DESCRIPTIONS OF THE COPEPODID STAGES OF THE MESOPELAGIC COPEPOD, *GAETANUS VARIABILIS* (BRODSKY, 1950) (CALANOIDA, AETIDEIDAE) FROM THE JAPAN SEA

BY

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ABSTRACT

Based on specimens collected from the Japan Sea, all copepodid stages of the mesopelagic copepod, *Gaetanus variabilis* are described and illustrated. Among the family Aetideidae, the development of the body segmentation and of the segmentation of the swimming legs in *G. variabilis* is more similar to that in *Gaetanus kruppii* than to that in *Aetideopsis armata*, *Chiridius gracilis*, or *Euchirella messinensis*. A sharp, spine-like crest on the frontal dorsal surface of the cephalothorax is a characteristic feature of copepodid stages II-IV of *G. variabilis*. This frontal crest of *G. variabilis*, lost in copepodid stages V-VI, is considered as "convergent morphology", relative to *G. kruppii*. Nucleotide sequences of the mitochondrial 16S rRNA gene confirmed that copepodid stages II and III with frontal crest and copepodid stage VI without frontal crest are the same species: *Gaetanus variabilis*. In the adult male, the mandible, maxillule, and maxilla degenerate, whence no feeding takes place: a phenomenon commonly seen in aetideid copepods.

RÉSUMÉ

A partir de specimens recoltés dans la mer du Japon, tous les stades copépodites du copépode méso-pélagique *Gaetanus variabilis* sont décrits et illustrés. Parmi la famille des Aetideidae, le développement de la segmentation corporelle et de la segmentation des pattes natatoires chez *G. variabilis* est plus semblable à ceux de *Gaetanus kruppi* qu'à ceux de *Aetideopsis armata*, *Chiridius gracilis* ou *Euchirella messinensis*. Une épine acérée en forme de crête sur la surface dorso-frontale du céphalothorax est caractéristique des stades copépodites II-IV chez *G. variabilis*. Cette crête frontale, perdue chez les stades copépodites V-VI, est considérée comme une "convergence morphologique" avec *G. kruppi*. La séquence des nucléotides du gêne mitochondrial 16S rRNA confirme que les stades copépodites II et III avec crête frontale et le stade copépodite VI sans crête frontale sont de la même espèce: *Gaetanus variabilis*. Chez les mâles adultes, les mandibules,

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Crustaceana 78 (7): 819-837

maxillules et maxilles dégénèrent, d'où une absence d'alimentation, un phénomène communément observé chez les copépodes Aetidéidés.

INTRODUCTION

Gaetanus variabilis (Brodsky, 1950) is a medium-sized calanoid copepod (Aetideidae) distributed throughout the mesopelagic zones of the Subarctic Pacific, the Bering Sea, the Sea of Okhotsk, and the Japan Sea (Brodsky, 1950; Tanaka, 1957; Tanaka & Omori, 1970). *G. variabilis* is indeed one of the dominant copepods in the mesopelagic realm of the Japan Sea (Sazhin & Vinogradov, 1979). This species was first classified in the genus *Gaidius* Giesbrecht, 1895 since it lacks a cephalic crest (Brodsky, 1950). Later, the genus *Gaidius* was regarded a synonym of *Gaetanus* Giesbrecht, 1888 because of close similarities in morphological features excepting the presence of the cephalic crest (Park, 1975; Markhaseva, 1996). While all copepodid stages of some aetideid copepods have been described by several authors (Matthews, 1964; MacLellan & Shih, 1974; Shih et al., 1981), currently available descriptions for *Gaetanus* species pertain to copepodid stages III-VI only (Mazza, 1965).

This paper aims to describe all copepodid stages of *Gaetanus variabilis*, based on specimens collected at four oceanic stations in the Japan Sea. In addition to morphological accounts, the nucleotide sequences of the mitochondrial 16S rRNA gene (272 bp) was analysed for several developmental stages to confirm conspecific affiliation. Developmental patterns in the segmentation of both body and swimming legs are compared with those of other aetideid copepods.

MATERIALS AND METHODS

Field sampling

Zooplankton samples were collected at St. C-8 (42°30′N 137°30′E) on 11-12 January 1997 and at St. J-7 (37°00′N 131°30′E) on 26-27 January 1997 on board the R/V "Kaiyo-Maru", and at St. HO97103 (40°48′N 138°19′E) and St. HO97104 (40°48′N 138°19′E), both on 19 September 1997 on board the T/S "Hokusei-Maru" (table I, fig. 1), all in the Japan Sea. Samplings were made with a closing net (60 cm mouth diameter, 0.1 mm mesh, cf. Kawamura, 1989) equipped with a Rigosha flow-meter in the mouth of the net, and a TSK Depth Distance Recorder (Tsurumi Seiki, Yokohama) or RMD Depth meter (Rigosha, Tokyo) on a suspender rope of the net. The net was towed vertically at a speed of 1 m·s^{-1} through four or five discrete depth strata from 2000 m (St. J-7, HO97103, and HO97104) or 3000 m depth (St. C-8) to the surface, mostly at night (one exception was daytime

TABLE I
Stratified sampling data with the closing net in the Japan Sea

Date	Time (local time)	Station	Location	Vessel	Sampling layer (number of stratified samples)
11-12 January 1997	2330-0340	C-8	42°30′N 137°30′E	“Kaiyo-Maru”	0-100, 100-500, 500-1000, 1000-2000, 2000-3000 m (5)
26-27 January 1997	2340-0350	J-7	37°00′N 131°30′E	“Kaiyo-Maru”	0-200, 200-500, 500-1000, 1000-2000 m (4)
19 September 1997	0040-0400	HO97103	40°48′N 138°19′E	“Hokusei-Maru”	0-100, 100-250, 250-500, 500-1000, 1000-2000 m (5)
19 September 1997	0810-1030	HO97104	40°48′N 138°19′E	“Hokusei-Maru”	0-100, 100-250, 250-500, 500-1000, 1000-2000 m (5)
5 December 2003	2246-2358	Y	38°20′N 138°04′E	“Mizuho-Maru”	600-1500 m used for molecular analysis

sampling at St. HO97104). After collection, zooplankton samples were preserved immediately in 5% formalin-seawater buffered with borax.

