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Article in *Journal of Natural History* - November 1999

DOI: 10.1080/002229399299770

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**A new deep-water calanoid copepod and the phylogeny of the genus
Nullosetigera nom. nov. in the Nullosetigeridae nom. nov.
(pro *Phyllopus*: Phyllopodidae) from Japanese waters**

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(Accepted: 10 December 1998)

Nullosetigeridae nom. nov. is proposed for Phyllopodidae Brodsky, 1950, nom. nud., and *Nullosetigera* nom. nov. is introduced for *Phyllopus* Brady, 1883, non Rafinesque, 1815. A new species, *Nullosetigera auctiseta*, is described from Japanese waters. *Nullosetigera mutica* comb. nov. (Sars, 1907) and *N. mutata* comb. nov. (Tanaka, 1964) are redescribed. Phylogenetic analysis implies that two groups, *N. auctiseta*–*N. mutica* group and *N. mutata*–*N. impar*–*N. bidentata*–*N. helgae* group, exist within the genus *Nullosetigera* and that the new species first diverges with *N. mutica*. The relatively advanced species, *N. impar*, *N. bidentata*, and *N. helgae* are the most widespread, and are vertically distributed from the epipelagic to the bathypelagic layers.

KEYWORDS: Calanoida, Nullosetigeridae, phylogeny, zoogeography.

Introduction

The deep-water copepod family Phyllopodidae Brodsky, 1950 has been placed in the superfamily Arietelloidea Sars, 1902 (Campaner, 1977; Bowman and Abele, 1982; Razouls, 1982, 1993). However, the family name based on *Phyllopus* Brady, 1883 is not available (Code, Art. 39), because it is a junior primary homonym of *Phyllopus* Rafinesque, 1815. In this paper the new family name, Nullosetigeridae, is proposed to maintain stability of the nomenclature.

This paper provides a description of a new species and redescription of two species, including the first recorded species from Japanese waters. Their phylogenetic relationships and geographical distributions are also discussed.

Materials and methods

Samples were collected by a ORI net (mouth diameter 160 cm, mesh size 0.33 mm) from Japanese waters during 1993–1996, and immediately preserved in 10% neutralized formalin/seawater after capture. Copepods were dissected and mounted in Gum-chloral medium, and observed and illustrated with a differential interference contrast microscope (Olympus BX-50) equipped with a drawing tube. Some appendages and the genital double-somites of females were also examined with a scanning electron microscope (SEM Jeol T-20). Type specimens are deposited in the Natural History Museum and Institute, Chiba, Japan. The morphological terminology is based on Huys and Boxshall (1991).

Description

Family NULLOSETIGERIDAE nom. nov. pro Phyllopodidae Brodsky, 1950 nom. nud.

Genus *Nullosetigera* nom. nov. (monotypic genus)

Synonymy: *Phyllopus* Brady, 1883: 78–79 (preoccupied).

Diagnosis

Calanoida, Arietelloidea. Body length *c.* 2 to 6 mm.

Female. Prosome regularly oval in dorsal view. First pedigerous somite separate from cephalosome; fourth and fifth pedigerous somites completely fused. Posterior corners of last pedigerous somite produced, sometimes asymmetrical. Urosome four-segmented; genital double-somite often asymmetrical, with paired copulatory pores and gonopores without operculum ventromedially or posteroventrally. Rostrum divided into paired rostral spines. Caudal rami symmetrical, with six setae; inner terminal seta V on right ramus sometimes much longer than left counterpart.

Antennule 24-segmented, asymmetrical; right slightly longer than left; ancestral segments I to III and XXVI to XXVIII completely fused, others separate. Aesthetasc usually present on ancestral segments I, III to XXI, XXV and XXVIII, but absent from some segments between IV and XX of *N. mutica* and *N. auctiseta* sp. nov. Antenna biramous; coxa with or without seta; basis with two setae; endopod two-segmented, first endopodal segment with one seta at midlength, second segment with seven and six setae on inner and outer lobes, respectively; exopod eight-segmented, with setation formula 0, 0, 1, 1, 1, 1, 3. Mandible with well developed gnathobase; mandibular basis unarmed; endopod two-segmented, with two setae on first segment and seven setae on second segment; exopod five-segmented, with setation formula 1, 1, 1, 1, 2. Labrum large, very broad, ornamented with spinule rows posteriorly; seven integumental pores antero- and postero-distally. Maxillule with strongly enlarged praecoxal arthrite bearing 16 elements; coxal endite with two long setae, coxal epipodite unarmed; basis lacking outer seta; basal endites usually with one seta each, distal endite rarely unarmed; endopod minute, one-segmented, with three or four setae; exopod bearing five or seven small setae. Maxilla well developed; praecoxa and coxa fused to form large syncoxa; first syncoxal endite with three or four setae and vestigial element, second to fourth endites with setation formula 2, 3, 3; basis with four setae; endopod four-segmented, with setation formula 4, 3, 2, 2. Maxilliped with short, stout syncoxa, setation formula 0 or 1, 2, 1 or 2, 1 or 3; basis elongate, with three setae, plus two distal setae representing incorporated first

endopodal segment; free endopod five-segmented, with setal formula 3 or 4, 4, 3, 3, 2 to 4.

Legs 1 to 4 with three-segmented rami. Basis of leg 1 with inner seta situated on anterior surface, and process medially on posterior surface. Leg 4 with reduced inner and outer setae on coxa and basis, respectively. Spine and seta formula as follows:

	coxa	basis	exopod	endopod
Leg 1	0-1	1-1	I-1; I-1; II, I, 4	0-1; 0-2; 1, 2, 2
Leg 2	0-1	0-0	I-1; I-1; III, I, 5	0-1; 0-2; 2, 2, 4
Leg 3	0-1	0-0	I-1; I-1; III, I, 5	0-1; 0-2; 2, 2, 4
Leg 4	0-0 or 1	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 2, 2, 3

Fifth legs nearly symmetrical, with common base formed by fusion of coxae and intercoxal plate; basis with outer seta; exopod three-segmented; first exopodal segment with outer spine; second segment with outer spinous process and long inner seta; third segment irregularly serrated along outer margin, with one distal spine.

Male. Body similar to female, but with five-segmented urosome; single genital aperture located ventrolaterally on right side at posterior rim of genital somite. Left antennule geniculate, 20-segmented; segments I–IV, XXI–XXIII, XIV–XXV and XXVI–XXVIII completely fused; segments II and III each with one seta; segments XIX and XX each with one process; segment XXI with two processes; segment XXV with or without process. Mouthparts and legs 1–4 similar to female.

Fifth legs asymmetrical; intercoxal sclerite fused to coxae to form common base; common base with or without stout tapering spine on right inner side. Right leg uniramous; basis with outer spine; exopod three-segmented; first exopodal segment with outer spine, second and third segments incompletely fused and flattened. Left leg biramous, with unsegmented, flattened endopod and three-segmented exopod; first exopodal segment slender, with outer spine; second segment robust, produced into spiniform distal process; third segment forming movable spine.

Type species

Nullosetigera bidentata comb. nov. Brady, 1883.

Other species

Nullosetigera auctiseta sp. nov.; *N. mutica* comb. nov. (Sars, 1907); *N. helgae* comb. nov. (Farran, 1908); *N. impar* comb. nov. (Farran, 1908); *N. aequalis* comb. nov. (Sars, 1920); *N. giesbrechti* comb. nov. (A. Scott, 1909); *N. integer* comb. nov. (Esterly, 1911); *N. mutata* comb. nov. (Tanaka, 1964).

