

New diagnostic microcharacters of the cephalothoracic appendages in *Cyclops* O. F. Müller, 1776 (Crustacea, Copepoda, Cyclopoida)

Maria HOŁYŃSKA

Museum and Institute of Zoology, Polish Academy of Sciences,
Wilcza 64, PL-00 679 Warsaw (Poland)
mariahoh@robal.miiz.waw.pl

Hans-Uwe DAHMS

Carl von Ossietzky Universität, FB 7, AG Zoosystematik und Morphologie,
Oldenburg (Germany)
hans.uwe.dahms@mail.uni-oldenburg.de

Hołyńska M. & Dahms H.-U. 2004. — New diagnostic microcharacters of the cephalothoracic appendages in *Cyclops* O. F. Müller, 1776 (Crustacea, Copepoda, Cyclopoida). *Zoosystema* 26 (2) : 175-198.

ABSTRACT

The morphology of the cephalothoracic appendages is compared among 12 taxa of *Cyclops* O. F. Müller, 1776: *C. strenuus strenuus* Fischer, 1851, *C. strenuus landei* Koźmiński, 1933, *C. abyssorum* Sars, 1863, *C. furcifer* Claus, 1857, *C. heberti* Einsle, 1996, *C. singularis* Einstle, 1996, *C. scutifer* Sars, 1863, *C. kolensis* Lilljeborg, 1901, *C. insignis* Claus, 1857, *C. canadensis* Einstle, 1988, *C. columbianus* Lindberg, 1956, and *C. alaskaensis* Lindberg, 1956. Diagnostic microcharacters found to be new or rarely mentioned in the earlier descriptions are: the relative length of the aesthetascs on the ancestral XXI antennular segment; the spinule ornamentation on the caudal surface of the antennal coxobasis; spinule ornamentation of the maxillular palp, and setulation of the maxillular palp setae; spinule ornamentation on the frontal surface of the maxilliped syncoxopodite; setulation of the medial spine and spinule ornamentation on the frontal surface of leg 1 basipodite. Hypothetical roles of the elongate aesthetascs on the ancestral XXI antennular segment in the pelagic *Cyclops* species, and long pinnate setae on the maxillilar palp are discussed. *C. strenuus landei* is synonymized with *C. strenuus strenuus*, and *C. strenuus strenuus* sensu Koźmiński, 1933 is found to be conspecific with *C. heberti*. Refined morphological delimitation of the taxa resulted in obtaining new data on the geographical distribution of *C. heberti* (southern France, central Italy, northern Germany and Poland) and *C. singularis* (Hungary and Slovakia). Nearctic occurrence of *C. strenuus* has not been confirmed.

KEY WORDS

Crustacea,
Copepoda,
Cyclops,
morphology,
cephalothoracic appendages,
microcharacters,
adaptive value,
geographical distribution.

RÉSUMÉ

Nouveaux microcaractères diagnostiques des appendices céphalothoraciques de Cyclops O. F. Müller, 1776 (Crustacea, Copepoda, Cyclopoida).

La morphologie des appendices céphalothoraciques de 12 taxons de *Cyclops* O. F. Müller, 1776 est comparée : *C. strenuus strenuus* Fischer, 1851, *C. strenuus landei* Koźmiński, 1933, *C. abyssorum* Sars, 1863, *C. furcifer* Claus, 1857, *C. heberti* Einsle, 1996, *C. singularis* Einsle, 1996, *C. scutifer* Sars, 1863, *C. kolensis* Lilljeborg, 1901, *C. insignis* Claus, 1857, *C. canadensis* Einsle, 1988, *C. columbianus* Lindberg, 1956 et *C. alaskaensis* Lindberg, 1956. Les microcaractères diagnostiques suivants sont nouveaux ou rarement mentionnés dans les descriptions précédentes : longueur relative des aesthetasques sur le segment antennulaire ancestral XXI ; l'ornementation des spinules sur la surface caudale des coxobasis antennaires ; l'ornementation des spinules du palpe maxillulaire et la sétation des soies du palpe maxillulaire ; l'ornementation des spinules sur la surface frontale des syncoxopodites maxillipèdes ; la sétation des épines médiales et l'ornementation des spinules sur la surface frontale du basipode de la patte 1. Les rôles hypothétiques des aesthetasques allongés sur le segment antennulaire ancestral XXI dans les espèces pélagiques de *Cyclops* et celui des longues soies spiniformes sur le palpe maxillulaire, sont discutés. *C. strenuus landei* est mis en synonymie avec *C. strenuus strenuus* et il est montré que *C. strenuus strenuus* sensu Koźmiński, 1933 est conspécifique avec *C. heberti*. Une délimitation morphologique affinée des taxons a permis l'obtention de nouvelles données sur la distribution géographique de *C. heberti* (sud de la France, centre de l'Italie, nord de l'Allemagne et Pologne) et *C. singularis* (Hongrie et Slovaquie). L'occurrence néarctique de *C. strenuus* n'est pas confirmée.

MOTS CLÉS

Crustacea,
Copepoda,
Cyclops,
morphologie,
appendices céphalothoraciques,
microcaractères,
valeur adaptative,
distribution géographique.

INTRODUCTION

Cyclops O. F. Müller, 1776 is a predominantly Palaearctic group, represented only by a few taxa in northern North America. The group occurs from the hot desert to the arctic areas, from the lowland to the high-altitude lakes of Tibet.

Cyclops became ill-famed because of the great morphological plasticity displayed in several of its members, large numbers of local forms, ecotypes and subspecies of usually obscure taxonomic position, and lack of morphological discontinuity between the taxa, making identification at the species level often very difficult. In this situation, *Cyclops* has been the focus of several studies applying different approaches (morphometry-ecology: Koźmiński 1927, 1933, 1936; Rzóska 1930, 1932; Lindberg 1957; Einsle 1975; Nilssen 1979; Elgmork & Halvorsen 1971, 1998; reproductive

biology [cross-breeding experiments]: Lowndes 1932; Wierzbicka 1934; cytogenetics [chromatin diminution, chromosome number, DNA content]: Einsle 1975, 1996a; Grishanin & Akif'ev 2000; Grishanin & Dahms in press; biochemical methods [enzyme electrophoresis]: Einsle 1994, 1996a) to resolve the taxonomical relationships within the group. Surprisingly, except for a few studies (Fiers & Van de Velde 1984; Einsle 1985, 1996b) on some qualitative and meristic characters, no intensive efforts have been made towards collecting new data on the morphology of the genus. The relatively slow progress in this field is reflected in that while the genus as currently known contains about 60 species and subspecies (Lindberg 1957; Einsle 1996b), the most recent compendium on *Cyclops* (Einsle 1996b) provides an identification key to 14 species, and gives descriptions of no more than 25 taxa.

One of the most problematic taxa is the type species of the genus, *Cyclops strenuus* Fischer, 1851, described from the neighbourhood of St Petersburg (Peterhof) in Russia. There are vast records of *C. strenuus* in both the literature and museum collections; nevertheless unequivocal morphological diagnosis of the species is missing even in Einsle's monograph (1996b), where the distinguishing morphological features are, for want of something better, partly replaced by ecological and cytogenetic traits. To amend the morphological delimitation of *C. strenuus*, for which type specimens are not extant, topotype material has been compared with other specimens identified by different authors as *C. strenuus* from remote localities of Europe, and North America, and also 11 other taxa considered as closer or more distant relatives of *C. strenuus*. In the earlier taxonomic literature (Koźmiński 1927; Lindberg 1957; Einsle 1985, 1988), the term "strenuus-group" was used as a synonym of the genus *Cyclops* of the currently accepted, restricted sense. No hypothesis has been proposed on the phylogenetic relationships within *Cyclops* yet, so the availability and reliable identification were decisive in the choice of the species here compared. Of our observations, here we will only report those on the cephalothoracic appendages, since these structures are especially poorly known and neglected in *Cyclops* taxonomy.

MATERIALS AND METHODS

ABBREVIATIONS

- SMNK Staatliches Museum für Naturkunde, Karlsruhe;
 UNOL University of Oldenburg;
 USNM Smithsonian Institution, National Museum of Natural History, Washington.

Those specimens for which no institution as place of the deposition is given, are in the senior author's collection deposited in the Museum and Institute of Zoology, Warsaw.

LIST OF THE MATERIAL EXAMINED

Cyclops strenuus Fischer, 1851

Russia. St Petersburg, Peterhof (type locality), 59°52'N, 29°55'E, coll. V. Alekseev, 5 ♀♀, 1 ♂.

Norway. Frognerjern, 60°48'N, 11°10'E, 20.II.1995, leg. S. B. Wærvågen, 1 ♀, 2 ♂♂; 25.V.1995, leg. S.

B. Wærvågen, 4 ♀♀; 3.X.1995, leg. S. B. Wærvågen, 1 ♂, 1 CV ♀; Hellesørtjenna, 59°01'N, 9°53'E, oligotrophic lake, 9.II.1984, leg. S. B. Wærvågen, 1 ♂, 1 CV ♀, 1 CIV ♀; Omlandstjenn, 58°42'N, 9°09'E, oligotrophic lake, 21.II.2000, leg. J. P. Nilssen, 2 ♀♀, 1 ♂; Barbuli-Temp, 58°43'N, 9°14'E, oligotrophic pool, 23.III.2000, leg. J. P. Nilssen, 2 ♀♀ and 2 ♂♂; Ura Basseng, 58°43'N, 9°14'E, oligotrophic lake, 22.III.2000, leg. J. P. Nilssen, 2 ♀♀, 1 ♂; Ura-Dam, 58°43'N, 9°14'E, oligotrophic lake, 22.III.2000, leg. J. P. Nilssen, 2 ♀♀; Stavsjøen, 60°49'N, 10°50'E, eutrophic lake, 26.V.2000, leg. S. B. Wærvågen, 2 ♀♀; Stordammen, 59°46'N, 10°23'E, oligotrophic lake, 12.IX.2000, leg. J. P. Nilssen & S. B. Wærvågen, 1 ♀ and 1 ♂.

Germany. "Spreit" Göttingen, 47°45'N, 8°59'E, 7.I.1988, 1 ♀ (UNOL: 3037-3038); Gottmadingen-Bietingen, 47°44'N, 8°46'E "Tümpel", 12.IV.1957, leg. F. Kiefer, 1 ♀ (SMNK: 6285-6286); "Weingartener Moor bei Karlsruhe", 49°00'N, 8°23'E, 4.V.1935, leg. F. Kiefer, 3 ♀♀ (SMNK: 3274-3275).

France. Camargue (74), Tour du Valat, 27.IV.1958, 1 ♀ (UNOL: 1928-1929).

Italy. Lago Maggiore, XII.1962, 2 ♀♀ (UNOL: 3033-3036).

"*Cyclops strenuus landei*"

Poland. NE Poland, "Suchar bei Wigryseen" (terra typica), 28.III.1928, leg. et det. Z. Koźmiński, 2 ♀♀ (SMNK: 4399-4400).

Germany. Bodensee/Gnadensee, plankton, 21.XI.1939, leg. Muckle-Ritzl, 5 ♀♀ (SMNK: 4390, 4392); "Hemenhof.-Steckborn Bodensee, Stat. 1383", 18.I.1956, 1 ♀ (SMNK: 5999-6000); Radolfzell, 47°44'N, 8°59'E, "mittl. Buchensee", 16.III.1966, 1 ♀, 2 ♂♂ (SMNK: 5034, "Glas").

Cyclops abyssorum Sars, 1863

Norway. Oslo, Steinsfjord, 60°02'N, 10°10'E (28 km W of the type locality, Maridalsvann), slightly eutrophic, 1972, leg. Herbst, 3 ♀♀ and 1 ♂ (SMNK: 5100, "Glas"); Lønnavatn, 60°41'N, 6°28'E, oligotrophic lake, 30.V.1973, leg. J. P. Nilssen, 3 ♀♀ and 3 ♂♂; Rockpool VS-XI, 58°42'N, 9°17'E, 31.V.1983, leg. J. P. Nilssen, 2 ♀♀; Mosvatn, 58°58'N, 5°43'E, eutrophic lake, 28.IV.1994, leg. Å. Molversmyr & S. B. Wærvågen, 2 ♀♀, 1 ♂; 19.VII.1994, leg. Å. Molversmyr & S. B. Wærvågen, 2 ♀♀, 2 ♂♂; 15.X.1989, leg. Å. Molversmyr & S. B. Wærvågen, 1 ♀, 1 ♂; Hellestveitvann, 59°04'N, 9°30'E, oligotrophic lake, 9.VIII.2002, leg. J. P. Nilssen & S. B. Wærvågen, 2 ♀♀, 1 ♂; Lake Berse, 58°19'N, 8°13'E, mesotrophic lake, 20.VIII.2002, leg. J. P. Nilssen, 2 ♀♀, 1 ♂; Ljosevannet, 58°31'N, 8°08'E, oligotrophic lake, 22.VIII.2002, leg. J. P. Nilssen, 3 ♀♀, 1 ♂; Formuvann, 58°39'N, 8°12'E, oligotrophic lake, 22.VIII.2002, leg. J. P. Nilssen, 1 ♂; Rockpool VS IX, 58°42'N, 9°14'E, mesotrophic, 21.IV.1983, leg. J. P. Nilssen, 2 ♀♀, 2 ♂♂;

Rockpool VS III, 58°42'N, 9°14'E, eutrophic, 13.IX.1983, leg. J. P. Nilssen, 1 ♀, 1 ♂; Frøylandsvatn, 58°46'N, 5°41'E, 30.III.1999 and 14.IV.1999, leg. Å. Molversmyr & S. B. Wærvågen, 2 ♀♀, 2 ♂♂; 10.IX.1998 and 29.IX.1998, leg. Å. Molversmyr & S. B. Wærvågen, 1 ♀, 1 ♂.

