



Towards a revision of *Ameira* Boeck, 1865 (Harpacticoida, Ameiridae): re-examination of the *A. tenella*-group and the establishment of *Filexilia* gen. n. and *Glabrameira* gen. n.

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A new genus *Filexilia*, is established to accommodate the *A. tenella*-group of *Ameira* Boeck, 1865 (Harpacticoida, Ameiridae), comprising *A. attenuata* Thompson, 1893; *A. tenella* Sars, 1907; *A. longicaudata* Nicholls, 1939; *A. brevipes* Kunz, 1954; *A. pestae* Petkovski, 1955; *A. longifurca* Bodin, 1964; *A. gravellicola* Guille & Soyer, 1966; *A. intermedia* Galhano, 1970; *A. brevipes pestae* Petkovski, 1955 *sensu* Marinov (1971); *A. brevipes* Kunz, 1954 *sensu* Apostolov (1977); and *A. tenella* Sars, 1907 *sensu* Kunz (1983).

Ameira longicaudata Nicholls, 1939, a permanently invalid name as a primary homonym of *A. longicaudata* T. Scott, 1892 (now type-species of *Stenocopia* Sars, 1907), is replaced by *Filexilia trisetosa* nom. n. and designated as the type-species. As a result of re-examination of the type material, *A. attenuata* is reinstated from its status of *species incertae sedis* in *Ameira* (Lang, 1948) as *Filexilia attenuata* (Thompson, 1893) comb. n., and *A. tenella* Sars, 1907 is relegated to a junior synonym of the latter. *Ameira tenella* Sars, 1907 *sensu* Kunz (1983) is regarded as a distinct species *F. azorica* sp. n. *Ameira longifurca*, previously considered a probable synonym of *A. tenella* by Moore (1976), is confirmed as a valid species *F. longifurca* (Bodin, 1964) comb. n. *Ameira pestae*, relegated to a subspecies or forma of *A. brevipes* (Lang, 1965), is reinstated at the species level. *Ameira brevipes pestae* Petkovski, 1955 *sensu* Marinov (1971) is sufficiently distinct from the latter to warrant the erection of a new species *F. marinovi* sp. n. *Ameira brevipes* Kunz, 1954 *sensu* Apostolov (1977) is regarded as *species inquirenda* in *Filexilia* whereas *A. brevipes* f. *pontica* Apostolov, 1969 is rejected.

Updated descriptions are given for both sexes of *F. trisetosa*, *F. attenuata* and *F. longifurca*. Keys to the species of *Filexilia* and *Sicameira* Klie, 1950 are presented and the phylogenetic relationships of both genera are discussed. *Ameira bengalensis* Rao & Ganapati, 1969 is transferred as the type-species of *Glabrameira* gen. n. © 1997 The Norwegian Academy of Science and Letters

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Introduction

The harpacticoid family Ameiridae currently contains 300 valid species and subspecies accommodated in 31 genera and is, in terms of species number, third only to the Canthocamptidae and Diosaccidae. Ameirids inhabit a wide range of sediment types and occur in virtually all salinity regimes. The family has a marine origin yet its successful secondary radiation in freshwater is exemplified by numerous species of the genera *Nitocrella* Chappuis, *Stygonitocrella* Petkovski, *Nitocrellopsis* Petkovski and *Parapseudoleptomesochra* Lang living in inland caves, karstic systems and other surface or subterranean habitats (Rouch 1986). Several members have colonized specialized habitats such as *Nitokra malaica* Kiefer living in hot-water springs (Heberer & Kiefer 1932) or species of *Psammonitocrella* Rouch inhabiting the hyporheic zone of rivers (Rouch 1992). Others have entered into loose associations

with invertebrate host organisms such as *Nitokra bdelluræ* (Liddell) living in the egg capsules of two parasitic flatworms *Bdellura propinqua* Wheeler and *B. candida* Girard associated with the horseshoe crab *Limulus* (Liddell 1912), *N. spinipes* Boeck (as *N. medusæa* Humes) on the exumbrellar surface of medusæ (Humes 1953), *N. divaricata* Chappuis living in the gill chambers of freshwater crayfish (Chappuis 1926; Jakubisiak 1939; Štraškraba 1956) and *N. sphaeromata* Bowman associated with the marine flabelliferan isopod *Sphaeroma peruvianum* Richardson (Bowman 1988).

The family is notorious for its numerous ill-defined genera and the fine-level systematics of the group is considered a taxonomic nightmare by many workers. The classification of the Ameiridae suffered a false start when Boeck (1865) inadequately defined two new genera, *Ameira* and *Nitokra*, on the basis of fragmentary descriptions totally lacking in illustrations. Most of the other

traditional marine genera were described and delineated in the early part of this century, notably by Sars (1907b, 1911) who split up *Ameira* into *Parameira* Sars, 1907 (replaced by *Sarsameira* Wilson, 1924), *Ameiropsis* Sars, 1907 and *Pseudameira* Sars, 1911. This course of action was the subject of severe criticism by Lang (1935, 1936) who rejected *Ameiropsis* as a valid genus, however, later he (Lang 1944, 1948) recognised the necessity of further subdividing *Ameira*, resulting in the erection of two new genera, *Proameira* and *Pseudosarsameira*, and the reinstatement of *Sarsameira*. Ironically, this progressive subdivision of *Ameira* did not lead to a better definition of the type-genus. Most authors have taken the conservative approach in utilizing the genus as a taxonomic repository and in one instance its boundaries were even further blurred by the amalgamation with *Psammameira* Noodt (Mielke 1975). Particularly in recent years the taxon has seen the addition of species of doubtful affinity, such as *A. confluens* Ranga Reddy, 1984 which unquestionably would warrant the erection of new genera.

Despite being the most speciose and morphologically diverse marine genus of the family no attempts have been made to delineate species groups within *Ameira*, except for Kunz (1983) who recognised the *A. tenella*-group as a distinct lineage. This paper is the first in a series towards the revision of the genus and removes the *tenella*-group to a new genus *Filexilia*.

Material and methods

Before dissection, body length measurements were made from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactic acid, and the parts mounted in lactophenol. Preparations were then sealed with glyceel (Gurr[®], BDH Chemicals Ltd, Poole, UK). All drawings have been prepared using a camera lucida on a Leitz Diaplan or Zeiss Axioskop differential interference contrast microscope. The descriptive terminology for body and appendage morphology is adopted from Huys & Boxshall (1991). Abbreviations used in the text are: ae, aesthetasc; P1–P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal(middle, distal) segment of a ramus. The type series is deposited in the collections of the Department of Zoology, The Natural History Museum, London.

Family AMEIRIDAE Monard, 1927

Genus *Filexilia* gen. n.

Diagnosis. *Ameiridae*. Body cylindrical and slender, without clear demarcation between prosome and urosome; integument pitted, not strongly chitinized. Hyaline frills of cephalothorax and somites bearing P2–P4 plain or minutely denticulate (abdominal somites). Female genital and first abdominal somites completely fused to form genital double-somite; transverse internal ribs marking original segmentation completely absent. Anal operculum minutely spinulose. Caudal ramus cylindrical, elongate; with 7 setae in both sexes. Sexual dimorphism in body size, antennule, P1 (inner basal spine), P5, P6, and in genital segmentation.

Rostrum small, bell-shaped; not demarcated at base. Antennule slender and elongate; setae smooth and slender except for single seta on segments 1 and 2, extremely long on distal segments; 8-segmented in ♀, with aesthetasc on

segments 4 and 8; 9-segmented and haplocer in ♂, with geniculation between segments 7 and 8 and aesthetasc on segments 5 and 9. Antenna with basis and proximal endopod segment incompletely fused forming allobasis; endopod with 3 lateral and 6 distal elements (outermost one with proximal tuft of setules). Antennary exopod distinctive, 2-segmented; armature formula [1,2]; exp-1 tapering proximally, with convex outer margin bearing fine spinule row(s); exp-2 minute, with lateral seta distinctly recurved. Mandibular palp uniramous, 2-segmented, comprising basis and 1-segmented endopod; basis with 1 pectinate and 1 flaccid densely plumose element; endopod with 1 lateral and 4 apical setae. Maxillule with 1 element on coxal endite; basis with 1 flaccid plumose element and 4 naked setae; endopod minute, with 2 setae; exopod absent. Maxillary syncoxa with 2 well developed endites, proximal one expanded distally and with 2 flaccid plumose setae; allobasis drawn out into a claw and with pectinate spine; endopod 1-segmented, with 2 elements. Maxilliped subchelate; syncoxa with 1 seta; endopod represented by pinnate claw with 2 accessory setae.

P1–P4 with 3-segmented rami. P1 exopod without inner seta on exp-2; exp-3 with 3 outer spines and 2 geniculate setae distally. P1 endopod prehensile, with enp-1 longer than enp-2 and -3 combined, and about as long as exopod; inner seta of enp-2 well developed. P2–P3 without inner setae exp-2 and P2–P4 without inner setae enp-1. Armature formula as follows:

	Exopod	Endopod
P1	0.0.023	1.1.111
P2	0.0.[0–1]23	0.1.121
P3	0.0.[0–1]23	0.1.[1–2]21
P4	0.[0–1].[2–3*]23	0.1.[0–1]21

*: when present, distal inner seta minute and displaced onto posterior surface.

P5 with separate baseoendopod and exopod in both sexes; baseoendopods fused medially in ♂; ♀ with 4 distal setae on baseoendopod (innermost 2 minutely serrate apically), exopod elongate and slender, with 5–6 setae; ♂ with 2–3 setae on baseoendopod and 5–6 setae on exopod. Female genital field positioned far anteriorly; with large copulatory pore leading via chitinized copulatory duct to median seminal receptacle; gonopores covered by common genital operculum derived from P6 with plumose seta and 2 spinous processes on either side. Male P6 slightly asymmetrical, with 3 simple setae, of which middle one longest.

Type-species. *Ameira longicaudata* Nicholls, 1939 = *F. trisetosa* nom. n.

Other species. *Ameira attenuata* Thompson, 1893 = *F. attenuata* (Thompson, 1893) comb. n.; *Ameira brevipes* Kunz, 1954 = *F. brevipes* (Kunz, 1954) comb. n.; *Ameira pestae* Petkovski, 1955 = *F. pestae* (Petkovski, 1955) comb. n.; *Ameira longifurca* Bodin, 1964 = *F. longifurca* (Bodin, 1964) comb. n.; *Ameira gravellicola* Guille & Soyer, 1966 = *F. gravellicola* (Guille & Soyer, 1966) comb. n.; *Ameira intermedia* Galhano, 1970 = *F. intermedia* (Galhano, 1970) comb. n.; *Ameira brevipes* Kunz subsp. *pestae* Petkovski, 1955 sensu Marinov (1971) = *F. marinovi* sp. n.; *Ameira tenella* Sars, 1907 sensu Kunz (1983) = *F. azorica* sp. n.

Species inquirenda. *Ameira brevipes* Kunz, 1954 sensu Apostolov (1977).

Etymology. The generic name is derived from the Latin *filum*, meaning

thread, and *exilis*, meaning slender, and refers to the slender nature of the antennule, bearing extremely long setae. Gender: feminine.

Filexilixia trisetosa nom. n.

Synonym. *Ameira longicaudata* Nicholls, 1939.

Material examined and type locality. 4 ♀♀, 2 ♂♂, 1 CV ♀ and 1 CV ♂ from the Natural History Museum, London deposited as: Types *Ameira longicaudata* (reg. no. 1940.5.1.29–34). Collected from Baie de Mille Vaches, north shore St. Lawrence River (Canada); washings of coarse sand; 8 m depth. Lectotype ♀ designated and dissected on 13 slides (reg. no. 1996.1115), paralectotypes (reg. no. 1996.1116–1122) are 3 ♀♀, 2 ♂♂ (P1–P4 and urosome of 1 ♂ dissected on 3 slides), 1 CV ♀ and 1 CV ♂ in alcohol.

Etymology. The trivial name refers to the presence of 3 setae/spines on P4 enp-3.

Redescription

Female. (Figs 1A–D, 2A–E, 3A–E, 5C, 8A–B.) Total body length 650 µm measured from tip of rostrum to posterior margin of caudal rami. Largest width 105 µm measured at posterior margin of P2-bearing somite.

Body cylindrical, slender (Fig. 1A), without distinct demarcation between prosome and urosome. Integument pitted, not strongly chitinized. Hyaline frill of cephalothorax and somites bearing P2–P5 smooth (Fig. 1A), minutely denticulate on genital double-somite and abdominal somites (Figs 1A, 2E, 5C). Cephalothorax and somites bearing P2–P4 without surface ornamentation (Fig. 1A). P5-bearing somite with minute spinule rows laterodorsally (Fig. 1A). Genital double-somite elongate; without internal chitinous ribs marking original segmentation (Figs 1A, 5C); with paired laterodorsal spinule rows both anteriorly and posteriorly; ventral posterior margin with median and paired ventrolateral spinule rows. Second abdominal somite (Figs 1A, 5C) with paired spinule rows laterodorsally and ventrolaterally, and median row ventrally. Third abdominal (Figs 1A, 5C) somite with midventral spinule row. Anal somite distinctly cleft medially (Figs 1A, 2E, 5C); with paired ventral, lateroventral and ventrolateral spinule rows anteriorly (largely concealed under hyaline frill of preceding somite); large spinules present around ventral hind margin; anal operculum slightly rounded, with minute spinules. Caudal rami (Figs 1A, 2E, 5C) elongate, slightly conical, 2.95 times as long as maximum width; inner margin with short rows of fine spinules proximally and distally; additional spinules present around ventral hind margin and outer distal corner; dorsal hind margin with minutely incised frill; with 3 secretory pores and 7 setae: seta I relatively long (Fig. 2E); seta III slightly displaced to ventral subdistal position (Fig. 2E); setae IV and V well developed and spinulose in distal portion; seta VI partially fused to inner distal margin of caudal ramus (Fig. 2E); seta VII triarticulate at base and located at insertion level of setae I–II.