Remarks

Brodsky (1950) established a new subfamily, Phyllopininae within the Arietellidae to accommodate the genus *Phyllopus* Brady, 1883. Campaner (1977) redefined the Arietellidae and raised the Phyllopininae to a separate family on the basis of the following characters: 1) a well developed endopod on the mandibular palp; 2) the form of the maxillule; 3) the armature of the maxillary basis; 4) the relative lengths of the maxillipedal segments; 5) the form of the fifth legs. The name *Phyllopus* Brady, 1883 is a junior primary homonym of *Phyllopus* Rafinesque, 1815. The latter has been suppressed for the purposes of the Principle of Priority, but not for those of the Principle of Homonymy (ICZN Opinion 502). No junior synonym being available (Code, Art. 60c), we consider it necessary to propose a new replacement

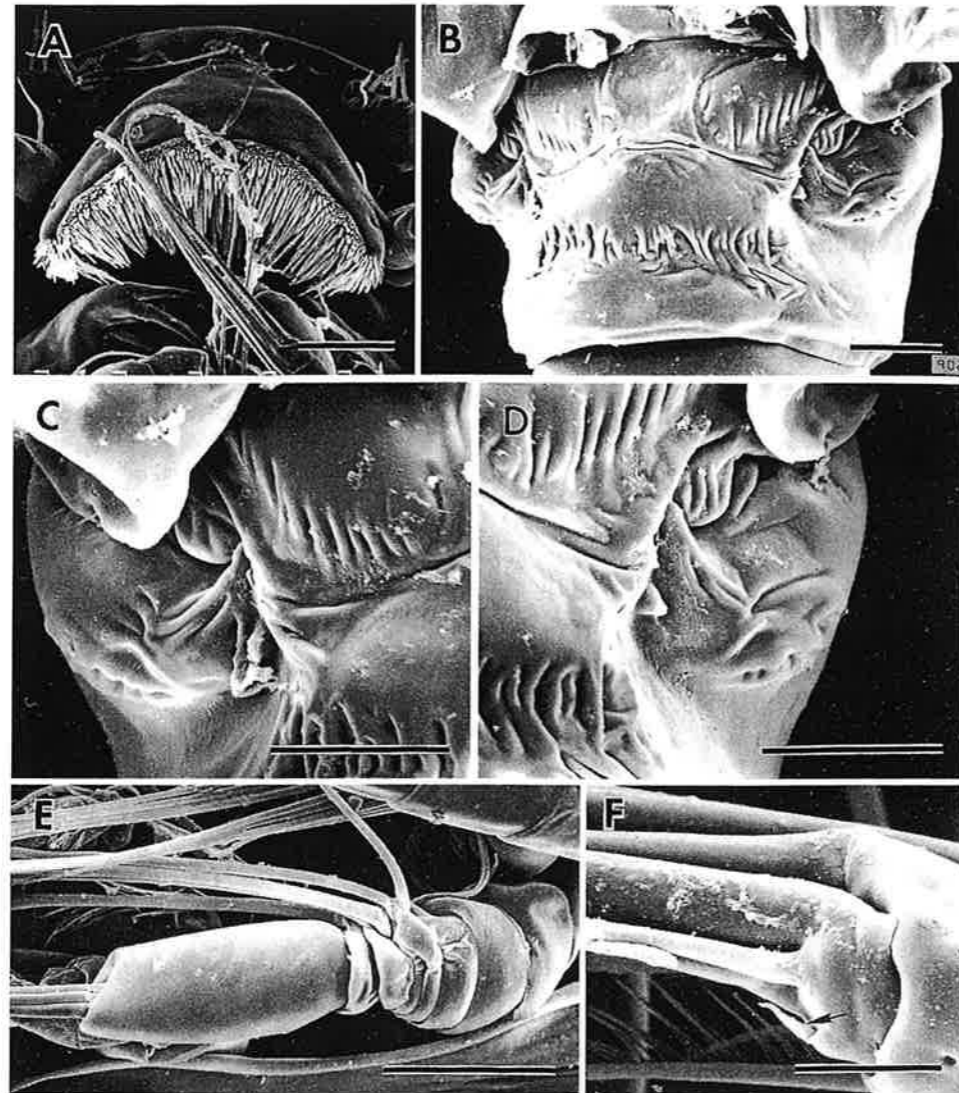


FIG. 2. *Nullosetigera auctiseta* sp. nov., female: (A) Labrum, scale bar = 200 μ m; (B) Genital double-somite, ventral view, scale bar = 50 μ m; (C) Right gonopore and copulatory pore, scale bar = 50 μ m; (D) Left gonopore and copulatory pore, scale bar = 50 μ m; (E) Exopod of left antenna, scale bar = 100 μ m; (F) Fifth and sixth endopodal segments of maxilliped, scale bar = 20 μ m (arrow pointing to tiny seta b on sixth endopodal segment).

exopod (figures 1D, 2E) eight-segmented. Mandibular gnathobase (figure 3A) with four bi- or multicuspid teeth and small chitinized dorsal setae. Maxillule (figure 3B) conspicuously modified: seven out of 16 elements on praecoxal arthrite heavily chitinized; distal endite of basis completely incorporated into segment, unarmed; endopod with three setae. First syncoxal endite of maxilla (figure 3C) with four setae and vestigial element; basis with luminescent pore. Maxilliped (figure 3D): syncoxa with setation formula 0, 2, 1, 1; second endopodal with three setae; sixth

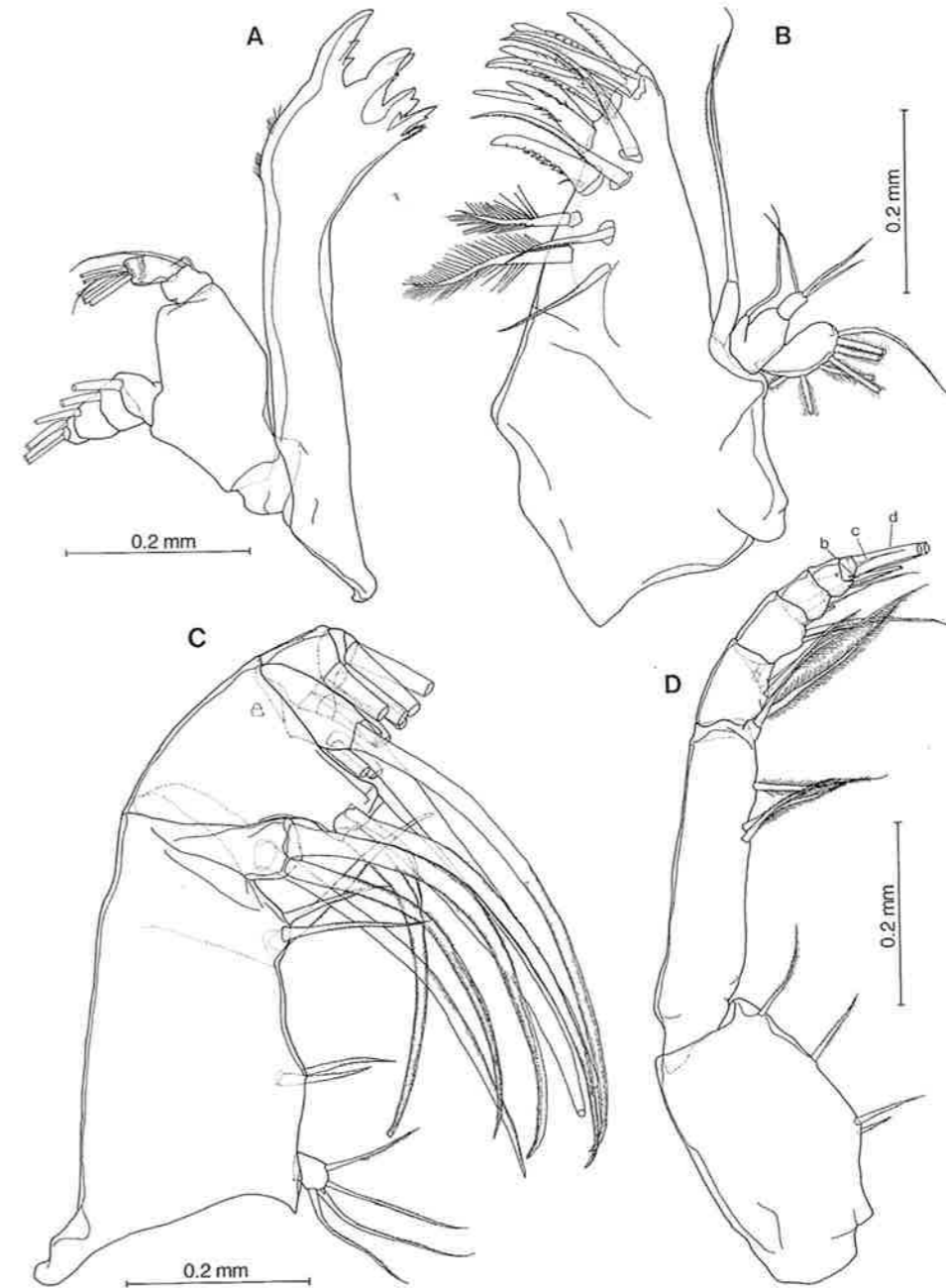


FIG. 3. *Nullosetigera auctiseta*, sp. nov., female (holotype): (A) Left mandible; (B) Left maxillule; (C) Left maxilla; (D) Left maxilliped. Setation elements on sixth endopodal segment of maxilliped indicated by letters b to d.

endopodal segment with elongate seta d, short seta c and vestigial seta b (figures 2F, 3D).

