Meiofauna Marina, Vol. 19, pp. 127–160, 18 figs., 5 tabs., 1 app., September 2011
 – ISSN 1611-7557

Revision of the taxon *Fultonia* T. Scott (Copepoda: Harpacticoida: Argestidae), including the (re)description of some species, discontinuation of the genus *Parargestes* Lang, and erection of Argestinae Por, subfam. nov.

Kai Horst George*

Abstract

In the frame of a phylogenetic analysis of Argestidae Por, the genus *Fultonia* T. Scott is reviewed. Apart from the redescription of *Fultonia hirsuta* T. Scott – including the first description of the male – and of *F. gascognensis* Bodin, *F. wilhelmsenae* sp. nov. is described. Thus, together with *F. bougisi* Soyer, four *Fultonia* species have been reported up to date. They share eight morphological synapomorphies (two of which still vague for *F. hirsuta*), supporting a hypothesis of monophyletism of that genus. Comparison with *Argestes* Sars supports the monophyly of an *Argestes*–*Fultonia*-group that is established as Argestinae Por, subfam. nov. and characterized by three apomorphies: (i) body densely covered with small cuticular spinules; (ii) female A1 with remarkably strong seta laterally at sixth segment; (iii) dorsal thoracic sensilla distinctly elongate. Finally, *Parargestes tenuis* Sars var. *arcticus* Lang is transferred into *Argestes*, while the usage of the genus *Parargestes* Lang is discontinued.

Keywords: Systematics, meiofauna, deep sea, taxonomy, phylogeny, morphology, *Argestes*

Introduction

Representatives of Argestidae Por, 1986 (Copepoda, Harpacticoida) are considered as "typical" deep-sea taxa (Noodt 1971, Hicks & Coull 1983). They show a world-wide distribution (cf. George 2004) and form one of the dominant groups of meiobenthic deep-sea Harpacticoida (Menzel & George 2009, Rose et al. 2005). Therefore, Argestidae may be a useful representative for chorological and biogeographical investigation on deep-sea Harpacticoida and perhaps even on deep-sea meiofauna in general (Menzel & George 2009). However, as already remarked in the past, for such purposes the so far questionable phylogeny of Argestidae has to be cleared up (George 2004, 2008). Consequently, the number of recent phylogenetic studies on Argestidae increases notable (e. g. George 2004, 2008; Menzel & George 2009; Corgosinho & Martínez Arbizu 2010; Menzel 2011, in press). While Menzel (2011, in press) and Menzel & George (2009) concentrate on

* Senckenberg am Meer, Abt. Deutsches Zentrum für Marine Biodiversitätsforschung DZMB, Südstrand 44, D-26382 Wilhelmshaven, Germany; e-mail: kgeorge@senckenberg.de

supposed derived argestid taxa (e. g. *Eurycletodes* Sars, 1910, *Mesocletodes* Sars, 1910), George (2004, 2008; present contribution) focuses on genera that may form a rather primitive group inside the family: *Argestes* Sars, 1910, *Bodinia* George, 2004, *Dizahavia* Por, 1979, *Fultonia* T. Scott, 1902, and *Parargestes* Lang, 1944. Corgosinho & Martínez Arbizu (2010) compare the systematic relationships of Argestidae, Ameiridae Boeck, 1865, and Parameiropsidae Corgosinho & Martínez Arbizu, 2010, allocating the former ameirid genera *Anoplosomella* Strand, 1929 and *Malacopsyllus* Sars, 1911 into Argestidae.

As announced by George (2008), a phylogenetic analysis of the taxon *Fultonia* is presented here. Moreover, new insights into the phylogeny of basal Argestidae and the description of *F. wilhelmsenae* sp. nov. is given. It clears some morphological discrepancies between the original description of *F. hirsuta* T. Scott, 1902 and its redescription provided by Sars (1910). Additionally, *Fultonia gascognensis* Bodin, 1968 and *Parargestes tenuis* (Sars, 1921) var. *arcticus* Lang, 1936 are partly redescribed, and the monophyly of an *Argestes*-*Fultonia*-group is discussed, leading finally to the establishment of a new monophylum Argestinae Por, 1986 subfam. nov.

Material and Methods

Material examined: *F. wilhelmsenae* sp. nov., two females, G. O. Sars collection of the Natural History Museums and Botanical Gardens, Zoological Museum, University of Oslo, Norway (coll. no. F 24008). One female dissected, the second female preserved in alcohol. One additional female is kept in the P. Bodin collection of the Museum National D'Histoire Naturelle, Dept. "Milieux et peuplements aquatiques", Paris, France [coll. nos. MNHN–Cp 2448(1–3)].

Fultonia hirsuta, three females, G. O. Sars collection of the Natural History Museums and Botanical Gardens, Zoological Museum, University of Oslo, Norway (coll. no. F 23017). Two females preserved in alcohol (coll. no. 23017a), one female dissected (coll. no. 23017b). The description of the male is based on material of the P. Bodin collection of the Museum National D'Histoire Naturelle, Dept. "Milieux et peuplements aquatiques", Paris, France [coll. nos. MNHN-Cp 2449(1–3)].

F. gascognensis, one female, P. Bodin collection of the Museum National D'Histoire Naturelle, Dept. "Milieux et peuplements aquatiques", Paris, France (coll. nos. MNHN-Cp 3254–3256).

Parargestes tenuis var. *arcticus*, three females, K. Lang collection of the Swedish Museum of Natural History, Dept. of Invertebrate Zoology, Stockholm, Sweden (coll. no. Type-2269); all specimens preserved in alcohol.

Drawings were made with the aid of a camera lucida on a Leica-DMR compound microscope equipped with an interference contrast 100 × objective. General terminology is mainly adopted from Lang (1948) and Huys & Boxshall (1991). Terminology referring to phylogenetics follows Ax (1984). The terms "telson" and "furca" are used according to Schminke (1976).

Abbreviations used in the text: **A1**, antennule; **A2**, antenna; **aes**, aesthetasc; **benp(s)**, basendopod(s); **cphth**, cephalothorax; **enp(s)**, endopod(s); **exp(s)**, exopod(s); **exp1**, first segment of exp; **FR**, furcal ramus/rami; **GF**, genital field; **md**, mandible; **mxl**, maxillule; **mx**, maxilla; **mxp**, maxilliped; **P1–P6**, swimming legs 1–6; **STE**, Subapical Tubular Extension.

Results

Family: Argestidae Por, 1986

Subfamily: Argestinae Por, 1986 subfam. nov.

Diagnosis. Copepoda Harpacticoida, Argestidae Por, 1986. Generic diagnosis: Body elongate, cylindrical to slightly depressed, and covered with small cuticular spinules. Cephalothorax posteriorly at most as broad as following thoracic somites. Cephalothoracic integument posteriorly accompanied with rudimentary pleurotergite of fused first thoracic somite. FR of variable length, covered with spinules. Female genital double somite dorsally with suture, indicating former division. Telson more or less square, reaching length of at least the preceding 2 abdominal somites. Anal operculum dentate or with spinules. Body somites dorsally and laterally with long sensilla, arising or not from tubercles. Female A1 7–8-segmented, sixth segment terminally with 1 very strong seta. Male A1 9–11-segmented, penultimate or antepenultimate segment terminally with strong seta. A2 with basis or allobasis and 1-segmented exp bearing 1 seta. Gnathobase of md terminally with several teeth or with broad, grinder-like, finely striped structure, then additionally with 1–2 strong cuticular elements; inner seta present or absent. Mandibular palp biramous. Mxl praecoxal arthrite with 5–7 spines, with 1 seta at inner side, and with 2 setae at its surface. Exp 1-segmented, enp absent. Maxilla with distinct or fused basis and 2 endites, the proximal one bearing 1 seta, the distal one with 2–3 setae. Maxillar enp present or absent, with or represented by 2 setae. Syncoxa of mxp with 1–2 setae, enp produced into slender claw; additionally with 1–2 long setae at its base. P1–P4 with 3-segmented exps; P1 enp 2–3-segmented, P2–P4 enps 3-segmented. P2–P4 enps3 with 3–5 setae. P5 benps fused, endopodal lobe completely reduced, being represented by 1–2 setae. Exp distinct, elongate, number of setae differing from 5–9.

Type genus: *Argestes* Sars, 1910. Additional genera: *Fultonia* T. Scott, 1902.

Type species: *Argestes mollis* Sars, 1910. Additional species: *A. tenuis* Sars, 1921 var. *arcticus* (Lang, 1944), *A. reductus* (Itô, 1983), *A. angolaensis* George, 2008, *Fultonia hirsuta* T. Scott, 1902, *F. bougisi* Soyer, 1964, *F. gascognensis* Bodin, 1968, *F. wilhelmsenae* sp. nov. (present contribution); species *incertae sedis*: *Argestes sarsi* Smirnov, 1946.

Genus: *Fultonia* T. Scott, 1902

Generic diagnosis. Body elongate, cylindrical, and covered with small cuticular spinules. Cephalothorax posteriorly as broad as following thoracic somites. Cephalothoracic integument posteriorly accompanied with rudimentary pleurotergite of fused first thoracic somite. FR small, more or less square, covered with spinules. Female genital double somite dorsally with suture, indicating former division. Telson more or less square, reaching length of at least the preceding 2 abdominal somites. Anal operculum dentate or with spinules. Body somites dorsally and laterally with long sensilla. Female A1 7–8-segmented, sixth segment terminally with 1 very strong seta. A2 with basis or allobasis and 1-segmented exp, bearing 1 seta. Gnathobase of md terminally with broad, grinder-like, finely striped structure. Additionally with 1–2 strong cuticular elements; inner seta present or absent. Mandibular palp biramous; basis with 2, enp with 4–5, exp with 2–4 setae. Mxl praecoxal arthrite with 5–6 spines, with 1 seta at inner side, and with 2 setae at its surface. Exp 1-segmented, enp absent. Maxilla with distinct basis and 2 endites, the proximal one bearing 1 seta, the distal one with 2–3 setae. Maxillar enp present or absent, with or represented by 2 setae. Syncoxa of mxp with 1 seta, enp produced into slender claw that bears few but strong pinnae at its distal half; additionally with 1 long seta at its base. P1–P4 with 3-segmented rami, except P1 enp, which is 2-segmented. P2–P4 enps3 with at most 4 setae. P5 benps fused, endopodal lobe completely reduced, being represented by 1 seta. Exp distinct, elongate, number of setae differing from 5–9.

Type species: *F. hirsuta* T. Scott, 1902. Additional species: *F. bougisi* Soyer, 1964, *F. gascognensis* Bodin, 1968, *F. wilhelmsenae* sp. nov. (present contribution); species *incertae sedis*: *Argestes sarsi* Smirnov, 1946.

Description of *Fultonia wilhelmsenae* sp. nov.
Figs. 1–4

Type material: 2 females, sampled by G. O. Sars as *Fultonia hirsuta* "at Farsund and Korshavn, south coast of Norway, in depths ranging from 20 to 50 fathoms" [i. e. 36.6–64.4 m] (Sars 1910, p. 342). Sampling sites form the locus typicus. G. O. Sars collection of the Natural History Museums and Botanical Gardens, Zoological Museum, University of Oslo, Norway. Both females show damaged body parts and appendages. For the description, the female presenting better conditions was dissected and distributed over 10 slides (coll. nos. Zool. Mus. Oslo F24008a–j).

Additional material: 1 female, collected by P. Bodin at Manche, Roscoff (France) on 14.05.1992; dissected, distributed over 3 slides, and labelled MNHN-Cp2448(1–3).

Etymology: The species name *Fultonia wilhelmsenae* is gratefully dedicated to Mrs. Åse Wilhelmsen, Zoological Museum of the University of Oslo, Norge.

Female

Habitus (Fig. 1 A,B) moderately slender, body length including FR of approximately 420 µm. Cphth less than ⅓ of total body length. Whole body densely covered with small spinules, except

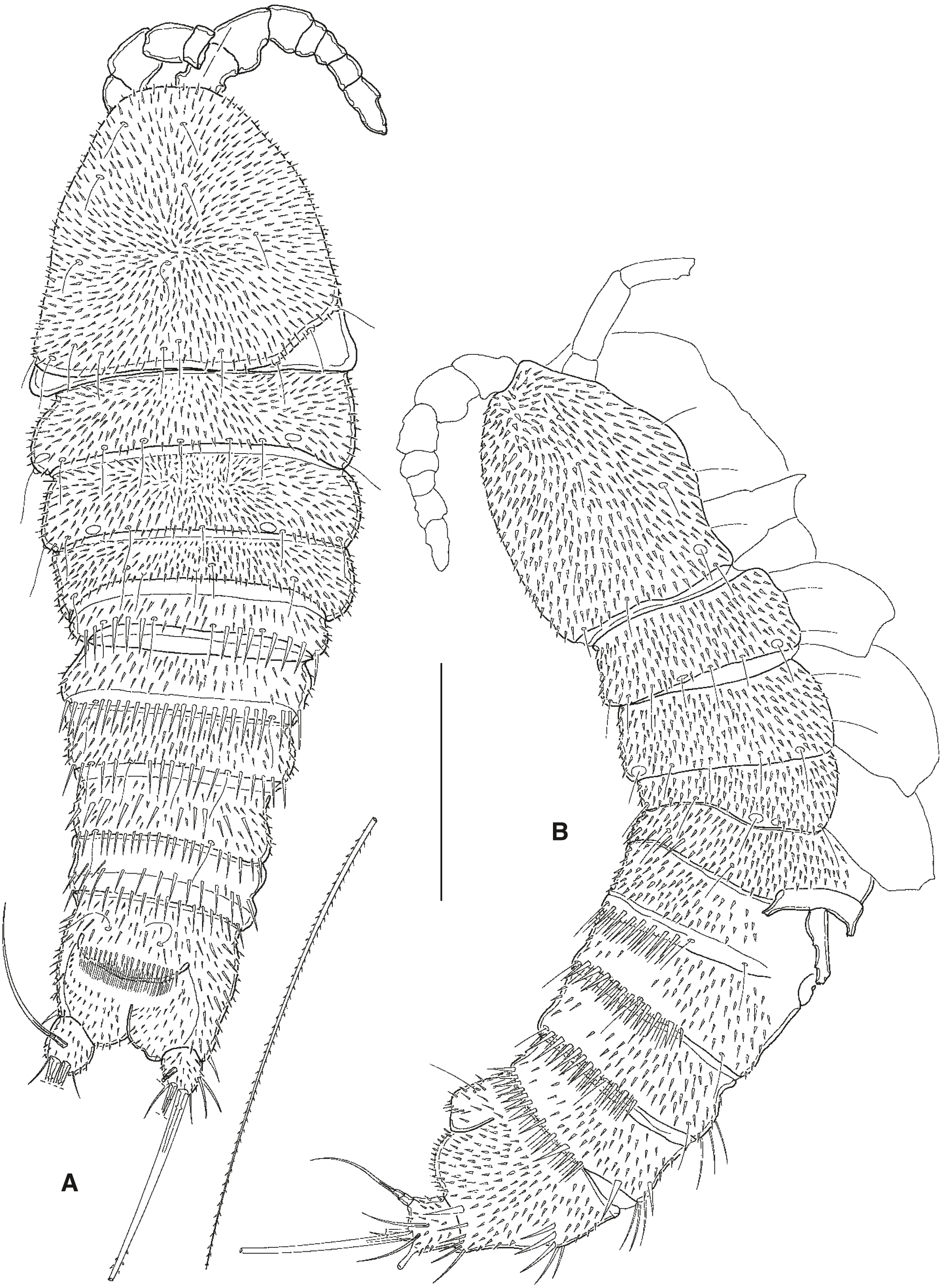


Fig. 1. *Fultonia wilhelmsenae* sp. nov., female. **A.** Habitus dorsal; **B**. Habitus lateral. Scale: 100 µm.

