Taxonomy, biology and phylogeny of Miraciidae (Copepoda: Harpacticoida)

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TAXONOMY, BIOLOGY AND PHYLOGENY OF MIRACIIDAE (COPEPODA: HARPACTICOIDA)

RONY HUYS & RUTH BÖTTGER-SCHNACK

SARSIA

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The holoplanktonic family Miraciidae (Copepoda, Harpacticoida) is revised and a key to the four monotypic genera presented. Amended diagnoses are given for *Miracia* DANA, *Oculosetella* DAHL and *Macrosetella* A. SCOTT, based on complete redescriptions of their respective type species *M. efferata* DANA, 1849, *O. gracilis* (DANA, 1849) and *M. gracilis* (DANA, 1847). A fourth genus *Distioculus* gen. nov. is proposed to accommodate *Miracia minor* T. SCOTT, 1894. The occurrence of two size-morphs of *M. gracilis* in the Red Sea is discussed, and reliable distribution records of the problematic *O. gracilis* are compiled. The first nauplius of *M. gracilis* is described in detail and changes in the structure of the antennule, P2 endopod and caudal ramus during copepodid development are illustrated. Phylogenetic analysis revealed that *Miracia* is closest to the miraciid ancestor and placed *Oculosetella-Macrosetella* at the terminal branch of the cladogram. Various aspects of miraciid biology are reviewed, including reproduction, postembryonic development, vertical and geographical distribution, bioluminescence, photoreception and their association with filamentous Cyanobacteria (*Trichodesmium*).

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INTRODUCTION

There is ample evidence that harpacticoid copepods can enter into the water column, either by active migration or passively as a result of erosion and subsequent advection from sediments (see PALMER 1988 for review). HICKS (1988a) listed 18 families of harpacticoids for which in at least some representatives sustained swimming activity had been observed, and YEATMAN (1962) showed how littoral harpacticoids can be carried into the open ocean by algal rafting. Truly planktonic species which permanently reside in the water column, however, form only a tiny minority in the order Harpacticoida. At present, out of a total of 3372 species of Harpacticoida only 17, belonging to seven families, can be regarded as permanent members of the plankton (BOXSHALL 1979). As in most other copepod orders, the invasion of the pelagic zone is clearly a secondary event in the evolution of the harpacticoids (HUYS & BOXSHALL 1991). The colonization of the marine planktonic environment happened independently by the Aegisthidae, Clytemnestridae and Miraciidae, and by isolated members of other families. The majority of these harpacticoids are morphologically not well adapted for life in the plankton, and some of them are not significantly different from their benthic relatives. Interestingly, it has been shown that at least two lineages are associated with 'pelagic' substrates that are essentially benthic in nature, serving a dual function as physical substrate for attachment and as food source. The attachment and feeding of *Microsetella* spp. (Ectinosomatidae) on discarded and occupied larvacean houses (Appendicularia) is well documented (ALLDREDGE 1972; OHTSUKA & al. 1993). An alternative strategy is adopted by the Miraciidae which are closely associated with blooms of marine filamentous Cyanobacteria (O'NEIL & ROMAN 1992).

The family Miraciidae currently contains four species accommodated in three genera: *Miracia* DANA, *Oculosetella* DAHL and *Macrosetella* A. SCOTT. All species were described before the turn of the century, and three of them were discovered during the monumental U.S. Exploring Expedition undertaken in the late 1830s and early 1840s (DANA 1847, 1849a, 1854).

Despite their early discovery and overall high abundance in subtropical and tropical oceanic waters, little is known about the biology of the Miraciidae and good species descriptions are still wanting. This lack has led to several misidentifications in the past, and fueled certain problematic issues such as the occurrence of two size morphs of *Macrosetella gracilis* in the Red Sea (BÖTTGER-SCHNACK 1989, 1991) and the uncertain taxonomic status of *Oculosetella gracilis* (cf. BOXSHALL 1979). The family received relatively little attention in LANG's (1948) monograph. His cursory treatment of the family, largely based on STEUER's (1935) review, did not consider some important papers (e.g. CLAUS 1891) and unfortunately contained several errors such as the setal formula given for *Miracia* and the diagnosis of *Oculosetella* which was based on illustrations of *Miracia minor*.

This paper gives full redescriptions of all species, presents the hypothetical phylogenetic relationships between the genera, and reviews our current knowledge on the biology of the family.

MATERIAL AND METHODS

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England). All drawings have been prepared using a camera lucida on a Leitz Diaplan differential interference contrast microscope. Females and males were examined with a Hitachi S-800 scanning electron microscope. Specimens were prepared by dehydration through graded ethanol, critical point dried, mounted on stubs and sputter-coated with palladium.

The descriptive terminology is adopted from HUYS & BOXSHALL (1991). Abbreviations used in the text are: P1–P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus; NI–NVI, first to sixth nauplius stage; CI–CV, first to fifth copepodid stage.

Copepods collected from the Red Sea, Gulf of Aden, Arabian Sea and eastern Mediterranean were obtained using a multiple opening-closing net system (MSN) equipped with five fine mesh nets (WEIKERT & JOHN 1981).

Phylogenetic relationships between genera were analyzed using the phylogenetic computer package PAUP version 3.1 prepared by D. Swofford, Laboratory of Molecular Systematics, Smithsonian Institution. A multistate scoring system was employed and missing characters were scored 9. A hypothetical composite ancestor was included in the analysis which scored 0 for all characters. The options employed in the analysis were BRANCH AND BOUND, which guarantees to find all most parsimonious trees, and the DELTRAN optimisation, which delays character transformation within the tree. All characters were set irreversible using the Camin-Sokal option.

SYSTEMATICS AND MORPHOLOGY

Family Miraciidae DANA, 1846

Macrosetellidae A. SCOTT, 1909.

The family name Miracidae DANA, 1846 takes its stem from the type genus *Miracia*. It constitutes therefore an original incorrect spelling which, despite its common usage, must be emended to Miraciidae.

History. The taxonomic history of the Miraciidae dates back to the first half of the 1800s when DANA first defined the family. Illustrations and full text descriptions of the various species were published in DANA's second volume of the Crustacea of the United States Exploring Expedition. Diagnoses of the families, genera and most species were given earlier in a series of papers (sometimes in different versions), forming part of a 'Conspectus Crustaceorum', and made available when the full Report on the Crustacea of the Expedition was still in the course of preparation. The exact publication dates of DANA's papers and their relative priority are not always clear from the literature. This inconsistency has caused some confusion with regard to the publication dates of the miraciid taxa.

DANA (1846a). This paper contains a classification of the Tribus Cyclopacea encompassing five families. The new genus *Setella* and *Arpactus* (*lapsus calami* of *Arpacticus* MILNE EDWARDS, 1840) are referred to the Arpactidae. The family Miracidae is established to accommodate the new genus *Miracia*. English diagnoses are given for *Setella* and *Miracia* but no reference is made to species. In the brief diagnosis of the family Miracidae, DANA already indicates the close resemblance with *Setella*. This paper was published in March 1846.

DANA (1846b). Except for slight typographical changes, this paper is identical in content with DANA (1846a). Presumably this version, contained in the volume that is dated 1846 on the title page, was published in the second half of 1846 since the editor acknowledged the American version and its publication date in a footnote on p. 185. The diagnoses presented in the English version therefore lose in priority.

DANA (1847). This is the first part of DANA's 'Conspectus Crustaceorum' series, covering the families Cyclopidae and Harpactidae. It includes a slightly more extensive Latin diagnosis of *Setella*, which is now placed in the Harpactidae with *Harpacticus* and the new genus *Clytemnestra*. Latin diagnoses are also given for five *Setella* species: *S. tenuicornis, S. longicauda, S. gracilis, S. crassicornis* and *S. aciculus*. The paper was published in volume I of the Proceedings of the American Academy of Arts and Sciences bearing a printing date of 1848 on the title page

which also indicates that the papers contained in the volume were selected from the records during the period May 1846 to May 1848. Most authors have adopted this date, overlooking that at least some of the papers were issued before 1848, including DANA's. A pamphlet found in the collection of W.T. Calman in The Natural History Museum is dated 1847 on the cover and includes a separate of DANA's first part of the Conspectus. The content is unchanged, but a few typographical changes are found in the title (p. 1), which is repeated in an abbreviated form on p. 3. The pamphlet pagination (pp. 1–8) is different from the journal one which is erroneously listed in parentheses (pp. 149–154) on every page but does not match with the original text (pp. 149–155). The exact publication date is after 4 May 1847, which was the date of the proceedings of the last meeting printed on p. 3 of the separate and also cited in DANA (1849b: 276).

DANA (1849a). This is the second part of the Conspectus, including the families Calanidae, Corycaeidae and Miracidae. Latin diagnoses are presented of the family Miracidae, its only genus *Miracia* and the two species included, *M. efferata* and *M. gracilis*. This paper was published in volume II of the Proceedings of the American Academy of Arts and Sciences bearing a printing date of 1852 on the title page which also indicates that the papers contained in the volume were selected from the records during the period May 1848 to May 1852. The date 1952 mistakenly became established in the literature (see e.g. LANG 1948). DANA's contribution forms part of the proceedings of the 311th meeting of the American Academy of Arts and Sciences which were issued together (pages 1–160 of the volume) in 1849. As for Pars I, DANA's pages were also published and distributed in 1849 as a pamphlet bearing a printing date of 1847–1849 on the title page.

DANA (1849b). This is a summary of Pars I and II of the 'Conspectus Crustaceorum' (DANA 1847, 1849a) repeating the Latin diagnoses of the families and genera and mentioning the constituent species without diagnoses. The publication date of the journal issue is September 1849.

DANA (1854). A great deal of controversy exists over the real publication dates of DANA's two volumes on Crustacea of the United States Exploring Expedition. The official set of volumes authorized by the Congress includes Vol. XIII (Crustacea, Part 1, James D. Dana, 1852) and Vol. XIV (Crustacea, Part 2, James D. Dana, 1853, with Atlas, 1855). The Act of Congress provided for a series of volumes to be issued in 100 copies. These were distributed as follows: one copy to the Captains Wilkes, Hudson and Ringgold, one to the Naval Lyceum at Brooklyn, one to each State of the Union, one to each friendly power and one copy each to France and Great Britain (COLLINS 1912). The number of copies available for general distribution must therefore have been small. Fifty-eigth copies of volumes XIII and XIV sent to the Department of State (Washington) were shipped from Philadelphia on 4 February 1853 and 4 February 1854, respectively (HASKELL 1942). The real publication date of Vol. XIV (containing the copepods) is therefore 1854 and not 1853 as printed on the title page. However, a fire at Washington, 11 April 1856, destroyed 21 copies which were never replaced. It is likely that none of the official copies authorized by the Congress ever reached the general public (COLLINS 1912).

Due to protests from scientific and other societies against the limitation of the edition, authors were permitted to have additional copies printed at their own expense. These author-distributed copies are what one finds in various public and scientific libraries. Since these volumes were generally placed by the authors in the hands of publishers, it were usually slight variations from the official set that were printed. In DANA's case both volumes were reprinted as Parts 1 and 2 of Vol. XIII and mention 1852 as the printing date on the title page. A copy of this public issue was for instance acquired by The Natural History Museum, London and by the Rijksmuseum voor Natuurlijke Historie, Leiden; without doubt this was also the edition cited by LANG (1948) in his monograph. As for the offical set, the author-distributed copies of Part 2 could not have reached the public before 1854, which is considered here as the real date of publication.

As pointed out by A. SCOTT (1909) and WILSON (1924), the genus name *Setella* had already been used for a lepidopteran genus. A. SCOTT (1909) proposed *Macrosetella* as a new replacement name and regarded it as the type of a new family Macrosetellidae. WILSON's (1924) replacement name *Dwightia* loses in priority. The family name Macrosetellidae gained wide acceptance but became subsequently a junior subjective synonym of DANA's Miraciidae when WILSON (1932) and STEUER (1935) included *Miracia* (and *Oculosetella*) in the family. Most plankton workers failed to recognize this synonymy even though LANG (1948) pointed out the existence of DANA's family name. This has occasionally led to the ambiguous situation whereby both family names are listed in the same paper (e.g. OWRE & FOYO 1967).

Diagnosis. Harpacticoida. P1-bearing somite fused to cephalosome to form a cephalothorax. Dorsal surface of thoracic and abdominal somites without spinular ornamentation. Genital and first abdominal somites in ♀ fused to form genital double-somite. Anal somite without well developed anal operculum; pseudoperculum also absent. Caudal rami parallel, as long or longer than last 2 abdominal somites combined; each with 7 setae; setae I–III closely set together; setae IV–V spinulose.

Cephalothorax with paired cuticular lenses anteriorly (secondarily reduced in *Macrosetella*). Antennule slender and 7- or 8-segmented in ♀; haplocer and 10-segmented in ♂, geniculation located between segments 7 and 8. Antenna with basis and proximal endopod segment incompletely or completely fused to form allobasis; free endopod 1-segmented, with 1–2 lateral spines, and 3–5 non-geniculate setae distally; exopod absent or at most represented by bisetose segment. Mouthparts reduced. Mandible with reduced gnathobase and small 1-segmented palp with 1–2 setae. Maxillule with arthrite bearing stubby armature elements and reduced palp with up to 4 setae; exopod (or endopod?) represented by 1 seta on non-articulated knob or minute free segment. Maxilla with 2 endites on syncoxa, each with 1 or 2 setae; allobasis drawn out

into short strong claw; endopod fully incorporated. Maxilliped powerful, subchelate; syncoxa elongate, with 1 or 3 setae, usually with sclerite around base; basis elongate, with 2 vestigial setae and distal concavity delineated by anterior chitinous ridge; endopod represented by anteriorly recurved claw and 2–3 accessory setae.

P1 with 3-segmented exopod and 2-segmented endopod; basis with inner and outer seta/spine; enp-1 elongate, twice as long as enp-2; exp-1 without inner seta; exp-3 with 3-4 setae.

P2-P4 with 3-segmented rami; protopods without surface ornamentation. Spine and seta formula:

	Exopod	Endopod
P1	0.1.02[1–2]	[0–1].021
P2	0.1.222	[0–1].2.121
P3	0.1.32[2–3]	[0–1].[1–2].221
P4	0.1.32[2–3]	1.1.221

Fifth pair of legs fused medially in ♂, free in ♀; exopod and baseoendopod separate in both sexes; exopod with 5–6 setae/spines in ♀, with 4–6 in ♂; endopodal lobe with 3–5 setae/spines in ♀, with 2–3 setae/spines in ♂.

Genital field with genital apertures located close to anterior margin of genital double-somite, separate or fused to common genital slit. Seminal receptacle unpaired, transversely expanded to form tripartite chamber. Copulatory pore single, minute; flanked by 3 secretory pores on either side. Genital operculum derived from P6 with 1 very long and 1–2 short setae.

Male sixth pair of legs symmetrical, slightly fused medially; with 1–3 setae.

Sexual dimorphism in antennule, P1 basis (inner margin with raised spinular comb or distally produced process), P2 endopod (2-segmented; enp-2 a compound segment with 1 seta fewer than in ♀, drawn out into spinous process derived from outer apical seta, outer margin with modified spine), P5, P6 and in genital segmentation.

Females with paired egg-sacs; males with 1 spermatophore.

Planktonic. Marine.

Type genus. *Miracia* DANA, 1846

Other genera. *Oculosetella* DAHL, 1895; *Macrosetella* A. SCOTT, 1909; *Distioculus* gen. nov.

KEY TO GENERA

1. Paired cephalic cuticular lenses absent; P1 exp-3 with 3 setae/spines ..... *Macrosetella* A. SCOTT.

   Paired cephalic cuticular lenses present; P1 exp-3 with 4 setae/spines ..... 2.

2. Cephalic cuticular lenses not touching middorsally; P1 enp-2 with 2 setae .. *Distioculus* gen. nov.

   Cephalic cuticular lenses touching middorsally; P1 enp-2 with 3 setae/spines ..... 3.

3. Rostrum well developed, defined at base; antennule ♀ 7-segmented; antennary exopod absent; P5 baseoendopod with 3 setae in ♀, 2 setae in ♂ ..... *Oculosetella* DAHL.

   Rostrum minute, fused to cephalothorax; antennule ♀ 8-segmented; antennary exopod present; P5 baseoendopod with 5 setae in ♀, 3 setae in ♂ ..... *Miracia* DANA.

Genus *Miracia* DANA, 1846a

History. DANA diagnosed the genus in 1846, however mentions the two species it originally contained not until 1849. According to Art. 11c(i) of the International Code of Zoological Nomenclature (3rd ed.), works published before 1931, containing uninominal genus-group names without associated nominal species, are accepted as consistent with the Principle of Binominal Nomenclature. DANA did not designate a type species, but *M. efferata* DANA, 1849 became the type and only species when *M. gracilis* DANA, 1849 was proposed as the type of a distinct genus *Oculosetella* (DAHL 1895).

Previous complete or partial redescriptions of *M. efferata* were given by BRADY (1883), CLAUS (1891), GIESBRECHT (1892), MRÁZEK (1895), WHEELER (1901), LEGARÉ (1964), BOXSHALL (1979) and ZHENG ZHANG & al. (1982).

Diagnosis (amended). Miraciidae. Body more or less cyclopiform; boundary between prosome and urosome distinct. Cephalothorax rounded anteriorly, distinctly wider than first free pedigerous somite, ventrally deflexed; with pair of large cuticular lenses touching in the median line. Thorax and abdomen with distinct constrictions between somites. Integument strongly chitinized, pitted. Original segmentation of genital double-somite marked by lateral constriction. Caudal ramus 3 times as long as wide; seta V shorter than urosome; setae IV and V not fused at base; seta VI not fused to ramus.

Rostrum small, largely integrated in cephalothorax. Antennule 8-segmented in ♀; aesthetasc on segments 4 and 8; seta on segment 1 present. Antenna with completely fused allobasis; bisetose exopod; endopod with 1 lateral and 5 distal armature

elements. Mandibular palp bisetose. Maxillule with gnathobase and palp separate; palp with free unisegmented endopod (or exopod) and 3 setae on basal endite. Maxillary endites each with 2 spines. Maxillipedal syncoxa as long as basis, with 1 seta; inner margin of basis concave.

P1 with inner seta on exp-2, 4 setae on exp-3; enp-1 with inner seta, enp-2 with 3 setae. Inner margin of basis with comb of spinules in ♂. P2–P4 with wide intercoxal sclerites; basis with outer seta. P2 enp-1 ♂ with inner seta. Spine and setal formula as follows:

	Endopod	Exopod
P1	0.1.022	1.021
P2	0.1.222	1.2.121
P3	0.1.32[2–3]	1.2.221
P4	0.1.323	1.1.221

P5 in ♀ with 6 setae on exopod and 5 setae on endopodal lobe of baseoendopod; in ♂ with 6 setae on exopod and 3 setae on endopodal lobe.

P6 with 1 short and 2 long setae in both sexes.

Type and only species. *Miracia efferata* DANA, 1849 (description in DANA (1854): 1260–1261, Plate 88, fig. 11).

Miracia efferata DANA, 1849

(Female: Figs 1; 2A; 3; 4A–C, F; 5; 6B–E; 7A–C. Male: Figs 2B–E; 4D, E, G, H; 6A; 7D,F)

Type locality. DANA (1854) did not specify a type locality, but mentioned that the species occurred in the Atlantic between 4–7° N and 20–21°30' W, and at 4°30' S, 25°W

Material examined. 1. Natural History Museum, London: (a) reg. no. 93.4.22.333–339: Gulf of Guinea (no station specified), R/V *Buccaneer*, leg. J. Rattray, det. T. Scott, 1894: 9 ♀♀, 2 ♂♂ in alcohol; (b) reg. no. 1930.1.1.1571-80: *Terra Nova* Expedition 1910, Stn 52; det. G.P. Farran: 2 vials, numerous ♀♀ and ♂♂ in alcohol; (c) *Discovery* collections (leg. IOS), northeastern Atlantic, off Cap Verde Islands, Stn 7089; 18° N, 25° W; November 1969; collected with RMT 1+8: 25 ♀♀ (reg. no. 1977.196–205) and 5 ♂♂ (reg. no. 1977. 206–213) in alcohol; (d) reg. no. C.C. 40.412: H.M.S. *Challenger* Expedition, Atlantic, off Sierra Leone; 15 August 1873: 1 ♀ *in toto* on slide; (e) reg. no. C.C. 41.412: H.M.S. *Challenger* Expedition, Atlantic, off Sierra Leone; 15 August 1873: 2 ovigerous ♀♀ *in toto* on slide; (f) reg. no. C.C. 42.412: H.M.S. *Challenger* Expedition, Atlantic, off Sierra Leone; 13 April 1876: 1 ♀ *in toto* on slide; (g) reg. no. C.C. 75.412: H.M.S. *Challenger* Expedition, Atlantic, off Sierra Leone; 11 April 1896: 1 ♀ *in toto* on slide together with *Eucalanus attenuatus, Temora dubia* and *Corycaeus varius*; (h) reg. no. 1951.8.10.754, 81E: H.M.S. *Challenger* Expedition, Atlantic, off Africa; 10 April 1896: 1 ♀ dissected on slide.

2. Royal Museum of Scotland: W.S. Bruce collection, Scottish National Antarctic Expedition, R/V *Scotia*, reg. no. 1921.143.1054, (a) Stn 59, 12 Dec 1902, 2°30' S, 32°42' W, townet 40: 11 ♀♀, 10 ♂♂, 1 CV♀; (b) Stn 36, 5 Dec 1902, 7°35' N, 25°32' W, townet 25: 100+ specimens; (c) Stn 44, 8 Dec 1902, 3°42' N, 26°26' W, townet 31: 2 ♀♀, 1 ♂; (d) Stn 30, 4 Dec 1902, 11°15' N, 25°20' W, townet 20: 5 ♀♀, 4 ♂♂;

3. Arabian Sea: R/V *Meteor* cruise 5 (leg 3b); Stn 496; 18° 00' N, 66° 25' E; haul 4, net 1; 12 May 1987 at night; depth 0–50 m (water depth ca 3000 m); collected with MSN, mesh size 0.055 mm; leg. R. Böttger-Schnack: 1 cop. IV♀.

Redescription (Illustrations based on *Discovery* material.)

Female. – Body length 1.55–1.85 mm measured from anterior margin of cephalothorax to posterior rim of caudal rami. Maximum width measured at posterior margin of cephalic shield.

Body more or less cyclopiform (Fig. 1) with distinct boundary between prosome and urosome. Integument strongly chitinized, pitted; somatic hyaline frills not developed but well developed connecting membranes between somites present (Figs 1; 7A). Cephalothorax ventrally deflexed; distinctly wider than first prosomite; rounded anteriorly but with straight margin posteriorly; typically with slight middorsal hump in lateral aspect (Fig. 1A); with pair of large cuticular lenses touching in the median line (Figs 1B; 5A). Body with largely symmetrical pattern of integumental pores and sensilla in particular on dorsal surface (Fig. 1A) and on both sides of the cuticular lenses (Fig. 5A, B). Thorax and abdomen with distinct constrictions between somites; epimeral areas rounded in dorsal aspect in prosomites, angular in P5-bearing somite (Fig. 1B). Original segmentation of genital double-somite marked by lateral constriction (Figs 1B; 7A). Posterolateral corners of genital double-somite and abdominal somites with tuft of spinules (Figs 1; 5C; 6C; 7A). Anal somite narrow (Figs 1B; 6C), without distinct anal operculum; ventral posterior margin with small spinules (Fig. 6D). Caudal ramus (Fig. 6C–E) 3 times as long as wide; outer margin stepped at two-thirds the ramus length; with 7 setae and several integumental pores; setae I–III closely set together and surrounded by spinular patch (Fig. 6E); seta I spiniform, seta II arrow-shaped, seta III long and naked, setae IV-V not fused at base, implanted subterminally and multipinnate (Fig. 6C), the latter being the longest but distinctly shorter than urosome (Fig. 1B); seta VI minute; seta VII located near inner margin, small and bi-articulated at base.

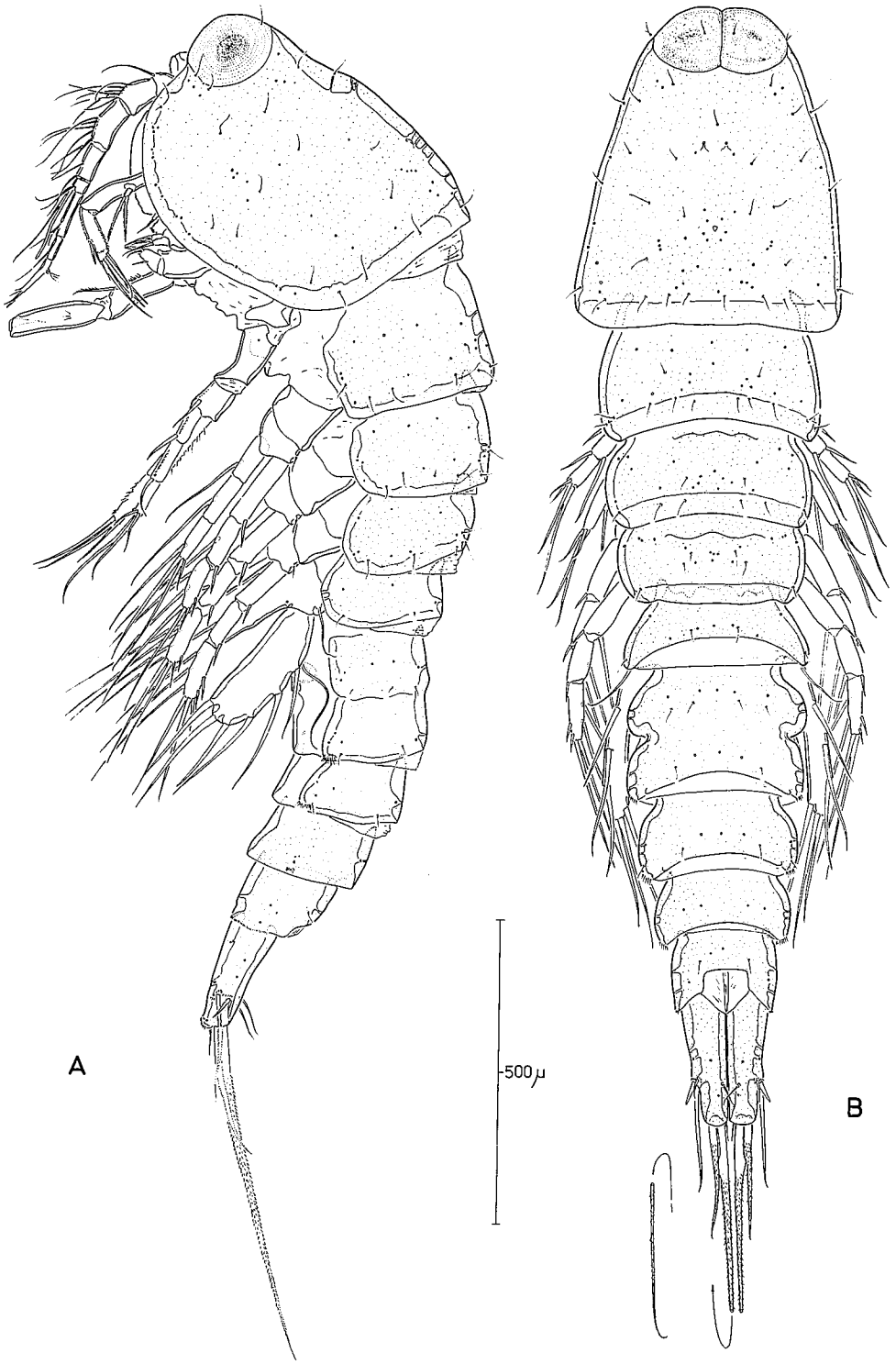

Fig. 1. *Miracia efferata* DANA, 1849. Female. A. Habitus, lateral. B. Habitus, dorsal.

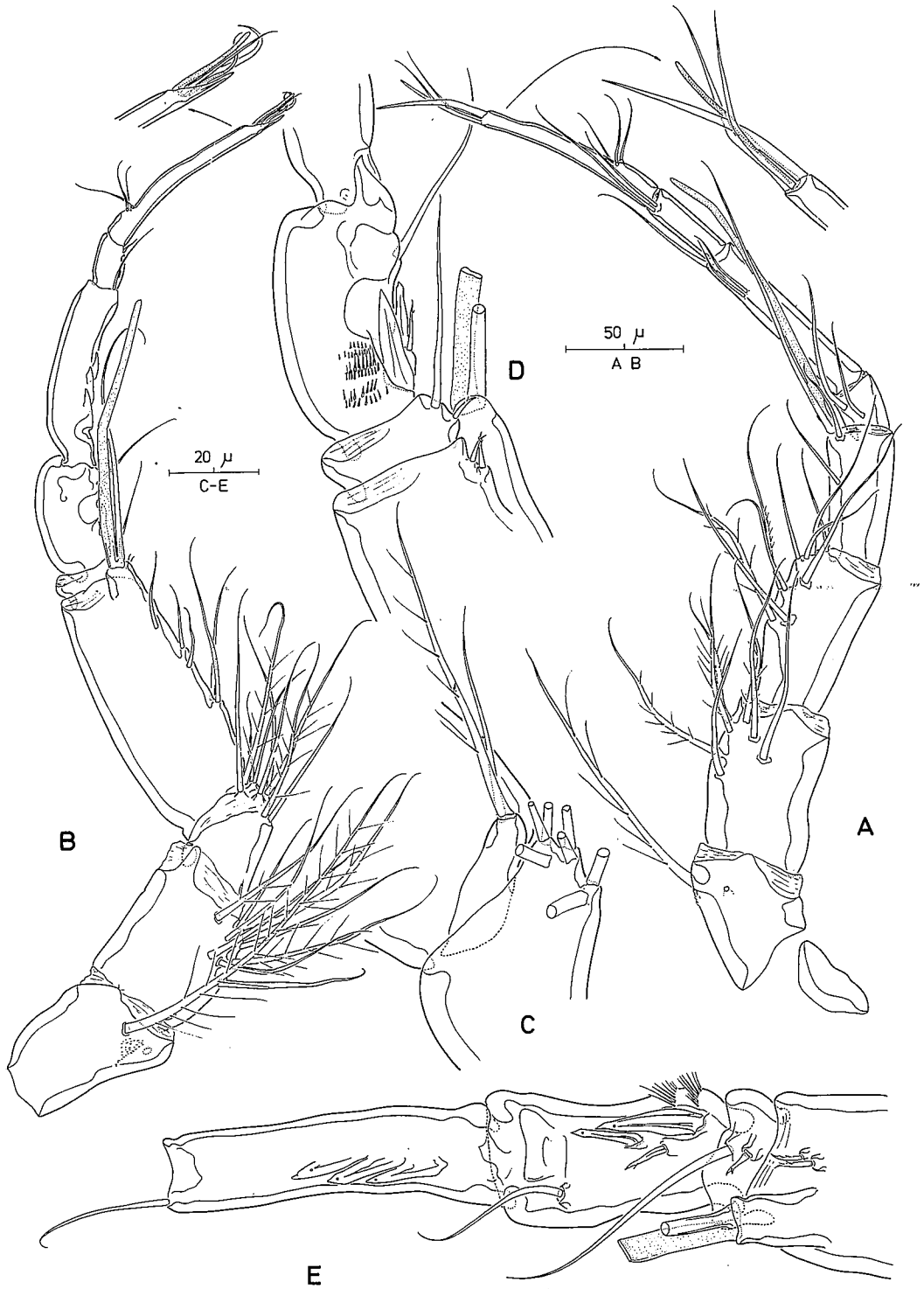

Fig. 2. *Miracia efferata* DANA, 1849. Female. A. Antennule, ventral. Male. B. Antennule, ventral. C. Same, segments 3–4, dorsal. D. Same, segments 5–7, dorsal. E. Same, segments 5–8, anterior.

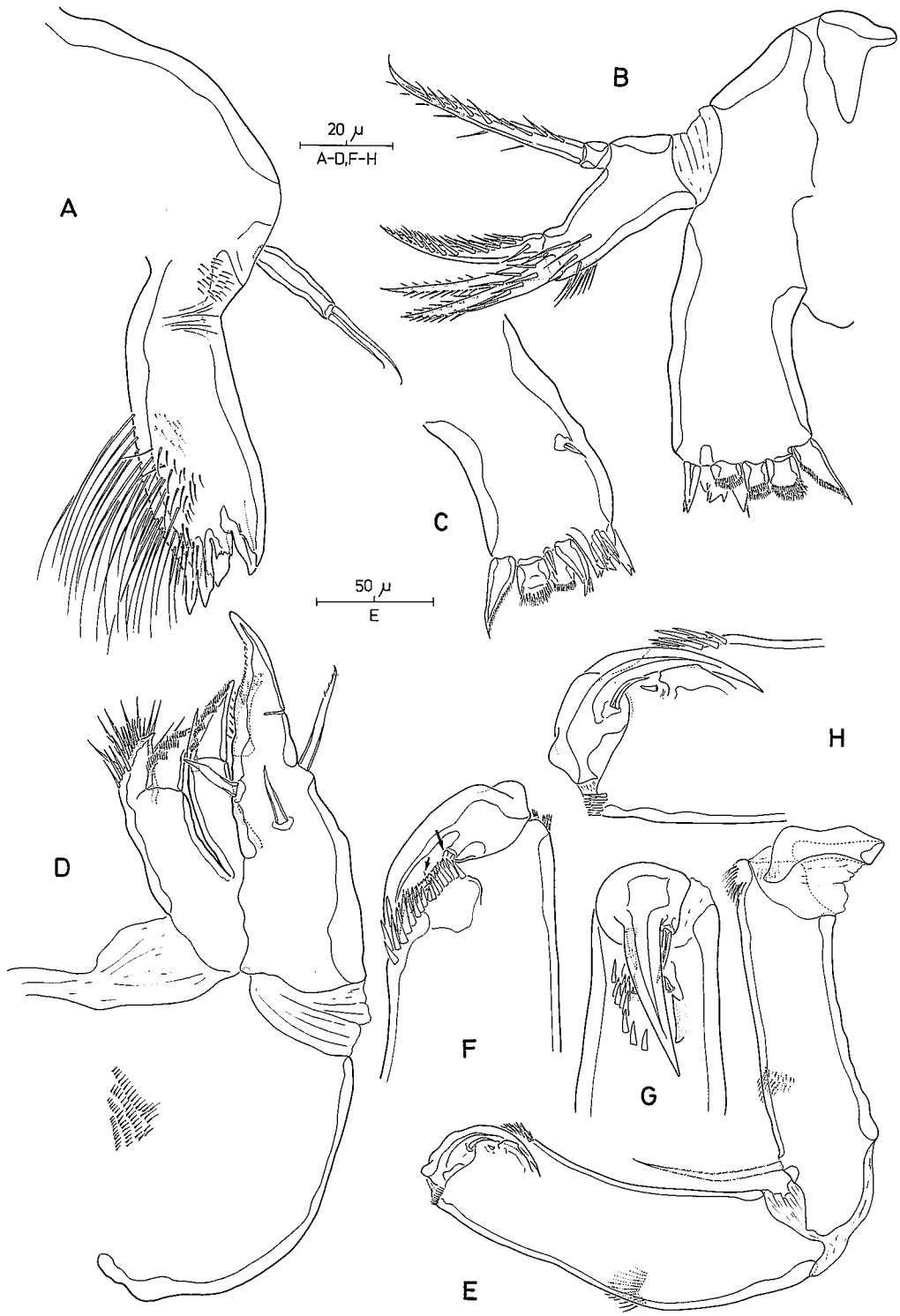

Fig. 3. *Miracia efferata* DANA, 1849. Female. A. Mandible. B. Maxillule, posterior. C. Maxillulary arthrite, anterior. D. Maxilla. E. Maxilliped, anterior. F. Same, endopod and distal part of basis, posterior (minute setae arrowed). G. Same, inner. H. Same, anterior.

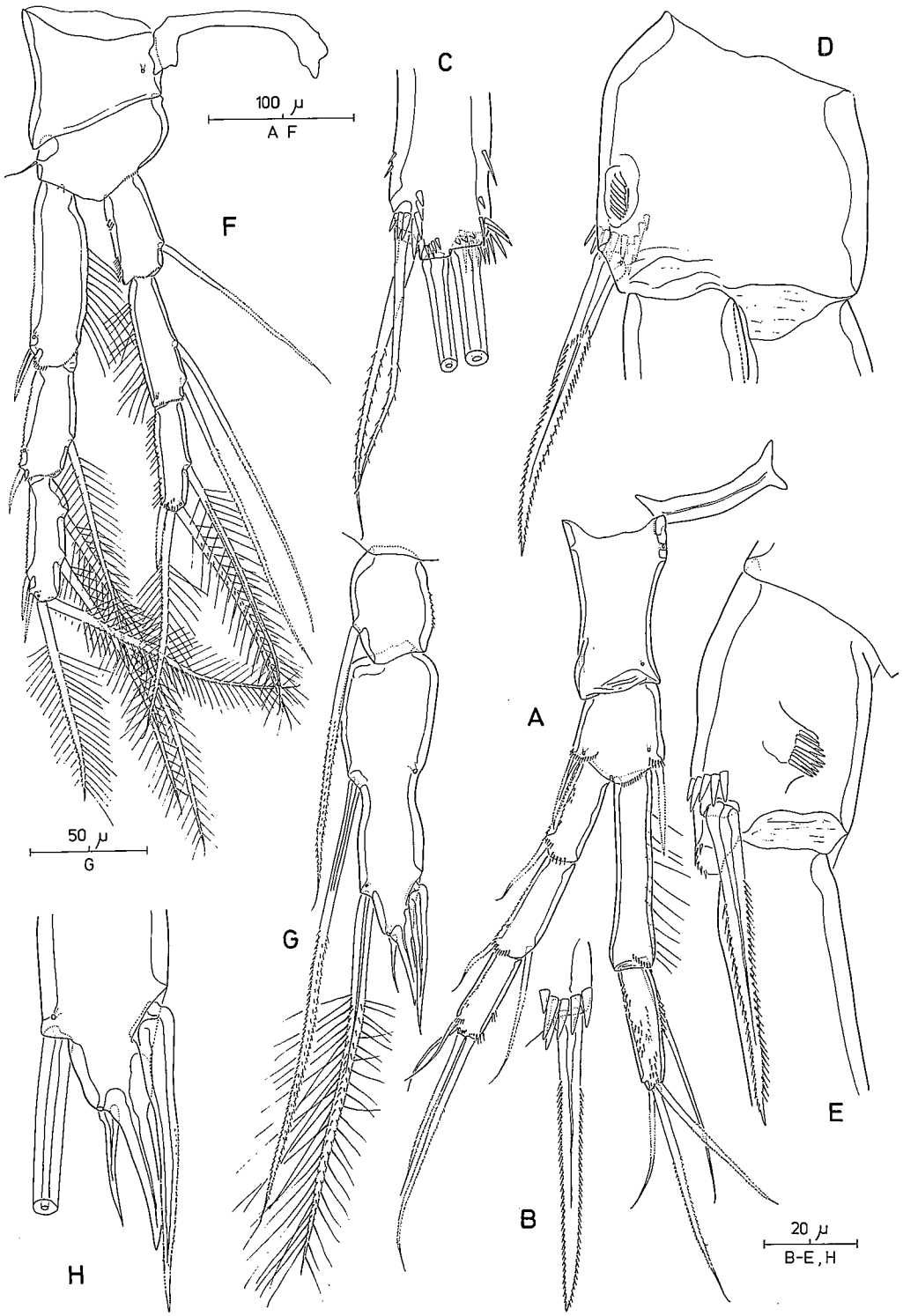

Fig. 4. *Miracia efferata* DANA, 1849. Female. A. P1, anterior. B. Same, inner basal spine. C. Same, distal margin of exp–3. D. P1 basis, posterior. E. Same, lateral. F. P2, anterior. Male. G. P2 endopod, anterior. H. Same, distal part of enp–2.

