

COMPARATIVE ANALYSIS OF THE ANTENNULES OF ASTEROCHERID
FEMALES (COPEPODA, SIPHONOSTOMATOIDA) — SYMBIONTS OF
MARINE INVERTEBRATES

BY

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ABSTRACT

Segmentation and armature of the antennule of adult females of the copepods representing the primitive siphonostomatoid family Asterocheridae Giesbrecht, 1899 (including 44 nominal genera) are analyzed. The comparison is based on a definition of the position of two articulating segments used as markers for determining segment correspondence and the decision not to presume presence of a segment without morphological proof. The first marker is the short segment bearing up to 8 setae; the second marker is the only segment carrying an aesthetasc. A number of variations in fusion and loss of segments are revealed. The presence of a complex of 3 segments lacking arthrodistal membranes and having 6 or fewer articulating segments in the section between the two markers in a group of four genera (*Cecidomyzon*, *Cystomyzon*, *Hammatimyzon*, and *Oedomyzon* of Stock, 1981), renders these significantly different from other asterocherids. These features are interpreted as neotenic. Two new states characterizing the asterocherids have been found: the short multi-setae segment is separated by an arthrodistal membrane proximally, and the section of the antennule between the two markers has 6-8 articulating segments, armed with up to 2 setae (with the exception of the four genera indicated).

INTRODUCTION

Asterocheridae Giesbrecht, 1899 is a heterogeneous and abundant family of presumably primitive cyclopiform copepods of the order Siphonostomatoida, including about 150 species in 44 genera (fig. 1, appendix I). Asterocherids are found in the benthos from various geographic regions, mostly associated with marine invertebrates such as sponges, cnidarians, echinoderms, and bryozoans, living above, within, or in galls of the hosts. Asterocherids were intensively investigated taxonomically over the last four decades and 32 new genera were described during this period of time. The distribution of species over the genera

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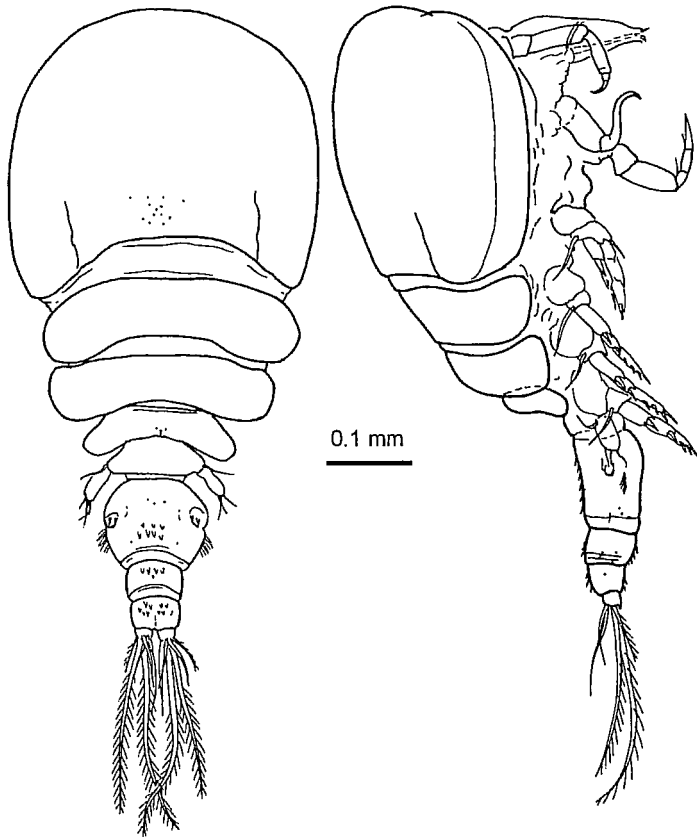


Fig. 1. Female of *Asterocheres simulans* (T. Scott, 1898) (after Ivanenko, 1997): body dorsal and lateral.

is asymmetrical: there is one group of 28 genera, each with one species, and, at the other extreme, one genus with more than 40 nominal species (fig. 2). Despite the considerable morphological variation within the family and the difficulty of distinguishing asterocherids from other families (Stock, 1992), the structure of the family as a whole has not been studied recently.