Identification and drawing of specimens

In the land laboratory, *Gaetanus variabilis* specimens were sorted from the entire samples. Descriptions of developmental stages other than the adults are not available for this species. To identify the copepodid stages, we referred to descriptions of copepodids of other species of the family Aetideidae, i.e., *Aetideopsis armata* (Boeck, 1872) (= *Chiridius armatus*) and *Bradyidius bradyi* (G.O. Sars, 1902) (cf. Matthews, 1964), and *Chiridius gracilis* Farran, 1908 (cf. MacLellan & Shih, 1974). Based on the presence (males) or absence (females) of a fifth pair of swimming legs, identification into males and females was made for copepodid stages IV (CIV) to adult (CVI). The mesh size of the nets used (0.10 mm) in this study was small enough to retain the stages CI through adult of *G. variabilis* (diagonal distance of the mesh is 0.14 mm, as compared with the prosome width of 0.20 mm for CI).

Intact specimens of *Gaetanus variabilis* of the stages CI, CII, CIII, CIV female (CIV F), CIV male (CIV M), CV F, CV M, CVI F, and CVI M were transferred to glycerine on microscope slides. Prosome length was measured from lateral view in 30 specimens under a dissecting microscope. Specimens used for length measurements were those from St. HO97103, where *G. variabilis* occurred most

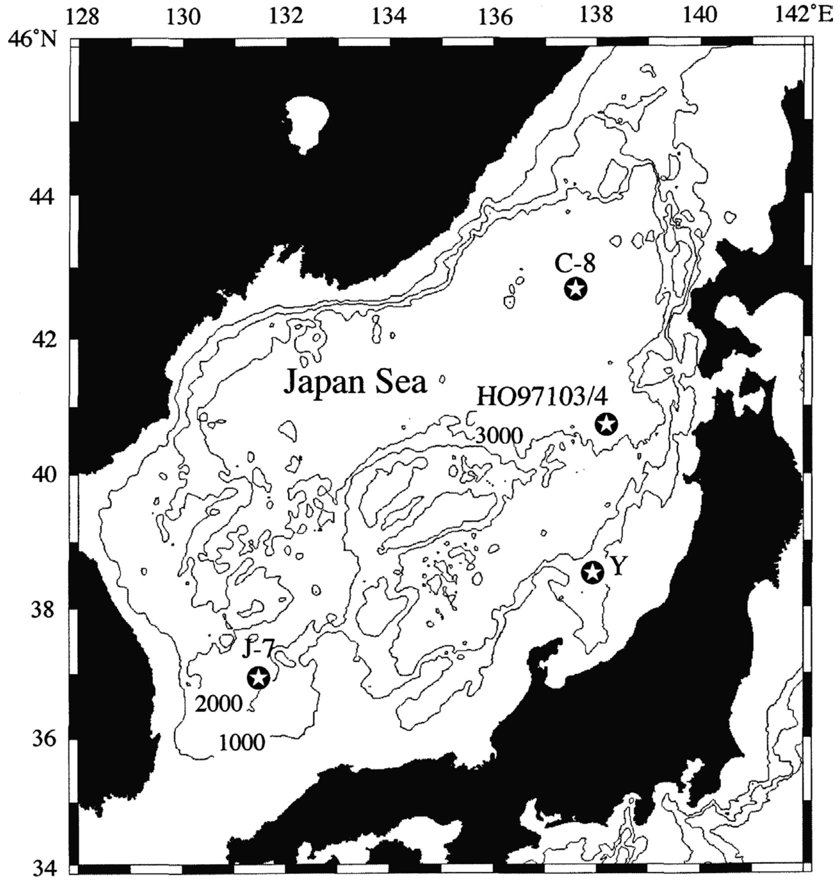


Fig. 1. Location of sampling stations St. C-8, J-7, HO97103, HO97104, and Y in the Japan Sea. Bathymetric contours (1000, 2000, and 3000 m) are superimposed.

abundantly. Specimens were dissected in glycerine. Dissected appendages were immersed in a drop of glycerine on a cover slip for observation. All drawings were made with the aid of a camera lucida. Some plumosity on the setae has been omitted. Morphological terms used in this study are mainly those of Huys & Boxshall (1991).

Nucleotide sequencing of the 16S rRNA gene

Additional zooplankton samples were collected at 600-1500 m at St. Y (38°20′N 138°00′E) with a 0.33 mm PCP closing net on 5 December 2003 (fig. 1, table I). Samples were preserved in 95% ethanol and stored at $<10°C$ in the dark. A batch of CII (5 specimens), and CIII (3), or single specimens of CVI F of *Gaetanus variabilis* were rehydrated in distilled water for 10-12 h and homogenized using a grinder. A 100 μl quantity of homogenate of rehydrated specimens was mixed with

200 μl of 5% Chelex 100 (Sigma) and incubated for 30 min. at 56°C and then for 8 min. in boiling water. The Chelex-treated homogenate was centrifuged for 5 min. at 20,000 *g*, and the supernatant was stored at −30°C before PCR amplification. The 16S rRNA gene was amplified from Chelex-treated homogenates with the primers 16S-arL (Palumbi & Benzie, 1991) and 16S-CB (Braga et al., 1999). The 100 μl of PCR mixture comprised the following: 10 μl of Chelex-treated supernatant including mtDNA, 1× PCR buffer, 200 μM of each dNTPs, 1.5 mM $MgCl_2$, 0.2 μM 16S-arL and 16S-CB primer set, and 2.5 U of "Taq" DNA polymerase (Promega). The PCR conditions were as follows: initial denaturation for 5 min. at 96°C, followed by 30 cycles of denaturation (96°C for 1 min.), annealing (50°C for 1.5 min.), and extension (72°C for 2 min.). PCR products were purified for sequencing by the Wizard PCR Preps kit (Promega) and directly sequenced using an ABI Prism 310 Genetic Analyzer.

RESULTS

Description of copepodid stages

Copepodid stage I (figs. 2, 11, 18, 27, 36, 45, 54, 63, and 72)

Prosome length 0.74 ± 0.02 mm. Body 5-segmented. Prosome composed of cephalothorax and 2-segmented metasome, with rounded posterior margin. Urosome 2-segmented. Second urosomal somite twice the length of the first. Ratio of prosome to urosome about 4.