Leg 1 (figure 4A): basis with tongue-like process medially on posterior surface.

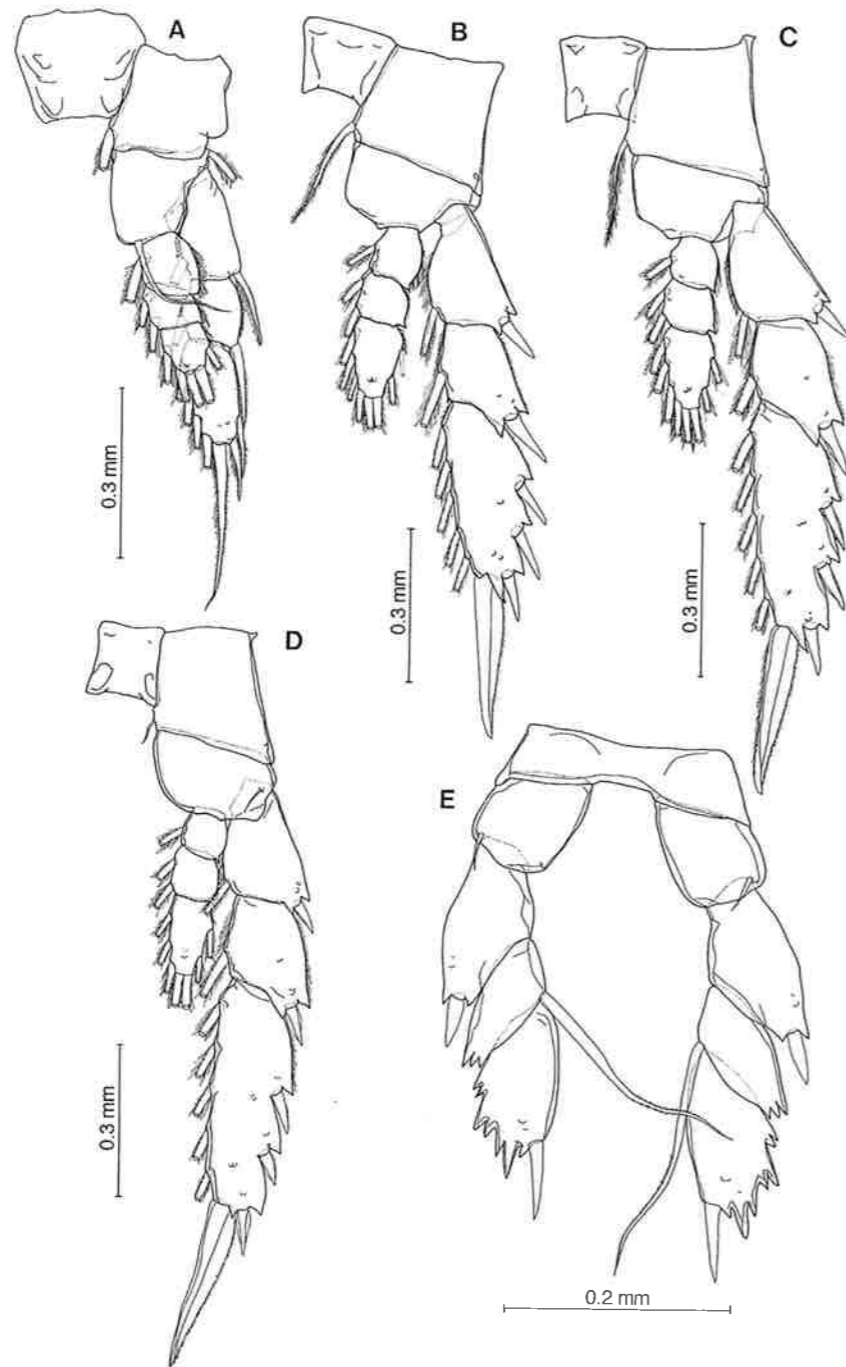


FIG. 4. *Nullosetigera auctiseta*, sp. nov., female (holotype): (A) Left leg 1; (B) Left leg 2; (C) Left leg 3; (D) Left leg 4; (E) Fifth legs.

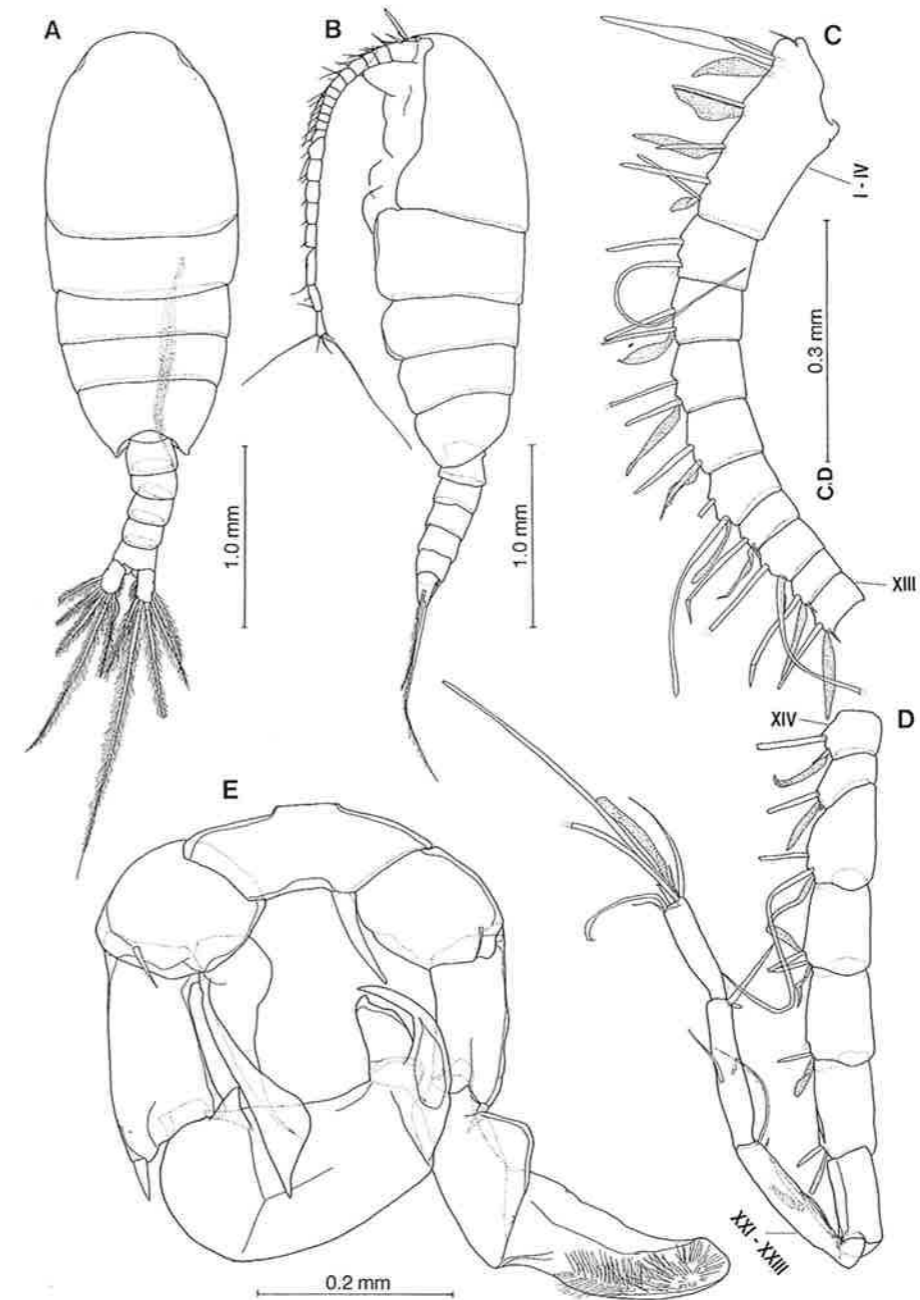


FIG. 5. *Nullosetigera auctiseta*, sp. nov., male (paratype): (A) Habitus, dorsal view; (B) Habitus, lateral view; (C) Left antennular segments I to XIII; (D) Left antennular segments XIV to XXVIII; (E) Fifth legs.