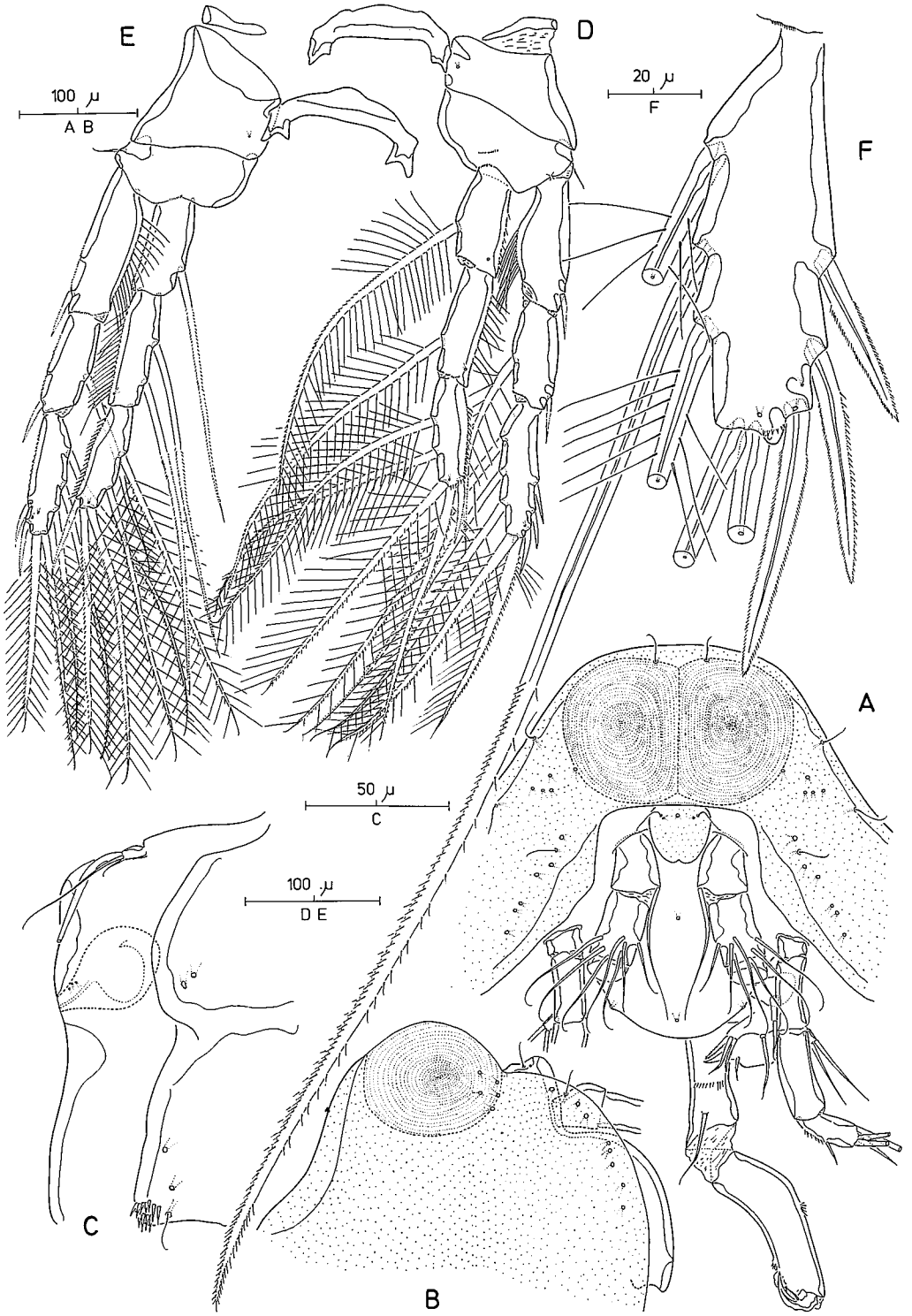

Fig. 5. *Miracia efferata* DANA, 1849. Female. A. Rostral area, anterior. B. Same, lateral. C. Genital field, lateral. D. P4, anterior. E. P3, anterior. F. P4 exp–3, anterior, showing modified seta.

Rostrum not discernible in dorsal aspect (Fig. 1B), small, blunt and largely integrated in ventral wall of cephalothorax (Fig. 5B); anterior margin slightly bilobed, with 2 sensilla and 3 integumental pores (Fig. 5A).

Antennule (Fig. 2A) 8-segmented, segments 6 and 8 longest; with pinnate setae on segments 1–3; segment 1 with ventral pore and 1 plumose seta; segment 2 with 3 naked and 4 pinnate setae; segment 3 with 6 naked and 3 pinnate setae; segment 4 with 2 short setae plus a long seta fused to an aesthetasc (125 μm); segment 5 smallest, with 2 setae; segment 6 with 3 setae; segment 7 with 2 setae: segment 8 with 3 lateral setae and apex (see inset) with 1 curved spine, 1 articulated seta and 1 seta fused to an aesthetasc (37 μm).

Antenna (Fig. 6B). Coxa bare. Basis and proximal endopod segment completely fused to form allobasis. Exopod 1-segmented, with 1 subapical and 1 apical pinnate spine. Endopod with 2 spinular patches, 1 lateral seta and 5 pinnate setae/spines around distal margin.

Labrum (Fig. 5A, B) distinctly pronounced ventrally; with 2 median and 2 lateral secretory pores.

Mandible (Fig. 3A). Coxa with fine spinules near implantation of palp and very long setules along dorsal margin; gnathobase with 6 irregularly shaped teeth. Palp minute, 1-segmented, with 2 apical setae.

Maxillule (Fig. 3B, C). Praecoxa with well developed, rectangular arthrite bearing minute armature elements; distal margin with 4 stubby, pinnate elements, 3 articulate spines and 1 spine fused to arthrite; anterior surface with rudimentary seta (Fig. 3C). Palp with 3 pinnate spines distally and with small, unisetose segment laterally (representing either endopod or exopod).

Maxilla (Fig. 3D). Syncoxa large, with 2 cylindrical endites; proximal endite with 1 articulate spine and 1 spine fused to endite, distal endite smaller and with 2 articulate spines. Allobasis drawn out into strong, short pinnate claw; with 4 setae.

Maxilliped (Fig. 3E–H). Subchelate. Syncoxa and basis elongate, joined at right angle. Syncoxa with pinnate seta near articulation with basis; with small, U-shaped sclerite at base. Basis as long as syncoxa (Fig. 3E); with concave inner margin and spinular row midway outer margin; distal part with concavity delineated anteriorly by vestigial seta (Fig. 3G) and integumental ridge (Fig. 3H), posteriorly by spinular row and vestigial seta (small arrow in Fig. 3F). Endopod represented by anteriorly recurved claw bearing 2 short accessory setae (arrowed in Fig. 3F) and fitting in basal concavity (Fig. 3G).

P1 (Fig. 4A-C). Praecoxa small (Fig. 1A; not figured in Fig. 4A). Basis with long inner pinnate spine (Fig. 4B). Exopod with inner seta on exp-2; exp-3 with 2 outer and 2 long apical setae (Fig. 4C). Endopod slightly longer than exopod; inner margin of enp-1 with long setules and long inner seta; enp-2 with numerous pinules and 3 setae.

P2–P4 (Figs 4F; 5D-F) with wide intercoxal sclerites. Praecoxae small. Basis with short, outer seta. P2–P3 enp-1 and enp-2 with bipinnate inner setae. Middle inner seta of P4 exp-3 tripinnate (Fig. 5F). Seta and spine formula as in generic diagnosis.

P5 large (Figs 1A; 7C); baseoendopod with outer basal seta, 7 pores and with 5 spines/setae on well developed endopodal lobe; exopod with 6 spines/setae and 5 pores; all armature elements delicately pinnate.

Genital apertures (Fig. 7A) fused, covered by vestigial sixth legs (Figs 5C; 7B) bearing vestigial outer seta, short middle and long inner seta. Copulatory pore minute, flanked by 3 secretory pores on either side; seminal receptacle trilobate.

Male. – Body length 1.30–1.65 mm measured from anterior margin of cephalothorax to posterior rim of caudal rami.

Antennule (Fig. 2B–E) 10-segmented, haplocer; geniculation between segments 7 and 8. Segment 1 with pore, spinular patch and 1 plumose seta; segment 2 with 6 naked and 3 plumose setae; segment 3 with 4 naked and 3 plumose setae; segment 4 minute, U-shaped sclerite, with 1 naked and 1 plumose seta (Fig. 2C); segment 5 longest, with 7 setae along anterior margin (distal 2 minute) and 1 seta plus an aesthetasc (115 μm) on a distal process (Fig. 2D, E); segment 6 with 1 vestigial and 1 long seta; segment 7 with 1 minute seta, 1 long seta, and 2 modified spines; segment 8 with 3 modified spines and 1 distal seta; segment 9 with 1 minute seta; distal segment drawn out into spinous process, with 3 lateral setae and 3 setae plus an aesthetasc apically (23 μm). Modified spines on segments 7 and 8 with minute pore on tip (Fig. 2E).

P1 basis (Fig. 4D, E). Inner margin with row of posteriorly directed spinules closely set on weak cuticular bump.

P2 endopod (Fig. 4G, H) 2-segmented. Enp-1 smaller than in female, with tripinnate inner seta. Enp-2 slightly constricted at about halfway the segment; proximal half with tripinnate inner seta; distal half with plumose inner seta, stout outer spine and spinous process plus a minute seta at the apex (Fig. 4H).

Fifth pair of legs fused medially (Fig. 7D, E); baseoendopod with 6 pores, endopodal lobe with 1

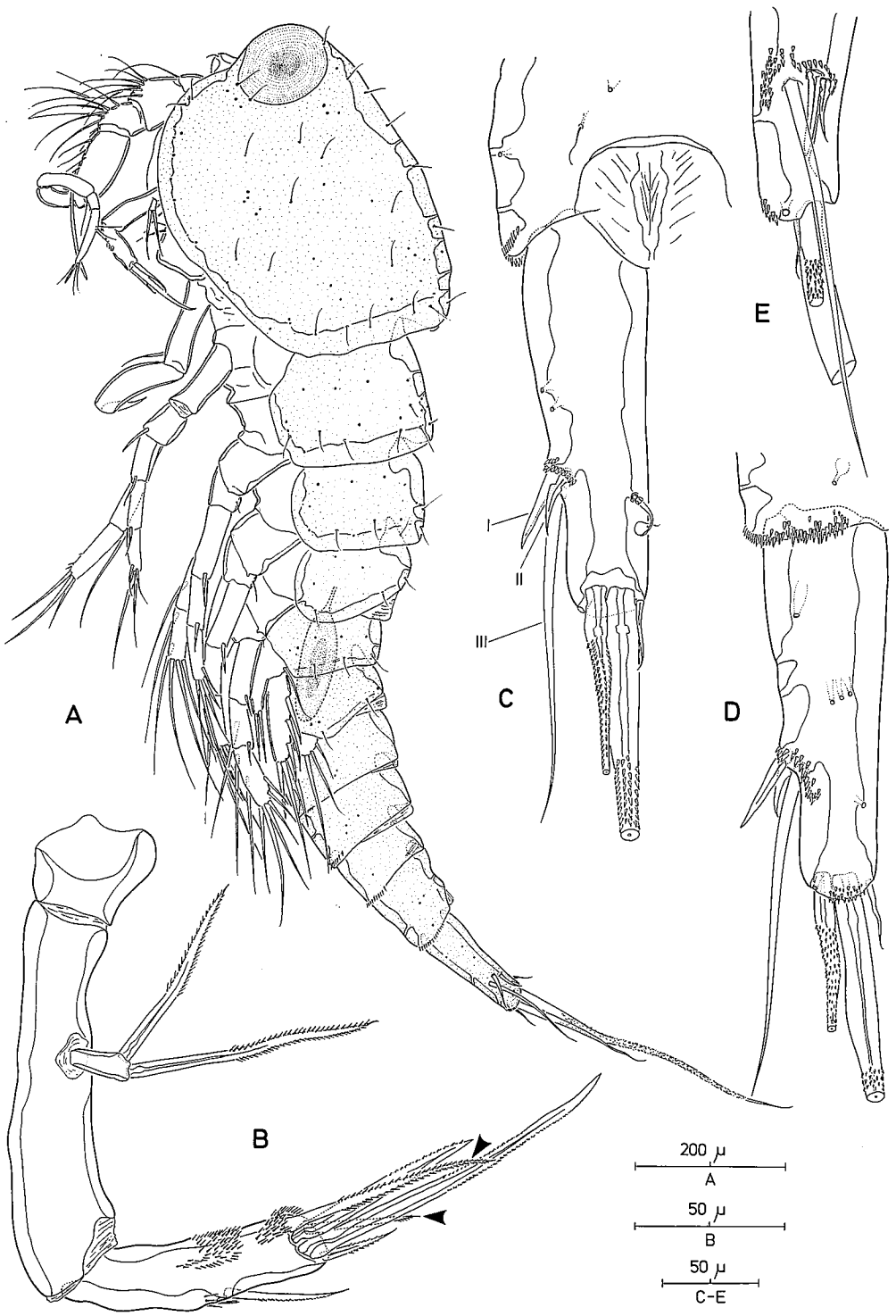

Fig. 6. *Miracia efferata* DANA, 1849. Male. A. Habitus, lateral. Female. B. Antenna. C. Anal somite and left caudal ramus, dorsal. D. Right caudal ramus, ventral. E. Left caudal ramus, posterior half, lateral.

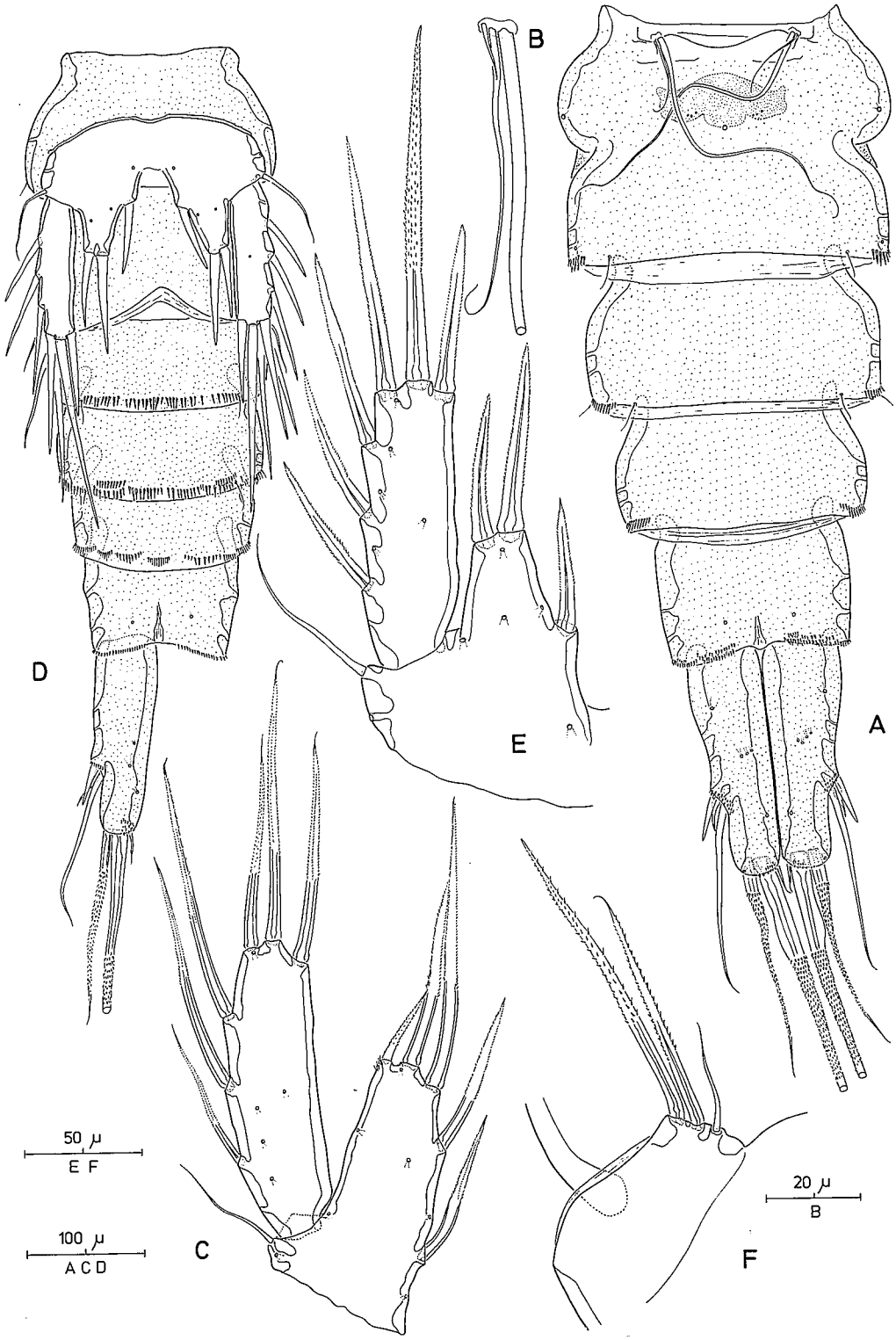

Fig. 7. *Miracia efferata* DANA, 1849. Female. A. Urosome (excluding P5–bearing somite), ventral. B. Armature of P6. C. P5, anterior. Male. D. Urosome, ventral. E. P5, anterior. F. Right P6, lateral.

lateral and 2 distal spines; exopod without spinules along inner margin, with 3 lateral and 3 distal spines.

Sixth pair of legs (Fig. 7D, F) symmetrical; fused to somite; outer margin with 1 naked and 2 pinnate setae.

Postgenital somites (Fig. 7D) with spinular rows at ventral posterior margin.

Remarks. BOXSHALL (1979) remarked that LANG's (1948) seta- and spine formula of P2–P4 given for the genus *Miracia* differed considerably from that of *M. efferata* and suspected that it was based only on data of *M. minor*. Indicative for this assumption is the absence of the inner seta on P2-P4 enp-1 in LANG's (1948) formula. This seta was noted in all previous descriptions of *M. efferata* that gave illustrations of these legs (BRADY 1883; CLAUS 1891; GIESBRECHT 1892). In a footnote LANG (1948: 767) expressed severe doubts about the validity of BRADY's (1883) observation but did not give any justification.

A second difference noted by BOXSHALL (1979) is the presence of 3 outer spines on P3–P4 exp-3 in his *Discovery* material from the northeastern Atlantic, as opposed to 2 spines given in LANG (1948). Although BOXSHALL's observation is correct for the P4, examination of a wider range of material has proven the number of outer spines on P3 exp-3 to be variable. In fact, in most specimens (including the majority of the *Discovery* material; see Fig. 5D) only 2 spines were found and the same number was also recorded by BRADY (1883), CLAUS (1891) and GIESBRECHT (1892).

ZHENG ZHANG & al. (1982) show a unisetose mandibular palp, but no such variability could be detected in our material.

Both sexes of *M. efferata* are a brilliant bluish purple (e.g. BRADY 1883; MRÁZEK 1895) even after a considerable time in preservative (BOXSHALL 1979). A vivid description of the colour pattern in live specimens is given by WILSON (1932; taken from R. Rathbun's unpublished coloration notes). According to WHEELER (1901) and WILSON (1932) the males are much paler than the females.

Genus *Oculosetella* DAHL, 1895

Miracia DANA, 1846a (partim).

History. The taxonomic history of *Oculosetella* and its only species *O. gracilis* (DANA, 1849) is intricate. Originally diagnosed as *Miracia gracilis* by DANA (1849a), the species, together with all *Setella* species known at that time (DANA 1847; CLAUS 1863; LUBBOCK 1860), was subsequently synonymized with *Setella gracilis* DANA, 1847 by GIESBRECHT (1892). Only in a later paper GIESBRECHT (1895) explained that his decision was based on the similarity in the rostrum between *M. gracilis* and *S. gracilis*, and on the fact that DANA's observations of corneal lenses (as in *M. gracilis*) were not always reliable as he had occasionally illustrated them in oncaeids (Poecilostomatoida). Meanwhile, MRÁZEK (1895) had redescribed the male of *M. gracilis* and re-instated it as a valid species. However, DAHL (1895) remarked that the specimens that formed the basis for MRÁZEK's redescription actually belonged to another *Miracia* species previously described by T. SCOTT (1894) under the name *M. minor*. DAHL also recognized the true identity of *M. gracilis* by pointing out that the cuticular lenses represent its only character in common with *Miracia* whilst in all other respects the species resembles *Setella* (= now *Macrosetella*) very closely. This intermediate position led DAHL to propose the new genus *Oculosetella* to accommodate *M. gracilis*, an act that was apparently overlooked by SARS (1916) who transferred *M. gracilis* to *Setella* and, in order to avoid homonymy, replaced it by the new name *S. oculata*. *Setella* DANA is a junior homonym of *Setella* SCHRANK, 1802 (Lepidoptera) and was therefore replaced by *Macrosetella* A. SCOTT, 1909. As a result, both ROSE (1929) and WILSON (1932) altered SARS' name to *Macrosetella oculata* (SARS, 1916). Finally, STEUER (1935) drew attention to DAHL's (1895) forgotten name and resurrected *O. gracilis*. Regrettably, the species is still occasionally referred to as *M. oculata* in the recent literature (e.g. HURE & SCOTTO DI CARLO 1968).

Diagnosis. Miraciidae. Body fusiform, elongate; boundary between prosome and urosome not well defined. Cephalothorax rounded anteriorly, only slightly wider than prosome, not ventrally deflected; with pair of large cuticular lenses touching in dorsal midline. Thorax and abdomen without distinct constrictions between somites. Integument weakly chitinized, smooth. Original segmentation of genital double-somite marked by dorsal superficial suture line. Caudal ramus about 3 times as long as wide; seta V distinctly longer than urosome; setae IV and V free at base; seta VI fused to ramus.

Rostrum large, ventrally projected, defined at base. Antennule 7-segmented in ♀; aesthetasc on segments 3 and 7; seta on segment 1 absent. Antenna with completely fused allobasis; exopod absent; endopod with 1 lateral and 3 distal armature elements. Mandibular palp unisetose. Maxillule with gnathobase and palp fused; palp without free ra-

mus, with 3 setae in total. Maxillary endites each with 1 spine. Maxillipedal syncoxa with 1 seta; basis distinctly longer than syncoxa, inner margin straight.

P1 with inner seta on exp-2, 4 setae on exp-3; enp-1 without inner seta, enp-2 with 3 setae. Inner distal corner of basis with large, bulbous process in ♂. P2–P4 with narrow intercoxal sclerites; basis without outer seta. P2 enp-1 ♂ without inner seta. Spine and setal formula as follows:

	Exopod	Endopod
P1	0.1.022	0.021
P2	0.1.222	0.2.121
P3	0.1.322	0.1.221
P4	0.1.322	1.1.221

P5 in ♀ with 6 setae on exopod, with 3 setae on endopodal lobe of baseoendopod; in ♂ with 4 setae on exopod, with 2 setae on endopodal lobe.

P6 with 1 short and 1 long seta in both sexes.

Type and only species. *Oculosetella gracilis* (DANA, 1849) DAHL, 1895 [description in DANA (1854): 1261–1262, plate 88, fig. 12a–c].

Oculosetella gracilis (DANA, 1849)

(Female: Figs 8–10; 11A, B, D; 12B, C; 13. Male: Figs 11C, E, F; 12A; 14)

Miracia gracilis DANA, 1849; *Setella oculata* SARS, 1916; *Macrosetella oculata* (SARS, 1916) ROSE 1929.

Type locality. No type locality was specified. The species was found in two localities in the South Pacific, one off Sunday Island, the other north of New Zealand at 32°24' S, 177° E (DANA 1854).

Material examined. 1. National Museum of Natural History (Smithsonian Institution), Washington, D.C.: (a) USNM 70764: between Easter and Galapagos Islands, 20°29' S, 103°26' W; R/V *Albatross*, Stn 4700; depth 2200 fms; 25 December 1904; 4 specimens in alcohol, labelled *Macrosetella oculata* (SARS); identified by C.B. Wilson; this vial contains only *Distioculus minor* (4 ♀♀); (b) USNM 74015: China Sea, near Hong Kong, 20°58' N, 120°03' E; R/V *Albatross*, Stn 5320; depth 0–500 m; labelled *Oculosetella oculata* (SARS); identified by C.B. Wilson; 1 Cop. IV stage in alcohol, belonging to *Miracia efferata*; (c) USNM 80276: 12°54' N, 56°15' W; Last cruise of the R/V *Carnegie*, Stn 30; surface tow; 15 September 1928; 12 specimens in alcohol, labelled *Macrosetella oculata* (SARS), presumably identified by C.B. Wilson but not indicated on label; this vial contains a mixture of *Distioculus minor* (1♀, 2♂♂), *Miracia efferata* (1 Cop. IV, 1 Cop. V♀) and *Oculosetella gracilis* (5 ♀♀, 2 ♂ ♂); (d) USNM 80277: south of Easter Islands, 31°49' S, 109°04' W; Last cruise of the R/V *Carnegie*, Stn 56; depth 100 m; 18 December 1928; 25 specimens in alcohol, labelled *Macrosetella oculata* (SARS), identified by C.B. Wilson; this vial contains a mixture of *Distioculus minor* (17 ♀♀, 6 ♂ ♂), *Miracia efferata* (1 Cop. III, 1 Cop. IV) and *Farranula* sp. (1 ♀, 1 ♂); (e) USNM 192049: N. Atlantic Ocean, U.S. A., off New Jersey, 34° 41'12' N, 73° 3'48' W; depth 69 m; 9 November 1976; collected and identified by D.J. Barr; 1 ♂ in alcohol;

2. Rijksmuseum van Natuurlijke Historie, Leiden: 44°05' S, 147°35' E; B.A.N.Z.A.R. [British, Australian and New Zealand Antarctic Research] Expedition 1929–31, Stn 77; net N70 V, 50–0 m; 23 November 1930; 1 ♀ in alcohol.

3. Royal Museum of Scotland: W.S. Bruce collection, Scottish National Antarctic Expedition, R/V *Scotia*, reg. no. 1921.143.1053, several vials labelled *Setella gracilis* (a) Stn 94, 26 Dec 1902, 30°25' S, 45°45' W, townet 69: 1 ♀ of *O. gracilis*; (b) Stn 65, 14 Dec 1902, 6°52' S, 34°32' W, townet 88: containing 1 ♀ of *O. gracilis* and 2 ♀♀ of *M. gracilis*; (c) Stn 99, 29 Dec 1902, 35°20' S, 50°18' W, townet 73: containing 8 ♀♀ and 2 ♂♂ of *O. gracilis* and 50+ specimens of *M. gracilis*; other vials containing only *M. gracilis* (see under *Macrosetella*)

Redescription (Illustrations based on *Carnegie* material)

Female. – Body length 1.20–1.30 mm measured from anterior margin of cephalothorax to posterior rim of caudal rami. Maximum width measured at posterior margin of cephalic shield.

Body fusiform, slender, elongate (Fig. 8) without distinct boundary between prosome and urosome. Integument weakly chitinized, smooth; somatic hyaline frills and intersomatic membranes moderately developed (Figs 8; 13E). Cephalothorax relatively small, not ventrally deflexed; only slightly wider than first prosomite; rounded anteriorly and with slightly concave dorsal margin in lateral aspect (Fig. 8B); with pair of large cuticular lenses touching in dorsal midline (Figs 8A; 9A, B; 10F). Body with largely symmetrical pattern of integumental pores and sensilla in particular on dorsal surface (Fig. 8A) and around cuticular lenses (Figs 8C; 9A). Thorax and abdomen without distinct constrictions between somites; none of somites laterally produced. Original segmentation of genital double-somite marked by superficial suture line dorsally (Fig. 8A, B) and internal chitinous patches ventrally (Fig. 13B). Posterior margin with spinules laterally and midventrally in genital double-somite, ventrally in free abdominal somites (Figs 8B; 13A). Anal somite narrow (Figs 8A; 13A, E), without distinct anal operculum; dorsolateral corners with small spinules (Fig. 13E). Caudal ramus (Fig. 13C–E) about 3 times as long as wide; outer margin almost straight; with 7 setae and several integumental pores; all setae located in posterior 1/6; setae I–III closely set together; setae I–II spiniform and pinnate, seta III long and naked, setae IV–V spinulose, not fused at base

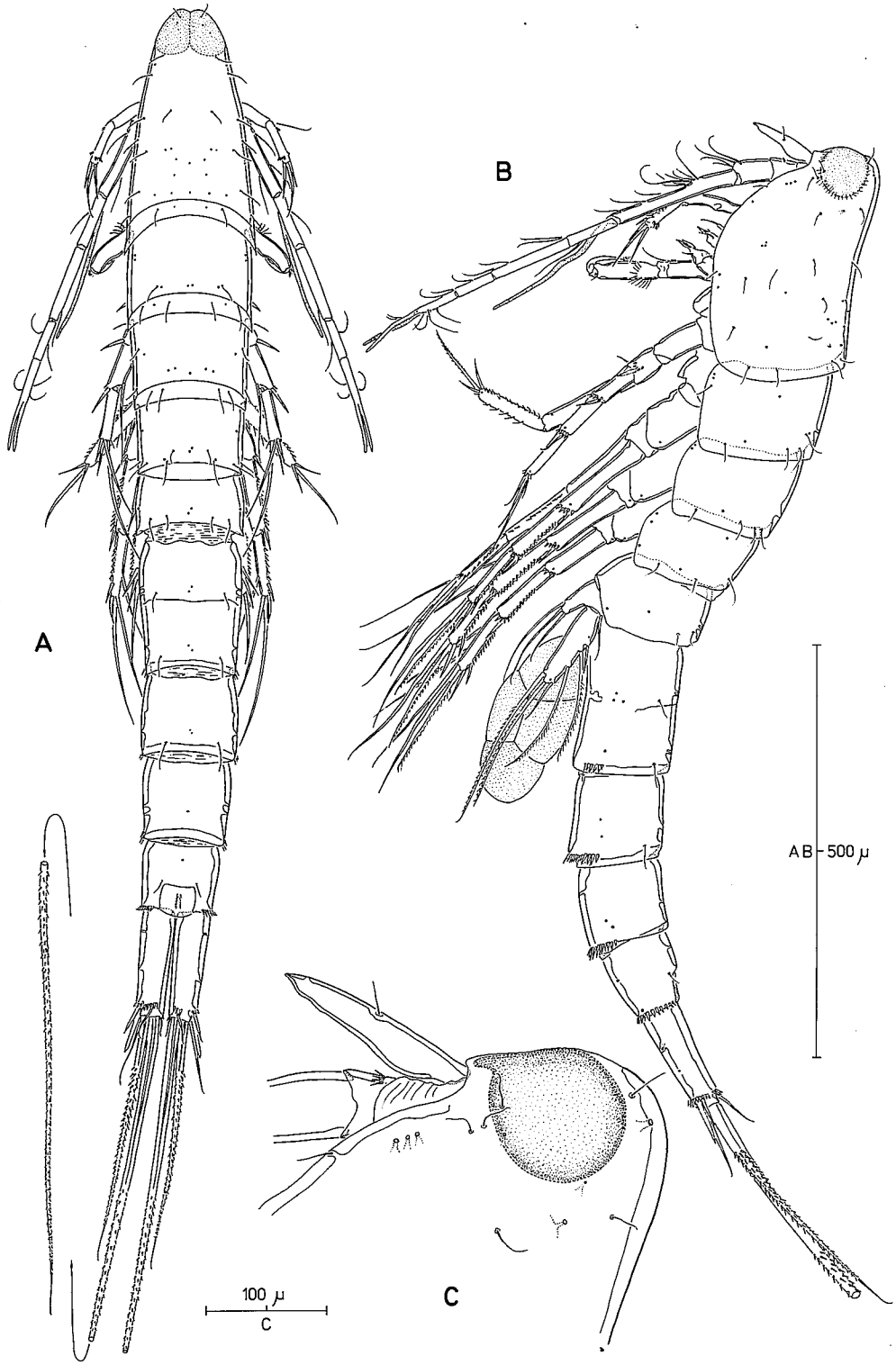

Fig. 8. *Oculosetella gracilis* (DANA, 1849). Female. A. Habitus, dorsal. B. Same, lateral. C. Rostral area, lateral.

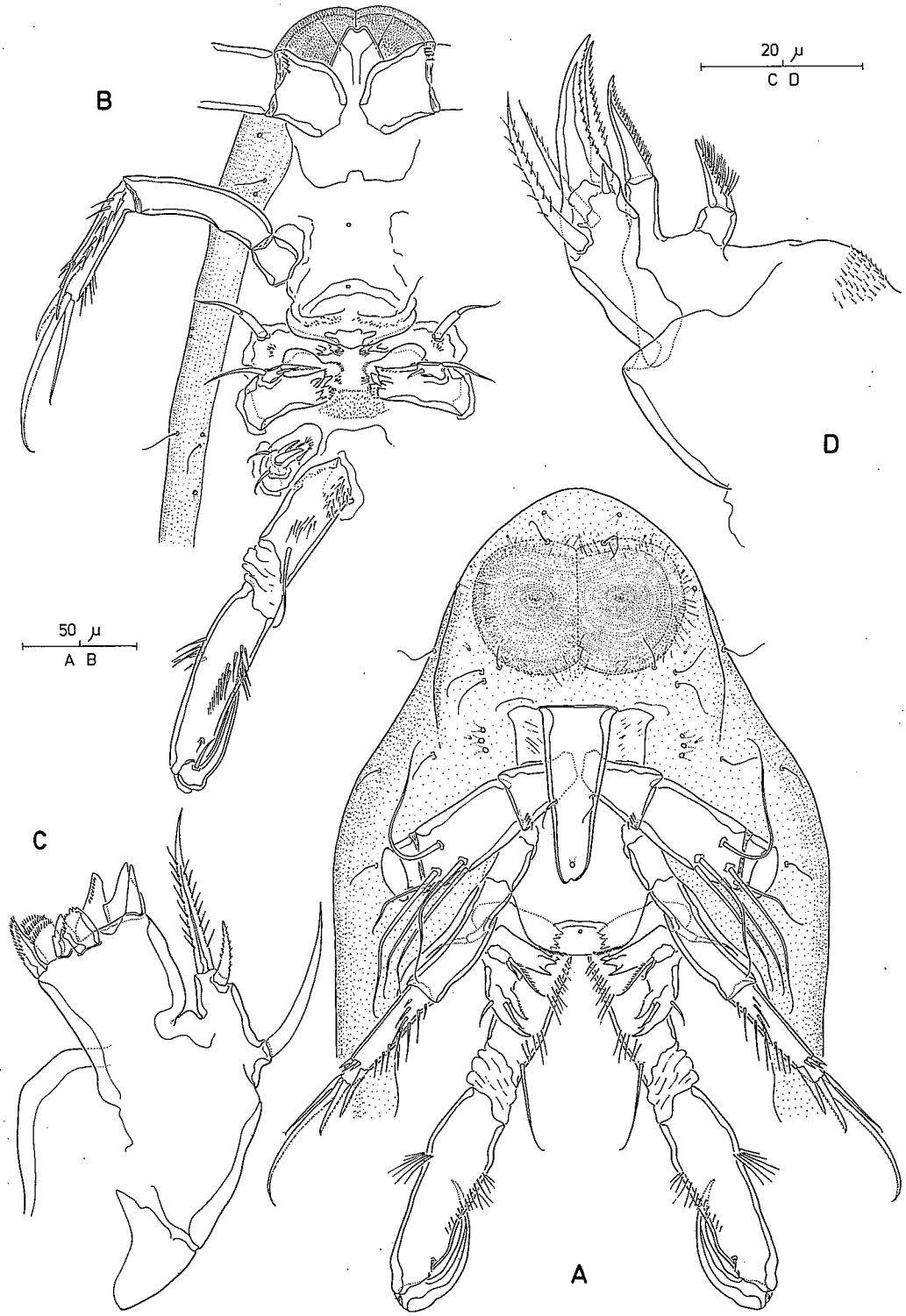

Fig. 9. *Oculosetella gracilis* (DANA, 1849). Female. A. Cephalothorax, rostral view. B. Same, ventral. C. Maxillule. D. Maxilla.

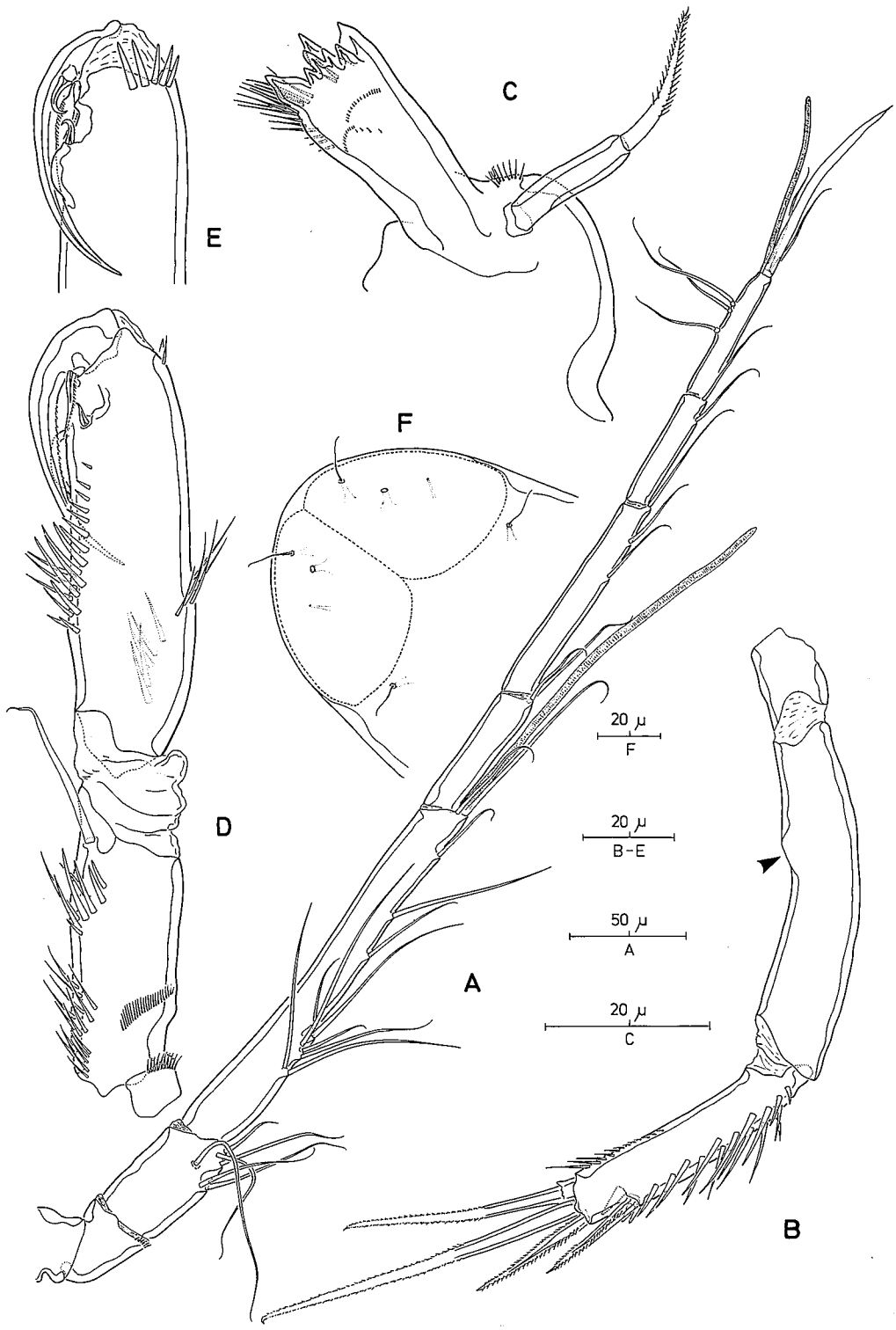

Fig. 10. *Oculosetella gracilis* (DANA, 1849). Female. A. Antennule, ventral. B. Antenna (arrow indicating position of lost exopod). C. Mandible. D. Maxilliped, anterior. E. Same, endopod and distal part of basis, posterior. F. Cephalic shield, anterior part, dorsal.