Rostrum (Fig. 1A; see also Fig. 2F) small, bell-shaped not demarcated at base; with 2 dorsal sensilla and a ventral tube pore apically; shorter than first antennular segment.

Antennule (Fig. 1B) elongate and slender, 8-segmented. Segment 1 with 1 anterior spinule row. Segment 2 longest. Armature formula: 1-[1 pinnate], 2-[1 pinnate + 8 bare], 3-

[8], 4-[3 + (1 + ae)], 5-[2], 6-[4], 7-[4], 8-[5 + acrothek]. Apical acrothek consisting of 2 extremely long setae fused basally to slender aesthetasc. Very long setae present on segments 4–6 and 8.

Antenna (Fig. 1C) arising from distinct pedestal. Coxa minute, bare. Basis and proximal endopod segment incompletely fused forming allobasis; original segmentation marked by surface suture; with spinule rows in basal half as illustrated in Fig. 1C. Endopod with 2 surface frills subdistally; lateral armature consisting of 2 spines flanking a small seta arrowed in Fig. 1C; apical armature consisting of 5 geniculate setae, with longest one bearing spinules around geniculation and fused basally to smaller seta bearing proximal tuft of fine setules. Exopod 2-segmented (Fig. 1C); armature formula [1,2]; exp-1 elongate, tapering proximally, with convex outer margin bearing 2 fine spinule rows; exp-2 minute, with 2 pinnate setae, lateral seta distinctly recurved.

Mandible. Gnathobase with coarse teeth ventrally, 1 pinnate seta dorsally and row of smaller teeth in between. Palp (Fig. 2A) uniramous, 2-segmented; comprising basis and 1-segmented endopod. Basis with 1 pectinate and 1 flaccid, densely plumose seta. Endopod with 1 short pinnate seta laterally, 1 pinnate and 3 basally fused, naked setae apically.

Maxillule (Fig. 2B) with praecoxa and coxa largely fused. Praecoxal arthrite rectangular; with 2 anterior surface setae, 2 lateral elements and distal armature consisting of 3 bare spines and 2 pectinate/serrate spines. Coxal endite with long distally pinnate spine. Basis with 1 flaccid, plumose element and 3 naked setae distally and 1 naked seta laterally. Endopod represented by minute segment with 1 bipinnate and 1 smaller, unipinnate seta. Exopod absent.

Maxilla (Fig. 2C) with 2 well developed endites on syncoxa; proximal endite of distinctive shape, with 2 flaccid, plumose setae; distal endite with 1 apically serrate and 2 naked setae. Allobasis drawn out into claw; with pectinate spine at base. Endopod a discrete segment with 2 naked setae.

Maxilliped subchelate. Syncoxa with 1 pinnate seta; with spinule rows on anterior surface. Basis with 2 groups of spinules along outer margin. Endopod represented by long distally pinnate claw accompanied at base by short tube seta and longer bare seta.

P1 (Figs 1D, 3A) with well developed praecoxa. Coxa with 4 spinule rows. Basis with pinnate outer seta and unipinnate outer spine. Exopod 3-segmented; exp-2 without inner seta; exp-3 with 3 outer pinnate spines and 2 geniculate setae distally. Endopod 3-segmented, prehensile; with enp-1 longer than enp-2 and -3 combined and very slightly shorter than exopod, with subdistal serrate seta; enp-2 short, inner seta plumose and well developed; enp-3 long, 3.1 times as long as enp-2 (measured along inner margin), with unipinnate claw, 1 geniculate and 1 plumose seta.

P2–P4 (Fig. 3B–E) with 3-segmented rami; endopods shorter than exopods. P2 (Fig. 3B) exopod identical to P3 exopod (Fig. 3C). P2–P4 exp-3 and enp-3 elongate. Coxae well developed sclerites with spinule rows on both anterior and posterior surfaces. Bases with naked slender seta. Anterior surface of most endopodal and exopodal seg-

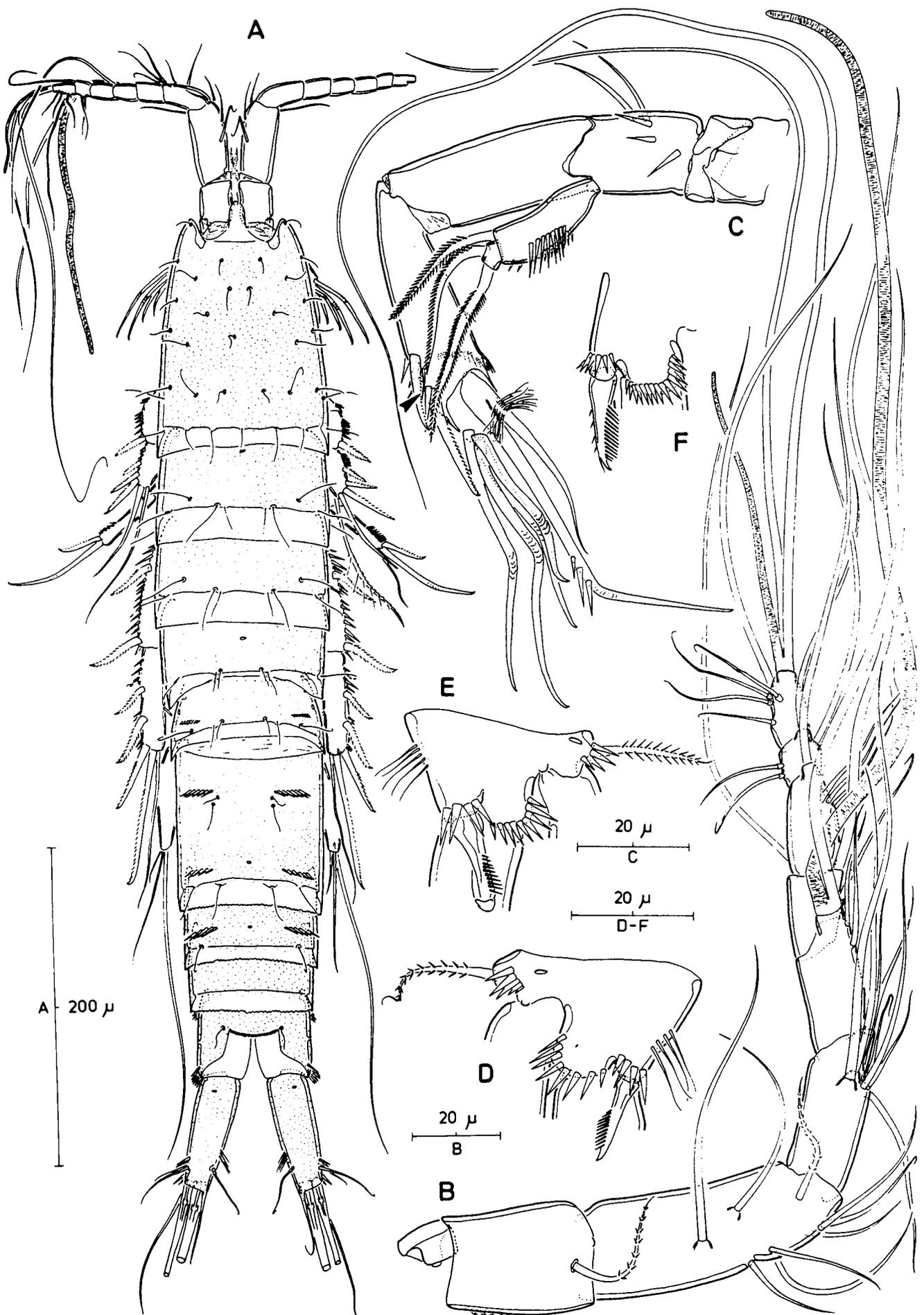


Fig. 1. *Filixilia trisetosa* nom. n.—A. Habitus ♀, dorsal.—B. Antennule ♀, ventral.—C. Antenna ♀ (arrow indicating small lateral seta).—D. P1 ♀, basis anterior.—E. P1 ♂, basis, anterior.—F. P1 CV ♂, inner basal spine.

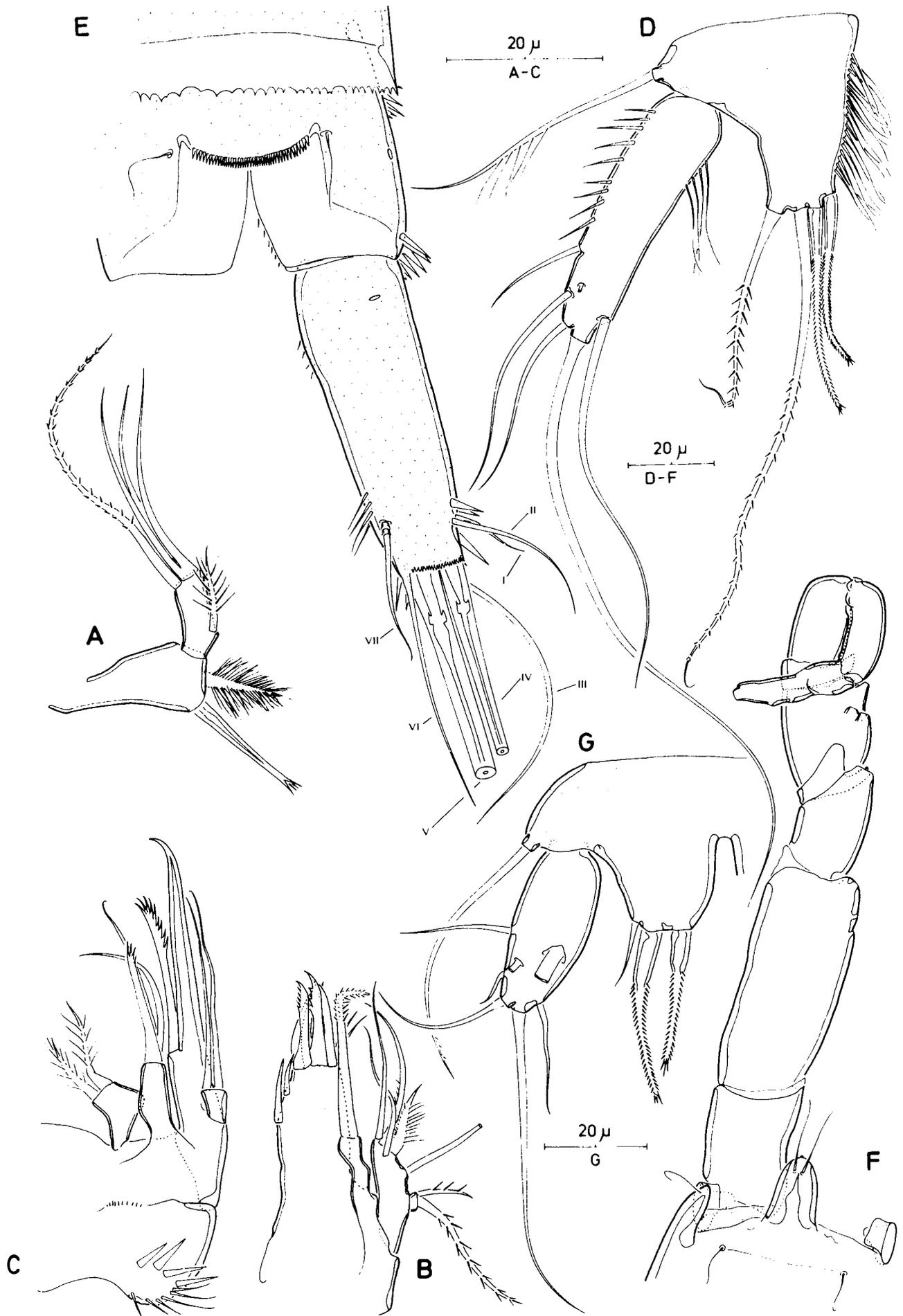


Fig. 2. *Filexilia trisetosa* nom. n.—A. Mandibular palp ♀.—B. Maxillule ♀.—C. Maxilla ♀.—D. P5 ♀, anterior.—E. Anal somite and right caudal ramus ♀, dorsal.—F. Rostrum and antennule ♂, dorsal (armature omitted).—G. Right P5 ♂, anterior.

ments with secretory pores. P4 (Fig. 3D); exp-2 inner seta small, 0.44 times segment length, arrowed in Fig. 3D; inner margin exp-3 with enlarged and strongly serrate middle seta and small recurved distal seta slightly displaced onto posterior surface (Fig. 3D–E). Armature formula as follows:

	Exopod	Endopod
P2	0.0.123	0.1.121
P3	0.0.123	0.1.121
P4	0.1.323	0.1.021

P5 (Fig. 2D) biramous. Baseoendopod with outer basal seta arising from short setophore. Endopodal lobe rectangular, inner margin with row of long setules; with 4 pinnate setae arranged around distal margin, innermost 2 minutely serrate apically. Exopod very long and slender, 3.8 times as long as maximum width; inner margin with few long setules and 1 naked seta; outer margin with spinule row and 3 bare setae; apex with 1 long naked seta; anterior surface with 1 secretory tube pore.