The family includes siphonostomatoid copepods, which can be grouped by two character states (Stock, 1987): the mandibular palp is present, and (or) the antennule of the female has an aesthetasc on the 2nd, or 3rd, or 4th articulating segment, numbered from the distal end. Both states, together with other states of the asterocherids, correspond to the ancestor of the siphonostomatoids, as proposed by Huys & Boxshall (1991). The primitive family Asterocheridae can be a key group for understanding the phylogeny of siphonostomatoids, but this has not been considered until now.

Number of species in genera of
Asterocheridae Giesbrecht, 1899

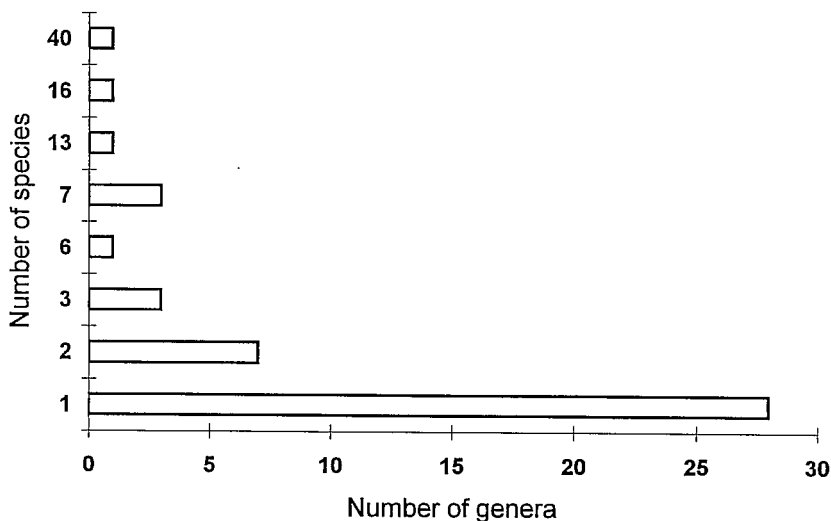


Fig. 2. The distribution of species in genera of the family Asterocheridae Giesbrecht, 1899.

The results of a comparative analysis of currently available data on the morphology of adult female antennules are presented here as a step to a revision of the family Asterocheridae.

METHODS

It is accepted that the setation of segments of copepod antennules is very conservative and can be used for estimating the homology of segments and their complexes. It is assumed that not only the number of setae and aesthetascs, but also their positions on a segment are conserved, even when segments form complexes due to the absence of arthrodial membranes, which usually define an articulating segment.

The 28-segmented state of the antennule as the most primitive for the Copepoda, is used as one of the systems created for homologization of antennular segments in different orders (Huys & Boxshall, 1991). According to this system, it is assumed that each ancestral segment was separated from its adjacent proximal and distal segments by an arthrodial membrane. Roman numerals indicate the ancestral segment.

In this paper, it was decided not to presume the presence of a segment without strong morphological proof. The presence of a segment in the antennule of adult or subadult stages should be demonstrated by setae, aesthetascs, or arthro-

dial membranes. Absence of morphological and (or) developmental indications of presence of a segment is interpreted as a segment lost. Therefore, it is not preferable to suggest that an articulating segment represents more than one ancestral segment without developmental evidence, if a segment separated from other segments by arthrodistal membranes lacks setae or carries only one seta (or aesthetasc). The problem with the identification of homology for some segments reflects current knowledge, and it allows us to recognize the section(s) of the antennule that need more investigation. Loss of segments is a type of characteristic not used actively for comparative analysis of copepods, but it has the same value as other characteristics such as setal groups and articulations.