Segmentation and setation of legs 1 to 4 (figures 4A–D) as for familial diagnosis. Fifth legs (figure 4E) nearly symmetrical: basis with small outer seta; second exopodal segment with long inner serrated seta, third exopodal segment with seven denticles on outer margin and terminal spine.

Male. Body (figure 5A, B) similar to the female; body length 3.06 to 3.16 mm long. Urosome five-segmented. Fusion pattern and armature of left antennule as follows (figure 5C, D): I–IV–7+4 aesthetascs, V–2+aesthetasc (missing in figure 5C), VI–2+aesthetasc, VII–2+aesthetasc, VIII–2+aesthetasc, IX–2+aesthetasc, X–2+aesthetasc, XI–2+aesthetasc, XII–2+aesthetasc, XIII–2+aesthetasc, XIV–2+aesthetasc, XV–2+aesthetasc, XVI–2+aesthetasc, XVII–2+aesthetasc, XVIII–2+aesthetasc (missing in figure 5D), XIX–1+process+aesthetasc, XX–1+process+aesthetasc, XXI–XXIII–2+2 processes+aesthetasc, XXIV–XXV–4+aesthetasc, XXVI–XXVIII–8 (one seta missing in figure 5D)+aesthetasc. Fusion pattern of segments of right antennule as in female; aesthetasc pattern as in male left antennule (figure 9A).

Leg 5 (figure 5E) asymmetrical; coxae and intercoxal sclerite completely fused, with long tapering spine on right inner side. Left leg with three-segmented exopod; second exopodal segment with triangular process proximally on inner side; third segment transformed as claw-like spine; one-segmented endopod foliate.

Remarks

This species is very similar to *Nullosetigera aequalis* (Sars, 1920) in the general body shape, but it is easily distinguished by the asymmetrical caudal seta, particularly the inner terminal seta V, and by the structure of the female leg 5. The elongate seta on the right caudal ramus is also found in *N. mutica* (Sars, 1907), but the species is well defined by the following characters: 1) female antennular segments II, IV, VI, VIII–X, XXII–XXIII, XV, XVII, XIX and XX lacking aesthetascs; 2) the unarmed antennary coxa; 3) the first endopodal segment of the antenna having one seta; 4) the coxal endite of the maxillule with two setae of nearly equal length; 5) the distal endite of the maxillular basis unarmed; 6) the first endite of the maxillary syncoxa with five elements; 7) the fourth endite of the maxillipedal syncoxa with one seta; 8) the sixth endopodal segment of the maxilliped with three elements.

Etymology

The specific name *auctiseta* (Latin, *auctus*: growth; *seta*: bristle) refers to the long stout spine on the first segment of the antennule.

Nullosetigera mutica (Sars, 1907) comb. nov. (figure 6)

Phyllopus muticus Sars, 1907: 26; Sars, 1925: 345, pl. cxxiv, figs. 10–16; Sewell, 1947: 238, fig. 64; Wilson, 1950: 289, pl. 15, fig. 189; Grice and Hulsemann, 1967: 38, figs. 266–270; Owre and Foyo, 1967: 91, figs. 648, 651.

Materials examined

Two ♀♀. Off Tanega Island, Kagoshima, southern Japan, 31°00.00'N 131°40.00'E, 30°56.04'N 131°40.03'E, depth 0–872 m, local time 0804–1015, 14 November 1993 (one ♀); off Honshyu, southern Japan, 32°58.93'N 135°17.62'E, 32°57.95'N 135°14.24'E, depth 0–2246 m, local time 2055–2342, 13 May 1996 (one ♀).

Diagnosis

Female. Body (figure 6A, B) 4.55 to 4.63 mm long; last pedigerous somite symmetrical. Posterior corner of prosome rounded in lateral view (figure 6B). Genital double-somite (figure 6C) completely symmetrical, undulated on both sides, with

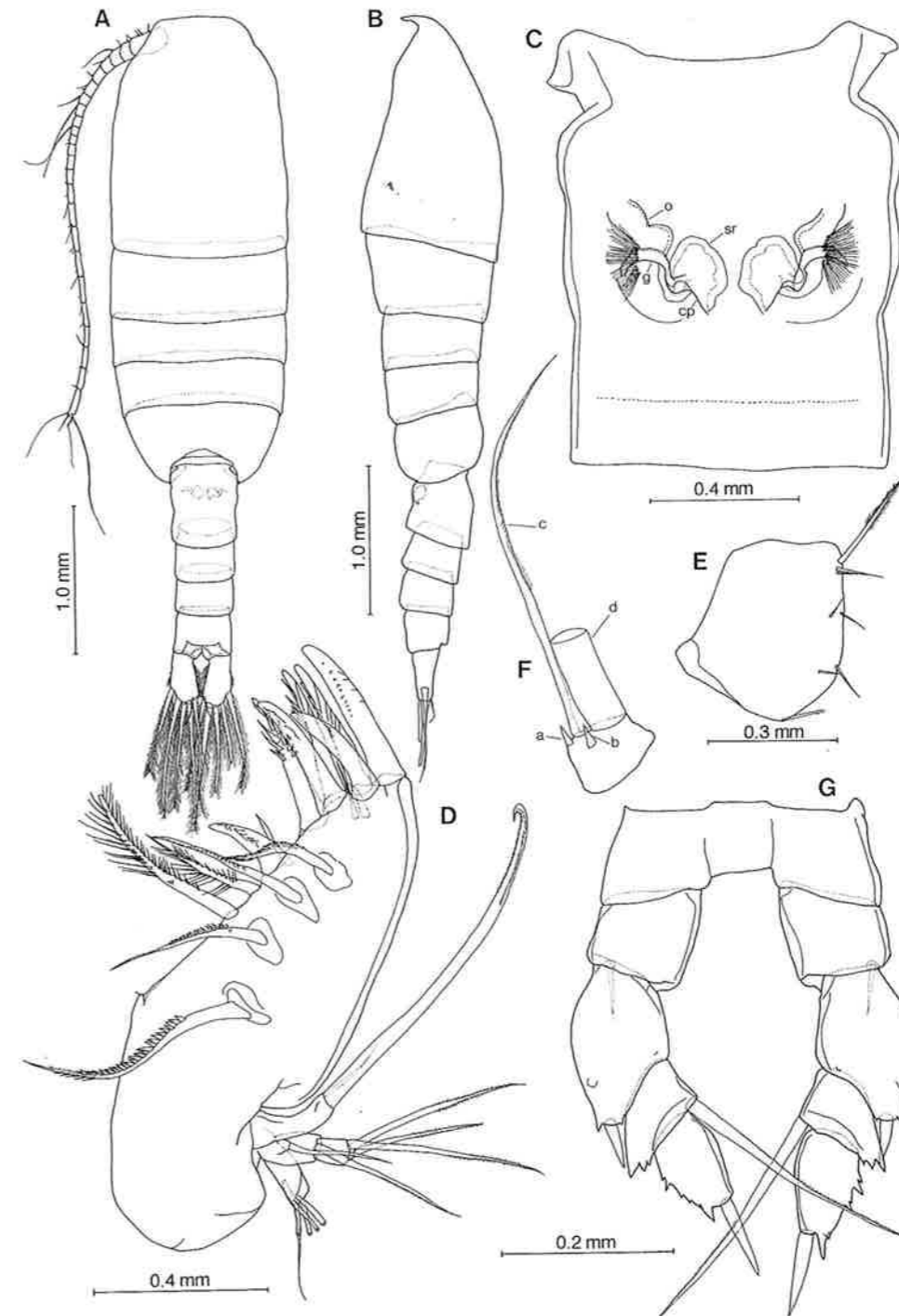


FIG. 6. *Nullosetigera mutica*, female: (A) Habitus, dorsal view; (B) Habitus, lateral view; (C) Genital double-somite, ventral view, cp: copulatory pore; sr: seminal receptacle; g: gonopore; o: oviduct; (D) Left maxillule; (E) Syncoxa of left maxilliped; (F) Sixth endopodal segment of left maxilliped; (G) Fifth legs. Setation elements on sixth endopodal segment of maxilliped indicated by letters a to d.

paired gonopores and copulatory pores without operculum ventromedially. Caudal rami symmetrical; outer and inner terminal setae each with luminescent organ; inner terminal seta of right caudal ramus (cut in figure 6A) much longer than its counterpart.

