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Phylogenetic Relationships of the Family Metridinidae (Copepoda: Calanoida)

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Several differences are revealed in the segmentation and setation of the antennule, maxillule, maxilliped and fifth legs between three genera of the family Metridinidae, *Metridia*, *Pleuromamma*, and *Gaussia*. The phylogenetic relationships are cladistically analyzed on the basis of 10 morphological characters. The cladogram shows that *Gaussia* and *Pleuromamma* form a sister group, with *Metridia* which is the first branch to diverge within the family. The presence of quadritheks on the male antennules of *Metridia* and *Pleuromamma* seems to be an important synapomorphy. The loss of quadritheks in *Gaussia* represents likely evidence of a character reversal into the ancestral condition.

Key words: Phylogenetic analysis, Copepoda, Calanoida, Metridinidae, Antennule dimorphism.

Introduction

The family Metridinidae Sars, 1902, comprising three genera, *Metridia* Boeck, 1864, *Pleuromamma* Giesbrecht, 1898, and *Gaussia* Wolfenden, 1905, is one of the most primitive group in the superfamily Arietelloidea Sars, 1902 (Soh, 1998). In this family, nevertheless, there are many morphological variations in element patterns of antennules and the fifth legs between the genera. For example, *Metridia* and *Pleuromamma* have additional aesthetascs on the proximal parts of their antennules (Boxshall and Huys, 1998; Soh, 1998). Some species of *Metridia* and *Pleuromamma* form a geniculation on either the left or the right one of male antennule (Sars, 1924; Ferrari, 1984; Soh, 19 98). *Metridia* species also show variable setation and segmentation in the fifth legs of the female. However, the polarities of these characters have been rarely studied.

This study aims to clarify relationships among three different genera in the family Metridinidae and to trace what the number of aesthetascs and the geniculation of male antennule are proceeded in their evolutionary processes.

Materials and methods

Copepods were collected from the Nansei Islands, southern Japan in 1993, using an ORI net (mesh size 0.33 mm). The net was obliquely towed between ca. 1,070-m depth and the surface at a speed of ca. 2 knots by the TR/V *Toyoshio-maru* of Hiroshima University. Samples were fixed immediately after collection with 10 % neutralized formalin/seawater. Additional specimens examined were loaned from the Institute of Oceanic Research & Development, Tokai University (Kubota et al., 1992; Kubota and Sawamoto, 1993).

For the phylogenetic analysis of the generic relationships within the family Metridinidae, specimens examined inclueled: 6 species of the genus *Metridia* including *M. princeps* Giesbrecht, 1889, *M. macrura* Sars, 1905, *M. pacifica* Brodsky, 1950, *M. boecki* Giesbrecht, 1889, *M. okhotensis* Brodsky, 1950, *Metridia* sp. sensu Hattori, 1996; 5 species of the genus *Pleuromamma* including *P. xiphias* (Giesbrecht, 1889), *P. abdominalis* (Lubbock, 1856), *P. scutullata* Brodsky, 1950, *P. indica*

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Wolfenden, 1905, *P. gracilis* (Claus, 1863); 2 species of the genus *Gaussia* including *G. princeps* (Scott, 1894), *G. sewelli* Saraswathy, 1973. Phylogenetic relationships between the genera were analyzed using PAUP (Version 4.0b, Swofford, 1998). BRANCH AND BOUND and DELTRAN options were employed to find the most parsimonious cladogram and to delay character transformation within the tree, respectively. A hypothetical composite ancestor, scored 0 for all characters, was included in the analysis. The morphological terminology and the setal homology of the 5th leg of female are based on Huys and Boxshall (1991) and Ferrari (1991), respectively

Results

Systematic account

Superfamily Arietelloidea Sars, 1902

Family Metridinidae Sars, 1902

Diagnosis. Body length, ca. 2 to 12 mm, remarkably variable.

Female. Prosome comprising cephalosome and four pedigerous somites; first pedigerous somite separated from cephalosome, and 4th and 5th pedigerous somites completely fused. Forehead usually rounded, sometimes with dorsal papilla or small sharp process. Posterior corner of prosome usually rounded, but with stout process in *Gaussia*. First pedigerous somite with dark-pigmented spot on one side in *Pleuromamma*. Rostrum divided into paired rostral filaments. Urosome usually elongated with three segments. Genital apparatus variable; all genera with paired gonopores located anteriorly on ventral surface of genital double-somite; copulatory pores paired in *Gaussia* and *Metridia*, but seminal receptacles absent in *Gaussia*; unpaired copulatory pore and seminal receptacle present in *Pleuromamma*. Caudal rami nearly symmetrical, with six setae.

