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DESCRIPTION OF NAUPLIAR STAGES IN *ACARTIA STEUERI* SMIRNOV (COPEPODA: CALANOIDA)

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A B S T R A C T

The six naupliar stages of *Acartia* (*Acanthacartia*) *steueri* Smirnov, a calanoid copepod of the family Acartiidae, are described by both light microscopy and scanning electron microscopy. Each stage is discriminated by the number of setae on the distal segment of the antennule. The nauplii of *A. steueri* can be distinguished from those of two con-subgeneric species, *Acartia* (*A.*) *californiensis* Trinast and *A.* (*A.*) *bifilosa* Giesbrecht, by both the combination and the constancy in all naupliar stages of the exopodal setal counts of the antenna and mandible.

KEY WORDS: *Acartia steueri*, Copepoda, nauplius larvae

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INTRODUCTION

The genus *Acartia* in the calanoid copepod family Acartiidae is distributed worldwide, and its species are especially common and abundant in estuarine and coastal waters (Jeffries, 1962; Madhupratap and Haridas, 1994). Steuer (1924) divided *Acartia* into eight subgenera, and six of these subgenera are still recognized. Although 97 species of the *Acartia* have been described to date, the naupliar stages have been known for only 9 species (Table 1). Moreover, some of the naupliar descriptions were incomplete (Oberg, 1906; Sazhina, 1982).

Acartia steueri Smirnov, 1936 belongs to the subgenus *Acanthacartia* and occurs in the Russian coastal waters of the Sea of Japan (Smirnov, 1936), the Pacific coast of the Japanese Islands (Tanaka et al., 1987; Uye, 1980, 1981, 1983; Kurihara et al., 2004; Onoue et al., 2004), and the East China Sea (Ueda, 1980; Kang and Kang, 2005). It is one of the dominant species of copepod in these coastal waters and is considered to be a food source for fish larvae (Tanaka et al., 1987). In this connection, many biological parameters such as growth rate (Uye, 1980), egg production (Uye, 1981), egg development (Onoue et al., 2004), and production rate (Kang and Kang, 2005) have been investigated.

The objectives of the present study were to describe the naupliar stages of *A. steueri* by both light microscopy and scanning electron microscopy (SEM) and to compare these nauplii with those of two con-subgeneric species, *Acartia* (*Acanthacartia*) *californiensis* Trinast, 1976, described by Trujillo-Ortiz (1986) and *A.* (*A.*) *bifilosa* Giesbrecht, 1881, described by Yoon et al. (1998).

MATERIALS AND METHODS

Sampling Site

The plankton samples used in this study were collected in Manazuru Port (35°09′49″N, 139°10′33″E; depth 5.5 m), Manazuru Peninsula, which is located near the north shore of Sagami Bay, Japan. The mouth of Sagami Bay faces the Pacific Ocean and its hydrography is primarily related to fluctuations of the Kuroshio Current axis and to waters originating from the Sagami and Sakawa Rivers as well as waters from Tokyo Bay (Hogetsu and Taga, 1977). The Manazuru Peninsula is a temperate zone site that has been methodically studied for both variability in environmental factors and distribution and abundance of plankton (Shimode et al., 1998, 2006; Kuwahara et al., 2000; Satoh et al., 2000; Toda et al., 2000; Miyaguchi et al., 2006). *Acartia steueri* is one of the dominant species of copepods along the coast of Sagami Bay (Onoue et al., 2004).

Collection of Naupliar Stages of *Acartia steueri*

The six naupliar stages of *A. steueri* were obtained both from the field by plankton net and from the laboratory by keeping adult females.

To collect nauplii in the field, plankton samples were taken by gently towing a 50 μm mesh net obliquely from bottom to surface in May, 2003. The samples were transferred to the laboratory, and were fixed in 5% neutralized formaldehyde solution diluted with seawater which had been filtered through 0.22 μm Millipore® membrane filters. The nauplii of *A. steueri* were then sorted by Pasteur pipette under a dissecting microscope.

To obtain eggs of *A. steueri* in the laboratory, plankton samples were collected by oblique tows using a 180 μm mesh net from the bottom to the surface from March to July, 2006. Adult females were sorted under a dissecting microscope. Each was then individually maintained for 12 hrs at ambient temperature conditions at 15.0°C, in a 10-ml beaker filled with seawater that had been filtered through Whatman® glass-fiber filters (Type GF/F) to avoid contamination with other eggs and remove other zooplankton. Eggs spawned by these females were placed in 12-hole NUNC® multi-well dishes (one egg per well) with ca 5 ml of seawater that had been filtered through 0.22-μm Millipore® membrane filters, and incubated at 15.0°C. Hatching and molting from N I to N II were monitored under a dissecting microscope every day. Then first and second nauplii were picked up with Pasteur pipette and fixed in 5% neutralized formaldehyde solution diluted with seawater that had been filtered through 0.22-μm Millipore® membrane filters.