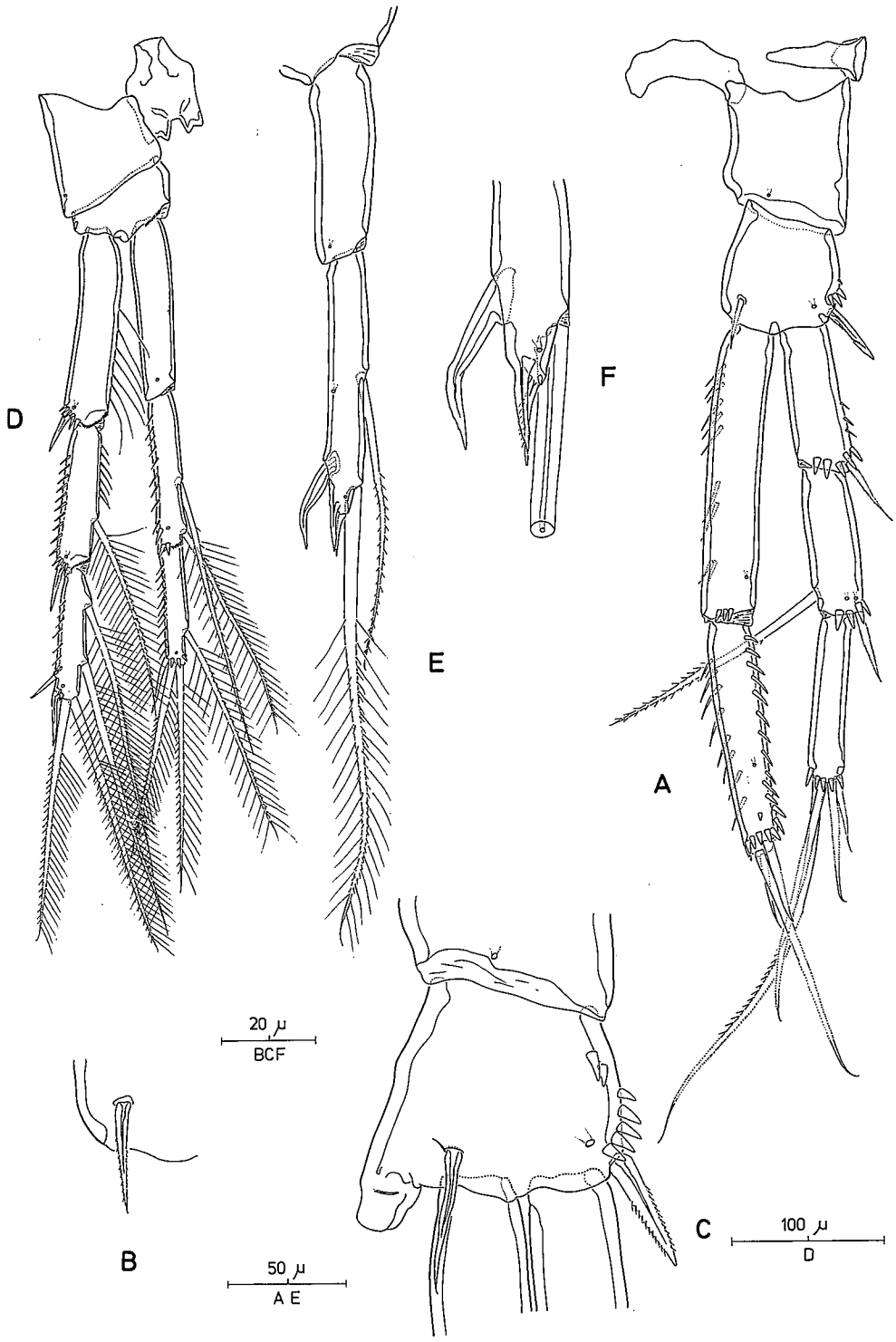

Fig. 11. *Oculosetella gracilis* (DANA, 1849). Female. A. P1, anterior. B. P1, inner basal spine. D. P2, anterior. Male. C. P1, basis, anterior. E. P2 endopod, anterior. F. Same, distal part of enp–2, anterior.

(Fig. 13C, E), seta V longest and about 75% of total body length (Fig. 8A); seta VI minute and fused to ramus (Fig. 13D); seta VII located middorsally, small and bi-articulated at base.

Rostrum large, elongate (Figs 8A, C; 9A), not discernible in dorsal aspect (Fig. 8A); defined at base,ventrally projected, slightly bifid at tip; with 2 sensilla and 1 integumental pore (Figs 8C; 9A).

Antennule (Fig. 10A) inserted on small pedestal; 7-segmented, segment 3 longest; without pinnate setae; segment 1 with few spinules distally, without seta; segment 2 with 6 setae; segment 3 with 11 setae, plus a long seta fused to an aesthetasc (165 μm) distally; segment 4 with 2 setae; segment 5 with 3 setae; segment 6 with 2 setae: segment 7 with 3 setae laterally, and 1 curved spine, 1 articulate seta and 1 seta fused to an aesthetasc (80 μm) apically.

Antenna (Fig. 10B). Coxa bare. Basis and proximal endopod segment completely fused to form allobasis; no armature or ornamentation. Exopod absent in adult but original position marked by area of thin cuticle (arrowed in Fig. 10B). Endopod with large spinules and 1 lateral spine along the abexopodal margin; with fine spinules along exopodal margin; with 3 pinnate setae/spines around distal margin, the longest one being recurved (Fig. 9A–B).

Labrum (Fig. 9A, B) distinctly pronounced ventrally; with 2 median secretory pores anteriorly and fine spinules at distal margin.

Mandible (Fig. 10C). Coxa with fine spinules near implantation of palp and long setules near dorsal corner; gnathobase with 7 pointed teeth. Palp small, 1-segmented, with 1 pinnate spine apically.

Maxillule (Fig. 9C) with fused praecoxa and palp. Praecoxa with well developed arthrite bearing minute armature elements; distal margin with 4 stubby, pinnate elements and 3 articulate spines; anterior surface with rudimentary seta. Palp with 2 pinnate spines distally and with small knob bearing bare spine laterally (representing either endopod or exopod).

Maxilla (Fig. 9D). Syncoxa large, with tiny spinules proximally and 2 cylindrical endites distally; each endite with 1 articulate, bipinnate spine. Allobasis drawn out into strong, short pinnate claw; with 1 small spine and 3 pinnate setae.

Maxilliped (Fig. 10D, E). Subchelate. Syncoxa and basis elongate, joined in linear arrangement. Syncoxa with several spinular rows and with naked seta near articulation with basis; with small, U-shaped sclerite at base. Basis longer than syncoxa (Fig. 10D), with 2 vestigial setae near articulation with endopod; inner margin straight, with coarse spinules; with spinular row midway outer margin; distal part with concavity delineated anteriorly by integumental ridge (Fig. 10E). Endopod represented by anteriorly recurved, pinnate claw bearing 2 short accessory setae and fitting in basal concavity (Fig. 10E).

P1 (Fig. 11A, B). Praecoxa a small sclerite. Basis with short, inner pinnate spine (Fig. 11B). Exopod with inner seta on middle segment; exp-3 with 2 outer and 2 long apical setae. Endopod distinctly longer than exopod; inner margin of enp-1 with spinules but without inner seta; enp-2 with spinular inner and outer margins and 3 setae/spines distally.

P2–P4 (Figs 11D; 12B, C) with narrow intercoxal sclerite. Praecoxae small. Basis without outer seta. P2–P3 enp-1 without inner seta. Middle inner seta of P4 exp-3 tripinnate (marked in Fig. 12C; see also inset). Seta and spine formula as in generic diagnosis.

P5 large (Figs 8B; 13F); baseoendopod with outer basal seta, 4 pores and with 3 setae on weakly developed endopodal lobe; exopod with 6 spines/setae and 4 pores; all long armature elements pinnate.

Genital apertures (Fig. 13B) separate, covered by vestigial sixth legs bearing short outer seta and long, basally swollen, inner seta. Copulatory pore minute, flanked by 3 secretory pores on either side; seminal receptacle transversely elongate. Egg-sacs each with 4 large eggs.

Male. – Body length 0.82 mm measured from anterior margin of cephalothorax to posterior rim of caudal rami.

Antennule (Fig. 14A-D) 10-segmented, haplocer; geniculation between segments 7 and 8. Segment 1 with spinular row distally, without seta; segment 2 with 7 setae; segment 3 with 8 setae (Fig. 14B); segment 4 minute, U-shaped sclerite, with 2 setae (Fig. 14B); segment 5 longest, with 7 setae along anterior margin (distal 2 minute) and 1 seta plus an aesthetasc (175 μm) on a distal process; segment 6 with 1 vestigial and 1 long seta; segment 7 with 2 spinular rows, 2 setae and 2 modified spines (Fig. 14C); segment 8 with 3 modified spines and 1 distal seta (Fig. 14C); segment 9 with 2 minute setae; distal segment drawn out into spinous process (derived from fused spine), with 3 lateral setae and 2 minute setae plus an aesthetasc apically (75 μm) (Fig. 14D). Modified spines on segments 7 and 8 with minute pore (Fig. 14C).

P1 basis (Fig. 11C). Inner margin produced into large, bulbous, ventrally directed process at distal corner; inner basal spine naked.

P2 endopod (Fig. 11E, F) 2-segmented. Enp-1 only slightly smaller than in female, without inner

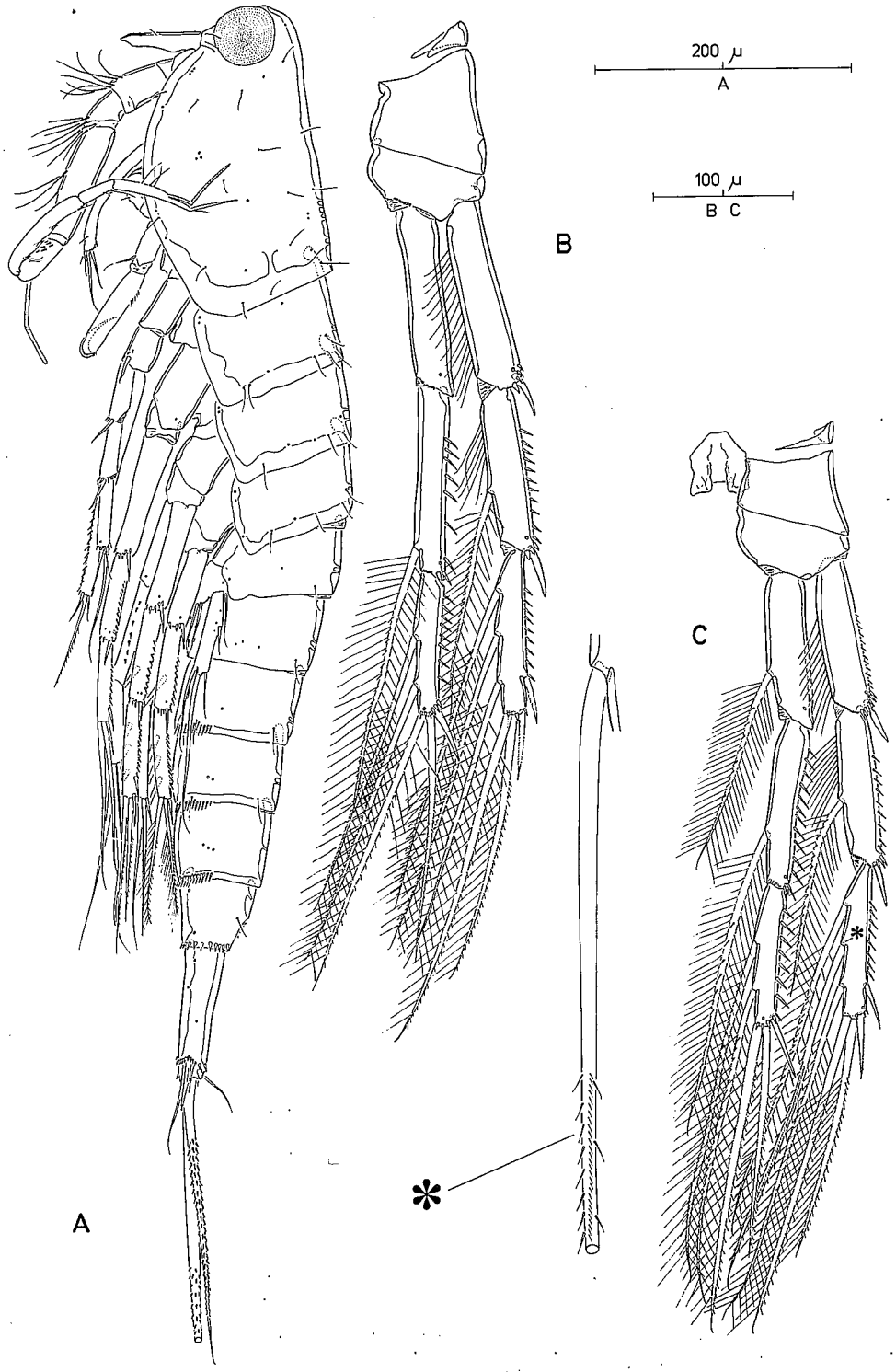

Fig. 12. *Oculosetella gracilis* (DANA, 1849). Male. A. habitus, lateral. Female. B. P3, anterior. C. P4, anterior (inset: modified middle inner seta of exp-3).

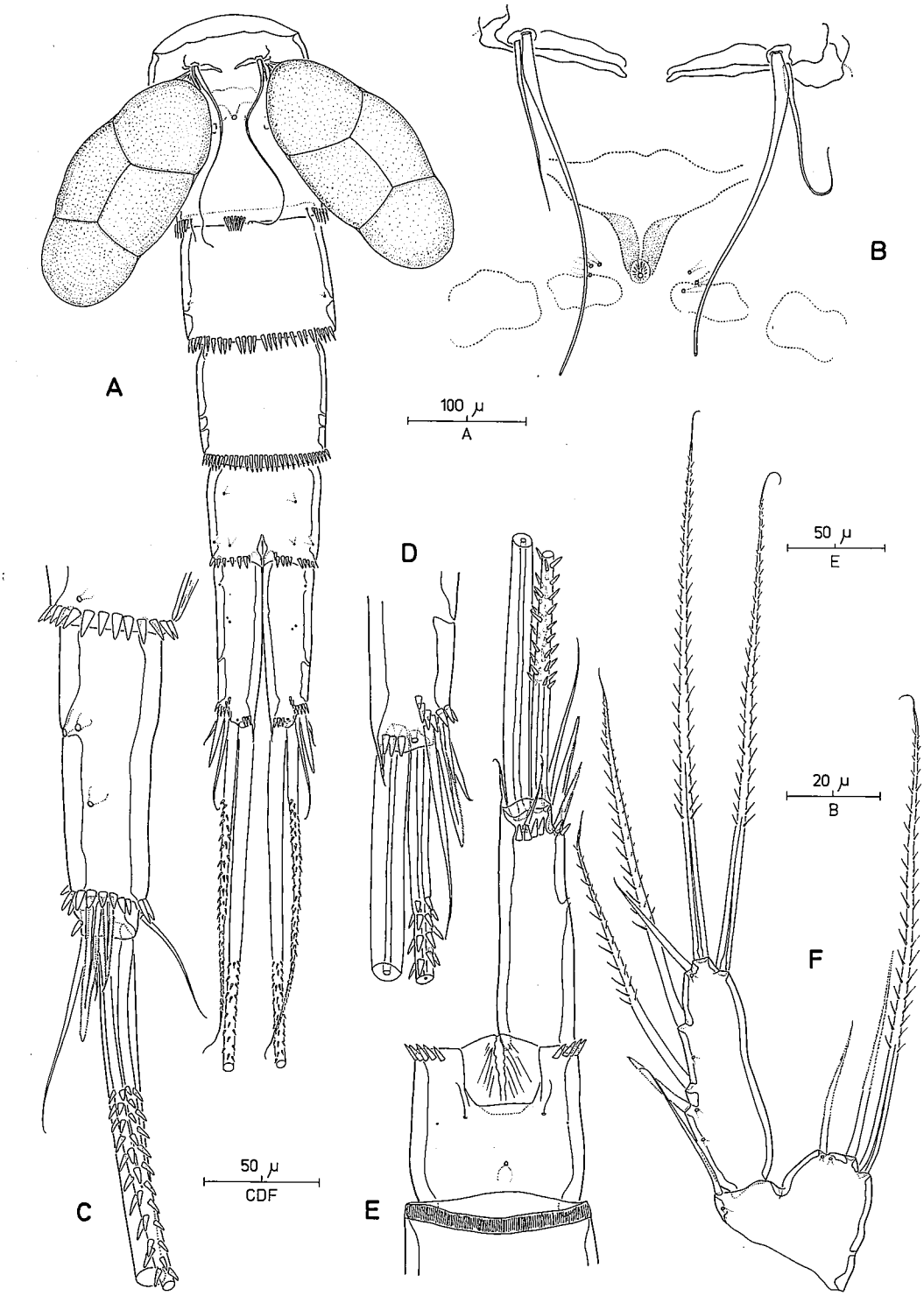

Fig. 13. *Oculosetella gracilis* (DANA, 1849). Female. A. Urosome (excluding P5–bearing somite) of ovigerous ♀, ventral. B. Genital field. C. Left caudal ramus, lateral. D. Distal half of left caudal ramus, ventral. E. Anal somite and left caudal ramus, dorsal. F. P5, anterior.

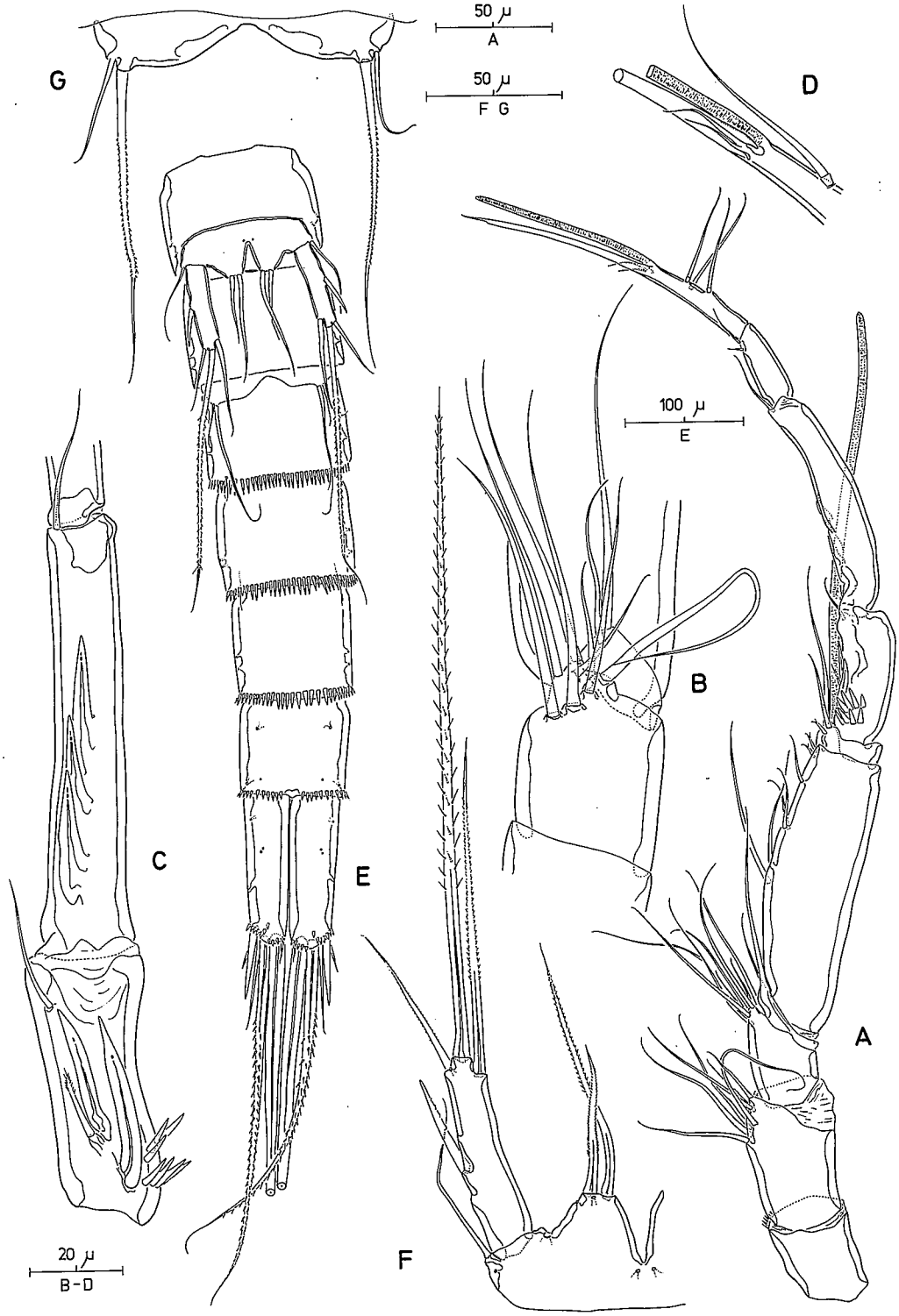

Fig. 14. *Oculosetella gracilis* (DANA, 1849). Male. A. Antennule, dorsal. B. Same, segments 3–4, anterior. C. Same, segments 7–8, anterior. D. Same, distal part of segment 10, ventral. E. Urosome, ventral. F. P5, anterior. G. Sixth pair of legs.

seta. Enp-2 with pinnate, inner seta in proximal half; distal half with strong, plumose inner seta subdistally, a stout, recurved spine at the outer margin, and spinous process plus a pinnate, basally fused seta at the apex (Fig. 11F).

Fifth pair of legs fused medially (Fig. 14E, F); baseoendopod with 3 pores, endopodal lobe with 2 distal setae; exopod without spinules along inner margin, with 1 lateral and 3 distal spines.

Sixth pair of legs (Fig. 14E, G) symmetrical; fused medially but not fused to somite; outer corner with 1 naked and 1 pinnate seta.

Postgenital somites (Fig. 14E) with spinular rows at ventral posterior margin.

Remarks. Previous descriptions of *Oculosetella gracilis* did not go beyond the level of merely illustrating the habitus (SARS 1916; STEUER 1935), except for OWRE & FOYO (1967) who provided illustrations of the antennules and fifth legs in both sexes. *O. gracilis* has been confounded at numerous occasions with other 'lens-bearing' copepods, usually *Miracia* species but also Corycaeidae (Poecilostomatoida; see material examined). An example how this confusion perpetuated in the literature is given by WILSON's (1932) description (as *Macrosetella oculata*) mistakenly based on specimens of *Distioculus minor* comb. nov. (see below). WILSON's illustrations formed the basis for the diagnosis of *O. gracilis* in LANG's (1948) monograph and were also reproduced in WELLS' (1970) Zooplankton Fiches to aid in the identification of planktonic harpacticoids and more recently in BOLTOVSKOY's (1981) zooplankton atlas of the southwestern Atlantic. Furthermore, WELLS' (1970) original drawings of the cephalothorax and the maxilliped are also taken from *D. minor* specimens. BOXSHALL (1979) pointed out that SEWELL's (1947) specimens were also misidentified and really belong to *D. minor*, and the present study revealed that at least part of the material collected during the last cruise of the *Carnegie* (WILSON 1942) is based on a mixture of other miraciids. The significance of WILSON's (1942) statements that *O. gracilis* is negatively phototactic and has a bright blue body colour and red eyes are therefore doubtful. Similarly, it is conceivable that WILSON's (1950) *Albatross* material from the Pacific, contrarily to his report, did not contain any *O. gracilis* at all. The four females from Stn 4700 mentioned by WILSON (p. 270) proved upon examination to belong to *D. minor*.

Genus *Macrosetella* A. SCOTT, 1909

Setella DANA 1846 (partim), *Dwightia* C.B. WILSON, 1924.

History. DANA (1847) presented Latin diagnoses of five *Setella* species, two from the Atlantic and three from the Indo-Pacific, which were subsequently described and illustrated in 1854: *S. tenuicornis, S. longicauda, S. gracilis, S. crassicornis* and *S. aciculus*. LUBBOCK (1860) described *S. tenuis* from the Gulf of Guinea and CLAUS (1863) added a seventh species *S. messinensis* from the Mediterranean. BRADY (1883), who had at his disposal the extensive collections made during the H.M.S. *Challenger* Voyage, identified all the *Setella* material as *S. gracilis*, though stated that "... the differences between this species and *Setella tenuicornis* appear to be of the very slightest character". BRADY's material came from a wide range of localities, and this led GIESBRECHT (1892) to conclude that all *Setella* species described at that time were conspecific. According to GIESBRECHT, both *S. crassicornis* and *S. aciculus* were based on juvenile stages (though the latter species was based on an ovigerous specimen), and *S. longicauda* corresponds with the male of either *S. tenuicornis*, as DANA (1854) already suspected, or *S. gracilis*. DANA (1847, 1849b, 1854) did not designate a type species for *Setella*, but GIESBRECHT (1892), acting as the first reviser, singled out *S. gracilis*, presumably on the ground of BRADY's (1883) redescription.

Both A. SCOTT (1909) and WILSON (1924) pointed out that *Setella* DANA, 1846 is a junior homonym of *Setella* SCHRANK, 1802 (Lepidoptera), and replaced it by *Macrosetella* and *Dwightia*, respectively, the former of which takes priority.

Previous complete or partial redescriptions of *M. gracilis* were given by BRADY (1883, 1910), GIESBRECHT (1892), WHEELER (1901), PESTA (1912), MORI (1929, 1937), ROSE (1933), DAKIN & COLEFAX (1940), CARVALHO (1952), LEGARÉ (1964), OWRE & FOYO (1967), CHEN & al. (1974), BOXSHALL (1979) and ZHENG ZHANG & al. (1982).

Diagnosis. Miraciidae. Body fusiform, elongate; boundary between prosome and urosome not well defined. Cephalothorax pointed anteriorly, only slightly wider than prosome, not ventrally deflected; without cuticular lenses. Thorax and abdomen without distinct constrictions between somites. Integument weakly chitinized, smooth. Original segmentation of genital double-somite marked by dorsal superficial suture line. Caudal ramus about 11 times as long as wide; seta V distinctly longer than entire body; setae IV and V fused at base; seta VI fused to ramus.

Rostrum moderate in size, ventrally projected, defined at base. Antennule 8-segmented in ♀; aesthetasc on segments 4 and 8; seta on segment 1

absent. Antenna with completely fused allobasis; exopod absent; endopod with 1 lateral and 3 distal armature elements. Mandibular palp unisetose. Maxillule with gnathobase and rudimentary palp fused; palp represented by 1 seta. Maxillary endites with 1 spine each. Maxillipedal syncoxa with 1 seta; basis slightly longer than syncoxa, inner margin convex.

P1 without inner seta on exp-2, 3 setae on exp-3; enp-1 with inner seta, enp-2 with 3 setae. Inner distal corner of basis with large, bulbous process in ♂. P2-P4 with narrow intercoxal sclerites; basis without outer seta. P2 enp-1 ♂ without inner seta. Spine and setal formula as follows:

	Exopod	Endopod
P1	0.0.021	1.021
P2	0.1.222	0.2.121
P3	0.1.322	1.1.221
P4	0.1.322	1.1.221

P5 in ♀ with 6 setae on exopod, with 4 setae on endopodal lobe of baseoendopod; in ♂ with 4 setae on exopod and 2 setae fused to endopodal lobe.

P6 with 1 short and 1 long seta in ♀; with 1–2 short setae in ♂.

Type and only species. *Macrosetella gracilis* (DANA, 1847) A. SCOTT, 1909 [description in DANA (1854): 1198–1199, table 84, fig. 3a–g].

Macrosetella gracilis (DANA, 1847)

(Female: Figs 15; 16; 17A, B; 18; 19B–E; 20B–D; 21A–C, E; 22. Male: Figs 17C–F; 19A; 20A, E; 21D, F, G)

Setella gracilis DANA, 1847; *Setella longicauda* DANA, 1847; *Setella tenuicornis* DANA, 1847; *Setella crassicornis* DANA, 1847; *Setella aciculus* DANA, 1847; *Setella tenuis* LUBBOCK, 1860; *Setella messinensis* CLAUS, 1863.

Type locality. DANA's (1854) material came from two localities in the Pacific, one near the Kermadec Islands, the other near Tongatabu.

Material examined. 1. Natural History Museum, London: (a) reg. no. 1985.310: *Discovery* collections (leg. IOS), northeastern Atlantic, Stn 11261, haul 819; 28 June 1985; collected with RMT 1+8, 600–840 m depth: 1 ovigerous ♀ in alcohol; (b) reg. no. 1977.214–223: *Discovery* collections (leg. IOS), northeastern Atlantic, off Cap Verde Islands, Stn 7089; 18° N, 25° W; November 1969; collected with RMT 1+8: 21 ♀♀ in alcohol; (c) reg. no. 1977.224: *Discovery* collections (leg. IOS), northeastern Atlantic, off Cap Verde Islands, Stn 7089; 18° N, 25° W; November 1969; collected with RMT 1+8: 1 ♂ in alcohol; (d) reg. no. 1949.12.31.583: John Murray Expedition, Stn 56 (SEWELL 1947); 4 November 1933; taken with surface net: 2 ♀♀, 3 ♂♂ in alcohol; (e) reg. no. 84.14; H.M.S. *Challenger* Expedition, Zamboanga; labelled *Setella gracilis*: this vial contained 1 ♀ and 2 ♂♂ of *M. gracilis*, and 2 ♀♀ and 2 ♂♂ of *Microsetella* sp., in alcohol; (f) reg. no. 84.14; H.M.S. *Challenger* Expedition; 2 vials labelled *Setella gracilis*: 1 ♀, 5 copepodids (10 April 1876; 1 ♀, 1 ♂ (6 February 1875); in alcohol; (g) reg. no. 93.4.22.554–558: 4 ♀♀ in alcohol, labelled *Setella gracilis*; locality data unknown; (h) reg. no. 1915.7.5.62–64: Durban Bay; leg. E.C. Chubb: 3 ♀♀ in alcohol;

2. Royal Museum of Scotland: W.S. Bruce collection, Scottish National Antarctic Expedition, R/V *Scotia*, reg. no. 1921.143.1053, several vials labelled *Setella gracilis*, (a) Stn 77, 19 December 1902, 15°03' S, 36°53' W, townet 57: 1 ♀; (b) Stn 83, 22 December 1902, 22°32' S, 39°22' W, townet 61: 2 ♀♀, 2CV ♀♀; (c) Stn 98, 28 Dec 1902, 34° 02' S, 49° 07' W: 20 ♀♀, 1CV ♀; (d) No locality details: 19 ♀♀, 2 ♂ ♂; for other vials see under *Oculosetella*;

3. Northern Red Sea: (a) R/V *Meteor* cruise 5 (leg 5); Stn 660; 23°39.6' N, 36°36.8' E; depth 0–50 m; 18 July 1987; collected with MSN, mesh size 0.055 mm; 77 copepodids; (b) R/V *Meteor* cruise 5 (leg 5); Stn 663; 22°58.2' N, 37°18.8' E; depth 0–50 m; 20 July 1987; collected with MSN, mesh size 0.055 mm; 62 copepodids;

4. Central Red Sea: (a) R/V *Valdivia* cruise 29; Stn 130, 21°25.5' N, 38°01.9' E; depth 0–50 m; 28 October 1980; collected with MSN, mesh size 0.1 mm: 25 copepodids; (b) R/V *Meteor* cruise 5 (leg 2); Stn 72, 23°21.5' N, 36°47.0' E; depth 200–500 m; 4 February 1987; collected with MSN, mesh size 0.1 mm: 1 ♂; (c) R/V *Meteor* cruise 5 (leg 5); Stn 679; 20° 57.9' N, 38°09.4' E; depth 0–50 m; 24 July 1987; collected with MSN, mesh size 0.055 mm; 15 ♀♀, 11 ♂♂, 7 copepodids; (d) R/V *Meteor* cruise 5 (leg 5); Stn 673; 19°43.8' N, 37°29.1' E; depth 0–50 m; 22 July 1987; collected with MSN, mesh size 0.055 mm; 10 ♀♀, 8 ♂♂;

5. Southern Red Sea: (a) R/V *Meteor* cruise 5 (leg 5); Stn 703, 15°34.0' N, 41°54.9' E; depth 50–100 m; 03 August 1987; collected with MSN, mesh size 0.055 mm: 10 ♀♀ (with nauplii); (b) R/V *Meteor* cruise 5 (leg 5); Stn 705, 14°56.1' N, 41°59.8' E; depths 0–50 and 50–100 m; 4 August 1987; collected with MSN, mesh size 0.055 mm: 15 ♀♀, 15 ♂♂, 75 copepodids, 30 nauplii;

6. Gulf of Aden: (a) R/V *Meteor* cruise 5 (leg 2); collected with MSN, mesh size 0.1 mm; depth 50–100 m; (i) Stn 246, 12°20.1' N, 44°21.1' E, 7 March 1987; (ii) Stn 255, 13°01.0' N, 47°52.9' E, 10 March 1987; (iii) Stn 269, 13°09.8' N, 47°05.4' E, 13 March 1987; (iv) Stn 274, 13°27.8' N, 47°19.9' E, 14 March 1987: numerous ♀♀ and ♂♂ for length frequency analysis; (b) R/V *Meteor* cruise 5 (leg 5); Stn 631, 11°55.3' N, 43°37.3' E; depth 0–50 m; 11 April 1987; collected with MSN, mesh size 0.055 mm: 25 ♀ ♀, 17 ♂♂;

7. Arabian Sea: (a) near coast of Oman; R/V *Meteor* cruise 5 (leg 3a); Stn 344 and 347, 20°44.6' N, 59°40.0' E; depth 0–50 m; 4–5 May 1987; collected with MSN, mesh size 0.055 mm: numerous ♀♀ and ♂♂ for length frequency analysis; (b) central part; R/V *Meteor* cruise 5 (leg 3b); Stn 496, 17°58.4' N, 66°26.4' E; depth 0–50 m; 12 May 1987; collected with MSN, mesh size 0.055 mm: numerous ♀♀ and ♂♂ for length frequency distribution;

8. Atlantic, north-west Africa, upwelling zone: R/V *Meteor* cruise 64; Stn 92, ca 17° N, 20° W; depth 120–150 m; spring 1983; collected with MSN, mesh size 0.3 mm: 2 ♂ ♂;

9. From Dr S. Nishida: south-eastern Indian Ocean; cruise KH 76–5; Stn 11, 04°47.9' S, 87°12.9' E; depth 10 m;

24 January 1977; collected with horizontal Motoda net, mesh size 0.1 mm: 9 ♀♀, 4 ♂♂;

10. From Dr H. Ueda: Nago Bay, Okinawa (Japan); collected near the surface with plankton net, mesh size 0.1 mm; 6 November 1989: 21 ♀♀, 5 ♂♂;

11. From Prof. B. Kimor: Gulf of Aqaba: Stn A; 29°30' N, 34°57' E; depth 0–150 m; 6 July 1987; collected with vertical net, mesh size 0.065 mm: 2 ♀♀, 4 ♂♂.

Distribution. *Macrosetella gracilis* is distributed worldwide in tropical and subtropical seas. In the Red Sea, the species is represented by two distinct size morphs among adults, with females being < 1.2 mm and > 1.2 mm in length, and males being < 1.1 mm and > 1.1 mm, respectively (Böttger-Schnack 1989, 1991). Both size groups differ considerably in spatio-temporal distribution, and functional differences of the size variants have been inferred from the existing data (Böttger-Schnack & Schnack 1989; Böttger-Schnack 1991). It needed to be tested, however, whether the two size groups are morphs of the same species, or two closely related *Macrosetella* species restricted to the Red Sea. Previous taxonomic descriptions of *M. gracilis* from the Mediterranean and the North Atlantic (Giesbrecht 1892; Boxshall 1979) were based on large specimens only. The distribution of the smaller size group appears to be restricted to the Red Sea and western Indian Ocean (see Böttger-Schnack 1989 for literature review). The following redescription is based on careful examination of both Red Sea morphs, and specimens from other Indo-Pacific regions as well as from the Atlantic were used for comparison.

Redescription. (Illustrations based on large specimens from Central Red Sea (d))

Female. – Body length: see Table 1. Maximum width measured at posterior margin of cephalic shield.

Body (Fig. 15) fusiform, slender, elongate without distinct boundary between prosome and urosome. Integument weakly chitinized, smooth; somatic hyaline frills and intersomatic membranes moderately developed (Figs 15; 16E). Cephalothorax relatively large, about 1/3 of body (excluding rami), not ventrally deflexed; about as wide as first prosomite; abruptly tapering and pointed anteriorly and with straight dorsal margin in lateral aspect (Fig. 15B); cuticular lenses absent (Figs 15; 17B). Body with largely symmetrical pattern of integumental pores and sensilla in particular on dorsal surface (Fig. 15A) and around anterior end of cephalothorax (Fig. 17B). Thorax and abdomen without distinct constrictions between somites; none of somites laterally produced. Original segmentation of genital double-somite marked by superficial suture line dorsally (Fig. 16A, C), no trace ventrally (Fig. 16B). Posterior margin of all somites without spinules, except for ventral margin of penultimate somite, and ventral and lateral margins of anal somite (Fig. 16B, C, E). Anal somite narrow (Fig. 16), without distinct anal operculum. Caudal ramus (Figs 16A–D; 20B, C) about 11 times as long as wide, narrowest halfway its length; outer margin slightly concave; with 7 setae located around distal margin and several integumental pores; setae I–III closely set together (Fig. 20C); setae I–II spiniform and pinnate, seta III long and naked, setae IV–V spinulose, fused at base (Figs 16D; 20B, C), seta V very long, distinctly longer than total body length (Fig. 15B); seta VI minute and fused to ramus (Fig. 16D); seta VII located middorsally, small and biarticulated at base (Fig. 20B).

Rostrum moderately large, elongate (Figs 15B; 17A, B), not discernible in dorsal aspect (Fig. 15A); defined at base, ventrally projected, rounded at tip; with 2 sensilla and 1 integumental pore (Fig. 17B).

Antennule inserted on small pedestal (Fig. 17B); 8-segmented (Fig. 17A), segment 3 longest; without pinnate setae; segment 1 with few spinules distally, without seta; segment 2 with 6 setae; segment 3 with 9 setae; segment 4 with 2 setae, plus a long seta fused to an aesthetasc (210 μm) distally; segment 5 with 2 setae; segment 6 with 3 setae; segment 7 with 2 setae: segment 8 with 3 setae laterally and 1 swollen spine, 2 small setae and short aesthetasc (120 μm) apically.

