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Morpho-functional grounds of life mode of "Cladocera". XI. On comparative morphology of antenna in Anomopoda (Phyllopoda: Crustacea)

Морфо-функциональные основы образа жизни ветвистоусых ракообразных. XI. К сравнительной морфологии антенны у Anomopoda (Phyllopoda: Crustacea)

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КЛЮЧЕВЫЕ СЛОВА: антенна, Crustacea, Anomopoda.

ABSTRACT: The antenna (the 2nd antenna) of cladocera is mostly not shown in figures, its features are usually not mentioned in descriptions in many recent publications. Attention here is drawn to the fact that it manifests a certain morphological diversity which may be useful in taxomomic diagnoses and in discussions of modes of life of different species.

РЕЗЮМЕ: Антенну (антенну 2-й пары) кладоцер обычно не изображают на рисунках, особенности её строения даже не упоминают в описаниях во многих сводках последнего времени. Однако, имеется значительное морфологическое разнообразие строения антенны, которое должно использоваться в таксономических диагнозах и при обсуждении образа жизни различных видов.

Introduction

While the morphology of thoracic limbs has now become a necessary and generally accepted tool in systematics of the Anomopoda, the structure of other appendages remains less known and less used in systematics. This is true especially of the antenna (the 2nd antenna, AII). This is a large and well-developed structure, consisting of 2-segmented basipodite and two branches. The presence (and size) of setae and spines on particular segments varies and is described as the antennal formula. Its is assumed that the upper (inner) branch (in position when AII is directed posteriorly) is the endopodite and the lower (outer) branch is the exopodite. The exopodite is 4-segmented (3-segmented in the Chydoridae), the endopodite is 3-segmented.

Initial publications on Cladocera represented full habit view of species, including antennae [Mueller, 1785; Jurine, 1820; Leydig, 1860; Sars, 1861]. Lilljeborg [1901] represents AII in most species or at least for one representative of most genera. Chiang Sieh-chih and Du Nan-shan [1979] show AII in all species, mostly in sufficient detail.

However, in many widely used summaries, as those by Behning [1941], Manuilova [1964], Sramek-Husek et al. [1962], Herbst [1962], Smirnov [1971], Flossner [1972, 2000], Margaritora [1985], Negrea [1983], the authors did not indicate AII on figures and did not describe it in sufficient detail, assuming at that time that it will not supply useful characters. and to avoid obstruction of the habit view.

On *Alona diaphana,* Sars [1888: 49] noted: "The antennae exhibit the usual structure". Guerne and Richard [1893: 242] describing their *Alona cambouei* Guerne et Richard, 1893 wrote: "Les antennes posterieurs ne present rien de particulier". In descriptions of *Alona monacantha* Sars, 1901*; A. glabra* Sars, 1901; *A. verrucosa* Sars, 1901; *Alonella lineolata* Sars, 1901; *A. dentifera* Sars, 1901; *A. sculpta* Sars, 1901; *A. nitidula* Sars, 1901, Sars [1901] does not mention AII, evidently as having no useful features characterizing species. Gauthier [1939] does not mention it in the description of *Leydigia propinqua* var. *ciliata* Gauthier, 1939.

However, when AII is obviously different, as in *Alona macrocopa*, Sars [1894] describes it in sufficient detail. It follows, on the other hand, that unspecialized structure of AII in some other species is also characteristic.

Green [1962] paid special attention to structure of AII, finding differences at the species level. He notes that comparison of species is not possible "since most

