:P:P:2P2S:SP:P:PS:S	4P:8P-2PS2P:3S:S3F:SFPH:G	P:5P-5S:2S2P:SPCP:3P:G
VI	LD	S:P:P:PSPS:SP:S:PS:S	4P:8P-2PS2P:2SP:FS2F:PFSC:G	P:5P-5S:PSPS:PSCP:3P:G

CA, Conchoderma auritum; LA, Lepas anatifera; OM, Octolasmis mülleri, CM, Capitulum mitella; PP, Pollicipes polymerus; LD, Lithotrya dorsalis. Setal types: B, bristled; C, cuspidate; D, plumodenticulate; F, feathered; G, gnathobase; H, hispid; P, plumose; S, simple.

# DISCUSSION

The present species, known as Pollicipes mitella by Zevina (1981), was classified as Capitulum mitella after review of relationships between genera of Pedunculata. In Capitulum the rostrum is an important plate as it is in the balanomorph, while it is relatively unimportant in all species of Pollicipes (Foster, 1978; Newman, 1987). The larvae of C. mitella resemble previously known pedunculate larvae. However, the cephalic shield itself bears specific distal shield spines, not found in the same stages of other pedunculate barnacle larvae, which appear around the caudal spine in stages II-III. Dineen (1987) suggests that the most striking similarity occurs between the cephalic shield outlines of Lithotrya dorsalis and C. mitella among the five scapellid species such as Calantica spinosa, Scalpellum scalpellum, Pollicipes polymerus, L. dorsalis and P. mitella. He also explains that the same basic shield shape, along with the elongated and spinulated thoracoabdominal process and dorsal thoracic spine, and the elongated posterior shield spines in larval stages IV-VI are present in both species, while the nauplii of other scalpellid species have relatively abbreviated thoraco-abdominal

processes and dorsal thoracic spines and appear to lack posterior shield spines. The presence of a long posterior shield spine readily distinguishes the larvae of C. mitella from the larvae of *P. polymerus* with not posterior shield spine but a blunt posterior shield border in nauplius stages IV-VI although *C. mitella* and *P. polymerus* are recognized as belonging to the same genus by Zevina (1981). Lewis (1975) suggested that the setation of *P. polymerus* nauplii is similar to that of the balanomorph barnacle Microeuraphia aestuarii (Stubbings, 1967) in that the thoraco-abdominal processes grow longer than the caudal spines with succeeding larval stages and that a hispid seta is present on the antennal endopodite. She explained that the larvae of C. mitella resemble those of *P. polymerus* because of a similarity in the setation of the appendages and the presence of a hispid seta on the antennal endopodite. The larvae of the following sessile barnacles bearing hispid setae have been described: Octomeris angulosa Sowerby, 1825 (Sandison, 1954); Microeuraphia depressa (Poli, 1791) (Le Reste, 1965); Chthamalus dalli Pilsbry, 1916 (Korn & Ovsyannikova, 1979); Chthamalus fragilis Darwin, 1854 (Lang, 1979); Catomerus polymerus Darwin, 1854; Chthamalus antennatus Darwin, 1854; and Chamaesipho tasmanica Foster & Anderson, 1986

Journal of the Marine Biological Association of the United Kingdom (2000)

(Egan & Anderson, 1989), and Chthamalus challengeri Hoek, 1883 (Lee, 1999). Therefore, a hispid seta cannot be considered as a morphological characteristic of pedunculate barnacles because they have been similarly observed in the balanomorphs. Thus the larvae of Capitulum mitella, formerly assigned to Pollicipes Leach, 1817, can not help being separated from those of *P. polymerus* from a phylogenetic viewpoint because significant morphological differences were consistently observed in relation to the presence of distal cephalic shield spines around a caudal spine in stages II-III, a long caudal and elongated abdominal spine, and the presence of a posterior shield spine in stages IV-VI in the former nauplii, when compared with the absence of a distal cephalic shield spine around a caudal spine in stages II-III, a short caudal and abdominal spine, and the absence of a pair of posterior shield spines in stages IV-VI in the latter nauplii (Table 2).