Observation and Description of Naupliar Stages of *Acartia steueri*

Each naupliar stage, in undissected condition, was examined both by light microscopy (Carl Zeiss: Axioskop model 2) with white light source at 400 times magnification and by low-magnification scanning electron microscopy (SEM: JEOL JSM-5600) at low magnification. The specimens for SEM were prepared based on the protocol of Suzuki et al. (1995), but the freeze-drying method in the procedure was improved in this study. The

Table 1. Descriptions of naupliar stages in the genus *Acartia*.

Subgenus	Species	Literatures
Acartia	*danae* Giesbrecht	Björnberg, 1972
Acartia	*negligens* Dana	Björnberg, 1972
Acartiura	*clausi* Giesbrecht	Ogilvie, 1953; Klein-Breteler, 1982
Acartiura	*longiremis* Lilljeborg	Oberg, 1906
Acanthacartia	*bifilosa* Giesbrecht	Oberg, 1906, Yoon et al., 1998
Acanthacartia	*californiensis* Trinast	Trujillo-Ortiz, 1986
Acanthacartia	*tonsa* Dana	Sazhina, 1982
Acanthacartia	*tsuensis* Itô	Takahashi and Ohno, 1996
Odontacartia	*lilljeborgi* Giesbrecht	Björnberg, 1972

detailed method would be described elsewhere. We examined microstructures with SEM at high magnification.

The terminology used in the text is referred to Ferrari and Dahms (2007). In the text, tables, and figures, the following abbreviations are used: N I-N VI = first to sixth nauplius stages; A1, 2: antennule, antenna; Md = mandible; Mx 1, 2 = maxillule, maxilla; Mxp = maxilliped; P 1, 2 = swimming leg 1, swimming leg 2; Ex = exopod; En = endopod.

Results

The naupliar development of *A. steueri* consists of a series of six stages. The body is not significantly curved laterally. All naupliar stages are oval anteriorly, becoming narrower towards the bud of the caudal rami. There are short and thin setules in the labrum's inferior margin throughout the naupliar phase. The antennule is composed of 3 segments throughout the naupliar phase. The number of seta on the distal segment of the antennule is increased from 3 to 10 throughout the naupliar phase. There is no seta on the proximal segment of the antennule, and the middle segment bears 2 setae throughout the naupliar phase. The antenna is composed of the coxa, the basis, the endopod, and the exopod. The number of setae on the antenna and the mandible does not increase from N I to N III, but the number of setae on the endopod increases at N IV. The bud of the maxillule appears as a single seta at N III (Fig. 1c), then as an appendage lobe at N IV (Fig. 2d), becoming well differentiated at N VI (Fig. 2f). The bud of the maxilla appears as a setose lobe between the maxillule and the maxilliped at N VI (Fig. 2f). The bud of maxilliped appears as medial lobe at N VI with 6 setae. The bud of the swimming legs 1 and 2 appear at N VI. The total number of setae and spines of the bud of the caudal rami increases at N III and N IV. There are 2 sensory setae at N I and N II, and 2 dorsal terminal spines are added at N III. At N IV, 2 ventral terminal spines are added to the bud of the caudal rami. The two sensory setae bear thin, soft setules from N II (Fig. 3a). Each naupliar stage is described in detail below, with successive stage differences and changes highlighted. The meristic differences are summarized in Table 2.

Nauplius I (Fig. 1a)

The body length is 88 μm. The antennule is composed of 3 segments. The proximal segment bears no seta, the middle segment bears 2 setae (a long one and a short one), and the distal segment bears 3 setae. The antenna is biramous and is composed of the coxa, the basis, the endopod, and the exopod. The coxa bears a single seta and a arthrite, the basis bears 2 setae, the endopod bears 4 setae, there are 7 setae on the exopod. The mandible is biramous and is composed of the coxa, the basis, the endopod, and the exopod. The coxa bears 1 seta and the basipod bears 2 setae, one of which is a spinulose. The endopod bears 7 setae, and the exopod bears 6 setae. There are 2 sensory setae in the bud of the caudal rami, flanked by 2 rows of 4 spinules each.