Antenna (Fig. 19B). Coxa minute, bare. Basis and proximal endopod segment completely fused to form allobasis; no armature or ornamentation. Exopod absent in adult but original position marked by area of thin cuticle (arrowed in Fig. 19B). Endopod with large spinules and 1 lateral spine along the abexopodal margin; with fine spinules along exopodal margin; with 3 pinnate setae/spines around distal margin, the longest being recurved (Fig. 18A).

Labrum (Fig. 18A, B) distinctly pronounced ventrally; with 2 median and 2 lateral secretory pores anteriorly, fine spinules at distal margin and coarser spinules at lateral corners.

Mandible (Fig. 19C). Coxa with fine spinules near implantation of palp and long spinules near dorsal corner; gnathobase with 6 pointed teeth. Palp small, 1-segmented, with 1 pinnate spine apically.

Paragnaths well developed, setulose lobes (Fig. 18D).

Maxillule (Fig. 18C) with rudimentary palp fused to praecoxa. Praecoxa with well developed arthrite bearing minute armature elements; distal margin

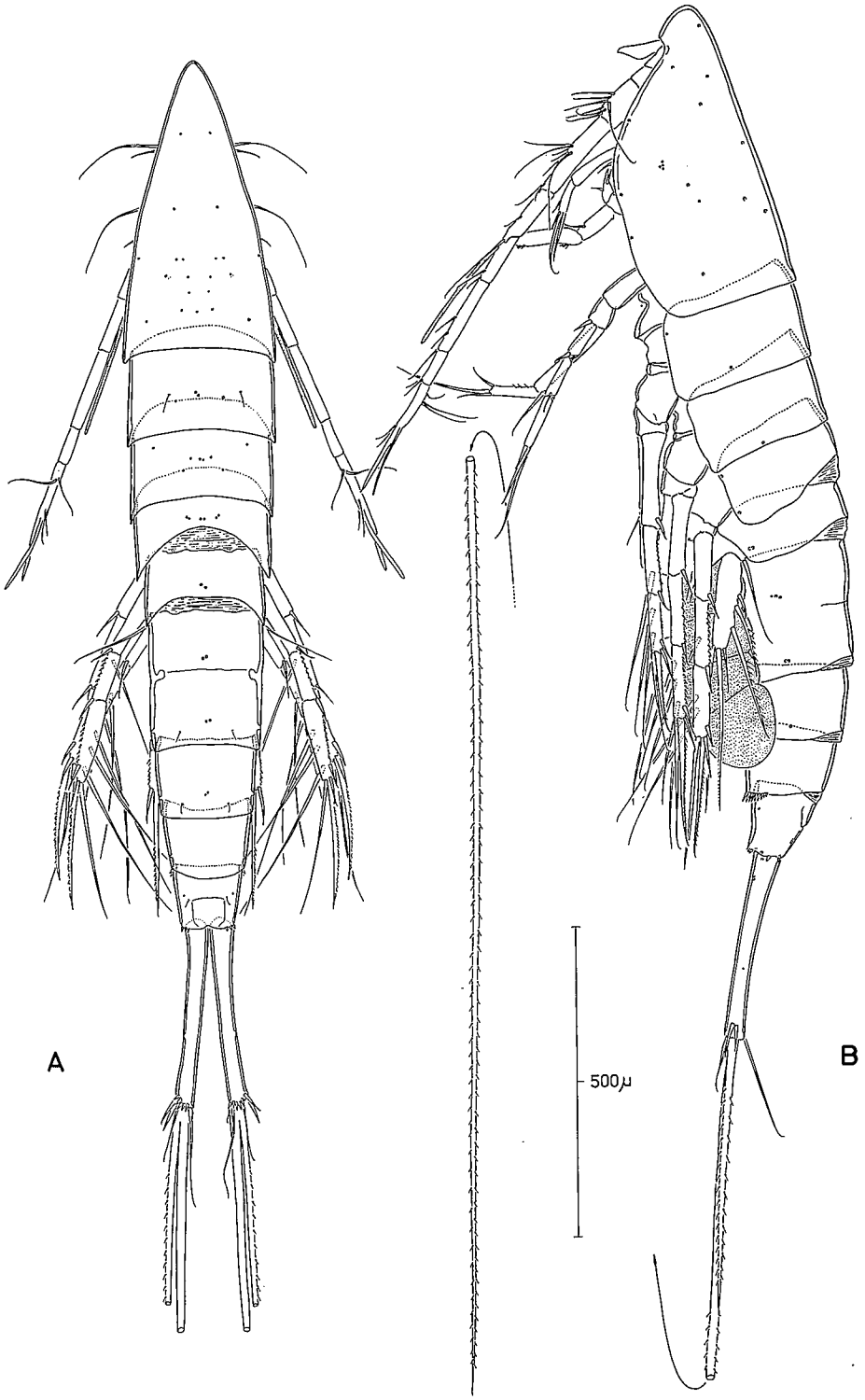

Fig. 15. *Macrosetella gracilis* (DANA, 1847). Female. A. Habitus, dorsal. B. Same, lateral.

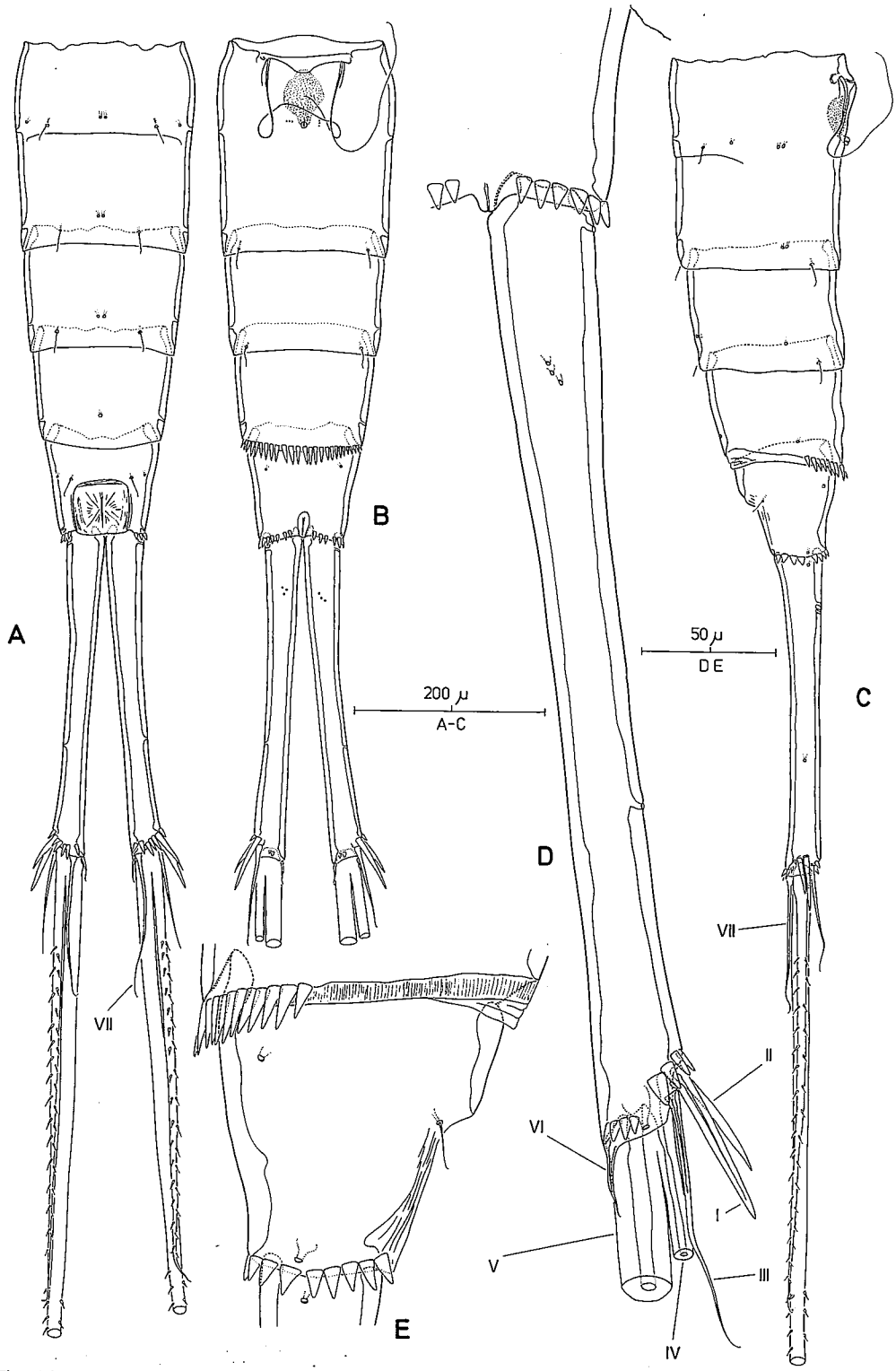

Fig. 16. *Macrosetella gracilis* (DANA, 1847). Female. A. Urosome (excluding P5–bearing somite), dorsal. B. Same, ventral. C. Same, lateral. D. Left caudal ramus, ventral. E. Anal somite, lateral.

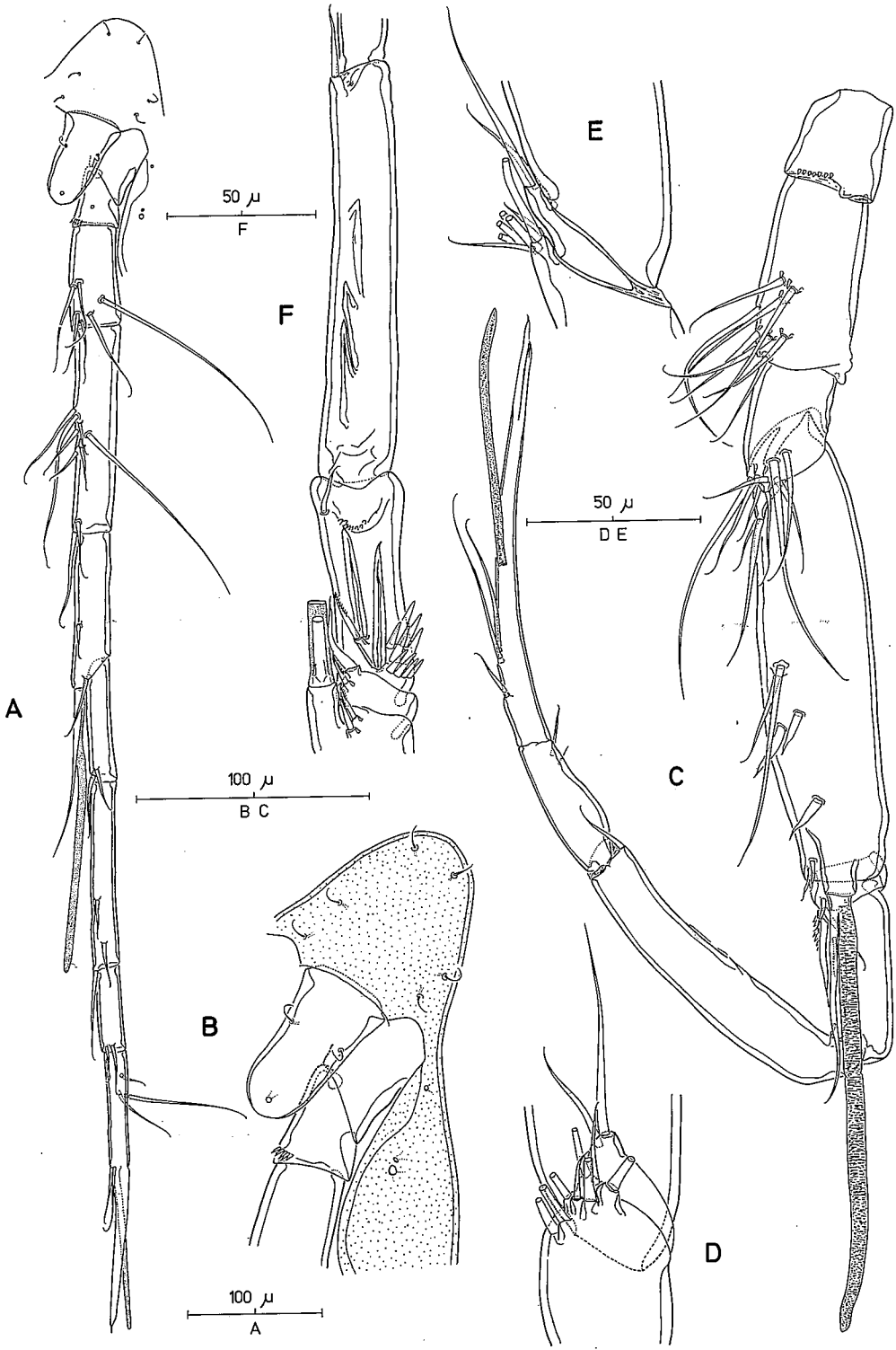

Fig. 17. *Macrosetella gracilis* (DANA, 1847). Female. A. Rostrum and antennule, dorsal. B. Rostral area. Male. C. Antennule, ventral. D. Same, segments 3–4, anterior. E. Same, segments 3–4, dorsal. F. Same, segments 5–8, anterior.

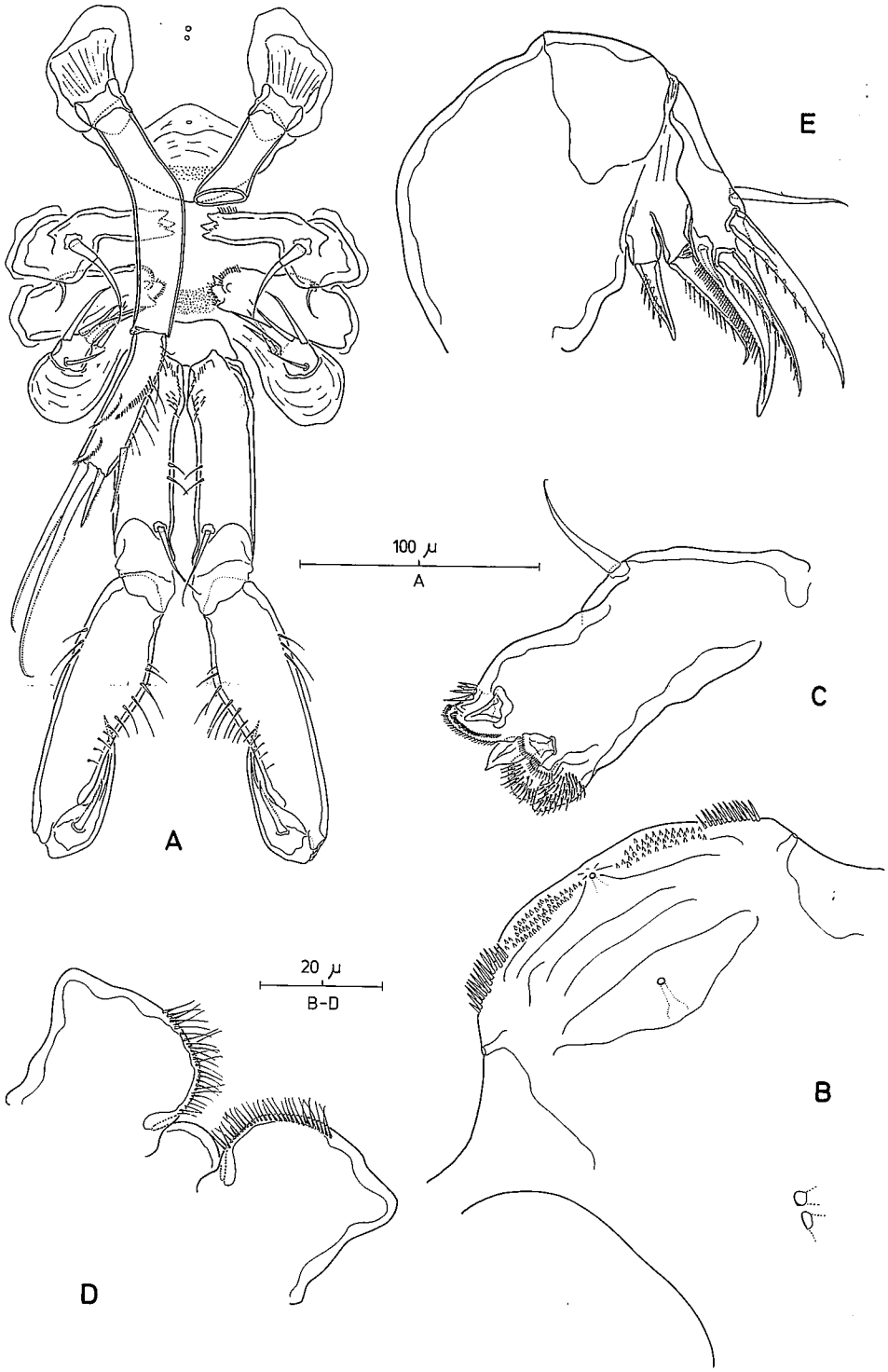

Fig. 18. *Macrosetella gracilis* (DANA, 1847). Female. A. Cephalic appendages and maxillipeds, ventral. B. Labrum, anterior. C. Maxillule. D. Paragnaths. E. Maxilla.

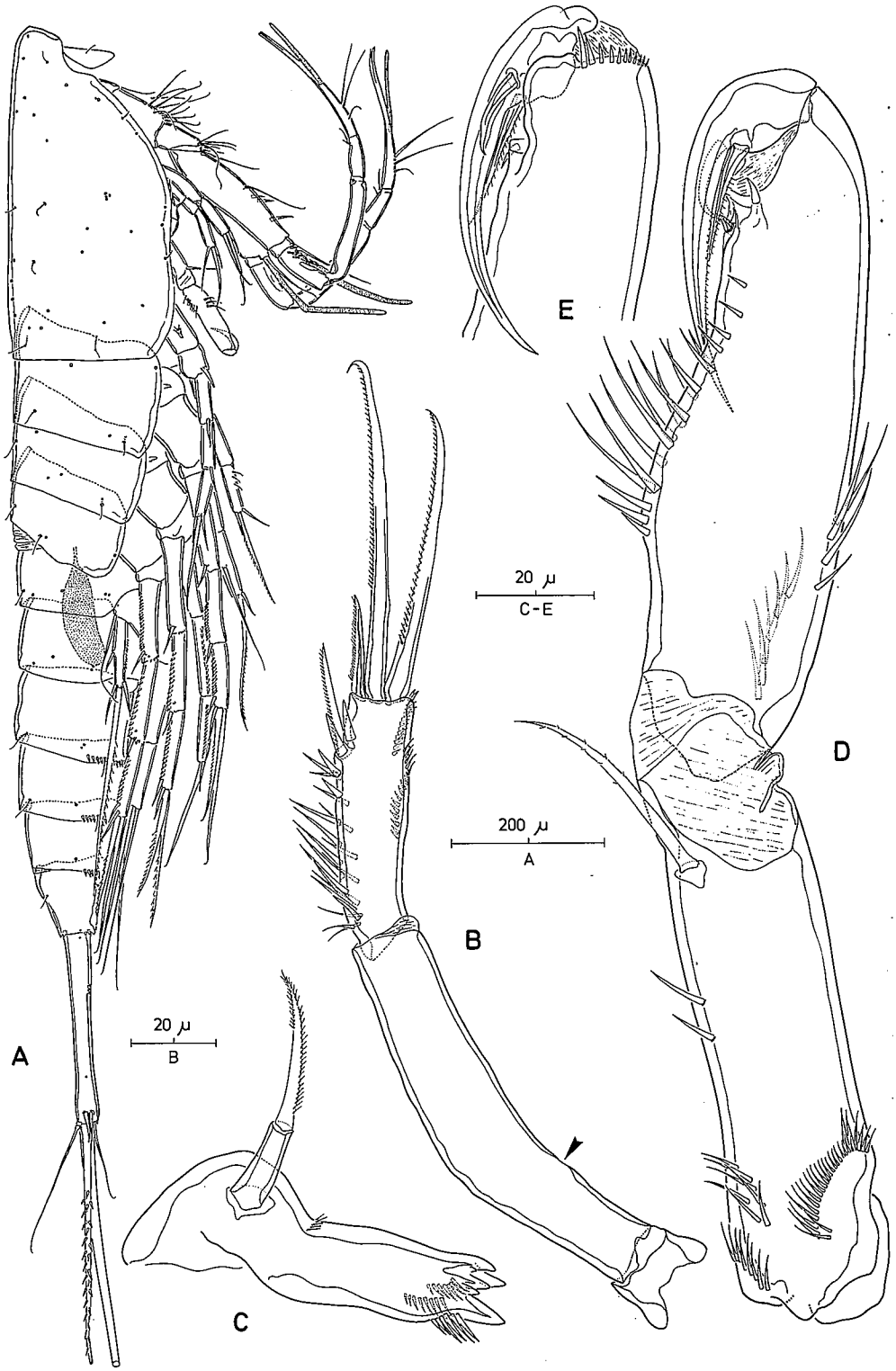

Fig. 19. *Macrosetella gracilis* (DANA, 1847). Male. A. Habitus, lateral. B. Antenna (arrow indicating position of lost exopod). C. Mandible. D. Maxilliped, anterior. E. Same, endopod and distal part of basis, posterior.

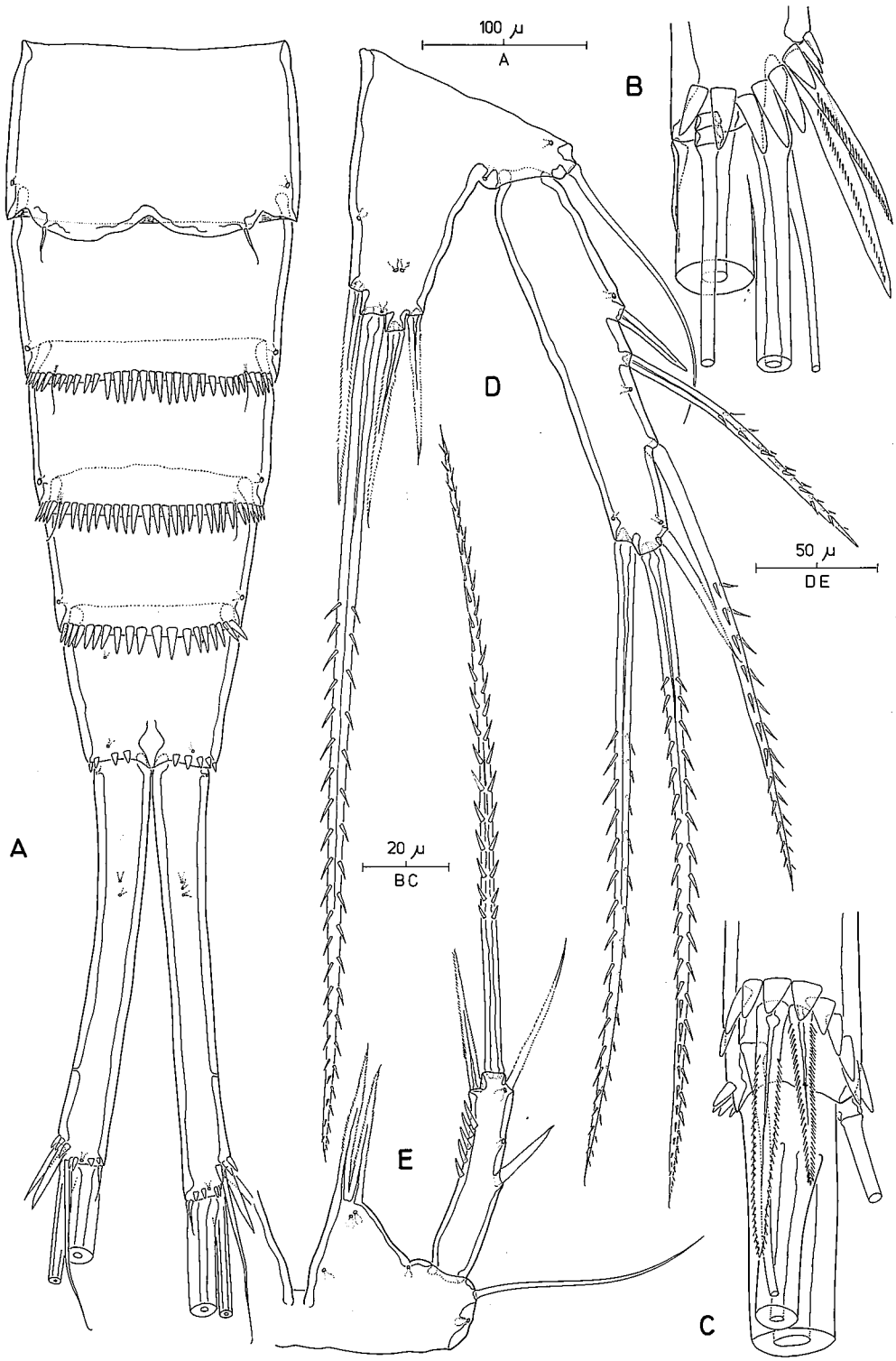

Fig. 20. *Macrosetella gracilis* (DANA, 1847). Male. A. Urosome (excluding P5-bearing somite). B. Right caudal ramus, distal margin, dorsal. C. Left caudal ramus, distal margin, lateral. E. P5, anterior. Female. D. P5, anterior.

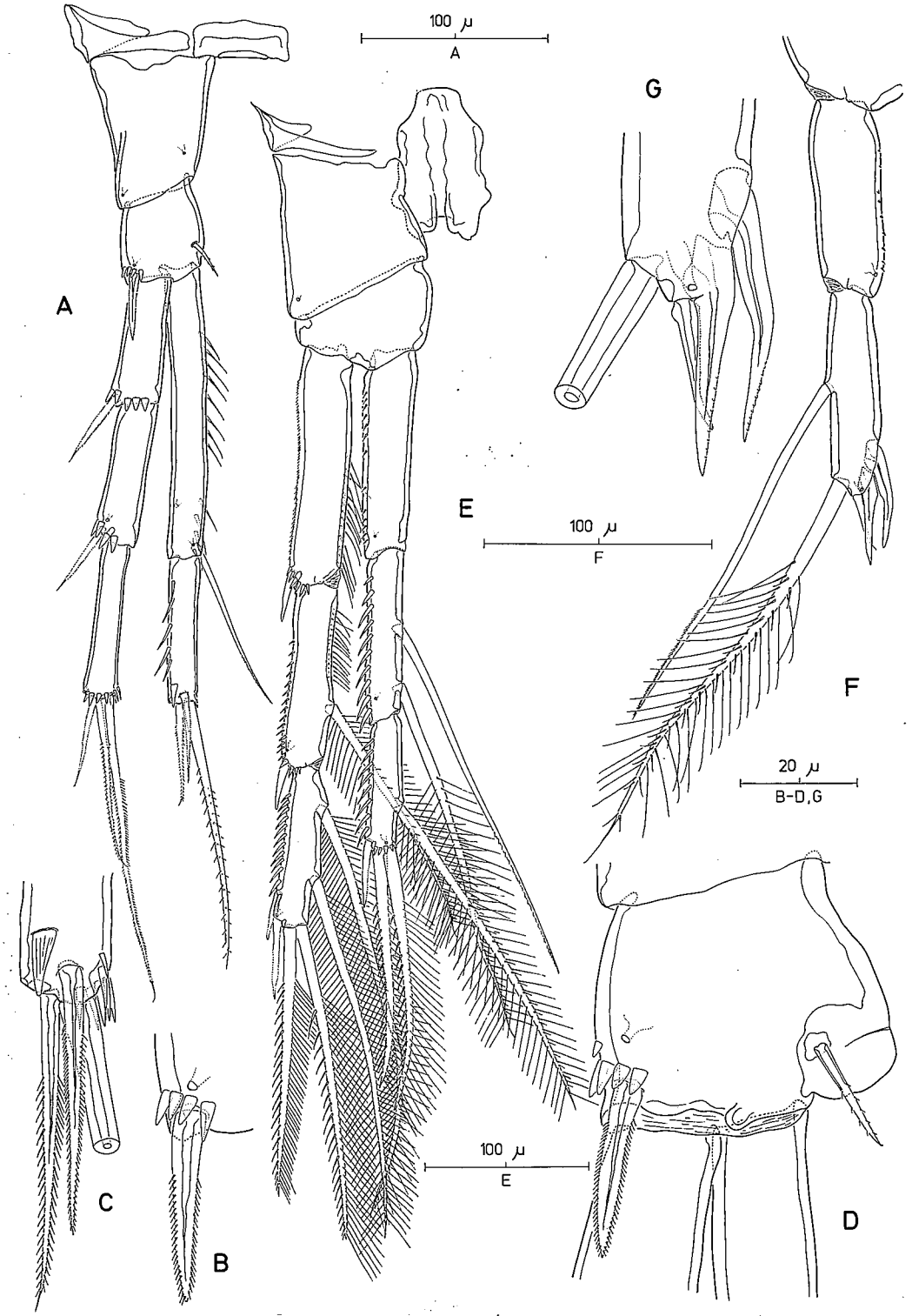

Fig. 21. *Macrosetella gracilis* (DANA, 1847). Female. A. P1, anterior. B. P1, outer basal spine. C. P1 enp-2, distal margin, anterior. E. P2, anterior. Male. D. P1 basis, anterior. F. P2 endopod, anterior. G. Same, distal part of enp-2, anterior.

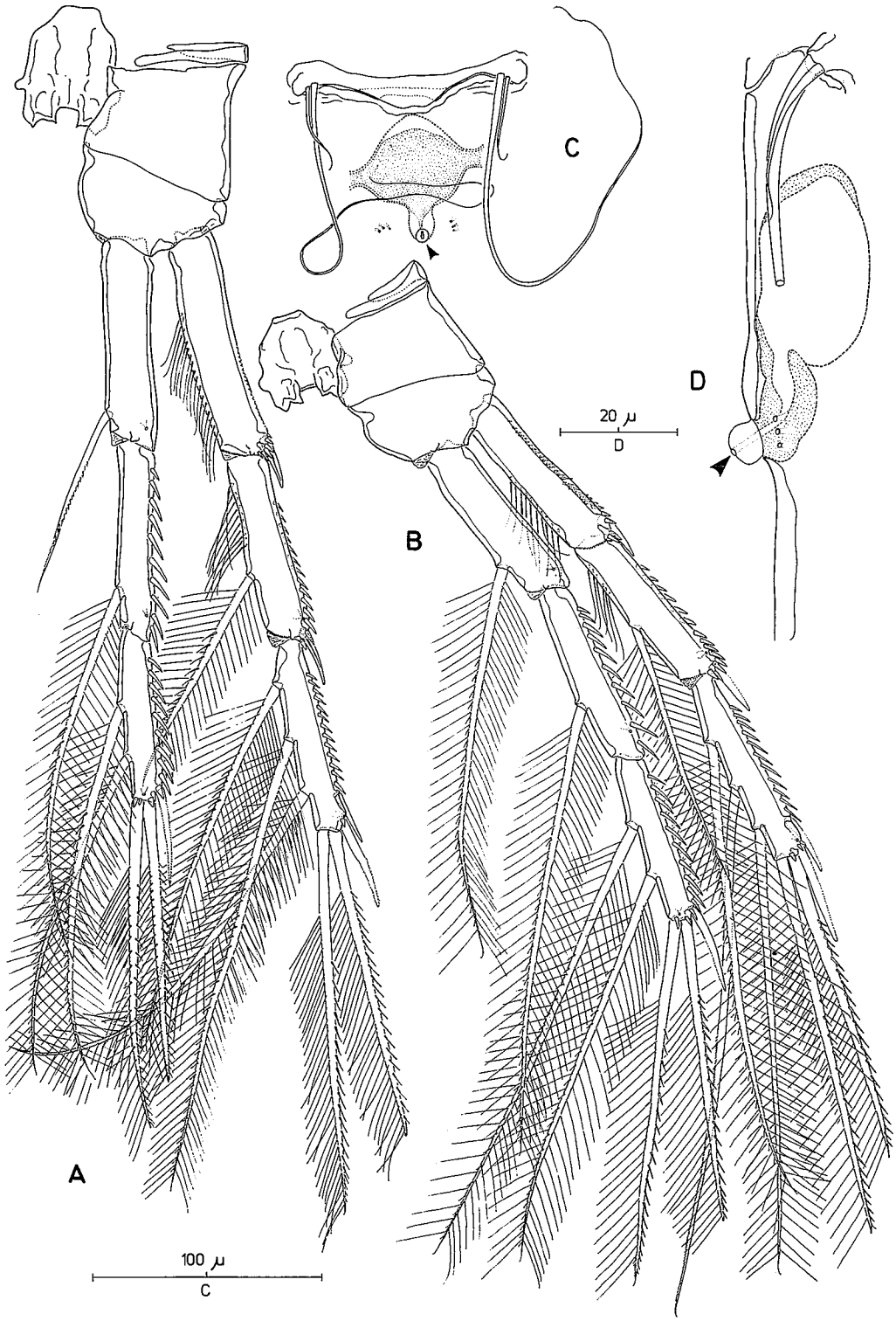

Fig. 22. *Macrosetella gracilis* (DANA, 1847). Female. A. P3, anterior. B. P4, anterior. C. Genital field, ventral. D. Same, lateral. (Copulatory pore arrowed in C-D).

with 4 stubby, pinnate and 4 spiniform elements; anterior surface without rudimentary seta. Palp represented by single seta only.

Maxilla (Fig. 18E). Syncoxa large, with 2 cylindrical endites distally; each endite with 1 articulate, pinnate spine. Allobasis drawn out into strong, short pinnate claw; with 2 naked setae and 2 pinnate spines.

Maxilliped (Figs 18A; 19D, E). Subchelate. Syncoxa and basis elongate, joined in linear arrangement. Syncoxa with several spinular rows and with pinnate seta near articulation with basis; with small sclerite at base. Basis longer than syncoxa (Fig. 19D), with 2 vestigial setae near articulation with endopod; inner margin slightly bulged, with double row of coarse spinules; with 2 spinular rows along proximal half of outer margin; distal part with small concavity delineated anteriorly by integumental ridge (Fig. 19E). Endopod represented by anteriorly recurved, pinnate claw bearing 2 short accessory setae.

P1 (Fig. 21A–C). Praecoxa a small U-shaped sclerite. Basis with short, inner pinnate seta and strong outer, pinnate spine (Fig. 21B). Exp-2 without inner seta; exp-3 with 1 outer and 2 long apical setae. Endopod about as long as exopod; inner margin of enp-1 with spinules and inner seta; enp-2 with spinular outer margin and 3 setae/spines distally (Fig. 21C).

P2–P4 (Figs 21E; 22A, B) with narrow intercoxal sclerites. Praecoxae small. Basis without outer seta. P2–P3 enp-1 without inner seta. Middle inner seta of P4 exp-3 tripinnate. Seta and spine formula as in generic diagnosis.

P5 large (Fig. 20D); baseoendopod with outer basal seta, 6 pores and with 4 setae (second inner one extremely long) on well developed endopodal lobe; exopod with 6 spines/setae and 4 pores; all long armature elements pinnate.

Genital apertures (Figs 16B, C; 22C, D) fused to form common genital slit, covered by vestigial sixth legs bearing short outer seta and very long inner seta. Copulatory pore minute, located on raised bulbous structure (arrowed in Fig. 22D) and flanked by 3 secretory pores on either side; seminal receptacle transversely elongate, tripartite.

Male. – Body length: see Table 1.

Antennule (Figs 17C–F; 19A) 10-segmented, haplocer; geniculation between segments 7 and 8. Segment 1 with spinular row distally, without seta; segment 2 with 8 setae; segment 3 with 8 setae (Fig. 17D); segment 4 minute, U-shaped sclerite, with 2 setae (Fig. 17D, E); segment 5 longest, slightly swollen, with 7 setae along anterior margin (distal 2 minute) and 1 seta plus an aesthetasc (185 μm) on distal process (Fig. 17F); segment 6 with 1 vestigial, pinnate seta and 1 large naked seta; segment 7 with spinular patch, 2 small setae and 2 strong spines (Fig. 17F); segment 8 with 3 modified spines and 1 distal seta (Fig. 17F); segment 9 with 2 minute setae; distal segment drawn out into spinous process (derived from fused spine), with 3 lateral setae and 2 minute setae (largely fused together to form a bifid process) plus an aesthetasc apically (110 μm) (Fig. 17C).

P1 basis (Fig. 21D). Inner margin produced into large, bulbous, inwardly directed process with

Table 1. Body length (mm) of adult *Macrosetella gracilis* sampled with fine mesh nets ($\leq$ 0.1 mm mesh size) in the Red Sea and different parts of the Indo-Pacific. ( ) = number of individuals measured; [ ] = outlier.

Region/season	Females	Males	Source
Red Sea			
Various regions, seasons and depths	0.98 - 1.60 (> 2000) [1.78]	0.88 - 1.34 (> 500)	BÖTTGER-SCHNACK (1989, 1991)
Gulf of Aden			
Winter 1987	1.04 - 1.56 (166)	1.00 - 1.30 (93)	Present account
Summer 1987	1.00 - 1.46 (71)	0.90 - 1.24 (91)	BÖTTGER-SCHNACK (1991)
Arabian Sea			
Spring 1987	0.88 - 1.40 (34)	0.86 - 1.12 (12)	Present account
Eastern Indian Ocean			
Winter 1977	1.18 - 1.40 (9)	1.20 - 1.30 (3)	Present account
Nago Bay, Okinawa			
Winter 1989	1.22 - 1.62 (17)	1.18 - 1.22 (4)	Present account

superficial transverse suture line; inner basal spine not modified.

P2 endopod (Fig. 21G, F) 2-segmented. Enp-1 broader than in female, without inner seta. Enp-2 with serrate, inner seta in proximal half; distal half with strong, plumose inner seta subdistally, a stout, curved spine at the outer margin, and spinous process plus a pinnate spine at apex (Fig. 21G).

Fifth pair of legs fused medially (Fig. 20E); baseoendopod with 5 pores, endopodal lobe with 2 distal setae confluent with the segment; exopod with coarse spinules along inner margin, with 1 lateral and 3 distal spines, the apical one very long and spinulose.

Sixth pair of legs (Fig. 20A) weakly developed; symmetrical, fused medially and to somite; outer corner with 1 or 2 naked setae.

Postgenital somites (Fig. 20A) with spinular rows at ventral posterior margin.

Variability. – 1. Body length: the body length of adult *M. gracilis* in the Red Sea has been analyzed in detail in earlier studies, by measuring females and males sampled at different depths, in various regions, and during three seasons (BÖTTGER-SCHNACK 1989, 1991). Body length was measured from the tip of the rostrum to the posterior margin of the caudal rami. The overall body length of the females ranged between 0.98 and 1.78 mm, males measured between 0.88 and 1.32 mm (Table 1). Two distinct size categories were recognized, with a size limit between the two groups at about 1.2(5) mm for females and at about 1.1 mm for males. A typical bimodal length frequency distribution of females and males, when both size morphs are co-occurring, is illustrated in Fig. 38.

The ranges in body length of *M. gracilis* females and males observed in fine mesh net samples outside the Red Sea are summarized in Table 1.

In the adjacent regions, the Gulf of Aden and the Arabian Sea, the length ranges of adults were generally similar to those found in the Red Sea. Notably, the smallest female *M. gracilis* yet discovered, measuring only 0.88 mm, was collected in the Arabian Sea near Oman (Table 1). In the eastern Indian Ocean and in neritic waters off Okinawa only large-sized specimens were found (females > 1.2 mm, males > 1.1 mm).

2. Caudal ramus length : width ratio: both rami of 12 females and 12 males (Red Sea), with both size morphs equally represented, were measured. Caudal ramus length was measured along the inner margin; width was measured posteriorly at the widest part, i.e. at the level of the base of seta I.