Antennules asymmetrical; right slightly longer, but not extending to last pedigerous somite; segments I to III incompletely fused. Fusion pattern of segments and armature (figure 8B) similar to preceding species except for segments VI, IX, XIII, XV, XVII and XIX, each bearing an aesthetasc, and loss of posterior seta on left segment XXV. Maxillule (figure 6D): coxal endite setae of extremely unequal length; basal endites each with one seta; one-segmented endopod with three setae; exopod with six setae. Maxillipedal syncoxa (figure 6E) with setation formula 1, 2, 2, 3; second endopodal segment with four setae; sixth endopodal segment (figure 6F) with tiny setae a and b, small seta c and elongate seta d.

Segmentation and setation of legs 1–4 as in *Nullosetigera auctiseta*. Fifth legs (figure 6G): denticles on outer margin of third exopodal segment rather irregular and slightly asymmetrical.

Remarks

Nullosetigera mutica from Japanese waters is slightly smaller than those from the Atlantic (4.80 mm long) and the Indian Oceans (7.21 mm long) measured by Sars (1925) and Grice and Hulsemann (1967), respectively. *Nullosetigera mutica* is easily discernible from other congeners in: 1) the large body size; 2) the extremely unequal length of setae on the coxal endite of the maxillule; 3) the maxillipedal syncoxa with setation formula 1, 2, 2, 3; 4) the sixth endopodal segment of the maxilliped with four elements. This is the first record of *Nullosetigera mutica* from Japanese waters.

Nullosetigera mutata (Tanaka, 1964) comb. nov. (figure 7)

Phyllopus mutatus Tanaka, 1964: 41, figure 226.

Material examined

One ♀. Off Kuchierabu Island, Kagoshima, southern Japan, 30°22.16'N 130°07.41'E, 30°22.16'N 130°08.35'E, depth 0–573 m, local time 1726–1756, 8 November 1994.

Diagnosis

Female. Body (figure 7A, B) 2.56 mm long. Last pedigerous somite asymmetrical; left side (figure 7B) produced posteriorly into apex having two minute spinules and a tiny hair on posterolateral margin; right side (figure 7C) narrowly rounded, with minute spine and a tiny hair on posterolateral margin. Genital double-somite asymmetrical and slightly sinuous on right anterolateral side. Caudal rami symmetrical, with seven setae; outer and inner terminal setae each with luminescent organ.

Antennules asymmetrical; right slightly longer, but not extending to last pedigerous somite; ancestral segments I to III completely fused. Fusion pattern of segments and armature as follows (figure 9F): I–III–7+2 aesthetascs, IV–2+ aesthetasc, V–2+ aesthetasc, VI–2+ aesthetasc, VII–2+ aesthetasc, VIII–2+ aesthetasc, IX–2+ aesthetasc, X–2+ aesthetasc, XI–2+ aesthetasc, XII–2+ aesthetasc, XIII–2+ aesthetasc, XIV–2+ aesthetasc, XV–2+ aesthetasc, XVI–2+ aesthetasc, XVII–2+

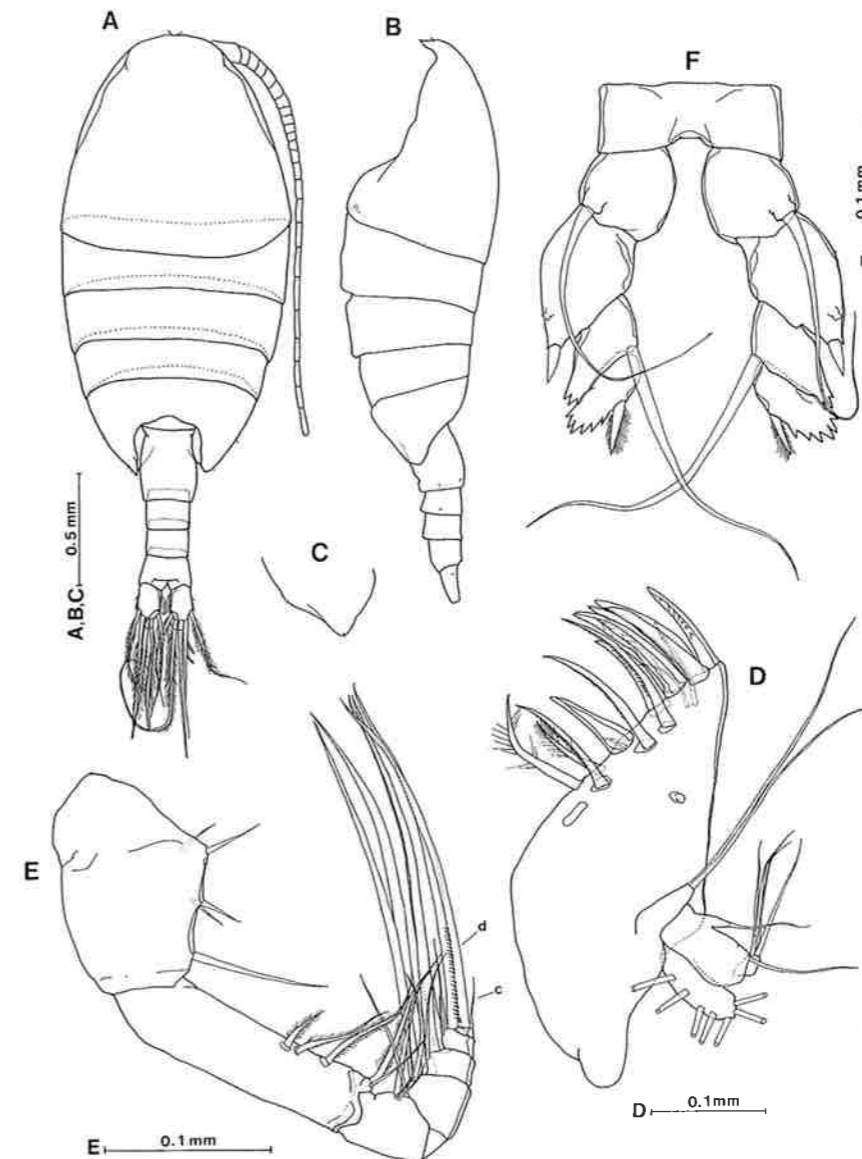


FIG. 7. *Nullosetigera mutata*, female: (A) Habitus, dorsal view; (B) Habitus, lateral view; (C) Last pedigerous somite, right lateral view; (D) Maxillule; (E) Maxilliped; (F) Fifth legs. Homologous setation elements on sixth endopodal segment of maxilliped indicated by letters c and d.

aesthetasc, XVIII–2+ aesthetasc, XIX–2+ aesthetasc, XX–2+ aesthetasc, XXI–2+ aesthetasc, XXII–1, XXIII–1, XXIV–1+1, XXV–1+ aesthetasc, XXVI–XXVIII–8+ aesthetasc; posterior seta on left segment XXV lost. Maxillule (figure 7D): coxal endite setae long; basal endite each with single seta; one-segmented endopod with four setae; exopod with seven setae. Maxillipedal syncoxa (figure 7E) with setation formula 0, 2, 2, 1; second endopodal segment with four setae; sixth endopodal segment with small seta c and elongate seta d.