Poland. NE Poland, Wigry lake, "Muliczne bei Wigry", 1.III.1927, leg. Z. Koźmiński, 1 ♂ (SMNK: 4403-4404).

Cyclops furcifer Claus, 1857

Germany. Eichener See (Baden), 13.IV.1935, leg. F. Kiefer, 7 ♀♀, 3 ♂♂ (SMNK: 2708-2709, 2716-2717).

Cyclops heberti Einsle, 1996

Germany. "Nägelsee, Steisslingen, Lkr. Konstanz", 47°48'N, 8°55'E, 25.I.1994, 3 ♀♀, 1 ♂ (paratypes) (SMNK); Kalkofen, 47°51'N, 9°05'E, "Tümpel", 26.III.1990, 2 ♀♀, (UNOL: 4912-4914); Litzelsee, 47°44'N, 9°01'E, 22.III.1983, 2 ♀♀ (UNOL: 4900-4902); Karlsruhe, 49°00'N, 8°23'E, "Weingartener Moor", 23.III.1935, leg. F. Kiefer, 1 ♂ (SMNK: 2860-2861); Oldenburg, 53°09'N, 8°12'E, ditch, "Johann Justus Weg", 28.X.2001, leg. M. Hołyńska, 1 ♀; Südschleswig, "Tümpel", 15.IV.1951, leg. H. Herbst, 1 ♀ (UNOL: 422, 426).

Poland. Truskaw, 52°18'N, 20°46'E, ditch on a meadow, 5.IV.1985, leg. R. Hołyński, 1 ♀; 1 km N of Truskaw, ditch at edge of forest, leg. R. Hołyński, 5.IV.1985, 1 ♀; *Cyclops strenuus strenuus* sensu Koźmiński, NE Poland, Wigry lake, "Tümpel", 6.IV.1927, leg. et det. Z. Koźmiński, 5 ♀♀, (SMNK: 4405-4407).

France. Camargue, Tour du Vallat, "Bach", 27.IV.1958, 1 ♀ (UNOL: 1843-1845); "Strassen-graben bei Salin de Badon", 11.IV.1958, 1 ♀ (UNOL: 1709-1711).

Italy. Lago di Chiusi, 43°00'N, 11°57'E, 2.IV.1968, 1 ♀ (UNOL).

Cyclops singularis Einsle, 1996

Germany. Litzelsee/Markelfingen, 47°44'N, 9°01'E, "Lkr. Konstanz", 4.IV.1994 4 ♀♀, 1 ♂ (paratypes) (SMNK); 22.III.1983, 1 ♀ (UNOL: 4906-4907); Kalkofen, 47°51'N, 9°05'E, "Tümpel", 26.III.1990, 1 ♀ (UNOL: 4915-4917).

Hungary. Tiszavasvári, 47°57'N, 21°21'E, Alkaloida, Sewage Plants, Oxidation lakes, 26.XI.1985, leg. M. Hołyńska, 1 ♀.

Slovakia. Nagysalló (Tekovské Šarluy), 48°06'N, 18°33'E, 14.IV.1932, leg. E. Dudich, 2 ♀♀ (SMNK: 11340-11342).

Cyclops scutifer Sars, 1863

Norway. Maridalsvann, 59°59'N, 10°46'E, oligotrophic lake, 6.VI.1980, leg. J. P. Nilssen, 2 ♀♀, 2 ♂♂; Lønnavatn, 60°41'N, 6°28'E, oligotrophic lake, 30.V.1973, leg. J. P. Nilssen, 2 ♀♀; Gjersjøen, 59°47'N, 10°47'E, eutrophic lake, 10.I.1979, leg. J. P.

Nilssen, 2 ♀♀; Roksjøen, 60°47'N, 11°27'E, oligotrophic lake, 7.VI. 2001, leg. S. B. Wærvågen, 2 ♀♀, 2 ♂♂; Vetlavatn, 60°43'N, 6°30'E, oligotrophic lake, 2.VI.1973, leg. J. P. Nilssen, 2 ♀♀, 1 ♂; Heilandsvann, 58°56'N, 8°50'E, oligotrophic lake, 14.VII.1977 and 5.VII.1978, leg. J. P. Nilssen, 1 ♀ and 1 ♂; Østre Kalvvann, 58°53'N, 9°09'E, oligotrophic lake, 30.V.1978, leg. J. P. Nilssen, 2 ♀♀, 2 ♂♂; 16.VIII.1978, leg. J. P. Nilssen, 4 ♀♀, 4 ♂♂.

Cyclops kolensis Lilljeborg, 1901

Poland. NE Poland, Wigry lake, southern bay, night, 21.III.1961, 4 ♀♀, 1 ♂.

Cyclops insignis Claus, 1857

Norway. Frognerjern, 60°48'N, 11°10'E, 20.II.1995, leg. S. B. Wærvågen, 2 ♀♀.

Hungary. Hortobágy, Nagymajor, 47°39'N, 20°59'E, puddle, 11.II.1995, leg. M. Hołyńska, 1 ♀.

Cyclops canadensis Einsle, 1988

USA. Alaska, Point Barrow, 71°23'N, 156°30'W, Arctic Ocean, 9.VII.1933, leg. J. Kalff & E. B. Reed, 2 ♀♀, 1 ♂ (USNM: 259924); Chatanika, 65°07'N, 147°31'W, grassy roadside pool, 4.VII.1947, leg. C. S. Wilson, 6 ♂♂ (USNM: 88010); Umati, 69°17'N, 152°12'W, 1953, leg. E. B. Reed, 1 ♀ (USNM: 259921); Barter Island, 1 ♀ (USNM: 204927).

Canada. Saskatchewan, Wakaw lake, 52°40'N, 105°35'W, 26.VI.1961, leg. E. B. Reed, 1 ♀, 1 CV (USNM: 259922); Yukon, Shingle Point, 68°56'N, 137°15'W, 1.IX.1974, leg. E. B. Reed, 1 CV (USNM: 259942).

Cyclops columbianus Lindberg, 1956

USA. Alaska, Karluk lake(?) (Kodiak Island), leg. T. Tobias, 4 ♀♀ (USNM: 231107).

Cyclops alaskaensis Lindberg, 1956

USA. Alaska, IX.1954, leg. E. B. Reed, 4 ♀♀, 1 ♂ (USNM: 259938).

METHODS

No characters on the mandible and maxilla varying between the species here compared have been found yet, therefore these appendages are not discussed further. No data on the frontal ornamentation of the syncoxopodite of the maxilliped in *C. furcifer* are provided here, because museum specimens available did not allow us to verify this feature. The drawings were made of specimens mounted in glycerin, by the aid of a camera lucida attached to an Olympus BX 50 compound light microscope. In the majority of the examinations, oil immersion and Nomarski (DIC) microscopy were applied.

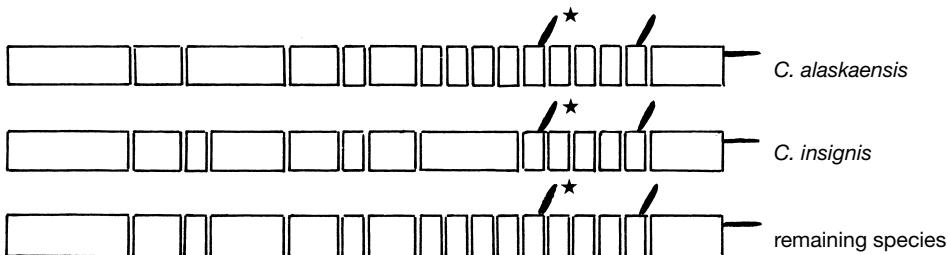


FIG. 1. — Schematic representation of the antennular segmentation in the females of *Cyclops* O. F. Müller, 1776. Asterisks mark the aesthetascs on the ancestral XXI segment. Proximal is left.

RESULTS

ANTENNULE

The antennule is 17-segmented in most *Cyclops* species. The only exceptions are *C. alaskaensis*, where usually the 16-segmented state and sometimes the 17-segmented state appears, and *C. insignis*, where the antennule consists of 14 segments. The same plesiomorphic assortment of the setae and aesthetascs [8, 4, 2, 6, 4, 2, 2, 1, 1, 0, 1, 1+ae, 0, 1, 2, 2+ae, 7+ae], retained also in several other lineages of Cyclopidae, is repeated in every species of *Cyclops*. There are interspecific differences in the relative length of the aesthetasc on the ancestral XXI segment (Huys & Boxshall 1991), which appears on the 9th segment in *C. insignis*, 11th in *C. alaskaensis*, and the 12th segment in the remaining species (Fig. 1). To the group with a long aesthetasc belong *C. strenuus*, *C. abyssorum*, *C. furcifer*, *C. kolensis*, and *C. columbianus* (Fig. 2). Intraspecific variability in the length of the aesthetasc is expressed in every member of this group: the aesthetasc may reach from the midlength to the distal margin of the second subsequent (14th) segment. To the group with relatively short aesthetascs belong: *C. heberti*, *C. insignis*, *C. alaskaensis*, and *C. canadensis* (Fig. 3). Intraspecific variability in this group occurs also: in *C. canadensis* the aesthetasc may reach from the distal margin of the next (13th) article to the midlength of the second subsequent (14th) segment; in *C. heberti*, the aesthetasc reaches the distal margin of the next (13th) article to the distal third of the second subsequent (14th) segment; in *C. insignis* the aesthe-

tasc reaches or just slightly passes beyond the distal margin of the next (10th) article. In *C. alaskaensis*, similarly to the taxa with long aesthetasc, the aesthetasc may reach from the midlength to the distal margin of the second subsequent (13th) article. However, this may be because of the antennular segments in this species are significantly compressed (Fig. 3E). An intermediate state between the short and long aesthetasc conditions is present in *C. scutifer* Sars, 1863, (Fig. 3G) and *C. singularis* (Fig. 3A), where the aesthetasc reaches from the proximal to the distal third of the second subsequent (14th) segment.

ANTENNA

The antenna is four-segmented, with a coxobasis bearing three setae, and a three-segmented endopodite with 1, 7-9, and 7 setae, respectively. One of the antennae of a single female of *C. strenuus* from Norway (Fig. 4B) bears an additional seta inserted on the mediocaudal surface of the coxobasis, near the base of the segment. The position of the seta suggests that this element structurally is homologous with the coxal seta, present within Podoplea only in *Cyclopicina longifurcata* (Scott, 1901). Since *C. longifurcata* retains several other ancestral features of Cyclopoida (Huys & Boxshall 1990) as well, the appearance of this additional seta on the coxobasis is considered here as an atavism. The second endopodal segment is armed with nine setae in *C. furcifer*, *C. heberti*, *C. singularis*, *C. scutifer*, *C. canadensis*, *C. columbianus*, *C. strenuus*, *C. abyssorum* and *C. kolensis*. In the latter three species sometimes the eight setae-