The length : width ratio was on average 11 : 1 (range 10.5–12.5 : 1) in females, and 10.5 : 1 (range 8.4–14 : 1) in males. Variation in the ratio of both caudal rami within a given specimen was considerably higher in males than in females. In 9 out of the 12 male specimens measured, the length to width ratio of the two rami differed by more than 5% and up to 21%; in females the ratio of both rami always differed by less than 5%.

3. Length of caudal ramus seta V (females): numerous females sampled at different depths and in two regions in the Red Sea during autumn and winter 1980–1981 were measured routinely during the course of the body length frequency analysis of females (see BÖTTGER-SCHNACK 1989).

The length of seta V (a) was slightly longer than the total body length (b), with an average ratio a : b of 1.3 : 1 (range 1.1–1.9 : 1). No systematic difference in the size relationship of caudal setae to body length was detected between the two size groups.

4. Male P6: observations are based on 53 specimens (40 large, 13 small) taken mainly from surface samples in the central Red Sea and Gulf of Aden during summer 1987, and with a few specimens collected from other areas (Table 2).

Table 2. Variability in the armature of leg 6 in male *Macrosetella gracilis* belonging to different size classes.

Region	Number of individuals with armature pattern		
	symmetrical		asymmetrical
	1 seta	2 setae	1/2 seta(e)
A. Small ♂♂ (< 1.1 mm)			
* Central Red Sea			
Summer 1987		1	
* Gulf of Aden			
Summer 1987	6	3	1
Winter 1987		1	
* Arabian Sea			
Spring 1987		1	
Total	6	6	1
B. Large ♂♂ (> 1.1 mm)			
* Red Sea			
Gulf of Aqaba			
(Northern Red Sea;			
Summer 1987)	1	3	
Central Red Sea			
Summer 1987	9	16	
Winter 1987		1	
* Gulf of Aden			
Summer 1987	2	4	1
* SE Indian Ocean		1	
* Atlantic, off NW Africa		2	
Total	12	27	1

Male *M. gracilis* exhibit a strong variability in the number of armature elements on the sixth legs (Table 2). In most cases a symmetrical pattern with either 1 seta (18 individuals) or 2 setae (33 individuals) on both sides was observed, but in two specimens the pattern was asymmetrical. The proportion of males possessing 2 setae seemed to be higher for the large size morph as compared to the smaller size group, but the number of small specimens examined was not sufficiently high for a statistical analysis.

Remarks. The present data on body length for adult specimens in different regions of the Indo-Pacific support BÖTTGER-SCHNACK's (1989) earlier findings that the distribution of the smaller size group (i.e. females < 1.2 mm, males < 1.1 mm) appears to be confined to the Red Sea and the western Indian Ocean. The number of individuals from the eastern Indo-Pacific available for length measurements during the present study was relatively low, however. Hence, more detailed information on length ranges of *M. gracilis* sampled with fine mesh nets outside the Red Sea is necessary, since most previous studies in those areas used nets with 0.2 or 0.3 mm mesh size, which cannot sample the adult population quantitatively (BÖTTGER-SCHNACK & SCHNACK 1989).

BOXSHALL (1979) reported sexual dimorphism in the antenna and the number of maxillary endites, but this could not be confirmed in the present study.

Genus *Distioculus* gen. nov.

Miracia DANA, 1846 (partim).

History. This genus is established to accommodate *Miracia minor* T. SCOTT, 1894, originally described from the eastern Atlantic (Gulf of Guinea). One year later MRÁZEK (1895) also discovered this species in the Indian Ocean and – being unaware of T. SCOTT's description – identified it with DANA's *Miracia gracilis*, previously relegated to a synonym of *Setella gracilis* by GIESBRECHT (1892). DAHL (1895) pointed out the confusion and so did GIESBRECHT (1895), who provided the first detailed description of both sexes.

Other redescriptions of *D. minor* comb. nov. have been given by KRISHNASWAMY (1956), OWRE & FOYO (1967) and BOXSHALL (1979).

Diagnosis. Miraciidae. Body more or less cylindrical; boundary between prosome and urosome not pronounced. Cephalothorax rounded anteriorly, slightly narrower than first pedigerous somite, not ventrally deflected; with pair of large cuticular lenses laterally, not touching in the median line. Thorax and abdomen without distinct constrictions between somites. Integument strongly chitinized, pitted. Original segmentation of genital double-somite marked by lateroventral chitinous ribs. Caudal ramus about three times as long as wide; seta V shorter than urosome; setae IV and V not fused at base.

Rostrum minute, integrated in cephalothorax. Antennule 8-segmented in ♀; aesthetasc on segments 4 and 8; seta on segment 1 present. Antenna with bisetose exopod; endopod with 2 lateral and 5 distal armature elements. Mandibular palp unisetose. Maxillule with gnathobase and palp separate; palp with 3 setae representing basal endite and incorporated endopod (or exopod). Maxillary endites with 2 spines each. Maxillipedal syncoxa with 3 setae, shorter than basis; inner margin of basis slightly concave.

P1 with inner seta on exp-2, 4 setae on exp-3; enp-1 with inner seta, enp-2 with 3 setae. Inner margin of basis with truncate striated process in ♂. P2-P4 with paired spinous processes on intercoxal sclerite; basis with outer seta. P2 enp-1 ♂ without inner seta. Spine and setal formula as follows:

	Exopod	Endopod
P1	0.1.022	1.021
P2	0.1.222	0.2.121
P3	0.1.322	0.2.221
P4	0.1.322	1.1.221

P5 in ♀ with 5 setae on exopod and 4 setae on baseoendopod; in ♂ with 4 setae on exopod and 2 setae on baseoendopod.

P6 with 1 long and 2 short setae in both sexes.

Type and only species. *Distioculus minor* (T. SCOTT, 1894) comb. nov. [description in T. SCOTT (1894): 102–104, plate XI, figs 18–30].

Etymology. The generic name is derived from the Latin *distans*, meaning standing apart, and *oculus*, meaning eye, and alludes to the laterally displaced cuticular lenses.

Distioculus minor (T. SCOTT, 1894) comb. nov.

(Female: Figs 23; 24A; 25; 26A, C; 27; 28B, C; 29C. Male: Figs 24B–D; 26B, D; 28A; 29A, B)

Miracia minor T. SCOTT, 1894; *Miracia gracilis* DANA, 1849 *sensu* MRÁZEK (1895).

Type locality. Gulf of Guinea, 5°58'1' S, 0°1'5' E, 235 fms.

Material examined. 1. Natural History Museum, London: (a) syntype series: Gulf of Guinea, R/V *Buccaneer*,

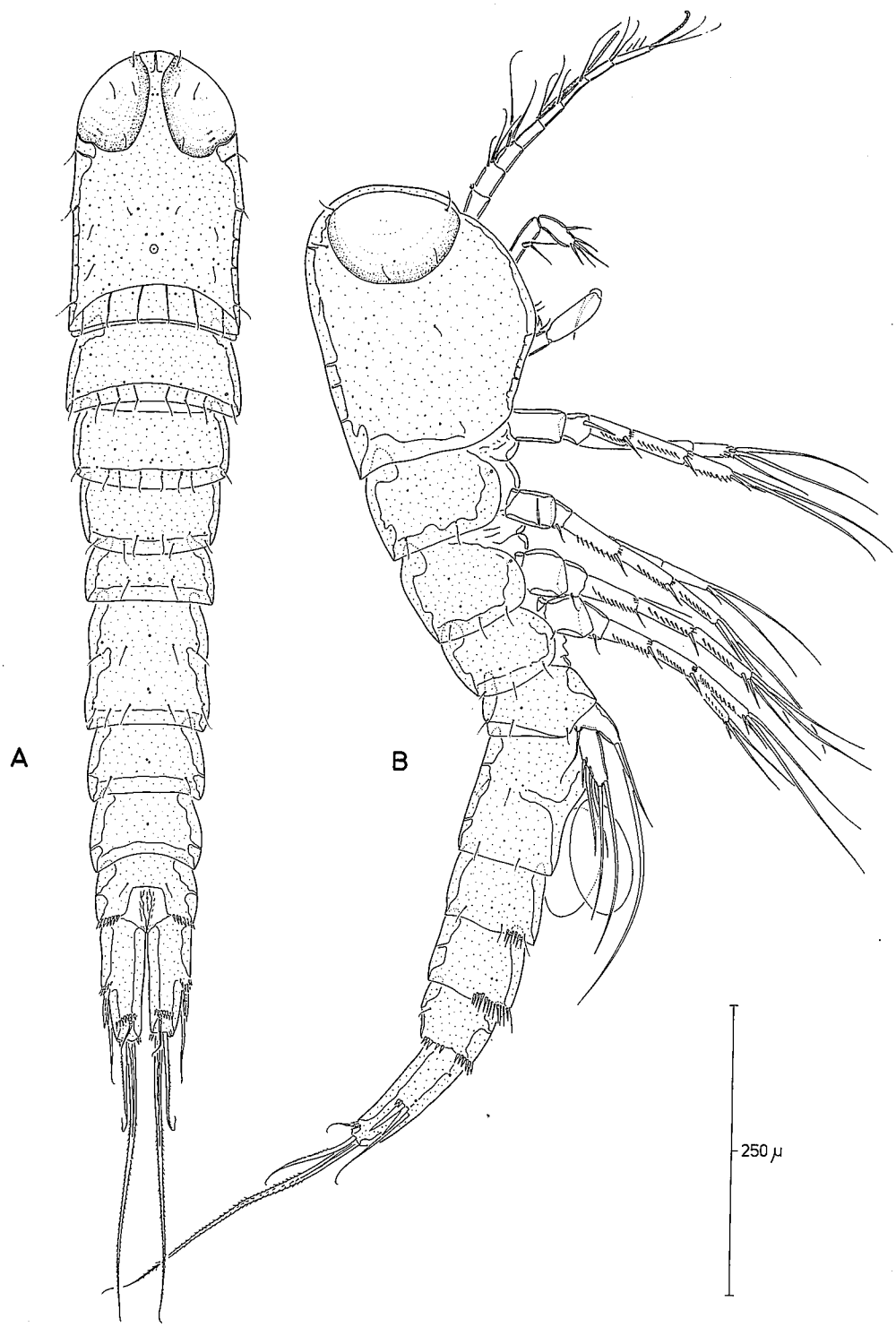

Fig. 23. *Distioculus minor* (T. Scott, 1894) comb. nov. Female. A. Habitus, dorsal. B. Habitus, lateral.

Stn 33, 5°58'1' S, 0°1'5" E, 235 fms; 5 February 1886; leg. J. Rattray, det. T. Scott, 1894; erroneously labelled *Miracia minuta* n.sp.; (i) reg. no. 1894.1.20.76–77, 79–87: 1 ♀ dissected on 6 slides [79–84], 1 ♂ dissected on 5 slides [76–77, 85–87]; (ii) reg. no. 1894.1.20.78: 1 ♀ in alcohol; (iii) reg. no. 1893.4.22.340: 2 ♂♂ in alcohol; (b) reg. no. 1984.198: Sargasso Sea, 150–200 m depth; 1 ♂ in alcohol; (c) reg. no. 1949.12.31.584–585: John Murray Expedition, Stn 61 (SEWELL 1947); 1 ♀ and 1 ♂ in alcohol, labelled *Macrosetella oculata*; (d) reg. no. 1911.11.8. 43199: Gulf of Aden, 1892; Norman collection (leg. A. Scott); 1 damaged ♂;

2. National Museum of Natural History (Smithsonian Institution), Washington, D.C.: see under *Oculosetella gracilis*.

3. Red Sea, Gulf of Aden, Arabian Sea, eastern Mediterranean: see Table 3 (leg. R. Böttger-Schnack).

Redescription. (Illustrations based on syntypes)

Female. – Body length 795–915 µm (n = 9; = 861 µm) measured from anterior margin of cephalothorax to posterior rim of caudal rami. Specimens from the Red Sea and Gulf of Aden are significantly smaller: 0.7 mm. Maximum width measured at posterior margin of cephalic shield.

Body more or less cylindrical (Fig. 23) with boundary between prosome and urosome not well defined. Integument strongly chitinized, pitted; somatic hyaline frills not developed. Cephalothorax not ventrally deflexed; slightly narrower than first prosomite; rounded anteriorly; with pair of large cuticular lenses bilaterally, not touching in the median line (Fig. 23A). Body with largely symmetrical pattern of integumental pores and sensilla, in particular on dorsal surface (Fig. 23A). Thorax and abdomen without distinct constrictions between somites; epimeral areas not well developed. Original segmentation of genital double-somite marked by internal chitinous ribs lateroventrally (Figs 23; 27A, B). Posterior ventral margin of genital double-somite without spinules (Fig. 27A, B). Ventrolateral corners of first free abdominal somite with double spinular row, consisting of tiny spinules distally and large spinules subdistally (Fig. 27A, B). Entire ventral margin of penultimate somite with similar ornamentation (Fig. 27A, B). Anal somite (Fig. 27), without distinct anal operculum; ventral and dorsolateral posterior margins with large spinules. Caudal ramus (Fig. 27) about 3 times as long as wide; outer margin stepped at about halfway the ramus length; with 7 setae and several integumental pores; setae I-III closely set together and surrounded by spinular patch (Fig. 27B); setae I and II spiniform, seta III long and pinnate; setae IV-V not

Table 3. Distribution of *Distoculus minor* in the Red Sea, the Gulf of Aden, the Arabian Sea and the eastern Mediterranean.

Station	Position	Date	Depth (m)	Number of specimens
Southern Red Sea				
705	14°56' N, 42°00' E	4 Aug 87	0 - 50	1 ♂
708	13°40' N, 42°37' E	5 Aug 87	40 - 60	1 ♀ (exuvium)
			60 - 85	1 ovigerous ♀
Strait of Bab al Mandab				
641	12°39.5' N, 42°14.5 E	12 Jul 87	20 - 40	1 ovigerous ♀
			40 - 60	1 ovigerous ♀
			60 - 80	4 ♀♀ (3 ovigerous)
			80 - 100	7 ♀♀ (4 ovigerous)
			100 - 120	1 ♀
			140 - 170	1 ovigerous ♀
717	3°32' N, 43°24.5' E	6 Aug 87	20 - 40	3 ♂♂
			40 - 60	2 ovigerous ♀♀, 1 ♂
Gulf of Aden				
631a	11°55.5' N, 43°38' E	11 Jul 87	50 - 100	2 ovigerous ♀ ♀; 1 cop.
631b			0 - 50	1 ovigerous ♀, 1 cop.
			50 - 100	2 ovigerous ♀♀
633	11°57' N, 43°47' E		40 - 60	3 ovigerous ♀♀
Arabian Sea				
347	20°44' N, 59°4' E	5 Apr 87	0 - 50	3 ♀♀
			50 - 100	5 ♀♀ (1 exuvium)
496	18°00' N, 66°25' E	12 May 87	0 - 50	2 ♀♀
			50 - 100	4 ♀♀
Eastern Mediterranean				
54	32°35' N, 33°39' E	27 Jan 87	0 - 50	1 ♀

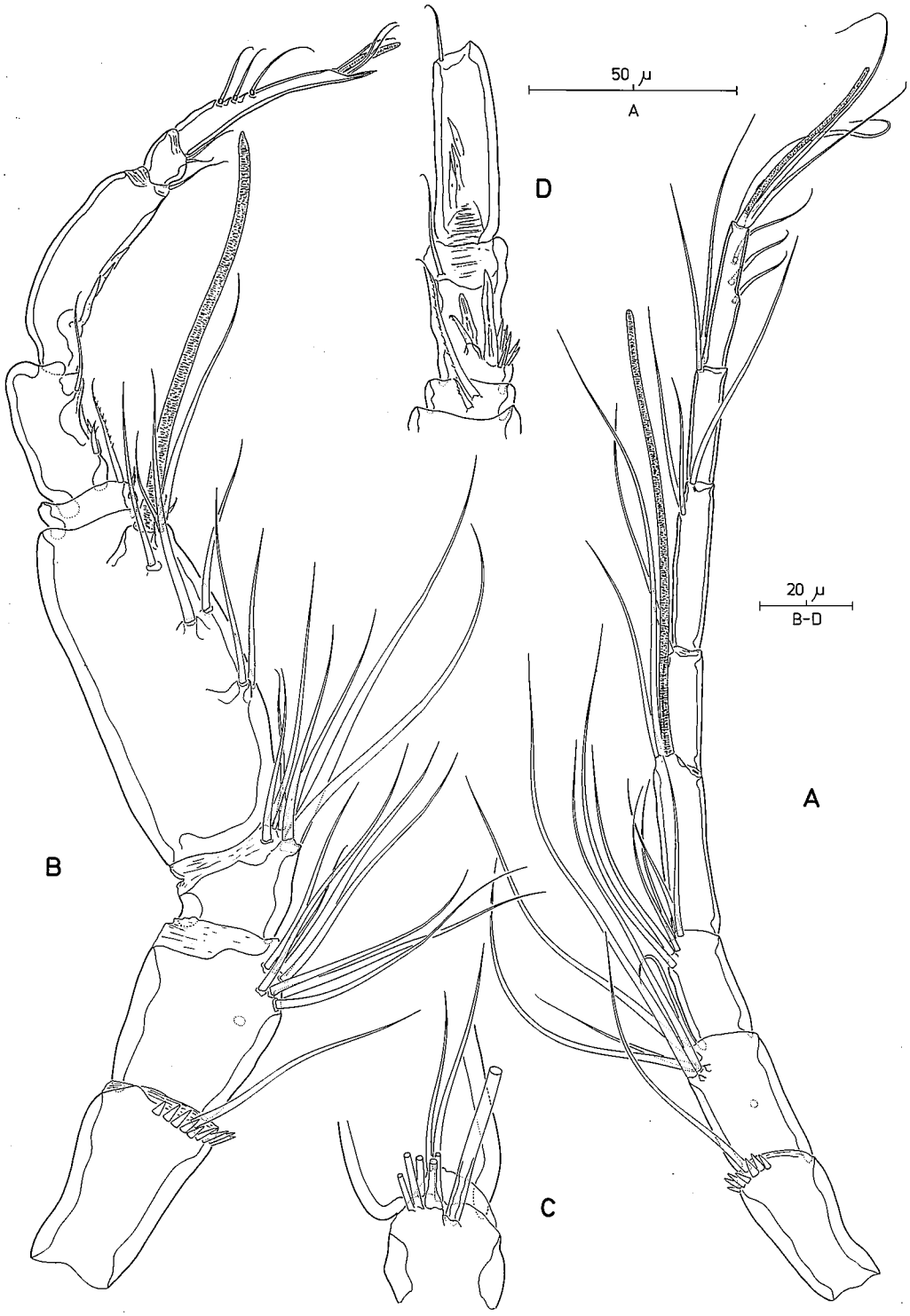

Fig. 24. *Distioculus minor* (T. Scott, 1894) comb. nov. Female. A. Antennule, ventral. Male. B. Antennule, ventral. C. Same, segments 3–4, anterior. D. Same, segments 6–8, anterior.

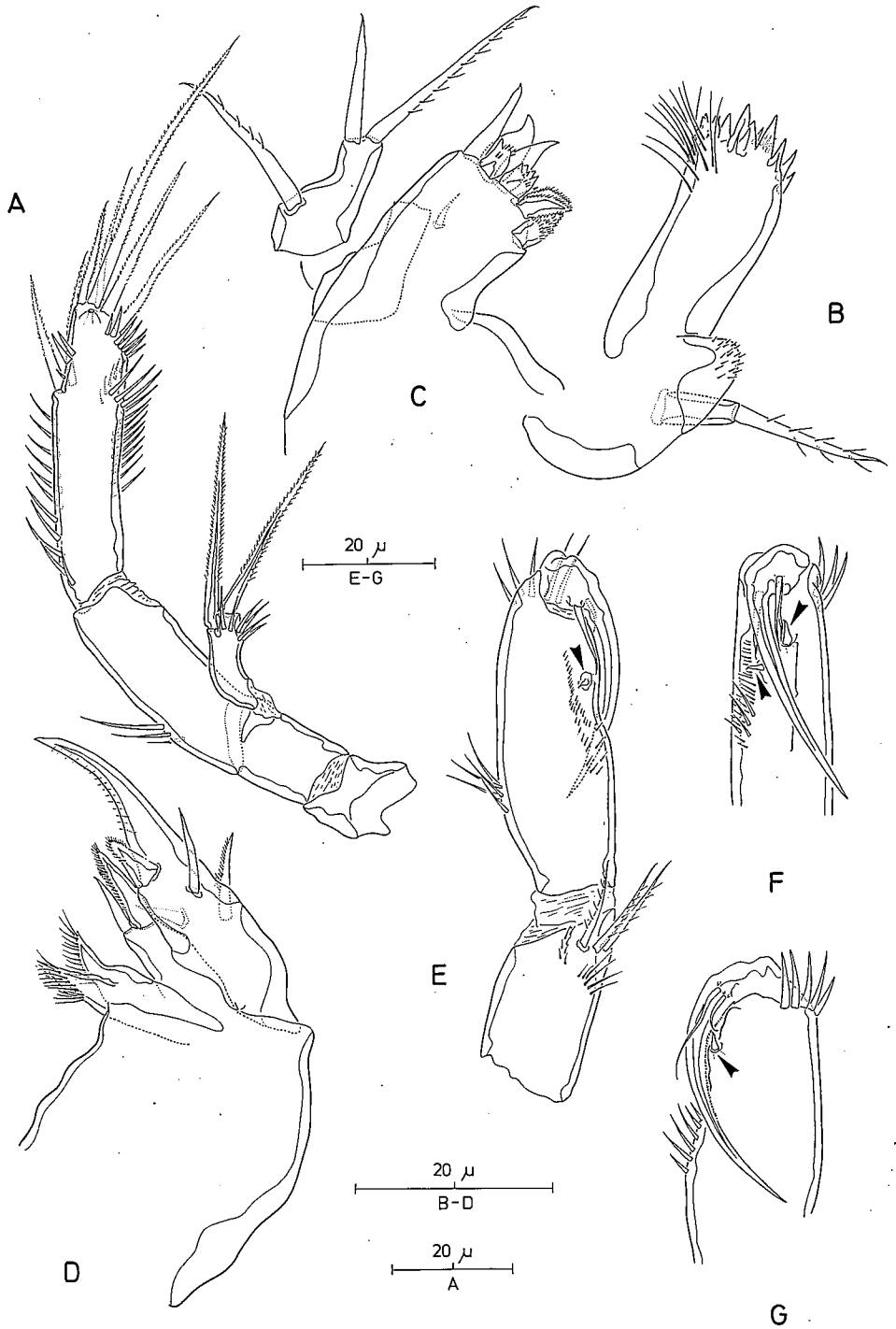

Fig. 25. *Distioculus minor* (T. Scott, 1894) comb. nov. Female. A. Antenna. B. Mandible. C. Maxillule (with disarticulated palp). D. Maxilla. E. Maxilliped, anterior. F. Maxilliped, endopod and distal part of basis, inner. G. Same, posterior. (Vestigial setae on basis arrowed in E-G).

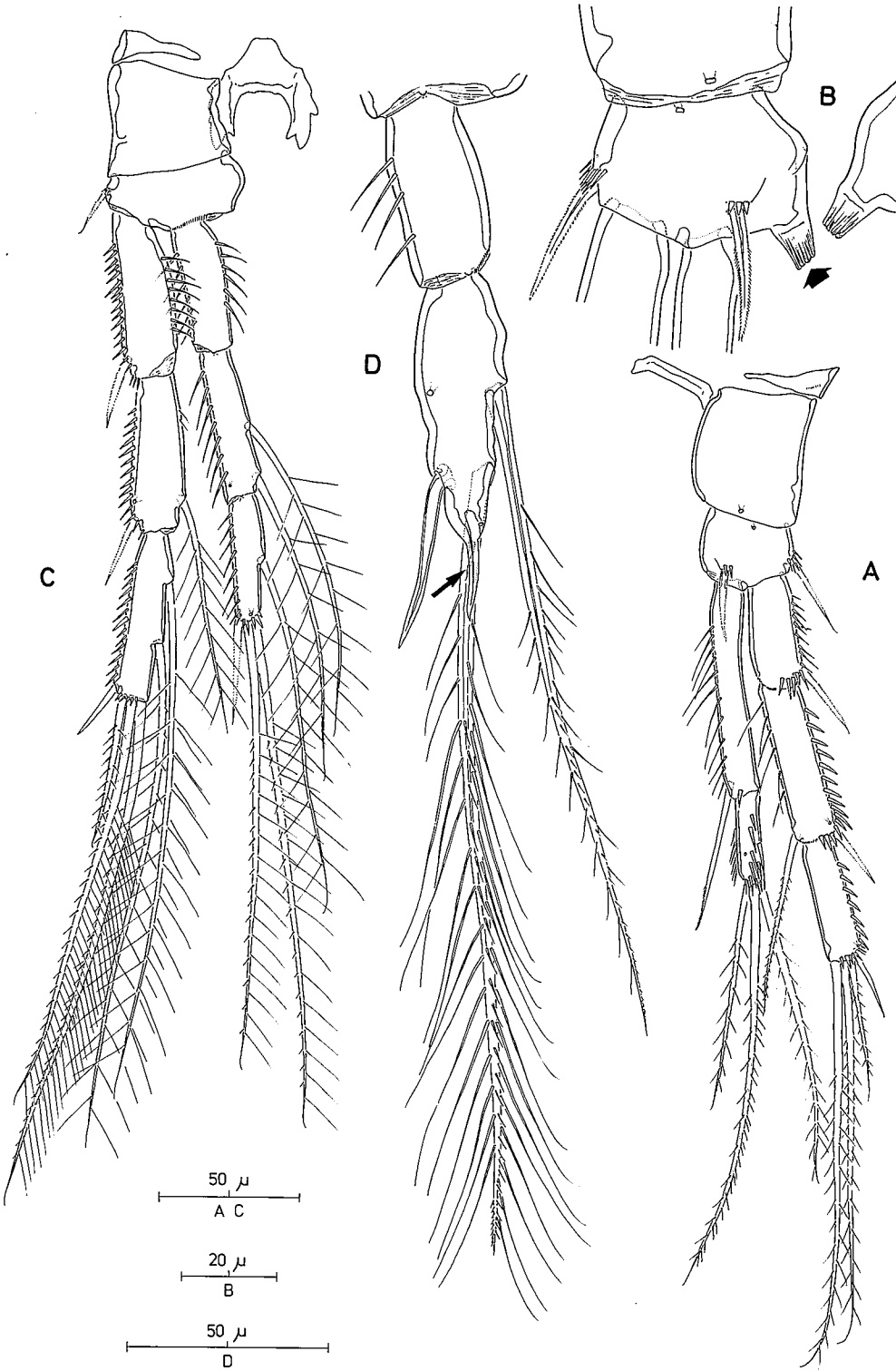

Fig. 26. *Distioculus minor* (T. Scott, 1894) comb. nov. Female. A. P1, anterior. C. P2, anterior. Male. B. P1 basis, anterior. (Inner process arrowed). D. P2 endopod, anterior. (Distal process arrowed).

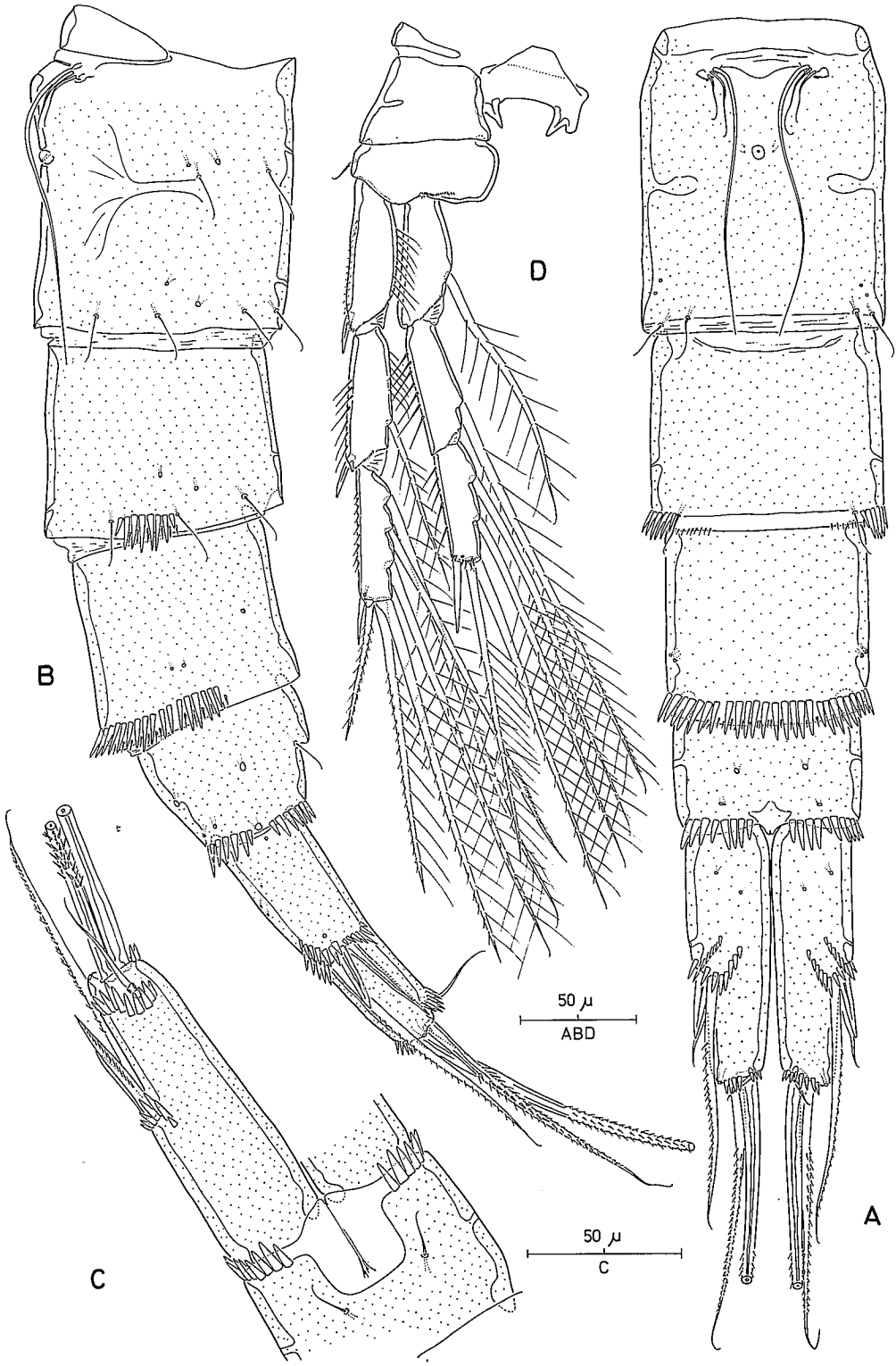

Fig. 27. *Distioculus minor* (T. Scott, 1894) comb. nov. Female. A. Urosome (excluding P5-bearing somite), ventral. B. Same, lateral. C. Anal somite and right caudal ramus, dorsal. D. P4, anterior.

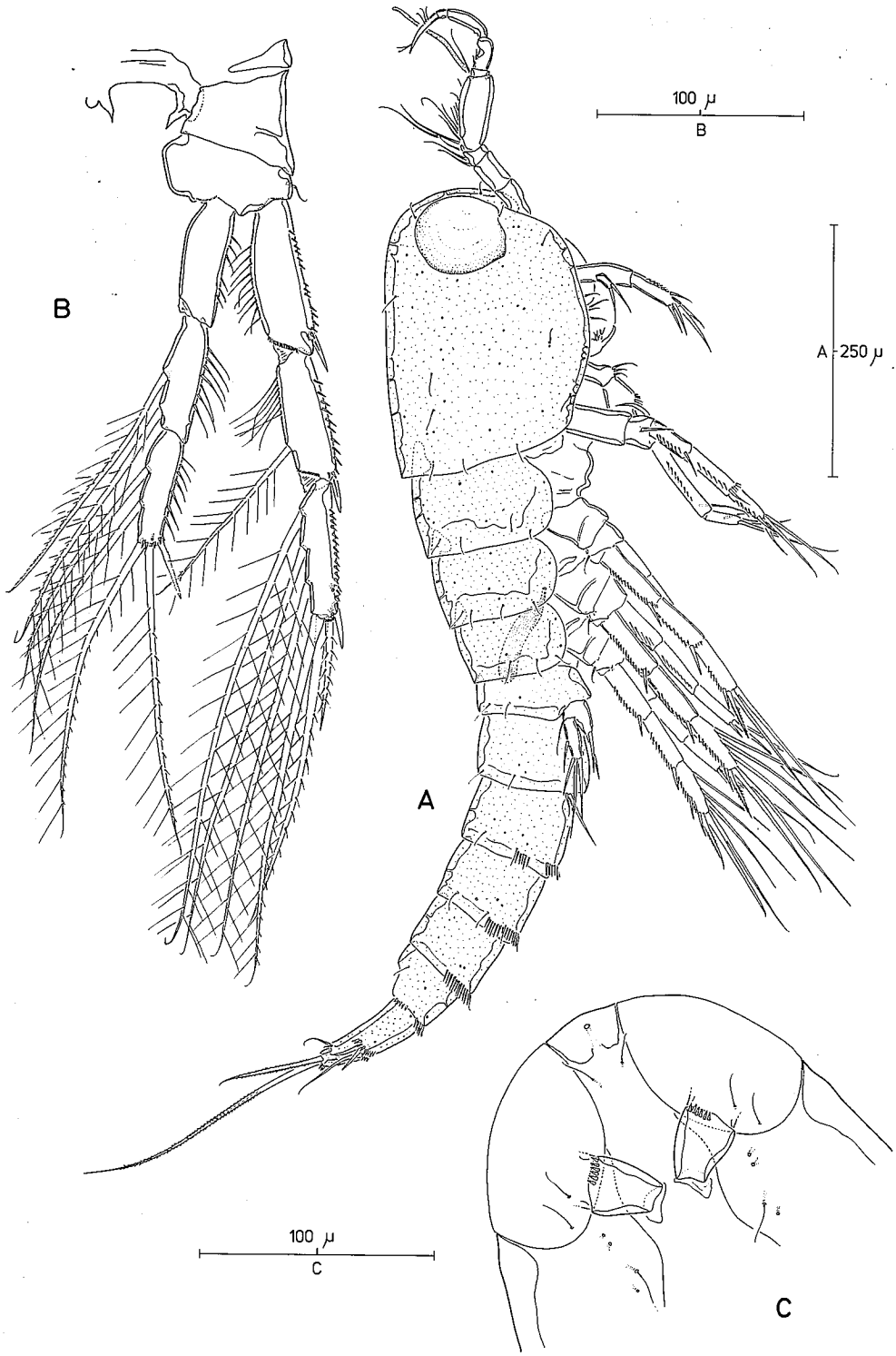

Fig. 28. *Distioculus minor* (T. Scott, 1894) comb. nov. Male. A. Habitus, lateral. Female. B. P3, anterior. C. Rostral area, frontal.

fused at base, multipinnate, the latter being the longest but distinctly shorter than urosome (Fig. 23); seta VI minute, outwardly directed; seta VII located near inner margin, small and bi-articulated at base.

Rostrum not discernible in dorsal aspect (Fig. 23A), minute, completely incorporated into ventral wall of cephalothorax (Fig. 28C).

Antennule (Fig. 24A) 8-segmented, segments 4 and 6 longest; all setae naked; segment 1 with spinular row and 1 slender seta distally; segment 2 with dorsal pore and 6 setae; segment 3 shortest, with 6 setae; segment 4 with 2 long setae, one which is fused to an aesthetasc (110 μm); segment 5 with 1 seta; segment 6 with 3 setae; segment 7 with 2 setae; segment 8 with 3 lateral setae and apex with 1 swollen seta and 2 simple setae fused to aesthetasc (50 μm).

Antenna (Fig. 25A). Coxa bare. Basis and proximal endopod segment incompletely fused to form allobasis; with few spinules midway along abexopodal margin. Exopod 1-segmented, curved; with 1 subapical and 1 apical pinnate spine; distal margin with spinular row. Endopod with spinules along inner and outer margins, 2 lateral setae and 5 pinnate setae around distal margin.

Mandible (Fig. 25B). Coxa with fine spinules on basal swelling near implantation of palp, and long setules at dorsal corner of gnathobase; gnathobase with 7 pointed teeth and several spinules. Palp minute, 1-segmented, with 1 pinnate seta apically.

Maxillule (Fig. 25C). Praecoxa with well developed, rectangular arthrite bearing minute armature elements; distal margin with 4 stubby, pinnate elements, 3 naked spines and 1 vestigial spine; anterior surface with rudimentary seta. Palp 1-segmented, distinct at base; with 1 naked and 1 pinnate seta distally, and 1 pinnate seta laterally.

Maxilla (Fig. 25D). Syncoxa large, with 2 cylindrical endites; proximal endite with 2 pinnate spines fused to endite, distal endite with 2 articulate spines (1 naked, 1 pinnate). Allobasis drawn out into strong, short pinnate claw; with 3 setae and 1 short pinnate spine.

Maxilliped (Fig. 25E–G). Subchelate. Syncoxa and basis joined in linear arrangement. Syncoxa with 3 pinnate setae near articulation with basis. Basis longer than syncoxa (Fig. 25E); with slightly concave inner margin and spinular row along outer margin; distal part with concavity delineated anteriorly by vestigial seta (arrowed in Fig. 25F, G) and integumental ridge (Fig. 25G), posteriorly by spinular row and second vestigial seta (Fig. 25F). Endopod represented by anteriorly recurved claw bearing 3 short accessory setae and fitting in basal concavity (Fig. 25F).

P1 (Fig. 26A). Praecoxa small. Basis with inner pinnate spine and outer pinnate seta. Exopod with inner seta on middle segment; exp-3 with 2 outer and 2 long apical setae. Endopod distinctly shorter than exopod; inner margin of enp-1 with long setules and serrate inner seta; enp-2 with numerous spinules and 3 setae.

P2–P4 (Figs 26C; 27D; 28B) with relatively narrow intercoxal sclerite bearing paired spinous processes; distal margin deeply concave. Praecoxae small. Basis with short, outer seta. P2–P3 enp-1 without inner seta. Middle inner seta of P4 exp-3 tripinnate. Seta and spine formula as in generic diagnosis.

P5 (Fig. 29C). Baseoendopod with outer basal seta and 3 pores; endopodal lobe well developed, with 4 setae, second inner one extremely long. Exopod with 5 spines/setae and 2 pores; all armature elements pinnate.

Genital apertures fused, covered by vestigial sixth legs (Fig. 27A) bearing 1 short outer and 1 middle setae, and very long inner seta. Copulatory pore minute, flanked by 2 secretory pores on either side; seminal receptacle trilobate.

Male. – Body length 770–920 μm (n = 7; x = 845 μm) measured from anterior margin of cephalothorax to posterior rim of caudal rami.

Antennule (Fig. 24B–D) 10-segmented, haplocer; geniculation between segments 7 and 8. Segment 1 with spinular row and 1 naked seta; segment 2 with dorsal pore and 8 naked setae; segment 3 with 6 naked setae (Fig. 24C); segment 4 minute, U-shaped sclerite, with 2 naked setae (Fig. 24C); segment 5 longest, slightly swollen, with 6 setae along anterior margin (distal 2 minute) and 1 seta plus aesthetasc (90 μm) on distal process; segment 6 with 1 vestigial and 1 pinnate seta; segment 7 with spinular patch, 1 vestigial seta, 1 naked seta, and 2 modified spines (Fig. 24D); segment 8 with 3 modified spines and 1 distal seta (Fig. 24D); segment 9 with 2 minute setae; distal segment drawn out into short spinous process, with 3 lateral setae and 3 small setae plus an aesthetasc apically (15 μm). Modified spines on segments 7 and 8 with minute pore (Fig. 24D).

