

Comparison of Female Antennules in Some Genera of Cyclopidae (Copepoda, Cyclopoida): Their Significance for Phylogeny*

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Abstract: The homology of the antennular segments of species belonging to some genera of Cyclopidae is determined by comparing the common setation patterns on female antennules. Comparison of the setation pattern has confirmed that there are always 44 setae and 3 aesthetascs on the female antennules of all the genera examined. This study shows that the strict application of homology is essential in order to resolve the phylogenetic relationships between the genera of Cyclopidae. Although both *Ectocyclops phaleratus* and *Paracyclops canadensis* have 11-segmented antennules, the analysis of segmental homologies has shown that the 11-segmented condition has occurred due to convergent evolution in these two species belonging to different genera. In addition, several segmental fusions of the female antennules have been identified as apomorphic states and can be used in phylogenetic studies.

Key Words: Copepoda, female antennule, homology, Cyclopidae

Cyclopidae (Copepoda: Cyclopoida) Familyasının Bazı Cinslerine Ait Türler Arasında Birinci Anten Karşılaştırması ve Filogenideki Önemi

Özet: Cyclopidae (Copepoda, Cyclopoida) familyasının bazı cinslerine ait temsili türlerin dişilerinin birinci antenleri arasındaki segment homolojileri antenler üzerindeki ortak setal düzen karşılaştırılarak belirlenmiştir. Setal düzenlerin karşılaştırılması, incelenen tüm cinslerine ait türlerde seta sayısının daima 44 ve aesthetasc sayısının ise daima 3 olduğunu ortaya çıkartmıştır. Cinsler arasındaki filogenetik ilişkilerin açığa çıkartılabilmesi için detaylı homoloji analizinin kesinlikle gerekli olduğu ortaya konulmuştur. *Ectocyclops phaleratus* ve *Paracyclops canadensis* türlerinin her ikisinde de antenler 11 segmentli olmasına rağmen, 11 segmentlilik durumu farklı cinslere ait bu türlerde konvergent evrim sonucu ortaya çıkmıştır. Bunlara ek olarak, dişi anten segmentlerinde meydana gelen pek çok segmental kaynaşma, filogenetik analizde kullanılacak birçok apomorfi ortaya çıkartmıştır.

Anahtar Sözcükler: Copepoda, dişi birinci anteni, homoloji, Cyclopidae

Introduction

The family Cyclopidae Dana, 1853, belonging to the order Cyclopoida, currently contains nearly 50 genera (Dussart and Defaye, 1985; Reid, 1988, 1993). There is no existing modern systematic study of the entire family Cyclopidae, nor of the subfamilies Eucyclopinæ and Cyclopinæ. Most of the genera in the Cyclopidae are in urgent need of revision (Karaytug, 1999).

The strict application of homology in inferring the copepod phylogeny by Huys and Boxshall (1991) has been a revolution in systematic studies on copepods. Boxshall and Huys (1992) strongly stressed that the identification of homologous characters and character states is a priority for phylogenetic analysis, and the most difficult task in any phylogenetic study is correctly identifying homologous shared derived character states (synapomorphies). They concluded that a failure to

devote sufficient attention to homology lies at the origin of many of the new phylogenetic schemes that appear and then disappear again with great rapidity. Phylogenetic analysis can best be improved by making positive statements on the homology of all the characters used in the analysis (Huys and Boxshall, 1991; Boxshall and Huys, 1992; Karaytug and Boxshall, 1996, 1998a, 1999).

The antennules of copepods are uniramous and comprise up to 27 expressed segments (Huys and Boxshall, 1991). The female antennules of the genera of Cyclopidae are basically cylindrical with no more than 21 expressed segments. The 21-segmented antennule has only been recorded in species of *Euryte* Philippi, 1843.

The first attempt to identify the pattern of setal and segmental homologies (with reference to the hypothetical 28-segmented antennule of the ancestral copepod

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proposed by Huys & Boxshall in 1991) of the female antennules within the family Cyclopidae was made between the species of *Paracyclops* Claus, 1893. This study showed that such examination of the female antennule could provide significant information for the rather confused systematics of the family Cyclopidae (Karaytug and Boxshall, 1998a).

In this paper, we attempt to show that the analysis of the setation pattern and hence the establishment of the homologies of the segments can be extended, simply by applying the similar procedure performed for the *Paracyclops* species (Karaytug and Boxshall, 1998a), to the other genera of the family Cyclopidae.