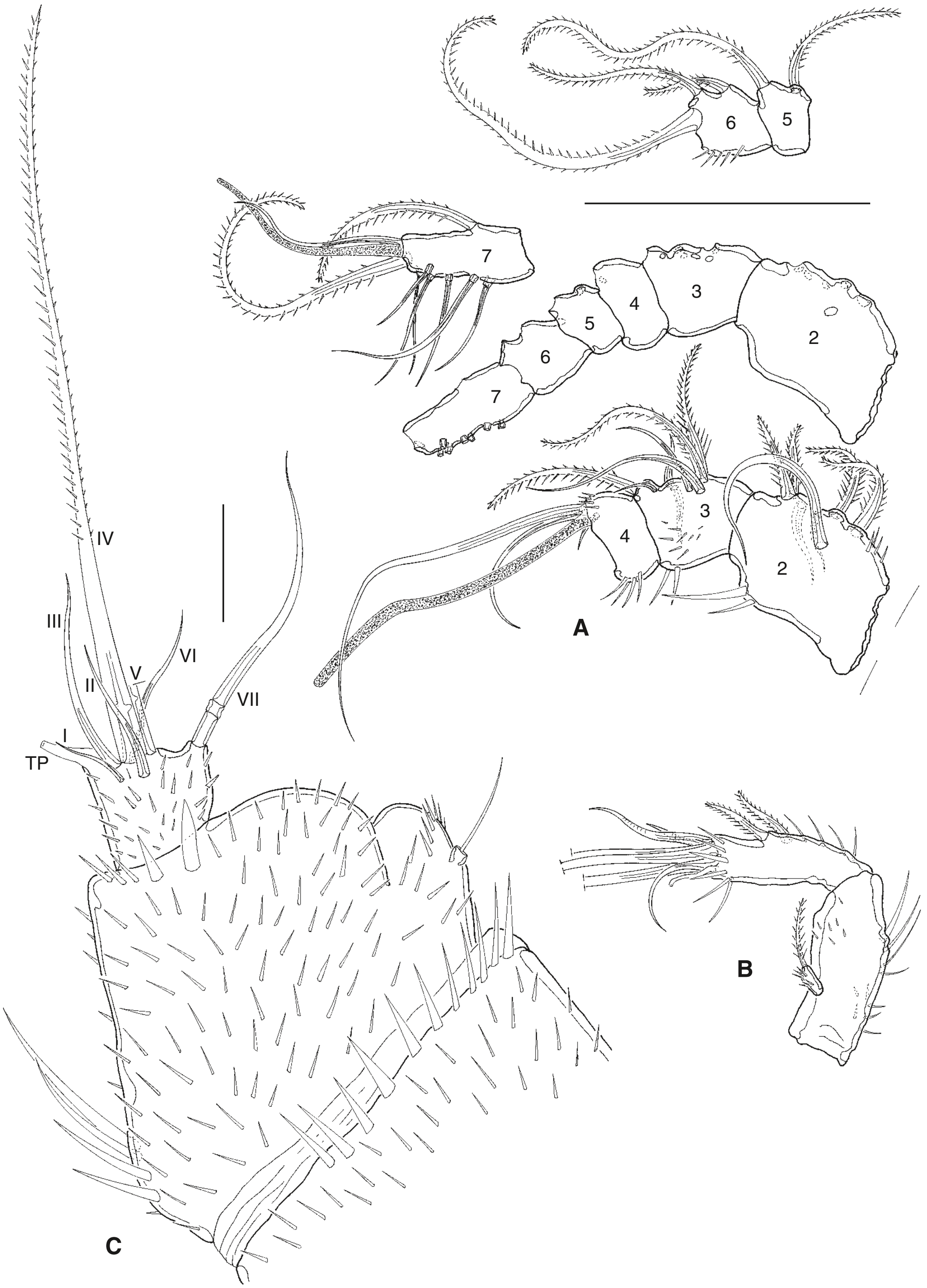


Fig. 2. *Fultonia wilhelmsenae* sp. nov., female. **A.** Antennula, segments numbered from 1–7; **B.** Antenna; **C.** Telson and FR, lateral view, furcal setae numbered I–VII; **TP**, tube pore. Scales: 20 µm.

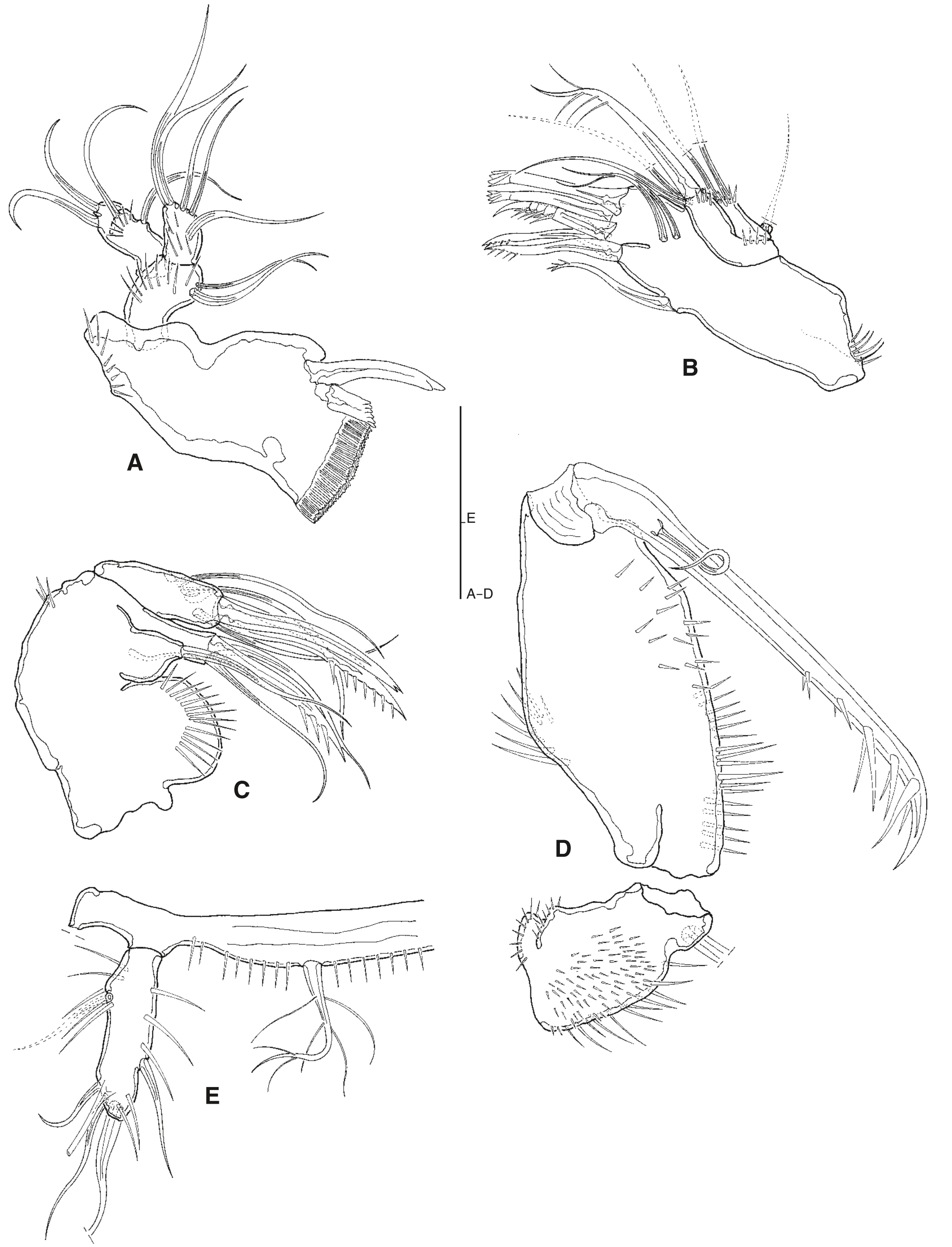
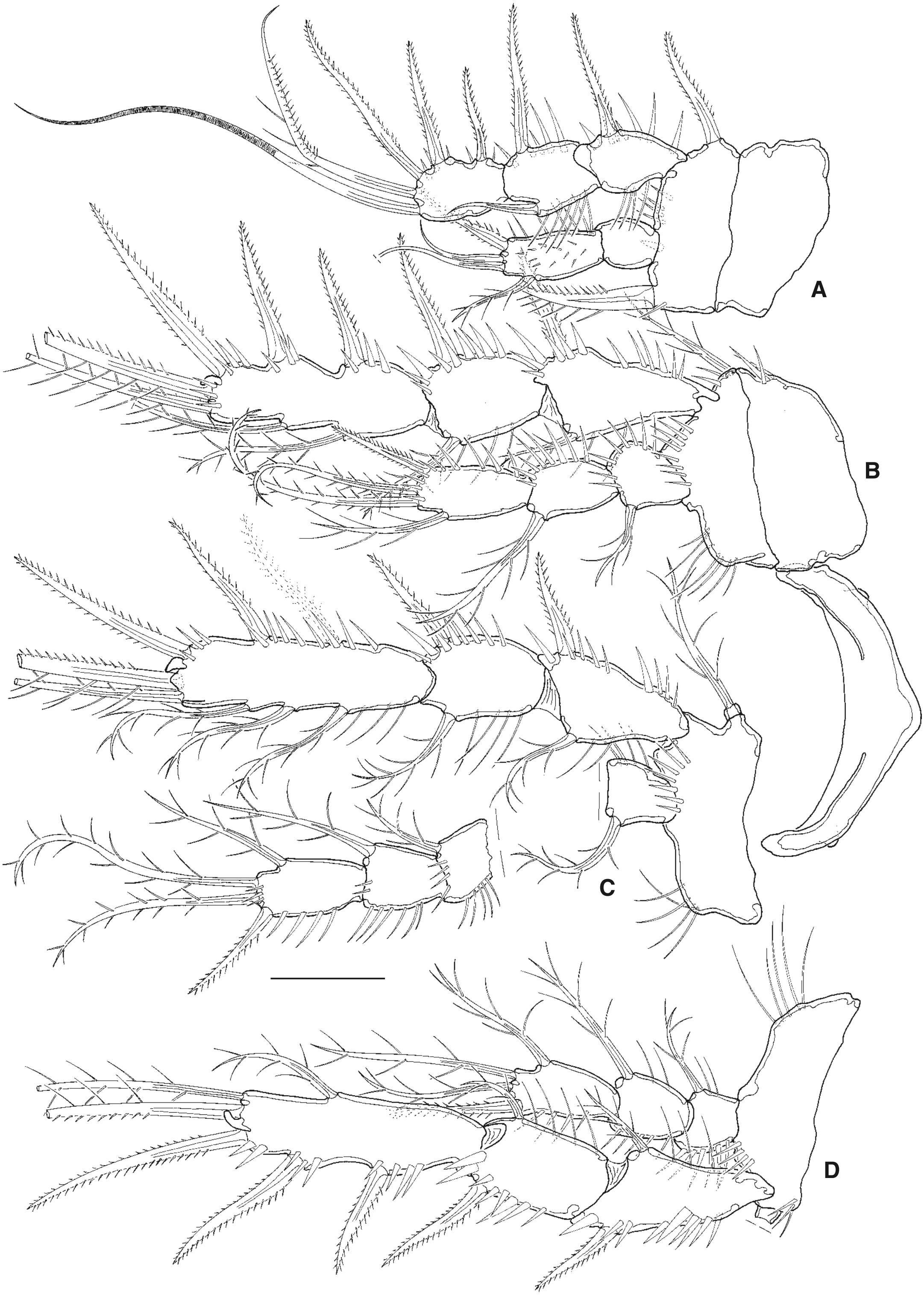


Fig. 3. *Fultonia wilhelmsenae* sp. nov., female. **A.** Md; **B.** Mxl, dotted setae according to counterpart; **C.** Mx; **D**. Mxp; **E.** P5. Scales: 20 µm.

Fig. 4. *Fultonia wilhelmsenae* sp. nov., female. **A.** P1; **B.** P2; **C.** P3; **D.** P4. Scale: 20 µm. ▷


A
B
C
D

for the penultimate body somite, which shows 2 rows of larger spinules dorsally. Spinule coverage less dense on abdomen than on cphth and thoracic somites. Thoracic part of genital double somite and first two abdominal somites dorsally with row of long spinules at distal margin. Body with several remarkably long sensilla. Rostrum small, fused with cphth. Cephalothoracic integument posteriorly accompanied with rudimentary pleurotergite of fused P1-bearing thoracic somite.

Telson (Figs. 1A, B, 2C) approximately as long as 2 preceding abdominal somites together, almost square in shape. Telson and 2 preceding abdominal somites ventrally with some strong spinules. Anal operculum weakly developed, with row of spinules at its distal margin; 2 sensilla arising basally.

FR (Fig. 2C) very small, almost square in shape, and covered with fine spinules. All 7 setae concentrated at terminal part: I and II subterminally on outer margin, I smaller than II and displaced subventrally. III subventrally at terminal margin, accompanied by strong but short tube pore. IV and V (broken in Fig. 2C) longest setae, inserting terminally, IV bipinnate. VI as long as III, arising from the inner terminal margin. VII dorsally, triarticulate.

A1 (Fig. 2A) 7-segmented (first segment broken in Fig. 2A). Segments 2, 3, 4, and 6 with few long spinules at posterior margins; segment 3 additionally with small spinules at its surface. Second segment with 4 bipinnate and 3 bare setae. Third segment almost half as long as second, with 3 bipinnate and 5 bare setae. Fourth segment small, with 3 bare setae, the longest basally fused with aes. Fifth segment smallest, with 2 bipinnate setae. Sixth segment with 3 bipinnate setae, the terminal one very long. Seventh segment terminally with small aes, and with 7 bare and 2 bipinnate setae, the subterminal one of which remarkably long.

Setal formula: 1/? (broken); 2/7; 3/8; 4/3 + aes; 5/2; 6/3; 7/9 + aes.

Table 1. *Fultonia wilhelmsenae* sp. nov., female, setation of P1–P4 (no. of outer spines in roman numbers).

Swimming leg	Exp1	Exp2	Exp3	Enp1	Enp2	Enp3
P1	I,0	I,1	III,2,0	0,0	I,2,1	–
P2	I,1	I,1	III,2,2	0,1	0,1	I,2,1
P3	I,1	I,1	III,2,3	0,1	0,1	I,2,1
P4	I,1	I,1	III,2,1	0,1	0,1	I,2,1

A2 (Fig. 2B) with allobasis and 1-segmented exp bearing 1 bipinnate seta and few small spinules. Enp laterally with 2 bipinnate setae. Terminally with 6 bare setae, at least 1 of which geniculate (3 setae broken in Fig. 2B). Subterminally with long tube pore and a row of long spinules.

