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ON THE HOMOLOGY OF ANTENNAL ARTICLES IN ISOPODA

BY

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INTRODUCTION

The antennae of Isopoda show important features which find application in taxonomy. To these features belong the number of peduncular articles, the length of the flagellum, the distribution of aesthetascs, remarkable setae and spines. In spite of the significance of these features, a survey of taxonomic literature of the last decade shows that often there is little knowledge about the identity of antennal articles and repeatedly peduncular and antennal articles have been confused. In the following attention shall be drawn on the results of early isopodologists, and moreover new features will be described as criteria for the identification of antennal articles.

FLAGELLUM

The distinction of peduncle and flagellum has its roots in the functional division of the crustacean antennae. The flagella bear sensory organs, especially chemosensoric aesthetascs on antenna one and mechanosensoric setae on antenna two (Schultz, 1969; Nielsen & Strömberg, 1973; Alexander, 1977; Risler, 1977, 1978 etc.), and they need the mechanical properties of an elastic rod, which can be moved in any direction to come into contact with the material that has to be investigated (water, food, substratum). The peduncle for the most part serves as shaft and carrier of these rods. Because of their function and morphology the broad and robust basal articles are ascribed to the peduncle, and the remaining small and short, usually numerous articles, to the flagellum. So it is not difficult to find out that in many Isopoda antenna one has 3 and antenna two 5 peduncular articles. For comparison of different types of antennae see figs. 34, 35 in Schultz, 1969 and fig. 1 in the present paper.

Unfortunately several isopods have no clear morphological differentiation of antennal segments. In these cases typical features of the setation help to discriminate the articles. Flagellar anatomy (muscles, proprioceptors) has not been taken into consideration.

THE FIRST ANTENNA

Early isopodologists (e.g., Racovitza, 1912, 1925; Hansen, 1925) had to name the structures of "their" crustacean group and helped themselves by

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THE STRUCTURE OF THE ALIMENTARY CANAL OF TWO FRESHWATER COPEPODS OF DIFFERENT FEEDING HABITS STUDIED BY LIGHT MICROSCOPE

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INTRODUCTION

Copepods play an important role in Lake Balaton, Hungary, as the most abundant planktonic crustaceans. Among them, the calanoid *Eudiaptomus gracilis* (G. O. Sars, 1863) and the cyclopoid *Cyclops vicinus vicinus* Ulianine, 1875, are the most significant (Ponyi, 1975). The way of feeding of these two copepods is different: the former being a filtering organism, the latter a predatory one. Hence, they are located on different levels in the food chain.

The microscopic structure of the alimentary canal of calanoid species has been investigated previously only in few representatives: *Calanus finmarchicus* (Gunnerus, 1770) (cf. Dakin, 1908; Lowe, 1935; Marshall & Orr, 1955), *Calanus helgolandicus* (Claus, 1863) (cf. Ong & Lake, 1969), *Centropages typicus* Krøyer, 1849 (cf. Arnaud et al., 1978), *Epilabidocera amphitrites* McMurrich, 1916 (cf. Park, 1966), and *Calanus* sp. (cf. Gauld, 1957), all marine species. I could not find any similar report on freshwater forms. Descriptions available on cyclopoid copepods are even less numerous (Hartog, 1888; Farkas, 1923; 1939), but all of these pertain, in contrast to those on calanoids, to freshwater species.

The aim of the present work was to compare the alimentary canal of two copepods with different feeding habits, by microscopic study, and to relate the differences found to their different ways of nutrition.

MATERIAL AND METHODS

Adult specimens, both male and female, of *Eudiaptomus gracilis* (G. O. Sars), occurring in Lake Balaton all the year round, and of *Cyclops vicinus vicinus* Ulianine, to be found mainly in autumn and in spring, were selected from samples collected by plankton hauls.