Antennule 23-segmented; ancestral segments I to III and XXVII and XXVIII completely fused; segments IX-X and XI incompletely fused; segments XI and XII, and XIV and XV almost separate; aesthetasc absent on segments XXII, XXIV, XXVI and XXVII, and occasionally on segment XXIII. Double aesthetascs present on any segment between ancestral segments II and XIII in some species of *Metridia*. Antenna biramous, unequal in length: coxa and basis separated, with one and two setae, respectively; endopod 2-segmented, first endopodal segment with two setae at midlength, second segment with nine and seven setae on inner and outer lobes, respectively; exopod 7-segmented, slightly longer than endopod; segmentation and setation formula: I-1, II-IV-2, V-1, VI-1, VII-1, VIII-1, IX-X-4. Mandible well-developed: cutting edge of gnathobasis with nine or ten teeth and a dorsalmost seta; basis of mandibular palp bearing four setae; endopod 2-segmented, with four and ten setae on first and second segments, respectively; exopod 5-segmented, with setation formula: 1, 1, 1, 1, 2. Maxillule well-developed: praecoxal arthrite with 16 elements; coxal endite with five setae, coxal epipodite with nine setae; basis with outer seta bearing typically four and five setae on first and second endites, but rarely seven setae on second endite; second 2-segmented, ancestral first and second segments fused; setation formula 6+4, 7 or 7+4, 7; exopod unsegmented, armed with 11 setae. Maxilla: praecoxa and coxa, completely or incompletely separated; first praecoxal endite with nine setae and one vestigial element, second endite with three setae; first and second coxal endites each with three setae; basis with four setae; endopod 4-segmented; segmental setation formula 4, 3, 2, 2. Maxilliped relatively short: syncoxa with endite setation formula 1, 2, 4, 4 bearing outer seta in *Metridia* and *Pleuromamma*; basis armed with patches of setules or spinules bearing two setae, plus two setae on incorporated first endopodal segment; five free endopodal segments with segmental setation formula 4, 4, 3, 3, 4.

Legs 1 to 4 biramous, with 3-segmented rami. Basis of leg 1 with an inner seta on anterior surface. Outer spines on second and third exopodal segments of leg 1 furnished with terminal lash. First endopodal segment of leg 2 lacking inner seta typically incised and ornamented with one or more hook-like spinous processes on inner margin.

Spine and seta formula primitively 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	0−0;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	0−1	1−0	I−1;I−1;III,I,5	0−1;0−2;2,2,3

Fifth legs uniramous, with transverse plate formed by fusion of coxae and intercoxal sclerite; basis bearing outer seta separated from coxa. Exopod

Table 1. Characters used in cladistic analysis of genera of the family Metridinidae. Code 0=ancestral (plesiomorphic) state, 1=derived (apomorphic) state

No.	Characters	States	Codes
1	Aesthetasc on female antennulary segment XXIII	present/absent	0/1
2	Fusion of male antennulary segments IX and X	separate/fused	0/1
3	Aesthetasc on mele non-geniculate antennulary segment XXII	present/absent	0/1
4	Number of setae on distal endite of basis of maxillue	7/5	0/1
5	Number of setae on first endopodal segment of maxillule	7/6	0/1
6	Outer spine b on 2nd exopodal segment of female leg 5	present/absent	0/1
7	Outer spine d on 3rd exopodal segment of female leg 5	present/absent	0/1
8	Outer spine e on 3rd exopodal segment of female leg 5	present/absent	0/1
9	Inner seta I on 3rd exopodal segment of female leg 5	present/absent	0/1
10	Fusion between 2nd and 3rd exopodal segments of male leg 5	separate/fused	0/1

originally 3-segmented, with armature formula of I −0;I−1;II,I,3 in *Metridia* sp. sensu Hattori (1996), but second and third exopodal segments often fused in other *Metridia* species and *Pleuromamma*, with reduced setation.