P1 basis (Fig. 26B). Inner margin enlarged, forming truncate process at inner distal corner (arrowed in Fig. 26B); process with longitudinal striations and marked at base by transverse superficial groove.

P2 endopod (Fig. 26D) 2-segmented. Enp-1 slightly shorter than in female, without inner seta. Enp-2 attenuated distally, produced into spinous process derived from outer apical seta; proximal half with tripinnate inner seta; distal half with plu-

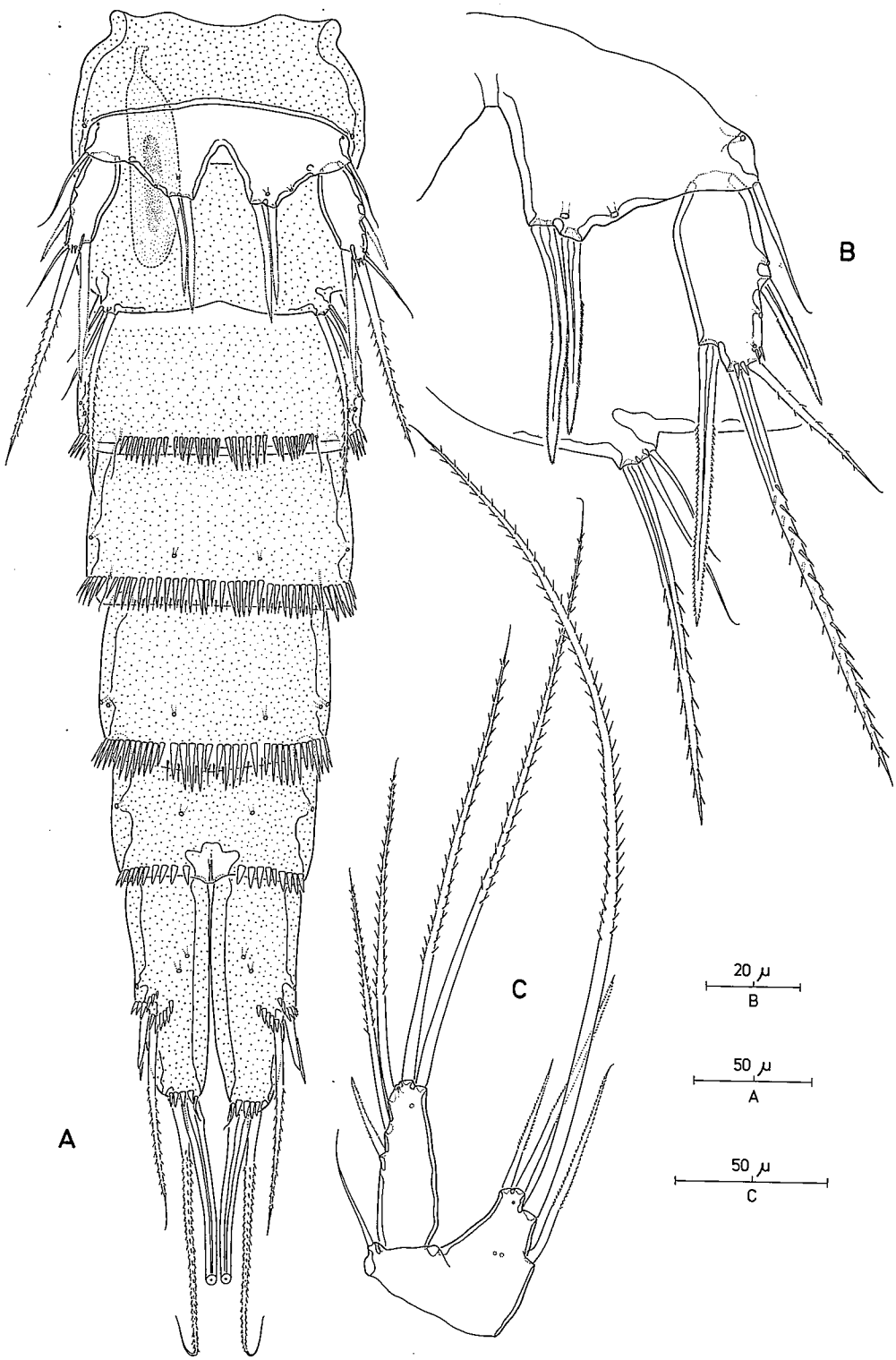

Fig. 29. *Distioculus minor* (T. Scott, 1894) comb. nov. Male. A. Urosome, ventral. B. Left P5 and P6, anterior. Female. C. P5, anterior.

mose inner seta, stout outer spine and minute seta at the apex (arrowed in Fig. 26D).

Fifth pair of legs fused medially (Fig. 29A, B); baseoendopod with 3 pores, endopodal lobe with 2 distal spines; exopod without spinules along inner margin, with 3 lateral pores, 1 inner, 1 outer and 2 apical setae/spines.

Sixth pair of legs (Fig. 29A, B) symmetrical; fused to somite; distal outer corner with 1 long pinnate and 2 short naked setae.

Postgenital somites (Fig. 29A) with spinular rows at ventral posterior margin. Ventral margin of urosomites 4 and 5 also with accessory row of tiny spinules.

Remarks. BOXSHALL (1979) re-examined the syntypes of *D. minor* and pointed out the confusion in the literature over the armature of the P5 in both sexes. This confusion mainly arose because of deficiencies in T. SCOTT's (1894) original description and the subsequent duplication of these mistakes by most authors who redrew their illustrations from A. SCOTT rather than from MRÁZEK's (1895; as *M. gracilis*) or GIESBRECHT's (1895) excellent redescriptions. WILSON's (1932) description of *Macrosetella oculata* (= *O. gracilis*) is based on copepodid V stages of *D. minor* comb. nov.

The sexual dimorphism in the maxilliped noted by T. SCOTT (1894) and adopted in some later papers (e.g. WELLS 1970) could not be confirmed by GIESBRECHT (1895) nor by our own observations.

BIOLOGY

Reproduction

BJÖRNBERG (1965) conducted rearing experiments with *Macrosetella gracilis, Oculosetella gracilis* and *Miracia efferata*, but did not observe the actual mating process. During the precopulatory phase males of *M. efferata* grasp the long terminal setae of the female's caudal rami (J. O'Neil pers. commn) and the same mate guarding posture has been reported for *M. gracilis* (BJÖRNBERG 1965).

The female reproductive system in *M. efferata* is paired along its entire course (CLAUS 1891) and examination of *M. gracilis* and *O. gracilis* has revealed a similar arrangement. The paired ovaries lie dorsal to the digestive tract in the middle part of the prosome, immediately posterior to the eyes. They are connected with the paired genital antra via paired oviducts which enter the genital doublesomite ventrally. The genital antra open to the exterior via a common median gonopore. The seminal receptacle is unpaired and typically trilobate by the presence of lateral diverticula. Spermatozoa are introduced via a small, median copulatory pore and a short midventral copulatory duct. During mating only one spermatophore is discharged at a time.

The male reproductive system is asymmetrical and developed either sinistrally or dextrally. The single testis is recurved in the posterior half of the cephalothorax and connected with the only functional gonopore (left or right) via a single vas deferens.

Females of all miraciid genera produce paired egg-sacs but this has rarely been reported in the literature. WILSON's (1932) statement that there is only one egg-sac in *Macrosetella* is contradicted by KRISHNASWAMY (1951) and our own observations. Both BRADY (1883) and MRÁZEK (1895) also figure only one egg-sac in *M. efferata*, but CLAUS (1891) and WHEELER (1901) clearly show two. The presence of paired egg-sacs is not widespread in the Harpacticoida. It is a diagnostic character for the benthic families Canuellidae and Diosaccidae and a few isolated cases in the Cylindropsyllidae and Huntemanniidae, however in all other planktonic harpacticoids a single median egg-sac is the rule.

Egg-sacs are typically biseriate, however, eggs can also be packed in a uniseriate arrangement when their number is sufficiently low. Freshly fertilized eggs are dark blue in all species, but their colour changes to red, orange or black as they mature (WILSON 1932; KRISHNASWAMY 1951; BJÖRNBERG 1965). The number of eggs per sac is usually low. In *O. gracilis* and *D. minor* each egg-sac typically contains 4 eggs (GIESBRECHT 1895; present account), and a similar number (4–6) is commonly found in *M. efferata*. Egg numbers, however, seem to be positively correlated with body size. Females of Red Sea *D. minor* for instance were distinctly smaller (0.7 mm) and usually had only 2 eggs per sac. In large Red Sea *M. gracilis* females an average of 8 eggs per sac were found with a range between 6 and 11. On average 6 eggs per sac (range: 3–8) were counted in the small females. The wide range in egg number, and the slight differences often observed between sacs of a single individual, result from the fact that nauplii are not hatching simultaneously. Eclosion usually starts first at the distal end of the egg-sac with the nauplii creeping forwards on the sac until they reach the female's fourth swimming legs. In *D. minor*, however, we observed several females, which had the proximal nauplii hatching first. In a single case in the Bahamas (J.M. O'Neil pers. commn.) observed an ovigerous female of *M. gracilis* actually removing all the eggs from the body and 'glueing' them to a colony of *T. thiebautii*. The female then swam around holding onto the colony until all the nauplii hatched (not simultaneously!) and started moving

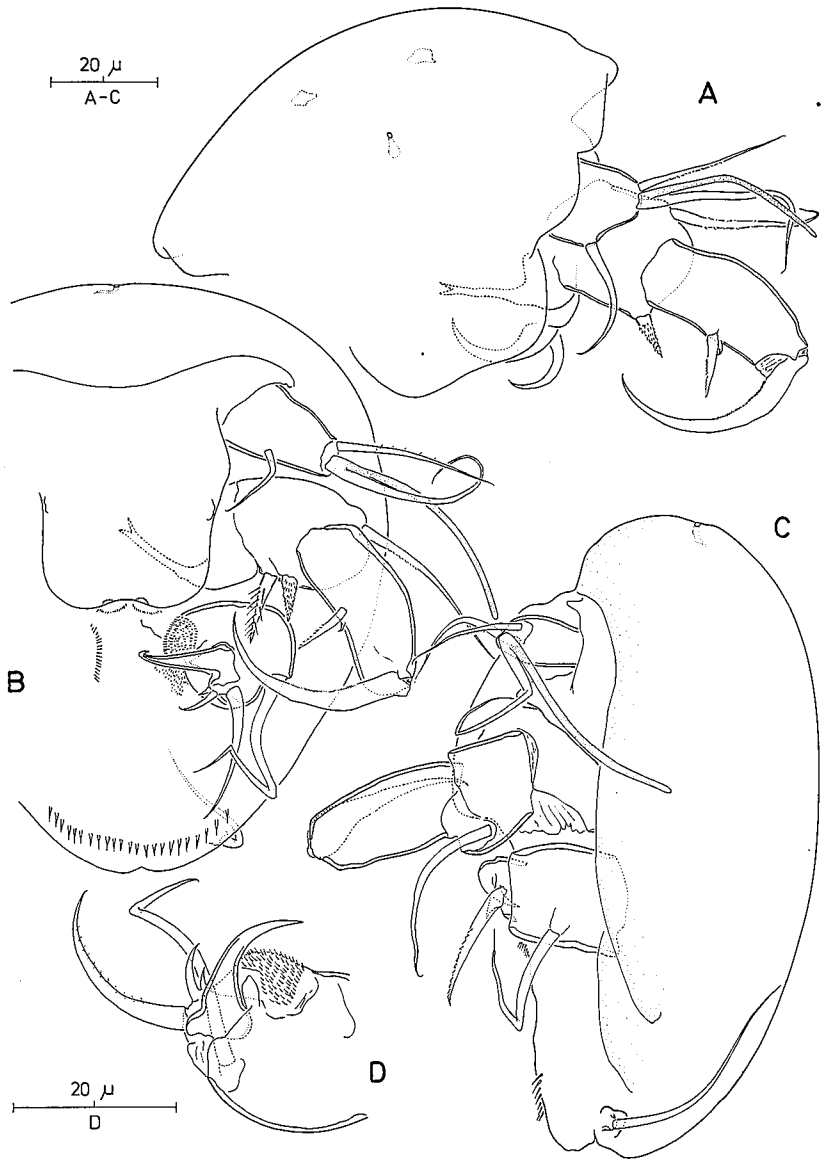

Fig. 30. *Macrosetella gracilis* (DANA, 1847). Nauplius I. A. Frontal view. B. Ventral view. C. Lateral view. D. Mandible, anterior.

about the small tufted colony, crawling up and down the trichomes. Occasionally, when no *Trichodesmium* is present, nauplii utilize the female's caudal rami and setae as a facultative, temporary substrate (J.M. O'Neil pers. commn.).

Naupliar development

The development of miraciid harpacticoids has been the subject of a considerable number of papers. No information is available for *D. minor* or *O. gracilis*, however, at least seven papers provide illustrations of one or several naupliar stages of *M. gracilis*. Unfortunately, the majority of these descriptions is largely deficient, lacking in detail, and in some cases based on the wrong instars.

The complete naupliar development has been described only for *M. gracilis* (KRISHNASWAMY 1951). Though some papers make no mention of the number of naupliar instars (BJÖRNBERG 1965), it is clear that the miraciids, like all other harpacti-

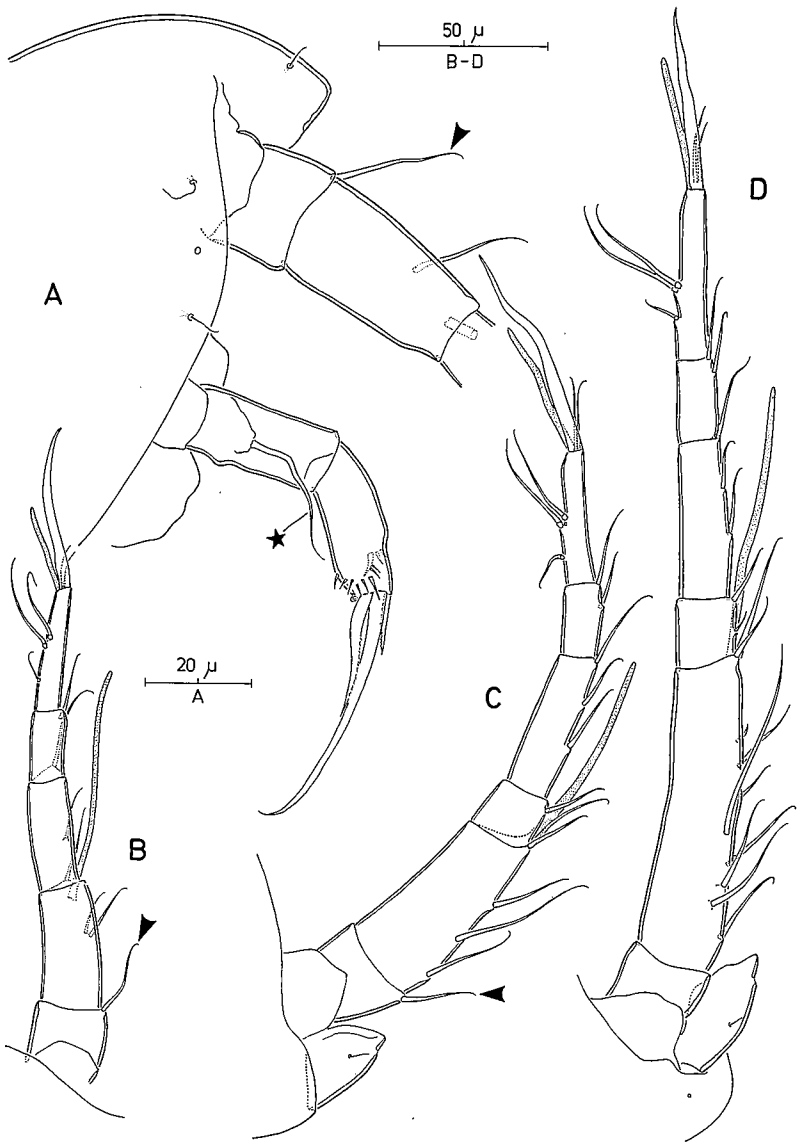

Fig. 31. *Macrosetella gracilis* (DANA, 1847). A. Copepodid I, anterior part of cephalothorax (asterisk indicating vestigial exopod). B. Copepodid I, antennule. C. Copepodid II, antennule. D. Copepodid III, antennule (seta on segment 1 arrowed in A-C).

coids, have six naupliar stages (KRISHNASWAMY 1949, 1951; DAHMS 1990). TOKIOKA & BIERI (1966) maintain that there are only five naupliar stages in *M. gracilis*. Comparison of their fifth stage with DAHMS' (1990) excellent illustration of the last nauplius proves that they were actually dealing with nauplius VI and one of the intermediate stages was overlooked. The sudden increase in size (from 330 to 815 µm) mentioned in KRISHNASWAMY's (1951) text description is undoubtedly a slip of the pen since it contradicts his table 2 and the author's previous measurements published in 1949.

The present description of the first nauplius of *M. gracilis* (Fig. 30A–D) agrees well with previous illustrations given by BJÖRNBERG (1965) and TOKIOKA & BIERI (1966), and as already presumed by DAHMS (1990) reinforces the presence of the antennary gnathobase from this stage onwards. This is in conflict with KRISHNASWAMY's (1951) view that the nauplii are non-feeding.

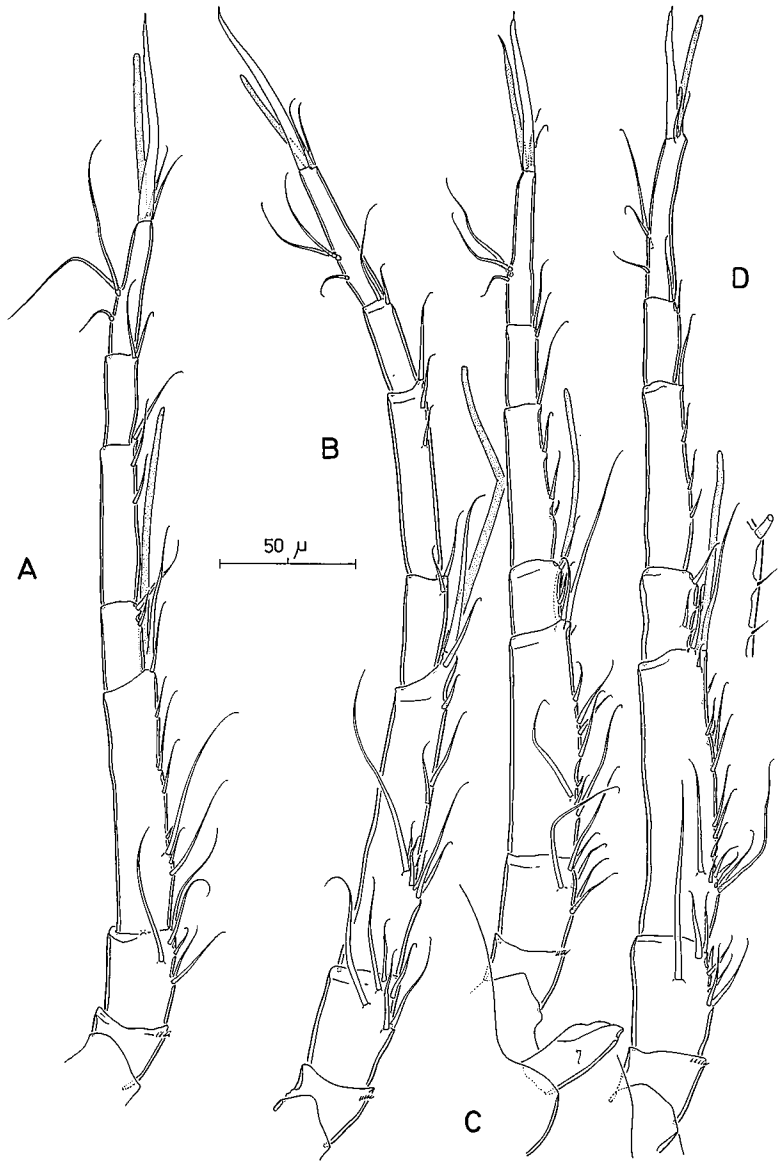

Fig. 32. *Macrosetella gracilis* (DANA, 1847). A. Copepodid IV♀, antennule. B. Copepodid V♀, antennule. C. Copepodid IV♂, antennule. D. Copepodid V♂, antennule (inset: anterior margin of segment 4).

BJÖRNBERG's (1965) detailed illustrations of the first, third and sixth nauplius of *M. efferata* were subsequently redrawn by SAZHINA (1986). In a previous paper SAZHINA (1982) also figured the sixth nauplius but this drawing is somewhat more difficult to interpret.

Copepodid development

The only information on the copepodids of *M. efferata* is given by KRISHNASWAMY (1950) whose sole figure of a CII stage in fact represents a first copepodid. Some authors (KRISHNASWAMY 1949, 1951; BJÖRNBERG 1965; TOKIOKA & BIERI 1966) report on the copepodid development of *M. gracilis* but their descriptions lack in detail and are of little help in deciding on the identity of the stages. No information is available on the copepodids of *O. gracilis* or *D. minor*.

We have not attempted to describe all copepodid stages of *M. gracilis* in detail. Instead, attention has

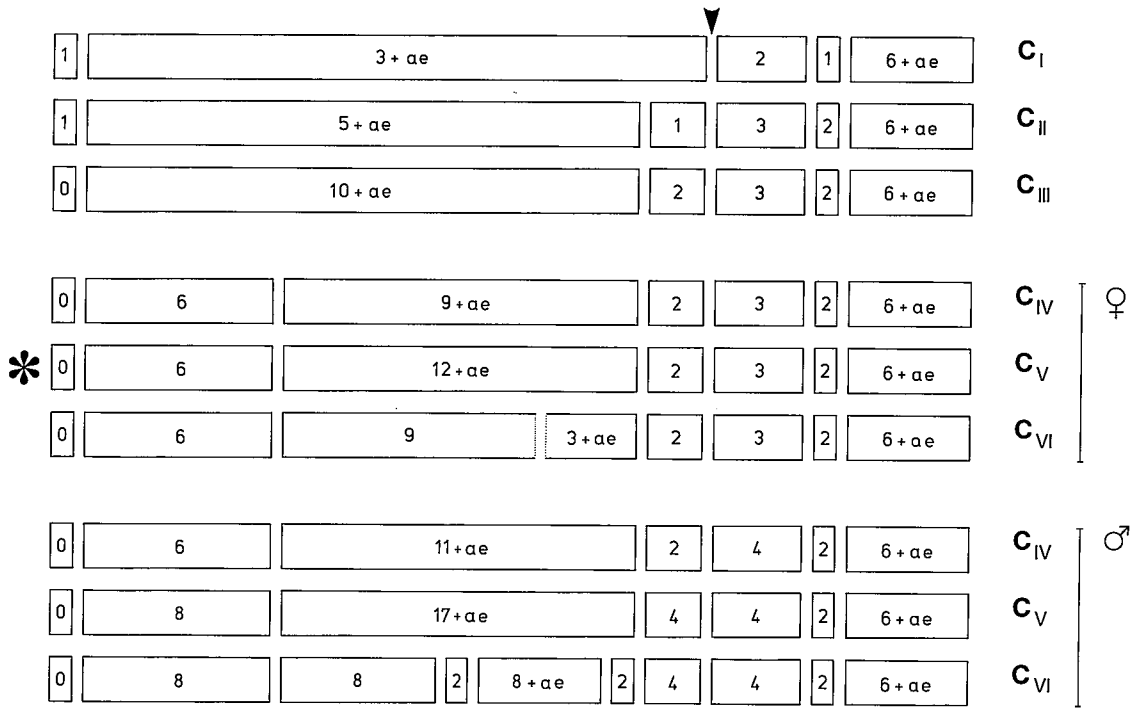

Fig. 33. *Macrosetella gracilis* (DANA, 1847). Diagram depicting segmentary homologies of antennules during copepodid development (arrow indicating position of geniculation. Asterisk denoting condition found in adult ♀ of *Oculosetella gracilis*).

been focussed on characters that undergo important changes during the copepodid phase or might provide some insights into the phylogenetic relationships in the family.

Antennules. The complete antennule development in *M. gracilis* copepodids is illustrated in Figs 31–32. A schematic comparison of segmental homologies during copepodid development is presented for both sexes in Fig. 33. Previous descriptions of the complete developmental sequence have been published by KRISHNASWAMY (1951) and DAHMS (1989). TOKIOKA & BIERI's (1966) figure of the antennule of CI contains several errors in the setal counts and is not considered any further.

KRISHNASWAMY's (1951) illustrations are grossly inadequate in various aspects such as the setation of the individual segments and the sexual dimorphism in CIV–CV. KRISHNASWAMY also failed to recognize the 6-segmented condition in CII-CIII since his description of the antennules in these stages is almost certainly based on a CI instar.

DAHMS' (1989) excellent description, also being based on material from the Red Sea, largely agrees with our observations, however differs in some of the setal counts (Fig. 33). In addition, DAHMS did not detect any sexual dimorphism prior to CV, whereas our study revealed that male CIV have 3 extra setae as opposed to the female, i.e. 2 on segment 3 and 1 on segment 5. This suggests that DAHMS' (1989) illustration of the CIV antennule was drawn from a male specimen.

The absence of the anterior seta on the first segment in adult *Macrosetella* and *Oculosetella* is an unusual character further being found in only very few harpacticoids such as the Hamondiidae and Ambunguipedidae (HUYS 1990a). As DAHMS (1989, 1991) pointed out this seta is present in the early copepodids but is lost at the moult from CII to CIII. In the more primitive genera *Miracia* and *Distioculus* it is still retained in all stages, including the adult. DAHMS (1991) maintained that this seta is replaced by a spinular row which is subsequently lost at CIV, however in this study we found this spinular row to persist in all later copepodids and adults of both sexes (Figs 18A–C; 32). The loss of one of the setae on segment 2 at the terminal moult towards the adult female (DAHMS 1989) could not be confirmed.

Comparison of the antennule development in *M. gracilis* with the adult female antennule in *Oculosetella* offers an explanation for the 7-segmented con-

dition in the latter. The segmental pattern and precise setal counts are completely identical in the adult female of *O. gracilis* and the CV♀ of *M. gracilis* (Fig. 33). Despite the absence of any information on the copepodids of *Oculosetella* this strongly suggests that the 7-segmented condition is due to heterochrony (neoteny) at the definitive moult rather than being the result of the formation of a compound third segment through secondary fusion of ancestral segments 3 and 4.

Other cephalic appendages. With the exception of the antenna, the other cephalic appendages undergo only minor structural changes during copepodid development. The maxillule, maxilla and maxilliped already have the full complement of armature elements at CI and only alterations in size and spinule ornamentation could be observed. The mandible takes its adult facies from CII onwards. At CI the palp is a larger, amorphous, membranous segment with a distal pinnate seta and several minor spinous processes along the inner margin (Fig. 36C). This degeneration resembles the condition found in other copepod orders such as the Poecilostomatoida and Cyclopoida where the mandibular palp is well developed in the nauplius phase and passes through a similar amorphous stage at CI before it is further reduced to a remnant or vanishes completely in the next copepodid stage.

The antenna in *Miracia* and *Distioculus* gen. nov. displays a well developed 1-segmented, bisetose exopod. Adults of *Oculosetella* and *Macrosetella* lack any trace of an exopod except for a small, circular area on the allobasis where the cuticle is thinner (arrowed in Figs 10B and 19B). Examination of this site in copepodid I stages of *M. gracilis* revealed a small, tubercular process bearing a long naked seta (Fig. 31A), which was overlooked in earlier descriptions of this stage (KRISHNASWAMY 1950; TOKIOKA & BIERI 1966). The subsequent loss of this knob leaving a membranous scar from copepodid II onwards is a synapomorphy for *Oculosetella* and *Macrosetella*.

A similar scar that persists in the adult antenna is found in members of the Cristacoxidae (HUYS 1990b). Recently, FERRARI (1993; based on unpublished data of F. Fiers) reported the presence of a small, unisetose segment at the position of the exopod in the copepodid I of *Noodtorthopsyllus* sp. and stated that the segment '... is absent in all later copepodids but the seta is retained'. The persistence of this seta throughout development is, however, doubtful since no setae can be found on the allobasis in the adult, suggesting that the entire exopod is lost at copepodid II. The developmental sequence of the antennary exopod is therefore identical in the Cristacoxidae and *Oculosetella-Macrosetella* and might be explained by a similar genetic mechanism. FERRARI (1993) suggested a simple genetic hypothesis in which a gene repressing system acts on a gene complex capable of developing an antenna with or without an exopod. Repression at copepodid II would explain the developmental pattern in *Oculosetella* and *Macrosetella* and in the Cristacoxidae. Such a mechanism could also be invoked to explain the loss of the antennary exopod in the Poecilostomatoida (see e.g. IZAWA 1986), however, contrary to FERRARI (1993), mere repression would not account for the condition in the Cyclopoida. In adults of primitive cyclopinids such as *Cyclopicina longifurcata*, the exopod is retained as a small process bearing 3 long setae (HUYS & BOXSHALL 1990), and in the Notodelphyidae, Oithonidae, Mantridae, and Speleoithonidae it is usually represented by 2 setae. This suggests that at least in these families phenotypic expression of the exopod was never completely suppressed during development and instead a different mechanism is involved. In contrast to the Poecilostomatoida and the harpacticoids mentioned above, the exopod in cyclopoids at copepodid I is usually a large, amorphous structure without distinct setae, often exceeding the endopod in size as in *Pygodelphys aquilonaris* (DUDLEY 1966). At copepodid II the entire ramus is reduced and replaced by 2 long setae implanted on a minute knob, a condition that persists in the adult.

Thoracopods P1 – P2. The male modification of the P1 basis is first noticeable as a slight swelling along the inner margin in CIII. This area gradually becomes more chitinized and elaborate in the later copepodids until it attains its full size and shape as in Fig. 11C.

All miraciids display sexual dimorphism on the P2 endopod. The ontogeny of this ramus during the copepodid phase is illustrated for both sexes in Fig. 34. Sexual dimorphism becomes apparent at CIV when the female acquires an extra inner seta on the distal segment (Fig. 34D–F) which is also distinctly longer than in the CIV♂. Male Miraciidae typically have one seta less than females. Examination of intermoult stages unequivocally revealed that it is the proximal inner seta of the middle endopod segment of the female that is missing. The transformation of the male endopod during later copepodid development involves the reduction of the 2 terminal setae. The outer terminal seta is reduced to a spine at CV (Fig. 34G) whereas CV intermoult stages (Fig. 34H) clearly illustrate that the inner

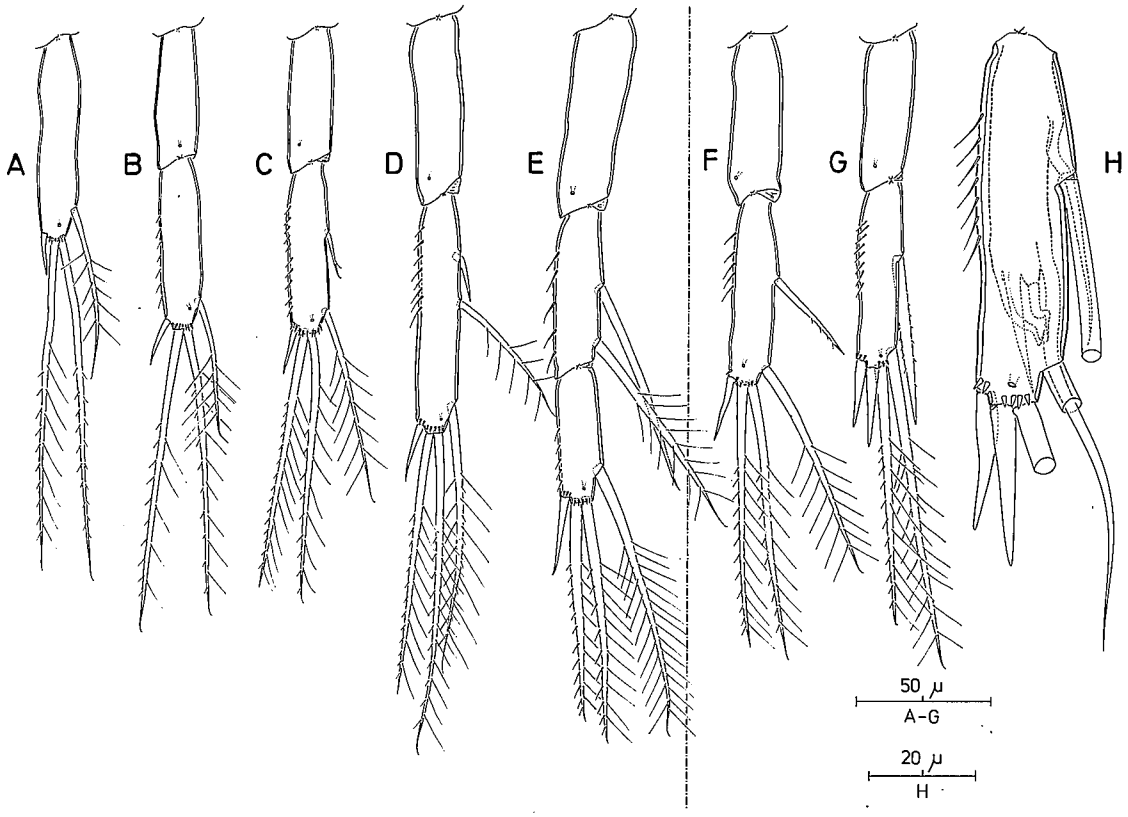

Fig. 34. *Macrosetella gracilis* (DANA, 1847). Development of P2 endopod in ♀ (A–E: copepodid I–V) and ♂ (A–C, F–G: copepodid I–V). H. Copepodid V♂, distal endopod segment, showing intermoult stage towards adult condition.

terminal seta undergoes similar reduction at the final moult (Fig. 21F, G). It is at this stage of the development that the outer spine becomes modified and the outer terminal spine is fully incorporated into the segment (Fig. 21F, G).

Caudal rami. The development of the caudal ramus in *M. gracilis* is puzzling. DAHMS (1993) pointed out the difference between the separate terminal setae at CI of *M. efferata* (cf. BJÖRNBERG 1965) and the fused branched seta-complex at the same stage in *M. gracilis*. Such a seta-complex is found at copepodid I in a wide range of families, and is assumed to be the common precursor of both terminal setae IV and V (DAHMS 1993). In the majority of these harpacticoids the branched seta-complex unfuses at the moult from CI to CII, but in a number of them such as some representatives of the Ectinosomatidae, Tetragonicipitidae and nearly all Laophontidae and Ancorabolidae the branched condition persists during the entire copepodid phase including the adult. In *M. gracilis* all copepodid stages including the adult also possess a similar branched seta (Figs 20A–C; 35; 36).

Through comparison of a wide range of species DAHMS (1993) illustrated the origin and fate of the three terminal setae IV, V and VI in harpacticoids that have a branched seta-complex at CI. DAHMS (1993) proposed that the branched seta of CI completely splits up to its base forming the two separate principal setae IV and V at CII. None of the branches undergoes reduction in size during this moult. Simultaneously, the terminal accessory seta VI shifts from the subdistal, posteromedial protuberance in CI to the inner distal corner (its final position), and the long setae IV and V shift outwards to fill the medial gap of the posterior margin usually found in CI.

In CI stages of *M. gracilis* there is no medial gap at the posterior margin of the caudal ramus, and none of the three terminal setae (if the branches of the seta-complex are counted as two prospective setae) is in a subdistal position (Fig. 35A, B). The outer distal seta is well developed, pinnate and originating from the same position as seta IV in the adult. The branched seta-complex consists of a short outer branch and a long inner branch, and is positioned in exactly the same plane as the outer distal

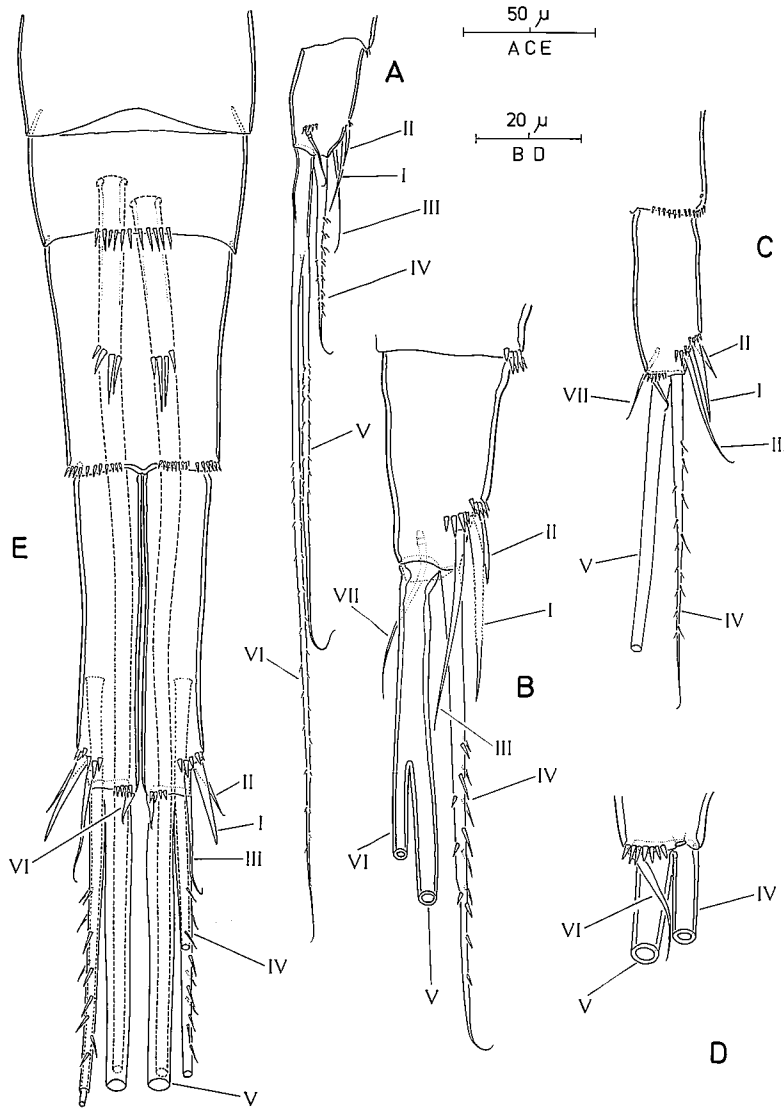

Fig. 35. *Macrosetella gracilis* (DANA, 1847). A. Copepodid I, caudal ramus (dorsal view). B. Same (ventral view). C. Copepodid II, caudal ramus (ventral view). D. Same, ventral posterior margin. E. Copepodid IV♂, urosome (ventral view), showing intermoult stage towards copepodid V.

seta. According to DAHMS (1993) the latter seta will assume a position at the inner distal corner during the moult to CII. In most harpacticoids this is achieved by minor displacement from a previous median, subdistal position, however, in *M. gracilis* this shift would require a much more significant 180° swap with the branched seta-complex.

Comparison with CII (Fig. 35C, D) suggests an alternative developmental scenario. The outer distal seta in CII is identical in ornamentation, position and relative size to its equivalent in CI (Fig. 35A), suggesting that no shifting of terminal setae has taken place. This seta is regarded as homologous with the outer terminal seta in the adult and is denoted IV in Fig. 35C. The branched seta-complex at CI therefore is regarded here as representing the fused setae V and VI which separate at the next moult (Fig. 35C, D). The very long, pinnate, inner branch corresponds to the terminal accessory seta VI and undergoes extreme reduction in size at the moult to CII (Fig. 35C, D). At the latter stage it is represented by a short, outwardly directed, naked

seta at the inner distal corner (Fig. 35D). Further reduction towards the adult stage will diminish it to a setule fused to the posterior margin of the ramus (Fig. 16D). The shorter outer branch representing the inner terminal seta V undergoes a considerable increase in length whereby it becomes the principal seta of the ramus at CII. During this moult it fuses at the base to the outer terminal seta IV to form a *de novo* branched seta-complex.