The specimens were fixed in toto in Bouin's solution, and after paraffin embedding serial sections of 7 μm were stained by the hematoxylin-eosin technique. Only freshly collected animals have been worked up. The following

comparing them to the morphology of other crustaceans. Since then there has been no doubt about the fact, that the antenna one of Isopoda has a peduncle with 3 segments. The rare occurrence of a second flagellum, or what remains of it, on the third article (*Bathynomus*; Epicaridea: fig. 1H) allows a homologization of this article with the last peduncular segment of other Malacostraca.

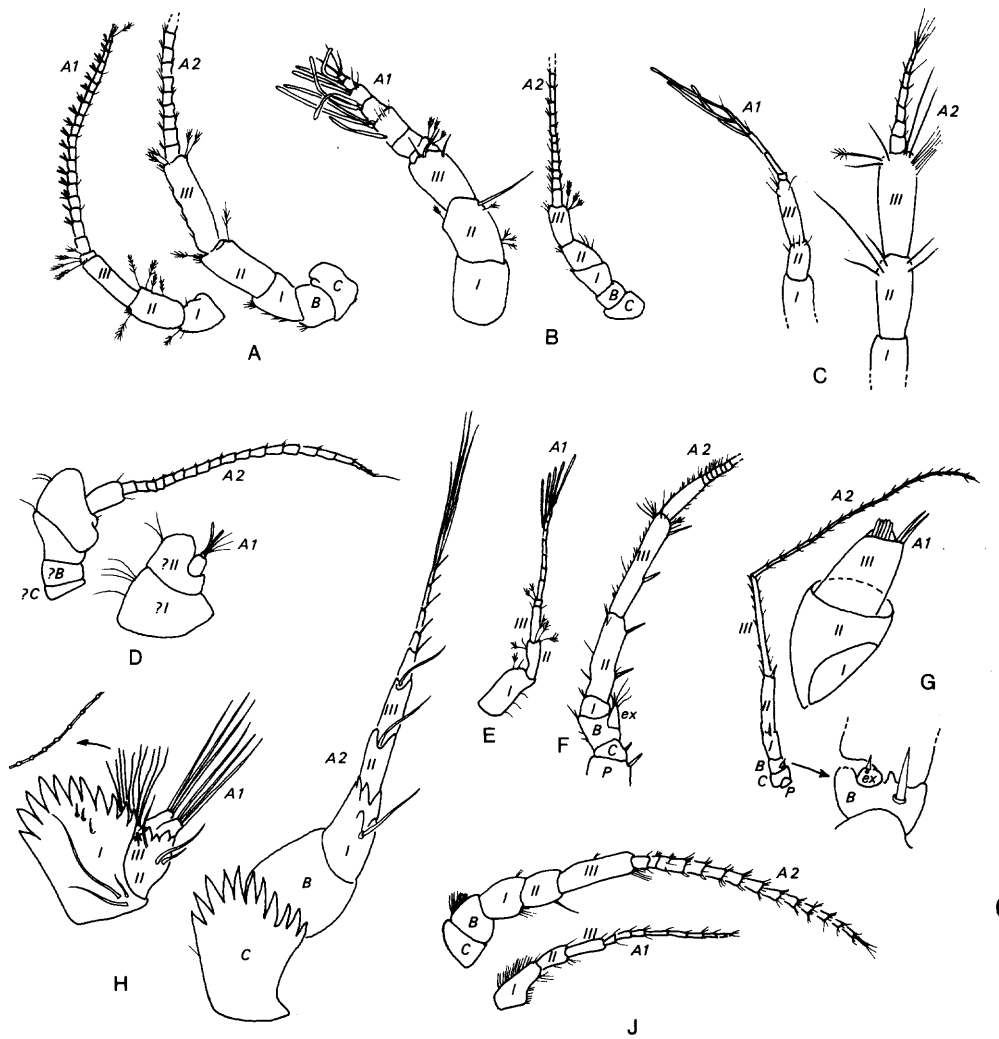

Fig. 1. Antennae of several isopod taxa. A, B, Cirolanidae: A, *Sphaeromides raymondi* Dollfus, after Racovitza, 1912; B, A1 of *Cirolana anadema* Glynn, 1972, A2 of *C. borealis* Lilljeborg, after Sars, 1897; C, Gnathiidea: A1 of *Gnathia wagneri* Monod, 1926, A2 of *G. vanhoeffeni* Menzies, 1962; D, Plakarthriidae: *Plakarthrium punctatissimum* (Pfeffer), after Wilson et al., 1976; E, F, Asellota: A1 of *Ianirella caribbica* Menzies, 1956, A2 of *Iathrippa longicauda* (Chilton), after Hurley, 1957; G, Oniscoidea: *Ligia italica* Fabricius, after Vandel, 1960; H, Epicaridea: *Clypeoniscus hanseni* Giard & Bonnier, after Nielsen, 1969; J, Phreatoicoidea: *Phreatomerus latipes* (Chilton), after Nicholls, 1942. A1, antenna 1; A2, antenna 2; P, praecoxa; C, coxa; B, Basis; ex, exopodite; I-III, peduncular segments.

Often the fusion of articles implies a shortening of the antennula and possibly a reduction of the number of peduncular segments. In these cases the counting of articles is of no use for the determination of homologies; features have to be found, which characterize single articles. This is not easy as the setation of isopod antennae is poorly known; unfortunately taxonomists seldom care much about a faithful reproduction of setation (fig. 1 shows some exceptions). A comparison of some species of different suborders proves that at least the limit between peduncle and flagellum can easily be found.