Md (Fig. 3A) gnathobase with broad and furrowed masticating front forming a mortar; dorsal seta lost, but ventrally with 2 sclerotized elements, being the outer one long and curved, whereas the second element being broad but short, not surpassing the gnathobase and ending in small teeth. Mandibular palp with spinules; basis with 2 bare setae. Enp 1-segmented, with bare 5 setae. Exp slightly longer than enp, with 2 outer and 2 terminal bare setae.

Mxl (Fig. 3B) with distinct exp. Praecoxal arthrite terminally with 4 spines, subterminally with another spine; laterally with 1 unipinnate seta, and on its surface with 2 bare setae. Coxa terminally with 3 setae, one of which very strong and plumose at its tip. Basis terminally with 2 setae. Enp absent. Exp 1-segmented, small and knob-like, terminally with 1 bare seta.

Mx (Fig. 3C). Syncoxa with 2 endites, the proximal one swollen and bearing 1 bare seta. Distal endite with 3 setae, the biggest one claw-like, terminally with pinnae. Basis distinct, terminally with 2 strong and claw-like spines, subterminally with bare seta. Enp incorporated into basis and represented by 2 bare setae.

Mxp (Fig. 3D) prehensile, syncoxa half as long as basis, with many spinules of different size, distally with 1 seta (broken in Fig. 3D). Basis with several long spinules. Enp produced into long claw showing strong denticles of increasing length at its distal part, additionally with 1 bare seta at its base.

P1 (Fig. 4A) with 3-segmented exp, and 2-segmented enp. Coxa and basis of approximately the same size. Basis with inner and outer bipinnate spine, the inner one very strong. Exp1 without, exp2 with inner seta. Exp3 with 3 outer bipinnate spines, and with 2 terminal setae, the outer one geniculate and bearing pinnae, the inner one bare and of "rat-tail" shape at its distal half. Enp1 without ornamentation and armature. Enp2 with 1 outer bipinnate spine, 2 terminal bare setae, and 1 plumose inner seta. For setal formula see Table 1.

P2–P4 (Figs. 4B–D) with 3-segmented exps and enps. Coxae slightly larger than bases, intercoxal sclerites big, bow-like (exemplified in

Fig. 4B), on outer side with few strong spinules. Bases much broader than long, exps and enps displaced outwardly. Bases with outer spines, at inner margin with long setules. Exps3 almost reaching length of exp1 and exp2 together, terminally with small, hook-like cuticular projection. Endopodal segments showing increasing length, enp1 being the shortest, and enp3 the longest segment. Setation of P2–P4 exp, and enp as in Table 1.

P5 (Fig. 3E) benps fused together, forming a narrow single plate. Endopodal lobe incorporated completely into basis, represented by 1 biplumose seta. Exp distinct, long and slender, with 2 outer, 2 terminal, and 1 inner seta. Additionally, outer distal margin with extremely long tube pore.

Male unknown.

Redescription of *Fultonia hirsuta* T. Scott, 1902

Material: Collected by G.O. Sars (1910) at Farsund/Korshavn, southern Norway. The sampled material comprises six individuals, three of which resulting to be *Fultonia hirsuta* females, two additional females belonging to the above described *F. wilhelmsenae* sp. nov., and the sixth specimen being no Argestidae. One female was dissected and placed on 12 slides, labelled as "Zool. Mus. Oslo, F20317 b–m". The remaining females were selected for further comparative examination without dissection, and returned into alcohol (coll. no. F20317a). Additional material: one male, collected by P. Bodin at Manche, Roscoff (France) on 14.05.1992; dissected, distributed over 3 slides, and labelled MNHN-Cp2449(1–3).

Female (Figs. 5–9)

Habitus (Figs. 5A,B) slender, body length from rostral tip to end of FR 620 µm. Cphth reaching at most ¼ of total body length. All body parts densely covered with small spinules, whose density decreases on the abdominal somites and the telson. Cphth and body somites except penultimate one with remarkably long sensilla at their distal margins. Thoracic somite bearing the P5 and abdominal somites additionally with row of long spinules at distal margins. Rostrum small, fused to cphth, with 2 sensilla and tube pore at its tip. Cephalothoracic integument posteriorly accompanied with rudimentary pleurotergite of fused P1-bearing thoracic somite.

Telson (Figs. 5A,B) almost square in shape, reaching at least length of preceding 2 abdominal somites together, dorsally with small anal operculum bearing a row of long spinules at distal margin, ventrally with interrupted row of larger spinules (Fig. 5B).

FR (Figs. 5B,C) small, square, with small spinules and 7 setae: I smallest, II and III of almost same length, all 3 setae arising subterminally at outer margin. IV and V longest setae, inserting terminally. VI slightly longer than setae II and III, bipinnate, inserting terminally at inner margin. VII triarticulated, arising subterminally on dorsal side, accompanied by small tube pore. FR ventrally with broad but short tube pore at distal margin.

A1 (Fig. 6A) 8-segmented. All segments with spinules of different length. First segment without seta. Second segment largest one, carrying 7 setae, at least 4 of which being bipinnate (3 setae broken). Third segment with 7 bipinnate setae. Fourth segment small, with 1 bipinnate seta and 1 long bare seta being basally fused to strong aes. Fifth segment smallest, with 1 bipinnate and 1 biplumose seta. Sixth segment with 2 bipinnate setae and 1 long bare seta arising subterminally. Seventh segment with 2 bipinnate and 2 bare setae. Eighth segment with 6 bare setae, terminally with small aes.

Setal formula: 1/0; 2/7; 3/7; 4/2+aes; 5/2; 6/3; 7/4; 8/6+aes.

A2 (Fig. 6B) with basis and 1-segmented exp bearing 1 bare seta but no spinules. Basis small, with few small spinules. Enp 2-segmented, enp1 without seta but few long spinules. Enp2 bearing several spinules and anteriorly 2 bipinnate setae, terminally with 5 setae, 4 of which geniculated. No tube pore.

Md missing, not drawn.

Mxl (Fig. 6C) badly damaged; thus, coxa and basis not drawn. Praecoxal arthrite with few spinules, terminally with 5 big spines (4 broken in Fig. 6C); laterally with 1 bare seta, and on its surface 2 with long and slender bare setae.

Mx (Fig. 6D) syncoxa with 2 endites, the proximal one small, cylindric, with 1 bare seta; the distal endite with 2 spines, one of which fused with segment and rounded at its tip. Basis distinct, with 2 strong terminal spines (one of which with rounded tip, the other broken), additionally with 2 setae. Enp reduced completely, represented by 2 bare setae.

Mxp (Fig. 6E) syncoxa small, covered with small fine spinules, terminally with 1 biplumose

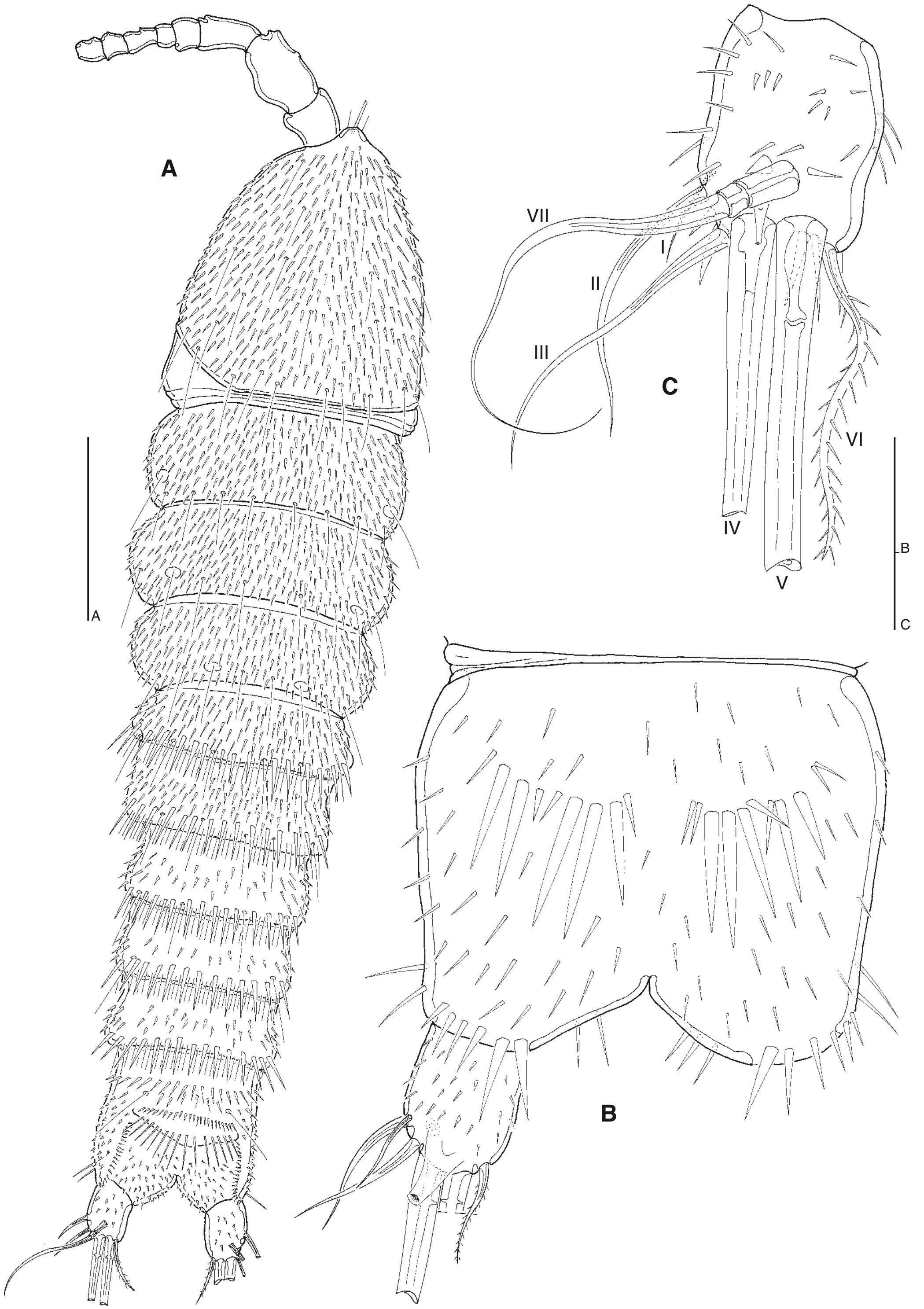


Fig. 5. *Fultonia hirsuta*, female. **A.** Habitus dorsal; **B.** Telson and FR, ventral view, furcal setae numbered I–VII; **C.** FR, dorsal view. Scales: A 100 µm, B–C 20 µm.

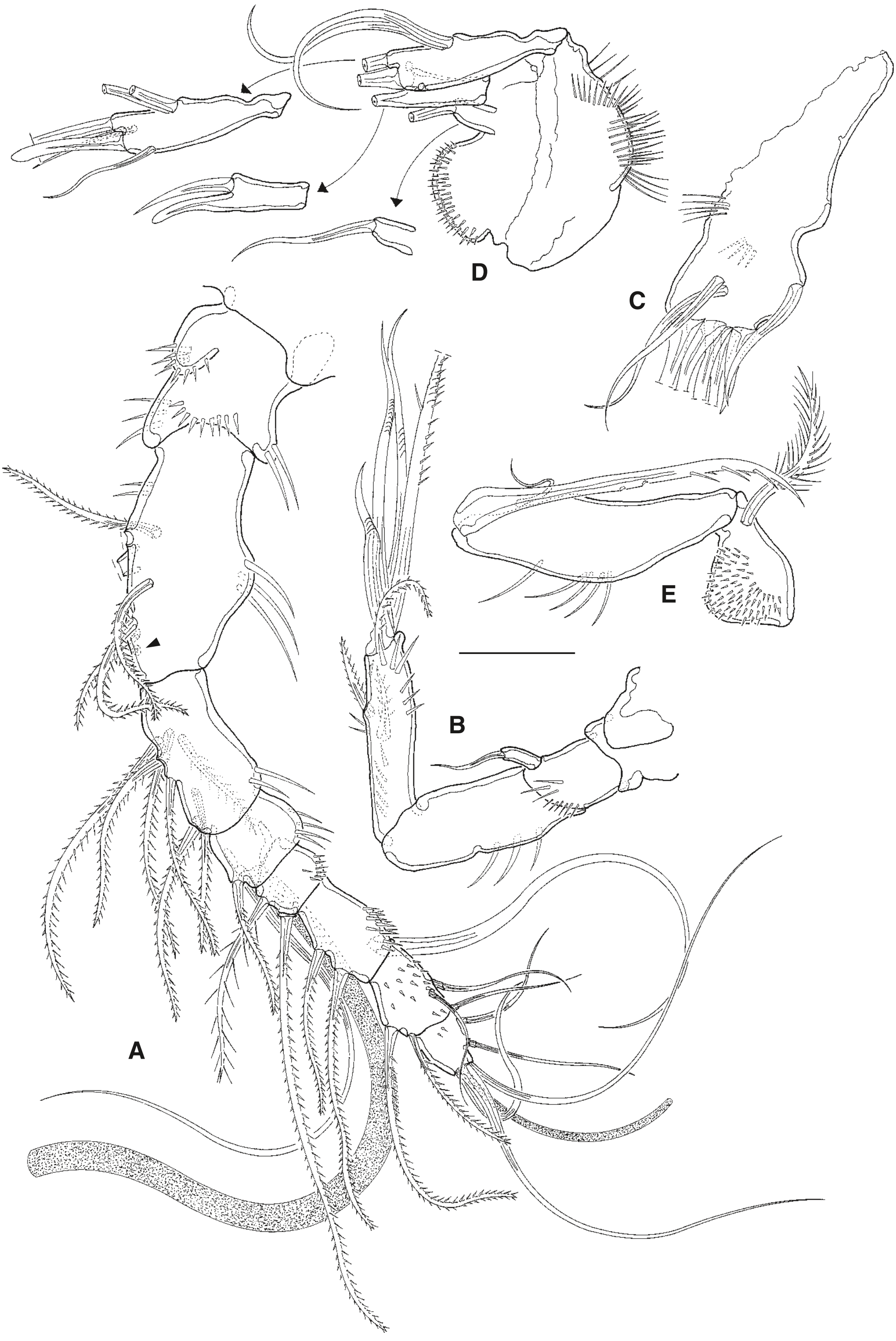


Fig. 6. *Fultonia hirsuta*, female. **A.** Antennula, arrowhead indicating base of (broken) seta; **B.** Antenna; **C.** Mxl, coxa and basis missing; **D.** Mx; **E.** Mxp. Scale: 20 µm.