Genital field positioned near anterior margin of genital double-somite (Fig. 5C); paired gonopores opening via common midventral slit covered by genital operculum forming interlocking mechanism derived from fused vestigial sixth legs. P6 with 1 plumose seta and 2 spinous processes (Figs 5C, 8A). Copulatory pore large (Fig. 8A), leading via chitinized copulatory duct with supporting chitinized rod (arrowed in Fig. 8B) to single median seminal receptacle; flanked by 2 pores anteriorly.

Single egg sac.

Male. (Figs 1E, 2F–G). Larger than female; total body length 680 μm measured from tip of rostrum to posterior margin of caudal rami. Sexual dimorphism in body size, antennule, P1, P5, P6 and genital segmentation.

Antennule (Fig. 2F) slender, 9-segmented and haplocer; geniculation between segments 7 and 8; segment 2 longest; segment 4 represented by U-shaped sclerite; with aesthetasc on segment 5 and as part of apical acrothek on segment 9; apical segment with superficial transverse mark indicating possible ancestral fusion plane. Armature formula: 1-[1 pinnate], 2-[10], 3-[7], 4-[2], 5-[1 pinnate, 3 bare + (1 + ae)], 6-[1 pinnate + 1 bare], 7-[1 + 2 modified], 8-[1 + 2 modified], 9-[8 + acrothek].

P1 inner basal spine modified (Fig. 1E); acutely recurved; outer margin with spinule row.

P5 (Fig. 2G) biramous. Baseoendopod with outer basal seta arising from short setophore. Endopodal lobe not extending beyond middle of exopod; distal margin with 2 pinnate setae (minutely serrate apically) and a small naked outer seta. Exopod oval in shape and much shorter than in female; 2.4 times as long as maximum width; all setae naked; inner margin with 1 seta; outer margin with 3 setae; apex with 1 long seta; anterior surface with 2 large secretory pores.

P6 fused, slightly asymmetrical; with 3 bare setae each, middle one longest.

Spermatophore 73 μm .

Copepodid V ♂. Inner basal spine of P1 (Fig. 1F) not yet modified and resembling condition of adult ♀ (cf. Fig. 1D).

Variability. None observed.

Remarks. *Ameira longicaudata* Nicholls, 1939 is a permanently invalid name as a primary homonym of *A. longicaudata* T. Scott, 1892 (now type-species of *Stenocopia* Sars, 1907) and consequently substituted here by the new replacement name *Filexilia trisetosa* nom. n. (ICZN 3rd ed., Art. 52b, 57b). The species has never been redescribed nor recorded since its discovery in the St. Lawrence River. Nicholls' (1939) original description contains several deficiencies which can be attributed to omission or misinterpretation of structures and associated armature elements: (a) the male antennule is described as 7-segmented (but illustrated as 6-segmented) and the segment boundaries proximal to the geniculation are not identified; (b) the antennary exopod is 1-segmented, the minute apical segment being overlooked; (c) mandibular palp with only the pectinate seta present (the flaccid, plumose element is easily dislodged during dissection); (d) the maxillule is incomplete with the coxal endite being superimposed on the basis; (e) maxilla with only the distal endite illustrated; the pectinate seta on the allobasis appears to be dislodged since its insertion site is indicated by a notch on the inner margin of the claw; (f) the recurved inner seta on P4 exp-3 is overlooked; this element is frequently missed in descriptions of ameirids due to shape, size and typically displaced position onto posterior surface; (g) P5 ♂ with 2 setae on baseoendopod (innermost spine absent) and only 4 setae on exopod (the small outer seta missing).

Nicholls (1939) recognized a certain similarity between *A. longicaudata* and *A. attenuata* in the elongate fifth legs and caudal rami. The affinity of this species to other members of the *tenella*-group has been alluded to by several authors (Kunz 1954, 1983; Bodin 1964; Guille & Soyer 1966; Galhano 1970). It can be readily distinguished by the loss of the inner seta on the distal endopod segment of P4 in conjunction with the presence of only 5 setae on the female P5 exopod.

Filexilia attenuata (Thompson, 1893) comb. n.

This species has been considered *incertae sedis* in *Ameira* by Lang (1948). Re-examination of the two type specimens (to be considered syntypes) held at the Natural History Museum, London, revealed them to represent two different species, the ♀ conforming to Sars' (1907a) description of *A. tenella*, the ♂ agreeing in almost every aspect to *A. brevipes* Kunz, 1954. The ♀ type is designated herein as the lectotype of *F. attenuata* and consequently *A. tenella* Sars, 1907 is relegated to a junior subjective synonym of the former.

Synonym. *Ameira tenella* Sars, 1907.

Material examined and type locality. (a) The Natural History Museum, London: 1 ♀ mounted *in toto* on slide, labelled Type (reg. no. 1959.2.9.5); from Port Erin, The Isle of Man (type locality); designated herein as lectotype; (b) The Natural History Museum, London: 1 damaged ♀ in

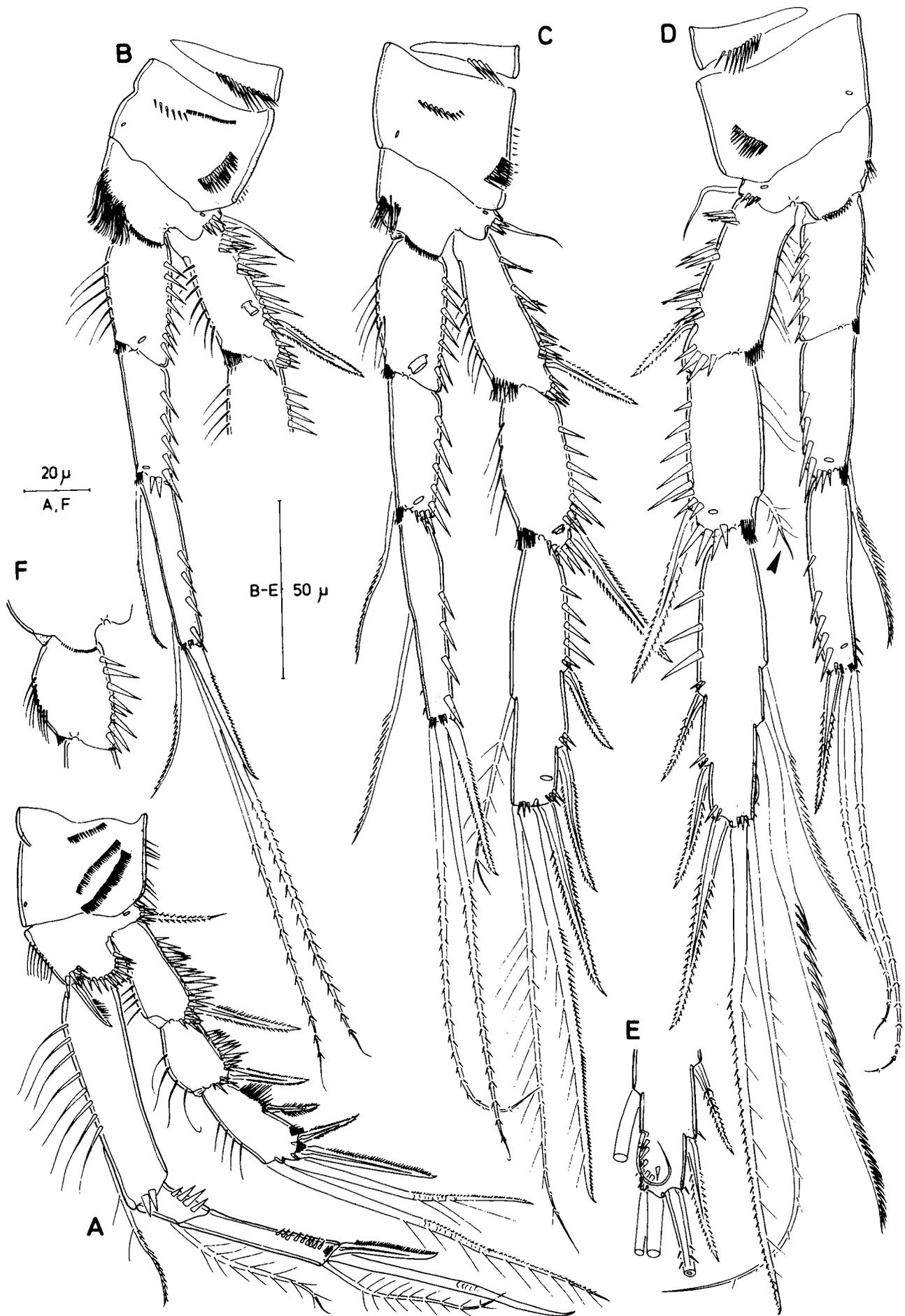


Fig. 3. *Filexilia trisetosa* nom. n.—A. P1 ♀, anterior.—B. P2 ♀, anterior (exp-2 and -3 omitted).—C. P3 ♀, anterior.—D. P4 ♀, anterior (arrow indicating small inner seta of exp-2).—E. P4 ♀, exp-3, distal portion, posterior. *Filexilia attenuata* comb. n.—F. P2 ♀, exp-1, anterior.

alcohol (reg. no. 1967.10.31.52), labelled *A. brevipes*; Isles of Scilly, Peninnis Head; det. J.B.J. Wells; (c) Zoologisches Museum, Kiel: Klie-collection, 1 ♀ dissected on slide (reg. no. Cop 145); labelled as *Ameira attenuata*; Helgoland, southeastern part of harbour entrance, from red algae taken at 8m depth; det. W. Klie, coll. H.W. Schäfer, 14 September 1935; (d) Zoologisches Museum, Kiel: Klie-collection, 1 ♀ dissected on slide (reg. no. Cop 146); labelled as *Ameira attenuata*; Helgoland, washings of *Laminaria digitata* holdfasts; det. W. Klie, coll. H.W. Schäfer, 14 September 1935; (e) 5 ♀♀ (1 ♀ damaged) and 1 damaged ♂ in alcohol (reg. no. 1996.1123–1127), 1 ♀ dissected on 6 slides (reg. no. 1996.1128) all from Frierfjord/Langesundfjord, Norway, 99 m deep mud, coll. R. Huys, 1985 (deposited in NHM).

Redescription (based on the Norwegian material)

Female. (Figs 3F, 4A–E, 5A, D, 7A, 8C–D). Total body length 554 µm measured from tip of rostrum to posterior margin of caudal rami (600 µm in lectotype).

Body cylindrical, slender. Integument pitted, not strongly chitinized. Hyaline frill of cephalothorax and somites bearing P2–P5 smooth, minutely denticulate on genital double-somite and abdominal somites (Figs 4A, 5D). Cephalothorax and somites bearing P2–P4 without surface ornamentation. P5-bearing somite with paired laterodorsal spinule rows. Genital double-somite elongate; without internal chitinous ribs marking original segmentation (Fig. 5D); with paired laterodorsal spinule rows both anteriorly and posteriorly; hind margin with spinule row dorsally and laterally but not ventrally. Second abdominal somite with paired spinule rows laterodorsally and ventrolaterally, and median row ventrally. Third abdominal somite with midventral spinule row (Fig. 5D). Anal somite distinctly cleft medially (Figs 4A, 5D); with paired ventral, lateroventral and ventrolateral spinule rows anteriorly (largely concealed under hyaline frill of preceding somite); spinules present around ventral hind margin; anal operculum slightly rounded with minute spinules (Fig. 4A). Caudal rami (Figs 4A, 5D) elongate, cylindrical, 2.85 times as long as maximum width; inner margin with short row fine setules proximally; spinules present around ventral hind margin and outer distal corner (Figs 4A, 5D); with 3 secretory pores and 7 setae: seta I long, almost as long as seta II (Fig. 4A); seta III slightly displaced to ventral subdistal position (Fig. 4A); seta IV and V well developed and spinulose in distal portion; seta VI partly fused to inner distal margin of caudal ramus (Fig. 4A); seta VII subdistal, triarticulate at base and located distal to insertion level of setae I–II.

Rostrum as in type-species.

Antennule (Fig. 5A) elongate, slender, 8-segmented. Segment 1 with 1 anterior spinule row. Segment 2 longest. Armature formula: 1-[1], 2-[9], 3-[8], 4-[3 + (1 + ae)], 5-[2], 6-[4], 7-[4], 8-[5 + acrothek]. Apical acrothek consisting of 2 long naked setae fused basally to slender aesthetasc.

Antenna arising from distinct pedestal. Coxa minute, bare. Basis and proximal endopod segment incompletely fused forming allobasis (Fig. 4B); original segmentation marked by surface suture; with spinule rows in basal half (Fig. 4B). Endopod armature and ornamentation as in type-species. Exopod 2-segmented (Fig. 4B); armature formula [1,2]; exp-1 elongate, tapering proximally, with convex outer margin bearing 2 fine spinule rows; exp-2 minute, with 2 pinnate setae, lateral seta distinctly recurved.

Mandible (Fig. 4C), maxillule, maxilla and maxilliped as for the type-species except for the following: (1) mandibular palp uniramous basis (Fig. 4C) more elongate and broader distally; lateral pinnate seta of endopod slightly larger than in type-species; (2) maxillary endopod minute with 1 pinnate seta and 1 smaller naked seta (cf. this seta is unipinnate in the type-species).

P1 (Fig. 7A) with well developed praecoxa. Coxa with 4 spinule rows. Basis with pinnate outer seta and bipinnate inner spine. Exopod as for type-species. Endopod 3-segmented, prehensile, with enp-1 longer than enp-2 and 3 combined and about as long as exopod, with subdistal strongly serrate seta; enp-2 short, with well developed inner plumose seta; enp-3 long, 4.8 times as long as enp-2 (measured along inner margin), with unipinnate claw, 1 geniculate and 1 long plumose seta.