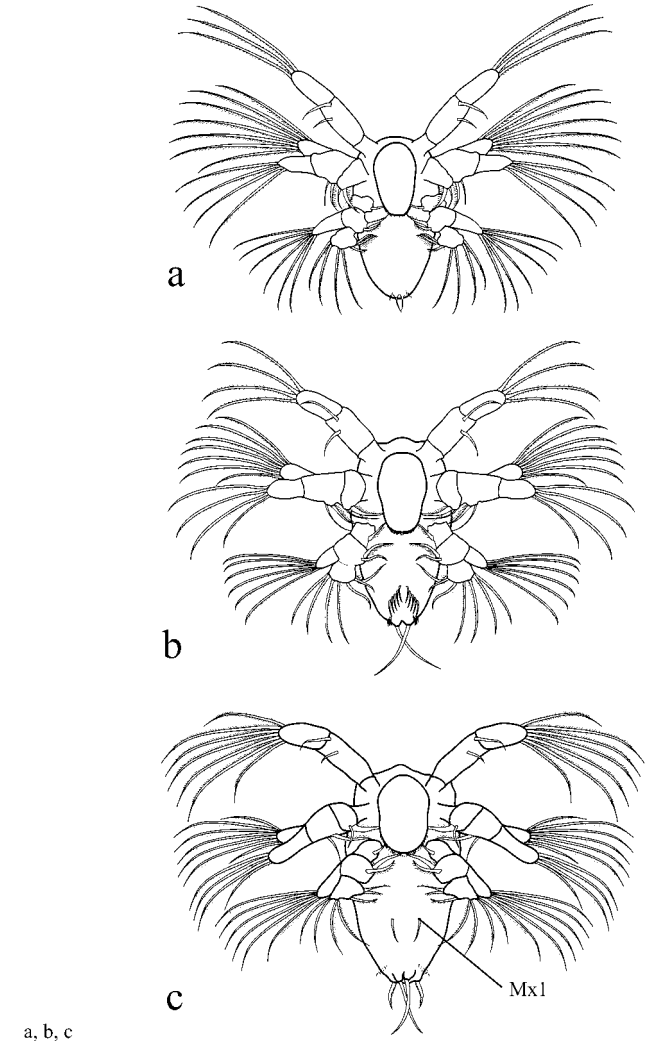

Fig. 1. Early naupliar stages of *Acartia steueri*: a, N I; b, N II; c, N III. Mx 1 = maxillule.

Nauplius II (Fig. 1b)

The body length is 107 μm. N II differs from N I as follows: the antennule bears 4 setae on its distal segment; there are 2 rows of 5 setae each on the posteroventral part of the body (Fig. 3b and 3c), which are uniquely characteristic to N II; the 2 sensory setae in the bud of the caudal rami are longer than in N II; the anus is newly observed behind the 2 sensory setae, elongated from side to side on the edge of the bud of the caudal rami.

Nauplius III (Fig. 1c)

The body length is 124 μm. N III differs from N II as follows: the antennule bears 7 setae on its distal segment; the bud of