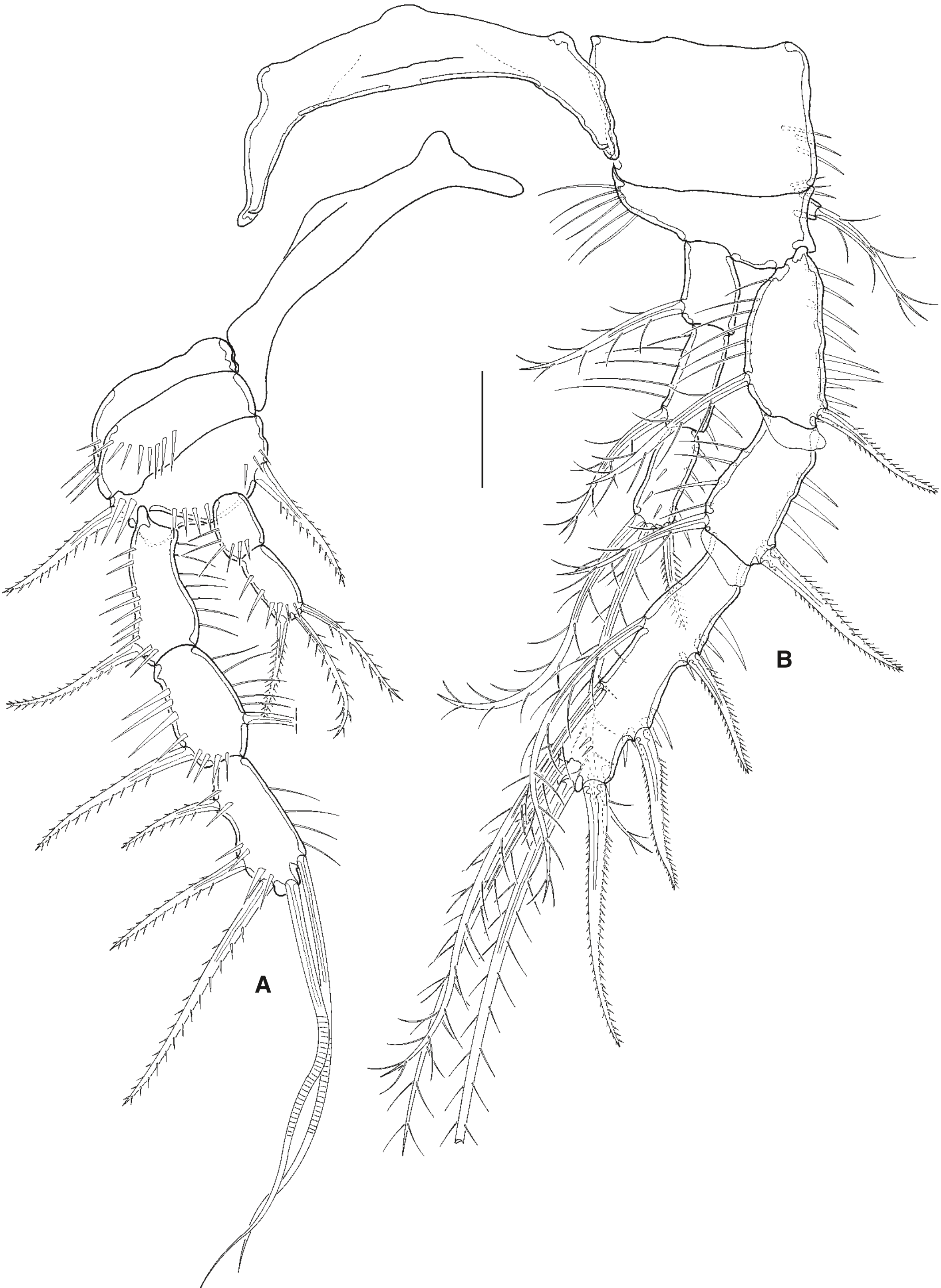


Fig. 7. *Fultonia hirsuta*, female. **A.** P1 with intercoxal sclerite; **B.** P2 with intercoxal sclerite. Scale: 20 µm.

seta. Basis with few long spinules. Enp produced into long and slender claw bearing long denticles at apical half and with 1 bare seta at its base.

P1 (Fig. 7A) with 3-segmented exp and 2-segmented enp. Praecoxa well developed. Coxa and basis of almost same size, coxa with some long spinules. Intercoxal sclerite elongate. Basis with inner and outer bipinnate spine and few long spinules. All exopodal segments of same size, exp2 with inner seta, exp3 with 3 outer spines and terminally with 2 geniculate bare setae. First endopodal segment with few spinules, without setae. Enp2 slightly longer than enp1, with 1 outer spine and 2 terminal bipinnate setae. For setal formula see Table 2.

P2–P4 (Figs. 7B, 8, 9A) with 3-segmented exps and enps. Intercoxal sclerites (Figs. 7B, 9A) narrow and bow-like. Coxae much bigger than bases, with few spinules. Bases broader than long, with outer seta; enp and exp displaced outwardly. P2 basis (Fig. 7B) with a few long setules at inner margin. Enps not surpassing second exopodal segment, enps3 with 1 outer spine and 2 terminal setae. Setation as shown in Table 2.

P5 (Fig. 9B) benps fused together, forming a narrow single plate. Endopodal lobe incorporated completely into basis, represented by 1 large biplumose seta. Exp distinct, long and slender, tapering posteriorly, with 2 outer, 2 terminal, and 1 inner seta. Additionally, outer distal margin with extremely long tube pore.

GF (Fig. 9C) with single gonopore; P6 reduced, without setae and forming 2 cuticular, laterally elongated rib-like projections with rounded tips.

Description of the male (Figs. 10–11)

As the only known male of *F. hirsuta* is dissected and distributed over three slides, no habitus could be drawn. Concluding from the intercoxal sclerites (cf. Figs. 7, 11), the male seems to be smaller

Table 2. *Fultonia hirsuta* T. Scott, 1902, setation of P1–P4 (no. of outer spines in roman numbers).

Swimming leg	Exp1	Exp2	Exp3	Enp1	Enp2	Enp3
P1	I,0	I,1	III,2,0	0,0	I,2,0	–
P2	I,1	I,1	III,2,2	0,1	0,1	I,2,0
P3	I,1	I,1	III,2,2	0,1	0,1	I,2,0
P4	I,1	I,1	III,2,1	0,1	0,1	I,2,0

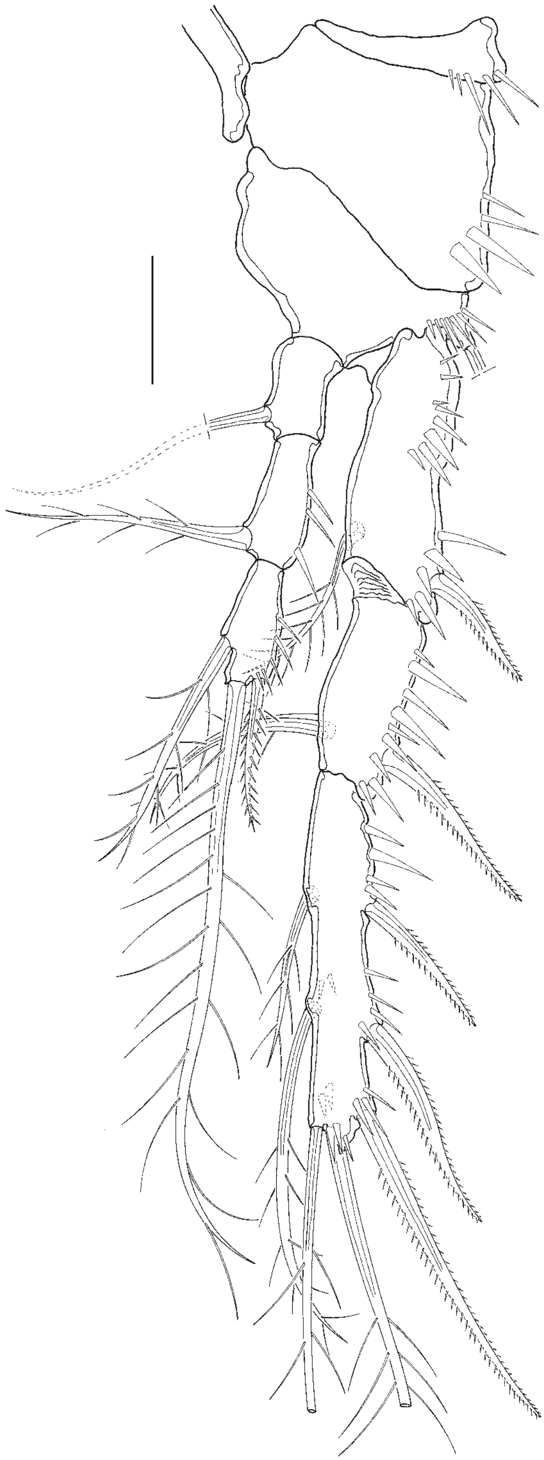


Fig. 8. *Fultonia hirsuta*, female. P3. Scale: 20 µm.

Fig. 9. *Fultonia hirsuta*, female. **A.** P4; **B.** P5; **C.** GF. Scale: 20 µm.

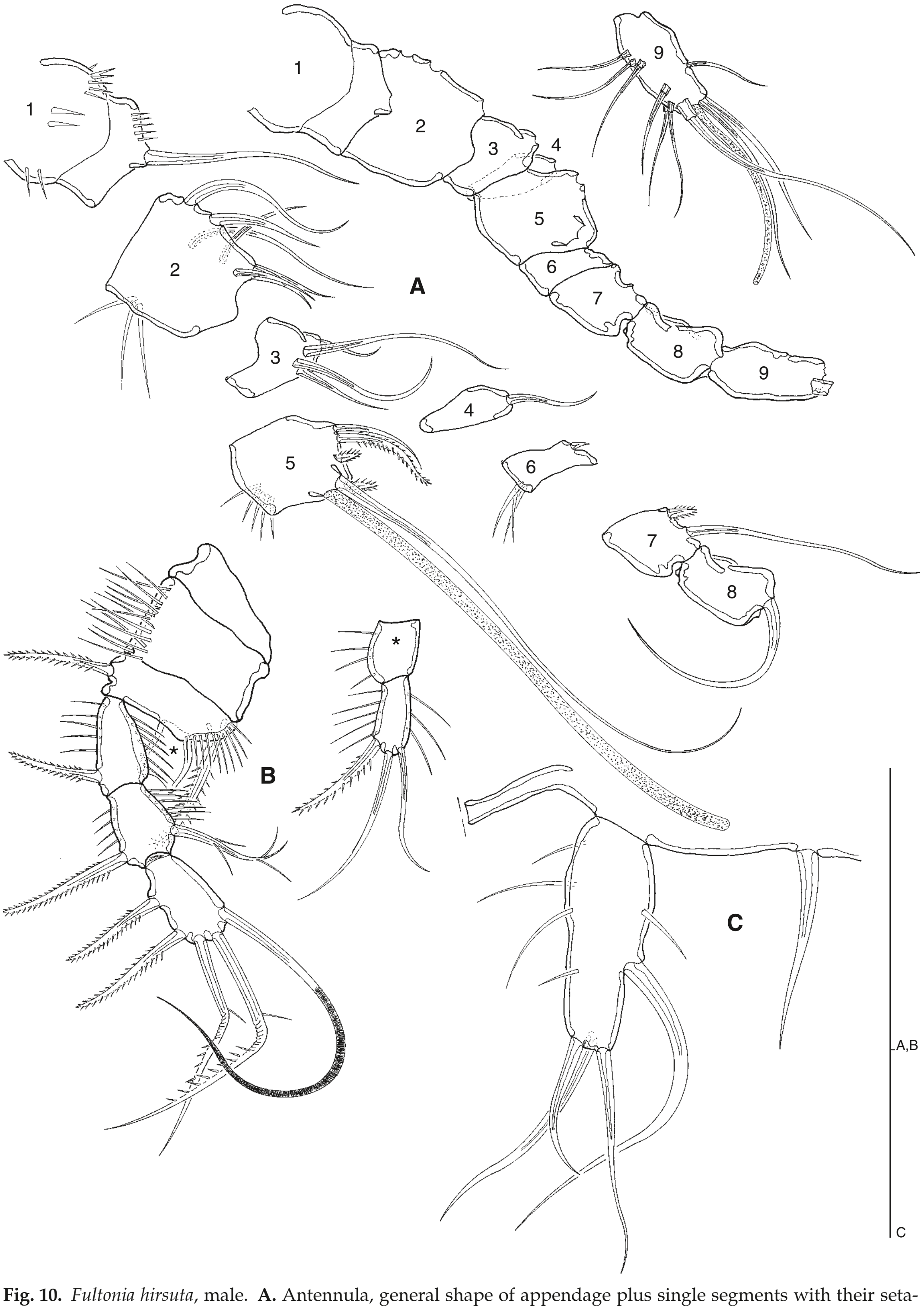


Fig. 10. *Fultonia hirsuta*, male. **A.** Antennula, general shape of appendage plus single segments with their setation; **B.** P1, asterisk marking position of enp; **C.** P5. Scales: 50 µm.

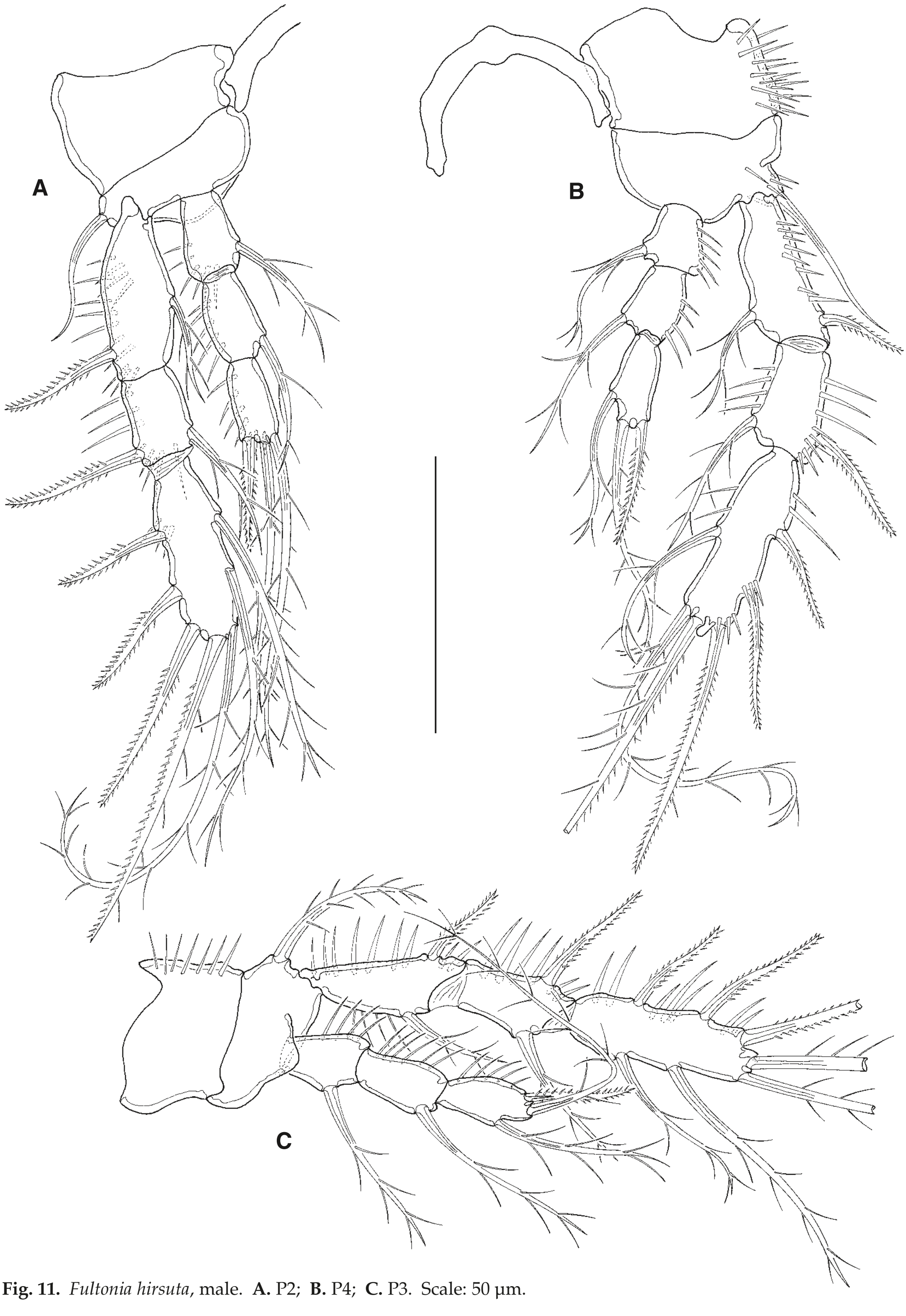


Fig. 11. *Fultonia hirsuta*, male. **A.** P2; **B.** P4; **C.** P3. Scale: 50 µm.

than the female. Moreover, the male swimming legs are less elongate than those of the female. Sexual dimorphism is discernible but not strongly expressed. The following male appendages are described: A1, P1–P5.