Two articulating segments were used as markers (or starting points) for revealing segmental correspondence in the adult female antennule of asterocherids (fig. 3). The first marker (A) is the only segment in the antennule of asterocherid

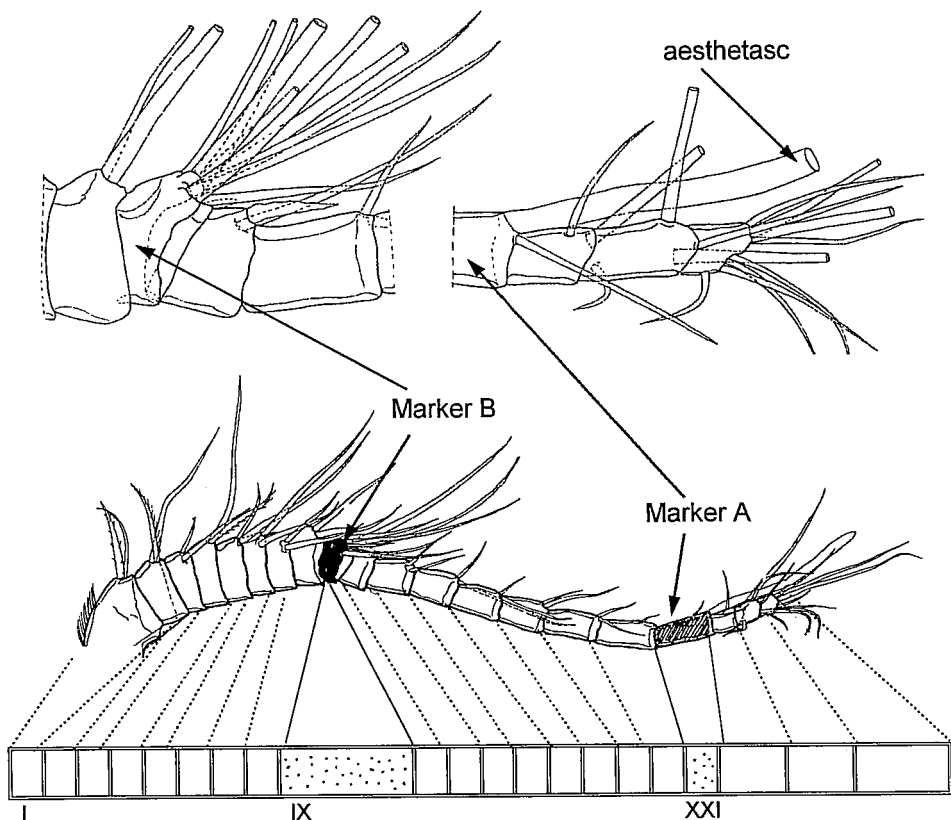


Fig. 3. Marker segments A and B and the ancestral state of the antennule of female asterocherids in correspondence to the adult female antennule of *Asterocheres* spp. (partly after Ivanenko, 1997; Ivanenko & Smurov, 1997). Roman numerals indicate ancestral segment.

females having one easily distinguished aesthetasc. This segment does not form complexes with other segments (with one exception) in either direction, proximal or distal. The second marker segment (B) is the short multi-setae segment armed with not more than 8 setae, not observed for one genus only. This segment does not form complexes proximally and, presumably, not distally either.

The antennules of asterocherids from 16 genera (marked with '*' in appendix I) were investigated during the preparation of this paper.

RESULTS AND DISCUSSION

The antennule of the asterocherid female (and of siphonostomatoids in general) consists of not more than 21 articulating segments, which state is shown in 3 genera of asterocherids (and all other siphonostomatoids): *Asterocheres* Boeck, 1859, *Australomyzon* Nicholls, 1944, and *Tuphacheres* Stock, 1965. This 21-segmented state can be interpreted as ancestral for asterocherids, which evolved due to the formation of 4 complexes: IX-XII, XXII-XXIII, XXIV-XXV, and XXVI-XXVIII, according to the system of Huys & Boxshall (1991).