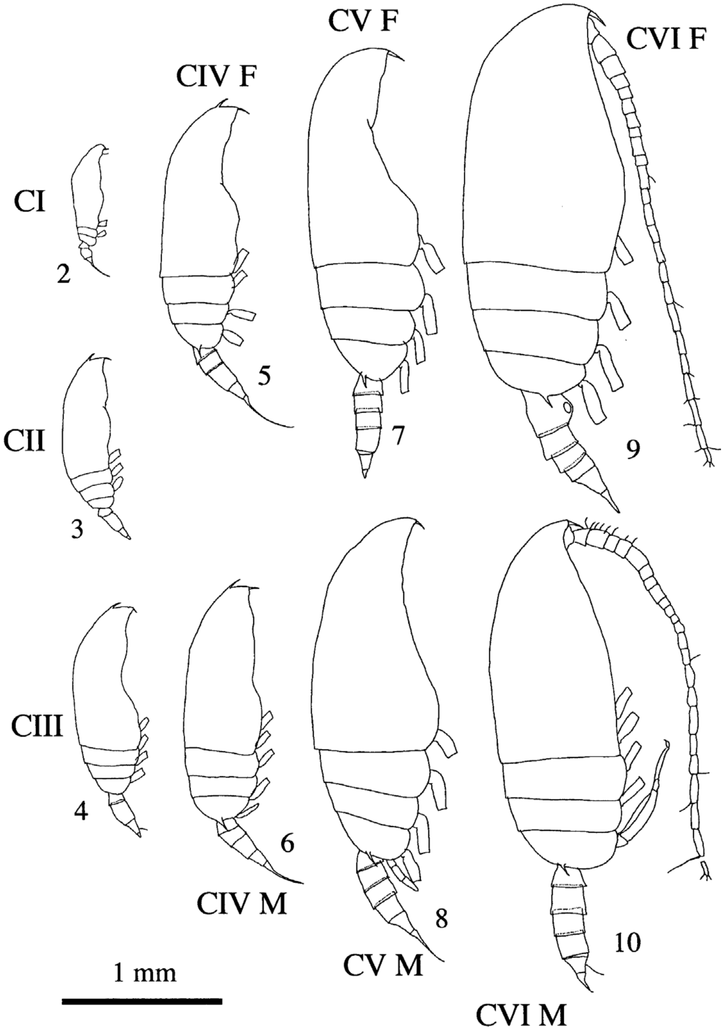
Antennule 10-segmented. Antenna with coxa, basis, 2-segmented endopod, and 7-segmented exopod. Mandible with coxa, basis, small 2-segmented endopod, and 4-segmented exopod; mandibular gnathobase with seven teeth. Maxillule constructed from non-segmented arthrite, endite, endopod, exopod, and small epipodite. Maxilla with five endites and unimerous endopod. Endopod of maxilliped 2-segmented.

P1 and P2 with 1-segmented rami. Formula for armature as follows (Roman and Arabic numerals representing spines and setae, respectively) (see table II).

P3 (lateral bud) to P5 absent.

TABLE II

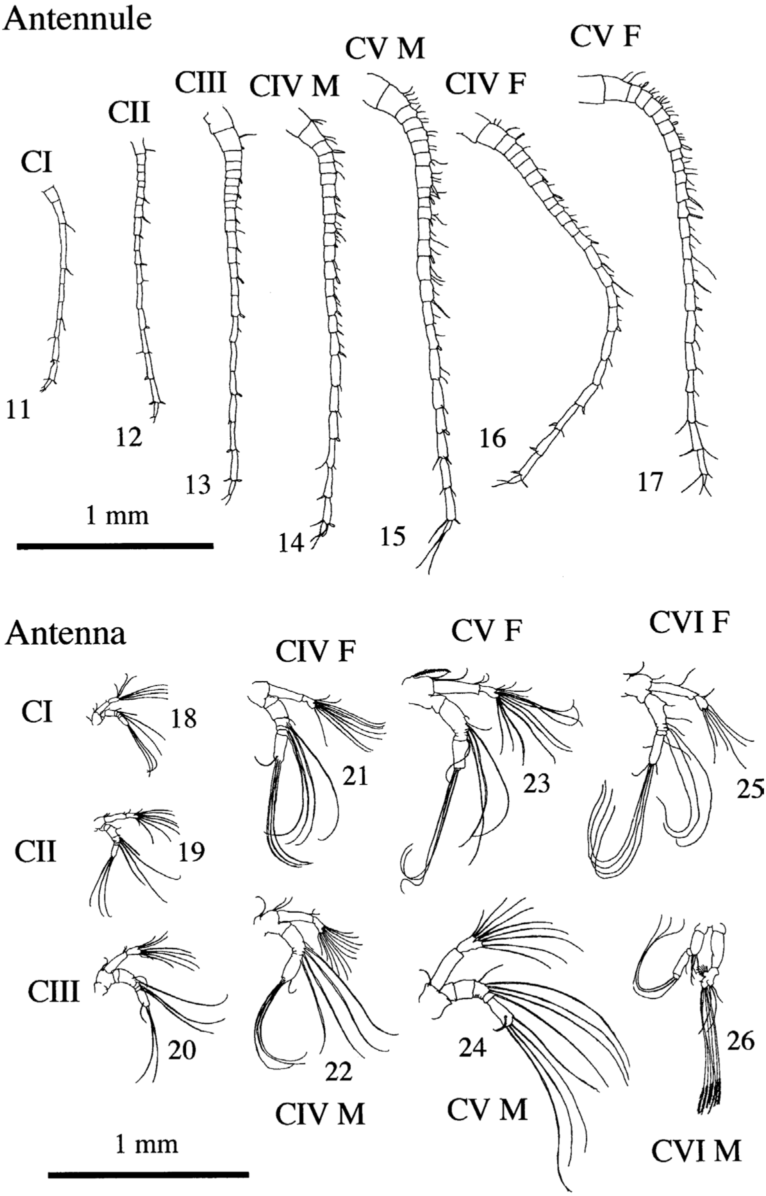
	Coxa	Basis	Exopod	Endopod
P1	0-0	0-1	II, 4	5
P2	0-0	0-0	III, I, 3	6



Figs 2-10. *Gaetanus variabilis* (Brodsky, 1950). Copepodid stage I (CI), CII, CIII, CIV female (CIV F), CIV male (CIV M), CV F, CV M, CVI F, and CVI M in lateral view. Antennules are shown in CVI F and CVI M.