A1 (Fig. 10A) sexually dimorphic, haplocer, with 9 segments. First segment with several spinules and 1 seta at its distal margin, showing mediolaterally a cuticular suture. Second segment as long as first, with 7 setae and few spinules. Third segment smaller than the preceding ones, at one side connected directly with the fifth segment, distally with 4 setae. Fourth segment very small, with 1 seta. Fifth segment bearing 5 setae, 3 of which bipinnate; two of the bipinnate setae short but broad. One bare seta long, arising together with 1 aes from a protrusion situated laterally on the segment. Sixth segment as small as fourth one, with 1 small, tooth-like seta. Seventh and eighth segments of almost same size and indication of geniculation. Seventh segment with 1 short but broad bipinnate and 1 long bare seta; eighth segment terminally with 1 strong bare seta at its lateral side. Ninth segment slightly longer than preceding one, with 10 bare setae and 1 small aes.

Setal formula: 1/1; 2/7; 3/4; 4/1; 5/5 + aes; 6/1; 7/2; 8/1; 9/10 + aes.

P1 (Fig. 10B) generally as in female, exp 3-, enp 2-segmented. Coxa with long spinules at outer margin, basis with long spinules at inner corner. Third outer element on exp3 transformed into geniculated seta, innermost terminal seta rat-tailed; enp2 with 1 outer spine and 2 terminal bare setae (bipinnate in female).

P2–P4 (Figs. 11A–C) segments not as long as in female; setation identical as in female (cf. Tab. 2).

P5 (Fig. 10C) exp shorter than in female, with 4 setae only, due to loss of 1 outer seta; distal outer seta shifted terminally; inner seta much stronger than in female; basendopodal seta bare. No tube pore discernible.

Fultonia gascognensis Bodin, 1968

Material: female holotype, collected by P. Bodin on 12.08.1963 in the Gulf of Gascogne (France; 46°21' N, 4°54' W), distributed over 3 slides (coll. nos. MNHN-Cp3254 [138-a], 3255 [138-b], 3256 [138c]). As the holotype has been dissected, no habitus could be drawn, inhibiting therefore the detection of an eventual coverage of the body with cuticular spinules. Furthermore, neither mxl nor P5 could be found and are therefore not drawn.

Redescription of female holotype (Figs. 12–14)

A1 (Fig. 12A) 7-segmented, most setae bipinnate; first segment laterally with 1 seta (broken) at distal margin; second segment with 6 setae (1 seta broken) and some strong spinules; third segment slightly smaller than second, with 8 setae; fourth segment with 1 long bare seta and 2 smaller bipinnate setae, additionally with aes arising from protrusion and accompanied by 1 bare seta; fifth segment smallest, with 2 bipinnate setae; sixth segment with 2 bipinnate setae, at its lateral distal margin with 1 additional long and biarticulated bipinnate seta; seventh segment as long as two preceding ones together, with 10 setae and terminally with 1 small aes.

Setal formula: 1/1; 2/6; 3/8; 4/4 + aes; 5/2; 6/3; 7/10 + aes.

A2 (Fig. 12B) with allobasis and 1-segmented exp that bears 1 bipinnate seta and apically several long and slender spinules. Enp anteriorly with 2 bipinnate setae, terminally with 6 setae, 4 of which geniculated, 1 bare, and 1 bipinnate. No tube pore.

Md (Fig. 12C) gnathobase with broad and furrowed masticating front, forming a mortar; 1 small seta dorsally; ventrally with 1 sclerotized broad and slightly curved element, barely surpassing the gnathobase and ending in small teeth. Mandibular palp: basis with no spinules but with 1 bare and 1 biplumose seta; enp 1-segmented, with 5 setae and several spinules; exp long and slender, with several spinules and 1 bare and 1 biplumose terminal seta.

Mx (Fig. 12D) with distinct basis and 2 endites; proximal endite small, terminally with 1 bare seta; distal endite slightly longer than proximal one, terminally with 2 bare setae and 1 unipinnate claw. Basis distinct, with 2 strong terminal spines (one of which fused to segment), additionally with 1 seta. Enp lost, represented by 2 setae.

Mxp (Fig. 12E) prehensile; syncoxa bearing 1 biplumose seta and several long spinules; basis longer than syncoxa, with row of spinules; enp produced into long claw being longer than basis and bearing massive denticles of increasing length at its distal part, additionally with 1 bare seta at its base.

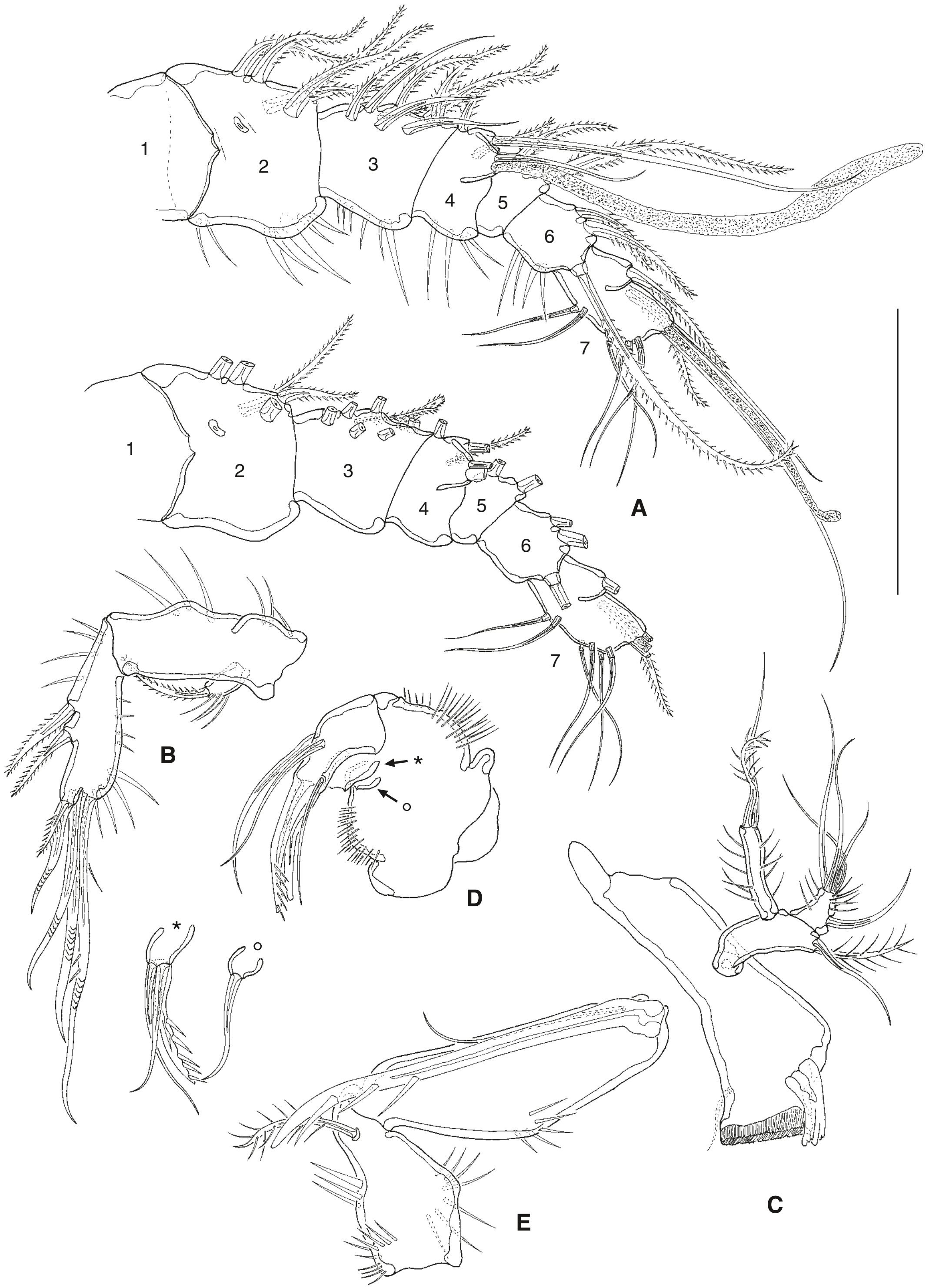


Fig. 12. *Fultonia gascognensis*, female. **A.** Antennula, lower illustration showing backmost setae; **B.** Antenna; **C.** Md; **D.** Mx, circle and asterisk showing proximal and distal endite, respectively; **E.** Mxp. Scale: 50 µm.

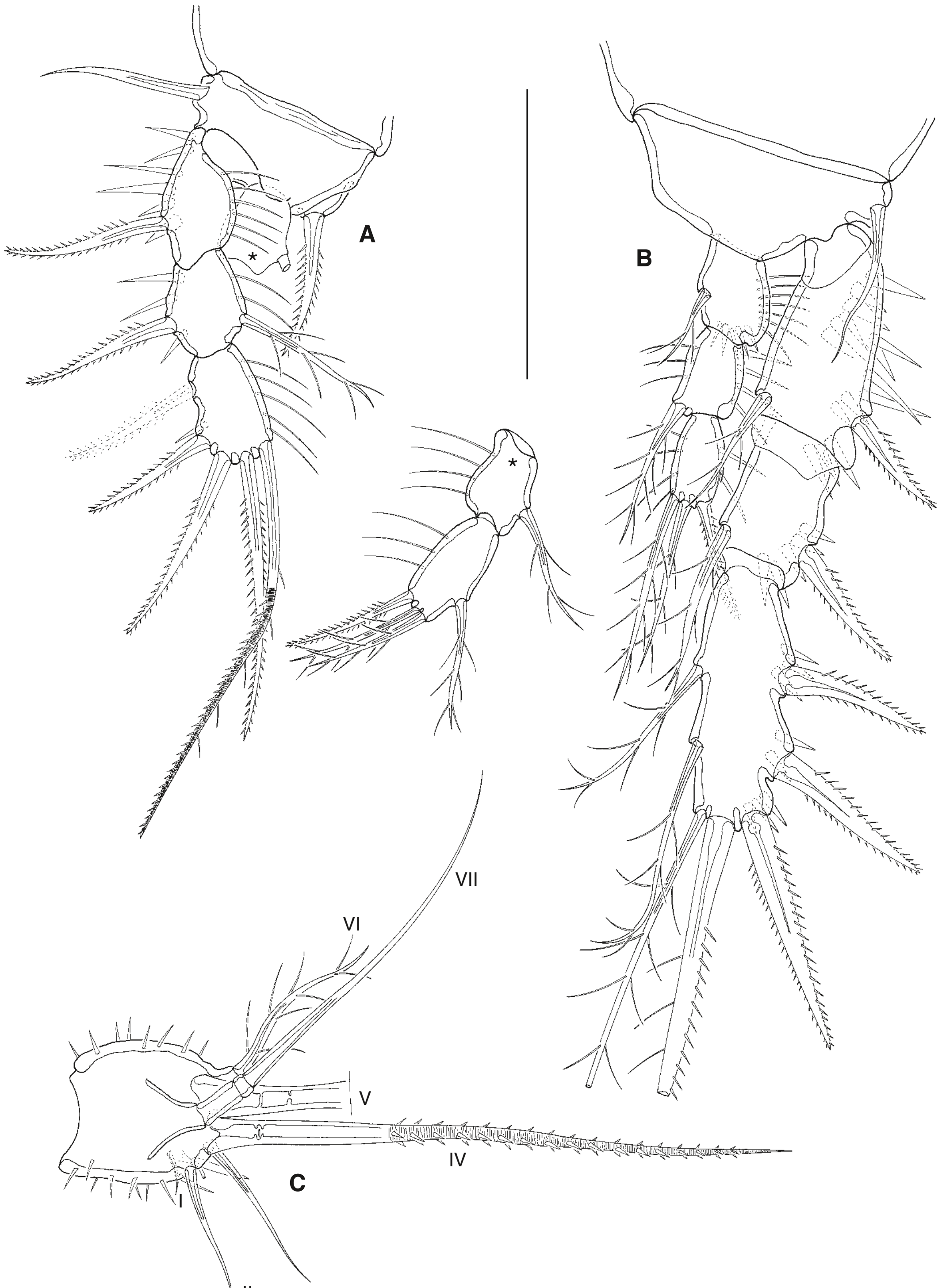


Fig. 13. *Fultonia gascognensis*, female. **A.** P1, asterisk marking position of enp; **B.** P2; **C.** FR, dorsal view, furcal setae numbered I–VII. Scale: 50 µm.