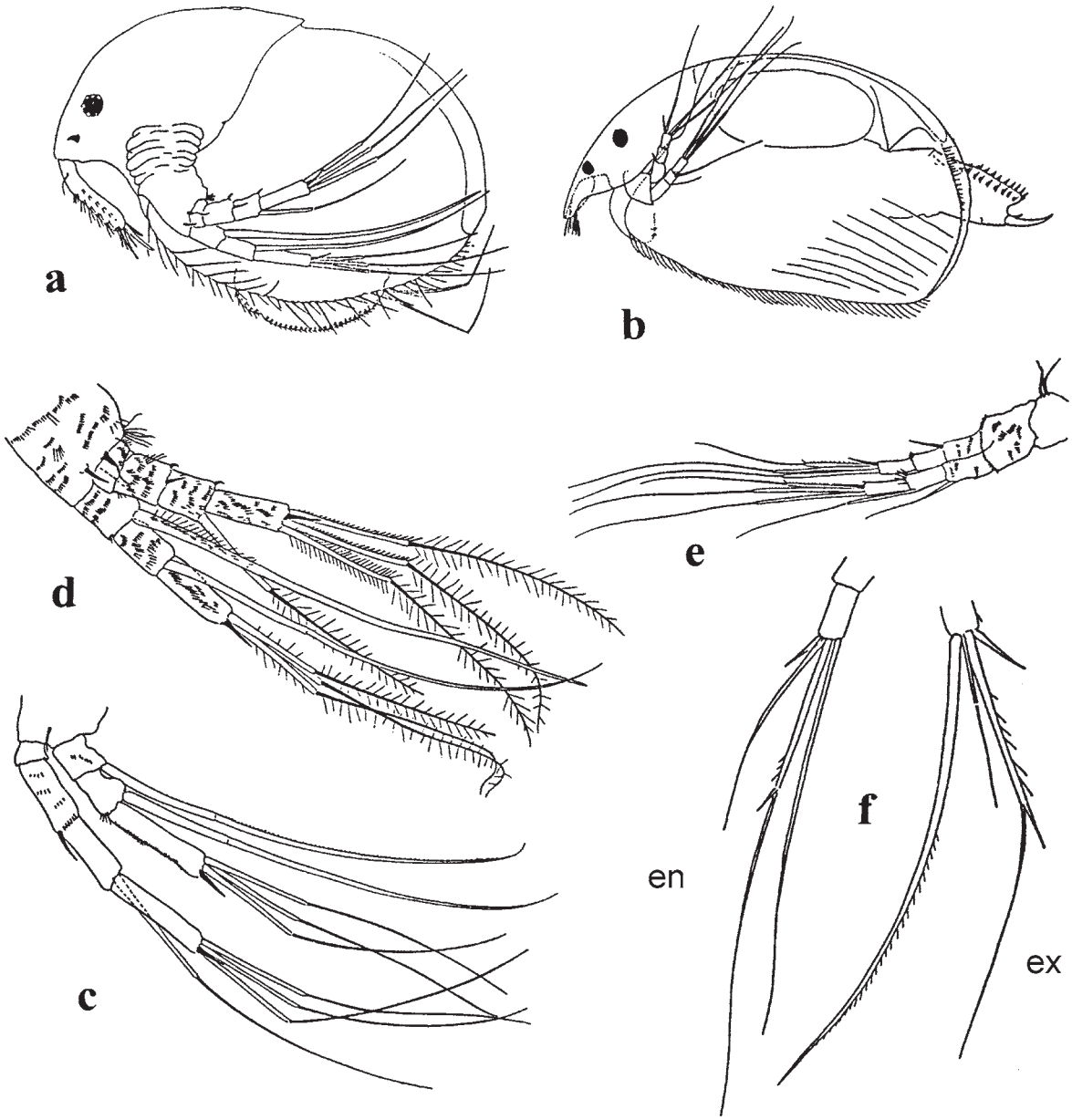

Fig. 1. Morphological radiation of AII in anomopods. A — *Macrothrix groenlandica* Lilljeborg, 1901 with a relatively large AII, B — *Alona costata* Sars, 1862 with a relatively small AII, C — AII of *Streblocerus serricaudatus* (Fischer, 1849) possessing generally similar (undifferentiated) setae, D — AII of *Macrothrix groenladica* with an extremely large proximal seta on the exopodite, E — AII of *Alona affinis* with a small proximal seta on the exopodite (absent in some species), distal setae possess a denticle at the articulation of their proximal and distal segments, in contrast to many species (e.g., as shown in Figs 1 C, D), F — Differentiation of setae on distal segments of the exopodite and endopodite of AII in *Alona gurneyi* (compare undifferentiated setae in Figs 1C–E). Figs 1A–C — from Alonso [1996], Fig. 1F — from Smirnov [1989].