P2–P4 with 3-segmented rami; endopods shorter than exopods. P2–P4 exp-3 and enp-3 elongate; enp-1 with rounded inner margin (P2 enp-1 see Fig. 3F). Coxae well developed sclerites with spinule rows on both anterior and posterior surfaces. Bases with naked slender seta. P4 exp-2 inner seta longer than in type-species, 1.23 times segment length; inner margin of exp-3 with enlarged, serrate middle seta and small recurved distal seta slightly displaced onto posterior surface. Armature formula as follows:

	Exopod	Endopod
P2	0.0.123	0.1.121
P3	0.0.123	0.1.221
P4	0.1.323	0.1.121

P5 (Fig. 4E) biramous. Baseoendopod truncate with outer basal seta arising from short setophore and with 2 anterior pores. Endopodal lobe slightly developed, inner margin with row of long setules; with 4 pinnate setae arranged around distal margin, innermost 2 minutely serrate apically. Exopod very long and slender, 4.9 times as long as maximum width; all setae naked; inner margin with few long setules and 1 seta; outer margin with spinule row and 4 setae; apex with 1 long seta.

Genital field positioned near anterior margin of genital double-somite (Fig. 5D); form and structure as in type-species (Fig. 8C–D) except for (1) copulatory pore circular and positioned more closely to genital slit, (2) copulatory duct less chitinized proximally and with bifid supporting rod, and (3) setae and spinous elements stubbier than in type-species.

Single egg sac.

Male. (Fig. 4F–G.) The exact body length could not be measured since the only ♂ specimen was damaged, but was approximately 520 µm measured from tip of rostrum to posterior margin of caudal rami; smaller than the female. Sexual dimorphism in body size, antennule, P1, P5, P6 and genital segmentation.

Antennule, 9-segmented, as in type-species.

P1 inner basal spine modified (Fig. 4F); acutely recurved; outer margin with spinule row.

P5 (Fig. 4G) biramous. Baseoendopod with outer basal seta arising from short setophore. Endopodal lobe not extending beyond middle of exopod; inner margin with

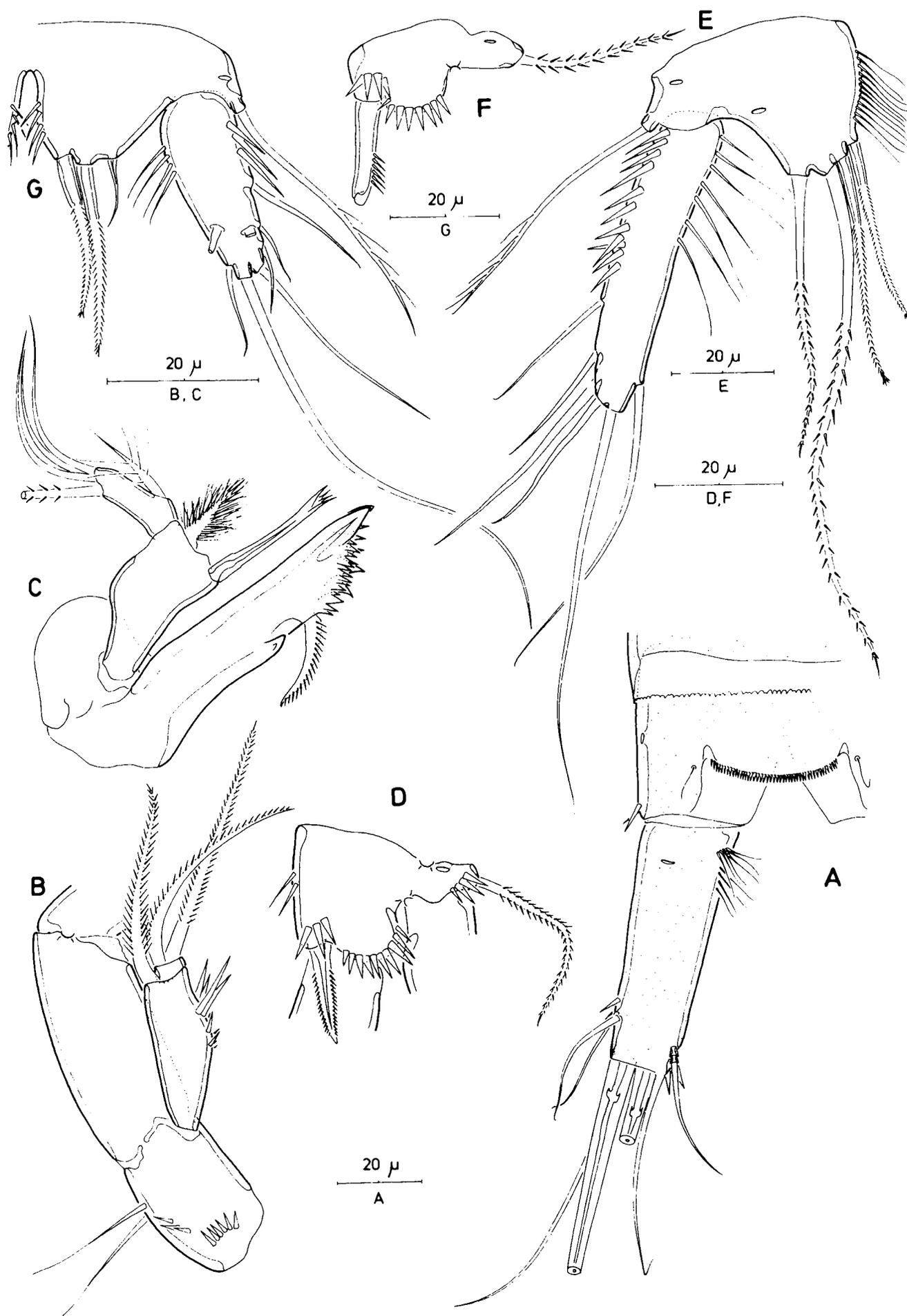


Fig. 4. *Filexilia attenuata* comb. n.—A. Anal somite and left caudal ramus ♀, dorsal.—B. Antenna ♀ (endopod omitted).—C. Mandible ♀.—D. P1 ♀, basis, anterior.—E. P5 ♀, anterior.—F. P1 ♂, basis, anterior.—G. Left P5 ♂, anterior.

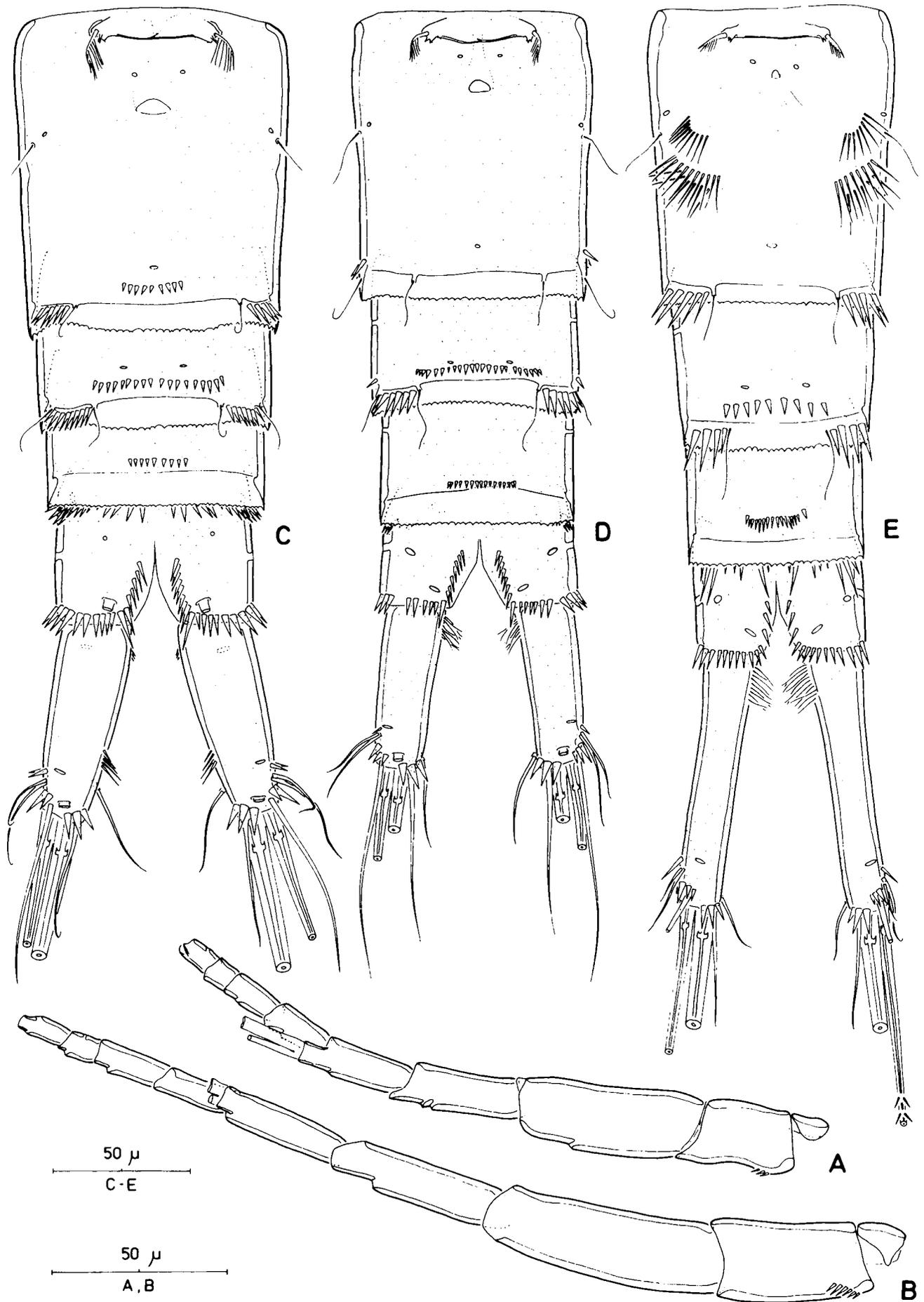


Fig. 5. *Filixilia attenuata* comb. n.—A. Antennule ♀, ventral (armature omitted).—D. Urosome ♀ (excluding P5-bearing somite), ventral. *Filixilia longifurca* comb. n.—B. Antennule ♀, ventral (armature omitted).—E. Urosome ♀ (excluding P5-bearing somite), ventral. *Filixilia trisetosa* nom. n.—C. Urosome ♀ (excluding P5-bearing somite), ventral.

spinule row; distal margin with 2 pinnate setae (minutely serrate apically) and a small naked outer seta. Exopod oval in shape and much shorter than in female; 2.5 times as long as maximum width; all setae naked; inner margin with few long setules and 1 seta; outer margin with spinule row and 4 setae; apex with 1 long seta; anterior surface with 2 large secretory pores.

P6 fused, slightly asymmetrical; with 3 bare setae each, middle one longest.

Variability. None observed.

Remarks. Sars (1911) himself, in his supplement to *The Crustacea of Norway*, relegates *A. tenella* Sars, 1907 with slight reservations to a synonym of *A. attenuata* Thompson, 1893. Lang (1948) does not exclude conspecificity but regards Thompson's description and illustrations of no value in validating this synonymy and retains *A. tenella* as a distinct species. He considers *A. attenuata* as unrecognizable and refers it to *species incertae et incertae sedis* of *Ameira*. Farran (1913) records a single specimen off Killary Harbour (Ireland) but mentions that it agrees with Sars' (1907a) illustrations of *A. tenella*. Holmes & O'Connor (1990) also found their single female from near Lough Hyne to conform with Sars' figures of *A. tenella* and considered its identity with Farran's (1913) specimen likely. Williams (1954), in his study of Strangford Lough, followed Sars' course of action and lists the species as *A. attenuata*. Apart from these three Irish records all other workers have followed Lang (1948) and ignored *A. attenuata*.

Our Norwegian specimens agree in every aspect with the lectotype of *A. attenuata*. The following key characters proved, upon comparison to be identical: (a) shape and setation of antennary exopod; (b) detailed morphology and morphometry of P1, including enp-3 length relative to enp-2 (4.6 times as long as maximum width); (c) ♀ P5 setation, length/width ratio of exopod (4.8 times as long as wide), and truncate shape of endopodal lobe. The P3 (enp-2 and -3) and P4 (exopod, enp-2 and -3) are incomplete, but the setal formula of the remaining segments are identical to that of the Norwegian specimens. There appears to be a slight deviation in the type specimen with regard to the caudal ramus length/width ratio being 2.4 compared to 2.85 in *F. attenuata*. The type specimen is, however, extremely squashed which would account for the difference observed.

The Norwegian material has also served as the basis for the first description of the male. Klie (1950) claims to have found the undiscovered male of *A. tenella*, but Kunz (1954) pointed out that it represents the unknown male of his new species *A. brevipes*.

There are only a few anomalies between Sars' (1907a) description of *Ameira tenella* based on specimens from Risør and Farsund, Norway, and the present redescription, namely: A2 exopod illustrated as 1-segmented bearing 2 setal elements; mandibular palp, basis with 1 element; P4 exp-3 with 2 inner distal setae; P5 ♀ exopod with only 5 setae. Since all of these slight discrepancies are conceivably the result of imperfect dissection or observation, we affirm Sars' (1911) supposition and relegate *A. tenella* to a junior synonym of *A. attenuata*. Coincidentally,

the same oversights were made by Nicholls (1939) in his original description of *A. longicaudata*.