Materials and Methods

Specimens of nine species representing eight genera were studied. Adult females were collected from different localities in Turkey and the observations were based on these materials except that the antennule of *P. canadensis* (Willey, 1934) was redrawn from Karaytug & Boxshall (1998b). The antennules were removed and mounted in lactophenol. Fragments of coverslip were placed between the slide and the coverslip to avoid crushing and to facilitate rotation, which allowed the antennules to be viewed from all angles. All drawings were made with the aid of a drawing tube using Nomarski differential interference contrast (DIC) attached to an Olympus BX 50 microscope, and an ocular micrometer was used to take measurements.

The homology of the antennular segments was established by comparing the distribution of the setae on each expressed segment with reference to their position and particular elements recognized here as markers (two arrows and a star are inserted in the Figure to indicate these). In the Figure, dotted lines indicate the homologous segments between the antennules.

Roman numerals that are shown in parenthesis in the results and discussion section indicate derivations from hypothetical 28-segmented ancestral antennule proposed by Huys and Boxshall (1991).

Species studied and collection data:

Megacyclops viridis Jurine, 1820: (Turkey, Karamandere, Tekirdağ, 30.04.2001, found in a small pond, coll. S. Karaytug and S. Sak).

Macrocyclus fuscus (Jurine, 1820): (Turkey, İkizcetepeler dam lake, Balıkesir, 25.05.2001, coll. S. Karaytug).

Acanthocyclus robustus (Sars, 1863): (Turkey, a creek in Ormanlı village, Istanbul, 30.04.2001, coll. S. Karaytug and S. Sak).

Cyclops strenuus Fischer, 1851: (Turkey, Seyhan dam lake, Adana, 14.10.1992, coll. S. Karaytug).

Diacyclops bicuspidatus (Claus, 1857): (Turkey, Uluabat lake, Balıkesir, 09.03.2002, coll. A. Alper).

Eucyclops serrulatus (Fischer, 1851): (Turkey, Riva creek, Ömerli village, İstanbul, 01.05.2001, coll. S. Karaytug and S. Sak).

Ectocyclus phaleratus (Koch, 1838): (Turkey, Yamansaz lake, Antalya, 06.07.2001, coll. S. Karaytug and S. Sak).

Paracyclops canadensis: (The antennule of this species was redrawn from Karaytug & Boxshall (1998b)).

P. imminutus Kiefer, 1929: (Turkey, Karasatı pond, Keşan, Edirne, 28.04.2001, coll. S. Karaytug and S. Sak).

Results and Discussion

Seventeen is the largest number of segments found for the antennules of adult females in this study. Seventeen segments are found in *Megacyclops viridis*, *Macrocyclus fuscus*, *Acanthocyclus robustus*, *Diacyclops bicuspidatus* and *Cyclops strenuus* and the segmental setation formula for each of these species is 8, 4, 2, 6, 4, 2, 2, 1, 1, 0, 1, 1 + aesthetasc, 0, 1, 2, 2 + aesthetasc, 7 + aesthetasc. By comparing the antennules with the *Paracyclops* antennules (Karaytug and Boxshall, 1998a) and the antennule of the female *Euryte robusta* Giesbrecht, 1900 (Huys and Boxshall, 1991), the ancestral segments (shown in Roman numerals below) of the 17-segmented antennules (shown in Arabic numerals) of the species studied can be identified as follows:

1 (I-V), 2 (VI-VII), 3 (VIII), 4 (IX-XI), 5 (XII-XIII), 6 (XIV), 7 (XV-XVI), 8 (XVII), 9 (XVIII), 10 (XIX), 11 (XX), 12 (XXI), 13 (XXII), 14 (XXIII), 15 (XXIV), 16 (XXV), 17 (XXVI-XXVIII). A comparison of the 17-segmented antennules of the species used in this study with those of *Er. robusta* revealed that the determinations of segment 7 of *Paracyclops waiariki* Lewis, 1974 as ancestral