In most isopods (fig. 1A, B, E; fig. 2) the fourth article of antenna one (= first flagellar article) is particularly short and a closer examination reveals the presence of one or a few plumose sensory setae, but there are no aesthetascs and few or no simple setae (fig. 2). Here we have the characteristic features of the first flagellar article, which enable us to find the limit between peduncle and flagellum in those cases, where a homologization is difficult. Aesthetascs can be found on some of the more distal articles. The last article primitively bears only simple setae and one plumose seta (*Asellus*: fig. 2A; *Cirolana*: fig. 2B), but often receives through fusion with other articles one or more aesthetascs (fig. 2E, F, G). Fig. 32 in Schultz (1969) shows such a generalized antennula.

Difficulties arise in cases of extreme reduction, where the first flagellar article disappeared completely or fused with other articles (Plakarthriidae, Oniscoidea, Epicaridea: figs. 1D, G, H). Comparative anatomy may yield some good results in these cases. Comparative morphology allows an analysis of the fate of single articles and setae in the phylogenetic process of fusion and reduction of the flagellum (e.g., Wägele, 1981: fig. 32).

It is not clear whether aesthetascs may appear inserting directly on the third peduncular segment, a phenomenon that can be explained by the fusion of the latter with the flagellum. Aesthetascs have been described on the peduncle of Oniscoidea (fig. 1G) and Epicaridea (fig. 1H), but it is not known whether vestiges of flagellar articles are present.

Among the Valvifera some Idoteidae show no first flagellar article which seems to be completely absent, but the original situation can be found in Arcturidae (figs. 2D, E).

THE SECOND ANTENNA

The second antenna of the Malacostraca primitively has the character of a biramous appendage with exo-, endopodite and a basipodite of 3 segments (praecoxa, coxa, basis: Hansen, 1893). A small exopodite still can be found in some Isopoda (Asellota, Ligiidae: figs. 1F, G) on the third peduncular article. In isopods as well as in some other Peracarida functionally three articles of the endopodite also belong to the peduncle, while the rest of the endopodite forms the flagellum. Most isopods only have 5 peduncular articles; the praecoxa usually is reduced or only detectable as small sclerites at the insertion of the

antenna (Racovitza, 1912, 1925; Hansen, 1925; Schmalfuß, 1974, etc.); sometimes further reductions may occur (coxa of *Paragnathia formica* (Hesse): Schmalfuß, 1974). Thus in Isopoda the seventh (with praecoxa) or sixth (without praecoxa) antennal article is the first article of the flagellum and accordingly has a "typical flagellar" morphology (figs. 1, 3A, B); and mostly