The specimens of *A. tenella* collected from the Isle of Man, partially redescribed and illustrated by Moore (1976) clearly belong to *F. attenuata*. The abdominal ornamentation pattern, the structure of the antennary exopod, all aspects of P5 ♀ (with exopod 4.5 times as long as maximum width) and the length of the caudal rami (2.9 times as long as maximum width) are all identical to those redescribed above. Kunz (1983) also redescribed *A. tenella*, but his material from the Azores displays a different setal formula and will be referred here to a new species *F. azorica*. There is no factual justification for Moore's (1976) proposal to synonymize *A. tenella* and *A. longifurca* Bodin, 1964 (see below).

With specific reference to the antennule and antennary exopod Lang (1948) distinguishes *A. attenuata* from *A. tenella*, and suggests the former more likely to be identical to *A. speciosa* Monard, 1935 based on the similarity of these two characters in both species and differences only in the length of the caudal rami and structure of the P5. Despite Thompson's (1893) description being grossly inadequate, a comparison of the original descriptions for each species reveals Lang's (1948) assumptions to be essentially unsubstantiated. Of the swimming legs of *A. attenuata* Thompson illustrates only the P1 and P4, the latter shown as an elongate appendage with fewer setae (notable absence of an inner seta on enp-1) and longer endopod than in *A. speciosa*. Additional evidence is found in the armature formula of P2–P4 which, taken from Monard's (1935) description, agrees with that found in the *longipes*-group of *Ameira*. The distinctive nature of the antenna and the truncate baseopod of the P5 in *A. attenuata* are indicated in Thompson's rudimentary drawings and are not comparable to those of *A. speciosa*. Hence, there is no evidence to suggest that *A. attenuata* and *A. speciosa* are synonymous or even closely related.

Filexilia attenuata and *F. longifurca* are the only species that have retained the maximum setation on the swimming legs and female P5. They differ in the detailed morphology of the antennule, antenna, swimming legs, P5 of both sexes, ♀ genital field, body ornamentation, caudal rami and size. A useful character to separate females of these species is the distinctive truncate endopodal lobe of the P5 in *F. attenuata*. Males can be readily distinguished on the basis of the P5. The species assumes a typically nordic distribution with records from Ireland (Farran 1913; Williams 1954; Holmes & O'Connor 1990), the Isle of Man (Thompson 1893; Herdman 1896; Moore 1976), Isles of Scilly (Wells 1961, 1970 (as *A. brevipes*)), southern Celtic Sea (Gee unpubl.), Helgoland (Klie 1950; Kunz 1954) and southern Norway (Sars 1907b). Other records from Portugal (Wells & Clark 1965), Romania (Por 1964a; Marcus 1970; Apostolov 1971) and Israel (Por 1964a) require confirmation.

Filexilia azorica sp. n.

Synonym. *Ameira tenella* Sars, 1907 *sensu* Kunz (1983).

Material examined. None.

Etymology. The trivial name refers to the type locality.

Remarks. Kunz (1983) pointed out that his female specimens of *A. tenella* from the Azores agreed closely with Moore's (1976) redescription based on Manx material. The author recognized particular similarities in the length:width ratio of the caudal rami, segmentation and setation of the antennary exopod, the presence of the tiny recurved seta on the P4 exopod and the armature formula of the P5 exopod. Kunz maintains that the Azorian population differs in the absence of the inner seta on P4 enp-3, a character which he considers to be typical for *A. brevipes*. Both statements are incorrect since the presence of only 3 setae on this segment (formula 021) is diagnostic for the type-species *F. trisetosa* only (see above) — not the *A. brevipes* complex — and both Kunz' text and illustrations clearly show the inner seta to be present in his material. It is obvious that this contradiction results from a *lapsus calami* and the author really referred to the P3. Comparison with other species assigned to the *tenella*-group reveals that the material from the Azores displays a unique setal formula and consequently deserves distinct species rank: *F. azorica* sp. n.

	Exopod	Endopod
P2	0.0.123	0.1.121
P3	0.0.123	0.1.121
P4	0.1.323	0.1.121

The elongate P5 exopod with parallel lateral margins relates the new species to *F. trisetosa*, *F. attenuata* and *F. longifurca*. Within this group *F. azorica* seems to be closest to *F. attenuata* and *F. longifurca* in the number of elements on P4 enp-3 and female P5 exopod but differs from these species in the setation of P3 enp-3. It can also be readily distinguished from the latter by the shorter caudal rami and the facies of the antennary exopod and differs from *F. attenuata* in the shape of the female baseoendopod (not truncate) and the first endopod segment of P2-P4 (with straight inner margin). Additional discrepancies between the new species and *F. attenuata* include the shorter caudal rami (L:W ratio 2.4 vs 2.85) and the relative length of the outer distal spine of P2 enp-3 (much longer in *F. azorica*).

Type locality: Ilha São Miguel, Ribeira Seca, Azores.

Filexilia longifurca (Bodin, 1964) comb. n.

Material examined. From Dr P. Bodin: paratypes, (a) 2 ♀♀ in alcohol, ♀ dissected on 2 slides [nos LXXXVI(h) and LXXXVI(c)], ♂ dissected on 1 slide [no. LXXXVI], retained in personal collection of Dr Bodin; (b) additional paratypes deposited at the Natural History Museum, London: 1 ♀ dissected on 9 slides [reg. no. 1996.1129], 1 ♂ damaged urosome on slide [reg. no. 1996.1130] and ♂ prosome in alcohol [reg. no. 1996.1131]. All paratypes from Plateau des Chèvres, Golfe de Marseille, France. The following redescription is based on the material listed under (b).

Redescription

Female. (Figs 5B, E, 6A–D, 7B–C, 8E–F). Total body length 658 µm ($\times=637$, $n=2$) measured from tip of rostrum to posterior margin of caudal rami.

Body cylindrical, slender. Integument pitted, not strongly chitinized. Hyaline frill of cephalothorax and somites bearing P2–P4 smooth, minutely denticulate on

genital double-somite and abdominal somites (Fig. 5E). Cephalothorax and somites bearing P2–P5 without surface ornamentation. Genital double-somite elongate; without internal chitinous ribs marking original segmentation (Fig. 5E); with paired laterodorsal spinule rows both anteriorly and posteriorly and with 3 pairs ventrolateral setule rows medially; posterior margin with paired ventrolateral spinule rows. Second abdominal somite with paired spinule rows laterodorsally and ventrolaterally, and median row ventrally. Third abdominal somite with midventral spinule row (Fig. 5E). Anal somite distinctly cleft medially (Figs 5E, 6D); with midventral and paired ventrolateral spinule rows anteriorly (largely concealed under hyaline frill of preceding somite); spinules present around ventral hind margin; anal operculum slightly rounded with minute spinules (Fig. 6D). Caudal rami (Figs 5E, 6D) extremely long, cylindrical, 4.6 times as long as maximum width; inner margin with row of fine setules proximally; spinules present around ventral hind margin and outer distal corner (Figs 5E, 6D); with 2 secretory pores and 7 setae: seta I relatively well developed (Fig. 6D); seta III slightly displaced to ventral subdistal position (Fig. 6D); seta IV and V well developed and spinulose in distal portion; seta VI partly fused to inner distal margin of caudal ramus (Fig. 6D); seta VII subdistal, triarticulate at base and located distal to insertion level of setae I–II.

Rostrum as in type-species, also see Fig. 7D.

Antennule (Fig. 5B) elongate, slender, 8-segmented. Segment 1 with 1 anterior spinule row. Segment 2 longest. Segment 8 with apical acrothek consisting of 2 long naked setae fused basally to slender aesthetasc.

Antenna in general more elongate than in type-species; arising from distinct pedestal. Coxa minute, bare. Basis and proximal endopod segment incompletely fused forming allobasis (Fig. 6A); original segmentation marked by surface suture; with spinule rows in basal half (Fig. 6A). Endopod armature and ornamentation as in type-species. Exopod 2-segmented (Fig. 6A); armature formula [1,2]; exp-1 very long and slender, tapering proximally, with convex outer margin bearing spinule row; exp-2 minute, with 2 pinnate setae, lateral seta distinctly recurved.

Mandible, maxillule, maxilla and maxilliped (Fig. 7C) as for the type-species except for the following: (1) mandibular gnathobase more elongate, with finer teeth dorsally (Fig. 6B); (2) minute maxillary endopod segment completely incorporated into basis, with 2 pinnate setal elements still present as in type-species.

P1 (Fig. 7B) with well developed praecoxa. Coxa with 5 spinule rows. Basis with pinnate outer seta and bipinnate inner spine. Exopod as for type-species. Endopod 3-segmented, prehensile, with enp-1 longer than enp-2 and -3 combined and about as long as exopod, with subdistal serrate seta; enp-2 short, with well developed inner plumose seta; enp-3 long, 4.58 times as long as enp-2 (measured along inner margin), with unipinnate claw, 1 geniculate and 1 long plumose seta.

P2–P4 with 3-segmented rami; endopods shorter than exopods. P2–P4 exp-3 and enp-3 very elongate. Coxae well developed sclerites with spinule rows on both anterior and posterior surfaces. Bases with weakly pinnate (P2) or naked slender (P3–P4) outer seta. P4 exp-2 inner seta longer than in type-species, 0.78 times segment length;

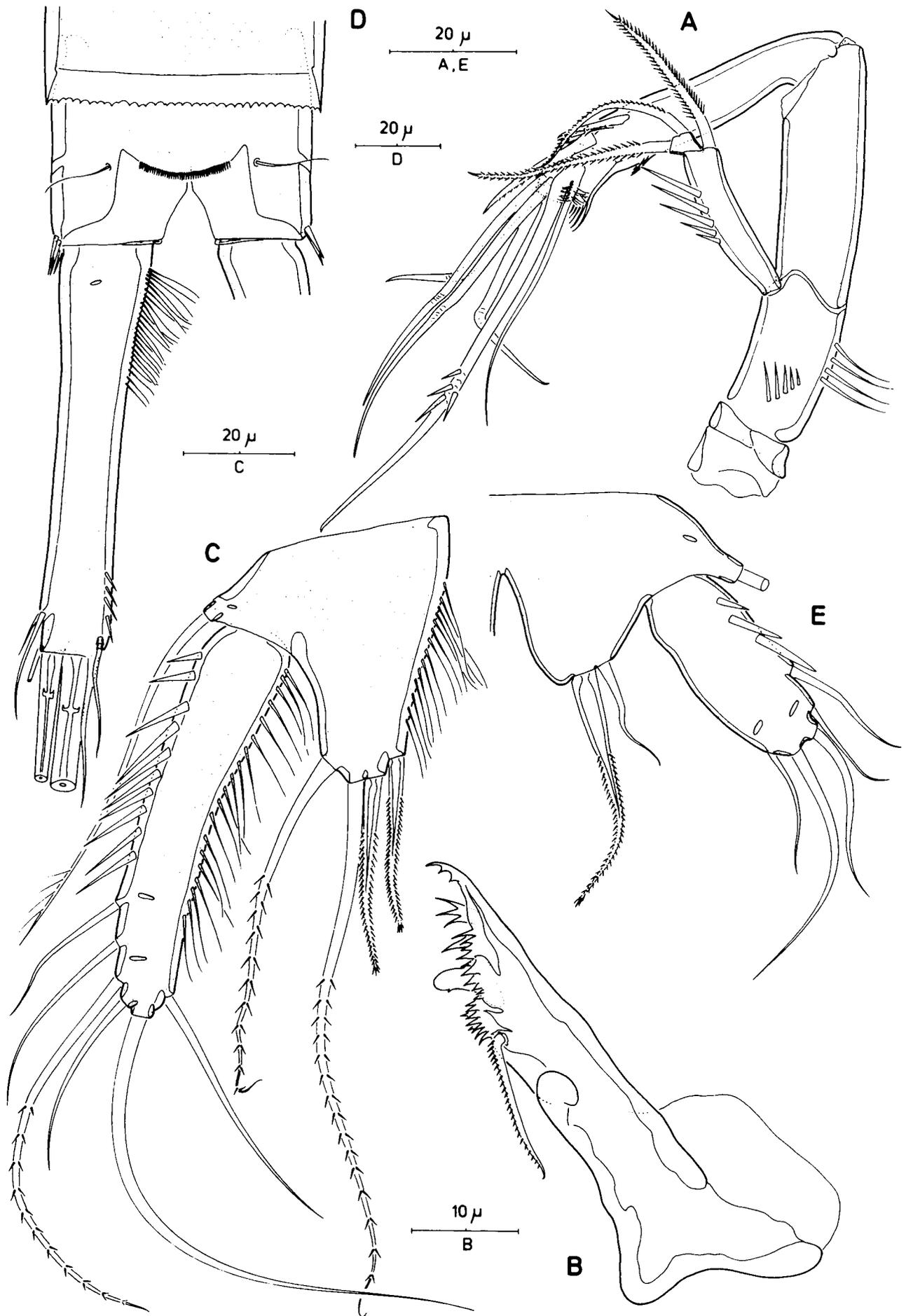


Fig. 6. *Filexilia longifurca* comb. n.—A. Antenna ♀.—B. Mandibular gnathobase ♀.—C. P5 ♀, anterior.—D. Anal somite and left caudal ramus ♀, dorsal.—E. Left P5 ♂, anterior.