This scenario does not require any setal displacement around the rear margin of the caudal ramus but is more complicated since it involves two major events condensed in a single moult: (1) unfusion of an existing branch complex and immediate formation of a new, non-homologous one, (2) gross reduction of the longest seta (branch) of CI and its replacement as principal seta through simultaneous elongation of another seta. In the absence of sound evidence this scenario would clearly be less favourable than DAHMS' (1993) proposal.

One reliable technique to trace homologies of armature elements vertically throughout ontogeny is the study of intermoult stages, particularly when newly formed elements are still in the exoskeletal sheaths of their precursors (HUYS & BOXSHALL 1991). If the branched seta-complex at CII and later stages is homologous to the one present at CI (i.e. if the former is the result of a neotenic event), then one would have to assume an identical origin. In the case of *M. gracilis* the evidence to reject such an identical origin is twofold.

First, examination of the CI intermoult stage revealed that the principal seta in CII is derived from the outer branch of the seta complex (Fig. 36A, B). Its precursor can be traced inside the old cuticle from the tip of the branch all the way up to the anterior margin of the urosome, foreshadowing the gross increase in length at the next moult. The long inner branch becomes obsolete since no major precursor can be detected inside. Instead, it will be replaced by a small seta whose Anlage can be discerned at the inner distal corner of the prospective ramus (denoted VI* in Fig. 36B). The outer distal seta also contains its precursor which is slightly longer. The intermoult clearly demonstrates that no shifting of terminal setae takes place and the components of the existing seta complex give rise to two separate setae.

Second, DAHMS (1992) examined the intermoult NVI instar of *Amonardia normani* (Diosaccidae) in detail and illustrated how at the metamorphic moult the principal bifid seta in the latter gives rise to the branched seta-complex in CI. Examination of later intermoult copepodids (II–V) of *M. gracilis* revealed that the seta-complex is not derived from such a branched precursor but that its constituent branches originate from completely separate Anlagen (Fig. 35E). The fusion in *M. gracilis* must therefore be a secondary process that happens at every moult during the copepodid phase. The exact timing is difficult to determine, but fusion probably takes place when the moult is nearing completion. The branched seta-complex retained in adult *M. gracilis* (though representing the same fused setae IV and V) is therefore not homologous with the seta-complex at CI in *A. normani* (or *M. gracilis*), or at later stages in those harpacticoids where it persists through neoteny. The third scenario that seta V is a bifid seta at CI and seta VI newly appears at the moult to CII is extremely unlikely since the latter seta is always present in the CI of harpacticoids, if not already in the late naupliar phase (DAHMS 1993).

The functional significance of the extremely long seta VI in CI is unknown but is probably related to the change in lifestyle from an intimate association with a filamentous substrate as nauplius to a looser relationship with the same substrate as copepodid I. Upon metamorphosis the locomotory tagma is not yet well developed and the antennules are still relatively short in comparison to early copepodids of calanoids and cyclopoids. It is possible that the branched seta-complex performs a role as balancer or prevents the copepodids from rapid sinking.

DAHMS (1993) recognized two major patterns of caudal ramus development but it is obvious that deviations occur in certain groups. One variation on the theme is the combined process of initial separation of setae and their subsequent re-fusion at a later stage in the copepodid phase. The latter takes place early on in development in *M. gracilis*, but HUYS (1992) recently showed that a similar fusion can also be acquired at the final moult towards the adult as in *Psammastacus confluens* (Leptastacidae).

Association with colonial cyanobacteria

The essentially tropical and subtropical occurrence of the Miraciidae is clearly paralleled by the distribution pattern of several filamentous colonial cyanophytes, collectively referred to under the genus name *Trichodesmium* (= formerly marine *Oscillatoria* species complex). These pelagic colonies act as a physical substrate for a diverse group of associated organisms, ranging in size from bacteria and diatoms up to copepods (O'NEIL & ROMAN 1992). Copepods are a common associate of *Trichodesmium* blooms. BOWMAN & LANCASTER (1965) found cyclopoid and harpacticoid copepods (belonging to non-pelagic genera) to be the only organisms asso-

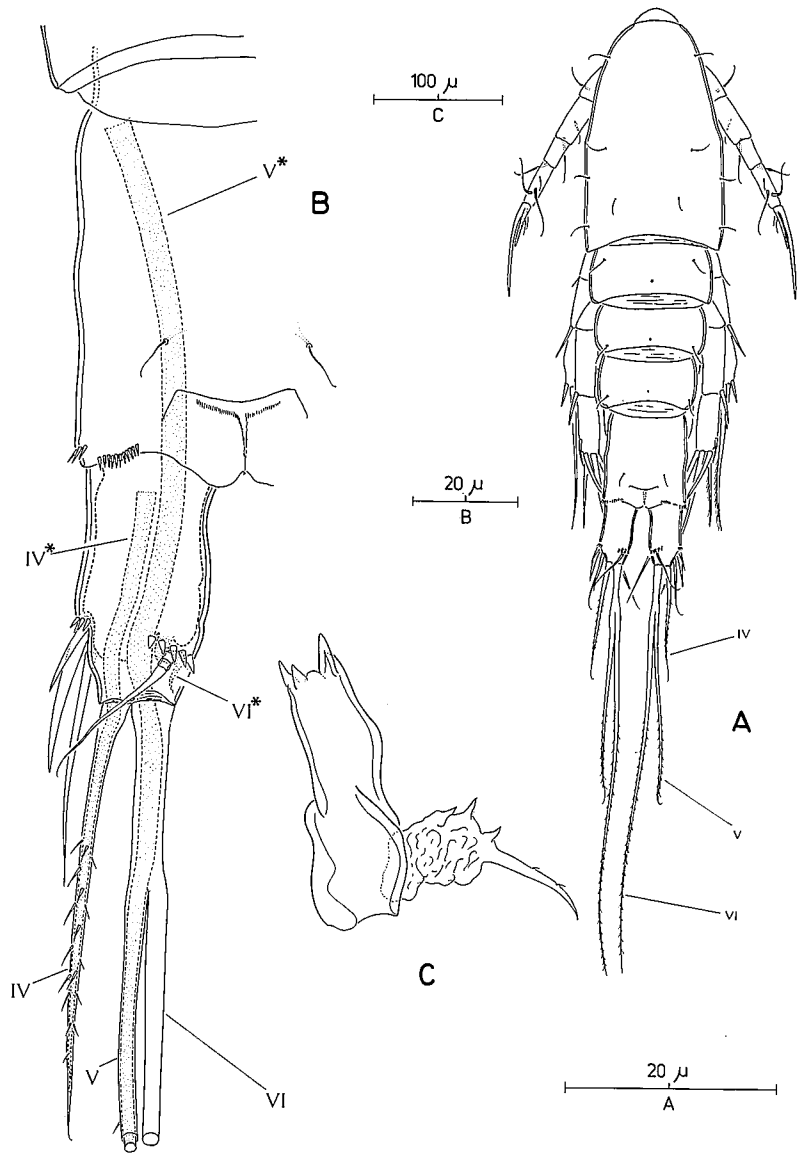

Fig. 36. *Macrosetella gracilis* (DANA, 1847). A. Copepodid I, dorsal. B. Anal somite and right caudal ramus of copepodid I intermoult (asterisks indicating precursors). C. Copepodid I, mandible.

ciated with a bloom in the Tonga Islands, whilst for other bloom samples they stated that calanoid copepods (mostly species of *Acartia* and *Paracalanus*) represented the dominant faunal element. A similar prevalence of copepods was observed in *Trichodesmium* blooms in the eastern Arabian Sea (DEVASSY & al. 1978; NAIR & al. 1980), though pteropods and the cladoceran *Evadne* sp. were also common. A brief summary of the *Trichodesmium*-zooplankton interactions is given by SELLNER (1992).

Trichodesmium as a physical substrate. The intimate association between *M. gracilis* and *Trichodesmium* was first observed by KRISHNASWAMY (1949) who found the nauplii and early copepodid stages clinging to floating *Trichodesmium* filaments in the Madras plankton. In a later report, describing all naupliar and copepodid stages, KRISHNASWAMY (1951) pointed out some of the morphological peculiarities of the juveniles and suspected them to be adaptations to life associated with a pelagic substrate.

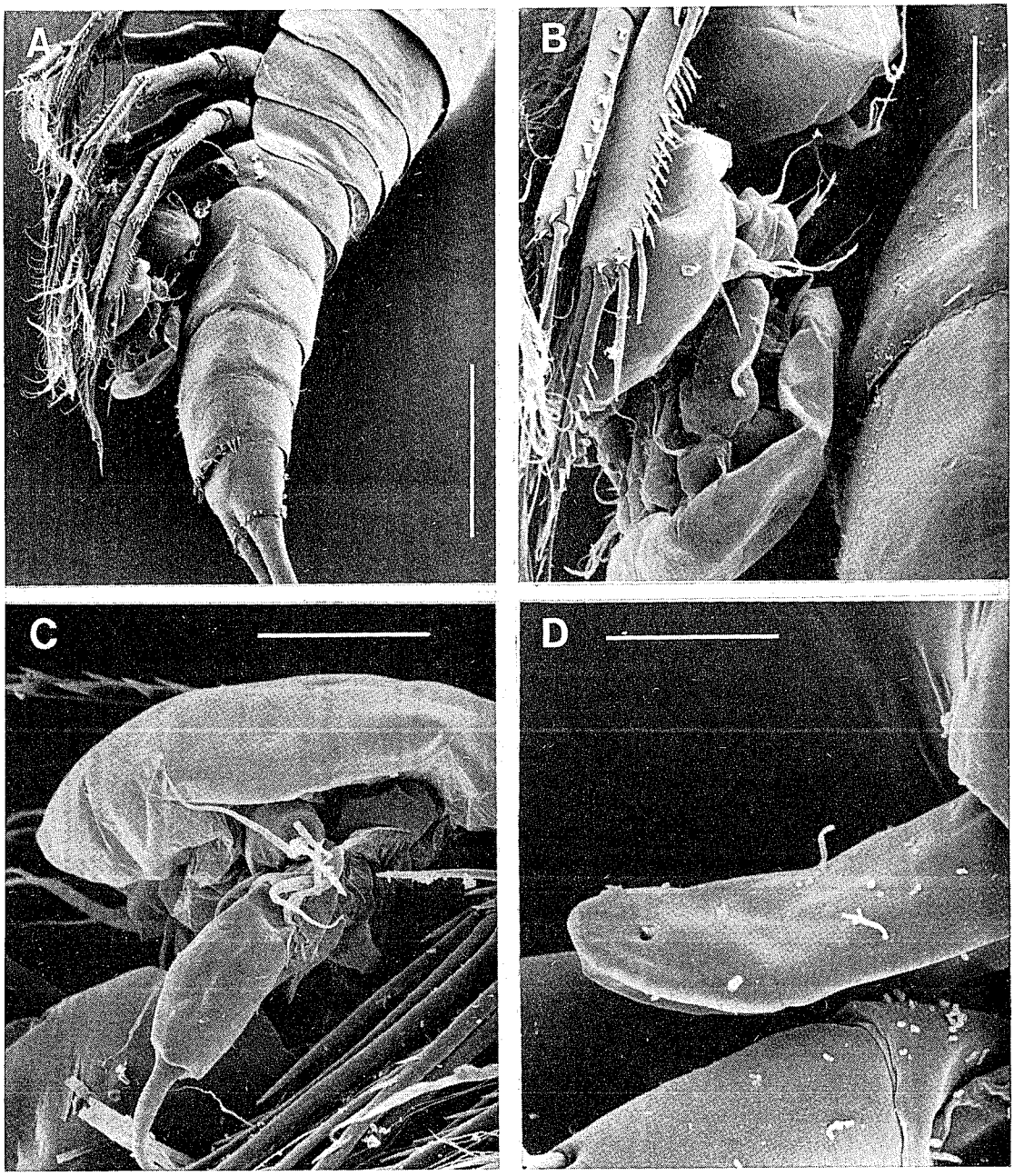

Fig. 37. *Macrosetella gracilis* (DANA, 1847). SEM micrographs. A. Ovigerous female with nauplii in process of eclosion. B. Close-up showing three nauplii. C. Nauplius, anterior view. D. Rostrum, female, dorsolateral. Scale bars: A = 150 μm, B = 43 μm, C = 25 μm, D = 15 μm.

The nauplius of the Miraciidae has been described as a creeping larva (KRISHNASWAMY 1951; BJÖRNBERG 1965) similar to the benthic nauplii of the majority of the harpacticoids. Clearly, the environmental constraints imposed on such a nauplius in the planktonic habitat are significant, since suitable physical substrates are scarce in the open ocean. BJÖRNBERG (1965) observed that the survival and development rate of freshly hatched nauplii was significantly higher when trichomes of *T. thie-*

bautii were added to cultures of *M. efferata, O. gracilis* and *M. gracilis*. Upon eclosion, nauplii typically remained associated with the parental female for some time (Fig. 37A,B) but soon attached themselves to a *Trichodesmium* filament by means of their hook-like antennae (Fig. 37C) and mandibles. However, it was shown in lab experiments that nauplii failing to clasp a filament were not able to develop further and died (BJÖRNBERG 1965). Field studies have reinforced the association of miraciid nauplii with Cyanobacteria. BJÖRNBERG found that nauplii of *M. gracilis* were abundantly attached to tufts of *Trichodesmium* off Curaçao and in the coastal and shelf waters of Brazil. The nauplii of *M. efferata* were also found clasping onto clusters of particulate debris in the plankton but the substrate preferences for this species are as yet unknown (BJÖRNBERG 1965). Similarly, BORSTAD (1978) found nauplii of *M. gracilis* in 4 % of all the *Trichodesmium* colonies inspected off Barbados but stated that they were more common on spherical (7%) than on parallel colonies (2 %). The athecate hydroid *Pelagiana trichodesmiae*, which is commonly found embedded in spherical colonies of *T. thiebautii*, may influence community structure significantly since it is known to be a voracious predator on chaetognaths and both nauplii and adults of *M. gracilis* (BORSTAD & BRINCKMANN-VOSS 1979). Several Japanese studies reported on the association of nauplii of *M. gracilis* with *T. erythraeum*. In the vicinity of Seto, TOKIOKA & BIERI (1966) observed several nauplii holding on to trichomes even after fixation with formalin. Nauplii are also a very common associate of *Trichodesmium* in the surface waters of the Kuroshio Current (OHKI & FUJITA 1982; OHKI & al. 1992) and in some extreme cases 99 % of the colonies were found to be 'infested' (OHKI & al. 1991).

Copepodids and adult Miraciidae are not good swimmers (BJÖRNBERG 1965) and some studies indicate that these stages too are dependent on *Trichodesmium* as a physical substrate, thereby utilizing the hooked maxillae and subchelate maxillipeds as the principal grasping devices. TOKIOKA & BIERI (1966) collected copepodids of *M. gracilis* from *Trichodesmium* colonies near Seto. BJÖRNBERG (1965) and O'NEIL (in O'NEIL & ROMAN 1992) observed copepodids and adults gliding forward on filaments using these as a kind of sledge. BJÖRNBERG (1965) suggested that miraciids might also use other pelagic substrates since they are frequently found free in the plankton, e.g. in the epipelagic zone during periods of *Trichodesmium* scarcity or in the meso- and bathypelagic zones where filamentous Cyanobacteria are absent (BÖTTGER-SCHNACK & SCHNACK 1989).

Trichodesmium as a potential food source. NAIR & al. (1980) claimed that there is no direct nutritional relationship between the zooplankton and *Trichodesmium*, the association being, however, based on enrichment caused by the blooms promoting the growth of diatoms and dinoflagellates. CALEF & GRICE (1966) found a strong linkage between the abundance of *M. gracilis* and the number of filaments in the upper 200 m of the northeast coast of South America, and interpreted this as supporting evidence for BJÖRNBERG's (1965) hypothesis that *Macrosetella* represents an important secondary link in the food-chain of impoverished tropical waters.

Although BJÖRNBERG (1965) claimed that *Trichodesmium* is a vital 'nursery' for successful growth and development of *M. gracilis*, it has not yet been determined whether the nauplii actually graze on the cyanobacterial colonies. KRISHNASWAMY (1951) suggested that the nauplii were non-feeding and lecithotrophic, however, this statement was largely based on the wrong assumption that the mouthparts lack masticatory spines. In the only lecithotrophic harpacticoid nauplius discovered thus far (DAHMS 1989b), a functional mouth, gut and anus are lacking and the masticatory parts of the antenna and mandible are at most rudimentary. The first nauplius of *M. gracilis* and *M. efferata* clearly possess a mouth, anal opening and a well developed antennary coxal seta (Fig. 30A, B), the latter being the primary feeding gnathobase pushing food particles beneath the labrum into the mouth. BORSTAD & BORSTAD (1977) reported on the possibility of nauplii feeding on one or more of the associated organisms (bacteria, other cyanobacteria, diatoms, dinoflagellates, protozoans, ...) since they failed to observe cell lysis or disappearance of any trichomes. This alternative feeding strategy is likely in view of the low nutritional value of cyanobacteria in general and the high energy expenditure during the manipulation of filamentous forms such as *Trichodesmium*. ROMAN (1978), however, repeated BJÖRNBERG's experiments and found that newly hatched nauplii and copepodids remained attached to the trichomes and fed continually on individual cells. Evidence that nauplii may derive nutrition from *Trichodesmium* directly, is provided by OHKI & al.'s (1991) study attempting to establish an artificial culture of *Trichodesmium* sp. Initial experiments with a *Trichodesmium* strain sampled from the Kuroshio Current were unsuccessful as the trichomes disappeared within a week. OHKI & al. (1991) attributed this failure to the presence of *M. gracilis* nauplii in the test tubes since removal of them resulted in survival of the colonies for longer periods of time.

Adult *M. gracilis* were observed eating individual filaments of *Trichodesmium* slowly ('... as if sucking it in...', cf. BJÖRNBERG (1965)) whilst holding on to other filaments immediately alongside. The energy transfer in the *Macrosetella-Trichodesmium* food chain alluded to by some authors (BJÖRNBERG 1965; CALEF & GRICE 1966; FOGG 1982) has been quantitatively demonstrated under controlled conditions since (ROMAN 1978; O'NEIL & ROMAN in press). Ingestion rates of *Trichodesmium* by *M. gracilis* adults were determined by comparing chlorophyll *a* concentrations between the experimental feeding jars and the control jars (containing only *Trichodesmium*). ROMAN (1978) calculated an overall mean ingestion rate of 1.08 µg copepod C µg copepod C^{-1} day^{-1} or 0.037 µg chl *a* $individual^{-1}$ day^{-1}. These values correspond to *M. gracilis* ingesting 90–126% of its body carbon per day during feeding on *Trichodesmium*, consuming 5.5 µg N daily. If the latter rates are converted to values per surface area, this would mean that *M. gracilis* consumes 0.14–2.75 mg C $(m^2\ day)^{-1}$ and 0.03–0.06 mg N $(m^2\ day)^{-1}$. The copepods used in ROMAN's study were collected from the Gulf Stream off Miami, and his results have recently been confirmed in more intensive grazing experiments using several planktonic copepods from the Bahamas and the eastern Caribbean (O'NEIL & ROMAN in press). By labelling *T. thiebautii* colonies with ^{14}C from photosynthesis and analyzing the subsequent enrichment of the labels in the copepods it was shown that no cyanobacteria were ingested by *Labidocera* sp., *Farranula gracilis* and the benthic harpacticoid *Tigriopus californicus* and ingestion rates were negligible for *Temora turbinata* and *Clausocalanus furcatus*. However, in all three miraciid species tested the grazing pressure on *Trichodesmium* was significant, the average ingestion rates expressed in µg C $copepod^{-1}$ $hour^{-1}$ being 0.173 (*M. gracilis*), 0.402 (*M. efferata*) and 0.126 (*O. gracilis*). *D. minor* was not included in the experiments, but it is conceivable that all members of the family have adopted the same feeding strategy. O'NEIL & ROMAN (in press) also found that grazing rates depend on the morphology of the *Trichodesmium* colonies since *M. gracilis* showed consistently higher rates on *T. thiebautii* puffs (spherical colonies) than on tufts. A possible explanation may be given by the more elaborate three-dimensional structure of the puffs providing a better surface for attachment, and thus offering certain nutritional advantages over the linear colonies which have fewer associated organisms and less organic matrix (BORSTAD & BORSTAD 1977; O'NEIL & ROMAN in press). Recent grazing experiments utilizing $^{15}N_2$-labelled *Trichodesmium* allowed determination of N-specific ingestion rates for *M. gracilis* and $^{15}NH_4$-isotope dilution experiments have allowed determination of regeneration of ammonium by this species. The preliminar results of these experiments indicate that *M. gracilis* is probably one of the major links in transferring 'new' biologically useful nitrogen from the N_2-fixing cyanobacteria to the higher trophic levels of the food web (J.M. O'Neil & al. pers. commn).

Ship-board experiments showed that Caribbean *T. thiebautii* bloom samples were toxic to the filter-feeding calanoid *Clausocalanus furcatus* and the poecilostomatoid *Farranula gracilis*, but not to the harpacticoid grazers *M. gracilis* and *M. efferata* (HAWSER & al. 1992). This suggests that Miraciidae possess a mechanism which confers resistance to *Trichodesmium* toxicity caused either by the cyanobacteria proper or by heterotrophic bacteria associated with the blooms and colonies. This apparent insensitivity to cyanobacterial toxigenic compounds might therefore be the key in the miraciid-*Trichodesmium* success story, since it enables them to graze on a major food-source in oligotrophic waters that is otherwise unavailable to the dominant copepod groups in the marine plankton, the calanoids and the poecilostomatoids. In addition, life associated with a toxic substrate might provide some protection against predation. *Macrosetella* and *Miracia* both have higher ingestion rates of *T. erythraeum* as compared to *T. thiebautii* (O'NEIL & ROMAN in press) and this preference might well be due to the fact that *T. erythraeum* lacks the neurotoxin found in *T. thiebautii*, and miraciids despite their resistance still have to expend energy to de-toxify it.

Trichodesmium is the most dominant and active diazotrophic cyanobacterium in the plankton of tropical and subtropical open oceanic waters (CARPENTER 1983) and plays a pivotal role in the input and output of carbon and nitrogen in these areas. Its overall rate of pelagic N_2 fixation is estimated at 5.4 Tg (= 10^{12}g) N $year^{-1}$ (CARPENTER & CAPONE 1992) which represents over one quarter of the total nitrogen fixation in the sea, and according to CARPENTER (1983) carbon fixation by *Trichodesmium* can contribute up to 20 % of phytoplankton production in the Caribbean. By consuming *Trichodesmium*, miraciid copepods (1) occupy a major link in the transfer of fixed carbon and nitrogen on to higher trophic levels, and (2) contribute significantly to the flux of organic material into deeper waters through the production of rapidly sinking fecal pellets (O'NEIL & ROMAN 1992) and through deep-living populations (BÖTTGER-SCHNACK & SCHNACK 1989).

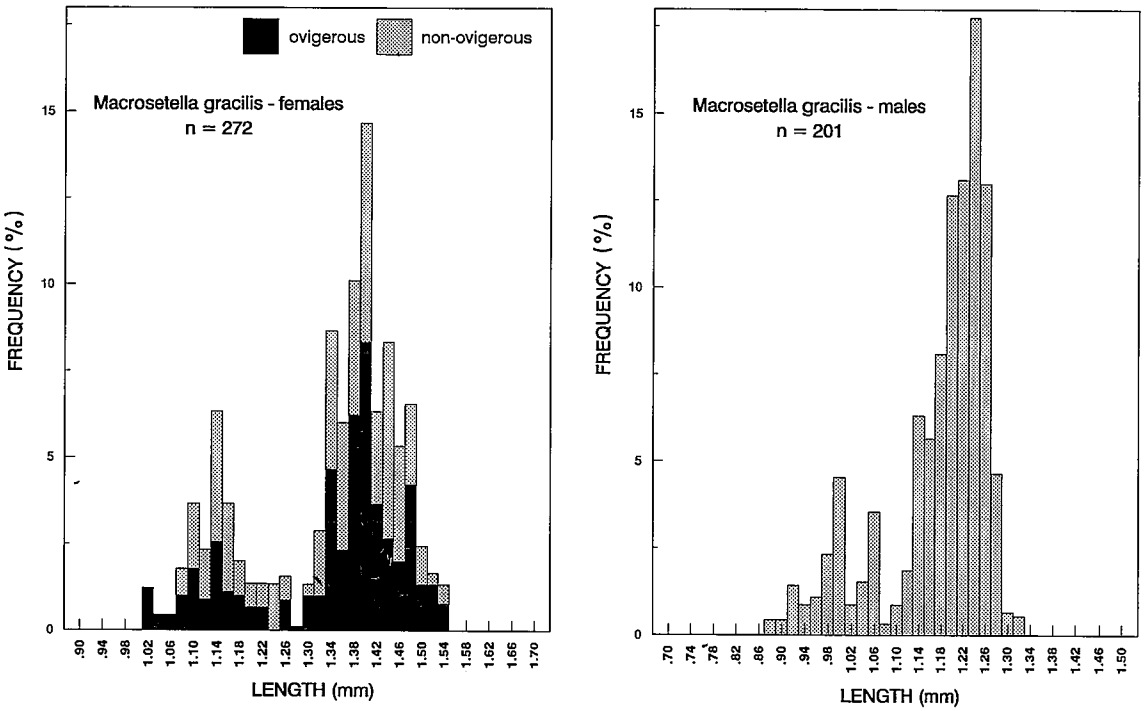

Fig. 38. *Macrosetella gracilis* (DANA, 1847). Length-frequency distribution of females and males from the epipelagic zone (0 to 50 m) in the central Red Sea, July-August 1987. Lengths of ovigerous females are shown by solid bars. n: number of specimens examined. (Adapted from BÖTTGER-SCHNACK (1991)).

Size dimorphism

A distinct size dimorphism has been found for adult *M. gracilis* in the Red Sea (BÖTTGER-SCHNACK 1989, 1991). Two separate size groups of adults were defined for both sexes (Fig. 38). The length of the females ranged between 0.98 and ca 1.2 mm (mode 1.1 to 1.2 mm) in the smaller size class, and 1.25 to 1.6 mm (mode 1.3 to 1.4 mm) in the larger size class. Males ranged between 0.88 and ca 1.1 mm (mode ca 1.0 mm), and between 1.1 and 1.34 mm (mode ca 1.2 mm) in the two size morphs, respectively.

Data on body length of adult *M. gracilis* in different regions of the Indo-Pacific Ocean are summarized in Table 1. They support earlier findings by BÖTTGER-SCHNACK (1989) that the occurrence of the smaller size group seems to be restricted to the Red Sea and western Indian Ocean. However, outside the Red Sea no detailed length measurements have yet been made on populations within *Trichodesmium* blooms where small females predominate. It may well be possible that the occurrence of the small size group of the species is more widespread in the blooms than indicated by the present data. In this context it is worth remarking that T. SCOTT (1894) already noted a gross disparity in size in his material from the Gulf of Guinea which led him '... to think that there were more than one species of *Setella* in the collection'.

No morphological differences other than size were noted among the two size groups of *M. gracilis*. For males there was some indication that the proportion of individuals exhibiting two spines on the P6 was higher within the larger size group, but the number of small specimens examined was not sufficient to allow for a statistical analysis of the data.

Distinct size dimorphism has not yet been proven for other miraciids, though large variability in length is found for some of them such as *M. efferata* and *D. minor*. The extraordinary range (♀♀: 0.93–1.74 mm; ♂♂: 0.83–1.45 mm) recorded for the latter species by STEUER (1935) might well be due to the presence of a rare large size morph in his samples.

Size variations among marine planktonic copepods are known to occur on temporal and/or spatial scales. Seasonal differences in copepod body length from tropical and subtropical areas have been reported by DEEVEY (1964), EL-MAGHRABY (1965), SANDER & MOORE (1983) and ASHJIAN &

WISHNER (1993, and references cited herein). Differences in copepod size due to the segregation of broods in different water masses (RUSSELL 1928), have been documented for instance by BRYLINSKI & al. (1988) and ASHJIAN & WISHNER (1993). ROE (1972) found two size morphs among female *Nannocalanus minor* and adult *Eucalanus attenuatus*, which differed according to their depth distribution and vertical migratory behaviour. Similar observations for *N. minor* size variants were made by AMBLER & MILLER (1987). Several species of the genera *Oncaea* (BOXSHALL 1977), *Sapphirina* (LEHNHOFER 1929) and *Oithona* (NISHIDA 1985) are known from two or more size morphs and differences in vertical distribution patterns, migratory behaviour or habitat preference have been reported for some of them, such as *Oithona simplex* (NISHIDA & MARUMO 1982), *Oncaea venusta* (BOXSHALL 1977) and *O. media* (BÖTTGER-SCHNACK 1990).

The main causes proposed in the literature for the development of different size morphs among pelagic copepod species include changes in hydrographic conditions (mainly temperature) and food availability. Temperature increase or decline in phytoplankton density are generally supposed to be the causative factors for the reduction in body size in suspension-feeding copepods (e.g. MCLAREN 1963; DEEVEY 1964; SANDER & MOORE 1983). ASHJIAN & WISHNER (1993), for instance, found that among *Nannocalanus minor*, body size in the slope waters of the NE Atlantic was inversely and linearly related to seasonal variations in temperature with no clear relationship to sea surface pigments, whilst in the Sargasso Sea there was an asymptotic, non-linear correlation with pigment concentrations but not with temperature. However, such effects have not been found for copepods which are assumed to be non-suspension-feeders, such as *Oncaea* or *Corycaeus* (MCLAREN 1969; SANDER & MOORE 1983). For the harpacticoid copepod *Microsetella norvegica* even a positive correlation between seasonal water temperatures and body length of females has been reported (EVANS & DIAZ 1978).

The causes for the existence of two size groups of *M. gracilis* in the Red Sea have not been investigated yet. Of the three major possible factors, (a) temperature changes, (b) food availability and (c) habitat differences, the availability of *Trichodesmium* filaments was presumed to have the greatest influence on body size in this species (BÖTTGER-SCHNACK 1989). However, only adult *M. gracilis* are known definitely to feed on these cyanobacteria (ROMAN 1978; O'NEIL & ROMAN 1992 in press), while different opinions exist on the feeding of the juvenile stages (see above).

The considerable differences in spatio-temporal distribution of the two size-groups of adult *M. gracilis* in the Red Sea indicate that they perform different roles in the life cycle. Large females might be produced at the end of the reproductive phase within a bloom, in order to survive periods of *Trichodesmium* scarcity during winter in resting phase at midwater depth. The larger size is possibly an advantage for higher lipid storage capacity and might induce a longer life span. In addition, the swimming speed (or sinking rate) might be lower as compared to their smaller relatives. During favourable conditions for reproduction mainly small individuals might be produced within a *Trichodesmium* bloom. The percentage of ovigerous females was found to be higher in the small size group during bloom conditions (34 %) as compared to the larger specimens (19 %) (BÖTTGER-SCHNACK & SCHNACK 1989). The number of eggs, however, was lower for the small individuals and the resulting reproductive rates of the females are as yet unknown. No information is available on the the development times of *M. gracilis* juveniles. *Trichodesmium* blooms represent a highly variable environment, developing and vanishing within only a few weeks (DEVASSY & al. 1978; CARPENTER & CAPONE 1992; DUPOUY 1992; FURNAS 1992). The ability of the copepod to reproduce in these blooms implies a relatively short generation time. For a limnetic cyclopoid copepod inhabiting temporary ponds the development time was found to be as low as 0.5 days at a temperature of 30° C (MAIER 1991). Such high temperatures can be observed in the Red Sea during summer and autumn (EDWARDS 1987), when *Trichodesmium* blooms are occurring.

Abundance and vertical distribution

Most published records of the four species of Miraciidae are from the epipelagic zone (0-200 m). Records from meso- and bathypelagic layers have been published several times for *M. gracilis* (MOORE & O'BERRY 1957; GRICE 1963; OWRE & FOYO 1964; DEEVEY & BROOKS 1977; BOXSHALL 1979; WEIKERT 1982; BÖTTGER 1987; BÖTTGER-SCHNACK & SCHNACK 1989; BÖTTGER-SCHNACK 1991), whereas only few records mention *M. efferata* (BOXSHALL 1979) or *D. minor* (OWRE & FOYO 1964). Except for the numerous finds of *M. gracilis* in the deep Red Sea (see below), the majority of the records refer to single individuals, and isolated specimens from deeper waters have usually been regarded as contaminants (BOXSHALL 1979). However, most published information on the occurrence of miraciids below 200 m is based on samples taken with 0.2 or 0.3 mm mesh nets which cannot sample the relatively small

and slender species quantitatively. Comparative studies in the Red Sea using nets of 0.3 mm and 0.1 mm mesh size have shown that the coarser mesh nets sample only 10 % of the adult *M. gracilis* standing stock (BÖTTGER 1985; BÖTTGER-SCHNACK & SCHNACK 1989). Recent studies in this area using finer mesh nets of 0.1 or 0.05 mm mesh size have revealed the existence of distinct deep populations of *M. gracilis*, occurring as deep as 1650 m depth during certain seasons. Since the structure of these deepwater populations differed considerably from those found at the surface during the same period it was assumed that contamination of the deep samples could only have been of minor importance (BÖTTGER-SCHNACK & SCHNACK 1989).

Life cycle of *Macrosetella gracilis*. The population biology and vertical distribution of *M. gracilis* was investigated in the central and northern Red Sea during autumn and winter 1980/81 (BÖTTGER 1985; BÖTTGER-SCHNACK & SCHNACK 1989; BÖTTGER-SCHNACK 1989) and in the central and southern Red Sea during winter and summer 1987 (BÖTTGER-SCHNACK 1991). The studies included analyses of ontogenetic composition, sex ratio, size distribution of adults and relative abundance of ovigerous females. The content of oil droplets, which can be regarded as an indirect measure of lipid storage, was also determined in adults. By relating the differences in the population structure to variations in abundance of *Trichodesmium* in the surface layers, a hypothetical life cycle for *M. gracilis* was proposed:

(1) Reproduction takes place only in surface waters during summer and autumn when massive blooms of *Trichodesmium* occur. The population has a balanced sex ratio and a high proportion of the females carries egg-sacs. The proportion of juvenile stages (nauplii and copepodids) strongly depends on the development of *Trichodesmium* bloom conditions: juveniles account for more than 50 % of the population inside the bloom, but are rare outside. During the reproductive phase at the surface, small individuals (females < 1.2 mm and males < 1.1 mm) dominate among the adults, although some large specimens are always present as well. Results from different phases of the *Trichodesmium* bloom indicate that the proportion of large adults at the surface increases towards the end of the bloom (BÖTTGER-SCHNACK 1989).

(2) During winter, at very low *Trichodesmium* abundances, *M. gracilis* occurs mainly at midwater depth (ca 300–450 m), in the upper part of the oxygen minimum-zone. The population consists mainly of large (>1.2 mm) non-ovigerous females, which are assumed to be in a resting phase. The mean depth of these midwater populations differs according to regional differences in oxygen distribution. Thus, it may be assumed that the decreasing oxygen concentrations act as a stimulus that prevents larger females from descending further. The high number of oil droplets observed in the deepwater females might indicate considerable lipid storage as this is typical for resting stages of some calanoids (ALLDREDGE & al. 1984) and benthic harpacticoids (COULL & GRANT 1981). In the absence of reliable data on lipid or enzyme content and information on various metabolic processes such as respiration and excretion, the presence of resting stages can only be inferred from the presence of oil droplets. Downward and upward migration of adults has not yet been directly observed, but migrations are assumed to take place in the transition periods, being late autumn and spring, respectively (BÖTTGER-SCHNACK 1991).

The role of the bathypelagic population of *M. gracilis* in the Red Sea, which occurred between 1050 and 1650 m depth during autumn 1980, remains enigmatic. The deep-sea population consisted exclusively of small-sized females and might represent a moribund population at the end of the autumn bloom period (BÖTTGER-SCHNACK & SCHNACK 1989). This hypothesis seems to be supported by the absence of deep-living individuals during late summer, at the beginning of a *Trichodesmium* bloom (BÖTTGER-SCHNACK 1991).

The existence of midwater and deepwater populations of *M. gracilis* in the Red Sea, though being only a temporary phenomenon, may have a significant impact on the nutrient cycle in these layers. NAQVI & al. (1986) estimated that nitrogen fixation by *Trichodesmium* may contribute 6 % to the total primary production in the Red Sea. This 'new' nitrogen is transferred into deeper zones by the copepods where it becomes available to other planktonic organisms after excretion or through the food web. Whether this cycle applies also to other oceanic areas is unknown at present, since distinct deepwater accumulations of *M. gracilis* (or any other miraciid) have never been reported in the literature. In view of the inadequate sampling methods (cf. mesh size), the scattered records from deeper layers outside the Red Sea might well be indicative for a similar depth distribution in these areas.

Diel vertical migration of *M. gracilis* has not yet been observed in the Red Sea. Depth distribution varies independently of daytime and is obviously correlated only with the abundance of *Trichodesmi-*

um filaments (BÖTTGER-SCHNACK & SCHNACK 1989). This is in agreement with the 'aberrant' behaviour previously reported from the Florida Current (MOORE & O' BERRY 1957; MOORE & FOYO 1963; ROEHR & MOORE 1965). In this area *M. gracilis* was concentrated at midwater depth (ca 330 m) or in the epipelagic zone (150–200 m), but did not display significant diel vertical movements, although it appeared to be active in captivity. MOORE & FOYO (1963) stated that '... instead of being insensitive to light it apparently regulates its depth by a rythm in its nul illumination, which just compensates for the diurnal changes taking place in the environment'.

Abundance of *Macrosetella gracilis*. The numerical abundance of *M. gracilis* adults in the Red Sea and other tropical areas where *Trichodesmium* blooms occur regularly, has been found to vary by several orders of magnitude from less than 0.08 to more than 100 individuals m^{-3} in the upper 20 or 50 m of the water column (CALEF & GRICE 1966; ROMAN 1978; BÖTTGER-SCHNACK & SCHNACK 1989). Maximum values always occurred within *Trichodesmium* bloom conditions. The abundance of early copepodid stages and nauplii has only rarely been reported quantitatively. From data reported by TOKIOKA & BIERI (1966), a mean abundance of 1.4 nauplii m^{-2} can be calculated for the upper 10 cm of the water column. Abundances were much higher in the Red Sea where nauplii and copepodids were found in concentrations up to 100 individuals m^{-3} within *Trichodesmium* bloom conditions (BÖTTGER-SCHNACK & SCHNACK 1989). Since these values are integrated over a relatively large depth zone of 20 or 50 m, density at the immediate surface where *Trichodesmium* filaments accumulate, might be much higher than indicated by the above values.