Pedunculate larvae, including those of C. mitella, have unique features, which clearly separate them from the larvae of balanomorphs. The former has long slender setae and setules on each appendage, and an inverted triangular cephalic shield (Lang, 1979; Dalley, 1984). In contrast, the latter have short setae and setules in each appendage, and pear-shaped cephalic shield. However, the larvae of the pedunculates and chthamalids possess common features in having a specific hispid or feathered seta in the fourth group of the antennal endopodite and a unilobed labrum. Lang (1979) found that at least 16 setae are present on the antennal endopodite of stage VI nauplii of all chthamalid and most pedunculate larvae but no more than 14 setae occur in balanid larvae. Newman & Ross (1976) suggested that the chthamalid bullate labrum of the adult form, inherited from the scalpellids, gave way to the thick but non-bullate condition, with concomitant changes in the nature of the mandibles to the more advanced balanid type from the viewpoint of a monophyletic diversification. Newman (1989) found that Neoverruca brachylepadoformis Newman, 1989, has the basic organization of the most primitive sessile barnacles, the extinct Brachylepadomorpha, and is further distinguished from higher sessile barnacles in passing through a number of well-developed pedunculated stages before undergoing an abrupt metamorphosis into the sessile mode. Derivation of the chthamalids from scalpellids is indicated by the morphological similarity between the larvae of P. polymerus and those of the chthamalid, the setal number in the antennal endopodite of stage VI of all chthamalid and most pedunculate larvae, fossil evidence, and comparison of morphological function (Newman, 1982; Anderson, 1983). However, significant differences exist between the larvae of C. mitella and those of the chthamalids in having a distal shield spine which appears in stages II and III, the prominent posterior shield spines in stages IV-VI, an elongated dorsal thoracic spine, and long setae of the appendages, when compared with absence of the distal shield spine and posterior shield spine, a short dorsal spine, and short setae of appendages in the latter larvae.

It is possible to identify the pedunculate larvae depending on total length, shield width, shape of the labrum, setation formulas, presence of posterior shield spine, and a specific setal type observed in the third and fourth segments of the antennal endopodite (Tables 3 & 4).

Octolasmis mülleri larvae have a tapered elliptical labrum while the larvae of Conchoderma auritum, Lepas anatifera, Capitulum mitella and P. polymerus possess a quadrate labrum. The labrum of Conchoderma auritum bears posteriorly directed hairs along each edge and a pair of spines at each corner of the distal margin. The labrum of P. polymerus and Capitulum mitella has two pairs of posterolateral spines at each corner of the distal edge, a median bilobed tooth, a few fine frontal hairs, and minute ventral teeth. The larvae of Conchoderma auritum, L. anatifera, C. mitella and Lithotrya dorsalis have a pair of posterior shield spines in stages IV-VI, whereas those of P. polymerus lack a posterior shield spine in the same stages. The distal shield spine of C. mitella appearing in stages II and III is absent in the same early stages in balanomorphs and pedunculates. Dineen (1987) noted that rudimentary posterior shield spines occur in L. dorsalis, which appear around the caudal spine, as observed in C. mitella naupliar stages II and III. We do not know whether it is a rudimentary posterior shield spine or not, but its phylogenetic significance needs to be investigated through detailed ontogeny of other pedunculate barnacles. The antennal endopodite of pedunculate nauplii in stage VI, known to function during feeding, also shows differences in the setal number depending on the habitat and other factors. For instance, the larvae of a commensal species, Octolasmis mülleri (Lang, 1976), which is attached to the gills of an edible crab, bear ten setae. But the non-commensal species have 16 setae in Conchoderma auritum (Dalley, 1984), 18 setae in Lepas anatifera (Moyse, 1987), 15 setae in Capitulum mitella from the present study, and 16 setae in *P. polymerus* (Lewis, 1975). The numerical setation formulae of the antennule are valuable for intraspecific identification of barnacle nauplius stages without dissection except for the commensal, Octolasmis mülleri, and non-commensal, Conchoderma auritum: stage I without preaxial setae and fine setule in all setae; stage II without preaxial setae but having some setae with fine setules; stage III with a preaxial seta and four postaxial setae; stage IV with two preaxial setae; stage V with three preaxial setae and five postaxial setae; stage VI with three preaxial setae and six postaxial setae (Table 4).