Male. Body similar to that of female, but urosome 5-segmented; a single genital aperture usually located ventrolaterally at posterior rim of genital somite on right side, but often on left side in *Metridia* and *Pleuromamma*.

Geniculate antennule 19 or 20-segmented, usually on left side, but occasionally on right side in *Metridia* and *Pleuromamma*; ancestral segments I-IV, IX-XII, XIV-XV, XVI-XVII, XXI-XXIII, XXIV-XXV and XXVII-XXVIII incompletely or completely fused. Two aesthetascs present on segments II to XIII except for those of *Gaussia*. Fifth legs asymmetrical; coxae and intercoxal sclerite completely fused. Right leg with basis bearing an outer seta and 3-segmented exopod. Second exopodal segment with an inner spinous process in some genera; third segment with two or three minute setae. Left leg with basis bearing outer seta and 2- or 3-segmented exopod; first exopodal segment with curved or straight inner process.

Type genus *Metridia* Boeck, 1864

Remarks. Dunn and Hulsemann (1979) requested a ruling from the International Commission of Zoological Nomenclature to eliminate the homonymy between the family Metridiidae Carlgren, 1893 based on the anthozoan genus *Metridium* Blainville, 1824 and the family Metridiidae Sars, 1902 based on the copepod genus *Metridia* Boeck, 1865. They also suggested that the Metridinidae Sars, 1902 (Copepoda) could be placed on the Official List of Family-Group Names in Zoology with the stem of the type genus *Metridia* Boeck, 1865 being designated as "Metridin-" for the purposes of Article 29. The family name Metridinidae Sars, 1902 was approved by the International Commission of Zoological Nomenclature (1984, Opinion 1269).

Ferrari (1985) analyzed the dimorphic asymmetry in both sexes of certain *Pleuromamma* species. Park and Mauchline (1994) showed that the integumental pore patterns on the urosome of *Pleuromamma* species could be useful for their phylogenetic study.

Phylogenetic analysis

Ten characters of the three genera, *Gaussia*, *Metridia*, and *Pleuromamma* in the family Metridinidae are used for the cladistic analysis (Table 1). There are several differences in the segmentation and setation of the antennule, maxillule, maxilliped, fifth leg and female's genital system between the genera.

1. Antennule of female (Fig. 1). In *Metridia* there are four types of armatures on the ancestral segments II-XIII. *Metridia* sp. sensu Hattori (1996) and *M. okhotensis* (Fig. 1D) possess a quadrithek of armature elements, consisting of two setae and two aesthetascs, on each of the segments II-XIII; *M. boecki* (Fig. 1B) on the segments II-IX and XI-XIII; *M. pacifica* (Fig. 1C) on the segments II-IX, XI and XIII. *M. princeps* (Fig. 1A) has the usual trithek (two setae plus one aesthetasc) through these ancestral segments. In *Pleuromamma* (Fig. 1E) and *Gaussia* (Fig. 1F) the armature elements are consistent.

2. Geniculate antennule of male (Fig. 2). *Metridia princeps* and *M. macrura* (Fig. 2A) exhibit a quadrithek on segments V, VII-IX, XI and XIII,