The relative abundance of *M. gracilis* within the copepod community (excluding nauplii) has been found to be in the range of 1 to 3 % in the upper 2000 m of the water column when sampled with 0.1 mm mesh nets (MICHEL & FOYO 1977; BÖTTGER 1987). At narrower depth layers, however, the contribution of the species to the total copepod density can be much higher. During periods of *Trichodesmium* bloom conditions in the Red Sea, the relative abundance of *M. gracilis* adults and copepodids in the upper 50 or 20 m depth layer was usually between 3 and 5 % of the total number of copepods, with single values up to 15 % (BÖTTGER 1985). Similarly, NAIR & al. (1980) reported a relative abundance of 6.3 % within *Trichodesmium* blooms near the Indian coast. During non-bloom conditions, however, the relative abundance within the surface copepod community is usually very low, with values ranging between <0.01 and 1% of the total density (BÖTTGER 1985; BÖTTGER-SCHNACK in press). In the mesopelagic zone, at 300 to 450 m depth, *M. gracilis* was found to account for up to 10 % of the total number of copepods during the winter period when the species is in a resting phase (fig. 24 in BÖTTGER 1985). The highest relative abundance of *M. gracilis*, however, was observed in the bathypelagic zone of the Red Sea during the autumn season where it accounted for 40 % of the total copepod density in the 1050-1650 m depth layer (BÖTTGER 1985, 1987).

Overall, the relative importance of *M. gracilis* within the copepod community of coastal and oceanic waters seems to be very variable, both in time and space, and largely depends on the occurrence and development of *Trichodesmium* bloom conditions. The present data indicate that the relative abundance of the species is locally much higher than previously estimated. Inefficient sampling and the lack of quantitative data obtained during periods of *Trichodesmium* bloom conditions may have underrepresented this species in marine plankton studies so far.

Other Miraciidae. The abundance and vertical distribution of other Miraciidae have only rarely been reported in the literature. OWRE & FOYO (1964) reported female *D. minor* at 146, 170, 250, and 750 m depth in the Florida Current where it was generally rare. The depth distribution of *D. minor* in the Gulf of Aden and southernmost part of the Red Sea based on fine mesh net samples is summarized in Table 3. The species was mainly concentrated in the subsurface layers between 25 and 175 m, but no specimens were caught below 250 m. *D. minor* does not penetrate further north into the Red Sea, its distribution obviously being limited by the increasing salinity (BÖTTGER-SCHNACK in press). BOXSHALL (1979) found *M. efferata* only within the upper 100 m of the water column both during the day and at night, and claimed that there is little evidence of any diurnal change in depth distribution. Isolated specimens caught between 305 and 1250 m depth were regarded as contaminants. STEUER (1935) reported *O. gracilis* from the upper 100 m. DEEVEY & BROOKS (1977) sampled *M. gracilis* and *O. gracilis* from the upper 1000 m in the Sargasso Sea, whilst *M. efferata* was found to occur in the upper 500 m only. The vertical resolution of their samples was rather coarse (500 m intervals), however, and the actual depth range of the species might be smaller than indicated by their data.

Studies with fine mesh nets in the upper 500 m of the Sargasso Sea revealed that *M. efferata* and *D. minor*, which were not quantitatively separated to species, were mainly confined to the upper 150 m of the water column (Table 4) (see BÖTTGER 1982 for location of stations and details of sampling methods). Maximum concentrations of up to 3 individuals m^{-3} were found in the upper 50 m. No diurnal vertical movement could be inferred from the data available.

Table 4. Vertical distribution of *Miracia* spp. (including *M. efferata* and *Distoculus minor*, formerly also placed in *Miracia*) in the upper 500 m of the Sargasso Sea. For location of stations and sampling details see BÖTTGER (1982). n = number of sampling series; D = day; N = night; $\bar{x}$ = individuals m^{-3} (arithmetic mean); R = range; - = no individuals present.

Depth (m)	n D/N	$\bar{x}$	R
0 - 25	6/4	0.53	0 - 2.9
25 - 50	6/4	1.00	0 - 3.0
50 - 100	6/4	0.44	0 - 1.3
100 - 150	6/4	0.23	0 - 1.6
150 - 200	6/4	0.05	0 - 0.47
200 - 300	2/2	0.01	0 - 0.04
300 - 400	2/2	-	
400 - 500	2/2	< 0.01	0 - 0.05

Seasonal aspects. Little is known about the seasonality in the occurrence of miraciids. In the Red Sea, surface populations of *M. gracilis* are present all year round (HALIM 1969; W. Beckmann pers. commn) with maximum concentrations occurring during summer and autumn, when *Trichodesmium* blooms are present (BÖTTGER-SCHNACK & SCHNACK 1989; BÖTTGER-SCHNACK 1991). Several other studies provide fragmentary data on seasonal distribution, however, without relating them to the occurrence of filamentous cyanobacteria in the surface waters. DEEVEY (1971) reported *M. gracilis* and *O. gracilis* at all times of the year in the Sargasso Sea off Bermuda, while *M. efferata* was present there only from August to February. SCOTTO DI CARLO & al. (1984) found *M. gracilis* all year round in small numbers in the western Mediterranean (Tyrrhenian Sea), whereas DAKIN & COLEFAX (1940) recorded higher numbers of *M. gracilis* during winter in the coastal waters of New South Wales. MOORE (1949) also provided information on the seasonality of *M. gracilis* and *O. gracilis*, but the reliability of her data is limited due to the great deal of inconsistency in sampling depth, geographical location and methodology applied.

Geographical distribution

The comprehensive compilation of distribution records predating 1935 given for each species by STEUER (1935) has subsequently been updated by LANG (1948) who suspected that STEUER had reversed the distribution maps of *M. efferata* and *D. minor*. Both species are found in the subtropical and tropical zones of all oceans, roughly between 40° N and 40° S (STEUER 1935; STEUER & HENTSCHEL 1937). *M. gracilis* assumes approximately the same distribution, mainly between the 15° C mean annual surface temperature isotherms, but has occasionally been recorded from higher latitudes. With the exception of a doubtful record of an undescribed species of *Setella* from the Arctic (OSTENFELD & WESENBERG-LUND 1909), the northernmost and probably deepest record of *M. gracilis* is that of THOMPSON (1903) who found it 'plentifully' in a gathering taken at 1670 fathoms (3000 m) west of Ireland. Though various authorities mistakenly cited BREEMEN (1908) as the source, *M. gracilis* has to our knowledge never been recorded from the North Sea. WILSON (1932) regarded the species as an immigrant in the Woods Hole region and unpublished observations revealed that it might even accidentally invade anchialine caves in the Bahamas and Bermuda (R. Huys pers. obs.).

High latitude records of *M. gracilis* in the southern hemisphere include those of BRADY (1910) and WOLFENDEN (1911) from the Kerguelen and the Antarctic. According to DE DECKER (1984) the species is widely distributed in warm water along both sides of the South African subcontinent, following the southernmost branch of the Agulhas Current on the West Wind Drift in the region south of Cape of Good Hope. In contrast to most other planktonic copepods which are confined to the warm core of the Current, *M. gracilis* seems to be the one that is most tolerant to lateral mixing.

The distribution of *M. gracilis* and *M. efferata* in the Indian Ocean has been mapped by HARIDAS & RAO (1981) as a result of the International Indian Ocean Expedition. *M. gracilis* seemed to be more abundant along the coasts of India and north-west Australia but appeared to be rare or absent in East African waters. *M. efferata* largely follows the same trend but is absent along the African continent and Arabian peninsula which seems to be in accordance with our results from the Red Sea and Arabian Sea. Overall, HARIDAS & RAO (1981) concluded that both species were more abundant near the land masses, i.e. in the northern and western Indian Ocean, corroborating previous observations made by EVANS (1961) whose series of transatlantic haul samples taken along the North Equatorial Current

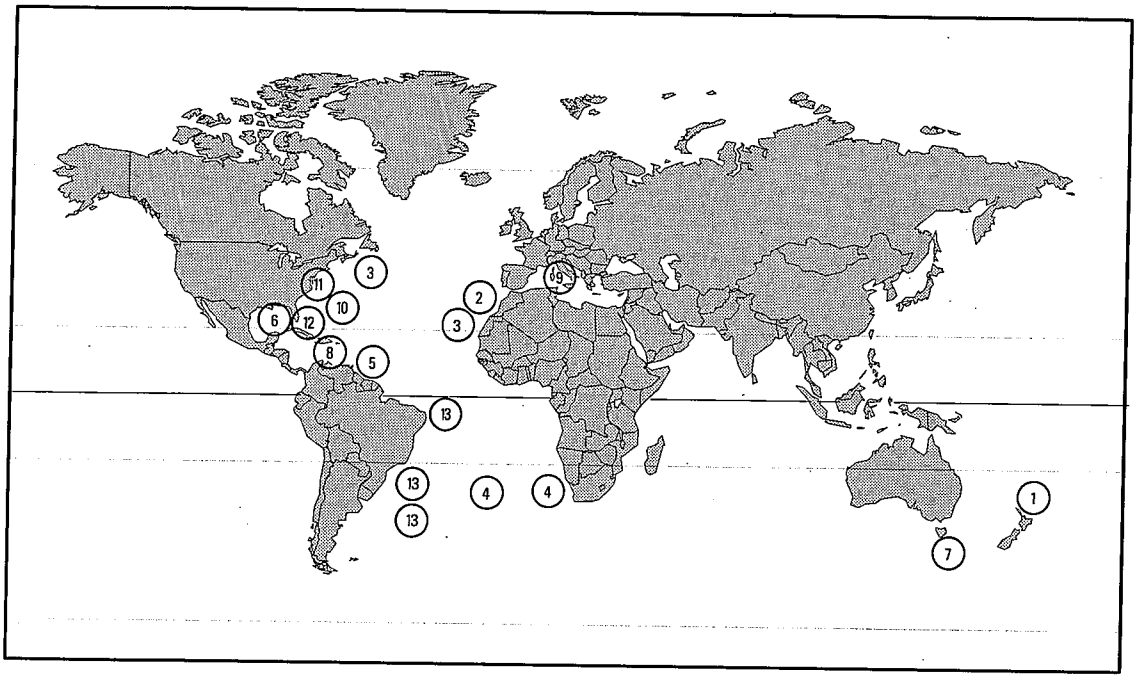

Fig. 39. Compilation of reliable distribution records of *Oculosetella gracilis* (DANA, 1849): 1 = DANA (1854); 2 = SARS (1916); 3 = ROSE (1929); 4 = STEUER (1935); 5 = WILSON (1942); 6 = KING (1950) and DAVIS (1950); 7 = VERVOORT (1957); 8 = OWRE & FOYO (1964); 9 = HURE & SCOTTO DI CARLO (1968); 10 = DEEVEY & BROOKS (1977); 11 = D. Barr (pers. commn); 12 = O'NEIL & ROMAN (in press); 13 = W.S. Bruce collection (Scottish National Antarctic Expedition) in Royal Museum of Scotland.

indicated that *M. gracilis* tends to neritic existence. STAR & MULLIN (1981), however, listed *Macrosetella* sp. as a numerically important species of the copepod assemblage in the North Pacific Central Gyre, whereas it was found to be absent or of minor importance in the Western California Current or in the nearshore stations. Although *D. minor* is a frequent member of the Red and Arabian Sea plankton (e.g. Table 3), and has occasionally been recorded from the Indian Ocean before (MRÁZEK 1895; THOMPSON & A. SCOTT 1903; WOLFENDEN 1905; KRISHNASWAMY 1956), the species surprisingly was not recorded by HARIDAS & RAO (1981). This, however, might just be a reflection of the sampling bias caused by hauling with the wrong mesh size. *Oculosetella gracilis* is a rare species and when recorded, usually represented only by one or two specimens in plankton hauls. A compilation of all valid records is presented in Fig. 39. DAHL (1895) and BJÖRNBERG (1965) did not give locality details, but it is clear from their notes that they were dealing with *O. gracilis*. JONES' (1952) record of '*Microsetella oculata*' from the Florida Straits requires confirmation. The species appears to assume a tropical and subtropical distribution between 40° N and 45° S, the southernmost record being south of Tasmania (VERVOORT 1957). Surprisingly, this is the only record from the Pacific since DANA (1854) described it from two localities north of New Zealand. *O. gracilis* seems to be widely distributed in the Atlantic, though in extremely low numbers. It has not been recorded yet from the Indian Ocean (HARIDAS & RAO 1981) or the Red Sea (R. Böttger-Schnack, pers. obs.). Since KASTURIRANGAN (1963) used WILSON's (1932) drawings in his key to the planktonic Copepoda of Indian coastal waters, his doubtful record of *O. gracilis* is probably based on specimens of *D. minor*.

Bioluminescence

Bioluminescence in Miraciidae has been reported by Russian investigators for *Macrosetella gracilis* in the Caribbean (ARTYOMKIN & al. 1966, 1969) and *Macrosetella* sp. in the Red Sea (RUDYAKOV & VORONINA 1967), but these cursory records have to be regarded uncertain pending further confirmation (HERRING 1988). It might well be that these observations are due to mistaken identification. The only harpacticoid for which luminescence has been demonstrated with confidence is *Aegisthus mucronatus* (HERRING 1985). *A. mucronatus* occurs at depths (DEEVEY & BROOKS 1977; BOXSHALL 1979) that fall

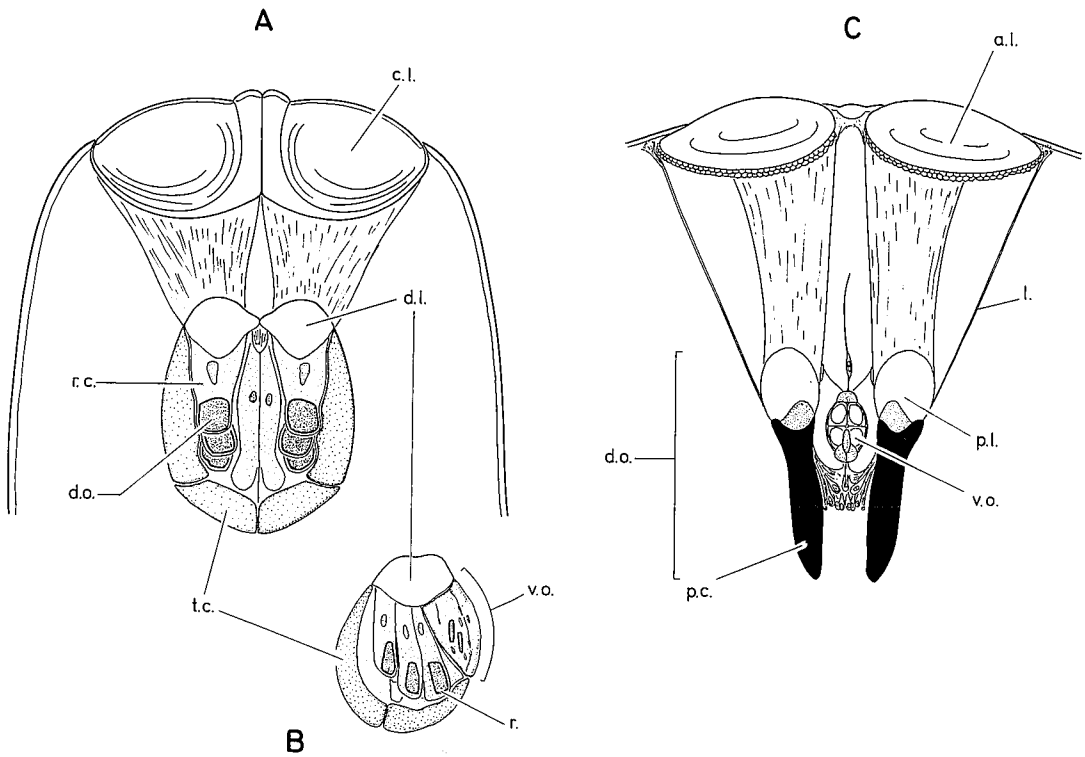

Fig. 40. Semi-diagrammatic comparison between elaborate nauplius eyes of *Miracia efferata* DANA, 1849 (A. Dorsal view. B. lateral view of ocelli; based on CLAUS (1891) and present account) and *Sapphirina maculosa* GIESBRECHT, 1892 (C. dorsal view; adapted from VAISSIÈRE (1961)); a.l. = anterior cuticular lens, c.l. = corneal lens, d.l. = double lens, d.o. = dorsolateral ocellus, l. = ligament, p.c. = pigment cup, p.l. = posterior lens, r. = rhabdomer, r.c. = retinal cell, t.c. = tube cell, v.o. = ventral ocellus.

within the vertical distribution of *M. gracilis* (BOXSHALL 1979; BÖTTGER 1987), and it is therefore conceivable that both species have been confounded in the past. It is noteworthy, however, that the genus *Aegisthus* has never been recorded from the Red Sea (HALIM 1965; WEIKERT 1982; R. Böttger-Schnack pers. obs.).

Photoreception

Most copepods have a single median, tripartite nauplius eye, consisting of a cluster of one ventral and two dorsolateral ocelli. In a number of genera one or more of the ocelli have separated from each other to form distinct eyes equipped with complex optical systems, including lenses, mirrors, or a combination of both. With the important exception of the cyclopoids, this specialization has evolved in planktonic representatives of virtually every order within the Copepoda, such as the Pontellidae in the Calanoida, the Caligidae in the Siphonostomatoida, the Corycaeidae and Sapphirinidae in the Poecilostomatoida and *Monstrillopsis* in the Monstrilloida. Little is known about modifications of harpacticoid eyes. FAHRENBACH (1962) described a simple modification in the algae-dwelling thalestrid *Diarthrodes*, involving the subdivision of the dorsolateral ocelli into double cups. In another thalestrid *Paradactylopodia trioculata,* HICKS (1988b) reported three curious 'lens'-like structures on the frontal part of the cephalothorax, however, only in the Miraciidae the basic nauplius eye has become specialized as an elaborate target detector.

The eye of *Miracia efferata* was studied in detail by CLAUS (1891), and his light microscopical study was corroborated and supplemented by ELOFSSON (1966). ELOFSSON recognized a morphological series of eyes within the Copepoda and pointed out that the highly specialised nauplius eye of *Miracia* is even more modified than in *Copilia, Corycaeus* and *Sapphirina.* A significant difference with the poecilostomatoid genera (Fig. 40C), however, is that the dorsolateral ocelli have not undergone lateral displacement and the basic tripartite arrangement of the nauplius eye is retained (Fig. 40A, B). The minute ventral cup is located between the anterior halfs of the dorsolateral cups and contains only a

few small cells. The large dorsolateral cups are fused medially and are enclosed in a thick tube. The nature of the tube is unknown. Each dorsolateral ocellus contains three large retinal cells which are stacked upon each other in a vertical plane. The retinal cells provide a setting for the lenses anteriorly and contain a rhabdomere in the posterior part. The rhabdomeres of the dorsolateral ocelli are large and developed along the ventral side of the cells. Smaller rhabdomeres are found in the ventral cup but their number and precise arrangement are obscure.

According to ELOFSSON (1966), each dorsolateral cup possesses a proximal and a distal lens which are contiguous, forming a single unit as opposed to the widely separated lenses in for instance *Copilia*. Anteriorly, two large, biconvex, cuticular lenses are found, touching in the middorsal line in *Miracia* and *Oculosetella* but being laterally displaced in *Distioculus* gen. nov. The only information about the lensless nauplius eye of *Macrosetella* is given by ELOFSSON (1966). The eye is minute but has retained the basic structure and components found in most other harpacticoids. Due to their small size, ELOFSSON was unable to discern the precise number of retinal cells, but estimated that there are about 5 to 7 in each ocellus. There are three conspicuous connections between the epidermis and the respective cups of the eye.

Phylogenetic analysis based on non-eye characters indicates that the absence of the modified nauplius eye in *Macrosetella* is secondary, and does not represent the ancestral condition of the family. A similar dramatic reduction is found in *Copilia* where specialized eyes are present in the females but not in the larger males. LAND (1984) therefore speculated on a possible role for the eyes in mate location and recognition, however, remarked that such sex difference is not present in the other sapphirinid genera *Vettoria* and *Sapphirina* or in the related Corycaeidae. This suggests that the elaborate eyes might also be involved in prey-capture and is supported by GOPHEN & HARRIS (1981) who found that both sexes of *Corycaeus anglicus* are presumably visual predators since they feed at much higher rates in the light than in the dark. An alternative explanation for the sex difference in *Copilia* is offered by the fact that the males, in contrast to males of Corycaeidae and other Sapphirinidae, have atrophied mouthparts and are presumably non-feeding as adults. In the Miraciidae there is no such sexual dimorphism in the eyes nor in the mouthparts, and recent observations (O'NEIL & ROMAN in press) suggest that the feeding strategies are similar in both lens-bearing (*M. efferata, O. gracilis*) and lensless species (*M. gracilis*). In other planktonic families with specialized eyes such as the Corycaeidae, nauplii lack any trace of cuticular lenses (GIBSON & GRICE 1978). Similarly, in pontellid calanoids such as *Labidocera*, elaborate eyes and their associated lenses do not occur until the first (JOHNSON 1935) or the second copepodid stage (GIBSON & GRICE 1977). The fact that the Anlagen of the cuticular lenses are already present in the first naupliar stage of *M. efferata* (BJÖRNBERG 1965) certainly indicates their early involvement in the life cycle of the Miraciidae and invites for further behavioural studies.

PHYLOGENETIC ANALYSIS

In his dendrogram LANG (1948) recognized a clear boundary between *Miracia-Oculosetella* and *Macrosetella* based on lens and antennary basis characters. With the removal of *M. minor* to *Distioculus* gen. nov., the family Miraciidae currently contains four monotypic genera. It needs to be tested, however, whether *Miracia* and *Distioculus* gen. nov. do not represent immediate sistergroups as this would make the splitting up of *Miracia* rather superfluous. The following characters compiled in Table 5 were included in the analysis.

1. Rostrum. Two types of rostrum are found in the family. Both *Miracia* and *Distioculus* gen. nov. have a small blunt rostrum that is not exposed in dorsal aspect and largely fused to the anterior margin of the labrum (Fig. 5B). In *Macrosetella* and *Oculosetella* the rostrum is a conspicuous elongate structure (Fig. 37D), completely delimited at the base and typically pointing ventrally (Figs 8B; 9A; 15B; 17B). This condition is regarded here as the plesiomorphic one. In *M. gracilis* the rostral area is not yet developed at CI (Fig. 31A), but becomes distinct at the base in CII and gradually enlarges in the later stages of the copepodid phase (Figs 31, 32). The *Distioculus* and *Miracia* conditions could have originated from the latter ontogenetic series through cessation in rostral development at CI and CII, respectively.

2. Eye lenses. Frontal cuticular lenses are present in *Miracia, Distioculus* gen. nov. and *Oculosetella* (Fig. 40A, B). On the basis of in-group comparison the minute lensless nauplius eye in *Macrosetella* is regarded here as secondary. This apomorphic state can easily be derived from the *Miracia* condition through simple loss of the integumental lenses. It does not require repositioning of the indi-

vidual ocelli into a single median unit, since the tripartite structure is retained in all lens-bearing genera. The presence of cuticular lenses in *Miracia* from the first nauplius onwards indicates that the *Macrosetella* condition cannot be explained solely by a heterochronic event. The contiguous arrangement of the cuticular lenses is considered the plesiomorphic condition for the family and is exhibited by *Miracia* and *Oculosetella*. The laterally displaced condition in *Distioculus* gen. nov. is therefore an autapomorphy for this genus.

3. Antennulary segmentation. Antennules are typically 8-segmented in females of *Miracia, Macrosetella* and *Distioculus* gen. nov., however, possess only 7 segments in *Oculosetella*. In the latter, segment 3 is clearly homologous to segments 3 and 4 of *Macrosetella* since the large aesthetasc is borne on this segment. Comparison with the antennulary development in female *M. gracilis* (Fig. 33), reveals a striking similarity between the latter's CV ♀ stage and the adult of *O. gracilis*. The identical segmentation and setal counts indicate that the 7-segmented condition in *Oculosetella* did not arise through segmental fusion at the final moult, but is undoubtedly the result of heterochrony.

4. Antennulary setation. Both sexes of *Miracia* and *Distioculus* gen. nov. differ from the other genera in the presence of an anterior seta on segment 1. The antennulary development in *M. gracilis* shows that this seta is present in the early copepodids but is subsequently lost, i.e. at the moult to CIII (Fig. 31; Dahms 1989). In the absence of copepodid stages it is accepted here that the seta on segment 1 was lost in a similar way in *Oculosetella*, and that this loss is a synapomorphy linking both genera.

In females the distal segment typically has a terminal articulate spine. This plesiomorphic condition is found in *Miracia, Distioculus* gen. nov. and *Oculosetella*, however, in *Macrosetella* this element is secondarily incorporated into the segment to form a rigid process (Fig. 17A).

5. Antennary exopod. Both *Miracia* and *Distioculus* gen. nov. possess a well developed 1-segmented, bisetose exopod which represents the plesiomorphic condition for the family. In adults of *Macrosetella* and *Oculosetella* no exopod is present and this apomorphic condition arose through loss at the moult towards CII (Fig. 31A).

6. Antennary endopod. The free endopod segment in *Miracia* and *Distioculus* gen. nov. has 5 setae/spines around the distal margin, whereas in *Macrosetella* and *Oculosetella* there are only 3 elements left. Comparison based on relative size and position of the individual armature elements suggests that it is the outermost and middle (= anterior) setae that are lost in the latter genera (arrowed in Fig. 6B). *Distioculus* gen. nov. is the only genus that has retained 2 lateral setae on the endopod.

7. Mandible. The palp is bisetose in *Miracia* (Fig. 3A). In the other genera it is represented by a small segment with one apical seta (Figs 10C; 20C; 25B).

8. Maxillule. A morphological series can be recognized in the maxillulary palp. The most primitive condition is found in *Miracia* where the palp is dis-

Table 5. Characters used in the phylogenetic analysis. Apomorphic states are referred to in square brackets. Characters 1, 10, 14, and 25 are multistate characters.

1 Rostrum elongate, free at base [state 1: blunt and short, fused to labrum, free dorsally; state 2: completely incorporated in cephalothorax]
2 Cuticular eye lenses present [absent]
3 Cuticular eye lenses contiguous [laterally displaced]
4 Antennule ♀ 8-segmented [7-segmented]
5 First antennulary segment ♀/♂ with seta [without]
6 Distal antennulary segment ♂ with articulate spine [with fused process]
7 Antennary exopod present [absent]
8 Antennary endopod with 5 distal spines/setae [3]
9 Mandibular palp with 2 setae [1]
10 Maxillulary palp defined at base, with 3 setae and discrete unisetose exopod [state 1: with 2 setae and exopod incorporated; state 2: palp fused to praecoxa; state 3: palp reduced to single seta]
11 Maxilla with 2 spines/setae on syncoxal endites [1]
12 Maxilliped stenopodial [with syncoxa and basis at right angle]
13 Maxillipedal syncoxa with 3 setae [1]
14 P1 basis ♂ with spinular row [state 1: truncate process; state 2: round process; state 3: entire inner margin swollen]
15 P2-P4 basis with outer seta [without]
16 P1 exopod with inner seta on exp-2 [without]
17 P1 exopod with 4 setae on exp-3 [3]
18 P4 exopod with 3 outer spines on exp-3 [2]
19 P1 endopod with inner seta on enp-1 [without]
20 P2 endopod with inner seta on enp-1 [without]
21 P3 endopod with inner seta on enp-1 [without]
22 P3 endopod with 2 inner setae on enp-2 [1]
23 P4 endopod with inner seta on enp-1 [without]
24 P5 ♀ with 6 setae/spines on exopod [5]
25 P5 ♀ with 5 setae/spines on baseoendopod [state 1: 4; state 2: 3]
26 P5 ♂ with 6 setae/spines on exopod [4]
27 P5 ♂ with 3 spines on baseoendopod [2]
28 P6 ♀/♂ with 3 setae [2]
29 Caudal ramus with setae IV and V free [fused at base]

crete, with three apical setae and a minute, 1-segmented endopod (or exopod) laterally (Fig. 3B). In *Distioculus* gen. nov. the palp is still free at the base, but one seta is lost apically and the endopod (or exopod) is incorporated (Fig. 25C). The condition in *Oculosetella* is similar to the previous one, except that the palp is no longer discrete but fused to the praecoxa (Fig. 9C). Finally, in *Macrosetella* the entire palp is reduced and represented by a single seta (Fig. 19C). The transformations of the maxillulary palp are scored using the multistate system.

9. Maxilla. In *Miracia* and *Distioculus* gen. nov. both syncoxal endites have two armature elements whereas only one is left in the other genera.

10. Maxilliped. Only in *Distioculus* gen. nov. are three setae retained on the syncoxa as opposed to one in the other genera. The general facies of the maxilliped in *Miracia* (Fig. 3E) differs significantly from the more 'stenopodial' type in *Oculosetella, Macrosetella* and *Distioculus* gen. nov. (Figs 10D; 20D; 25E), and is regarded here as an autapomorphy for the genus.

11. P1 basis ♂. The male modification of the inner margin of the P1 basis is a diagnostic character for the family. A distinct transformation series can be recognized for this character starting with the raised spinular row in *Miracia* (Fig. 4D, E). In the other genera the inner portion of the basis is medially expanded. In *Distioculus* gen. nov. this portion is produced into a striated, truncate process derived from the *Miracia* condition through basal fusion of the spinules (Fig. 27B). A similar process is found in *Oculosetella* (Fig. 11C) but the individual striations are lost. In *Macrosetella* the entire process is incorporated in the expanded inner portion forming a strongly chitinized, bulbous structure (Fig. 21D). The transformations of the male basis are scored using the multistate system.

12. P2–P4 basis. Only *Miracia* and *Distioculus* gen. nov. possess an outer seta on the P2–P4 basis. The loss of this seta is a synapomorphy linking *Macrosetella* and *Oculosetella*.

13. P1 exopod. The presence of three rather than four setae on exp-3 and the absence of the inner seta on exp-2 are autapomorphies for *Macrosetella*.

14. P3–P4 exopods. *Miracia* is the only genus that has retained three outer spines on the distal exopod segment of P3 (though being variable) and P4. The other genera are linked by the presence of only two outer spines on these segments. Only the number of outer spines on P4 exp-3 is scored in the present analysis.

15. P1–P3 endopods. The inner seta on the proximal segment of the 2-segmented endopod of P1 and the 3-segmented endopod of P2–P3 is lost only in *Oculosetella* and is regarded here as a (compound) autapomorphy for the genus. *Miracia* and *Distioculus* gen. nov. possess two inner setae on the middle endopod segment of P3, whereas only one seta (presumably the distal one) is retained in *Oculosetella* and *Macrosetella*. *Distioculus* gen. nov. is the only genus that has lost the inner seta of P4 enp-1.

16. P5 ♀. The basic number of six exopodal setae is present in *Miracia, Oculosetella* and *Macrosetella*. Comparison with the latter two genera shows that it is the outer distal seta that is absent in *Distioculus* gen. nov.. *Miracia* has the maximum number of five setae and spines on the baseoendopod. The proximal inner seta is missing in all other genera in which also the distal inner seta is very to extremely elongated. *Oculosetella* has also lost the middle inner seta.

17. P5 ♂. The most primitive condition is found in *Miracia* with six setae/spines on the exopod and three spines on the baseoendopod. In the other genera the exopod has only four setae (derived through loss of two outer spines) and the inner baseoendopodal spine is absent.

18. P6. Both sexes of *Miracia* and *Distioculus* gen. nov. have three setae on the P6. The outermost one is lost in the other two genera.

19. Caudal rami. In *Miracia, Distioculus* gen. nov. and *Oculosetella* the outer (IV) and inner terminal (V) setae are separate. In *Macrosetella* these setae are fused at the base to form a branched seta-complex. The ontogenetic sequence associated with the formation of this complex is explained above (section 'Copepodid development').

The distribution of the various character states are summarized in tabular form (Table 6) using the multistate scoring system. This character matrix was analysed using PAUP 3.1 with all characters set irreversible and employing the DELTRAN-option for character optimization. The analysis was performed at the species level using the BRANCH AND

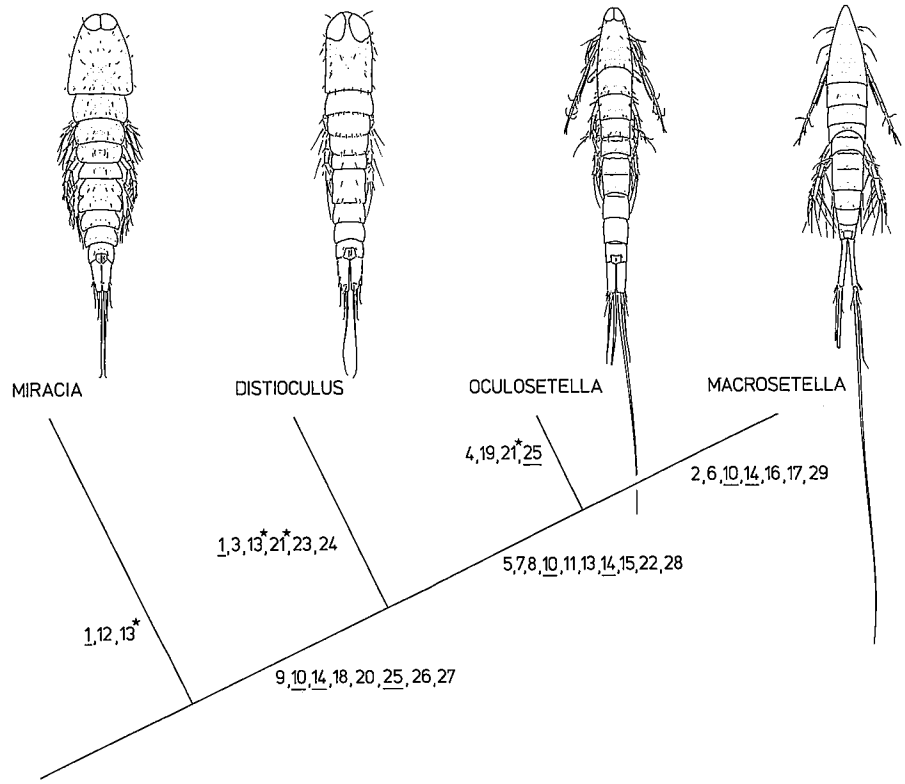

Fig. 41. Phylogenetic relationships within the Miraciidae. (For explanation see text; _ = multistate characters, * = convergence).

BOUND algorithm. The single tree obtained (tree length = 38 steps, consistency index 0.921, homoplasy index 0.079) reveals that the genus *Miracia* is a paraphyletic assemblage, corroborating the removal of *M. minor* to a new genus *Distioculus* (Fig. 41). The latter diverges as the sistergroup of the *Oculosetella-Macrosetella* branch. Superimposing the habitus on the cladogram shows that there is an evolutionary trend in body shape, changing from cyclopiform to fusiform types. Related to this trend are the changes in chitinization of the body, in width and shape of the intercoxal sclerites of P2-P4, and in the relative length of the inner terminal seta V. The tree shown in Fig. 41 contains two convergencies (character 13: loss of syncoxal setae of maxilliped in *Miracia* and *Oculosetella-Marcosetella* branch; character 21: loss of inner seta of P3 enp-1 in *Distioculus* gen. nov. and *Oculosetella*). Other characters that show up several times are 1, 10, 14, and 25 but this is a result of employing the multistate scoring system.

As in other harpacticoid families evolution in the

Table 6. Character data matrix (See Table 5). Characters are scored using the multistate system: 0 = ancestral (plesiomorphic) state, 1 = derived (apomorphic) state, 2 and 3 = further derived states, 9 = missing data, indicating that the structure is absent (character 3).

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Miracia	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oculosetella	0	0	0	1	1	0	1	1	1	2	1	0	1	2	1	0	0	1	1	1	1	1	0	0	2	1	1	1	0
Macrosetella	0	1	9	0	1	1	1	1	1	3	1	0	1	3	1	1	1	1	0	1	0	1	0	0	1	1	1	1	1
Distioculus	2	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	1	0	1	1	1	1	1	0	0

Miraciidae has followed the general crustacean trend of oligomerization, however, the underlying patterns and processes for this phenomenon are largely unknown. The study of developmental stages has illustrated that at least some of the reductions and losses (cf. rostrum, antennule, antenna, eye lenses) are due to arrest in ontogeny. Heterochrony, and neoteny in particular, seems to be one of the key events in copepod evolution and future studies in this area might help tremendously in elucidating relationships between genera and families. It does not, however, provide the answer to questions such as why the most successful miraciid species has lost its specialized eyes.

PERSPECTIVES

In this review we have already pointed out specific areas in need of more critical evaluation. There is, nevertheless, a need to re-emphasize some of the areas where deficiencies exist in our understanding, in the hope that future research will take them fully into account. It is conceivable that all four species are associated with filamentous cyanobacteria and it has been demonstrated that they can co-exist in blooms, however, to date there is no substantive evidence suggesting competition in space, time or food utilization. The evidence that these species are trophically dependent on *Trichodesmium* is accumulating at a rapid pace. Miraciids are extremely conservative in mouthpart structure, yet it is unknown whether there is any differential utilization of the available food resource in space and/or time. When co-occurring in *Trichodesmium* blooms, species of *Miracia*, *Oculosetella* and *Distioculus* are always numerically subordinate to *M. gracilis* which is the most successful miraciid world-wide but has lost its complex eyes. It remains an enigma why target detectors of this kind have disappeared in *Macrosetella* and how this can be linked to its success. Behavioural studies of all four species might prove to be a fruitful area of research to elucidate why evolution in this family has proceeded this way. In spite of being by far the best studied species, virtually nothing is known about the temporal aspects of feeding over the entire life cycle of *M. gracilis*, and how these aspects affect functional responses and population dynamics. It remains unresolved whether *Trichodesmium* is vital either to sustain the entire life cycle, to promote rapid maturation or to increase fecundity. HEINLE & al. (1977) for instance found for *Coullana canadensis* (Canuellidae) that detritus provided most of the energy required, but that the addition of algal cells to the copepod's diet remained necessary for egg production. Species incapable of trophic plasticity, are likely to be constrained to a narrow specialized range of food items which might only be available at certain times of the year, thereby controlling the reproductive pattern and numerical abundance. The only opportunity these species might have to assimilate sufficient energy from a particular nutritional resource for conversion into reproductive products is at a time when this food source goes into surplus, such as during *Trichodesmium* bloom conditions. It is not known whether miraciids can subsist on a diet of *Trichodesmium* alone and future ecological studies on *M. gracilis* would undoubtedly benefit from data on the quantitative relationship between the copepod and the cyanobacteria. The phasing of development and subsequent decay of a particular bloom could regulate substantially the aspects of the consumer's biology. Several aspects of the population dynamics of *M. gracilis*, including the development times of the copepodid stages and the alternation of size groups among adults as hypothesized in the testable model of BÖTTGER-SCHNACK & SCHNACK (1989), need to be investigated in an integrated study during drift experiments following the seasonal cycling of *Trichodesmium*. This should necessarily be parallelled by mesoscale observations on *Trichodesmium* distribution, e.g. by remote sensing via satellite (BÖTTGER 1985; FURNAS 1992). The complete life cycle of *M. gracilis* can only be elucidated by a continuous year-round study in areas of regular *Trichodesmium* occurrence at neritic and oceanic stations, covering both the epi- and mesopelagic zones. By doing so it can be shown whether a seasonal vertical migration of *M. gracilis*, as observed in the Red Sea, can be viewed as a universal phenomenon or merely as a local event in that particular area. In our view this kind of integrated studies is the essence of research into trophodynamics in tropical and subtropical marine areas. The presence of oil (lipid) droplets in miraciids is another unusual phenomenon among harpacticoids. It remains to be fully elucidated whether they are utilized for basal metabolic needs during downward migration when normal feeding might cease or for rapid incorporation into eggs, however, other explanations for their precise function should also be addressed. Finally, the use of radioisotopes as a device for tracing ingestion, assimilation, excretion and utilization of nutritional resources in metabolic processes is a fundamental area of research which deserves a greater injection of future effort.

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