The section proximal to the marker segment B includes not more than 8 articulating segments. The exception of *Chelacheres longipalpus* Stock & Humes (1995), allegedly having 9 articulating segments (more clearly shown for the male of *Chelacheres optans* Stock & Humes, 1995) according to the original description, was not confirmed, and it actually has 8 articulating segments. This section has the distal segment separated from the marker in all genera, and this state separates the asterocherids from a number of siphonostomatoid families characterized by fusion of the marker segment B with one or more segments of this section. Despite the number of possible variants of the segmental fusion, loss of segments characterizes only *Cystomyzon* and *Oedomyzon*, who have two articulating segments in this section. The first articulating segment corresponds to segment I. The identification of the second articulating segment is complicated and needs additional information: it is armed with 3 to 9 setae and can correspond to 3 to 8 ancestral segments in the section II-VIII. Variants include different cases of entire or partial loss of the arthrodistal membrane, and these variants have diagnostic value for genera (fig. 4).

The section between the markers A and B includes not more than 8 articulating segments. The exception for *Hermacheres montastreae* Stock, 1988, allegedly having 9 articulating segments according to the original description, was not confirmed, and it actually has 8 articulating segments also. One or 2 segments may be lost and the section can include only 7 or even 6 articulating segments (fig. 4). Data show that the number of articulating segments can vary among