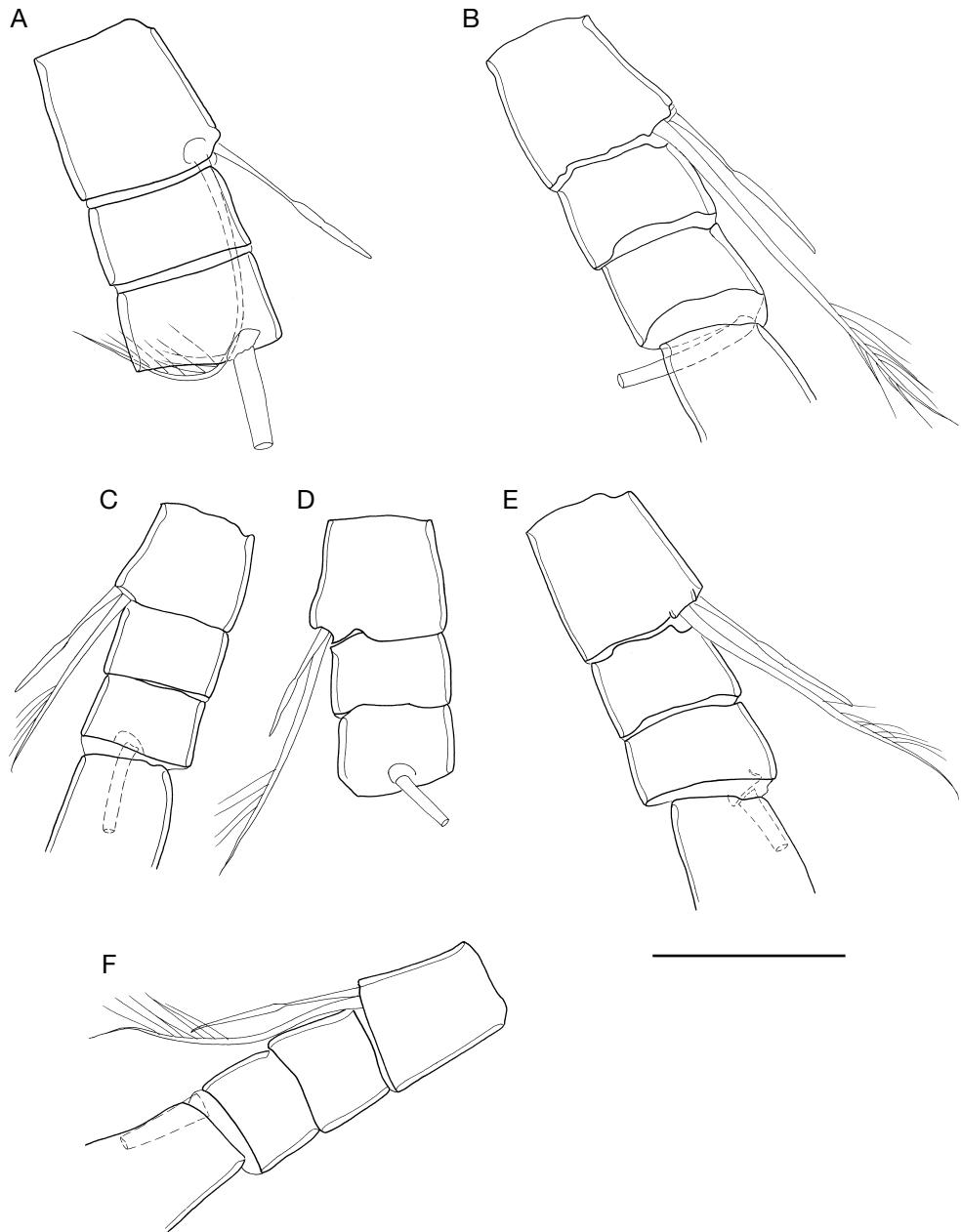


FIG. 2. — Interspecific variability of the aesthetasc on the ancestral XXI antennular segment, female; **A**, *Cyclops strenuus* Fischer, 1851 (Russia, Peterhof); **B**, *C. abyssorum* Sars, 1863 (Norway, Lønnavatn); **C**, **D**, *C. furcifer* Claus, 1857 (Germany, Baden); **E**, *C. kolensis* Lilljeborg, 1901 (Poland, L. Wigry); **F**, *C. columbianus* Lindberg, 1956 (Alaska, Karluk lake[?]). Scale bar: 50 µm.

state is expressed. *Cyclops alaskaensis* usually bears eight, sometimes seven setae, and *C. insignis* has seven setae on the second endopodal segment.

The spinule pattern on the caudal surface of the coxobasis – a feature highly diversified and successfully used as a diagnostic character in other cyclopid

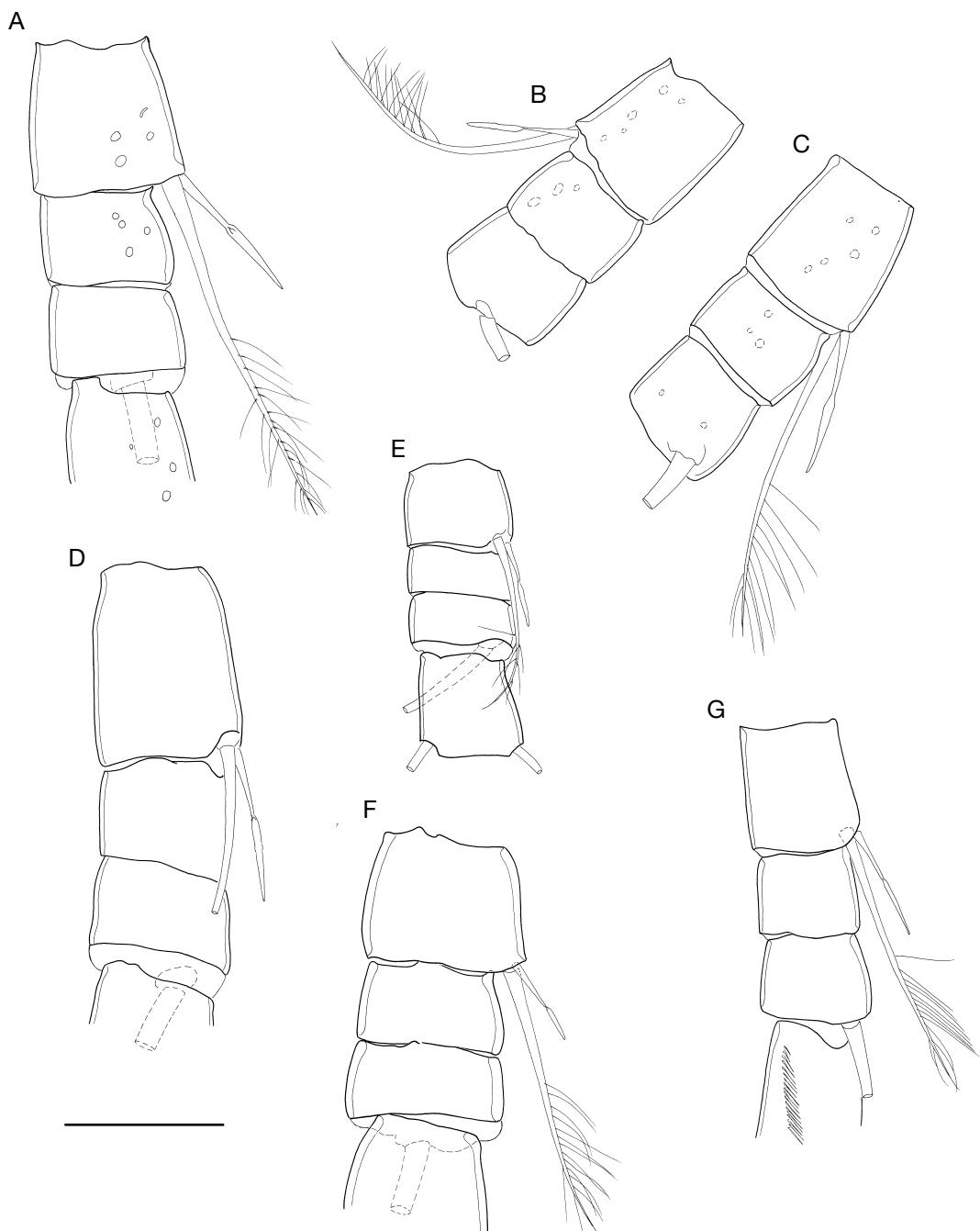


FIG. 3. — Interspecific variability of the aesthetasc on the ancestral XXI antennular segment, female; **A**, *Cyclops singularis* Einsle, 1996 (Germany, paratype); **B**, *C. heberti* Einsle, 1996; **B**, Poland, Wigry (*Cyclops strenuus strenuus* Fischer, 1851 *sensu* Koźmiński, 1933); **C**, Germany (paratype); **D**, *C. insignis* Claus, 1857 (Norway, Frognerjern); **E**, *C. alaskaensis* Lindberg, 1956 (Alaska); **F**, *C. canadensis* Einsle, 1988 (Alaska, Point Barrow); **G**, *C. scutifer* Sars, 1863 (Norway, Lønnavatn). Scale bar: 50 µm.

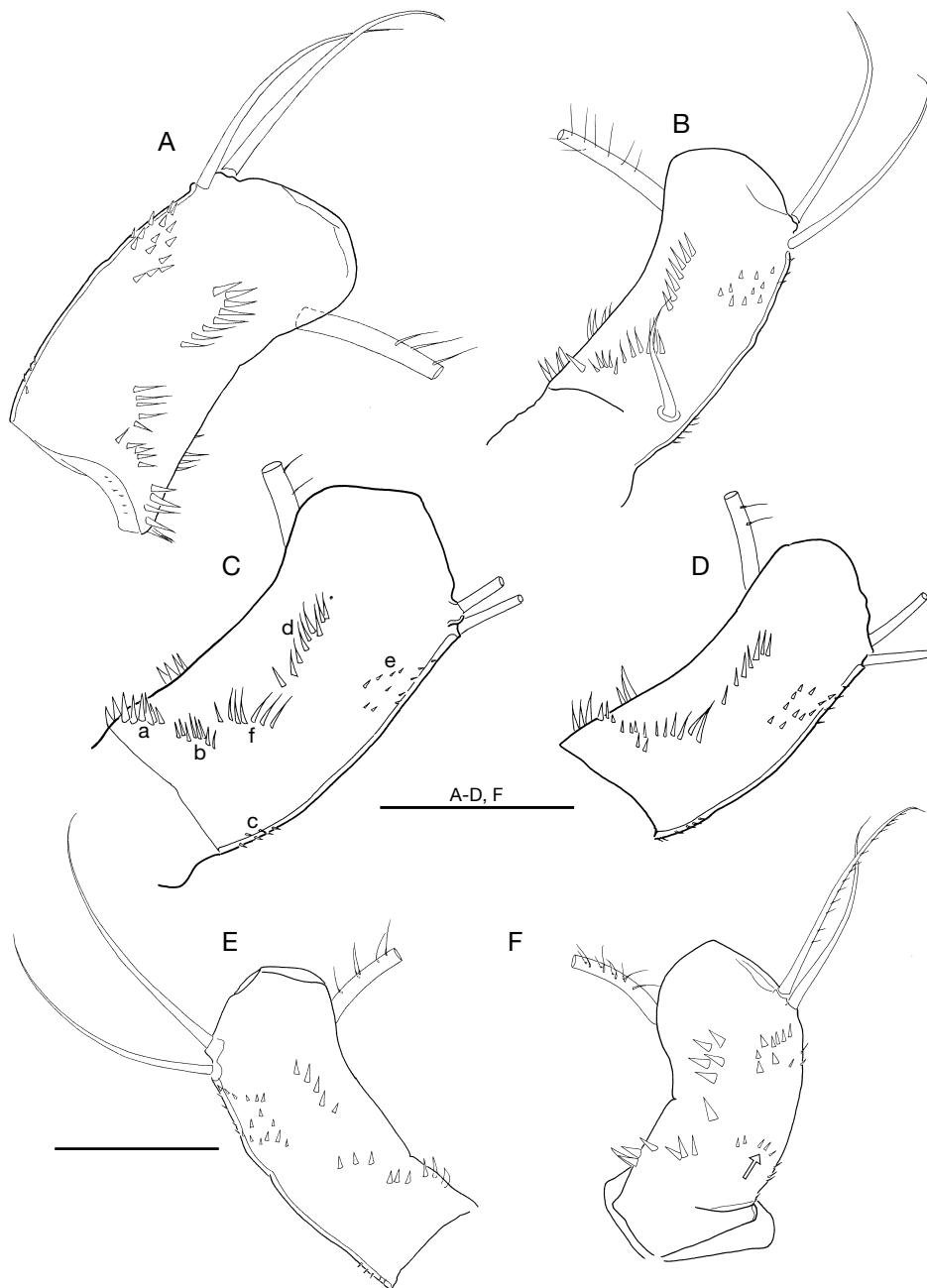


FIG. 4. — Spinule ornamentation on the caudal surface of the antennal coxobasis, female; **A-D**, *Cyclops strenuus* Fischer, 1851; **A**, Russia, Peterhof; **B**, Norway, Fagnertjern; **C**, Germany, Gottmadingen; **D**, Germany, Untersee, "C. strenuus landeri" Koźmiński, 1933; **E**, *C. abyssorum* Sars, 1863 (Norway, Lønavatn); **F**, *C. furcifer* Claus, 1857 (Germany, Baden). Scale bars: 50 µm.