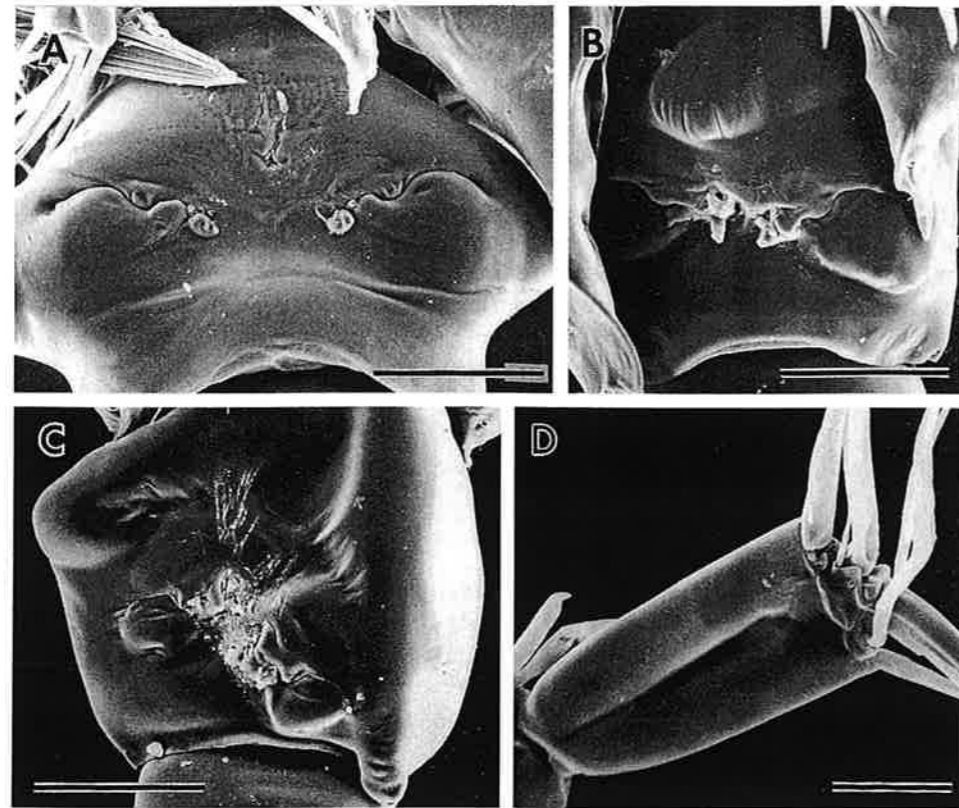


FIG. 8. SEM micrographs of genital double-somite and antennule of female: (A) *Nullosetigera impar*, ventral view, scale bar = 100 μm; (B) *N. bidentata*, ventral view, scale bar = 100 μm; (C) *N. helgae*, ventral view, scale bar = 100 μm; (D) Antennular segment XXV and antennular compound segment XXVI–XXVIII of *N. helgae*, scale bar = 25 μm.

Fourth swimming legs without inner coxal seta. Fifth legs (figure 7F): coxa with very long outer seta; second exopodal segment with long inner seta; third exopodal segment with regular denticles on outer margin and stout seta on inner margin.

Male. Unknown.

Remarks

Tanaka (1964) described this species from Suruga Bay, Japan. This study is the second record of the species. The present specimen differs slightly from Tanaka's illustrations (1964) in having a tiny spinule on the posteroventral margin of the right side of the last pedigerous somite. However, Tanaka might have overlooked this feature in his description.

Phylogenetic analysis

Characters

Nullosetigera species mainly differ in the segmentation and setation patterns of the antennule, maxillule, maxilla, maxilliped, and legs 4 and 5. Nineteen characters

were chosen for the cladistic analysis (table 1). Autapomorphies were excluded from the character matrix (table 2).

Genital double-somite. The genital double-somite of *Nullosetigera auctiseta* (figure 2B) and *N. mutica* (figure 6C) is symmetrical, while those of *N. mutata* (figure 7A), *N. bidentata* (figure 8B), and *N. helgae* (figure 8C) are asymmetrical.

Table 1. Characters used in the cladistic analysis of the species of the genus *Nullosetigera* nom. nov. Code 0 and 1 refer to plesiomorphic and apomorphic states, respectively.

No.	Characters	States	Codes
1.	Genital double somite	symmetrical/asymmetrical	0/1
2.	Fusion of female antennular segments I and II	incomplete/complete	0/1
3.	Fusion of female antennular segments II and III	incomplete/complete	0/1
4.	Aesthetasc on female antennular segment IV	present/absent	0/1
5.	Aesthetasc on female antennular segment VIII	present/absent	0/1
6.	Aesthetasc on female antennular segment X	present/absent	0/1
7.	Aesthetasc on female antennular segment XII	present/absent	0/1
8.	Aesthetasc on female antennular segment XX	present/absent	0/1
9.	Posterior seta of female left antennular segment XXV	present/absent	0/1
10.	Fusion of male antennular segments III and VI	incomplete/complete	0/1
11.	Aesthetasc on male antennular segment II	present/absent	0/1
12.	Number of setae on endopodal segment of maxillule	4/3	0/1
13.	Number of elements on first endite of maxillary syncoxa	5/4	0/1
14.	Seta on first endite of maxillipedal syncoxa	present/absent	0/1
15.	Number of setae on fourth endite of maxillipedal syncoxa	3/1	0/1
16.	Tiny seta a on sixth endopodal segment of maxilliped	present/absent	0/1
17.	Tiny spine b on sixth endopodal segment of maxilliped	present/absent	0/1
18.	Coxal inner seta on leg 4	present/absent	0/1
19.	Tapering spine on right inner part of compound proximal segment of male fifth legs	present/absent	0/1

Table 2. Character data matrix. 0 = plesiomorphic state; 1 = apomorphic state; 9 = missing data.

Species	Characters																		
	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	1
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>N. auctiseta</i> sp. nov.	0	1	1	1	1	1	1	1	0	1	0	1	0	1	1	1	1	0	0
<i>N. mutica</i> comb. nov.	0	0	0	1	1	1	1	1	1	0*	0*	1	1	0	0	0	0	0	0*
<i>N. mutata</i> comb. nov.	1	1	1	0	0	0	0	0	0	1	9	9	0	1	1	1	1	1	1
<i>N. impar</i> comb. nov.	0	1	1	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1
<i>N. bidentata</i> comb. nov.	1	1	1	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1
<i>N. helgae</i> comb. nov.	1	1	1	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1

* According to Sewell (1947).

The genital double-somite of *N. impar* (figure 8A) is considerably expanded on both sides, although it is symmetrical.

Female left antennule. In *Nullosetigera mutica* ancestral segments I, II, and III are incompletely fused, each retaining a suture line on the anterior side; in *N. auctiseta*, *N. impar*, *N. helgae*, *N. bidentatus* and *N. mutata* these segments are completely fused. *Nullosetigera auctiseta* (figure 9A) and *N. mutica* (figure 9B) lack of aesthetasc on segments IV, VIII, X and XII. In *Nullosetigera auctiseta* the aesthetasc is also absent from segments VI, IX, XIII, XV, XVII, and XIX. However, *Nullosetigera impar* (figure 9C), *N. helgae* (figure 9D), *N. bidentata* (figure 9E) and *N. mutata* (figure 9F) have an aesthetasc on each of these segments. The loss of aesthetascs on female antennules may be an ontogenetic suppression. These states are therefore synapomorphies of *Nullosetigera auctiseta* and *N. mutica*. *Nullosetigera auctiseta* is unique in displaying one postero-distal seta on segment XXV; the rest of the species have lost it.

Male left antennule. *Nullosetigera auctiseta* (figure 10A) and *N. impar* (figure 10B) retain an aesthetasc on ancestral segment II, whereas *N. helgae* (figure 10C) and *N. bidentata* (figure 10D) have lost it.

Maxillule. *Nullosetigera impar*, *N. helgae*, *N. bidentata* and *N. mutata* (figure 7D) have four elements on the single endopodal segment, whereas *N. auctiseta* (figure 3B) and *N. mutica* (figure 6D) bear three elements. *Nullosetigera auctiseta* (figure 3B) lacks also a seta on the distal endite of basis.

Maxilla. *Nullosetigera auctiseta* is unique in displaying five setae plus element on the proximal endite of syncoxa (figure 3C); the other five species display three setae and a single element only.

Maxilliped. *Nullosetigera mutica* (figure 6E) retains the most primitive setation formula 1, 2, 2, 3 for the syncoxa. In *Nullosetigera auctiseta* (figure 3D), *N. mutata* (figure 7E), *N. impar*, *N. helgae* and *N. bidentata*, the seta on the proximal endite is lost, and the number of setae on the fourth endite of the syncoxa is reduced to a single seta only. *Nullosetigera mutica* (figure 6F) also has four setae (tiny setae a and b, small seta c and elongate seta d) on the sixth endopodal segment, whereas

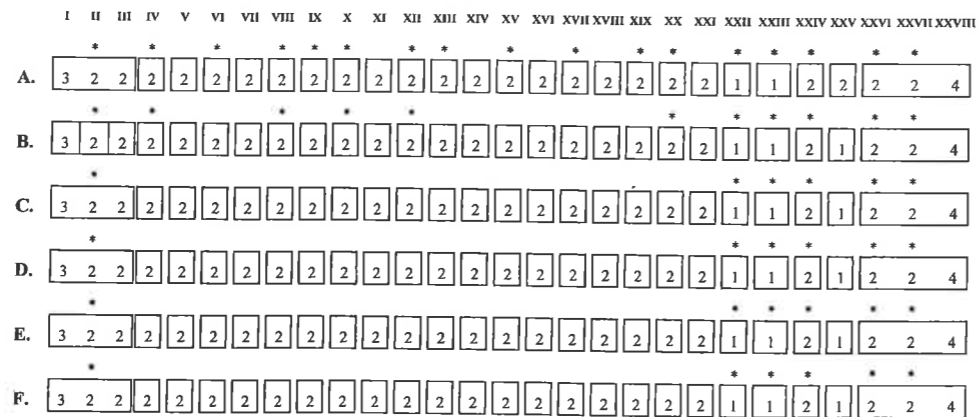


FIG. 9. Schematic illustration of segmental pattern and armature of female antennule in some nullosetigerids: (A) *Nullosetigera auctiseta*, sp. nov.; (B) *N. mutica*; (C) *N. impar*; (D) *N. helgae*; (E) *N. bidentata*; (F) *N. mutata*. The number indicates setae on each segment. Asterisks indicate segments without aesthetasc. Line in triple segment I-III shows degree of separation.