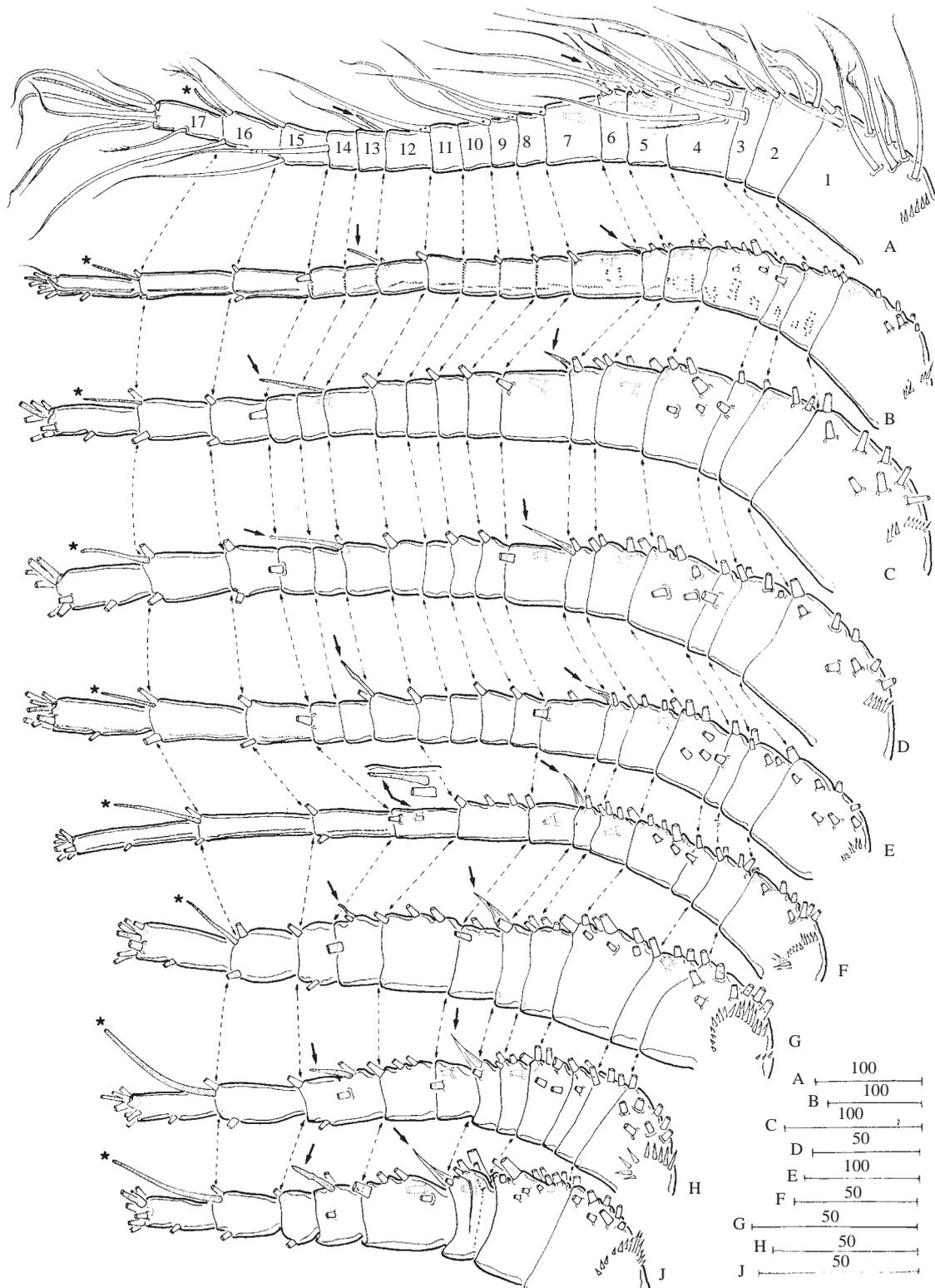


Figure. Comparison of adult female antennules of some cyclopoid species belonging to family Cyclopidae. Antennules are all in ventral view. A. *Megacyclops viridis*; B. *Macrocyclops fuscus*; C. *Acanthocyclops robustus*; D. *Diacyclops bicuspidatus*; E. *Cyclops strenuus*; F. *Eucyclops serrulatus*; G. *Ectocyclops phaleratus*; H. *Paracyclops canadensis*; J. *Paracyclops imminutus*. Scale bars in mm.

segment XV and segment 8 as ancestral segments XVI-XX by Karaytug and Boxshall (1998a) are erroneous. The correct identification should be as follows: segment 7 of *P. waiariki* is derived from ancestral segments XV-XVI and segment 8 is derived from ancestral segments XVII-XX.