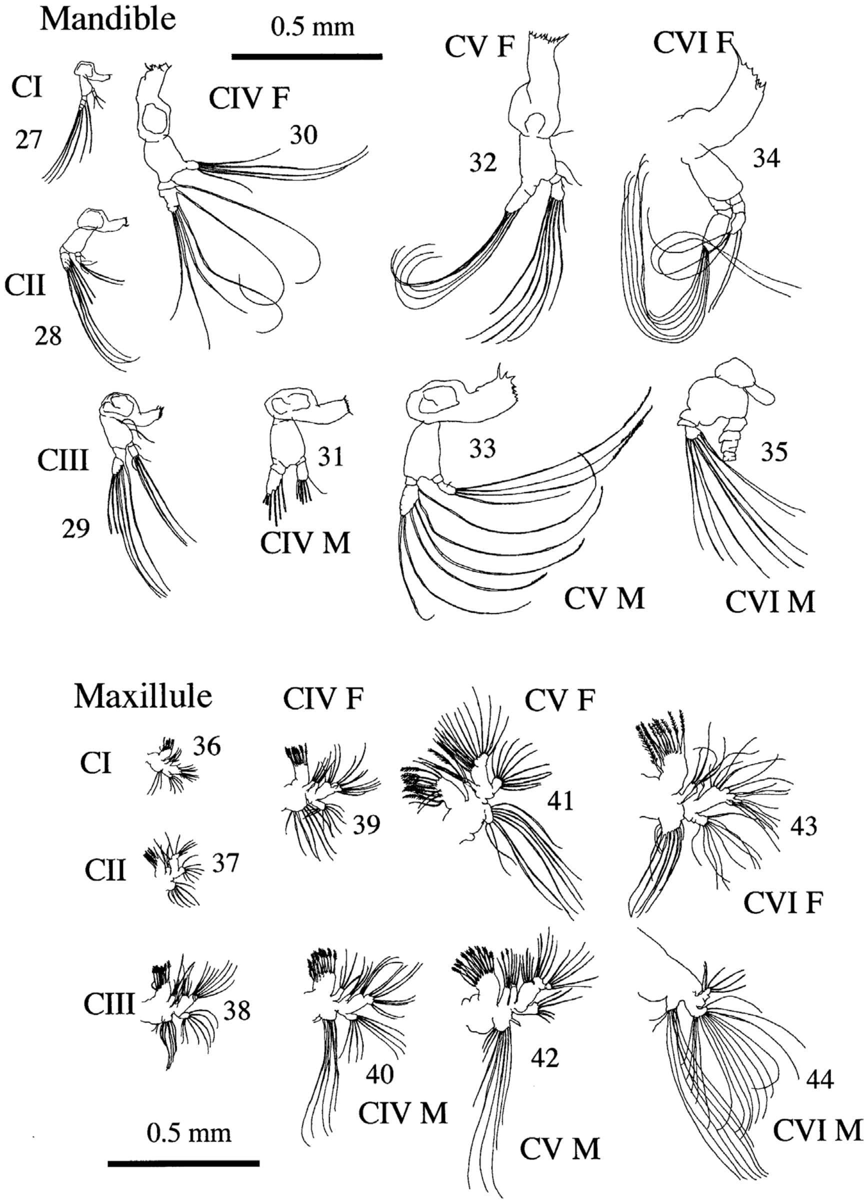
Copepodid stage II (figs. 3, 12, 19, 28, 37, 46, 55, 64, 73, 81)

Prosome length 1.05 ± 0.05 mm. Body 6-segmented. Prosome composed of cephalothorax and 3-segmented metasome, with rounded posterior margin. Sharply pointed, small spine-like crest present on anterior dorsal surface of cephalothorax. Urosome 2-segmented. Second urosomal somite twice the length of the first. Ratio of prosome to urosome about 4.



Figs 11-26. *Gaetanus variabilis* (Brodsky, 1950). 11-17, antennule: copepodid stage I (CI), CII, CIII, CIV female (CIV F), CV F, CIV male (CIV M), and CV M; 18-26, antenna: CI, CII, CIII, CIV F, CIV M, CV F, CV M, CVI F, and CVI M.

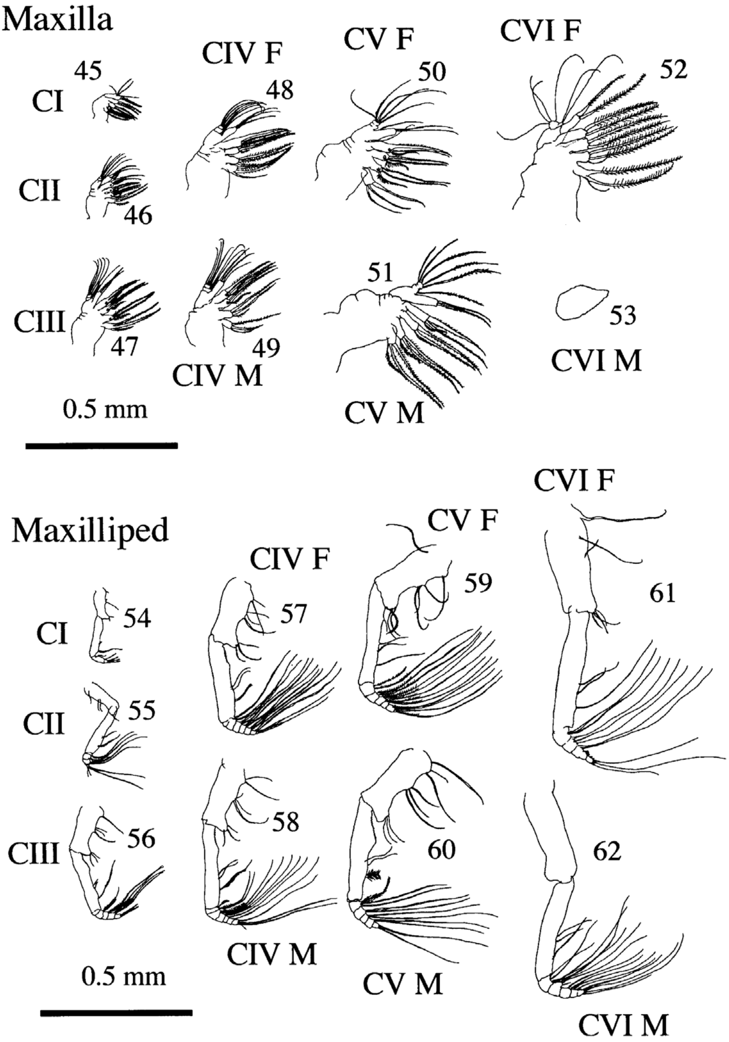
Antennule 17-segmented. Mandible with coxa, basis, 2-segmented small endopod, and 5-segmented exopod; mandibular gnathobase with seven teeth. Maxilla with five endites and 3-segmented endopod. Endopod of maxilliped 3-segmented.