Different variants of female antennules in Asterocheridae

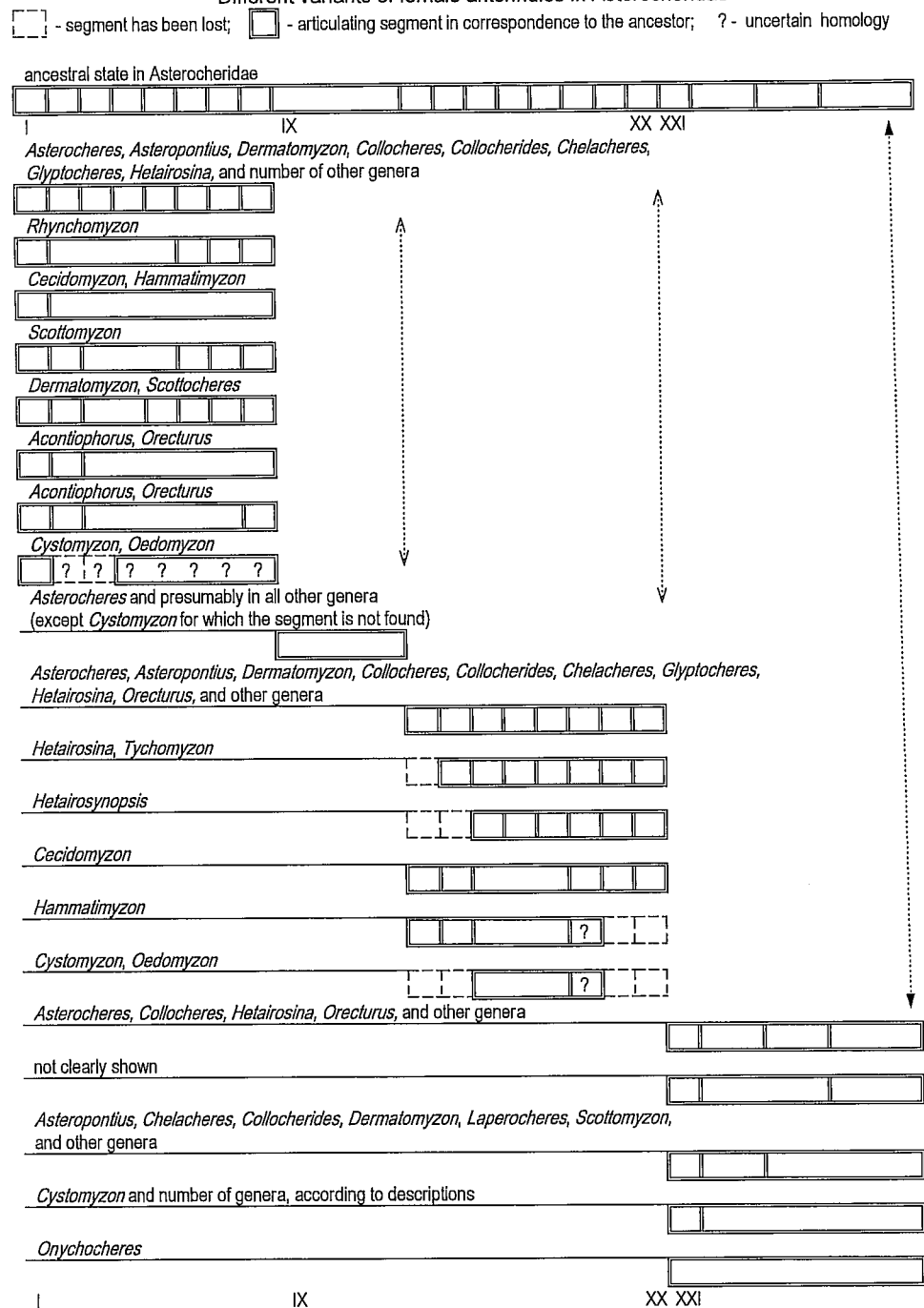


Fig. 4. Different variants of fusion and loss of segments in the antennules of adult females of the family Asterocheridae. Roman numerals indicate ancestral segment.

congeneric species. This variability can partly result from an overlooked, short segment following marker B. This section is not characterized by the formation of segmental complexes, except for a 3-segmented complex in four deep-sea genera *Cecidomyzon*, *Cystomyzon*, *Hammatimyzon*, and *Oedomyzon* (of Stock, 1981) representing one group. Additionally, the genus *Hammatimyzon* and the two genera *Cystomyzon* and *Oedomyzon*, are characterized by loss of 2 and 4 segments, respectively. Correspondence of the remaining segments is complicated, but the 3-segmented complex comprises, segments XV-XVII of the ancestral copepod. Correspondence of one articulating segment located proximal to the complex XV-XVII in *Cystomyzon*, *Hammatimyzon*, and *Oedomyzon* cannot be established now and will depend on the pattern of the antennule's ontogeny. This segment can correspond to one of the segments XVIII to XX. The presence of 6-8 articulating segments being separated is a characteristic of asterocherids (exception in 4 genera, as above) which (with other characteristics) allows to differentiate them from other siphonostomatoids.

The marker segment B was not observed in *Cystomyzon*. However, the presence of marker A and the triple segment (XV-XVII), which can be used as an additional marker, suggests that this multi-setae segment was lost or is represented by the distal part of the second articulating segment. The pattern of setation and articulation of this antennule is much closer to that of the third copepodid stage of *Asterocheres*, than to any other copepodid stages described by Boxshall & Huys (1998).

The section of the antennule following the marker segment A includes not more than 3 articulating segments, which may lose all their arthrodistal membranes except the one with the marker segment. The remarkable exception is the genus *Onychocheres* Stock & Gooding, 1986. In this animal, the marker segment is included in one segment with the distal part of the antennule. This is exceptional for the asterocherids' state, but it is common for most other siphonostomatoids and presumably corresponds to the state of these segments in the first copepodid stage of *Asterocheres* (see Boxshall & Huys, 1998). The difficulty of observing arthrodistal membranes in this tiny section of the antennule complicates determination of the number of arthrodistal membranes in many genera. Nevertheless, the available data suggest that all variants of arthrodistal membrane loss are possible, but always result in the presence of 3 segments in all genera (fig. 4).