The pattern of setation elements on cyclopoid antennules permits the unequivocal identification of the pattern of ancestral segmental homologies (Karaytug and Boxshall, 1996, 1998a). The common setation pattern contains a number of elements which act as reference points along the antennule. On segment 6 (XIV) of *Megacyclops viridis* there is a spine located distally (arrowed in the Figure), which provides an important reference. In addition, on segment 12, the aesthetasc (indicated by an arrow in the Figure) derived from ancestral segment XXI provides another significant reference point in concert with the other aesthetasc (indicated by a star in the Figure) on segment 16, corresponding to ancestral segment XXV (Karaytug and Boxshall, 1996, 1998a).

The key point is that each seta present on every segment of the antennules of one species has a homologue in all the other species examined. Careful attention to the position of every seta on every segment permits the identification of its homologue. Segmental boundaries and the patterns of segmental fusions with respect to the ancestral 28-segmented antennule postulated by Huys and Boxshall (1991) can then be identified by back-tracking from the antennule of the adult female, with reference to the number and position of the setae on each segment and, principally, to the position of the marker setae and aesthetasc (Karaytug and Boxshall, 1996, 1998a).

It has long been considered that the multi-segmented antennule is more primitive than the antennule with few expressed segments (Boxshall et al. 1984; Ho, 1986; Huys and Boxshall, 1991; Reid, 1993). The assumption that the evolution of copepods has proceeded predominantly by oligomerisation has always been present in studies on the phylogeny (Huys and Boxshall, 1991). Such treatments indicate that, in the evolution of copepods the most widely accepted process has been the trend towards fusion and reduction in the number of segments; the multi-segmented antennule being inferred to be more primitive than the antennule with few

expressed segments (Boxshall et al. 1984). Methodologically, however, polarisation of the characters found on the antennules of the species used in this study can also be achieved by outgroup comparison in cladistic analysis (Başbüyük and Çıplak, 1997) using, for example, the antennules of *Euryte robusta* as an outgroup.

The antennules of *Eucyclops serrulatus*, *Ectocyclops phaleratus*, *Paracyclops canadensis* and *P. imminutus* shown in the Figure exhibit one or more segmental fusions between segments homologous with the second and fifteenth segments of the antennules of *Megacyclops viridis*, *Macrocyclus fuscus*, *Acanthocyclops robustus*, *Diacyclops bicuspidatus* and *Cyclops strenuus*. Comparative studies indicate that several segmental fusions on the antennules of some species examined can be defined as apomorphies: these fusions are as follows:

The condition where no fusion occurs between the second (VI-VII) and third (VIII) (this segment corresponds to ancestral segments VIII-XI in *Ec. phaleratus*) segments is observed in *Me. viridis*, *Ma. fuscus*, *A. robustus*, *D. bicuspidatus*, *C. strenuus*, *Eu. serrulatus*, *Ec. phaleratus* and *P. canadensis*. The fusion of these two segments appears only in *P. imminutus*, and this derived condition is putatively an autoapomorphy of *P. imminutus*.

The condition that no fusion occurs between third (VIII) and fourth (IX-XI) segments is observed in *Me. viridis*, *Ma. fuscus*, *A. robustus*, *D. bicuspidatus*, *C. strenuus*, *Eu. serrulatus* and *P. canadensis*. The fusion of these two segments appears in *Ec. phaleratus* and *P. imminutus*, and this derived condition is a synapomorphy of these two species.

The condition where no fusion occurs between the fifth (XII-XIII) and sixth (XIV) segments is observed in *Me. viridis*, *Ma. fuscus*, *A. robustus*, *D. bicuspidatus*, *C. strenuus*, *Eu. serrulatus* and *P. canadensis*. This condition is found between the fourth (XII-XIII) and fifth (XIV) segments of *Ec. phaleratus*. The partial fusion of these two segments appears only in *P. imminutus*, and this derived condition is another derived state for *P. imminutus*.

The condition where no fusion occurs between the seventh (XV-XVI) and eighth (XVII) segments is observed in *Me. viridis*, *Ma. fuscus*, *A. robustus*, *D. bicuspidatus*, *C. strenuus*, *Eu. serrulatus* and *P. canadensis*. This condition is observed between the sixth (XV-XVI) and seventh (XVII-

XX) segments of *Ec. phaleratus*. The fusion of these two segments appears only in *P. imminutus*, and this derived condition is also a derived state seen only in *P. imminutus*.