Figs 27-44. *Gaetanus variabilis* (Brodsky, 1950). 27-35, mandible: copepodid stage I (CI), CII, CIII, CIV female (CIV F), CIV male (CIV M), CV F, CV M, CVI F, and CVI M; 36-44, maxillule: CI, CII, CIII, CIV F, CIV M, CV F, CV M, CVI F, and CVI M.

P1, P2, and P3 with 1-segmented rami. Formula for armature as follows (see table III).

P4 (lateral bud) and P5 absent.

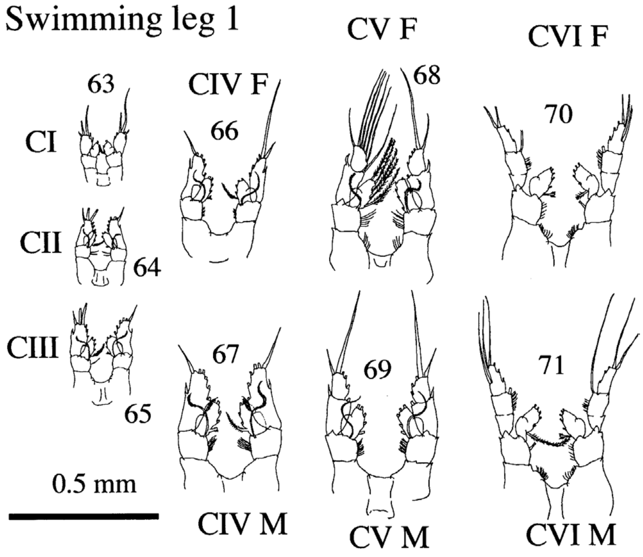


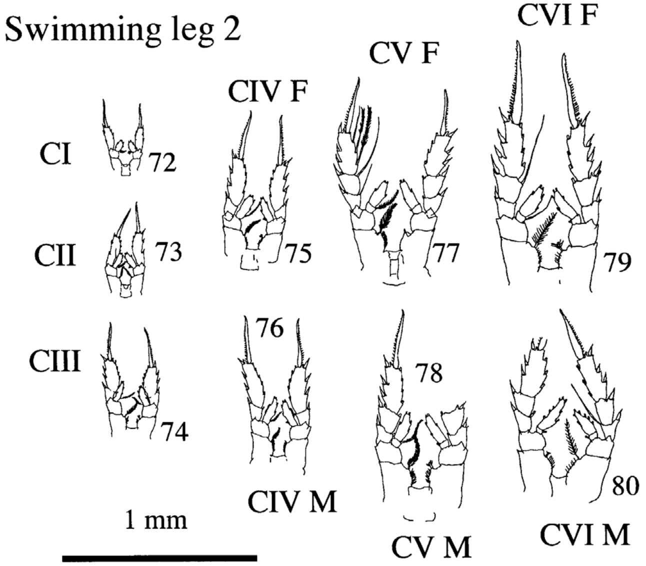
Figs 45-62. *Gaetanus variabilis* (Brodsky, 1950). 45-53, maxilla: copepodid stage I (CI), CII, CIII, CIV female (CIV F), CIV male (CIV M), CV F, CV M, CVI F, and CVI M; 54-62, maxilliped: CI, CII, CIII, CIV F, CIV M, CV F, CV M, CVI F, and CVI M.

Copepodid stage III (figs. 4, 13, 20, 29, 38, 47, 56, 65, 74, 82, 89)

Prosome length 1.39 ± 0.07 mm. Body 6-segmented. Prosome composed of cephalothorax and 3-segmented metasome, with rounded posterior margin. Sharply pointed, small spine-like crest present on anterior dorsal surface of cephalothorax. Urosome 2-segmented. Second urosomal somite twice the length of the first. Ratio of prosome to urosome about 4.

Antennule 22-segmented. Endopod of maxilliped 4-segmented.