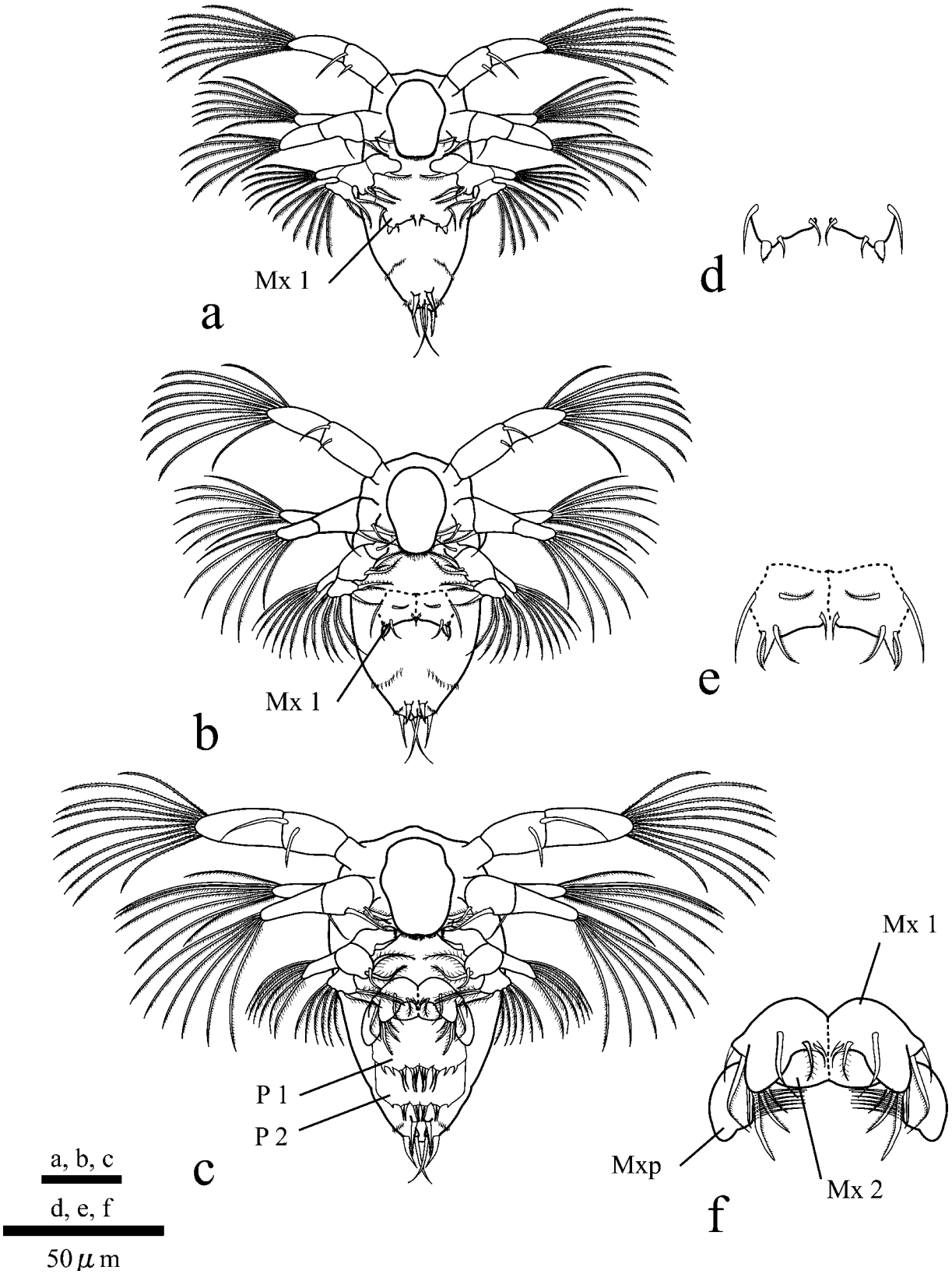

Fig. 2. Late naupliar stages of *Acartia steueri*: a, N IV; b, N V; c, N VI; d, maxillule of N IV; e, maxillule of N V; f, maxillule, maxilla and maxilliped of N VI. Mx 1 = maxillule, Mx 2 = maxilla, Mxp = maxilliped, P 1 = swimming leg 1, P 2 = swimming leg 2.