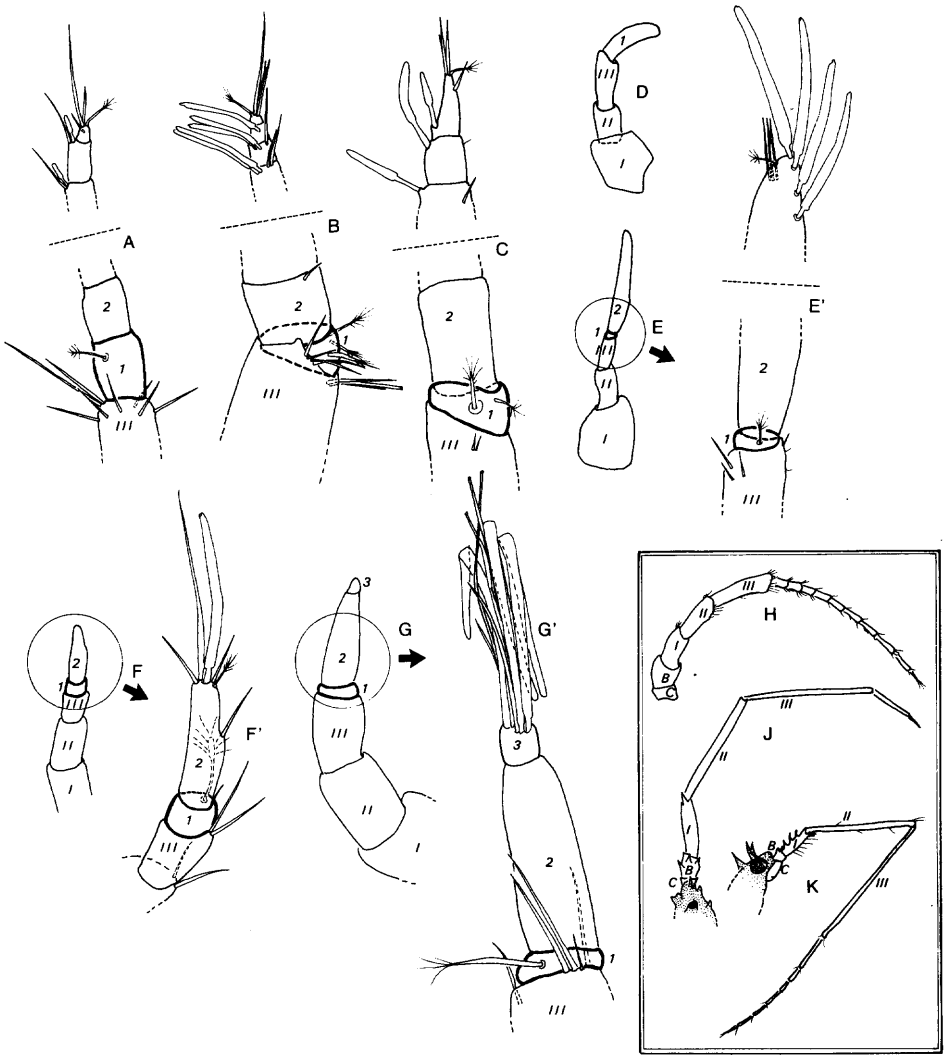

Fig. 2. Details of antenna one. A, Asellota: *Asellus aquaticus* (L.); B, Cirolanidae: *Cirolana borealis* Lilljeborg; C, Sphaeromatidae: *Sphaeroma hookeri* Leach; D, E, Valvifera: D, *Idotea baltica* (Pallas); E, *Astacilla longicornis* (Sowerby); F, Microcerberidea: *Microcerberus mirabilis* Chappuis & Delamare Deboutteville; G, Anthuridea: *Anthura gracilis* (Montagu). Inset: Elongation of peduncular articles of antenna two in Valvifera: H, *Idotea chelipes* (Pallas) after Sars, 1897; J, *Pleuroprion fabulosum* Gurjanova, 1955; K, *Antarcturus dentatus* (Whitelegge), after Monod, 1970.
C = coxa, B = basis, I-III = peduncular segments, 1 = first flagellar article.