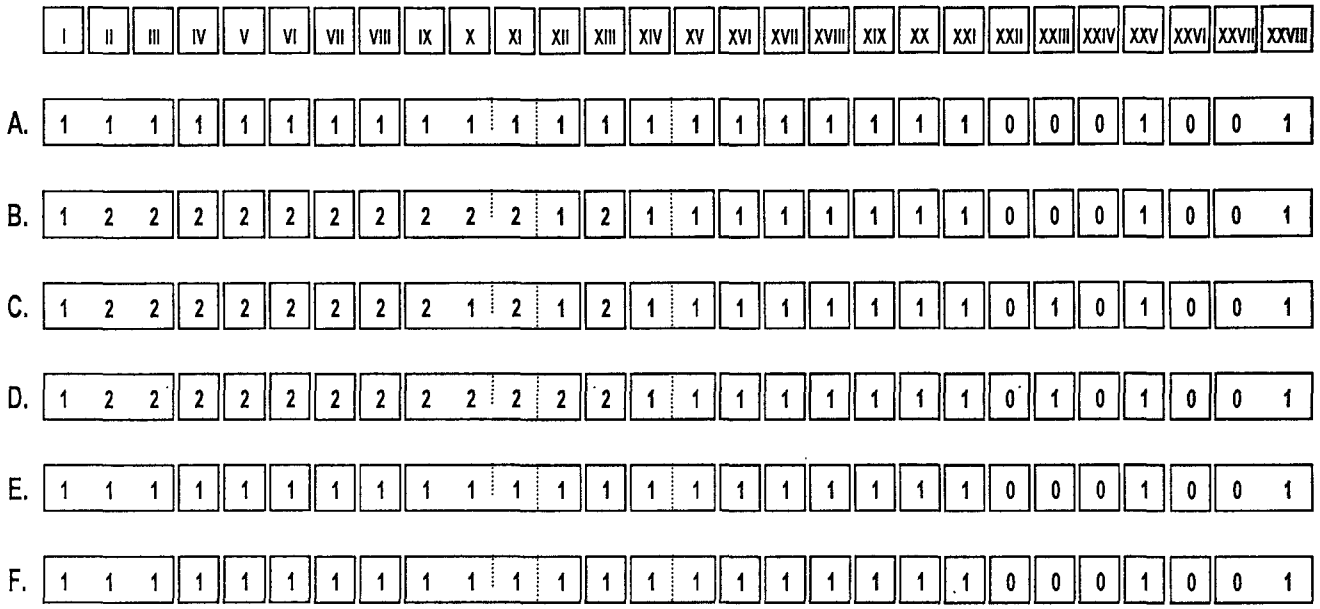

Fig. 1. Schematic comparison of segmentation and segmental aesthetasc numbers of female antennules in some metridinid species. A. *Metridia princeps*; B. *M. boecki*; C. *M. pacifica*; D. *M. okhotensis*; E. *Pleuromamma xiphias, P. abdominalis, P. scutullata* and *P. indica*; F. *Gaussia princeps* and *G. sewelli*. Dot lines show degree of separation.