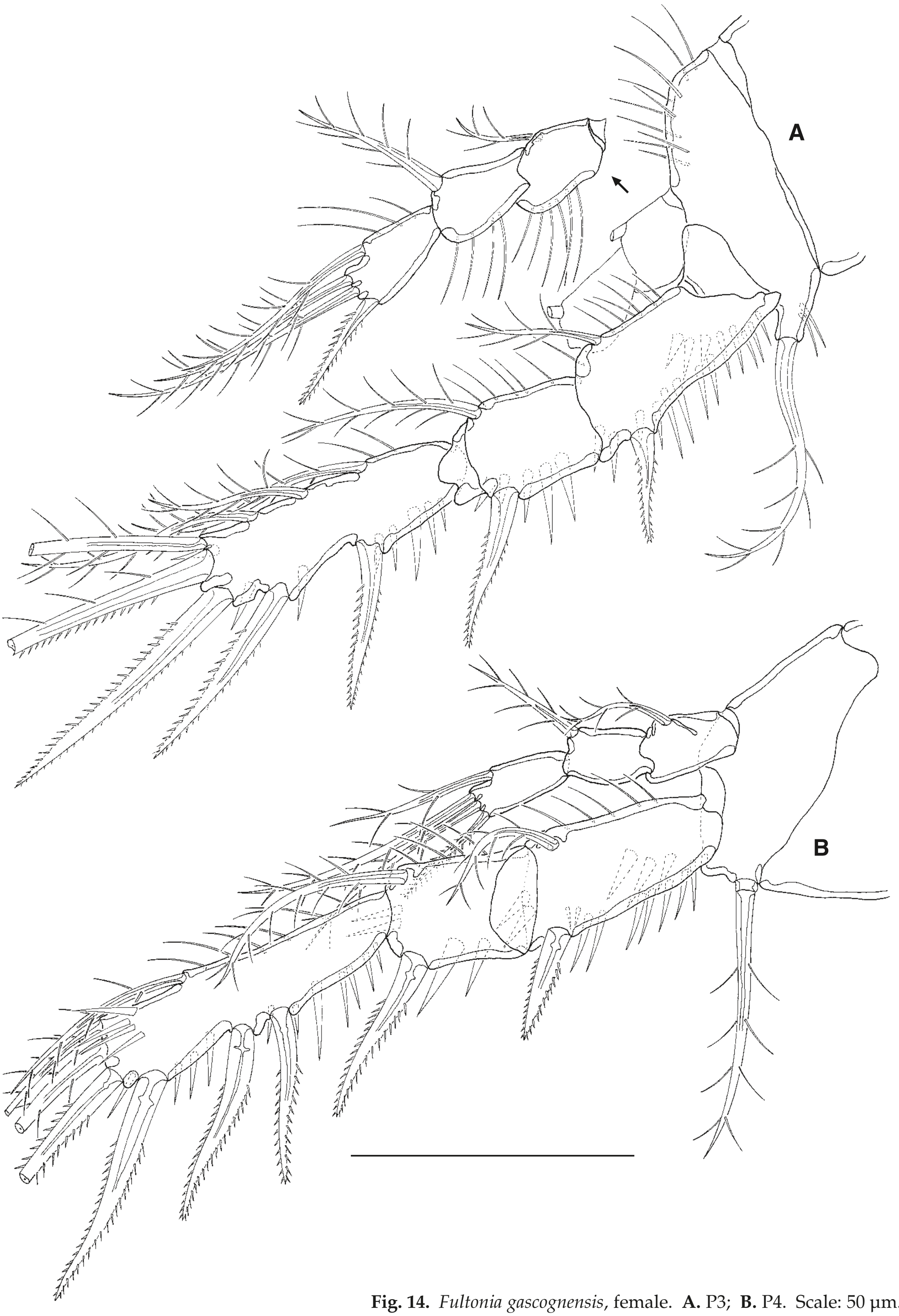


Fig. 14. *Fultonia gascognensis*, female. **A.** P3; **B.** P4. Scale: 50 µm.

P1 (Fig. 13A) with 3-segmented exp and 2-segmented enp. Basis broader than long, with outer bare and inner bipinnate seta. Outer terminal seta of P1 exp3 bipinnate, non-geniculate; inner terminal seta rat-tailed, bipinnate. Enp1 with 1 inner biplumose seta, enp2 with 1 inner biplumose seta and 2 terminal biplumose setae of almost same length, additionally with 1 outer bipinnate spine.

P2–P4 (Figs. 13B, 14A, B) with 3-segmented enps and exps. P2–P4 enps not reaching boundary between exp2 and exp3. Setation as shown in Table 3; P4 exp3 with additional outer spine (Fig. 14B); P2 enp3 with 2 terminal setae and 1 outer spine (Fig. 13B), whereas P3 (Fig. 14A) and P4 enp3 additionally with 1 inner seta.

FR (Fig. 13C) short, square in size, with seven setae: I bare, very small, inserting ventrally; II bare, about 3.5 times longer than I, subterminally; III bare, as long as II, inserting terminally at the ventral side; IV long, rat-tailed and tripinnate; V broken, apparently longest seta; VI slightly longer than II and III, bipinnate; VII triarticulate, longer than VI, arising dorsally from triangular protrusion.

Remarks. The here presented redescription of *F. gascognensis* differs in some minor features from the original one provided by Bodin (1968): re-examination of the A2 showed that it bears an allobasis instead of a basis; careful examination of the mx revealed no enp, with former endopodal setae arising directly from the basis; shape of several setae differs concerning their ornamentation (pinnate, plumose, bare), e.g. most setae on mandibular palp, endopodal seta of mxp, P1 exp3, FR, etc.).

Parargestes tenuis (Sars, 1921) var. *arcticus* Lang, 1936

Material: *P. tenuis* var. *arcticus* from the K. Lang collection (coll. no. Type-2269) of the Swedish Museum of Natural History. The label says:

"*Parargestes tenuis* (G. O. Sars), var. *arcticus* Lang. Spetsbergen. 76°46'n – 15°22'ö. 210 m. Bottentemp. +2,38 Fin, svartgrå lera, 26/6 1898. Coll. Spetsb.-exp. 1898. St. 9. Det. K. Lang."

The material consists of 3 female specimens. All individuals show remarkable damages in the appendages and are covered with fine and very compact, cement-like detritus, inhibiting a

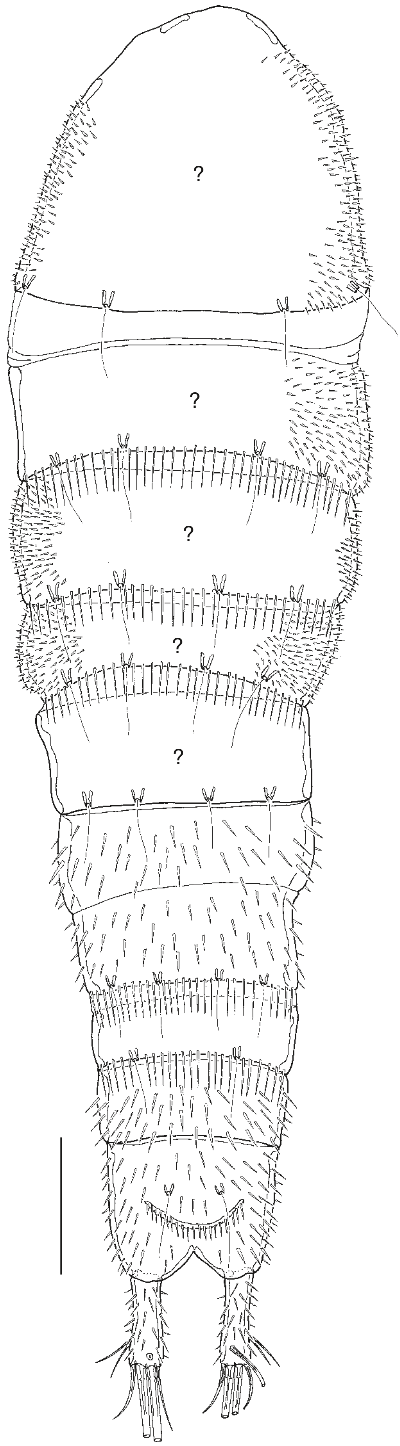


Fig. 15. *Argestes tenuis* var. *arcticus* nom. nov., female. Habitus, dorsal view. Scale: 100 µm.

Fig. 16. *Argestes tenuis* var. *arcticus* nom. nov., female. **A.** Habitus, lateral view, furcal setae numbered II–VII; **B.** P1. Scales: A 100 µm, B 20 µm.

detailed observation. Thus, and because dissection was not done (to maintain the individuals in the original conditions), only a partial redescription of the species could be made. It includes a description of the female's body, P1, P4, and P5.

Partly redescription of female (Figs. 15–17)

Habitus (Figs. 15, 16A) long and slender, body length from rostral tip to end of FR varying between approximately 830 µm and 1000 µm. Cphth occupying approximately ¼ of whole body length. All body parts presumably covered densely with small spinules; however, it could not be confirmed unequivocally for cphth and thorax, due to the compact coverage of the body with detritus (interrogatives in Figs. 15, 16A). Thoracic somites bearing P2–P4 as well as abdominal somites 1 and 2 dorsally with remarkably elongate spinules at their distal margins. Thoracic somite bearing the P5 and abdominal somites covered with longer spinules than preceding somites. Cphth and body somites except penultimate one at their distal margins with remarkable long sensilla arising from tubercles. Rostrum virtually absent. Cephalothoracic integument posteriorly accompanied with rudimentary pleurotergite of fused first thoracic somite. Telson almost square from dorsal view (Fig. 15) but trapezoid from lateral view, being the ventral side 2 times longer than the dorsal side (Fig. 16A). FR elongate, about 3 times longer than broad, presenting seven setae: I and II (Fig. 16A) laterally at distal half, III terminally at outer margin (Fig. 15), IV and V longest setae, terminally (Fig. 15), VI as long as III, inserting terminally at inner margin, VII triarticulate (Figs. 15, 16A). Due to compact coverage with detritus, verification of a rat-tailed shape of the furcal setae was impossible. Anal operculum weakly developed, with spinules at its distal margin and flanked by 2 sensilla.

P1 (Fig. 16B) coxa smaller than basis, without ornamentation. Basis with outer spine and inner strong bipinnate seta. Exp 3-segmented, all segments of same size, outer spines of exp2 and exp3 with STEs (not discernible in P1 exp1). Enp 3-segmented, as long as exp, all segments of same size. Setal formula as given in Table 3.

P4 (Fig. 17A) coxa and basis not drawn. Exp large, 3-segmented, exp2 shortest. Distal half of exp3 shortened, so both distal outer spines stay close together and arise subterminally. Enp 3-segmented, slightly shorter and more slender than exp. Setal formula shown in Table 4.

P5 (Fig. 17B) benps fused together, forming a narrow single plate. Endopodal lobe incorporated completely into basis, represented by 2 biplumose setae of nearly equal length. Exp distinct, long and slender, not reaching length of basendopodal setae, with 2 outer, 2 terminal, and 1 inner seta. In addition terminally with tube pore (broken[?] in Fig. 17B).

Table 3. *Fultonia gascognensis* Bodin, 1968, setation of P1–P4 (no. of outer spines in roman numbers).

Swimming leg	Exp1	Exp2	Exp3	Enp1	Enp2	Enp3
P1	I,0	I,1	III,2,0	0,1	I,2,1	–
P2	I,1	I,1	III,2,2	0,1	0,1	I,2,0
P3	I,1	I,1	III,2,3	0,1	0,1	I,2,1
P4	I,1	I,1	IV,2,1	0,1	0,1	I,2,1

Discussion

In the frame of clearing the phylogeny of a supposed monophylum Argestidae (cf. George 2004, 2008, Corgosinho & Martínez Arbizu 2010), the here presented contribution is the second of a series dealing with those argestid genera that apparently represent the most primitive ones of the family (cf. Por 1986; George 2004, 2008). While George (2008) confirmed a monophylum *Argestes* Sars, 1910, the here presented paper focuses on the genus *Fultonia*. Furthermore, new evidences confirm the necessity of re-allocation of *Parargestes tenuis* (Sars, 1921) into *Argestes*, already suggested by George (2008) and now undertaken (see below).

According to Wells (2007), three *Fultonia* species are known up to date: *F. hirsuta*, *F. bougisi* Soyer, 1964, and *F. gascognensis*. *F. bougisi* was subsequently split into two subspecies by Soyer (1966), namely *F. bougisi bougisi* Soyer, 1966 and *F. bougisi corallicola* Soyer, 1966, but later on synonymised again by that author (Soyer 1971).

Table 4. *Argestes tenuis* var. *arcticus* nom. nov., female, setation of P1 and P4 (no. of outer spines in roman numbers).

Swimming leg	Exp1	Exp2	Exp3	Enp1	Enp2	Enp3
P1	I,0	I,1	III,2,0	0,0	0,1	I,2,0
P4	I,1	I,1	III,2,1	0,1	0,1	I,2,2

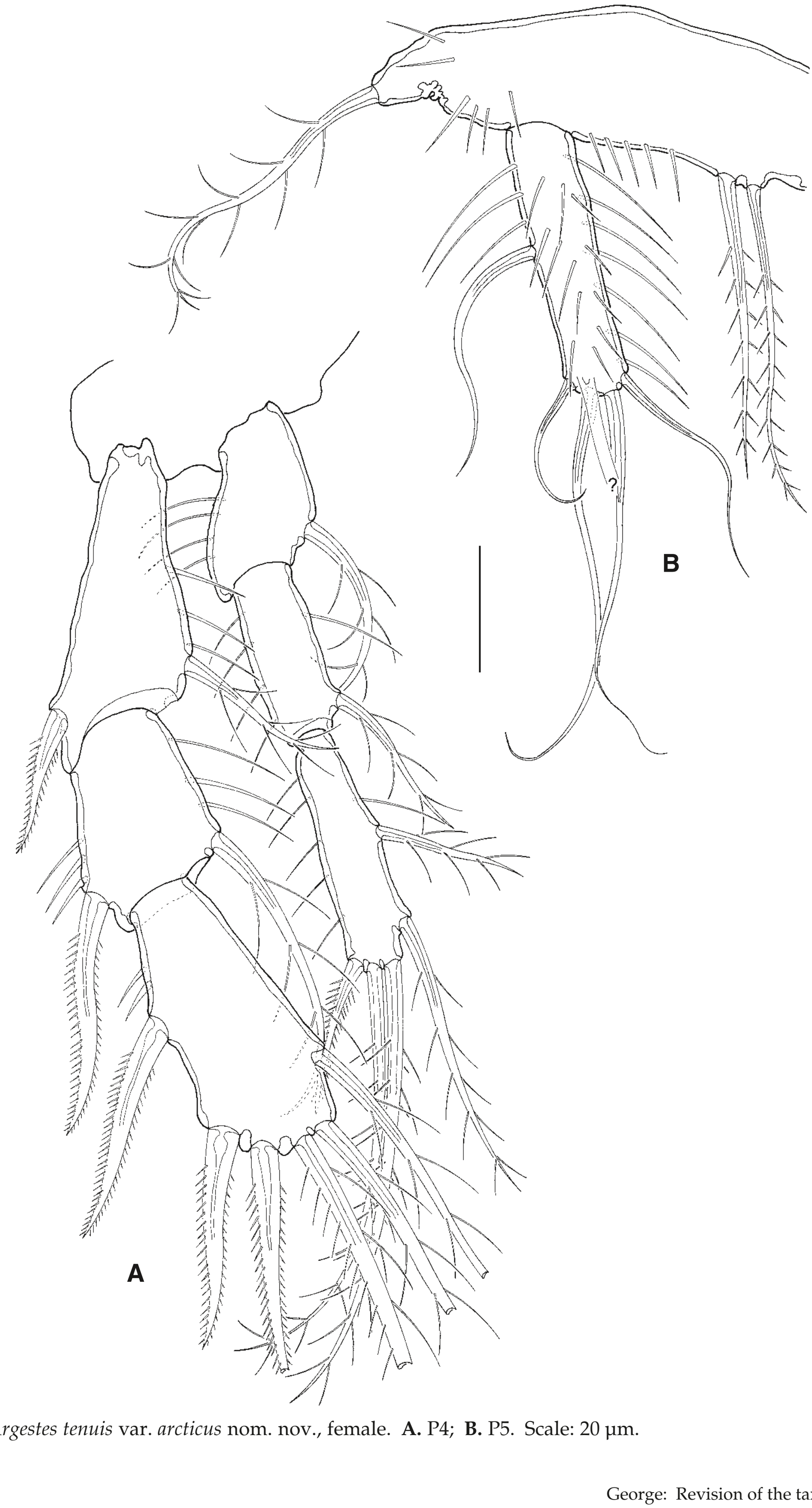


Fig. 17. *Argestes tenuis* var. *arcticus* nom. nov., female. **A.** P4; **B.** P5. Scale: 20 µm.