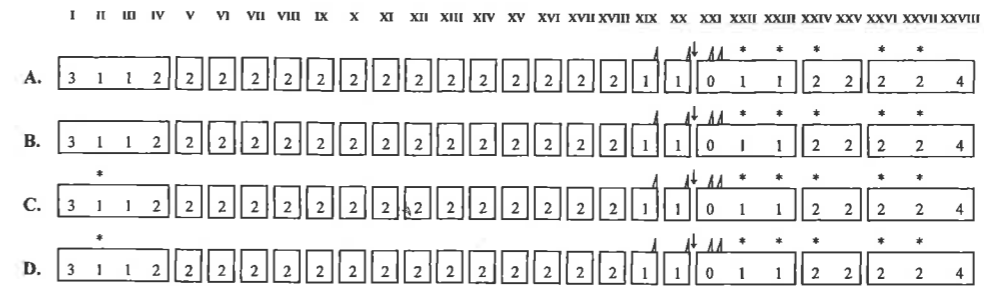


FIG. 10. Schematic illustration of segmental pattern and armature of male left antennule in some nullosetigerids: (A) *Nullosetigera auctiseta*, sp. nov.; (B) *N. impar*; (C) *N. helgae*; (D) *N. bidentata*. The number indicates setae on each segment. Asterisks indicate segments without aesthetasc. Arrow indicates position of geniculation.

Nullosetigera auctiseta (figures 2F, 3D) has lost the vestigial seta a on the sixth endopodal segment. *Nullosetigera mutata* (figure 7E), *N. impar*, *N. helgae* and *N. bidentata* lack setae a and b on the sixth endopodal segment.

Female leg 4. *Nullosetigera auctiseta* (figure 5E) and *N. mutica* retain the inner coxal seta while *N. impar*, *N. helgae*, *N. bidentata* and *N. mutata* have lost it.

Male leg 5. *Nullosetigera auctiseta* and *N. mutica* have a long tapering spine on the right inner side of compound segment formed by the fusion of the intercoxal sclerite and the coxae, whereas *N. impar*, *N. helgae* and *N. bidentata* lack of it. This off spine seems to derived from the ancestral inner seta of the coxa of the right leg, because it is completely separated from the compound segment.

Phylogenetic relationships between *Nullosetigera* species from Japanese waters

The phylogenetic relationship between species was analyzed using the phylogenetic computer package PAUP 3.1.1 (Swofford, 1993). BRANCH AND BOUND and DELTRAN options were employed to find the most parsimonious cladogram and to delay character transformation for character optimization within the tree, respectively. A hypothetical ancestor, which scored 0 for all characters, was included in the analysis. Four trees were obtained, with equal tree length (=27 steps), consistency index (=0.704) and retention index (=0.833). The f-value of tree 1 was 0.2154, that of tree 2 was 0.2171, that of tree 3 was 0.4923, and that of tree 4 was 0.4961. Tree 4 (figure 11) was therefore selected as having the highest f-ratio.

The *Nullosetigera auctiseta*-*N. mutica* group is well defined by the following synapomorphic character states: the absence of an aesthetasc on female antennular segments IV, VIII, X, XII and XX (characters 4, 5, 6, 7 and 8); and the reduction of the number of setae on the endopodal segment of the maxillule (character 12). The *Nullosetigera impar*-*N. mutata*-*N. helgae*-*N. bidentata* group is characterized by the following synapomorphic characters:

- (1) the complete fusion of female antennular segments I-III (characters 2 and 3);
- (2) the absence of a posterior seta on the female left antennular segment XXV (character 9);
- (3) the fusion of male antennular segments III and IV (character 10);
- (4) the reduction of the number of setae on the first endite of the maxillary syncoxa (character 13);

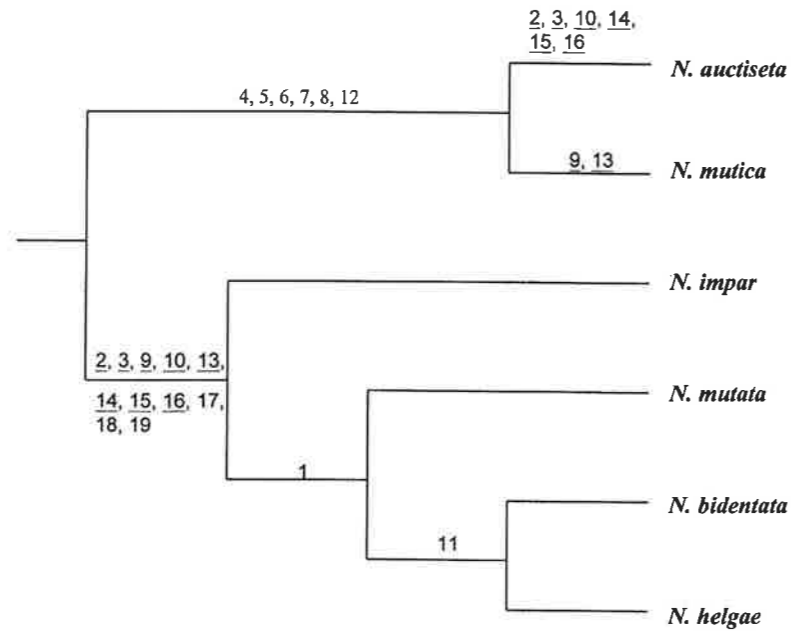


FIG. 11. Phylogenetic relationships of *Nullosetigera* species from Japanese waters. Arabic numerals refer to characters discussed in text (— below Roman numeral = convergence).

- (5) the absence of the praecoxal seta on the syncoxa (character 14);
- (6) the reduction of the setal number on the fourth endite of the maxillipedal syncoxa (character 15);
- (7) the loss of tiny setae a and b on the sixth endopodal segment of the maxilliped (characters 16 and 17);
- (8) the absence of the inner coxal seta on leg 4 (character 18);
- (9) the absence of a spine on the right side of the compound proximal segment of the male leg 5 (character 19).

However, the phylogenetic relationships indicated here are tentative since *Nullosetigera giesbrechti* and *N. integer* were not included in this study.

Feeding ecology and distribution

Gut contents were observed in five females each of *Nullosetigera impar*, *N. helgae* and *N. bidentatus*, but no materials were found apart from oil droplets. However, stout setae on the basal endite and the endopodal segments of the maxilla indicate that they are carnivores.

Nullosetigera mutica has been recorded from the Atlantic, Pacific and Indian Oceans between 40°N and 25°S (Sars, 1925; Sewell, 1947; Wilson, 1950; Grice, 1963; Owre and Foyo, 1964; Grice and Hulsemann, 1967; present study) and ranges vertically in the bathypelagic zone below c.1000 m (Grice, 1963; Owre and Foyo, 1964; Grice and Hulsemann, 1967) (figure 12). *Nullosetigera impar*, *N. helgae* and *N. bidentata* are widely distributed from the tropical to the temperate regions of the world oceans, and range vertically from the epipelagic to the bathypelagic zones (Brady, 1883; Giesbrecht, 1892; Scott, 1894, 1909; Wolfenden, 1911; Lysholm and Nordgaard, 1921; Sars, 1925; Jespersen, 1934, 1940; Tanaka, 1964; Sewell, 1947;