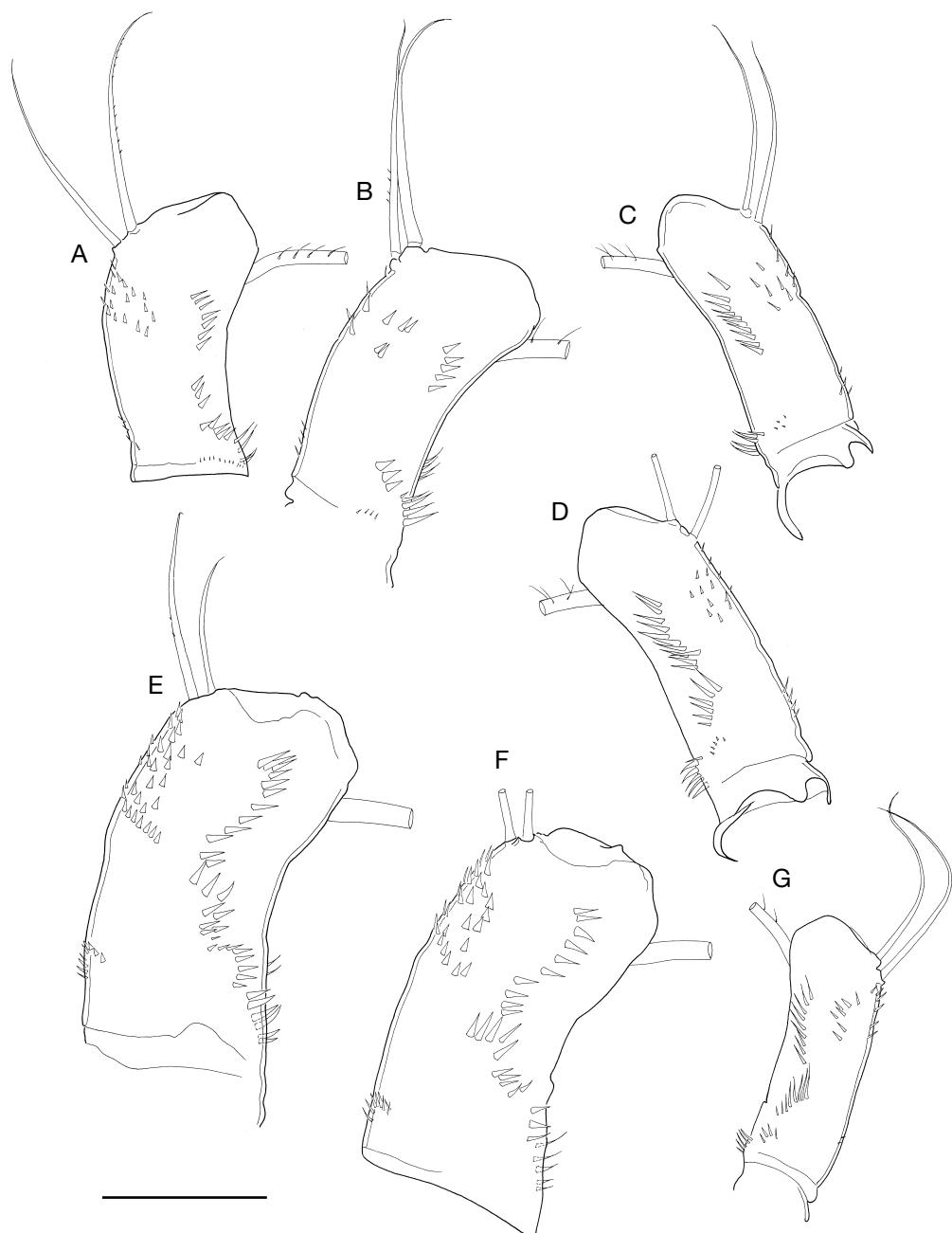


FIG. 5. — Spinule ornamentation on the caudal surface of the antennal coxobasis, female; **A, B**, *Cyclops heberti* Einsle, 1996; **A**, Germany, Oldenburg; **B**, Germany (paratype); **C, D**, *C. scutifer* Sars, 1863; **C**, Norway, Maridalsvann; **D**, Norway, Lønnavatn; **E, F**, *C. insignis* Claus, 1857 (Norway, Frognerjern); **G**, *C. columbianus* Lindberg, 1956 (Alaska, Karluk lake[?]). Scale bar: 50 µm.

genera (e.g., *Mesocyclops* Sars, 1914, *Paracyclops*) – is very similar among *Cyclops* species (Figs 4–6). The basic (but not necessarily plesiomorphic) cyclopid ornamentation, consisting of long spinules on the lateral margin near the base of the segment (Fig. 4C, a), an oblique row next to the former group at the proximolateral angle (Fig. 4C, b), spinules on the medial margin near the base (Fig. 4C, c), and a longitudinal row near the lateral margin (Fig. 4C, d), is supplemented with an oblique field of spinules, proximally to the insertion of the medial setae (Fig. 4C, e), and a second group of spinules usually is added next to the oblique row at the proximolateral angle (Fig. 4C, f). Differences between the species are mainly in the relative size and robustness of the spinules in a particular spinule group. A stable diagnostic character, helping in the identification of *C. strenuus*, is the presence of conspicuously elongate spinules (Fig. 4C, f), next to the oblique row at the proximolateral angle. This feature sometimes also appears in *C. scutifer*, *C. columbianus*, and *C. kolenensis*, but these species differ from *C. strenuus* in other easily discernible characters (pediger 4 and 5 are widely pointed in *C. scutifer* and *C. columbianus*; spine formula of the swimming legs is 2, 3, 3, 3 in *C. kolenensis*). *Cyclops furcifer* has an additional transverse row near the medial margin (verified on five females) (Fig. 4F, arrowed). While the spinules in the longitudinal row near the lateral margin are thin and elongate in *C. strenuus* (Fig. 4A–D), *C. scutifer* (Fig. 5C, D), *C. columbianus* (Fig. 5G), and *C. alaskaensis* (Fig. 6C, D), they are robust in *C. furcifer* (Fig. 4F), and *C. singularis* (Fig. 6A, B). In the remaining species, however, both the size and shape of the spinules are variable. Spinules between the longitudinal row near the lateral margin, and long lateral spinules near the base are arranged in a single row in *C. alaskaensis* (Fig. 6C, D), and usually in two rows in the remaining species. Although, sometimes triple rows (*C. strenuus*) or a single row (*C. abyssorum*, *C. heberti*, *C. scutifer*, *C. kolenensis*, *C. canadensis*, *C. columbianus*) appears.

MAXILLULE

The segmentation and setation follow the typical cyclopine pattern. Interspecific differences have

been found in the spinule ornamentation of the palp, and setulation of its two proximalmost setae. While the palp is bare in *C. alaskaensis* (Fig. 8F), and the spinules if present are extremely tiny on the maxillular palp of *C. abyssorum* (Fig. 7D), the palp is adorned with easily visible spinules in all the other species. A unique ornamentation, with a row of very large spinules near the base and tiny spinules apically to the row, appears in *C. singularis* (Fig. 7F). One of the three dissected Peterhof females of *C. strenuus* bears a field of tiny spinules on the praecoxopodite, proximally to the insertion of the palp (Fig. 7A). A similar ornamentation appears in *C. canadensis* from Point Barrow (verified by one female) (Fig. 7B), but this group is absent in specimens from Chatanika (Fig. 7C). Both the proximalmost seta of the lateral lobe, and proximalmost seta of the palp bear long setules in *C. furcifer* and *C. heberti*. However, while the setules extend along the whole length of the setae in *C. furcifer* (Fig. 7E), they are restricted to the proximal half in *C. heberti* (Fig. 8A, B). Long setules are present only on the proximalmost seta of the palp (the proximalmost seta of lateral lobe of the palp is spinulose) in *C. abyssorum* (Fig. 7D) and *C. singularis* (Fig. 7F). In all the other species the lobe setae and proximalmost seta of the palp are spinulose.

MAXILLIPED

The maxilliped consists of syncoxopodite, basipodite, and two-segmented endopodite, with 3, 2, 1, and 3 setae, respectively. Differences between the species are in the frontal spinule ornamentation of the syncoxopodite, and the shape of a membranous element slightly standing out from the frontal surface of the syncoxopodite. The spinules between the level of the insertions of the median and distalmost setae, present in every species, vary in size: they are conspicuously large in *C. scutifer* (Fig. 9G), *C. columbianus* (Fig. 10A), and *C. kolenensis* (Fig. 10E), but tiny in *C. heberti* (Fig. 9D–F) and *C. insignis* (Fig. 10B); in *C. abyssorum* (Fig. 9B, C) they are either small or large. This group is supplemented with distinct groups of tiny spinules in *C. abyssorum*

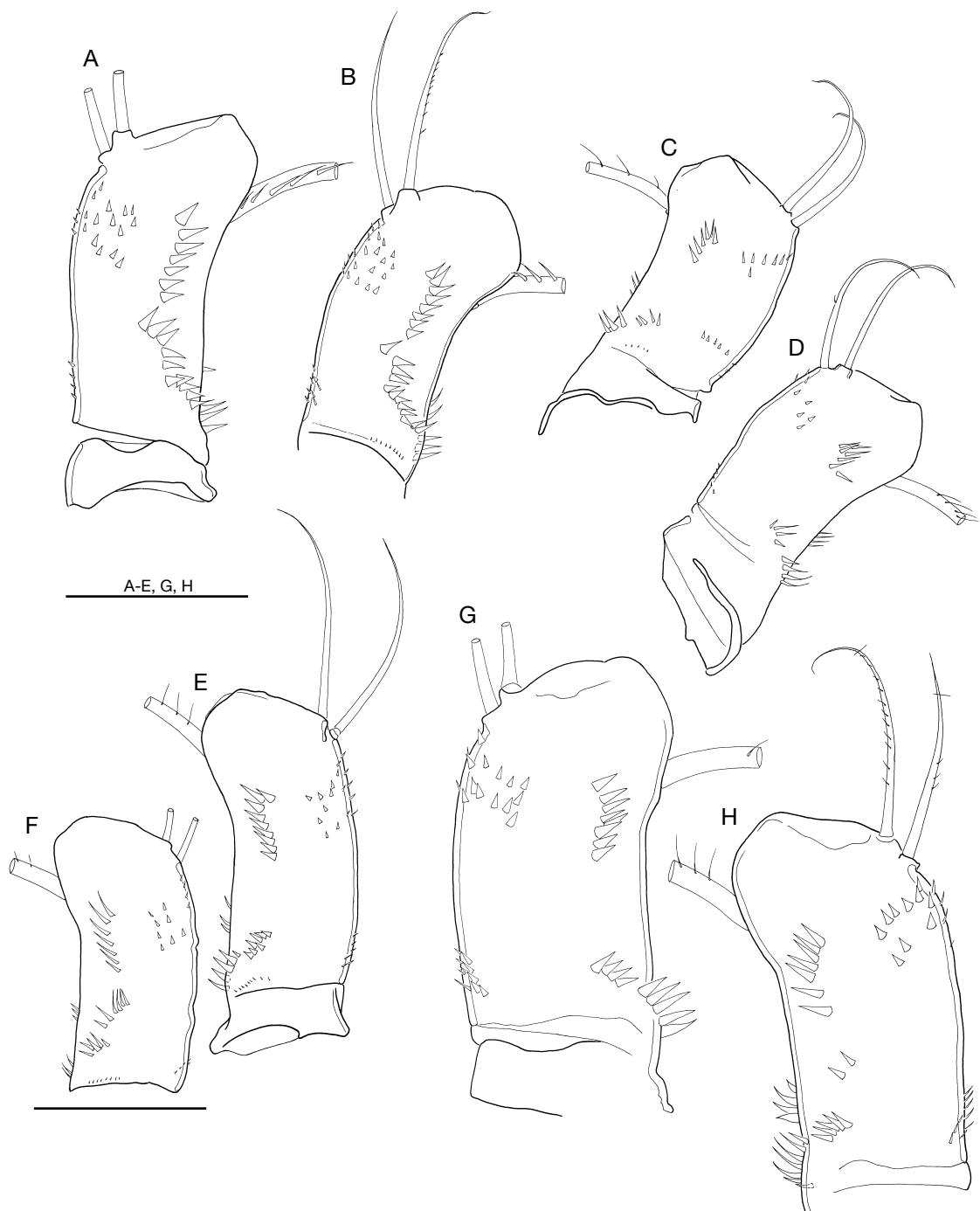


FIG. 6. — Spinule ornamentation on the caudal surface of the antennal coxobasis, female; **A, B**, *Cyclops singularis* Einsle, 1996; **A**, Hungary, Tiszavasvári; **B**, Germany (paratype); **C, D**, *C. alaskaensis* Lindberg, 1956 (Alaska); **E, F**, *C. kolensis* Lilljeborg, 1901 (Poland, L. Wigry); **G, H**, *C. canadensis* Einsle, 1988 (Alaska, Point Barrow). Scale bars: 50 µm.

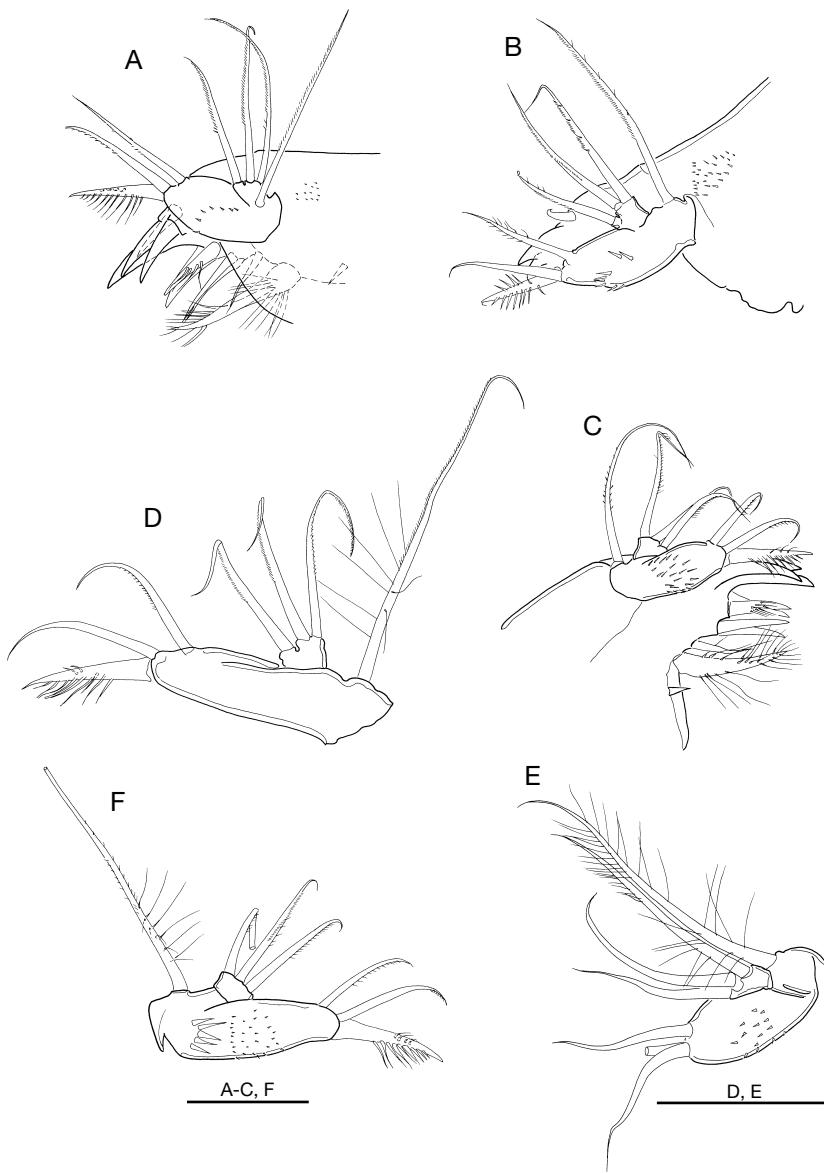


FIG. 7. — Ornamentation of the maxillular palp, and setulation of the palp setae, female; **A**, *Cyclops strenuus* Fischer, 1851 (Russia, Peterhof); **B**, **C**, *C. canadensis* Einstle, 1988; **B**, Alaska, Point Barrow; **C**, Alaska, Chatanika; **D**, *C. abyssorum* Sars, 1863 (Norway, Lønnavatn); **E**, *C. furcifer* Claus, 1857 (Germany, Baden); **F**, *C. singularis* Einstle, 1996 (Germany, paratype). Scale bars: 50 µm.