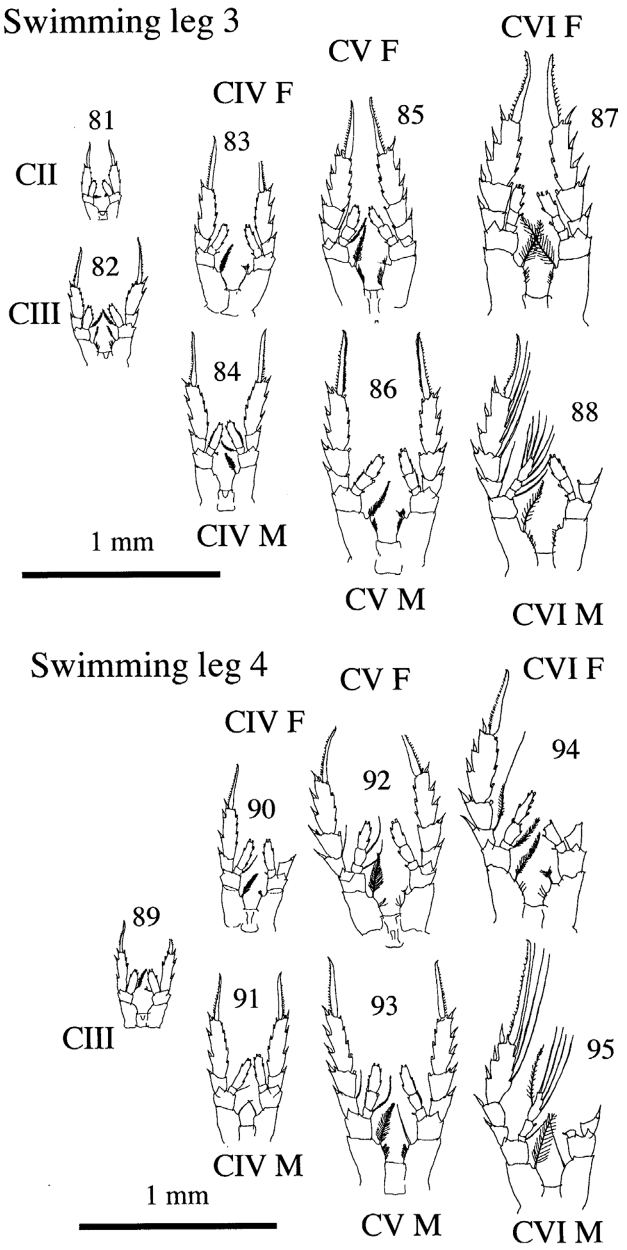




Figs 63-80. *Gaetanus variabilis* (Brodsky, 1950). 63-71, swimming leg 1: copepodid stage I (CI), CII, CIII, CIV female (CIV F), CIV male (CIV M), CV F, CV M, CVI F, and CVI M; 72-80, swimming leg 2: CI, CII, CIII, CIV F, CIV M, CV F, CV M, CVI F, and CVI M.

P1, P2, and P4 with 1-segmented rami. Segmentation of P2 exopod fused and obscure. Exopod of P3 2-segmented. Formula for armature as follows see (table IV).

P5 (lateral bud) absent.



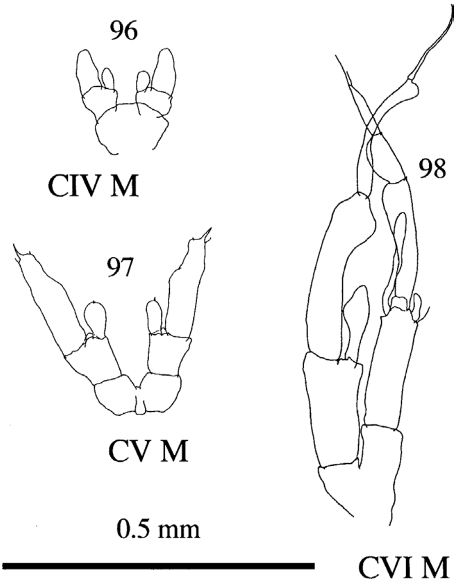
Figs 81-95. *Gaetanus variabilis* (Brodsky, 1950). 81-88, swimming leg 3: copepodid stage II (CII), CIII, CIV female (CIV F), CIV male (CIV M), CV F, CV M, CVI F, and CVI M; 89-95, swimming leg 4: CIII, CIV F, CIV M, CV F, CV M, CVI F, and CVI M.

TABLE III

	Coxa	Basis	Exopod	Endopod
P1	0-0	0-1	II, 5	5
P2	0-1	0-0	III, I, 4	6
P3	0-0	0-0	III, I, 3	6

TABLE IV

	Coxa	Basis	Exopod	Endopod
P1	0-0	0-1	II, 5	5
P2	0-1	0-0	IV, I, 6	6
P3	0-1	0-0	I-0; II, I, 4	0-1; 6
P4	0-0	0-0	III, I, 3	6



Figs 96-98. *Gaetanus variabilis* (Brodsky, 1950). 96-98, swimming leg 5: copepodid stage IV male (CIV M), CV M, and CVI M.

Copepodid stage IV (female: figs. 5, 16, 21, 30, 39, 48, 57, 66, 75, 83, 90; male: figs. 6, 14, 22, 31, 40, 49, 58, 67, 76, 84, 91, 96)

Prosome length 1.92 ± 0.05 mm (female), 2.0 ± 0.10 mm (male). Sexes distinguishable on appearance of P5 in male. Body 7-segmented. Prosome composed of cephalothorax and 3-segmented metasome, with pointed posterior margin. Sharply

TABLE V

	Coxa	Basis	Exopod	Endopod
P1	0-0	0-1	II, 5	5
P2	0-1	0-0	I-0; IV, I, 5	6
P3	0-1	0-0	I-0; III, I, 5	0-1; 6
P4	0-1	0-0	I-0; III, I, 5	0-1; 6
P5 (male)	0-0	0-0	0	0

pointed, small, spine-like crest present on anterior dorsal surface of cephalothorax. Urosome 3-segmented. Third urosomal somite the longest. Ratio of prosome to urosome about 3.7 in female and 3.3 in male.

Antennule 23-segmented, with fusions at 8th-9th and 24th-25th segments. Endopod of maxilliped 5-segmented.

P1 and P5 of male with 1-segmented rami. Exopods of P2, P3, and P4 are 2-segmented. Endopods of P3 and P4 2-segmented. Hairs abundant on inner margin of coxa of P1 and P2. Formula for armature as follows (see table V).

Copepodid stage V (female: figs. 7, 17, 23, 32, 41, 50, 59, 68, 77, 85, 92; male: figs. 8, 15, 24, 33, 42, 51, 60, 69, 78, 86, 93, 97)

Prosome length 2.72 ± 0.07 mm (female), 2.68 ± 0.12 mm (male). Sexes distinguishable on appearance of P5 in male. Body 8-segmented. Prosome composed of cephalothorax and 3-segmented metasome, with pointed posterior margin. Anterior dorsal surface of cephalothorax smoothly rounded (sharply pointed, spine-like crest observed during CII-CIV now rudimentary only). Urosome 4-segmented. Length of urosomal somites nearly equal. Ratio of prosome to urosome about 3.5 in female and 3.3 in male.

Antennule 23-segmented, with fusions at 8th-9th and 24th-25th segments. Endopod of maxilliped 5-segmented.

P5 of male with 1-segmented rami. Segmentation of exopod and endopod 2 and 1 for P1, 3 and 2 for P2, and 3 and 3 for P3 and P4, respectively. Formula for armature as follows (see table VI).

Adult female (CVI F) (figs. 9, 25, 34, 43, 52, 61, 70, 79, 87, 94)

Prosome length 3.09 ± 0.10 mm. Body 8-segmented. Prosome composed of cephalothorax and 3-segmented metasome, with pointed posterior margin. Anterior dorsal surface of cephalothorax smoothly rounded (sharply pointed, spine-like crest observed during CII-CIV now rudimentary). Urosome 4-segmented. Length of urosomal somites nearly equal. Ratio of prosome to urosome about 3.0.