The condition where no fusion occurs between the eighth (XVII), ninth (XVIII), tenth (XIX) and eleventh (XX) segments is observed in *Me. viridis*, *Ma. fuscus*, *A. robustus*, *D. bicuspidatus* and *C. strenuus*. The fusion of these segments appears in *Eu. serrulatus*, *Ec. phaleratus*, *P. canadensis* and *P. imminutus*, and this derived condition is a synapomorphy of *Eu. serrulatus*, *Ec. phaleratus*, *P. canadensis* and *P. imminutus*.

The condition where no fusion occurs between the twelfth (XXI), thirteenth (XXII) and fourteenth (XXIII) segments is observed in *Me. viridis*, *Ma. fuscus*, *A. robustus*, *D. bicuspidatus* and *C. strenuus*. The fusion of these segments appears in *Eu. serrulatus*, *Ec. phaleratus*, *P. canadensis* and *P. imminutus*, and this derived condition is a synapomorphic state for those species.

The condition where no fusion occurs between the fourteenth (XXIII) and fifteenth (XXIV) segments is observed in *Me. viridis*, *Ma. fuscus*, *A. robustus*, *D. bicuspidatus*, *C. strenuus*. This condition is observed between the ninth (XXI-XXIII) and tenth (XXIV) segments of *Eu. serrulatus*, between the eighth (XXI-XXIII) and ninth (XXIV) segments of *Ec. phaleratus* and between the fifth (XXI-XXIII) and sixth (XXIV) segments of *P. imminutus*. The fusion of these two segments appears only in *P. canadensis*, and this condition is a derived state for *P. canadensis*.

The largest number of segments known for the antennules of females in the family Cyclopidae is 21, and this was determined in *Euryte*. The total number of setae and aesthetascs is 47 (44 setae and 3 aesthetascs) in *Euryte robusta* (Huys and Boxshall, 1991). Our comparative study revealed that the total number of setae and aesthetascs on the antennule of *Er. robusta* is exactly the same in every species of the genera examined in this study as well as in species of *Paracyclops* (Karaytug and Boxshall, 1998a). This proves that the setal elements are evolutionarily highly conservative, and particular attention should be given to the identification of every single setal element in the descriptions. Any loss or gain of a seta on the antennules of adult females should be

noted as this can provide a significant character in systematic studies of Cyclopidae (Karaytug and Boxshall, 1999).

Karaytug and Boxshall (1998a) pointed out that simple total segment numbers should not be used in the antennules of adult females as characters in cladistic analysis. This study showed that both *Ec. phaleratus* and *P. canadensis* have 11-segmented antennules but, as can be seen from the Figure the segments are not all homologous. Segments 3 and 4 (ancestral segments VIII and IX-XI) of *P. canadensis* failed to separate in *Ec. phaleratus* whereas segments 8 and 9 (ancestral segments XXI-XXIII and XXIV) of *Ec. Phaleratus*, failed to separate in *P. canadensis*. The 11-segmented state in these two species is convergently derived, and a similar convergence was determined between the antennules of *P. affinis* and *P. yeatmani* (Karaytug and Boxshall, 1998a).

The systematic concept of the Cyclopidae continues to be based primarily on the form and armature of the fifth leg. The subfamily Eucyclopinae is essentially defined by possession of three elements (setae or spines) on the terminal (or only) segment of this leg. Genera with two or fewer elements at this location are considered to belong to the subfamily Cyclopinae. The diagnoses of many genera of this group remain vague and somewhat controversial. The origin of many taxonomic problems within the Cyclopidae can be attributed to workers arbitrarily including newly discovered species into particular genera.

Detailed descriptions of species are necessary in order to have more characters available to establish rigorous modern diagnoses of the genera of Cyclopidae. Therefore, the fine structure of female antennules is a promising source for characters in future systematic studies of the genera of Cyclopidae. It has already been shown that the female and male antennules provide a considerable number of significant characters that are valuable both for taxonomic identification and for phylogenetic studies (Karaytug and Boxshall, 1998a, 1999). It should be pointed out that the correct identification of homologous elements is absolutely crucial to this process and necessitates careful comparative studies between species.

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