Our larval descriptions of C. mitella differ in several respects from that of Yasugi (1937). He explained that it passes through five nauplius stages, a metanauplis and a cyprid stage. His numerical formula of 114211 in the antennule of stage V and the metanauplius stage differs because we found it to be 11142111 in stage V and 11142121 in stage VI. He also described 11 setae and 13 setae in the mandibular endopodite of stages III-IV, and stages V–VI, respectively, while we found it to have consistently 15 setae in the mandibular endopodite of stages III-VI. The antennal setal type was similar but a difference was observed in the fourth group of the antennal endopodite by the presence of a specific hispid seta, not depicted in Yasugi's description. Therefore, the differences observed might reflect ecological or biogeographical variations or possibly he did not detect all of the setae in the antennule, antenna and mandible.

Our thanks go to Dr I.H. Kim of Kangnung National University, Korea for his advice with profound knowledge of barnacles. We thank two anonymous referees for their critical review of this manuscript.

#### REFERENCES

- Anderson, D.T., 1965. Embryonic and larval development and segment formation in Ibla quadrivalvis Cuv. (Cirripedia). Australian Journal of Zoology, 13, 1-15.
- Anderson, D.T., 1983. Catomerus polymerus and the evolution of the balanomorph form in barnacles (Cirripedia). Memoirs of the Australian Museum, 18, 7–20.
- Batham, E.J., 1945. Description of female, male and larval forms of a tiny stalked barnacle, Ibla idiotica n. sp. Transactions of the Royal Society of New Zealand, 75, 347–356.
- Batham, E.J., 1945. Pollicipes spinosus Quoy and Gaimard. II. Embryonic and larval development. Transactions of the Royal Society of New Zealand, 75, 405–418.
- Coker, R.E., 1902. Notes on a species of barnacle (Dichelaspis) parasitic on the gills of edible crabs. Bulletin of the United States Fisheries Commission, 21, 399–412.
- Dalley, R., 1984. The larval stages of the oceanic, pedunculate barnacle Conchoderma auritum (L.) (Cirripedia, Thoracica). Crustaceana, 46, 39-54.
- Darwin, C., 1851. A monograph on the subclass Cirripedia, with figures of all species. The Lepadidae or pedunculated cirripedes. London: The Ray Society.
- Dineen, J.E. Jr, 1987. The larval stages of Lithotrya dorsalis (Ellis & Solander, 1786): a burrowing thoracican barnacle. Biological Bulletin. Marine Biological Laboratory, Woods Hole, 172, 284-298.
- Egan, E.A. & Anderson, D.T., 1986. Larval development of Balanus amphitrite Darwin and Balanus variegatus Darwin (Cirripedia, Balanidae) from New South Wales, Australia. Crustaceana, 51, 188-207.
- Egan, E.A. & Anderson, D.T., 1989. Larval development of the chthamalid barnacle Catomerus polymerus Darwin, Chamaesipho tasmanica Foster & Anderson and Chthamalus antennatus Darwin (Crustacea: Cirripedia). Zoological Journal of the Linnean Society, 95, 1–28.
- Foster, B.A., 1978. The marine fauna of New Zealand: barnacles (Cirripedia: Thoracica). Memoirs of the New Zealand Oceanographic Institute, 69, 1-16.
- Groom, T.T., 1894. On the early development of Cirripedia. Philosophical Transactions of the Royal Society, 185, 110–232.
- Hoek, P.P.C., 1913. The Cirripedia of the Siboga Expedition. B. Cirripedia Sessilia. Siboga Expeditie Monography, 31, 129–275.
- Karande, A.A., 1974. Development of pedunculate barnacle Ibla cumingi Darwin. Indian Journal of Sciences, 3, 173-177.
- Kaufman, R., 1965. Zur embryonal und larvalentwicklung von Scalpellum scalpellum L. (Crust. Cirr.) mit einem Beitrag zur autokölogie dieser. Zeitschrift für Morphologie und Ökologie der Tiere, 55, 161–232.
- Kim, I.H., 1985. Korean barnacles (Crustacea, Cirripedia, Thoracica). PhD thesis, Seoul National University, Korea. [In Korean.]
- Kim, I.H., 1998. Illustrated encyclopedia of fauna and flora of Korea. Vol. 38. Cirripedia, Symbiotic Copepoda, Pycnogonida. Seoul: Ministry of Education of Korea. [In Korean.]
- Korn, O.M. & Ovsyannikova, I.I. 1979. Larval development of Chthamalus dalli. Biologia Morya (Vladivostok), 5, 60–69.