(Fig. 9B, C), *C. heberti* (Fig. 9D-F), *C. insignis* (Fig. 10B), and *C. singularis* (Fig. 10D). The membranous element near the lateral margin is distinctly claw-like in most species, but it is flap-shaped in *C. alaskaensis* (Fig. 10F), and is poorly developed in *C. scutifer* (Fig. 9G).

LEG 1

Interspecific differences exist not only in the number of spines on the third exopodal segment, a well known character and discussed by several former students, but also in the appearance of the medial spine and the frontal ornamentation of

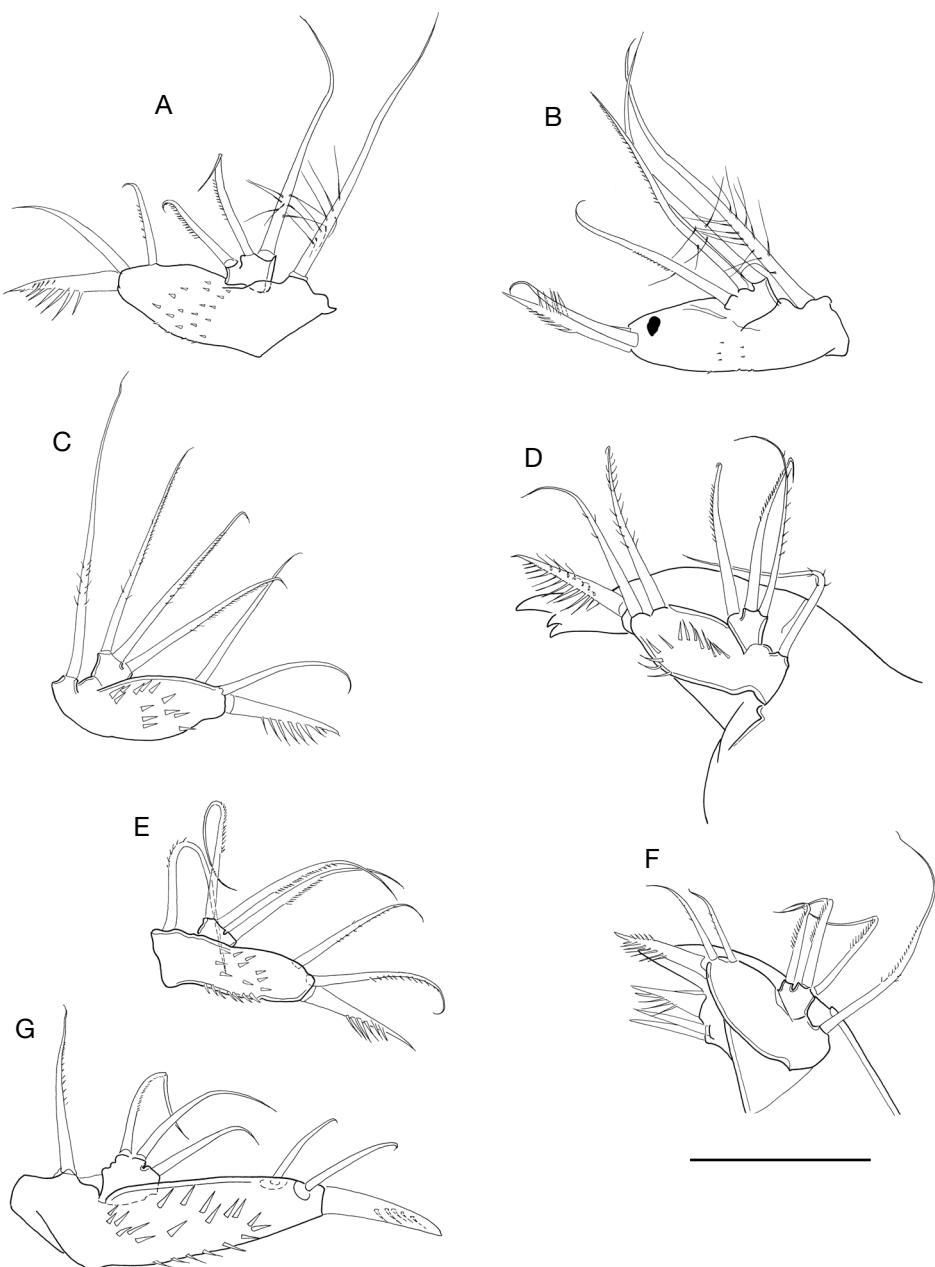


FIG. 8. — Ornamentation of the maxillular palp, and setulation of the palp setae, female; **A, B**, *Cyclops heberti* Einsle, 1996; **A**, Germany, paratype; **B**, Poland, Wigry (*Cyclops strenuus strenuus* Fischer, 1851 sensu Koźmiński, 1933); **C**, *C. scutifer* Sars, 1863 (Norway, Maridalsvann); **D**, *C. columbianus* Lindberg, 1956 (Alaska, Karluk lake[?]); **E**, *C. kolensis* Lilljeborg, 1901 (Poland, L. Wigry); **F**, *C. alaskaensis* Lindberg, 1956 (Alaska); **G**, *C. insignis* Claus, 1857 (Norway, Frognerjern). Scale bar: 50 µm.

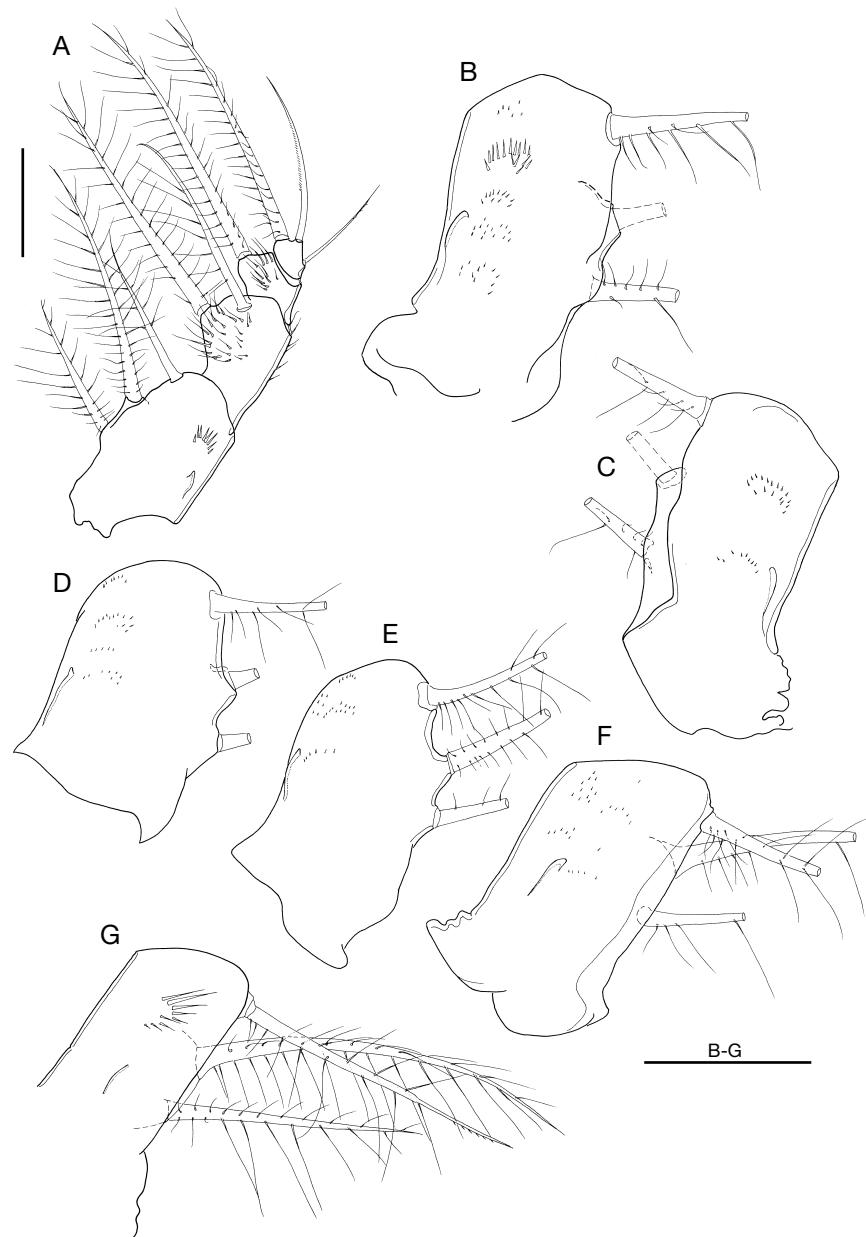


FIG. 9. — Ornamentation of the frontal surface of the maxilliped syncoxopodite, female; **A**, *Cyclops strenuus* Fischer, 1851 (Russia, Peterhof); **B, C**, *C. abyssorum* Sars, 1863; **B**, Norway, Rockpool VS-XI; **C**, Norway, Lonavatn; **D-F**, *C. heberti* Einsle, 1996; **D**, Poland, Wigry (*Cyclops strenuus strenuus* Fischer, 1851 *sensu* Koźmiński, 1933); **E**, Germany, Oldenburg; **F**, Germany, paratype; **G**, *C. scutifer* Sars, 1863 (Norway, Maridalsvann). Scale bars: 50 µm.

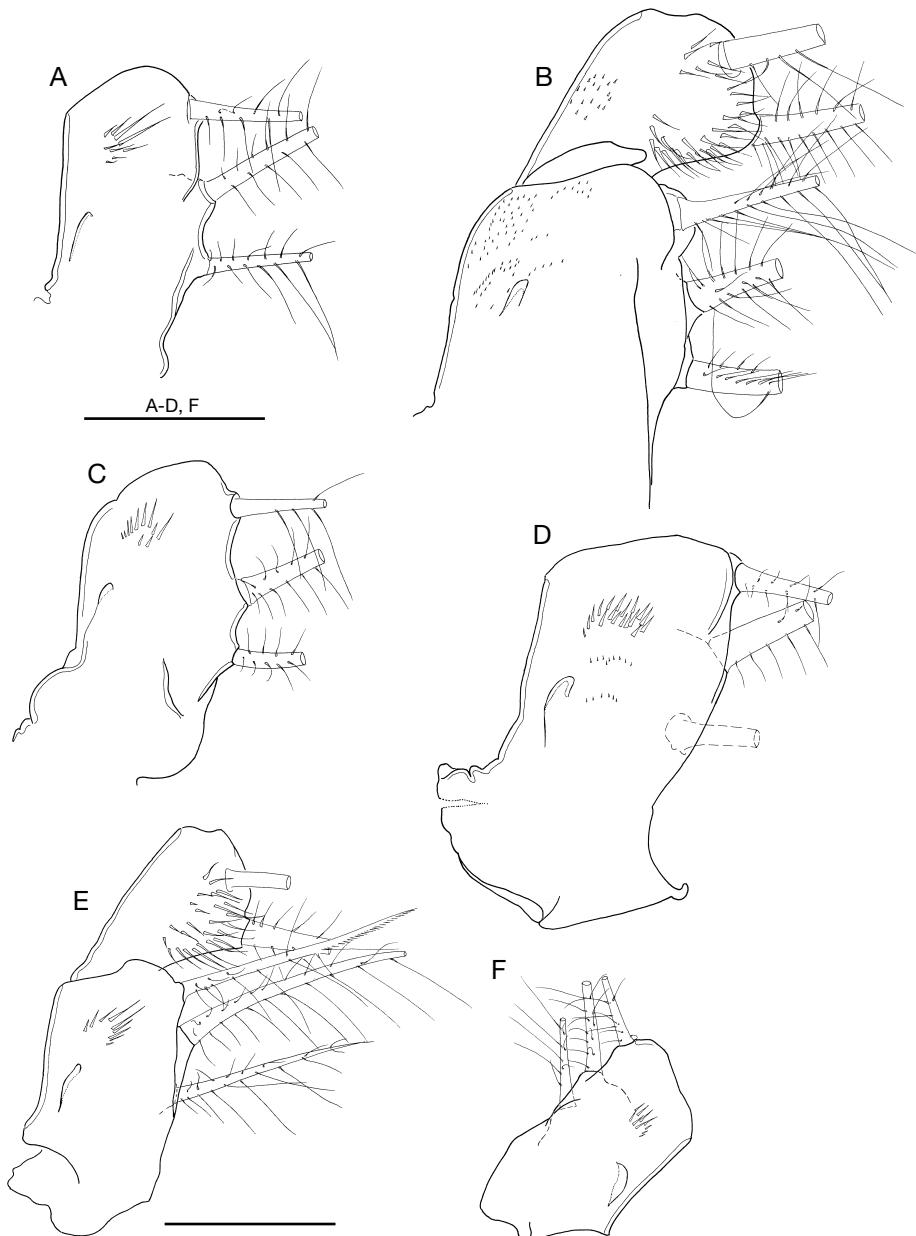


FIG. 10. — Ornamentation of the frontal surface of the maxilliped syncoxopodite, female; **A**, *Cyclops columbianus* Lindberg, 1956 (Alaska, Karluk lake[?]); **B**, *C. insignis* Claus, 1857 (Norway, Frognerfjern); **C**, *C. canadensis* Einsle, 1988 (Alaska, Chatanika); **D**, *C. singularis* Einsle, 1996 (Germany, paratype); **E**, *C. kolensis* Lilljeborg, 1901 (Poland, L. Wigry); **F**, *C. alaskaensis* Lindberg, 1956 (Alaska). Scale bars: 50 µm.