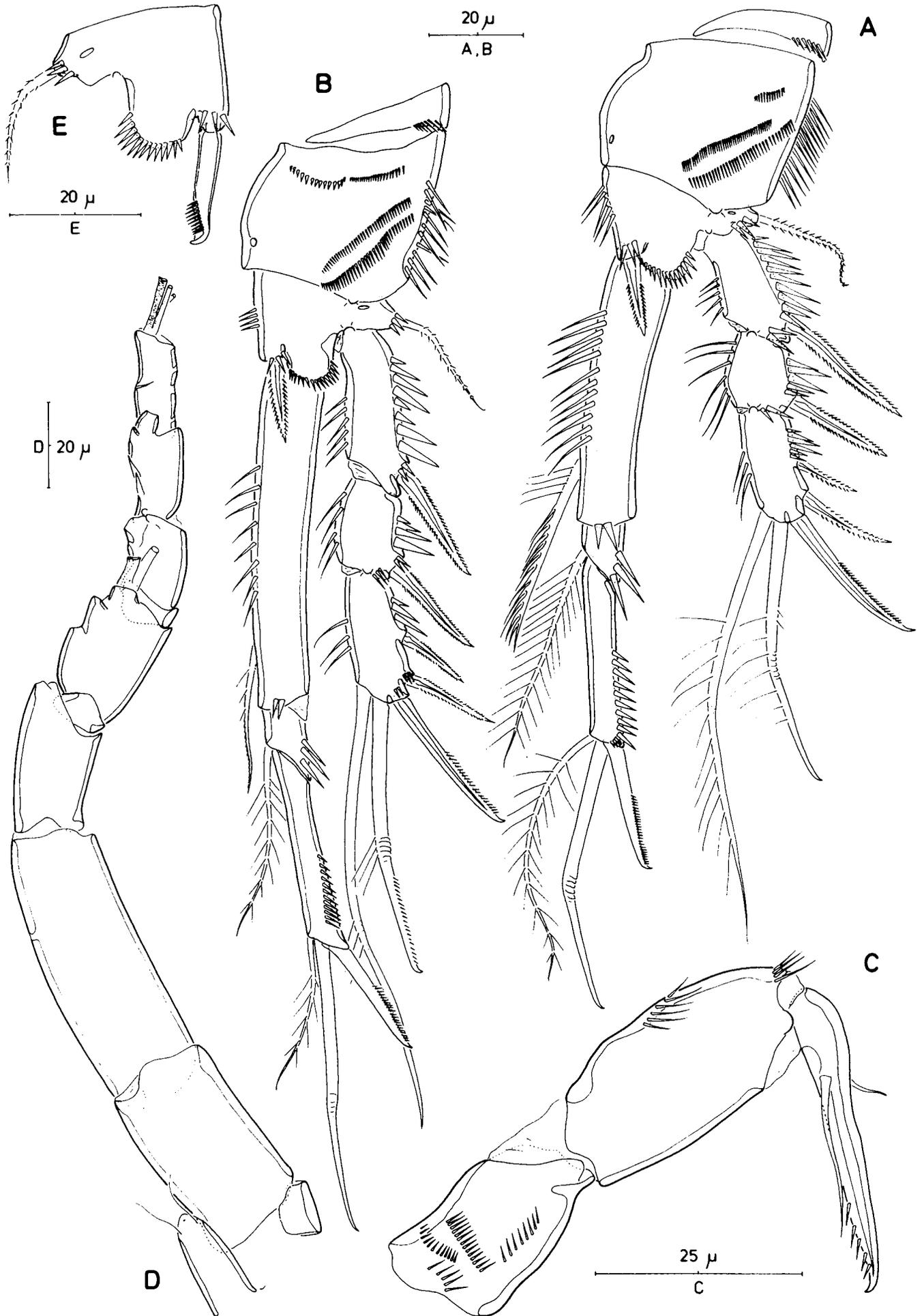


Fig. 7. *Filexilia attenuata* comb. n.—A. P1 ♀, anterior. *Filexilia longifurca* comb. n.—B. P1 ♀, anterior.—C. Maxilliped ♀, anterior.—D. Rostrum and antennule ♂, dorsal (armature omitted).—E. P1 ♂, basis, anterior.

inner margin of exp-3 with small recurved distal seta slightly displaced onto posterior surface. Armature formula of swimming legs as follows:

	Exopod	Endopod
P2	0.0.123	0.1.121
P3	0.0.123	0.1.221
P4	0.1.323	0.1.121

P5 (Fig. 6C) biramous. Baseoendopod with outer basal seta arising from short setophore and with 1 anterior pore. Endopodal lobe rectangular, inner margin with row of long setules; with 4 pinnate setae arranged around distal margin, innermost 2 minutely serrate apically. Exopod very long and slender, 4.7 times as long as maximum width; inner margin with row of long setules and 1 seta; outer margin with spinule row, 1 pinnate and 3 naked setae; apex with 1 long seta.

Genital field positioned near anterior margin of genital double-somite (Fig. 5E); form and structure as in type-species (Fig. 8E–F) except for: (1) copulatory pore smaller, circular and positioned more closely to genital slit; (2) copulatory duct less chitinized proximally and (3) setae, and spinous elements stubbier than in type-species.

Single egg sac.

Male. (Figs 6E, 7D–E). Body length 670 μm , measured from tip of rostrum to posterior margin of caudal rami; larger than the female. Sexual dimorphism in body size, antennule, P1 (inner basal spine), P5, P6 and genital segmentation.

Antennule (Fig. 7D), 9-segmented, as in type-species.

P1 inner basal spine modified (Fig. 7E); acutely recurved; outer margin with spinules.

P5 (Fig. 6E) biramous. Baseoendopod with outer basal seta arising from short setophore. Endopodal lobe not extending beyond middle of exopod; inner margin bare, distal corner slightly produced; distal margin with 1 pinnate seta (minutely serrate apically) and a small naked outer seta. Exopod oval in shape and much shorter than in female; 2.36 times as long as maximum width; all setae naked; inner margin with 1 seta; outer margin with spinule row and 3 setae; apex with 1 long seta; anterior surface with 2 large secretory pores.

P6 fused, slightly asymmetrical; with 3 bare setae each, middle one longest.

Variability. Female used for redescription with aberrant P2 (right enp-3 with additional outer spine).

Remarks. Bodin (1964) compared *A. longifurca* with *A. attenuata* [as *A. tenella*], *A. brevipes* [erroneously spelled *A. brevicornis*] and *A. longicaudata*. He comments on the fact that the P2–P4 setal formula of *A. longifurca* is the same as that of *A. tenella*, but that the caudal rami are much more elongate, and that although the swimming leg setal formula differs from that of *A. longicaudata* and *A. brevipes*, the P5 is very similar to the latter. Moore (1976) suggested that *A. longifurca* is a synonym of *A. tenella*, however, based his contention on a comparison of two characters only, i.e. the setation of the female P5 exopod

and the length:width ratio of the caudal ramus. He pointed out that the P5 exopod can have a variable setation in the genus *Ameira* and cited earlier reports of this variability in *A. brevipes* by Kunz (1954) and in *A. parvula* by Lang (1948). It should be noted however, that this 'variability' in *A. brevipes* was not recorded within the same population but results from a comparison of German and Mediterranean specimens. Furthermore, other characters reinforce that Kunz (1954) was comparing different species rather than populations of the same species. Lang's (1948) report on *A. parvula* is potentially misleading as it is based on the setation of the P5 and P4 exp-3 only with total neglect of other morphological features. As closely related *Ameira* species have been shown to co-exist in the field, the widespread belief of *A. parvula* being a highly variable species with cosmopolitan distribution should be critically reviewed. Further extrapolation of this concept to other species such as *A. attenuata* should be strongly discouraged and considered as unacceptable taxonomic practice. The presence of a sixth seta on the P5 exopod of female *A. longifurca* is therefore regarded as significant rather than a reflection of intraspecific variability. A similar misconception applies to the length:width ratio of the caudal rami in *A. longifurca* and *A. attenuata*. Moore (1976) considered the caudal ramus to be "... variable within wide limits..." as he found specimens of *A. attenuata* with ratios ranging between 2.4 and 2.9. Extending this range of variation further in order to include the elongate rami of *A. longifurca* (ratio 4.5) seems artificial, particularly since no variability has been recorded for the latter.

Re-examination of *F. longifurca* has revealed numerous additional differences with *F. attenuata* which in our view prevent conspecificity and confirm the former as a valid species. Both species differ markedly in size and body ornamentation (Fig. 5D–E). The antennule, antenna (allobasis, endopod and the characteristic exopod), P1–P4 enp-3 and P2–P4 exp-3 are all more elongate and slender in *F. longifurca*. Distinct differences are also found in the genital field with the copulatory pore being smaller and positioned more closely to the genital slit in *F. longifurca*, and the chitinized rod supporting the copulatory duct being simple rather than bifid. The present description of the males of both species has also revealed differences in the setation and ornamentation of the P5 (Figs 4G, 6E).

***Filexilia brevipes* (Kunz, 1954) comb. n.**

Synonym. *Ameira tenella* Sars, 1907 *sensu* Klie (1950) [δ only].

Material examined. (a) Zoologisches Museum, Kiel: Klie-collection, 1 δ dissected on slide (reg. no. Cop 144); labelled as *Ameira attenuata*; Helgoland, southeastern part of harbour entrance, from red algae taken at 8 m depth; det. W. Klie, coll. H.W. Schäfer, 14 September 1935; designated herein as lectotype; (b) The Natural History Museum, London: 1 δ mounted *in toto* on slide (reg. no. 1959.2.9.6); labelled as *Ameira attenuata* [Type]; Port Erin, Isle of Man, coll. and det. I.C. Thompson.

Remarks. Thompson's male specimen agrees in many aspects with *A. brevipes* Kunz, 1954: (a) total body length 444 μm [420 μm according to Klie (1950)]; (b) shape of antennary exopod (Fig. 9A; Kunz overlooked

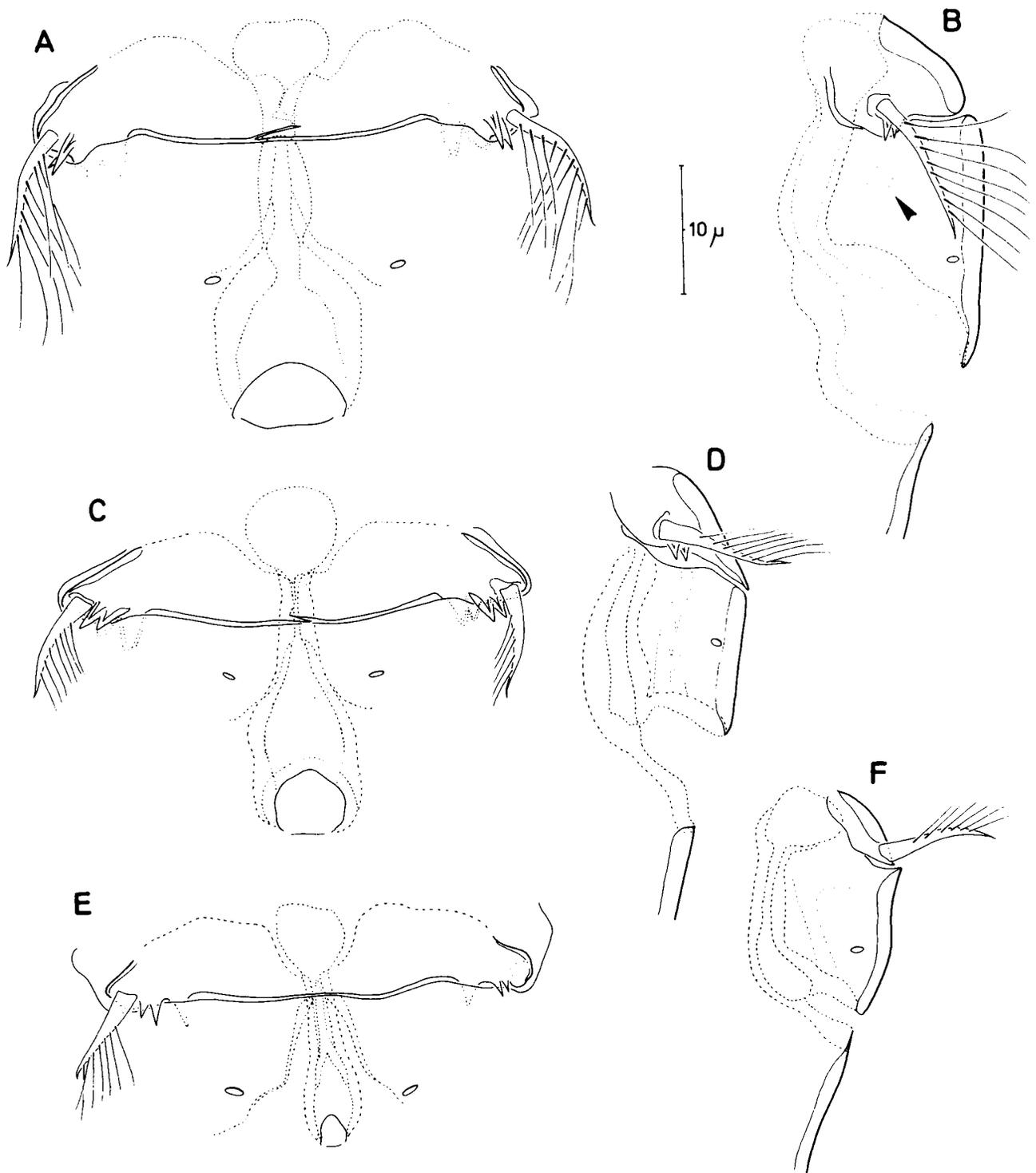


Fig. 8. *Filixilia trisetosa* nom. n.—A. Genital field ♀, ventral.—B. Same, lateral (arrow indicating chitinized supporting rod). *Filixilia attenuata* comb. n.—C. Genital field ♀, ventral.—D. Same, lateral. *Filixilia longifurca* comb. n.—E. Genital field ♀, ventral.—F. Same, lateral.