TABLE VI

	Coxa	Basis	Exopod	Endopod
P1	0-0	0-1	I-1; I, 4	5
P2	0-1	0-0	I-1; I-1; III, I, 4	0-1; 5
P3	0-1	0-0	I-1; I-1; III, I, 4	0-1; 0-1; 5
P4	0-1	0-0	I-1; I-1; III, I, 4	0-1; 0-1; 5
P5 (male)	0-0	0-0	I	0

TABLE VII

	Coxa	Basis	Exopod	Endopod
P1	0-0	0-1	I-1; I, 4	5
P2	0-1	0-0	I-1; I-1; III, I, 4	0-1; 5
P3	0-1	0-0	I-1; I-1; III, I, 4	0-1; 0-1; 5
P4	0-1	0-0	I-1; I-1; III, I, 4	0-1; 0-1; 5

Antennule symmetrical, 23-segmented with fusions of 8th-9th and 24th-25th segments, and reaching to tip of metasomal process.

Segmentation of exopod and endopod 2 and 1 for P1, 3 and 2 for P2, and 3 and 3 for P3 and P4, respectively. Exopod of P1 with obscure segmentation in first segment. Formula for armature as follows (see table VII).

Adult male (CVI M) (figs. 10, 26, 35, 44, 53, 62, 71, 80, 88, 95, 98)

Prosome length 2.77 ± 0.08 mm. Body 9-segmented. Prosome composed of cephalothorax and 3-segmented metasome, with pointed posterior margin. Anterior dorsal surface of cephalothorax smoothly rounded (sharply pointed, spine-like crest observed during CII-CIV now rudimentary). Urosome 5-segmented. Last urosomal somite very short. Ratio of prosome to urosome about 3.3.

Antennule symmetrical, 23-segmented with fusions of 8th-9th and 24th-25th segments, and reaching to tip of metasomal process. Feeding appendages of adult male degenerated, gnathobase of mandible degenerated to a weak and toothless remnant, maxillule of small size and all inner lobes degenerated, maxilla of small size and entire appendage reduced to a small, bulb-like structure bearing several lobular processes without setae.

Segmentation of P1-P4 similar to that of adult female. P5 asymmetrical. Exopod of P5 3-segmented for left and 2-segmented for right appendage. Endopod unimerous. Lobe-like structure and one small seta present on left outer margin of basis of P5.

Nucleotide sequence of the 16S rRNA gene

Partial sequences (272 bp) of the 16S rRNA gene of CII (n = 1), CIII (n = 1) and CVI F (n = 2) revealed a perfect match (no difference in the sequence). All these data are deposited in the GenBank/EMBL/DDBJ database under accession number: AY940161. This result, as compared with interspecific variations of the same gene in the order of 7-24% for *Calanus* spp. (cf. Bucklin et al., 1995) or 5-7% for *Neocalanus* spp. (cf. Taniguchi et al., 2004), suggest that the CII, CIII, and CVI F specimens are indeed monospecific (= *Gaetanus variabilis*).

DISCUSSION

For the purpose of an accurate description of the morphological development of copepods, laboratory-rearing is the best method (cf. Mauchline, 1998). Yamaguchi & Ikeda (2000) successfully raised *Gaetanus variabilis* (= *Gaidius variabilis*) eggs to CI, but further development beyond CI was unsuccessful due to the difficulty of providing appropriate food (CI is the first feeding stage). To date, successful laboratory raising of an aetideid copepod, i.e., *Aetideopsis armata* (= *Chiridius armatus*) from eggs to adults was achieved only by Matthews (1964), who used a mixture of phytoplankton (*Phaeodactylum tricornutum* Bohlin) and zooplankton (*Artemia* nauplii) as staple food in his experiments. Because of our use of field-collected specimens instead of laboratory-raised specimens, it can be argued that possible inclusion of aetideid copepods other than *G. variabilis* in the present study cannot be ruled out. However, we are quite confident that this is not the case for the following reasons.

As a marginal sea of the northern Pacific Ocean, the pelagic fauna of the Sea of Japan is characterized as species-poor (cf. Zenkevitch, 1963). All previous studies on aetideid copepods in the Japan Sea are consistent in that *Gaetanus variabilis* is the most numerous aetideid species. In addition to *G. variabilis*, *G. brevispinus* (G.O. Sars, 1902) (cf. Brodsky, 1950), *G. simplex* Brodsky, 1950 (cf. Sazhin & Vinogradov, 1979), *Gaetanus* sp. (cf. Hirakawa et al., 1990), and *Chiridius gracilis* (cf. Dolganova et al., 1999) have also been reported. Since *G. brevispinus* (total length of CVI F = 4.0-4.8 mm) is much larger than *G. variabilis* (3.2-3.6 mm, cf. Brodsky, 1950), there is little chance to confuse them. Sazhin & Vinogradov (1979) noted that *G. simplex* was distributed at 300-400 m depth at a station (41°22′N 136°06′E) near station C-8 of this study. While sampling seasons are different between Sazhin & Vinogradov's (June) and our surveys (January), no *G. simplex* occurred in our samples down to 3000 m depth. The morphology of *G. simplex* (presence of a spine-like crest in adults) is different from that of *G. variabilis* (no spine-like crest in adults). The *Gaetanus* sp. reported by Hirakawa et al. (1990)

from Toyama Bay, southern Japan Sea, is in fact stage CII-CIV of *G. variabilis* (cf. K. Hirakawa, pers. comm.). *C. gracilis*, found in waters around Yamato-Rise (central Japan Sea) is thought to be a warm-water species brought along with the Tsushima Warm Current (Dolganova et al., 1999). *C. gracilis* (total length of CVI F = 2.2-2.9 mm) is much smaller than *G. variabilis*. The two species could not be confused. According to a recent study, a total of eight aetideid copepods occurs in the Japan Sea, and *G. variabilis* contributes >96% of these total aetideid numbers (Hashizume & Shinagawa, 2003). For these reasons, we believe that confusion with other aetideids in identifying *G. variabilis* specimens in the present study is highly unlikely. The perfect match of the nucleotide sequences of the 16S rRNA gene in this study, supports our conclusion even further.