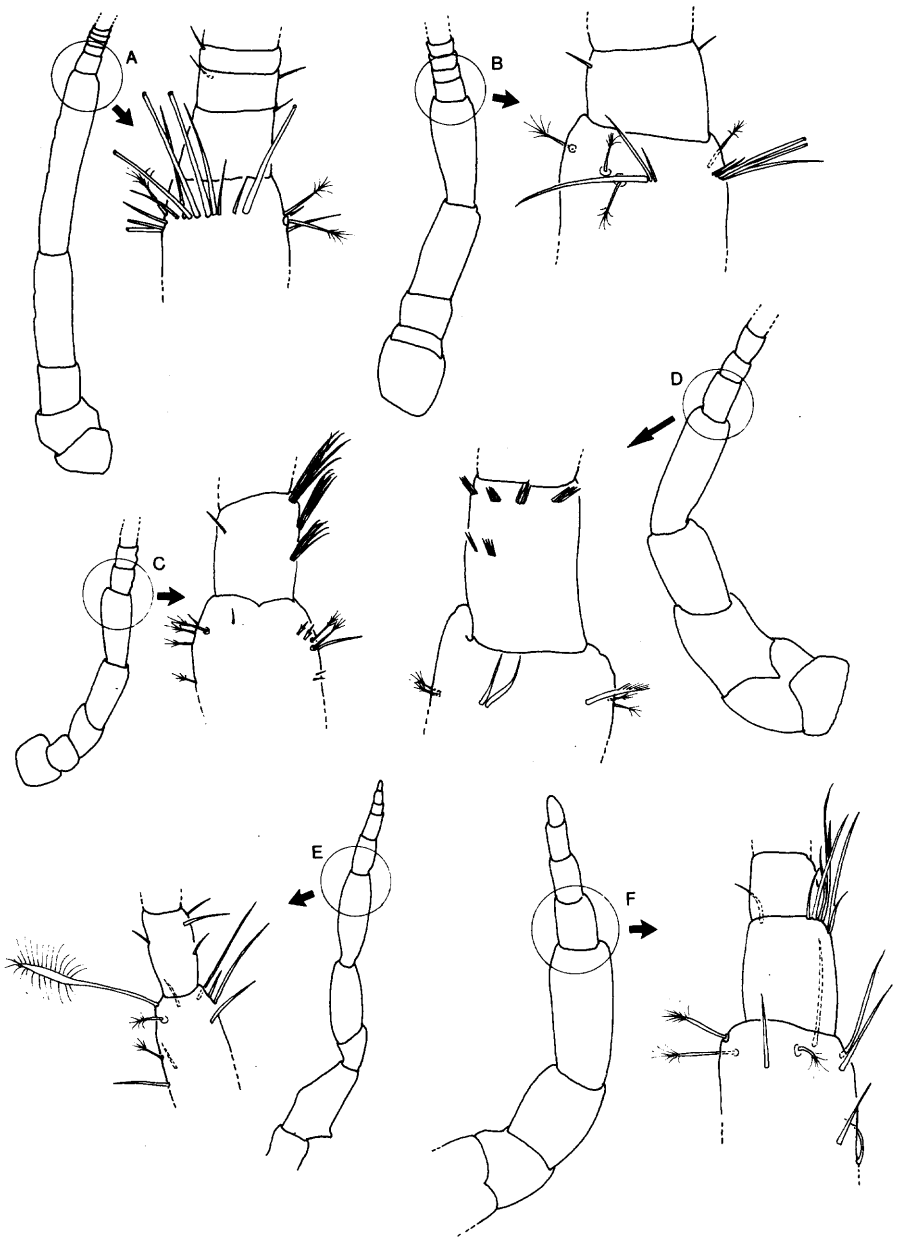

Fig. 3. Details of antenna two, insertion of the flagellum on the last peduncular segment. A, Asellota: *Asellus aquaticus* (L.); B, Cirolanidae: *Cirolana borealis* Lilljeborg; C, Sphaeromatidae: *Sphaeroma hookeri* Leach; D, Valvifera: *Idotea balthica* (Pallas); E. Microcerberidea: *Microcerberus mirabilis* Chappuis & Delamare Deboutteville; F, Anthuridea: *Anthura gracilis* (Montagu).

(when the praecoxa is reduced) the two first articles of antenna two are the coxo- and basipodites.

A closer examination reveals that the first flagellar article differs in its setation from the last peduncular segment, the latter bearing several plumose sensory setae, which are not present on the flagellum (fig. 3). This feature can be used to find the first article of the flagellum.

If the morphology of peduncle and flagellum is very similar and the setation is not known, the homology of the articles can be established through comparison with related genera. As an example we find in the less specialized Valvifera a peduncle, where the two last segments are somewhat longer than the foregoing segments, but some Arcturidae have unusual long and slender articles and in the case of e.g. *Antarcturus* (fig. 2K) it is difficult to find the limit between peduncle and flagellum, also because of the hidden position of the coxa. Comparing figs. 2H-K it seems probable, that in *Antarcturus* the first three peduncular segments remain short while the two following, very long segments are homologous with the segments 4 and 5 (in fig. 2: segments II and III) of other Valvifera; segment 6 would be the first flagellar article. For a verification other morphological or anatomical features are needed; this is also true for other problematic cases (Plakarthriidae: fig. 1D).

In some Oniscoidea aesthetascs have been found on the flagellum of antenna two (e.g., *Trichoniscoides picturarum* Vandel, 1952; cf. Vandel, 1960). This very unusual occurrence needs further investigation.