the minute apical segment); (c) elongate swimming legs, P2–P3 exp-2 and -3 without inner setae (setal formula see below); (d) setation and shape of P5 (compare Fig. 9B and 9E). The presence of the minute inner distal seta on P4 exp-3 is not indicated in Kunz' (1954) description, however scrupulous re-examination of Thompson's and Klie's males revealed that it is genuinely absent in both specimens (Fig. 9D). The swimming leg setal formula is therefore as follows:

	Exopod	Endopod
P2	0.0.023	0.1.121
P3	0.0.023	0.1.121
P4	0.1.223	0.1.121

Conversely, the caudal ramus (Fig. 9C) of the Manx specimen is 1.8 times as long as the maximum width and, although being squashed, appears to be distinctly shorter

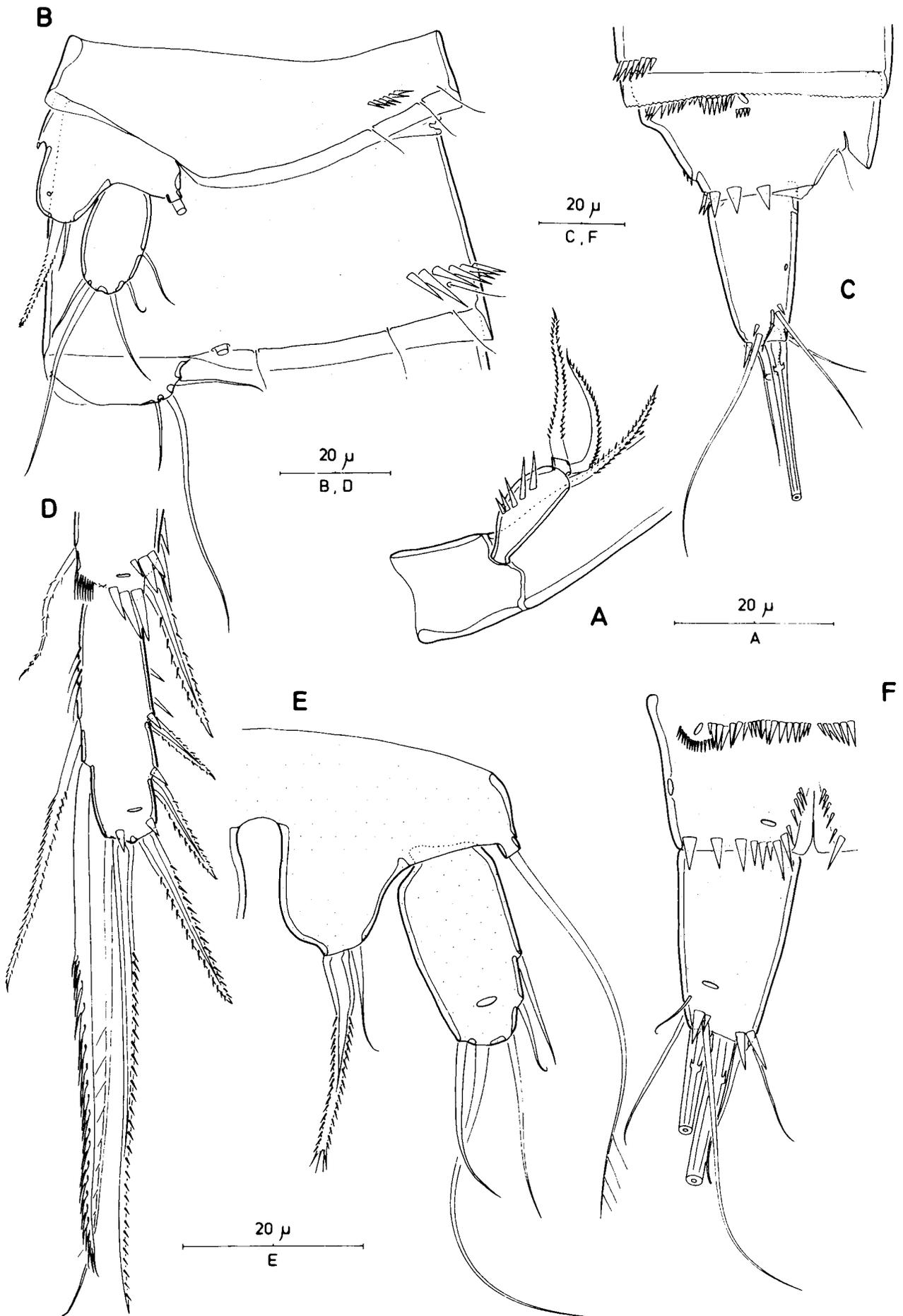


Fig. 9. *Filixilia* aff. *brevipes* (Male syntype *A. attenuata*).—A. Antennary exopod.—B. Somites bearing P5–P6, lateral.—C. Anal somite and left caudal ramus, lateral. *Filixilia brevipes* comb. n. (Male lectotype).—D. P4, distal portion exp-2 and exp-3, anterior.—E. P5, anterior.—F. Anal somite and right caudal ramus, ventral.

Table 1. Morphometric data and setal counts of P5 in species of *Filexilia*. [*: aberrant specimen, see text]

Species	Total body length (μm)		P5 exp ♀L:W ratio	P1 enp-1 vs exp	P1 ratio enp-3:enp-2	Caudal ramus L:W ratio	P5 ♀setae		P5 ♂exp		Reference
	♀	♂					exp	benp	exp	benp	
<i>irisetosa</i>	650	680	3.8	slightly shorter	3.1	2.95	5	4	5	3	this study
<i>attenuata</i>	554	520	4.9	equally long	4.8	2.85	6	4	6	3	this study
<i>tenella</i>	530	?	4.4	equally long	4.25	2.8	5	4	?	?	Sars (1907a)
<i>tenella</i>	563	?	4.5	?	?	2.9	6	4	?	?	Moore (1976)
<i>azorica</i>	?	?	4.8	?	?	2.3	6	4	?	?	Kunz (1983)
<i>longifurca</i>	658	670	4.7	equally long	4.58	4.6	6	4	5	2	this study
<i>gravellicola</i>	560	530	2.7	equally long	4.0	3.3	6	4	5	2	Guille & Soyer (1966)
<i>intermedia</i>	457	?	3	slightly longer	3.0	2.7	6	4	?	?	Galhano (1970)
<i>brevipes</i> (Helgoland)	400	420	2.6	equally long	4.75	1.7 ¹	6	4	5	2	Kunz (1954) and this study
<i>brevipes</i> (Agay)	?	?	2.2	equally long	4.75	3.0	5	4	5	2	Kunz (1954)
<i>pestaе</i>	480	400	3.3	slightly shorter	4.37	1.8	6	4	5	2	Petkovski (1955)
<i>marinovi</i>	?	?	3.7	longer	4.0	2.2	5	4	?	?	Marinov (1971)
<i>brevipes pestaе</i>	?	?	2	slightly longer	3.0	1.6	5	4	?	?	Apostolov (1973)
<i>brevipes pestaе</i>	?	?	2.8	shorter	2.0	2.3	5	4	?	?	Apostolov (1977)
<i>brevipes pontica</i>	?	?	3.2	?	?	1.6	5	6*	?	?	Apostolov (1969)

¹ Based on male lectotype.

enp-3 being 4.36 [4.75] times as long as enp-2, (c) relative lengths of P2–P4 enp-3. On the basis of these discrepancies we re-instate *A. brevipēs pestaе* at the species level. Petkovski (1955) interpreted the antennary exopod as 1-segmented but probably overlooked the minute apical segment. Its convex outer margin bearing fine spinules and the distinctly recurved lateral seta clearly indicate that *A. pestaе* should be placed in *Filexilia*. The species has also been recorded in three localities along the Bulgarian coast (Apostolov 1973). Another form *A. brevipēs* f. *pontica* illustrated by Apostolov (1969) is possibly based on aberrant specimens of *F. pestaе*.

Type locality: Budva, Southern Adriatic coast (Montenegro, Yugoslavia).

Filexilia gravellicola (Guille & Soyer, 1966) comb. n.

Material examined. None.

Remarks. The original description and illustrations leave no doubt that *A. gravellicola* shares many characters in common with the type-species and other members of the genus *Filexilia*. Guille & Soyer (1966) themselves remark on its affinities to *A. tenella*, *A. longicaudata*, *A. brevipēs* and *A. longifurca*. The description of the mouthparts contains a number of inaccuracies: (a) the antennary endopod shows a supernumerary element around the distal margin; (b) the second flaccid element of the mandibular palp is not figured; (c) the maxilla is illustrated and described as having 3 endites on the syncoxa; this configuration is extremely improbable since even in the most primitive ameirid genera (such as *Stenocopia* and *Ameiropsis*) only 2 (coxal) endites are retained which represents the ancestral condition for the family; the only plausible explanation is that the middle endite has been superimposed from another structure.

The notation of the setal formula for the distal exopod segments of P2–P4 is peculiar, and has been inadvertently

reversed (with outer spines counted first) for all the species described by Guille & Soyer (1966). The amended setal formula would then be as follows:

	Exopod	Endopod
P2	0.0.123	0.1.121
P3	0.0.123	0.1.121
P4	0.0.3*23	0.1.121

*: distal inner seta minute, and probably overlooked.

Filexilia gravellicola and *F. intermedia* (see below) are the only species in the genus that have lost the inner seta of P4 exp-2. Both species are extremely similar in most aspects including the P1 and P5, and the most significant discriminating feature appears to be the caudal ramus which is conical and long (3.3 times as long as maximum width) in *F. gravellicola* but slightly bulbous and shorter (L:W ratio 2.7) in *F. intermedia*. The species has thus far been recorded only from its type locality on Racou Beach, Banyuls-sur-Mer, France.

Filexilia intermedia (Galhano, 1970) comb. n.

Material examined. None

Remarks. Galhano (1970) recognized the close affinity of *F. intermedia* to *A. tenella*, *A. longicaudata*, *A. brevipēs*, *A. gravellicola*, *A. longifurca* and *A. attenuata*. The setal formula of the swimming legs is the same as the amended formula for *F. gravellicola* to which it is most closely related. Discovery of the male might provide additional characters to distinguish these two species. The species is only known from Francelos, near Porto, however it is possible that Wells & Clark's (1965) record of *A. tenella* from Peniche, further south along the Portuguese coast, also refers to *F. intermedia*.

***Filexilia marinovi* sp. n.**

Synonym. *Ameira brevipes pestae* Petkovski, 1955 *sensu* Marinov (1971).

Material examined. None.

Etymology. The species is named after Dr T. Marinov, who first recorded the species.

Remarks. Examination of Marinov's (1971) illustrations of *A. brevipes pestae* confirms that this species belongs in the genus *Filexilia*, but is distinct from *F. pestae*. The armature formula P2–P4 is identical in both species, however the main differences are found in (a) the caudal rami which are more elongate in the Bulgarian material (2.2 times as long as maximum width), (b) P1 with enp-1 longer than exopod and the relative lengths of enp-2 and -3 being different, (c) P5 exopod of the female longer (3.7 times as long as maximum width) and with 5 setae. With regard to the latter character it is considered unlikely that Marinov (1971) missed out 1 seta as the arrangement of the setae indicates that it is the same outer lateral seta that is lost in the type-species *F. trisetosa*. Although a detailed redescription would be desirable, there seems to be sufficient evidence to warrant the erection of a new species for Marinov's material which we name *F. marinovi* sp. n.

Key to species of *Filexilia* gen. n.

The following key is applicable to both sexes unless otherwise stated.

1. P2–P3 exp-3 without inner seta/spine, with armature formula 023 7.
P2–P3 exp-3 with inner seta/spine, with armature formula 123 2.
2. P4 enp-3 with 3 setae/spines; P5 exopod with 5 setae in both sexes *F. trisetosa* nom. n.
P4 enp-3 with 4 setae/spines; P5 exopod with 6 setae in ♀, 5 or 6 setae in ♂ 3.
3. P3 enp-3 with 4 setae/spines 4.
P3 enp-3 with 5 setae/spines 6.
4. Female P5 exopod elongate, 4.8 times as long as maximum width; P4 exp-2 with inner seta *F. azorica* sp. n.
Female P5 exopod at most 3 times as long as maximum width; P4 exp-2 without inner seta 5.
5. Caudal rami conical, 3.3 times as long as maximum width *F. gravellicola* (Guille & Soyer, 1966).
Caudal rami slightly bulbous, 2.7 times as long as maximum width *F. intermedia* (Galhano, 1970).
6. P2–P4 enp-1 with rounded inner margin; ♂ P5 exopod with 6 setae, baseoendopod with 3 setae; ♀ P5 baseoendopod truncate; caudal rami 2.8–2.9 times as long as maximum width *F. attenuata* (Thompson, 1893).
P2–P4 enp-1 with straight inner margin; ♂ P5 exopod with 5 setae, baseoendopod with 2 setae; ♀ P5 baseoendopod not truncate; caudal rami 4.6 times as long as maximum width *F. longifurca* (Bodin, 1964).
7. Female P5 exopod with 5 setae, 3.7 times as long as maximum width; caudal rami 2.2 times as long as maximum width *F. marinovi* sp. n.
Female P5 exopod with 6 setae 8.
8. P5 exopod ♀ 3.3 times as long as maximum width *F. pestae* (Petkovski, 1955).
P5 exopod ♀ 2.6 times as long as maximum width *F. brevipes* (Kunz, 1954).