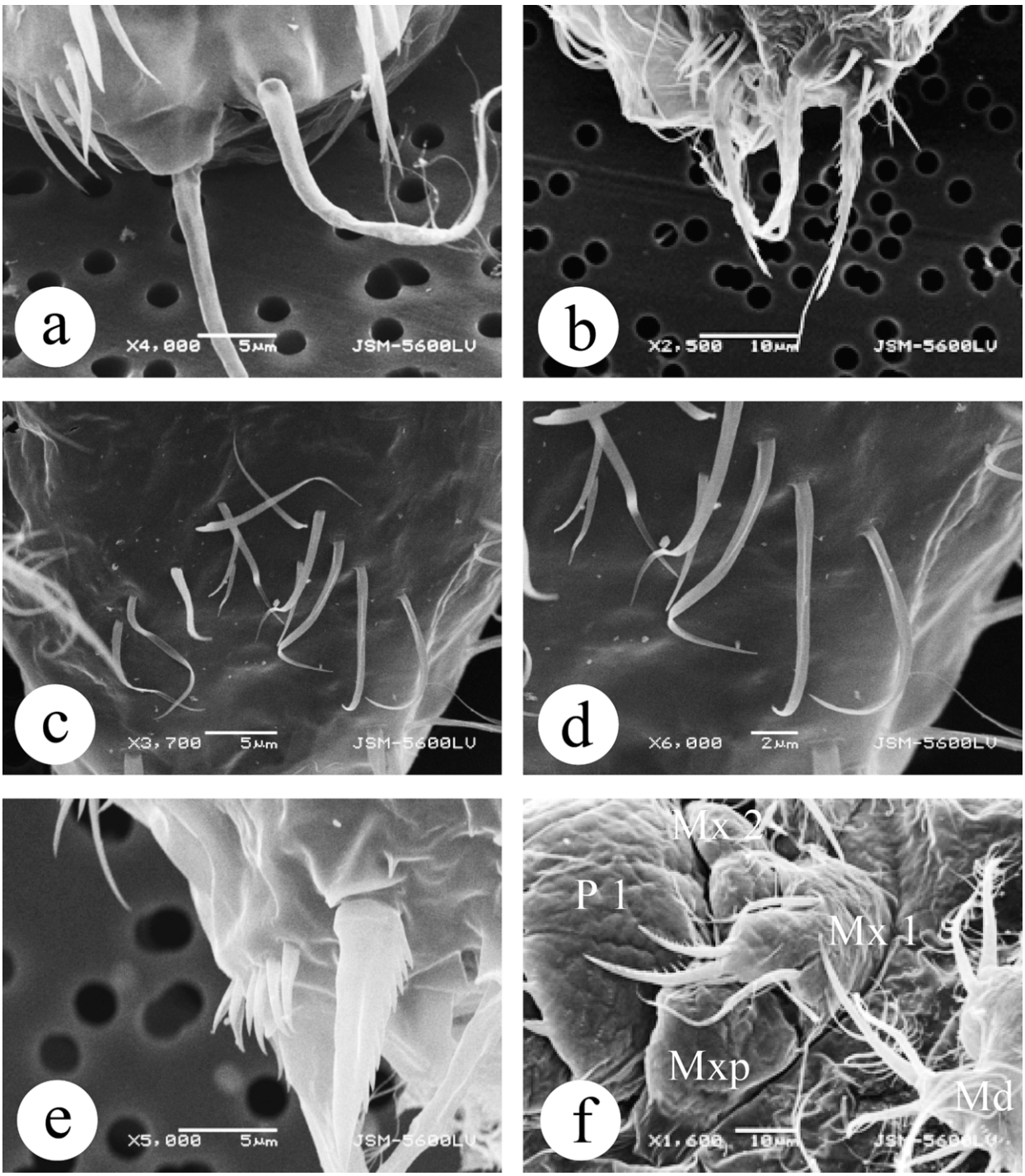

Fig. 3. Detailed structures of the naupliar stages on the body exoskeleton and the appendages of *Acartia steueri*: a, sensory setae on the bud of the caudal rami of N II; b, the bud of the caudal rami of N III; c and d, setae on the posteroventral part of the body; e, the bud of the caudal rami of N IV; f, the maxillule, the maxilla and the maxilliped of N VI. Md = mandible, Mx 1 = maxillule, Mx 2 = maxilla, Mxp = maxilliped.

the maxillule appears as a single seta; the 2 dorsal terminal spines join the sensory setae in the bud of the caudal rami (Fig. 3b), which is now flanked by 2 rows of 9 spinules each.

Nauplius IV (Fig. 2a and 2d)

The body length is 156 μm. N IV differs from N V as follows: the antennule bears 8 setae on its distal segment; the antenna bears 6 setae on its endopod; the mandible bears 3 setae on its basis and 9 setae on its endopod; the bud of the maxillule is expressed as a limb bud with 1 ventral seta, 1 terminal spine and 1 terminal seta, and 1 dorsal seta; 2 ventral terminal spines have been added to the bud of the caudal rami (Fig. 3b).

Table 2. Setae and spines on appendages of naupliar phase of *Acartia steueri*.

Stage:	N I	N II	N III	N IV	N V	N VI
A 1						
No. segments	3	3	3	3	3	3
No. setae	5	6	9	10	11	12
Proximal segment	0	0	0	0	0	0
Middle segment	2	2	2	2	2	2
Distal segment	3	4	7	8	9	10
A 2						
Coxa	1	1	1	1	1	1
Basis	2	2	2	2	2	2
Endopod	4	4	4	6	6	6
Exopod	7	7	7	7	7	7
Md						
Coxa	1	1	1	1	1	1
Basis	2	2	2	3	3	3
Endopod	7	7	7	9	9	9
Exopod	6	6	6	6	6	6
M 1						
Dorsal lobe	0	0	0	1	1	2
Terminal lobe	0	0	1	2	3	4
Ventral lobe	0	0	0	1	2	4
Basis	0	0	0	0	0	0
Endopod	0	0	0	0	0	0
Exopod	0	0	0	0	0	0
M 2						
Basis	0	0	0	0	0	0
Endopod	0	0	0	0	0	0
Exopod	0	0	0	0	0	0
Mxp						
Coxa	0	0	0	0	0	0
Basis	0	0	0	0	0	0
Endopod	0	0	0	0	0	6
Exopod	0	0	0	0	0	0
Caudal rami						
Sensory setae	2	2	2	2	2	2
Dorsal spines	0	0	2	2	2	2
Ventral spines	0	0	0	2	2	2
P 1						
Coxa	0	0	0	0	0	0
Basis	0	0	0	0	0	0
Endopod	0	0	0	0	0	3
Exopod	0	0	0	0	0	4
P 2						
Coxa	0	0	0	0	0	0
Basis	0	0	0	0	0	0
Endopod	0	0	0	0	0	2
Exopod	0	0	0	0	0	3

Nauplius V (Fig. 2b and 2e)

The body length is 183 μm. N V differs from N VI as follows: the antennule bears 9 setae on its distal segment; the bud of the maxillule bears 2 setae on its ventral lobe, 2 spines and 1 seta on its terminal lobe, and 1 seta on its dorsal lobe.

Nauplius VI (Fig. 2c and 2f)

The body length is 202 μm. N VI differs from N V as follows: the antennule bears 10 setae on its distal segment. the bud of the maxillule is well differentiated (Fig. 3f) and bears 4 setae each on its ventral and terminal lobe, and 2 setae on its dorsal lobe; the bud of the maxilla appears as an asetose lobe (Fig. 3f) between the maxillule and the newly appeared maxilliped with its 6 medially directed setae (Fig. 3f); the swimming legs 1 and 2 appear as single continuous lobe and more posteriorly; the swimming leg 1 bear 3 setae on its presumptive endopod, and 4 setae on its presumptive exopod; the swimming leg 2 bears 2 setae on its presumptive endopod, and 3 setae on its presumptive exopod.