- Lang, W.H., 1976. The larval development and metamorphosis of the pedunculate Octolasmis mülleri (Coker, 1902) reared in the laboratory. Biological Bulletin. Marine Biological Laboratory, Woods Hole, 150, 255-267.
- Lang, W.H., 1979. Larval development of shallow water barnacles of the Carolinas (Cirripedia: Thoracica) with keys to naupliar stages. National Oceanic and Atmospheric Administration Technical Report, NMFS, no. 421, 1–39.
- Lee, C., 1999. Larval development of Chthamalus challengeri Hoek (Cirripedia: Chthamalidae) with keys to barnacle larvae of Korean coastal waters. Korean Journal of Biological Sciences, 3,
- Lee, C. & Kim, C.H., 1991. Larval development of Balanus albicostatus Pilsbry (Cirripedia, Thoracica) reared in the laboratory. Journal of Experimental Marine Biology and Ecology, **147**, 231–244.
- Lee, C., Shim, J.M. & Kim, C.H., 1999. Larval development of Balanus reticulatus Utinomi, 1967 (Cirripedia, Thoracica) and a comparison with other barnacle larvae. Journal of Plankton Research, 21, 2125-2142.
- LeReste, L., 1965. Contribution a l'etude des larvaes de cirripedes dans le golfe de Marseille. Recueil des Travaux de la Station Marine d'Endoume. Bulletin, 38, 33–121.
- Lewis, C.A., 1975. Development of the gooseneck barnacle Pollicipes polymerus (Cirripedia: Lepadomorpha): fertilization through settlement. Marine Biology, 32, 141-153.
- Moyse, J., 1987. Larvae of lepadomorph barnacles. In Barnacle biology (ed. A.J. Southward), pp. 329-362. Rotterdam: A.A. Balkema. [Crustacean Issues, no. 5.]
- Newman, W.A., 1965. Prospectus on larval cirriped setation formulae. Crustaceana, 9, 51-56.
- Newman, W.A., 1982. Cirripedia. In The biology of Crustacea, vol. 1 (ed. L. Abele), pp. 197-220. New York: Academic Press.
- Newman, W.A., 1987. Evolution of cirripedes and their major groups. In Barnacle biology (ed. A.J. Southward), pp. 43-61. Rotterdam: A.A. Balkema. [Crustacean Issues, no. 5.]
- Newman, W.A., 1989. Juvenile ontogeny and metamorphosis in the most primitive living sessile barnacle, Neoverruca, from abyssal hydrothermal springs. Bulletin of Marine Science, 45,
- Newman, W.A. & Ross, A., 1976. Revision of the balanomorph barnacles; including a catalog of the species. Memoirs of the San Diego Society of Natural History, 9, 1-108.
- Nilsson-Cantell, C.A., 1927. Some barnacles in the British Museum (Natural History). Proceedings of the Zoological Society of London, 3, 734-790.
- Sandison, E.E., 1954. The identification of the nauplii of some South African barnacles with notes on their life histories. Transactions of the Royal Society of South Africa, 34, 69–101.
- Sandison, E.E., 1967. The naupliar stages of Balanus pallidus stutsburi Darwin and Chthamalus aestuarii Stubbings (Cirripedia, Thoracica). Crustaceana, 13, 161–174.
- Yasugi, R., 1937. On the swimming larvae of Mitella mitella L. Botany and Zoology, Tokyo, 5, 792-896.
- Zevina, G.B., 1981. Barnacles of the Suborder Lepadomorpha (Cirripedia Thoracica) of the world ocean. 1. Family Scalpellidae. Opredeliteli Fauna SSR, 127, 1–398. [In Russian.]

Submitted 18 June 1999. Accepted 11 January 2000.