Discussion

Several authors (Kunz 1954; Bodin 1964; Guille & Soyer 1966; Galhano 1970; Moore 1976) have alluded to the

affinities between *A. tenella*, *A. longicaudata*, *A. longifurca*, *A. brevipes*, *A. gravellicola* and *A. intermedia*, but it was Kunz (1983) who first formally recognized the *A. tenella* species-group. The author provides a summary and comparison of characters common to the various species and subspecies. An update of this overview of important morphometric data and P5 setal counts is presented in Table 1. Despite recognising the *tenella*-group as a distinct lineage, Kunz (1983) preferred to maintain its position in *Ameira*, suggesting instead that its constituent taxa might well be geographical varieties of the same species.

The following comparison is restricted to the species closely related to the type-species of *Ameira* [*A. longipes* Boeck, 1865], such as *A. parvula* (Claus, 1866) and *A. minuta* Boeck, 1865, and referred to as the *longipes*-group. Species of the *tenella*-group are typically more slender and elongate. This slenderness is also recognized in the various appendages such as the antennules, swimming legs, P5 exopod and caudal rami, and is best expressed in *A. longifurca* where even the antennary exopod is elongated. The anal operculum is provided with fine spinules whereas it is usually smooth in the *longipes*-group. The fusion of the genital double-somite is complete with the inner chitinous ribs marking the original segmentation being lost. The genital field in the *tenella*-group with the vestigial sixth legs bearing one pinnate seta and two spinous processes and the copulatory duct being strongly chitinized is distinctly different from that in the *longipes*-group which has a short pinnate seta, a long naked seta and one spinous process on the opercula, and a weakly defined copulatory duct. The caudal rami are elongate and slender as opposed to being very short (sometimes wider than long) in the *longipes*-group. Very distinctive features of the *tenella*-complex are the elongate antennules bearing very long setae on the distal segments and the form and shape of the antennary exopod (see below). In the *longipes*-group the latter invariably has a cluster of 2–4 coarse spinules wrapped around the outer lateral margin in the distal third of the proximal segment and supplementary ornamentation is present in the form of fine spinular rows or frills. The inner basal spine of the ♂P1 is modified in a different way, being acute and naked in the *longipes*-group but recurved and unipinnate in the *tenella*-lineage. Additional setal differences are found in the swimming legs (i.e. inner setae of P2–P3 exp-2 and P2–P4 enp-1 absent in the *tenella*-group) and in the male sixth legs (inner seta modified into spiniform element in the *longipes*-group) and members of the two lineages can be easily distinguished by the shape of the female P5 exopod.

The *tenella*-group occupies an isolated position in *Ameira* and a preliminary phylogenetic analysis of the genus revealed that none of its lineages shares a direct relationship with this group, corroborating its separate status and removal to a new genus. Due to the absence of elaborate sexual dimorphism on the swimming legs the generic boundaries in the Ameiridae have traditionally been based on differences in the setation and segmentation of the P1–P4, and to a lesser extent, the mouthparts. It is our contention that particularly the latter can provide information of high phylogenetic significance although it should be pointed out that authors have attributed too much significance to certain doubtful characters such as

the absence or presence of an antennary allobasis. Other structures such as the antennary exopod can be highly distinctive but have received little attention. For example, in *Filexilia* the exopod is typically 2-segmented with the distal segment being minute (and often not recognized in earlier descriptions) and the large proximal segment tapering towards the base, having a convex outer margin provided with fine spinule rows and furnished with a distinctly recurved lateral seta. The detailed morphology of the antennary exopod differs considerably among ameirids (Conroy-Dalton & Huys, unpubl.) and it is clear that its usefulness in elucidating relationships has been grossly underestimated in the past. For example, the *Filexilia*-condition is not found in any other member of the genus *Ameira* and is further displayed within the family only by representatives of *Sicameira* Klie, 1950. The modified exopod in *Filexilia* and *Sicameira* is clearly homologous and no doubt represents a uniquely derived condition within the family, supporting a sistergroup relationship between these genera. Evidence in support of such a relationship is also provided by the facies of the antennule which is equipped with extremely long setae on the apical segments giving the whole appendage a very slender appearance. As far as we can ascertain, this secondary elongation of antennular setae is unique within the Ameiridae and represents an additional synapomorphy for the *Filexilia*-*Sicameira* clade. Some other ameirids such as *Ameira tenuicornis* T. Scott, 1902 also have slender antennules but this condition is the result of secondary elongation of the proximal segments and is therefore not homologous.

With considerable foresight Sars (1907a) recognized a 'perplexing similarity' between *A. tenella* and *A. gracilis* A. Scott, 1896. Lang (1948) doubted the validity of *A. gracilis* and considered it *species incertae sedis*. The species was rediscovered by Por (1964b) who described both sexes and transferred it to *Sicameira*. Currently, *Sicameira* encompasses four interstitial species, all described from coarse sandy sediments in intertidal or shallow subtidal localities (Scott 1896; Klie 1950; Rao 1972; Marinov 1973). A key to the species is provided below:

1. P2-P3 exp-3 with inner seta *S. langi* Rao, 1972.
P2-P3 exp-3 without inner seta 2.
2. Antennule 8-segmented in ♀; P2-P3 exp-3 with 1 and 2 inner setae, respectively *S. gracilis* (A. Scott, 1896).
Antennule 7-segmented in ♀; P2 exp-3 without, P3 exp-3 with 1 inner seta 3.
3. P1 exp-1 as long as exopod; caudal ramus about 1.5 times as long as maximum width *S. leptoderma* Klie, 1950 [type-species].
P1 exp-1 distinctly shorter than exopod; caudal ramus about 3 times as long as maximum width *S. intermedia* Marinov, 1973.

Klie (1950) did not discuss the relationships of his new genus. Por (1964b) claimed that the antennary exopod of *S. gracilis* resembles the *Stenocopia*-*Ameiropsis* type and voiced the opinion that the genus appears to be related to *Pseudameira*, however without giving any reasons. From the evidence presented above it is clear that *Sicameira* is most closely related to *Filexilia*. It can be identified by the following suite of autapomorphies: (a) antennule with very short (aesthetasc-bearing) segment 4, much shorter than segment 5 [segment 4 not reduced and distinctly longer than segment 5 in *Filexilia*], (b) P2-P4 exp-3 without outer spine [outer spine always present in *Filexilia*], and (c) P5

baseoendopod of ♀ with 2 setae [with 4 setae in *Filexilia*]. The 9 valid species of *Filexilia* constitute a monophyletic group on the basis of (a) P2-P4 exp-1 without inner seta [seta always present in *Sicameira*], (b) P2-P4 exp-2 without inner seta [present in *Sicameira*], and (3) genital field with P6 bearing 1 well developed seta [2 well developed elements in *Sicameira*].

Within the genus *Ameira* the species *A. bengalensis* Rao & Ganapati, 1969 is of particular interest. This interstitial ameirid described from coarse sand of the Waltair coast (India) has lost the inner seta of P2-P4 exp-2, a character typical for *Filexilia*. It also shows the elongate caudal rami which are characteristic for both *Filexilia* and *Sicameira* and resembles the latter genus in the presence of only 2 setae on the female P5 baseoendopod and by the reduced fourth antennular segment. *Ameira bengalensis* is reminiscent of *Filexilia* in the structure of the genital field showing only 1 well developed armature element and in the presence of the outer spine on the distal endopod segments of P2-P4. This combination of characters suggests that *A. bengalensis* represents a transitional stage between *Sicameira* and *Filexilia*. Unfortunately, Rao & Ganapati's (1969) illustrations, which could have provided the conclusive evidence for this intermediate position, are extremely small and do not contain sufficient detail in order to assess the morphology of the antennary exopod and antennule. The reduced setal formula of the swimming legs and the presence of only 2 setae on the female P5 baseoendopod preclude *A. bengalensis* from being placed in *Ameira* and it is therefore transferred here to a new genus *Glabrameira* gen. nov.

Genus *Glabrameira* gen. n.

Diagnosis. Ameiridae. Body cylindrical and slender, without clear demarcation between prosome and urosome. Hyaline frills of cephalothorax and body somites unconfirmed. Female genital and first abdominal somites completely fused to form genital double-somite. Anal operculum with fringe of fine spinules. Caudal ramus cylindrical, elongate, about twice as long as wide; with 7 setae. Sexual dimorphism (and male) unknown but probably displayed in body size, antennule, P1 (inner basal spine), P5, P6, and in genital segmentation.

Rostrum prominent, triangular; not demarcated at base. Antennule slender and elongate; majority of setae smooth and slender, some being very long on distal segments; 7-segmented in ♀, with aesthetasc on reduced segment 4 and possibly on segment 7. Detailed setation patterns on mouthparts unconfirmed. Antenna with basis and proximal endopod segment free; exopod 1-(possibly 2)-segmented; armature formula [1 + 2; of equal length]. Mandibular palp uniramous, 2-segmented, comprising basis and 1-segmented endopod; basis with 2 elements. Maxillule with 2 elements on coxal endite; endopod minute, with 2 setae; exopod absent. Maxillary syncoxa with at least 1 well developed endite. Maxilliped subchelate; syncoxa with 1 seta; endopod represented by claw, presence of accessory setae unconfirmed.

P1-P4 with 3-segmented rami. P1 exopod without inner seta on exp-2; exp-3 with 3 outer spines and 2 geniculate

setae distally. P1 endopod prehensile, with enp-1 slightly longer than enp-2 and -3 combined, shorter than exopod; inner seta of enp-2 well developed. P2-P4 without inner setae on exp-1 and -2, with inner seta on enp-1. Armature formula as follows:

	Exopod	Endopod
P1	0.0.023	1.1.111
P2	0.0.123	1.1.121
P3	0.0.123	1.1.121
P4	0.0.2*23	1.1.121**

*: minute distal inner seta and possibly overlooked.

** : based on text description but 1.1.221 according to their Fig. 8.11.

P5♀ with separate baseoendopod and exopod; not fused medially; exopod oval, not elongate, with 5 setae, baseoendopod with 2 well developed setae. Female genital field with copulatory pore leading via chitinized copulatory duct to median seminal receptacle; gonopores covered by common genital operculum derived from P6 with long seta and 1 short element.

Type- and only species. *Ameira bengalensis* Rao & Ganapati, 1969 = *G. bengalensis* (Rao & Ganapati, 1969) comb. n.

Etymology. The generic name is derived from the Latin *glaber*, meaning smooth, and refers to the absence of the inner setae on P2-P4 exp-1 and -2.

A tentative cladogram depicting the relationships within the genus *Filexilia* is presented in Fig. 10. *Filexilia trisetosa*, *F. azorica*, *F. attenuata* and *F. longifurca* form a monophyletic group defined by the elongation of the P5 exopod. The *brevipes*-subgroup recognized by Kunz (1974) represents the terminal clade, containing *F. brevipes*, *F. pestae* and *F. marinovi* and is characterized by the short caudal rami and reduced swimming leg armature (loss of inner setae of P2-P3 exp-3 and P3 enp-3 and distal inner seta of P4 exp-3). The closely related species *F. intermedia* and *F. gravellicola* represent an intermediate group between the *attenuata*- and *brevipes* clades and share the unique loss of the inner seta of P4 exp-2.

The genus *Filexilia* assumes a typical boreo-mediterranean distribution extending into the Black Sea basin and with two outliers in the North Atlantic, *F. trisetosa* (Canada) and *F. azorica* (Azores).

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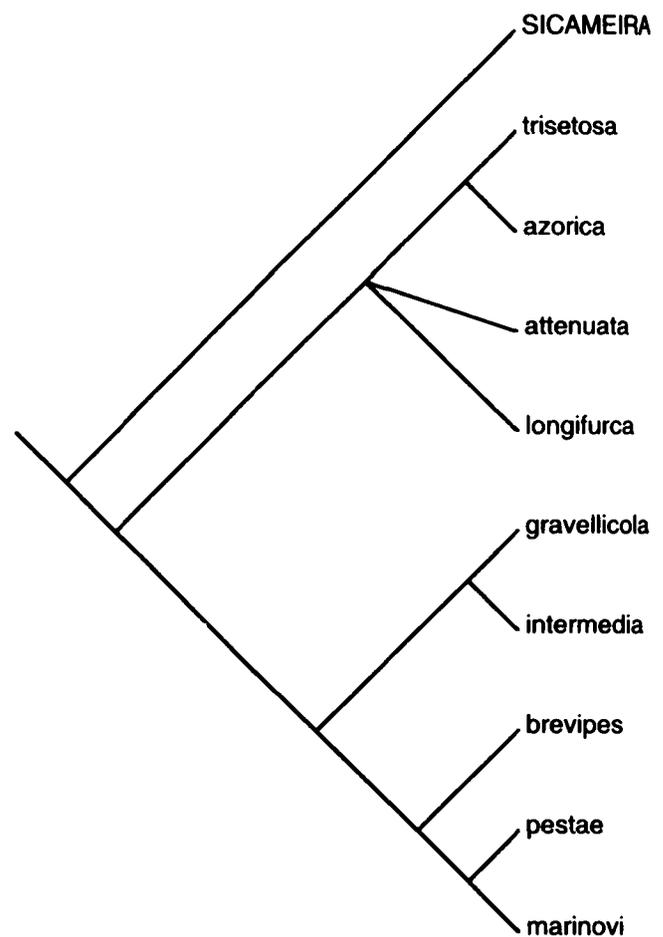


Fig. 10. Cladogram depicting relationships of valid *Filexilia* species.

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