Discussion

All six naupliar stages of *Acartia steueri* are described for the first time in this paper. Each stage can be discriminated by the number of seta on the distal segment of the antennule

Table 3. Setae and spines on appendages from N I to N III in *Acartia californiensis*, *A. bifilosa*, and *A. steueri*. N. D. = No data.

Stage:	N I			N II			N III		
Species:	*A. californiensis*	*A. bifilosa*	*A. steueri*	*A. californiensis*	*A. bifilosa*	*A. steueri*	*A. californiensis*	*A. bifilosa*	*A. steueri*
A 1									
No. segments	3	3	3	3	3	3	3	3	3
No. setae	5	5	5	6	6	6	8-9	8	9
Proximal segment	0	0	0	0	0	0	0	0	0
Middle segment	2	2	2	2	2	2	2	2	2
Distal segment	3	3	3	4	4	4	6-7	6	7
A 2									
Coxa	1	N. D.	1	1	N. D.	1	2	N. D.	1
Basis	1	1	2	2	2	2	2	2	2
Endopod	4	3	4	5	4	4	5	11	4
Exopod	5	5	7	5	6	7	5	11	7
Md									
Coxa	1	N. D.	1	1	N. D.	1	1	N. D.	1
Basis	2	2	2	2	2	2	2	2	2
Endopod	6	5	7	7	5	7	7	8	7
Exopod	3	4	6	4	6	6	5	5	6
Mx 1									
External lobe I	0	N. D.	0	0	N. D.	0	1	N. D.	0
External lobe II	0	N. D.	0	0	N. D.	0	0	N. D.	0
Internal lobe I	0	N. D.	0	0	N. D.	0	1	N. D.	0
Internal lobe II	0	N. D.	0	0	N. D.	0	0	N. D.	0
Internal lobe III	0	N. D.	0	0	N. D.	0	0	N. D.	0
Dorsal lobe	0	N. D.	0	0	N. D.	0	0	N. D.	0
Terminal lobe	0	N. D.	0	0	N. D.	0	0	N. D.	1
Ventral lobe	0	N. D.	0	0	N. D.	0	0	N. D.	0
Basis	0	N. D.	0	0	N. D.	0	0	N. D.	0
Endopod	0	N. D.	0	0	N. D.	0	0	N. D.	0
Exopod	0	N. D.	0	0	N. D.	0	0	N. D.	0
Caudal rami									
Sensory setae	2	N. D.	2	2	N. D.	2	2	N. D.	2
Dorsal spines	0	N. D.	0	0	N. D.	0	0	N. D.	2
Ventral spines	0	N. D.	0	0	N. D.	0	2	N. D.	2

(Table 3 and 4). The present findings were compared to the naupliar descriptions of two species belonging to the same subgenus, *Acartia* (*Acanthacartia*) *californiensis* (see Trujillo-Ortiz, 1986) and *A.* (*A.*) *bifilosa* (see Yoon et al., 1998). The naupliar stages of *A.* (*A.*) *tonsa* Dana, 1849 (see Sazhina, 1982) and *A.* (*A.*) *tsuensis* Ito, 1956 (see Takahashi and Ohno, 1996) were excluded from this comparison, because the former was only partially described (Sazhina, 1982), and in the latter the number of setae on the appendages at each developmental stage was not stated (Takahashi and Ohno, 1996). In *A. steueri*, the number of setae on the exopods of the antenna and the mandible do not increase throughout the naupliar phase. The antenna bears 7 setae on its exopod and the mandible bears 6 setae throughout the naupliar phase. In *A.* (*A.*) *californiensis*, the number of setae on the exopods of the antenna and the mandible is 5 and 3 respectively in N I, 5 and 4 in N II, 5 and 5 in N III, 7 and 5 in N IV, 7 and 5 in N V, and 7 and 5 in N VI. In *A.* (*A.*) *bifilosa*, the number of setae on the exopods of these appendages is 5 and 4 in N I, 6 and 6 in N II, 11 and 5 in N III, 11 and 5 in N IV, 10 and 6 in N V, and 8 and 5 in N VI. The nauplii of *A.* (*A.*) *steueri* can thus be distinguished from these by the combination of the number of setae on the exopods of the antenna and mandible.