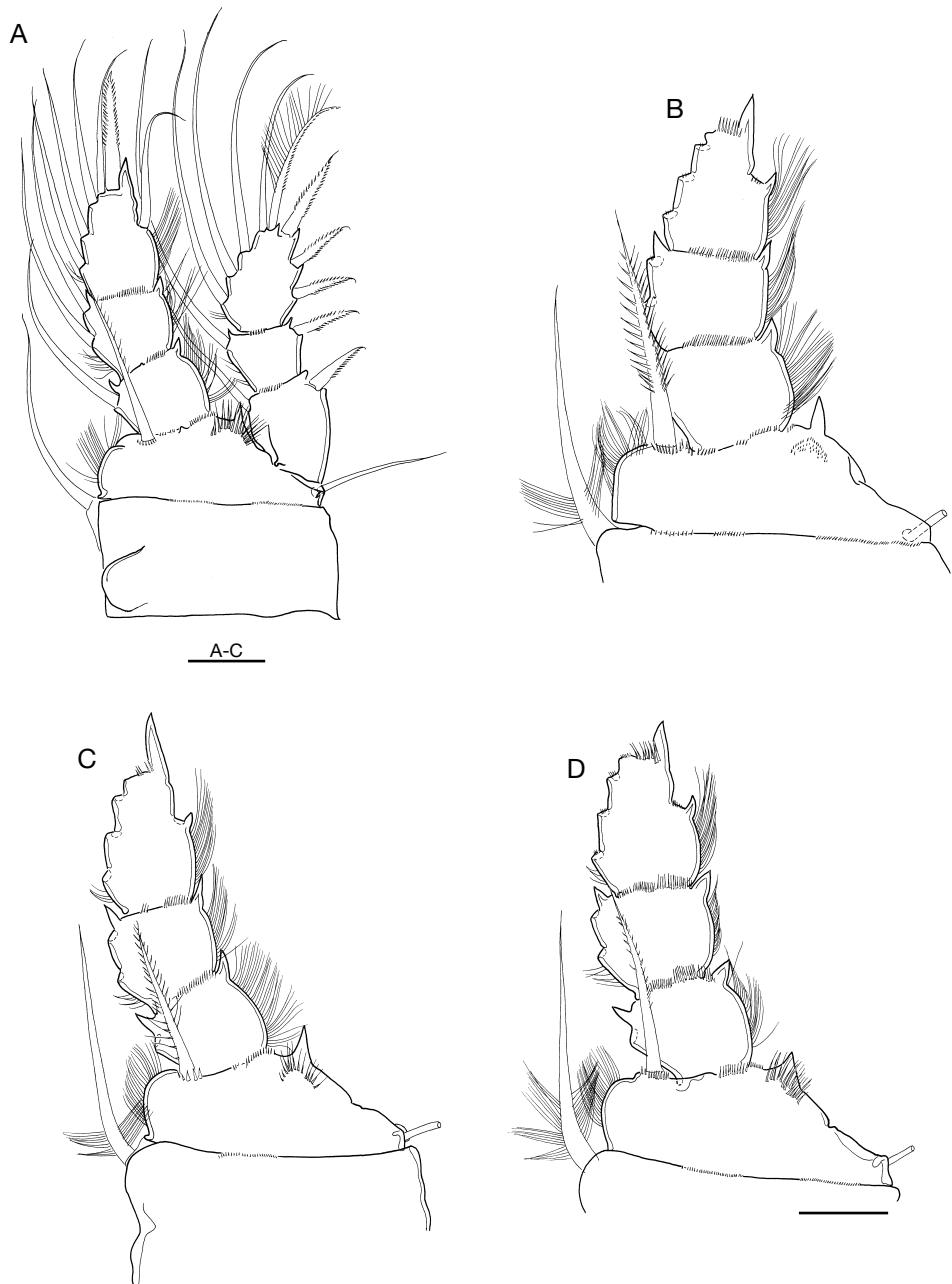


FIG. 11. — Setulation of the medial spine and ornamentation of the frontal surface of P1 basipodite, female; **A**, *Cyclops strenuus* Fischer, 1851 (Russia, Peterhof); **B**, *C. insignis* Claus, 1857 (Norway, Frognerjern); **C**, *C. singularis* Einsle, 1996 (Germany, paratype); **D**, *C. canadensis* Einsle, 1988 (Alaska, Point Barrow). Scale bars: 50 µm.

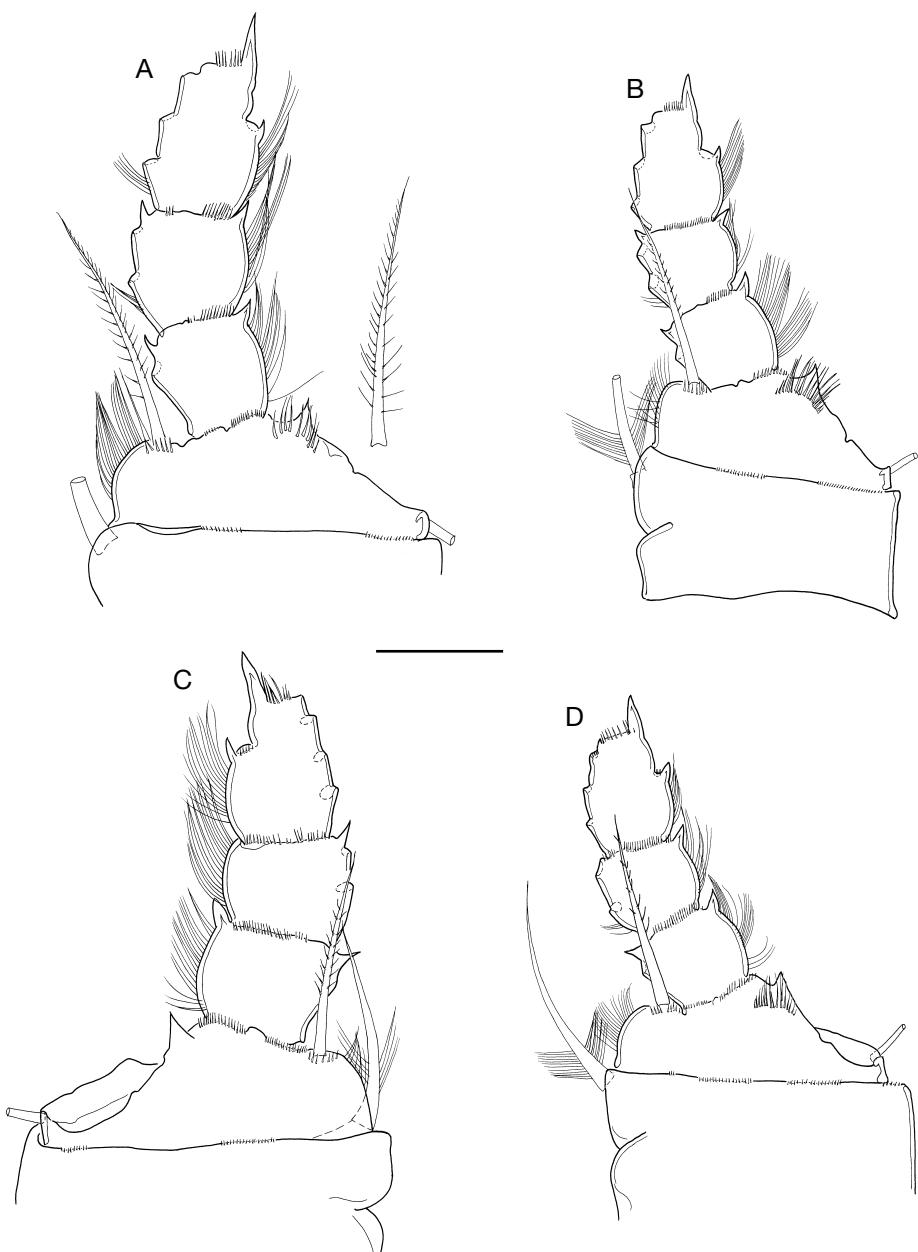


FIG. 12. — Setulation of the medial spine and ornamentation of the frontal surface of P1 basipodite, female; **A**, *Cyclops abyssorum* Sars, 1863 (Norway, Lonavatn); **B**, *C. kolensis* Lilljeborg, 1901 (Poland, L. Wigry); **C**, *C. furcifer* Claus, 1857 (Germany, Baden); **D**, *C. alaskaensis* Lindberg, 1956 (Alaska). Scale bar: 50 µm.

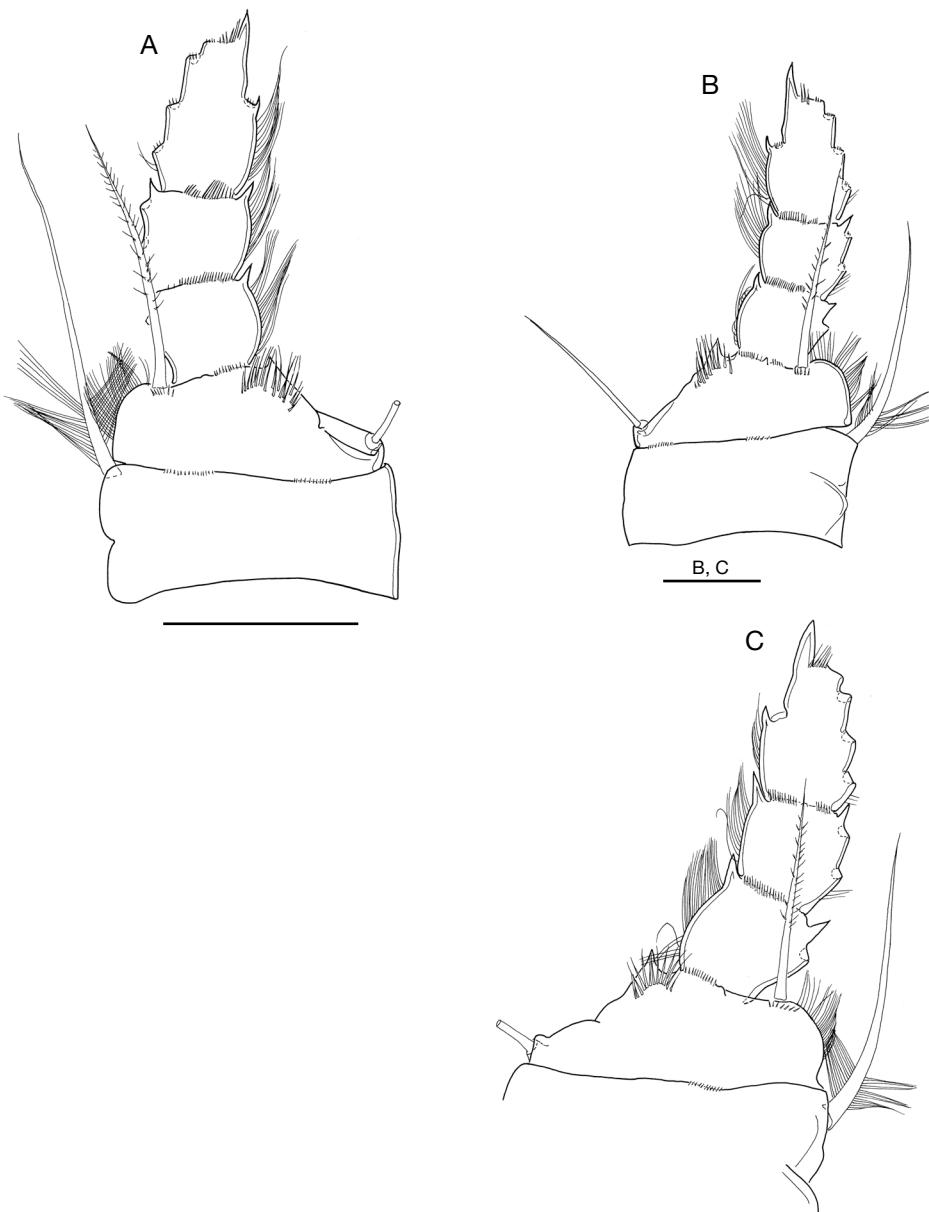


FIG. 13. — Setulation of the medial spine and ornamentation of the frontal surface of P1 basipodite, female; **A**, *C. columbianus* Lindberg, 1956 (Alaska, Karluk lake[?]); **B**, *C. scutifer* Sars, 1863 (Norway, Maridalsvann); **C**, *C. heberti* Einsle, 1996 (Germany, paratype). Scale bars: 50 µm.

the basipodite. In most species the basipodite frontally bears large spinules arranged in an arc between the insertions of the endo- and exopodites (Figs 11-13). No ornamentation, however,

is present in *C. furcifer* (Fig. 12C), and only tiny spinules arranged in a group appear in *C. insignis* (Fig. 11B). The medial spine of the basipodite is usually spinulose, but long setules are present on

the proximal half in *C. singularis* (Fig. 11C) and sometimes in *C. abyssorum* (Fig. 12A). In the latter species, this feature varies not only within the population, but even in the same specimen: one spine has long setules and the corresponding spine on the other side may not. The spinulose medial spine is conspicuously stout in *C. insignis* (Fig. 11B).