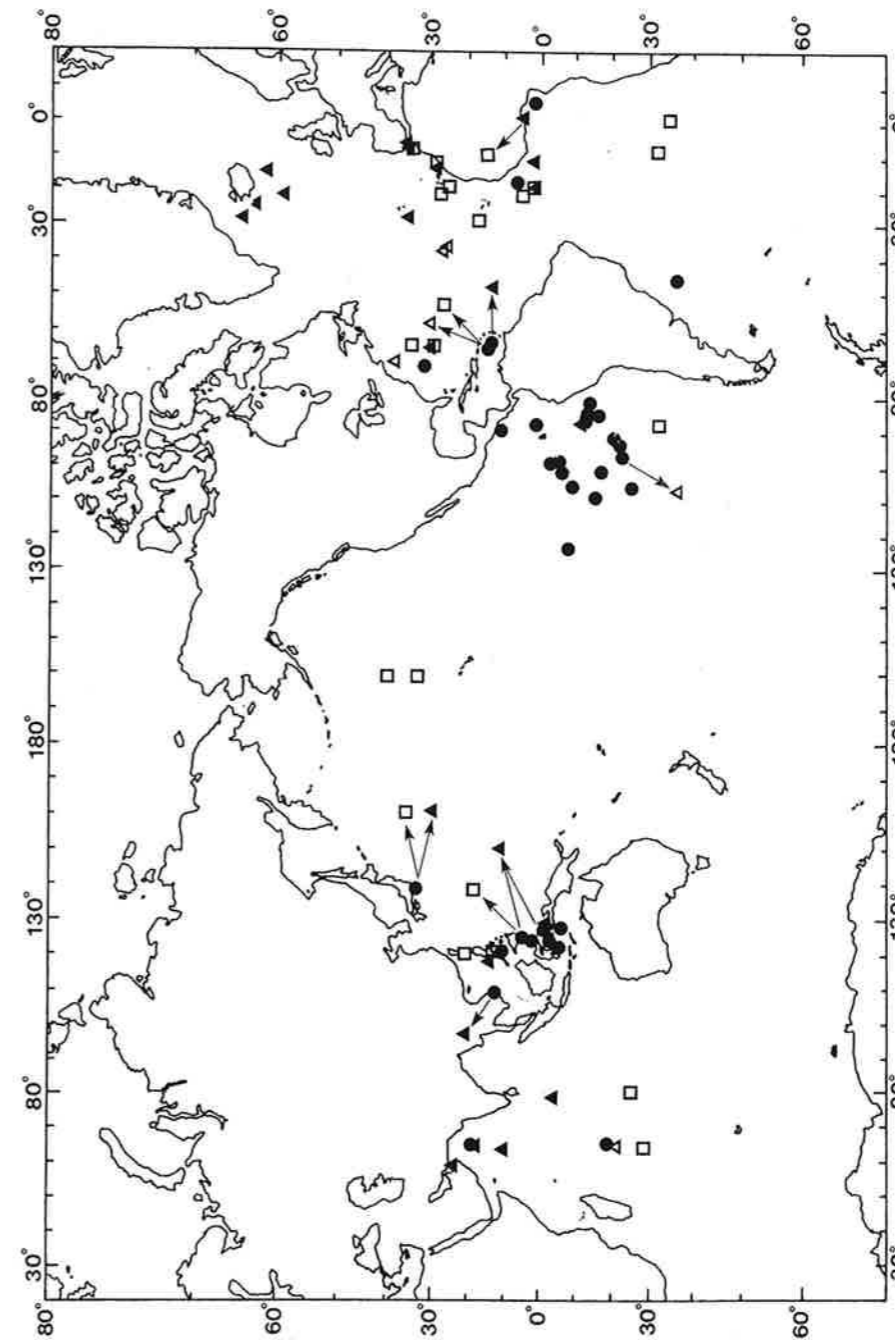


FIG. 12. Geographical distribution of *Nullosetigera mutica* (Δ), *N. impar* (\blacktriangledown), *N. bidentata* (\bullet) and *N. helgae* (\square).

Brodsky, 1950; Wilson, 1950; Rose, 1955, 1956; Grice, 1963; Grice and Hulsemann, 1967; Owre and Foyo, 1964, 1967; Vervoort, 1965; Morris, 1970; Roe, 1972) (figure 12). Roe (1972) pointed to the possibility of diurnal migration in *Nullosetigera helgae*.

Discussion

The present phylogenetic analysis of nullosestigerid species reveals two groups, a *Nullosetigera auctiseta*-*N. mutica* group and a *N. impar*-*N. mutata*-*N. helgae*-*N. bidentata* group. *Nullosetigera* has very great variation in the display of aesthetascs on antennular segments IV to XX of the female (see figure 8). The *Nullosetigera auctiseta*-*N. mutica* group has lost the aesthetasc on antennular segments IV, VIII, X, XII and XX. In addition, *Nullosetigera auctiseta* lacks of the aesthetasc on antennular segments VI, IX, XIII, XV, XVII and XIX. Reduction of aesthetascs on these segments of female antennules are found also in some *Euaugaptilus*, *Augaptilus*, *Pseudaugaptilus*, *Arietellus*, *Paraugaptilus* and *Metacalanus*; these genera are located in relatively advanced groups (see Ohtsuka *et al.*, 1994; Soh, 1998). On the other hand, the *Nullosetigera impar*-*N. mutata*-*N. helgae*-*N. bidentata* group shows apomorphic states in the setation of the maxillule, maxilla, maxilliped, leg 4 and male leg 5, although the female antennules retain a trithek (two setae + one aesthetasc) on segments. Aesthetascs seem to be easily added in the antennule, in contrast to setae (Boxshall and Huys, 1998). Therefore, the trithek on the female antennules of the *Nullosetigera impar*-*N. mutata*-*N. helgae*-*N. bidentata* group might be a character reversal to the ancestral condition. Additionally, the *Nullosetigera auctiseta*-*N. mutica* group has a stout tapering spine on the right inner margin of the proximal compound segment of the male fifth legs, whereas the *N. impar*-*N. helgae*-*N. bidentata* group lacks it.

Nullosetigera has asymmetrical antennules: the right antennule is slightly longer than the left one. Asymmetry of antennules is also found in some species of the genera *Paramisophria* T. Scott, 1897 and *Hyperbionyx* Ohtsuka *et al.*, 1993 included in the same superfamily Arietelloidea, and it has been related to their hyperbenthic habitats (Ohtsuka and Mitsuzumi, 1990; Ohtsuka *et al.*, 1993). Soh's phylogenetic tree (1998) for the superfamily Arietelloidea Sars, 1902 implies that the asymmetry of antennules in nullosestigerids might be derived from a hyperbenthic ancestor.

Key to species of *Nullosetigera* nom. nov.

- 1 Leg 4 with coxal inner seta (♀♂); male leg 5 with tapering process on intercoxal sclerite-coxae compound segment (♂) 2
 Leg 4 without coxal inner seta (♀♂); male leg 5 without any process on intercoxal sclerite-coxae compound segment (♂) 3
- 2 Coxal endite of maxillule with two extremely unequal setae (♀♂); four elements on sixth endopodal segment of maxilliped (♀♂) *N. mutica* comb. nov. (Sars, 1907)
 Coxal endite of maxillule with two nearly equal setae (♀♂); three elements on sixth endopodal segment of maxilliped (♀♂) *N. auctiseta* sp. nov.
- 3 Genital double-somite symmetrical, protruding on both sides (♀); left leg 5 without distinct demarcation between tooth and second exopodal segment (♂); right leg 5 with large tongue-like process on first exopodal segment (♂)
N. impar comb. nov. (Farran, 1908)
 Genital double-somite asymmetrical (♀); tooth on second exopodal segment of left leg 5 distinctly separated from third exopodal segment 4

- 4 Last pedigerous somite symmetrical (♀); genital double-somite protruding on right side (♀); third exopodal segment of left leg 5 very elongated (♂)
N. helgae comb. nov. (Farran, 1908)
 Last pedigerous somite asymmetrical, with posterior corners laterally modified into apically truncate lobes (♀); left leg 5 with small distal tooth and short curved claw on third exopodal segment (♂)
N. bidentata comb. nov. (Brady, 1883)
 Last pedigerous somite slightly asymmetrical, with tiny spines on posterior corners (♀)
N. mutata comb. nov. (Tanaka, 1964)

Acknowledgements

We thank Drs G. A. Boxshall, F. Ferrari, I. -H. Kim and M. J. Grygier for their comments on The International Code of Zoological Nomenclature. We also express our sincere thanks to Dr M. J. Grygier for critically reading the first draft. Thanks are extended to Drs T. Kubota and S. Sawamoto for loan of specimens of *Nullosetigera*. The captain and crew of TR/V Toyoshio-maru provided useful assistance for collections at sea. Dr M. Miya permitted us to use the PAUP computer software (version 3.1.1).

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