Morphological details of N VI are remarkably different in *A. steueri* were from those of other species of *Acantha-cartia*: *A.* (*A.*) *californiensis* (see Trujillo-Ortiz, 1986), and *A.* (*A.*) *bifilosa* (see Yoon et al., 1998) (Table 4), as well as *A.* (*A.*) *tsuensis* (see Takahashi and Ohno, 1996). In our study, unlike earlier studies, the naupliar stages of *A.* (*A.*) *steueri* were observed by using both light microscope and SEM. In observing of N VI in *A. steueri* by SEM, both swimming legs 1 and both swimming legs 2 were found to consist of a single continuous lobe (Fig. 4a and 4b), and those of distal end were divided slightly into the right and left legs and the presumptive endopods and exopods (Fig. 4c and 4d). In past descriptions of other species of *Acanthacartia*, both swimming legs 1 and both swimming legs 2 of N VI were illustrated as separated into the right and left legs and/or already divided into the endopod and exopod. The nauplii of copepods are small, and those of congeneric species resemble each other; therefore, it is difficult to establish which morphological characteristics are the key for species-level identification of nauplii. SEM has been employed in the descriptions of many adult acartiid copepods (Belmonte, 1998; Castro-Longoria and Williams, 1999; Soh and Suh, 2000). SEM makes it possible to observe external fine structures in detail, and clarify morphological characteristics. To describe such small naupliar stages in detail and correctly, observations by SEM are an unavoidable necessity.

Table 4. Setae and spines on appendages from N IV to N VI in *Acartia californiensis*, *A. bifilosa*, and *A. steueri*. N. D. = No data.

Stage:	N IV			N V			N VI		
Species:	*A. californiensis*	*A. bifilosa*	*A. steueri*	*A. californiensis*	*A. bifilosa*	*A. steueri*	*A. californiensis*	*A. bifilosa*	*A. steueri*
A1									
No. segments	3	3	3	3	3	3	3	3	3
No. setae	9-10	12	10	10-11	14	11	12-13	15	12
Proximal segment	0	0	0	0	0	0	0	0	0
Middle segment	2	2	2	2	2	2	2	2	2
Distal segment	7-8	10	8	8-9	12	9	10-11	13	10
A2									
Coxa	2	N. D.	1	2	N. D.	1	2	N. D.	1
Basis	2	2	2	2	2	2	2	2	2
Endopod	5	8	6	6	7	6	6	8	6
Exopod	7	11	7	7	10	7	7	8	7
Md									
Coxa	1	N. D.	1	1	N. D.	1	1	N. D.	1
Basis	2	2	3	2	2	3	2	2	3
Endopod	8	9	9	8	9	9	8	9	9
Exopod	5	5	6	5	6	6	5	5	6
Mx 1									
External lobe I	1	N. D.	0	1	N. D.	0	5	N. D.	0
External lobe II	0	N. D.	0	0	N. D.	0	0	N. D.	0
Internal lobe I	2	N. D.	0	1	N. D.	0	2	N. D.	0
Internal lobe II	0	N. D.	0	4	N. D.	0	5	N. D.	0
Internal lobe III	0	N. D.	0	0	N. D.	0	0	N. D.	0
Basis	0	N. D.	1	0	N. D.	2	0	N. D.	4
Endopod	0	N. D.	2	0	N. D.	3	0	N. D.	4
Exopod	0	N. D.	1	0	N. D.	1	0	N. D.	2
Mx 2									
Lobe I	0	N. D.	0	0	N. D.	0	0	N. D.	0
Lobe II	0	N. D.	0	0	N. D.	0	2	N. D.	0
Lobe III	0	N. D.	0	0	N. D.	0	4	N. D.	0
Lobe IV	0	N. D.	0	0	N. D.	0	4	N. D.	0
Lobe V	0	N. D.	0	0	N. D.	0	1	N. D.	0
Dorsal lobe	0	N. D.	1	0	N. D.	1	0	N. D.	2
Terminal lobe	0	N. D.	2	0	N. D.	3	0	N. D.	4
Ventral lobe	0	N. D.	1	0	N. D.	2	0	N. D.	4
Endopod	0	N. D.	0	0	N. D.	0	0	N. D.	0
Exopod	0	N. D.	0	0	N. D.	0	0	N. D.	0
Mxp									
Coxa	0	N. D.	0	0	N. D.	0	2	N. D.	0
Basis	0	N. D.	0	0	N. D.	0	0	N. D.	0
Endopod	0	N. D.	0	0	N. D.	0	0	N. D.	6
Exopod	0	N. D.	0	0	N. D.	0	0	N. D.	0
Caudal rami									
Sensory setae	2	N. D.	2	2	N. D.	2	2	N. D.	2
Dorsal spines	2	N. D.	2	2	N. D.	2	2	N. D.	2
Ventral spines	2	N. D.	2	2	N. D.	2	2	N. D.	2
P 1									
Coxa	0	N. D.	0	0	N. D.	0	0	N. D.	0
Basis	0	N. D.	0	0	N. D.	0	0	N. D.	0
Endopod	0	N. D.	0	0	N. D.	0	4	N. D.	3
Exopod	0	N. D.	0	0	N. D.	0	4	N. D.	4
P 2									
Coxa	0	N. D.	0	0	N. D.	0	0	N. D.	0
Basis	0	N. D.	0	0	N. D.	0	0	N. D.	0
Endopod	0	N. D.	0	0	N. D.	0	7	N. D.	2
Exopod	0	N. D.	0	0	N. D.	0	7	N. D.	3