DISCUSSION

COMMENTS ON THE DIAGNOSTIC SIGNIFICANCE OF SOME CEPHALOTHORACIC APPENDAGES

There is some intraspecific variability in the length of the aesthetasc on the ancestral XXI antennular segment, yet separation of the two groups of species with long and short aesthetascs is distinct. Our data indicate that those taxa which invaded the pelagic zone of lakes bear long aesthetascs (*C. strenuus*, *C. abyssorum*, *C. kolensis*, and *C. columbianus*), while inhabitants of ephemeral pools and shallow weedy biotopes have short aesthetascs (*C. heberti*, *C. insignis*, *C. alaskaensis*, and *C. canadensis*). One species, *C. furcifer* (small ephemeral waterbodies [Lindberg 1957; Einsle 1996b]) having a long aesthetasc does not fit in this tendency, and *Cyclops singularis* (pools [Einsle 1996a]) and *C. scutifer* (lakes [Lindberg 1957; Elgmork & Halvorsen 1998]) represent an intermediate state in the length of the aesthetasc. Nevertheless, the correlation between the habitat and aesthetasc length is supported by the observations made in another cyclopine genus, *Mesocyclops*, also: while the aesthetasc on the ancestral XXI segment in the plankters (e.g., *M. tobae*, *M. yutsil*, *M. edax*, *M. leuckarti*) reaches or passes beyond the distal margin of the subsequent article (13th segment), that in the species preferring small waterbodies (e.g., *M. aspericornis*, *M. woutersi*, *M. papuensis*, and *M. affinis*) is always shorter. Boxshall & Huys (1998) reported a similar phenomenon but on a much larger scale, namely an increase in the number or size of the aesthetascs in the pelagic lineages of Calanoida, Siphonostomatoida, Poecilstomatoida, Cyclopoida, and Harpacticoida. However, those transformations with a few

exceptions hold only for the male antennules. According to Boxshall & Huys' (1998) hypothesis, in open-pelagic environments, where the water is less turbulent and, therefore, the chemical signals persist longer, the enhancement of the chemosensory system permits males to detect pheromones at lower concentrations (i.e. to find and follow older pheromonal tracks laid by females), and as a consequence, location of the conspecific mate becomes faster. Thus, elongation of the aesthetasc on the ancestral XXI segment in the females of limnetic *Cyclops* species might be the result of a selection actually acting on their males. To test this presumption, we made some preliminary measurements on the relative lengths of the male aesthetascs in forms from lakes and small waterbodies (Table 1). Very few data are available on size of the aesthetascs distally to segment 9 (ancestral segment XV), because it is often difficult even to recognize these weakly chitinized structures on the geniculated sections of the antennule. This is especially true for the aesthetasc on the 15th segment (ancestral segments XXI-XXIII), which is homologous with the female aesthetasc in question showing an increase of size in the limnetic species.

The data in Table 1 do not indicate an elongation of the aesthetascs in the limnetic species, and a relationship between the relative size of the aesthetasc and the body length of the males. On the other hand, taking into account the small size of the sample (few taxa) involving supposedly very closely related species (*C. furcifer*-*C. singularis*-*C. heberti* [Einsle 1996a]), we cannot either exclude a shift in a direction opposite to what is observed in the females (that is the male aesthetascs increase in length towards smaller water bodies), or that size of the aesthetascs in males reflects phylogenetic relationships rather than the environmental influence.

If size of the aesthetasc in females is not directly controlled by a selection exerted on the males, what selection value might it have in limnetic *Cyclops* species? One possibility might be to make predation-avoidance behaviour more efficient. There is strong support from experiments (overview

TABLE 1. — Relative lengths of the aesthetascs in males of *Cyclops* O. F. Müller, 1776. Relative length of aesthetasc = length of aesthetasc/length of antennular segment 1. Numbers refer to antennular segments; **a**, **b**, **c**, proximal, median and distal aesthetasc on antennular segment 1; **L**, total body length excluding caudal setae. Numbers in parentheses show number of specimens examined. Letters in parentheses after the locality names refer to the month of sampling, if males were collected from the same locality, but at a different time. Unless one specimen was measured, data give the mean values. **Froylv.**, Froylandsvatn; *, aesthetasc absent; **r**, aesthetasc is reduced to short shaft; -, no data available.

Antennular segments	a	1 b	c	4	9	13	15	16	17	L (µm)
<i>C. strenuus</i>										
Frognerjern (M)	0.53(1)	0.53(1)	0.55(1)	-	0.56(1)	-	-	-	-	950(1)
Radolfzell	0.40(1)	0.41(2)	0.41(2)	0.42(2)	0.52(2)	-	-	0.30(1)	-	1020(2)
Hellesørdtjenna	0.44(1)	0.45(1)	0.44(1)	0.42(1)	0.48(1)	-	-	-	-	1095(1)
Ura Basseng	0.47(1)	0.48(1)	0.49(1)	-	0.58(1)	-	-	-	-	1120(1)
Frognerjern (F)	0.43(2)	0.43(2)	0.40(1)	0.44(1)	0.54(2)	0.43(1)	-	-	0.75(1)	1155(2)
Ura-Dam	0.42(1)	0.45(1)	0.45(1)	0.49(1)	0.58(1)	0.47(1)	-	-	0.90(1)	1160(1)
Omlandstjenn	-	0.44(1)	0.43(1)	0.47(1)	-	-	-	-	0.89(1)	1175(1)
Barbuli-Temp	0.41(1)	0.43(1)	0.48(1)	0.49(1)	0.55(1)	-	-	-	0.75(1)	1175(2)
Peterhof	0.36(1)	0.36(1)	0.36(1)	0.40(1)	0.49(1)	0.39(1)	0.43(1)	0.33(1)	0.72(1)	1185(1)
Stordammen	0.44(1)	0.44(1)	-	-	0.57(1)	-	-	-	0.69(10)	1255(1)
<i>C. abyssorum</i>										
Mosvatn (J)	0.43(1)	0.38(2)	-	0.40(1)	0.39(2)	-	-	-	0.81(1)	1145(2)
Froylv. (M/A)	0.42(1)	-	-	0.44(1)	0.45(1)	0.44(1)	-	-	-	1240(1)
Rockpool III	0.36(1)	0.34(1)	-	-	-	-	-	-	-	1315(1)
Steinsfjord	0.46(1)	0.46(1)	0.49(1)	0.55(1)	-	-	-	-	-	1330(1)
Lønnavatn	0.42(2)	0.41(2)	0.43(2)	0.46(2)	0.41(1)	0.44(1)	-	0.41(1)	0.65(1)	1350(2)
Mosvatn (A)	0.39(1)	0.41(1)	0.36(1)	0.49(1)	-	0.44(1)	0.43(1)	-	-	1465(1)
Berse	0.45(1)	0.44(1)	0.48(1)	0.45(1)	0.47(1)	-	-	-	0.80(1)	1515(1)
Rockpool IX	0.45(1)	0.41(1)	0.42(1)	-	-	0.44(1)	-	-	-	1525(1)
Hellestveitvann	0.46(1)	0.48(1)	0.46(1)	0.48(1)	-	-	-	-	-	1560(1)
Ljosevatn	-	0.46(1)	-	-	0.46(1)	-	-	-	-	1700(1)
<i>C. kolensis</i>										
Wigry	0.52(1)	0.52(1)	0.52(1)	0.57(1)	0.49(1)	0.49(1)	-	-	-	1070(1)
<i>C. scutifer</i>										
Maridalsvann	*(2)	*(2)	r(2)	r(2)	r(2)	-	-	0.25(1)	0.38(2)	1122(2)
Heilandsvann	*(1)	*(1)	r(1)	-	0.13	0.18	-	-	-	1080(1)
Roksjøen	*(2)	(2)	r(2)	r(2)	-	-	-	-	0.32(1)	1087(2)
Vetlavatn	*(1)	*(1)	r(1)	r(1)	-	-	-	-	-	1210(1)
<i>C. furcifer</i>										
Eichener See	0.47(2)	0.55(3)	0.49(2)	0.51(3)	0.52(2)	0.55(2)	0.43(1)	0.44(1)	-	-
<i>C. singularis</i>										
Type locality	0.57(1)	0.57(1)	-	0.65(1)	-	-	-	-	0.69(1)	1365(1)
<i>C. heberti</i>										
Type locality	0.52(1)	0.52(1)	-	0.56(1)	-	0.41(1)	-	-	0.79(1)	1375(1)
<i>C. alaskaensis</i>										
Alaska	-	-	0.75(1)	0.77(1)	-	0.60(1)	-	-	0.83(1)	990(1)

in Lampert 1993), that diel vertical migration (DVM) of cladocerans and diaptomids can be induced by waterborne chemicals released by the predator: non-migrating individuals showed vertical displacement after the addition of water from fish or invertebrate (*Chaoborus* spp.) predators. Such mechanism could enable limnetic *Cyclops* species to respond quickly to changes in the density of the predators (fish "smell"), by a shift from the

non-migration strategy to energetically supposedly costly migrating behaviour (or in the opposite direction). Einsle (1975, 1987) reported on the DVM of *C. vicinus* and *C. abyssorum praealpinus* in Lake Constance, and Makino & Ban (1998) described a "slight DVM" of *C. strenuus* in Lake Toya, Hokkaido (we did not verify the identity of these taxa). A fish-induced DVM of *C. abyssorum tatricus* in the alpine lakes of the Tatra

Mountains in Poland was documented by Gliwicz (1986). Entering a resting stage could be another alternative adaptation in order to avoid predation (Nilssen 1977; Dahms 1995), but such populations may fail to use the period when food organisms are most abundant (Maier 1989; Santer & Lampert 1995). It seems to be a plausible hypothesis, that strong selection acts on a predator (chemo-)sensory system that allows populations to exploit rich food sources at low mortality rates. This hypothesis generates the prediction that the longer and more intense predation is exerted on a limnetic species, the more pronounced is the size increase of the aesthetasc on the female antennule. Testing such a prediction is, however, beyond the scope of this paper.

As for the diagnostic and systematic importance of the relative length of the female aesthetasc on the ancestral XXI antennular segment, since there is no clear-cut separation in this feature among the species, and the length of the aesthetascs may be more influenced by the environment than by relatedness of the taxa, caution is needed in its application as either a species distinguishing or a phylogenetically diagnostic feature.

The setulation of the two proximalmost setae of the maxillulary palp is a stable, expressed in both female and male by the same character-state without intraspecific variability, and relatively easily verifiable feature. Fryer (1957) reported on the feeding of carnivorous cyclopids (*Macrocylops* and *Megacyclops*) as follows: "When the distal denticles of the maxillules are clamped into the prey the palps of these appendages embrace the latter and the setae of the palps are splayed over its surface. Any movement of the prey can thus be detected by these setae."