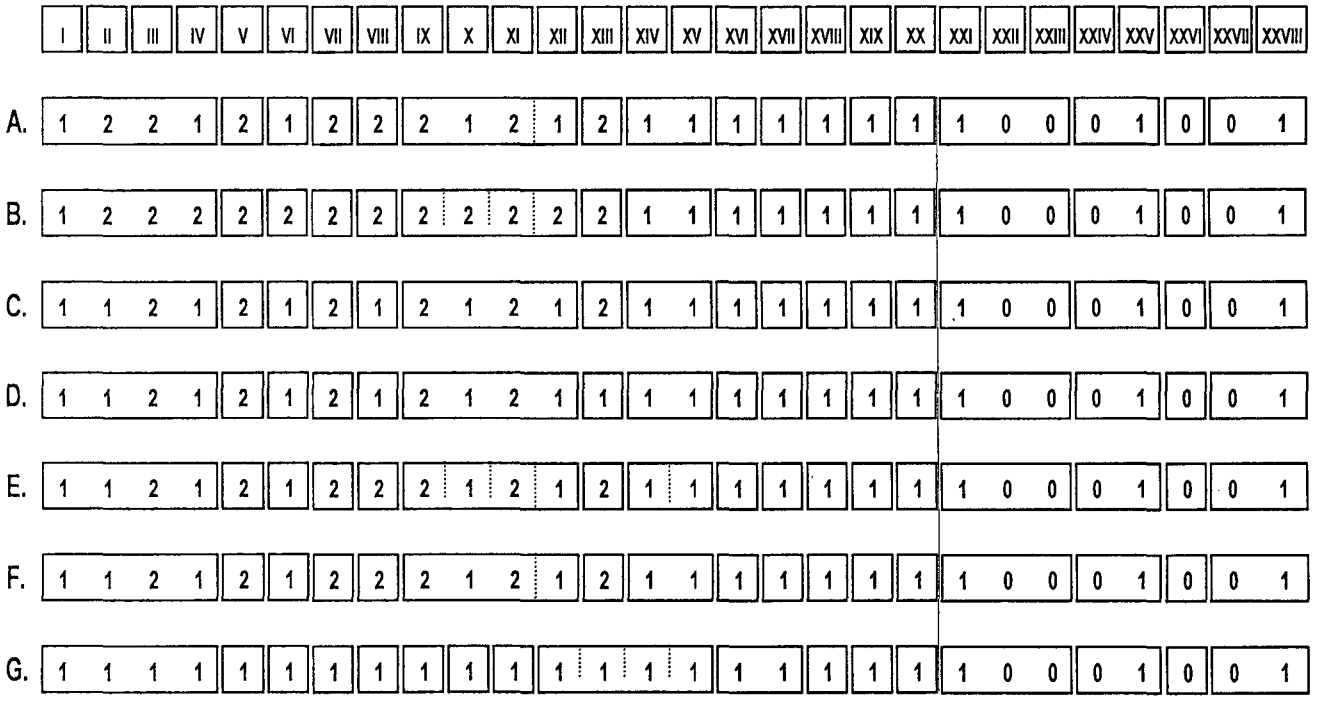

Fig. 2. Schematic comparison of segmentation and segmental aesthetasc numbers of male geniculate antennules in some metridinid species. A. *Metridia princeps* and *M. macrura*; B. *M. pacifica*; C. *Pleuromamma xiphias*; D. *P. abdominalis*; E. *P. scutullata*; F. *P. gracilis*; G. *Gaussia princeps* and *G. sewelli*. Dot lines show degree of separation. Solid line between segments XX and XXI indicates position of geniculation.

and *M. pacifica* (Fig. 2B) carries one on each segments IV-XIII. *Pleuromamma xiphias* (Fig. 2C) has a quadrithek on each segment V, VII, IX, XI and XIII, and *P. abdominalis* (Fig. 2D) is similar to *P. xiphias except* for segment XIII. *P. scutullata* (Fig. 2E) and *P. gracilis* (Fig. 2F) bear a quadrithek on segments V, VII-IX and XIII. *Gaussia princeps* (Fig. 2G) and *G. sewelli* retain a single aesthetasc on the proximal segments II to XIII.

3. Non-geniculate antennule of male. The quadrithek pattern is the same as that of geniculate antennule except for segments II and III having two setae, respectively. *Pleuromamma xiphias, P. abdominalis, Gaussia princeps* and *G. sewelli*, however, show the usual trithek pattern on those segments.

4. Maxillule. In *Metridia* sp. sensu Hattori (1996) the basal endite and the first endopodal segment each have seven setae, which could be the most plesiomorphic condition in calanoids. *M. pacifica* also has seven setae on the basal endite, but it retains six setae on the first endopodal segment. The other genera bear five setae on the basal endite and six setae on the first endopodal segment.

5. Maxilliped. *Metridia* and *Pleuromamma* possess a single outer seta on the syncoxa, but this represents a symplesiomorphy; *Gaussia* lacks this seta.

6. Female fifth leg. Fifth legs of metridinid females show variable segmentation and setation patterns (Fig. 3). The most plesiomorphic condition is found in *Metridia* sp. *Sensu* Hattori (1996): basis with single outer seta and 3-segmented exopod; first exopodal segment with a single outer spine (a in Fig. 3); second with a single outer spine (b in Fig. 3) and a single inner seta (k in Fig. 3); third with two outer spines (d, e in Fig. 3), one distal element (f in Fig. 3) and three inner setae (g, h and i in Fig. 3). Other congeners exhibit more advanced states; the exopod is 2-segmented and only distal spine f and inner setae, g and h are retained on the distal segment. *Pleuromamma* also has 2-segmented exopod and remain a distal spine f and inner setae, g and h. *Gaussia* possesses seta, k on the second exopodal segment and distal spine, f and seta, g on the third one. Therefore, 2-segmented exopod in *Metridia* and *Pleuromamma* may be interpreted as ontogenetic suppression.

A single tree was obtained on the basis of the character matrix (Table 2). The tree length and consistency index are 11 steps and 0.909, respectively. The cladogram shows that *Gaussia* and *Pleuromamma* form a sister group, with *Metridia* which is the first branch to diverge within the family (Fig. 4). The *Pleuromamma-Gaussia* clade is defined by the following synapomorphies: characters 1, 3, 4, 5, 6, 7, 8, 9, 10.