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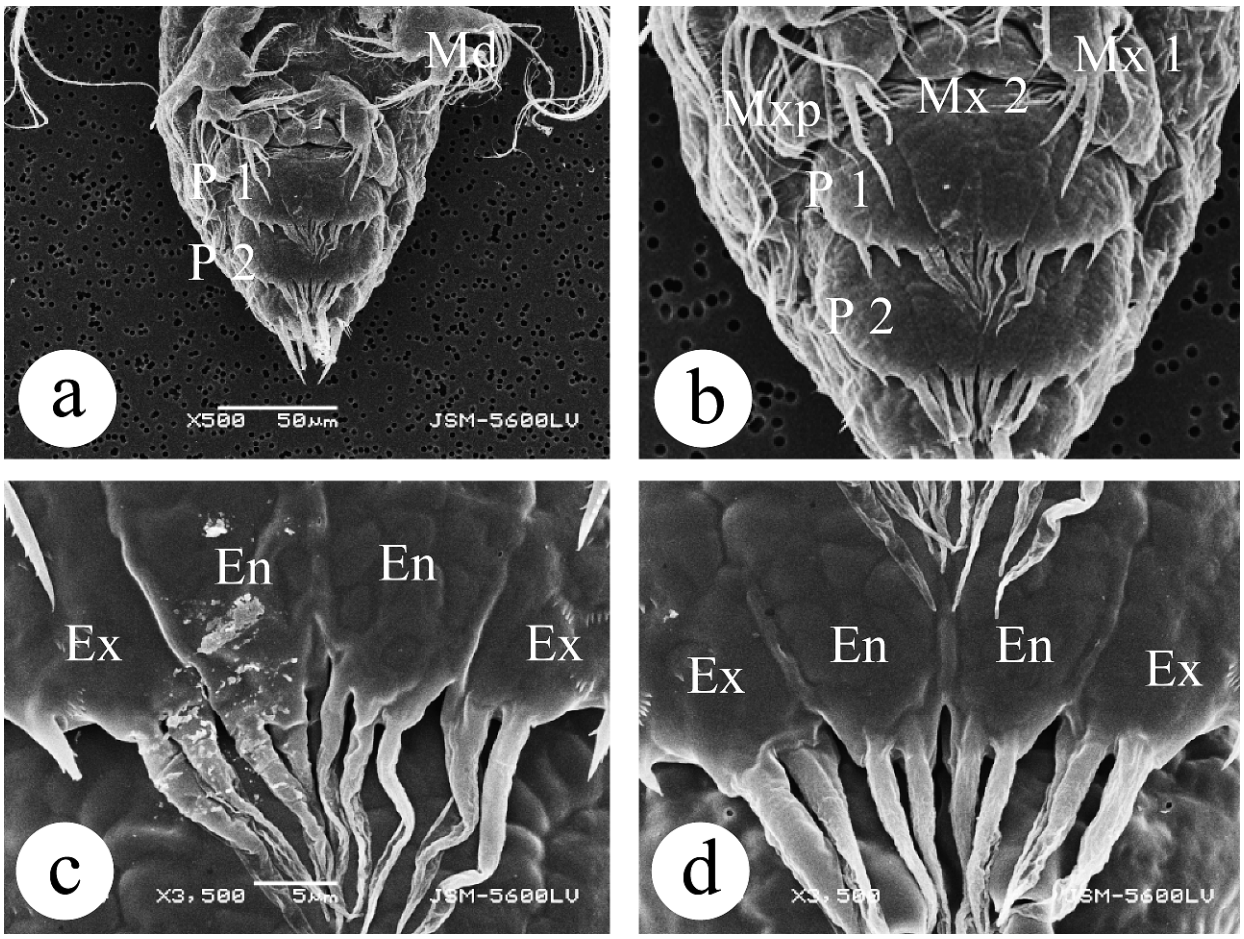

Fig. 4. SEM photographs of the swimming legs 1 and swimming legs 2 of *Acartia steueri*: a, ventral view of N VI; b, the swimming legs 1 and 2; c, the exopods and the endopods of the swimming legs 1; d, the exopods and the endopods of the swimming legs 2. Md = mandible, Mx 1 = maxillule, Mx 2 = maxilla, Mxp = maxilliped, P 1 = swimming leg 1, P 2 = swimming leg 2, Ex = exopod, En = endopod.

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