While copepodid stages of aetideid copepods have been described by several authors (Matthews, 1964; Mazza, 1965; MacLellan & Shih, 1974; Shih et al., 1981), only descriptions from CIII onward are available for a species of *Gaetanus* (Mazza, 1965). Among the species of *Chiridius*, the development of the segmentation of body and swimming legs is similar (MacLellan & Shih, 1974). The segmentation of the antennule during the development of *G. variabilis* is similar to that of *Chiridius* species (table VIII), though the segmentation pattern of the swimming legs is different between these two genera. In *Chiridius*, the exopod of P1 and P2 is 2-segmented in CII, but it is unimerous in the same stage of *Gaetanus*. While the exopod of P1-P3 is 2-segmented in CIII of *Chiridius*, a 2-segmented exopod is only observed for P3 in CIII of *Gaetanus* (table VIII). The development in segmentation of the swimming legs of *Chiridius* is faster than that of *Gaetanus*. As to the segmental development of the swimming legs of aetideid species given in table VIII, a species showing a pattern similar to that of *G. variabilis* is *Gaetanus kruppii* Giesbrecht, 1903 from the Mediterranean Sea (Mazza, 1965), except for the segmentation of the exopod of P2 in CIII and the exopod of P1 in CVI (cf. table VIII).

Degeneration of the feeding appendages in CVI M *Gaetanus variabilis* is a phenomenon commonly seen throughout aetideid copepods (Matthews, 1964; MacLellan & Shih, 1974; Shih et al., 1981). Degeneration of the mouthparts implies termination of feeding at CV M, resulting in loss of body weight during the moult to CVI M (cf. Yamaguchi & Ikeda, 2000).

The presence of a sharp, spine-like crest on the anterior dorsal surface of the cephalothorax is observed only in CII-CIV in *Gaetanus variabilis*. As viewed from the developmental patterns in the swimming legs, *G. variabilis* is closer to other *Gaetanus* species than to *Aetideopsis*, *Chiridius*, *Euchirella*, and *Bradyidius* (table VIII). Because the spine-like crest on the cephalothorax is characteristic for *Gaetanus* species, the spine-like crest of CII-CIV *G. variabilis* is considered as a morphological convergence in *Gaetanus* species. Developmental change in

Table VIII

Inter-species comparison in numbers of segments of antennule and swimming legs in aetideid copepods. Al, antennule; Pl-5, swimming legs 1-5. Segmentation of swimming legs is shown in the order of exopod and endopod; differences between left (L) and right (R) are noted for P5

Copepodid stage		Species					
		Gaetanus variabilis (Brodsky) (cf. this study)	*Aetideopsis armata* (Boeck) (cf. Matthews, 1964)	*Chiridius gracilis* Farran (cf. MacLellan & Shih, 1974)	*Gaetanus kruppii* Giesbrecht (cf. Mazza, 1965)	*Euchirella messinensis* (Claus) (cf. Mazza, 1965)	*Bradyidius similis* (G.O. Sars) (cf. Shih et al., 1981)
CI	A1	10	10	10			10
	P1	1, 1	1, 1	1, 1			1, 1
	P2	1, 1	1, 1	1, 1			1, 1
CII	A1	17	17	17			17
	P1	1, 1	2, 1	2, 1			2, 1
	P2	1, 1	2, 1	2, 1			2, 1
	P3	1, 1	1, 1	1, 1			1, 1
CIII	A1	22	22	22			23
	P1	1, 1	2, 1	2, 1	1, 1	1, 1	2, 1
	P2	1, 1	2, 1	2, 1	2, 1	2, 1	2, 1
	P3	2, 1	2, 1	2, 1	2, 1	2, 2	2, 1
	P4	1, 1	1, 1	1, 1	1, 1	1, 1	1, 1
CIV	A1	23	24	23			24
	P1	1, 1	2, 1	2, 1	1, 1	1, 1	2, 1
	P2	2, 1	2, 1	2, 1	2, 1	2, 1	2, 2
	P3	2, 2	2, 1	2, 1	2, 2	2, 2	2, 2
	P4	2, 2	2, 2	2, 1	2, 2	2, 2	2, 2
	P5	1, 1	1, 1	1	1, 1	1, 1	1, 1
CV	A1	23	24	23			24
	P1	2, 1	3, 1	3, 1	2, 1	2, 1	3, 1
	P2	3, 2	3, 1	3, 1	3, 2	3, 1	3, 2
	P3	3, 3	3, 2	3, 2 (♀) 3 (♂)	3, 3	3, 3	3, 3
	P4	3, 3	3, 3	3, 3	3, 3	3, 3	3, 3
	P5	1, 1	1, 1	1	1, 1	1, 1	2 (L) 1 (R), 1
CVI	A1	23		23			24
	P1	2, 1		3, 1	3, 1	2, 1	3, 1
	P2	3, 2		3, 1 (♀) 2 (♂)	3, 2	3, 1	3, 2
	P3	3, 3		3, 2 (♀) 3 (♂)	3, 3	3, 3	3, 3
	P4	3, 3		3, 3	3, 3	3, 3	3, 3
	P5	3 (L) 2 (R), 1		5 (L) 4 (R)	3 (L) 2 (R), 1	3 (L) 2 (R), 1	2 (L) 3 (R), 1

morphology of the spine-like crest (CVI M reduced in length) is known to occur in *Gaetanus* species (Bradford & Jillett, 1980). During the course of development, large morphological changes have been known to occur in some copepods: the crest on the frontal surface of the cephalothorax in the juvenile copepodid stage of *Neocalanus cristatus* (Krøyer, 1848) (= *Calanus cristatus*) is another good example (Brodsky, 1950).

ACKNOWLEDGEMENTS

We thank Dr. F. D. Ferrari (Smithsonian Institution, Washington, D.C.) and Dr. H.-U. Dahms (Universität Oldenburg, Oldenburg) for critical reading of the manuscript and for providing valuable comments. Dr. N. Iguchi (Japan Sea National Fisheries Research Institute, Niigata) provided zooplankton samples for determination of the mitochondrial 16S rRNA gene, and Dr. T. Sawabe (Hokkaido University, Hakodate) kindly assisted in interpreting the data. We thank the captains, officers, and crew members of R/V "Kaiyo-Maru" and T/S "Hokusei-Maru" for their cooperation in sampling at sea.

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First received 7 March 2005.
Final version accepted 15 April 2005.