We can summarize that in most Isopoda a homologization of the peduncular segments and the identification of the first flagellar articles of both pairs of antennae is possible whenever the morphology and setation is known. The discrimination is possible because of the different functional performance of the articles, which is expressed in the morphology and partly in the setation. Simple mechanosensoric setae can be found nearly everywhere; plumose setae (hydrodynamic receptors) are present on the peduncles and often on the first and the last article of antenna one; aesthetascs mostly seem to be restricted to the flagellum of antenna one. Whenever the phylogenetic ground-plan is known a homologization of more or less aberrant and specialized structures can be tried.

RÉSUMÉ

Une comparaison des antennes de tous les sous-ordres d'isopodes montre que la variabilité du nombre des articles, qui est apparente dans la littérature taxonomique, est dûe à une mauvaise interprétation de la morphologie des antennes. Par conséquent des caractéristiques sont décrites ici, qui rendent possible l'homologisation des articles antennaires.

La première antenne (antennule) comprend fondamentalement 3 articles pédonculaires et un flagelle multiarticulé. Sur ce qui est primitivement le premier article du flagelle on peut observer des soies sensorielles plumeuses, les articles suivants portant des soies simples et souvent des aesthetascs, et le dernier article n'ayant que des soies simples et une soie plumeuse.

La deuxième antenne se compose fondamentalement de 6 articles pédonculaires dont le premier surtout (praecoxa) est réduit, et un flagelle multiarticulé avec plusieurs soies simples. Le

dernier article du pédoncule diffère des articles du flagelle par ses soies sensorielles plumeuses. On peut rencontrer des difficultés pour déterminer les homologies à l'aide des caractéristiques décrites ici dans le cas des antennes extrêmement courtes (Epicarides, Oniscoïdes).

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