Discussion

The genera of *Metridia* and *Pleuromamma* retain additional aesthetascs on the antennulary segments II to XIII, while *Gaussia* has trithek (two setae plus aesthetasc) on those segments (Giesbrecht, 1892; Soh et al., 1998). These additional aesthetascs, which appear only in adult stage, are a widespread phenomenon among pelagic calanoid copepods (Ohtsuka et al., 1993, 1994; Soh, 1998; Boxshall and Huys, 1998). Huys and Boxshall (1991) considered these could be an adaptation to pelagic

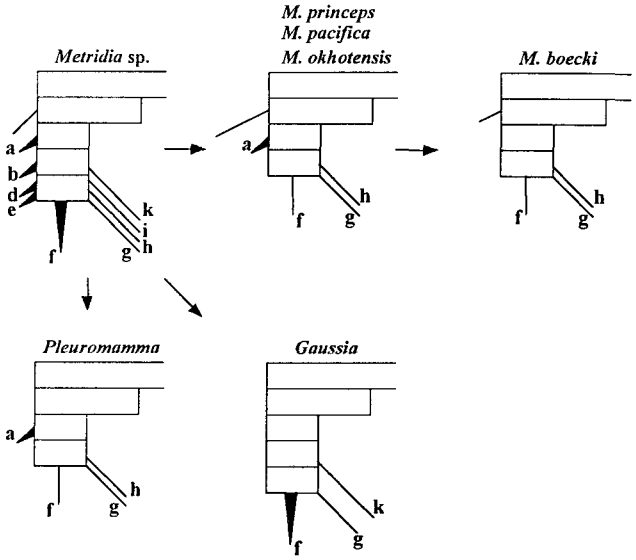

Fig. 3. Schematic illustration of segmental and armature patterns of female fifth legs in some metridinids. Arrows indicate possible derivations of segmentation and armature elemental patterns and are not indicative of ancestor-descendant relationships between taxa.

Table 2. Character data matrix (see Table 1)

Genus	Characters									
	1	2	3	4	5	6	7	8	9	10
Ancestor	0	0	0	0	0	0	0	0	0	0
Metridia	0	1	0	0	0	0	0	0	0	0
Pleuromamma	1	1	1	1	1	1	1	1	1	1
Gaussia	1	0	1	1	1	1	1	1	1	1

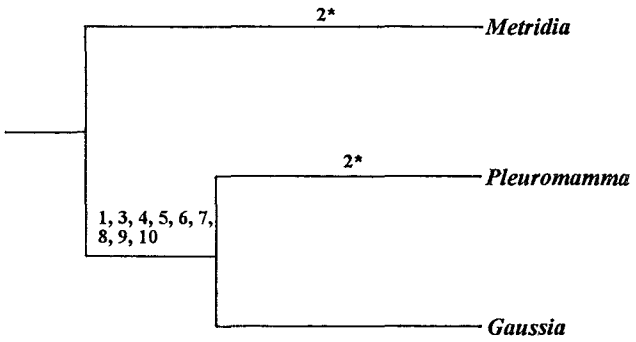

Fig. 4. Cladogram depicting the phylogenetic relationship between three genera of the family Metridinidae. Numbers refer to the characters. Asterisks indicate convergence of the character.

environments that appeared when a calanoid lineage having the usual trithek invaded the pelagic realm. Therefore, the quadritheks on the male antennule in the genera *Metridia* and *Pleuromamma* are probably a synapomorphy, and the loss of these in the genus *Gaussia* (Soh et al., 1998) may represent a character reversal into the ancestral condition. The quadritheks on the female antennule of some *Metridia* species are considered to be an autapomorphy. However, these characters are excluded in our analysis, because there are no evidence whether the quadritheks on these segments of the genera *Metridia* and *Pleuromamma* are plesiomorphic or apomorphic one. Boxshall and Huys (1998) also suggested that the use of aesthetasc patterns in phylogenetic analysis should be urged with caution, because the addition or loss of aesthetascs is evolutionarily more labile than that of other setation elements.

Males of *Metridia* and *Pleuromamma* have a geniculate antennule on either the left or the right one, while *Gaussia* only on the right. On the basis of dimorphic asymmetries of genital systems, antennules and legs 5, Ferrari (1984) suggested that a hypothetical metridinid ancestral male might have predominantly a right geniculate antennule. Although the present cladogram (Fig. 4) does not provide any information of the polarity of male geniculate antennule, Soh (1998)' s phylogenetic analysis of the superfamily Arietelloidea Sars, 1902 including the family Metridinidae indicates that the complete switching of antennule geniculation might occur from the right side to the left.

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