Рис. 1. Морфологическая радиация AII у аномопод. A — *Macrothrix groenlandica* Lilljeborg, 1901 с относительно большой AII, B — *Alona costata* Sars, 1862 с относительно маленькой AII, C — AII *Strelocerus serricaudatus* (Fischer, 1849) с единообразными (недифференцированными щетинками), D — AII *Macrothrix groenlandica* с очень большой проксимальной щетинкой на экзоподите, E — AII *Alona affinis* с маленькой проксимальной щетинкой на экзоподите (у некоторых видов отсутствующей), у дистальных щетинок есть шипик у сочленения проксимального и дистального сегментов, в отличие от многих видов (например, как показано на рисунках 1 C, D), F — Дифференциация щетинок на дистальных сегментах AII *Alona gurneyi* (сравнить с недифференцированными щетинками на рис. 1 C–E). Рис. 1A–C из Alonso [1996], рис. 1F — из Смирнова [1989].

authors do not describe the antennae of their specimens" (p. 424). Still, many later authors (as mentioned above) commonly did not supply details on structure of AII.

Discussion and conclusions

The available data clearly indicate that the size of AII in relation to the body size and the structure of AII are different and may supply useful features for species discrimination.

The branches consist of 3–4 segments, mostly bearing setae or spines (Fig. 1). The form (elongation) of antennal segments is different. It is known that functionally, AII is used for swimming in most daphniids, for attachment to substrata in *Simocephalus* Schoedler, 1858, and for swimming and crawling in chydorids [Fryer, 1968; Smirnov, 1999]. There are obvious differences between species in size of setae and spines. However, it was assumed that distal setae are generally similar. But even in this case there are obvious differences, as between *Alona affinis* (Leydig, 1860) and *A. quadrangularis* (Mueller, 1785), as well as striking specialization as in *A. gurneyi* Smirnov, 2001 [see Smirnov, 1989, 2001]. In the latter case, three distal setae are very different from each other (Fig. 1 f). The distal setae are three in number on each distal segment, with a sole exception of *Paralona pigra* (Sars, 1862) with 2 setae on the endopodite [Smirnov, 1996].

Thus AII manifests morphological dissimilarity in various cladocera species, as well as uniform structure in many of them. Also, there are some tendencies. Among chydorids, the spines on antennal segments in most species belonging to the subfamily Chydorinae (except *Disparalona*) are small. In the subfamily Aloninae, the spines are very diverse and mostly rather large. In the Chydoridae and Daphniidae the setae on proximal segments tend to be small or undeveloped. Striking contrast is made by *Macrothrix* Baird, 1843 with one of the proximal setae attaining a "gigantic" size (Fig. 1d). As well, the spines either are large, or small, or not pressent. A special case is the increase in the number of spines on antennal segments, known in *Macrothrix superaculeata* (Smirnov, 1982) vs *M. triserialis* Brady, 1886, and especially in *Leydigia* Kurz, 1875 species.

The structure of the basal part of AII was never sufficiently described. Sars [1894] indicated (for *Alona macrocopa*, sensu Sars, 1894) that it consists of two clearly separated segments. Presence of two segments in the basipodite was shown for many chydorids [Smirnov, 1971]. Basal area of the basal segment bears two setae, which may contribute to further elucidation of homology of this area, the setae potentially corresponding to segments. However in most species the basipodite is still poorly studied, especially in its proximal part, where it is concertina-like, ensuring mobility of AII. Investigation of II, e.g., in *Ilyocryptus* Sars, 1862 [Kotov, 2000; Kotov & Dumont, 2000; Kotov & Williams, 2000] brought extensive new information and demonstrated that further exploration is worthwhile.

In the practical aspect, the representation of a full range of morphological radiation of the same structure would supply a tool for decisions whether a newly found form deserves recognition as a new species. This is especially urgent in case of *Alona* species, frequently similar to each other, and when local variation vs geographical variation is unknown. Comparative investigation of antennal morphology may yield results revealing true relationships of anomopod species.

The diversity outlined above may be organized as morphological series. The morphological series of AII: 1) demonstrate the actual range of variation of each particular structure and the limits of modifications; 2) thus every constituent part of AII tends to undergo morphological radiation within such range; 3) there are certain trends in development, differently expressed in different groups; 4) the combination of modifications of particular structures (in combination with other body parts) characterizes forms described as different species; 5) functionally, modifications seem to be: unspecialized or (a) useful in particular habitats, or (b) restricting habitats of specialized species.

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