Our speculation is that long setules on the proximal setae of the palp (*C. abyssorum*, *C. furcifer*, *C. singularis*, *C. heberti*) by an increase of the perception area enhance the sensitivity of these setae, and help in holding the (small-sized?) prey more securely. Literature data (Makino & Ban 1998) suggest that even adult *Cyclops* are omnivorous, feeding on small cladocerans (e.g., *Bosmina*), rotifers and phytoplankton (diatoms and dinoflagel-

lates). On the other hand, the proximalmost seta of the maxillulary palp is conspicuously elongate (as long or longer than the seta next to it on the lateral lobe of the palp) in all the *Cyclops* species, which might suggest that the genus as a whole is adapted to smaller-sized food. In contrast, the proximalmost seta of the palp in *Mesocyclops* (except a few taxa like *M. yutsil* and *M. chaci*) (Hołyńska *et al.* 2003) and *Macrocylops* (verified on *M. albidus*, *M. fuscus*, and *M. neuter*) is short and spinulose. Some representatives of these genera hunt for large food items (e.g., mosquito larvae, calanoids). Interestingly, in those taxa which supposedly are entirely or predominantly herbivorous, like *Eucyclops* (Fryer 1957) and perhaps *Paracyclops* (Karaytug 1999), the proximalmost seta of the maxillulary palp is long, and – like at least the proximalmost seta of the lateral lobe – bears long setules (maxillule in *Eucyclops* was verified on *E. serrulatus*, *E. speratus*, and two unidentified species from Borneo and Taiwan).

ZOOGEOGRAPHICAL IMPLICATIONS

As a result of better morphological delimitation by the "microcharacters" shown here, new information has been gained on the geographical distribution of some taxa. Comparison of *C. strenuus strenuus* sensu Koźmiński, 1933 and *C. strenuus landei* Koźmiński, 1933 collected from the terra typica (NE Poland: Lake Wigry region) and identified by Koźmiński himself, helped in establishing the identities of these subspecies: while *C. strenuus strenuus* sensu Koźmiński is conspecific with *C. heberti*, *C. strenuus landei* is a form identical in all observed characters with *C. strenuus* s. str. Einsle (1975) investigated the seasonal and multi-annual changes in the morphometric characters of *Cyclops strenuus* in Lake Constance and its neighbourhood. Although a tendency toward the decrease of body length, width of pedigers 4 and 5, and the elongation of the caudal setae could be observed from the small-water/littoral toward the pelagic populations, large series of intermediate forms appeared between the two extremes distinguished by Einsle as *C. strenuus strenuus* (small-water/littoral ecotype) and *C. strenuus landei* (pelagic ecotype). The

mean values of the morphometric indices significantly changed in the same population during a year, and representatives of the pelagic and littoral-types were present even in the same sample. The five females we saw from the type locality (Peterhof) of *C. strenuus* are close to the littoral ecotype on the scale set up on Lake Constance specimens: body length, 1595–1715 mm; relative length (in proportion to the length of the body) of the caudal setae from the medialmost to the lateralmost: 113–133%, 259–286%, 230–256%, 79–84%. In the single undissected female of *C. strenuus landei* available for us from the terra typica, the body length is slightly smaller (1490 mm), but the relative lengths of the caudal setae are in the ranges measured for the Peterhof specimens of *C. strenuus*. Koźmiński (1933) described *C. strenuus landei*, having compared it with what he had considered as *C. strenuus strenuus* (actually another species, *C. heberti*). Besides the morphometric differences (smaller body length, narrower pediger 4 in *C. strenuus landei*), he found ecological separation between the two “subspecies” also: while “*C. strenuus strenuus*” (= *C. heberti*) appeared abundantly in small ephemeral pools, but never occurred in the plankton of the lakes, *C. strenuus landei* inhabited the open water of small lakes (not deeper than 8 m) called in the local language, “Suchary” and “Šlepaki” (dystrophic peatbog ponds of very low Ca content, without in- and outlets [Falk 1979]). Einsle, apparently influenced by Koźmiński’s observations, named the littoral type *C. strenuus strenuus* and the pelagic type *C. s. landei*. A trinomial name properly assigns a subspecies, an aggregate of populations living in a subdivision of the range (Mayr 1970); therefore its use for an ecological form is confusing, and should be avoided. Instead, it is better to refer to such variants as littoral- and pelagic types/forms, all the more that similar shifts in morphometric characters can occur in the small-water/littoral- and pelagic populations of other unrelated cyclopoid taxa as well.

Cyclops heberti, which has so far been known only from southern Germany, seems to be widely distributed in Europe (southern France, central Italy,

southern and northern Germany, Poland). Similarly, until recently *Cyclops singularis* was reported from southern Germany only, yet occurrences of this species in Belgium (Alekseev *et al.* 2002), England (the specimens were found and identified by J. Green [in a letter to G. A. Boxshall]), Hungary and Slovakia (records herein) indicate a much larger geographical range. We do have much better knowledge of the geographical distribution of a North American species, *C. canadensis*, often misidentified as *C. strenuus*. The fact that all specimens examined from the Arctic Canada and Alaska identified as *C. strenuus* were conspecific with *C. canadensis* supports Einsle’s hypothesis that the former species does not occur in the Nearctic (Einsle 1988, 1996b).

Acknowledgements

We thank Prof. Victor Alekseev for placing the topotypes of *C. strenuus* at our disposal. We are also grateful for the help of Mrs Janice Clark Walker (USNM), who made the material from North America available for us. The senior author wishes to thank Prof. Horst-Kurt Schminke and Dr Thomas Glatzel (Carl von Ossietzky Universität, Oldenburg) and Dr Hans-Walter Mittmann (SMNK), for their hospitality during her research visit sponsored by the “Deutscher Akademischer Austauschdienst” (No. A/01/02168) in September–October 2001. Last but not least we must mention Dr Jens Petter Nilssen and Dr Svein Birger Wærvågen, who, by sending several samples with *Cyclops* from Norway along with ample information on the collection sites in particular, and by critically reading the manuscript, helped us very much.

REFERENCES

- ALEKSEEV V., FEFILOVA F. & DUMONT H. J. 2002. — Some noteworthy free-living copepods from surface freshwater in Belgium. *Belgian Journal of Zoology* 132: 133–139.
- BOXSHALL G. A. & HUYS R. 1998. — The ontogeny and phylogeny of copepod antennules. *Philosophical*

- Transactions of the Royal Society of London B* 353: 765-786.
- DAHMS H.-U. 1995. — Dormancy in the Copepoda – an overview. *Hydrobiologia* 306: 199-211.
- EINSLE U. 1975. — Revision der Gattung *Cyclops* s. str. speziell der abyssorum-Gruppe. *Memorie dell'Istituto Italiano di Idrobiologia dott. Marco de Marchi* 32: 57-221.
- EINSLE U. 1985. — A further criterion for the identification of species in the genus *Cyclops* s. str. (Copepoda, Cyclopoida). *Crustaceana* 49: 299-309.
- EINSLE U. 1987. — Zur Vertikalwanderung planktischer Copepoden im Bodensee-Obersee. *Schweizerische Zeitschrift für Hydrologie* 49: 303-315.
- EINSLE U. 1988. — *Cyclops canadensis* n. sp. and *Cyclops scutifer* Sars, 1863 (Crustacea: Copepoda) from northern Canada. *Canadian Journal of Zoology* 66: 2146-2149.
- EINSLE U. 1994. — *Cyclops kikuchii* Smirnov, 1932 (Copepoda, Cyclopoida), eine selbständige Art aus süddeutschen Gewässern. *Crustaceana* 66: 240-246.
- EINSLE U. 1996a. — *Cyclops heberti* n. sp. and *Cyclops singularis* n. sp., two new species within the genus *Cyclops* ("strenuus-subgroup") (Crust. Copepoda) from ephemeral ponds in southern Germany. *Hydrobiologia* 319: 167-177.
- EINSLE U. 1996b. — Copepoda: Cyclopoida. Genera *Cyclops*, *Megacyclops*, *Acanthocyclops*. Volume 10, in DUMONT H. J. F. (ed.), *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*. Backhuys, Leiden, 82 p.
- ELGMORK K. & HALVORSEN G. 1971. — Reidentification of a freshwater, planktonic cyclopoid (Copepoda, Crustacea) from Greenland, Iceland, and the Faroe Islands. *Norwegian Journal of Zoology* 19: 267-274.
- ELGMORK K. & HALVORSEN G. 1998. — Intraspecific morphological variation in a freshwater copepod (Crustacea) in relation to geographic distribution and environment. *Canadian Journal of Zoology* 76: 751-762.
- FALK K.-O. 1979. — Z przeszłości i teraźniejszości wód wigierskich. Obrazy z życia rybaków augustowskich. [= Past and present of the Wigry waters. Pictures from the fishermen-life in the Augustów region.]. *Rozprawy i Monografie (Ośrodek Badania Naukowych w Białymostku)* 12: 26-91 (in Polish).
- FIERS F. & VAN DE VELDE I. 1984. — Morphology of the antenna and its importance in the systematics of the Cyclopidae. *Crustaceana* Suppl. 7: 182-199.
- FRYER G. 1957. — The feeding mechanism of some freshwater cyclopoid copepods. *Proceedings of the Zoological Society of London* 129: 1-25.
- GLIWICZ M. Z. 1986. — Predation and the evolution of vertical migration in zooplankton. *Nature* 320: 746-748.
- GRISHANIN A. K. & AKIF'EV A. P. 2000. — Inter-population differentiation within *C. kolensis* and *C. strenuus strenuus* (Crustacea: Copepoda): evidence from cytogenetic methods. *Hydrobiologia* 417: 37-42 (dated 1999, published 2000).
- GRISHANIN A. & DAHMS H.-U. (in press). — DNA-content of embryonic cells of *Cyclops kolensis* as evidenced by cytophotometry. *Zoological Studies*.
- HOŁYŃSKA M., REID J. W. & UEDA H. 2003. — Genus *Mesocyclops* Sars, 1914, in UEDA H. & REID J. W. (eds), *Copepoda: Cyclopoida. Genera Mesocyclops and Thermocyclops*. Volume 20, in DUMONT H. J. (ed.), *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*. Backhuys, Leiden: 12-213.
- HUY'S R. & BOXSHALL G. A. 1990. — The rediscovery of *Cyclopicina longifurcata* (Scott) (Copepoda: Cyclopinae) in deep water in the North Atlantic, with a key to genera of the subfamily Cyclopinae. *Sarsia* 75: 17-32.
- HUY'S R. & BOXSHALL G. A. 1991. — *Copepod Evolution*. The Ray Society, London, 468 p.
- KARAYTUG S. 1999. — Genera *Paracyclops*, *Ochridacyclops* and key to the Eucyclopinae. Volume 14, in DUMONT H. J. F. (ed.), *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*. Backhuys, Leiden, 217 p.
- KOŹMIŃSKI Z. 1927. — Über die Variabilität der Cyclopiden aus der *strenuus*-Gruppe auf Grund von quantitativen Untersuchungen. *Bulletin international de l'Académie polonaise des Sciences et des Lettres* sér. B, Suppl. 1: 1-114 + 19 pls.
- KOŹMIŃSKI Z. 1933. — Badania morfometryczne i ekologiczne nad oczlikami (Cyclopidae) z grupy *strenuus*. [= Morphometric and ecological studies on cyclopids from the *strenuus*-group]. *Archiwum Hydrobiologii i Rybactwa, Suwałki* 7: 59-140 + 5 pls (in Polish).
- KOŹMIŃSKI Z. 1936. — Morphometrische und ökologische Untersuchungen an Cyclopiden der *strenuus*-Gruppe. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 33: 161-240.
- LAMPERT W. 1993. — Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. *Archiv für Hydrobiologie Beih. Ergebn. Limnol.* 39: 79-98.
- LINDBERG K. 1957. — *Le groupe Cyclops rubens* (syn. *Cyclops strenuus*). *Révision du genre Cyclops s. str. (O. F. Müller 1770) (Crustacés copépodes)*. C. W. K. Gleerup, Lund, 335 p.
- LOWNDES A. G. 1932. — The results of further breeding experiments on four species of *Cyclops*. *Annals and Magazine of Natural History* Ser. 10, vol. 9: 265-297.
- MAIER G. 1989. — Variable life cycles in the freshwater copepod *Cyclops vicinus* (Uljanin, 1875): support for the predator avoidance hypothesis? *Archiv für Hydrobiologie* 115: 203-219.
- MAKINO W. & BAN S. 1998. — Diel changes in vertical overlap between *Cyclops strenuus* (Copepoda;

- Cyclopoida) and its prey in oligotrophic Lake Toya, Hokkaido, Japan. *Journal of Marine Systems* 15: 139-148.
- MAYR E. 1970. — *Populations, Species, and Evolution. An Abridgment of Animal Species and Evolution*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, 453 p.
- NILSEN J. P. 1977. — Cryptic predation and the demographic strategy of two limnetic cyclopoid copepods. *Memorie dell'Istituto Italiano di Idrobiologia dott. Marco de Marchi* 34: 187-196.
- NILSEN J. P. 1979. — Problems of subspecies recognition in freshwater cyclopoid copepods. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 17: 285-295.
- RZÓSKA J. 1930. — Biometrische Studien über die Variabilität einer Cyclopiden-gruppe. *Archiwum Hydrobiologii i Rybactwa* 5: 193-220.
- RZÓSKA J. 1932. — Some general remarks on the faunistics and variability of some Cyclopida. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 26: 424-430.
- SANTER B. & LAMPERT W. 1995. — Summer diapause in cyclopoid copepods: adaptive response to food bottleneck. *Journal of Animal Ecology* 64: 600-613.
- WIERZBICKA M. 1934. — Les résultats du croisement de certaines formes du groupe de *Cyclops strenuus* (*sensu lato*). *Mémoires de l'Académie polonaise des Sciences et des Lettres* Sér. III, B 6: 189-206 + pls 7, 8.

Submitted on 6 May 2003;
accepted on 5 September 2003.