Another species, *Argestes sarsi* Smirnov, 1946, was transferred into *Fultonia* by Lang (1965). However, mainly due to the insufficient description provided by Smirnov (1946), the systematic position of that species remains unclear until today. While Bodin (1968) adopted Lang's (1965) allocation, renaming the species *Fultonia sarsi* (Smirnov, 1946), Por (1979) proposed its translocation into the then newly erected genus *Dizahavia* Por, 1979 because of the 6-segmented A1 and the P4 exp3 retaining 2 inner setae instead of 1. Bodin (1997) and George (2004, 2008) adopted the name *Fultonia sarsi*, but Wells (2007) left the species in Argestidae as species *incertae sedis*, retaining Smirnov's (1946) *Argestes sarsi*. As the type material is not available for detailed redescription nor for phylogenetic discussion, I follow Wells (2007), excluding the species from the discussion on *Fultonia*. Thus, with the inclusion of the here presented *F. wilhelmsenae* sp. nov., the genus encloses four species so far.

An extensive phylogenetic revision of Argestidae including all so far enclosed taxa would go far beyond the scope of the present contribution. It must be noticed, however, that a well-based characterization of a monophylum Argestidae is still pending. George (2004) listed several presumably derived features (Fig. 18, characters I–VI) that may perhaps confirm the monophyletic status of Argestidae but are still awaiting their phylogenetic evaluation. Recently, Corgosinho & Martínez Arbizu (2010) discussed additional characters related to the shape and armature of the mx and considering them as apomorphies for Argestidae, namely the development of 1 very strong spine on each the distal maxillar endite and the basis close to the basal claw* (Fig. 18, characters VII–VIII).

In Fig. 18, characters I–VIII are listed tentatively as apomorphies for Argestidae without detailed phylogenetic discussion, which may be provided elsewhere. The result of the here presented phylogenetic analysis focuses instead on systematic relations of *Argestes* and *Fultonia*. Altogether, 38 morphological characters have been detected that may elucidate phylogenetic relationships of and within both genera. They are listed in the Appendix and discussed in detail below. Ameiridae was selected as outgroup, as that family has often be supposed to be closely related to Argestidae (e. g. Huys & Conroy-Dalton 1997, George 2004, but see Corgosinho & Martínez Arbizu 2010).

Twenty eight apomorphies (1–6, 8–29) are congruent, supporting the corresponding monophyla (Fig. 18) or characterizing the respective species (Appendix). Ten additional characters (7, 30–38) still remain questionable, as they are heterogeneously distributed over the species and do therefore not allow yet a clear detection of sistergroups within *Fultonia*. As there have recently been recorded several so far unknown *Fultonia* species from different deep-sea and seamount locations (George pers. obs.), their successive description and integration into future phylogenetic analyses may clear up the relations inside that genus.

Similarities between *Argestes* and *Fultonia*

Sars (1910) already noted a strong resemblance between *F. hirsuta* and *Argestes mollis* Sars, 1910. That similarity is confirmed here in a phylogenetic sense. *Fultonia* shares some derived characters with *Argestes* that have already been assigned to the latter by George (2008) [in the following, plesiomorphic conditions in square brackets]:

1. Body densely covered with small cuticular spinules [no spinule coverage];
2. A1 with very strong seta terminally on 6th segment in female [no strong seta developed].

The phylogenetic value of both apomorphies has been extensively discussed by George (2008). Both *Fultonia hirsuta* and *F. wilhelmsenae* sp. nov. fit with the derived conditions. Character 2 is also clearly detectable in *F. bougisi* (cf. Soyer 1964, 1966) and *F. gascognensis* (Fig. 12 A, see also Bodin 1968), whereas the body coverage with small cuticular spinules has still to be proved for both species. Further comparison of both genera reveals a third synapomorphy:

3. Dorsal thoracic sensilla remarkably elongate [sensilla small].

Character 3:
Dorsal thoracic sensilla remarkably elongate

The sensillar ornamentation may vary remarkably in Harpacticoida (cf. George 2008). However, the common shape of these sense organs is that of fine and small "hairs" never reaching the length

---

* Corgosinho & Martínez Arbizu (2010) adopt the mouthpart-terminology proposed by Ferrari & Ivanenko (2008), regarding the claw-bearing segment of the mx as first endopodal segment instead of the basis. In the present contribution, I do not follow that approach.

of a normal-sized seta. *Argestes* and *Fultonia* present, however, sensilla of considerable length, which may even surpass the distal margin of the following thoracic somite (cf. George 2008). Although such long sensilla have occasionally been observed in other harpacticoid taxa (e. g. *Isthmiocaris longitelson*, cf. George & Schminke 2003, some *Mesocletodes* species, cf. Menzel & George 2009), their occurrence is comparatively rare and in particular uncommon inside the here assumed outgroup, the Ameiridae Boeck, 1865. Therefore, the remarkable sensillar elongation in *Argestes* and *Fultonia* is regarded as synapomorphy for both taxa. Thus, apomorphies 1–3 support the monophyly of a taxon *Argestes*–*Fultonia* (Fig. 18, Appendix). Its designation as Argestinae Por, 1986 subfam. nov. is justified below.

In addition to synapomorphies 1–3, both *Fultonia* and *Argestes* share another feature, which according to Itô (1983) is the cephalothoracic integument being posteriorly accompanied by the rudimentary pleurotergite of the fused first thoracic somite. George (2008) accepted that explanation for this more or less hyaline structure present in all *Argestes* species. However, its presence also in *Fultonia* (Figs. 1 A, B, 5 A) (not yet confirmed for *F. bougisi* and *F. gascognensis*) and *Parargestes tenuis* var. *arcticus* (Figs. 15, 16), coupled with its simultaneous absence in more basal species like e. g. *Bodinia* George and *Dizahavia* Por may indicate a possible derived status of that feature. Instead of being a rudimentary remnant of the originally free P1-bearing thoracic somite, it might constitute a secondarily evolved kind of joint enabling a better agility of the cphth when the animal moves on or in the sediment, as assumed for other harpacticoid copepods (e. g. George & Schminke 2003). However, as this assumption is quite speculative so far, that character is ignored in the present phylogenetic analysis.

Differences between *Argestes* and *Fultonia*

Disregarding the above listed synapomorphies 1–3, *Argestes* and *Fultonia* show differences that justify their maintenance as distinct monophyla (Fig. 18, Appendix). George (2008) confirmed and discussed two apomorphies for *Argestes*:

4. Furcal setae I, II, III, VI rat-tailed [setae of normal shape];
5. Thoracic sensilla arising from long cylindrical tubercles [no tubercles developed].

Careful comparison of *Argestes* and *Fultonia* reveals that there is a third and even a fourth apomorphy for *Argestes*, obviously missing in the *Fultonia* groundpattern:

6. P1 exp2 and exp3 outer spines with Subapical Tubular Extensions [no Subapical Tubular Extensions developed].
7. A2 with allobasis [A2 with basis].

Character 6
P1 exp1 and exp2 outer spines with Subapical Tubular Extensions (STE)

STEs may be detected in different harpacticoid taxa. However, as most setae in Copepoda lack STEs (cf. Huys & Boxshall 1991, Seifried 2003), it is assumed that their expression is rather derived than basal. Inside Argestidae, Menzel & George (2009) confirmed STEs also for *Mesocletodes* Sars, 1909. They concluded that the presence of STEs in both the rather primitive *Argestes* (cf. George 2008) as well as in the more derived *Mesocletodes* may be the result of convergent development (Menzel & George 2009), which is adopted here. Concerning the here compared taxa, no *Fultonia* species shows that derived feature, but almost all *Argestes* species do (to be confirmed for *A. mollis* Sars, 1910). Thus, it is regarded as apomorphy for that genus.

Character 7
A2 with allobasis

The plesiomorphic condition of an antenna bearing a basis and a 2-segmented enp is still retained in *F. hirsuta* and *F. bougisi*. Thus, for the *Fultonia* groundpattern the possession of that plesiomorphic state has to be assumed, while its sistertaxon *Argestes* developed a derived A2 bearing an allobasis. However, the incorporation of the antennar enp1 into the basis occurs quite often within Harpacticoida, so it is not surprising that inside *Fultonia* there are species showing also that derived condition (*F. gascognensis* and *F. wilhelmsenae* sp. nov.), leading to the conclusion of a convergent development in *Argestes* and the named two *Fultonia* species. Nonetheless, the possession of an allobasis in all *Argestes* species allows the conclusion that this derived condition has evolved as autapomorphy in the *Argestes* ancestor, forming therefore a synapomorphy for all *Argestes* species.

On the other hand, *Fultonia* may be characterized by the following 8 apomorphies:

8. Md gnathobase with broad and furrowed masticating front forming a mortar instead of a cutting edge [gnathobase formed as indented cutting edge];
9. Md gnathobase with distinct strongly sclerotized element at its ventral margin [no strong element developed];
10. Mxp: syncoxa lost 1 seta, retaining 1 seta only [mxp syncoxa with 2 setae];
11. Mxp: claw with few but long denticles at its distal half [claw unipinnate or bare];
12. P1 enp 2-segmented [P1 enp 3-segmented];
13. P2–P4 enps remarkably reduced in size, reaching at most the distal margin of exp2 [P2–P4 enps, reaching at least half of length of exp3];
14. P2–P4 enps3 lost 1 inner setae, showing at most 4 setae [P2–P4 enps3 with 5 setae];
15. Female P5 benp with 1 seta only [female P5 benp with 2 setae].

Characters 8 and 9
Md gnathobase with broad and furrowed masticating front forming a mortar; additionally with strongly sclerotized element at its ventral margin

In the copepod groundpattern the mandibular gnathobase is produced into a sharp cutting edge and apart from 2 dorsal setae, no further distinct elements are present (Huys & Boxshall 1991). Such gnathobase is retained in almost all copepod orders and therefore is considered as constituting the groundpattern of Copepoda (cf. Huys & Boxshall 1991). In Harpacticoida and even Podogennonta, the only deviation from that groundpattern is the reduction of 1 dorsal seta (Seifried 2003). Thus, the development of a broad and furrowed masticating front in *Fultonia* has to be considered as derived condition. Same applies to the development of 1 distinct, strongly sclerotized and toothed element at the ventral margin of the gnathobase (not yet confirmed for *F. hirsuta*). It resembles what is called *lacinia mobilis* in some other crustaceans (e.g. Peracarida; cf. Mielke 1984). The exclusive presence of such particular gnathobase in almost all known *Fultonia* species (to be confirmed for *F. hirsuta*) is regarded as a synapomorphy of these taxa.

Character 10
Mxp: syncoxa lost 1 seta, retaining 1 single seta only

In *Argestes* all species bear 2 setae at the distal margin of the maxillipedal syncoxa, whereas all *Fultonia* species reduced 1 seta, being that reduction the derived state.

Character 11
Mxp: claw with few but long denticles at its distal half

While *Argestes mollis* and *A. reductus* show bare maxillipedal claws, it is unipinnate in *A. angolaensis* (George 2008). In contrast, all *Fultonia* species show a maxillipedal claw equipped with only few denticles that are restricted to its distal half but increase considerably in size (Figs. 3D, 6E, 12E, cf. Bodin 1968). Although it is impossible in the frame of the present contribution to clear whether a bare or unipinnate claw constitutes the ancestral condition (both states are widely distributed over Harpacticoida), it appears doubtless that the scarce development of few but strong denticles at the maxillipedal claw like in *Fultonia* is a derived state, certainly linked to any specific function of that appendage. This is regarded as a derived and synapomorphic condition for all *Fultonia* species.

Character 12
P1 enp 2-segmented

Inside the monophylum *Argestes–Fultonia*, all representatives of *Argestes* show a 3-segmented P1 enp, which reflects the groundpattern of even all Copepoda. In contrast, all *Fultonia* species bear a 2-segmented P1 enp; in combination with the remaining apomorphies it is considered as the apomorphic condition, pointing to the close relation of all respective species.

Character 13
P2–P4 enps remarkably reduced in size, reaching at most the distal margin of exp2

The basic condition in harpacticoid swimming legs includes enp and exp being of same length (cf. Huys & Boxshall 1991, Seifried 2003). However, in most Harpacticoida a deviation can be observed that often manifests in size reduction of mainly the endopods. *Argestes* shows P2–P4 enps being slightly smaller than the corresponding exps, but surpassing clearly the boundary between exp2 and exp3. In contrast, the *Fultonia* species show considerably shorter P2–P4 enps that hardly reach the boundary between exp2 and exp3. This further reduction in size is interpreted as apomorphic for the genus.

Character 14
P2–P4 enps3 lost 1 inner seta, showing at most 4 setae

While all known *Argestes* species show 2 inner setae on P2–P4 enps3, in *Fultonia* one inner seta became lost. Therefore, no *Fultonia* species bears more than 4 setae on its third segment of P2–P4. That loss of 1 element is a clear apomorphy for the genus.

Character 15
Female P5 benp with 1 seta only

All females of *Argestes* bear 2 setae at their P5 basendopodal lobe, while all *Fultonia* females present 1 seta only, a reduction that is considered as the derived, i.e. apomorphic condition.

As the derived states of characters 8–15 are present in all *Fultonia* species (despite some pending confirmations for *F. hirsuta*, cf. Appendix), they are interpreted as synapomorphic characters, supporting the monophyletic status of that genus.

***F. wilhelmsenae* sp. nov.:**
the "result" of former misinterpretations

Sars' (1910) redescription of *Fultonia hirsuta* differed considerably from the original one provided by T. Scott (1902) (Tab. 5). While Sars (1910) did not refer to these discrepancies, Lang (1948) put them down to insufficient and incorrect observations of T. Scott (1902).

As the type material of *F. hirsuta* is not available anymore, I decided to redescribe the species based on Sars' material. That material, consisting in 6 individuals, resulted to enclose 2 different species, showing (among others) the differences listed in Table 5. Thus, on one hand I was able to confirm the correctness of T. Scott's (1902) description; as demonstrated with the here presented redescription, *F. hirsuta* presents almost all characters described by T. Scott (1902). On the other hand, also Sars (1910) provided a correct species description. Unfortunately, he did not note that his material enclosed two different species, namely *F. hirsuta* and the here presented *F. wilhelmsenae* sp. nov. The latter was picked out and "redescribed" as *F. hirsuta* by Sars (1910). Lang (1948) trusted rather in Sars' (1910) than in T. Scott's (1902) description. As his Swedish material obviously fit the "redescription" of Sars (1910) (but actually showing *F. wilhelmsenae* sp. nov.), he concluded that T. Scott (1902) was mistaken (Lang 1948, pp. 1301–1302). Thus, the "discrepancies" between T. Scott's (1902) and Sars' (1910) descriptions are in fact features of two distinct species. Surprisingly, the 2 specimens (1 female, 1 male) collected by Bodin from the Gulf of Gascogne in 1992 and identified by that author as *F. hirsuta* (cf. Material and Methods) do also distribute over both *F. hirsuta* (the male specimen) and *F. wilhelmsenae* sp. nov. (the female specimen); this may certainly be due to the inconsistent descriptions Bodin found in literature. It seems that both species do commonly occur together at same locations.