The loss of arthrodistal membranes in the antennule of asterocherids does not change the position and number of setae (fig. 3) to any appreciable extent. Each seta has a more or less fixed position on each segment. There is a trend to loss of setae on the marker segment B and on the segments following the marker A. Loss of one seta is often found for the segments I and VIII, but loss of setae has

not clearly been shown for the segments between the markers A and B of the antennule.

The remarkable characteristics of the antennule in the group of four gall-inhabiting genera described by Stock (1981) can be interpreted as neotenic. These features, with others shown in the original descriptions, require reconsideration of the taxonomic status of this group, which should be recognized as a separate family.

The presence of 28 segments has been proposed a priori in all copepod species, and at any copepodid stages (Huys & Boxshall, 1991; Boxshall & Huys, 1998). In contrast, Ferrari & Benforado (1998) assumed a model in which segments as setal groups are added during copepodid development. However, it is obvious that the segment, as a structural unit, can be reduced due to different processes such as oligomerization or neoteny (Beklemishev, 1964a, b; Dogiel, 1936, 1954). Consequently, applying an assumption in comparative morphology by which the structure (a segment) is present in all groups of representatives without supplying phenotypic proof of its presence may produce numerous schemes that cannot be easily falsified. In the same manner, simply describing the number of articulating segments does not permit a correct interpretation of homologous parts of the antennule and so cannot be used effectively for taxonomic decisions on the level of more than one genus. Careful comparative analysis based on real morphological data, including the introduction of markers, is a productive tool for taxonomy and phylogeny.

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APPENDIX I

List of nominal genera of the family Asterocheridae (* = studied by the author):

1. *Acontiophorus* Brady, 1880
 - *2. *Asterocheres* Boeck, 1859 (syn. *Madacheres* Humes, 1996)
 3. *Asterocherooides* Malt, 1991
 4. *Asteropontella* Stock, 1988
 - *5. *Asteropontius* Thompson & A. Scott, 1903
 6. *Asteropontooides* Stock, 1975
 7. *Asteropontopsis* Stock, 1987
 8. *Australomyzon* Nicholls, 1944
 - *9. *Cecidomyzon* Stock, 1981
 - *10. *Chelacheres* Stock & Humes, 1995
 11. *Cheramomyzon* Humes, 1989
 12. *Cletopontius* Thompson & A. Scott, 1903
 - *13. *Collocheres* Canu, 1893
 - *14. *Collocherides* Stock, 1971
 - *15. *Cystomyzon* Stock, 1981
 - *16. *Dermatomyzon* Claus, 1889
 17. *Discopontius* Nicholls, 1944
 18. *Doropontius* Thompson & A. Scott, 1903
 - *19. *Glyptocheres* Humes, 1987
 20. *Gomumucheres* Humes, 1996
 21. *Hammatinmyzon* Stock, 1981
 - *22. *Hermacheres* Stock, 1987
 - *23. *Hetairosina* Humes, 1991
 24. *Hetairosynopsis* Humes, 1996
 25. *Indomyzon* Ummerkuty, 1966
 26. *Inermocheres* Boxshall, 1990
 - *27. *Laperocheres* Ivanenko, 1998
 28. *Meandromyzon* Stock, 1988
 29. *Mesocheres* Norman & T. Scott, 1905
 30. *Monocheres* Stock, 1966
 - *31. *Oedomyzon* Stock, 1981
 - *32. *Onychocheres* Stock & Gooding, 1986
 - *33. *Orecturus* Humes, 1992
 34. *Parasterocheres* Humes, 1996
 35. *Peltomyzon* Stock, 1975
 36. *Phyllocheres* Humes, 1996
 37. *Psilomyzon* Stock, 1965
 38. *Rhynchomyzon* Giesbrecht, 1895
 39. *Scottocheres* Giesbrecht, 1897
 - *40. *Scottomyzon* Giesbrecht, 1897
 41. *Sinopontius* Boxshall, 1990
 42. *Siphonopontius* Malt, 1991
 43. *Tuphacheres* Stock, 1965
 44. *Tychomyzon* Humes, 1991
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