Table 5. Differences between the descriptions of *Fultonia hirsuta* (only females) provided by T. Scott (1902) and Sars (1910):

No.	Character	T. Scott (1902)	Sars (1910)
1	A1	8-segmented	7-segmented
2	P1 enp-2	No inner seta	1 inner seta
3	P4 enp-3	No inner seta	1 inner seta
4	P5 exp	6 setae	7 setae

Phylogenetic characterization of the *Fultonia* species

Fultonia hirsuta

That species is easily to characterize by the following 6 apomorphies:

16 Second segment of female A1 elongate [segment not longer than first];
17. Mx: distal endite with 1 seta fused to endite [all setae distinct];
18. P1 enp2 inner seta lost [P1 enp2 still with inner seta];
19. P3 exp3 1 inner seta lost (2 setae present) [P3 exp3 with all 3 inner setae];
20. P3 enp3 inner seta lost [P3 enp3 inner present];
21. P4 enp3 inner seta lost [P4 enp3 inner present].

In *Argestes* and the remaining *Fultonia* species, the second segment of female A1 (16) is more or less squared in size, reflecting that the rather primitive condition. Thus, elongation of that antennular segment in *F. hirsuta* has to be regarded as apomorphic state.

The fusion of 1 seta to the distal maxillar endite (17) is a clearly derived condition; all remaining *Fultonia* species and also *Argestes* retain the distinct seta.

The loss of setae (18–21) is always considered as the secondary, i. e. the derived state, while their retention (here: in all remaining *Fultonia* species and in *Argestes*) shows the original condition.

Fultonia gascognensis

Three apomorphies confirm the maintenance of that species:

22. Md palp: exp lateral setae lost [exp with 2 lateral setae];
23. Mx: one of the claw-like setae fused with basis [all setae distinct];
24. P4 exp3 with additional outer seta (= 4 outer setae) [no additional seta (= 3 outer setae)].

F. bougisi and *F. wilhelmsenae* sp. nov. show 2 lateral setae at their mandibular exp (22), whereas *F. gascognensis* lost them, being this a clear apomorphy. This character is, however, of certain weakness, as the md of *F. hirsuta* is still unknown.

The fusion of one of the claw-like maxillar setae (23) must also be considered as deviation, as all setae of the maxillar basis originally are distinct (cf. Seifried 2003), which is retained in all remaining *Fultonia* species. It has to be remarked, however, that also *Argestes angolaensis* and *A. mollis* show fused setae at their maxillar bases. However, this coincidence may rather be due to convergent development, as much more weighty characters confirm the distinctness of *Fultonia* and *Argestes* (Fig. 18).

The development of additional setae (24) is a quite rare and uncommon event and inside Harpacticoida known from Superornatiremidae only (cf. Huys 1996). Such superior setal number might be the result of a malformation; however, as *F. gascognensis* shows that additional seta in both P4 exps coupled with no other indication of any malformation, it has to be concerned as apomorphic character for that species. Nonetheless it has to be taken into account that up to now only one single specimen, the female holotype, is available. Future comparison with additional material of that species may confirm the phylogenetic value of that character.

***Fultonia wilhelmsenae* sp. nov.**

The here described *Fultonia wilhelmsenae* sp. nov. is characterized by 2 apomorphies that justify its establishment as distinct species:

25. Md gnathobase ventrally with second long and curved sclerotized spine [no second ventral spine developed];
26. Mx: proximal endite large, remarkably swollen [endite small, of cylindrical or slightly triangular shape].

The derived shape of the md in *Fultonia* as well as its possession of a strongly sclerotized toothed spine has already been discussed in detail (cf. characters 8, 9). Deviating from all remaining *Fultonia* species (not yet confirmed for *F. hirsuta*), the new species bears a second strongly sclerotized element at the ventral margin of the mandibular gnathobase, just beside the first one (25; cf. Fig. 3A). This is regarded as apomorphy for the species.

The proximal endite of the mx (26) is small and of more or less cylindrical shape not only in *Argestes* and the remaining *Fultonia* species, but in almost all Argestidae. In contrast, *Fultonia wilhelmsenae* sp. nov. develops a considerably larger endite of a swollen shape (Fig. 3C), being interpreted as apomorphic.

Fultonia bougisi

Three apomorphies for that species were detected basing on Soyer's (1964) description:

27. Md palpus: one terminal seta of enp lost [all 4 terminal setae still present];
28. Md palpus: basal setae set widely apart from each other [setae standing closely together];
29. P1: inner basal seta strong, longer than enp [seta not reaching end of enp].

While all remaining *Fultonia* species (not yet confirmed for *F. hirsuta*) bear 4 terminal setae at the mandibular enp (27), *F. bougisi* lost 1 seta; moreover, the basal setae of the mandibular palp are standing closely together in *Argestes* and in all remaining *Fultonia* species (not yet confirmed for *F. hirsuta*) (28), but they are set widely apart in *F. bougisi*; the inner seta of P1 basis is elongate and strong in *F. bougisi*, surpassing the length of the whole enp (29), while reaching at most the end of the enp in all remaining *Fultonia* species; all these features are considered as derived and therefore interpreted as apomorphies for *F. bougisi*.

Phylogeny inside *Fultonia*

The relation of the so far known four *Fultonia* species cannot be resolved at the moment; too many characters (30–38, Appendix) are incongruently distributed over the corresponding species. Moreover, some features remain uncertain, because their condition could not be proved for all known species so far.

F. bougisi, *F. gascognensis*, and *F. wilhelmsenae* sp. nov. share 2 apomorphies:

30. Palpus of the md cylindrical, curved [palpus more or less trapezoid];
31. Maxillar basis with 3 setae [basis with 4 setae].

As remarked above, the shape of the mandibular palp is unknown from *F. hirsuta*, as T. Scott (1902) did not describe it, and the here redescribed specimens were damaged and lacked the md. Thus, character 30 is of weak phylogenetic value so far, until an examination of additional *F. hirsuta* material. If that species would bear a cylindrical curved md palp like the remaining species, that feature would turn into another apomorphy for whole *Fultonia*.

Therefore there is just one character (31) that seems to point towards a closer relation of *F. bougisi*, *F. gascognensis*, and *F. wilhelmsenae* sp. nov., as *F. hirsuta* still bears a fourth seta at its maxillar basis.

On the other hand, apomorphy number

32. Mx enp lost, represented by 2 setae only [mx with small enp bearing 2 setae]

may indicate to a closer relationship of *F. gascognensis*, *F. hirsuta*, and *F. wilhelmsenae* sp. nov., as these taxa share that apomorphy, while *Argestes* and *F. bougisi* present the plesiomorphic state. It has to be objected, however, that Bodin (1968) also described a maxillar enp for *F. gascognensis*, which could not be confirmed in the here presented redescription. Unfortunately, it was impossible for the author to get the type material of *F. bougisi* for re-examination, so a doubtless clearance of that character is still pending.

Nevertheless, as shown by characters

33 Female A1 7-segmented [female A1 8-segmented];

34 Maxillipedal claw: denticles extremely strong [denticles of moderate size].

there may be a closer relation between *F. gascognensis* and *F. wilhelmsenae*; they share the derived 7-segmented female A1 (33) (8-segmented in remaining *Fultonia* species, but also 7-segmented in *Argestes*) and in both species the distal maxillipedal denticles are reaching largest size (34), as compared with *F. bougisi* and *F. hirsuta*.

So at last it has to be admitted, however, that none of the characters 30–38 serves yet to elucidate phylogenetic relations inside *Fultonia*. This has to be postponed until the availability and examination of additional *Fultonia* material.

Allocation of *Parargestes tenuis* into *Argestes*

George (2008) recognized and confirmed the monophyly of a taxon *Argestes*, suggesting that the usage of the genus *Parargestes* should be discontinued. Unfortunately, a re-examination of *Parargestes tenuis* basing on the type material was not possible, as the type material of that species is not available anymore (Åse Wilhelmsen and Jens Petter Nilssen [Norway], personal communication). Thus, examination had to be done using material of the subspecies *P. tenuis* var. *arcticus*. The Lang collection at the Swedish Museum of Natural History comprises three individuals of that taxon. To avoid destruction of specimens by dissection, and because of the condition of the material (specimens remarkably damaged and covered with compact detritus), a detailed redescription was not possible. However, examination of the individuals did enable a phylogenetic comparison with *Fultonia* and *Argestes*.

George (2008) already presented a detailed discussion on the formerly supposed five differences between *Argestes* and *Parargestes*, demonstrating that none of them can be maintained. On the other hand, *P. tenuis* var. *arcticus* fits the following derived *Argestes* characters (see above):

5. Thoracic sensilla arising from long cylindrical tubercles (Figs. 15, 16A);
6. P1 exp outer spines with subterminal tubular extensions [not in P1 exp1] (Fig. 16B);
7. A2 with allobasis (cf. Sars 1921, Lang 1948).

Unfortunately, apomorphy no. 4 (furcal setae I, II, III, VI rat-tailed; cf. Appendix) could not be verified, due to the conditions of the material. New material is needed to prove the quality of that character. Nonetheless, due to the congruence of at least the above listed apomorphies 5–7 justify the transfer of *P. tenuis* var. *arcticus* into *Argestes*, which is therefore renamed *Argestes tenuis* Sars, 1921 var. *arcticus* (Lang, 1936) nom. nov. With *A. angolaensis* George, 2008 the species shares elongation of the FR and the possession of 5 setae at P5 exp (cf. George 2008). *A. tenuis* var. *arcticus*

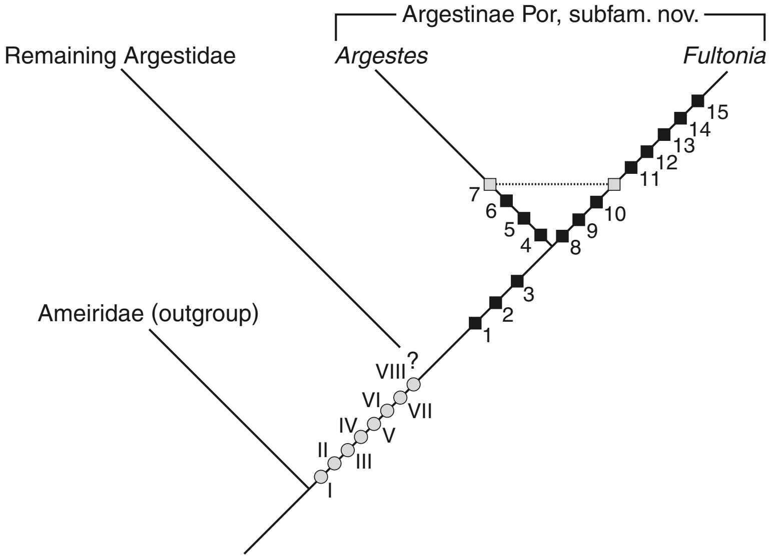


Fig. 18. Cladogram summarizing the phylogenetic relation of *Argestes* and *Fultonia* according to the apomorphies discussed in the text (cf. Appendix). Presumptive apomorphies for Argestidae modified after George (2004) (I–VI) and according to Corgosinho & Martínez Arbizu (2010) (VII–VIII): **I**, integument poorly chitinized; **II**, telson nearly square, large; **III**, anal operculum shifted anteriorly; **IV**, FR set wide apart at corners of the telson; **V**, A2 exp 1-segmented; **VI**, P2–P4 rami displaced towards outer margin of basis; **VII**, distal maxillar endite armed with very strong spine; **VIII**, maxillar basis with 1 very strong spine in addition to the basal claw, giving a scissor-shape.

nom. nov. is unique in showing a remarkable shortening of P4 exp3, so the two distal outer spines arise terminally together with the terminal setae (cf. Fig. 17A). Detection of further specific apomorphies as well as detailed phylogenetic analyses inside *Argestes* requires more material of *Argestes tenuis* var. *arcticus* nom. nov.

Establishment of a monophylum Argestinae Por, 1986 subfam. nov.

Recently, Argestidae become of increasing interest in faunistic and biogeographic studies on marine meiobenthos, as they form a dominant taxon particularly of deep-sea Harpacticoida (George 2004, 2008; Menzel & George 2009; Menzel 2011; in press). However, as stated before (George 2004, 2008, Corgosinho & Martínez Arbizu 2010), their systematic status remains absolutely unclear so far. Even when establishing the family, Por (1986: p. 422) already noted "much evolutionary distance between the primitive and the advanced genera". Up to now, no unequivocal apomorphies have been detected to justify a monophylum Argestidae, despite some derived characters (cf. George 2004) that may be shared by all argestid taxa but are still waiting extensive checking. Recently, Corgosinho & Martínez (2010) provided new morphological evidence supporting a monophylum Argestidae, namely the shape and armature of the maxilla. Another step towards recognition of Argestidae as monophylum is presented here. As demonstrated above, inside Argestidae a group of taxa may be pooled and justified basing on apomorphic characters. *Argestes* and *Fultonia* share three apomorphies justifying the erection of a monophylum *Argestes–Fultonia* (see above). Aiming its clear distinction inside Argestidae, it is named Argestinae Por, 1986 and lifted up to subfamily range. Future investigation will show whether there are further taxa (e. g. *Dizahavia*) that fit Argestinae, and whose characters may reveal its relation to the remaining argestid genera.

Acknowledgements

I am indebted to Mrs. Å. Wilhelmsen (Oslo, Norway) for providing the material of *Fultonia hirsuta* and *F. wilhelmsenae* sp. nov.; Mrs. K. Sindemark-Krønestedt (Stockholm, Sweden) kindly put the material of *A. tenuis* var. *arcticus* to my disposal, and Dr. D. Defaye (Paris, France) made available additional material of *F. hirsuta* and *F. wilhelmsenae* sp. nov. as well as the type material of *F. gascognensis*. I very much appreciate the valuable, constructive and helpful critics on the manuscript by two reviewers.

References

Ax, P. (1984). Das Phylogenetische System. Gustav Fischer Verlag Stuttgart, 349 pp.

Bodin, P. (1968). Copépodes Harpacticoides des étages bathyal et abyssal du Golfe de Gascogne. Mémoires du Muséum National d'Histoire Naturelle A 55: 1–107.

— (1997). Catalogue of the new marine harpacticoid Copepods. Documents de travail de l'Institut royal des Sciences naturelles de Belgique, Bruxelles, 304 pp.

Corgosinho, P. H. C. & P. Martínez Arbizu (2010). Ameiridae Boeck and Argestidae Por revisited, with establishment of Parameiropsidae, a new family of Harpacticoida (Crustacea, Copepoda) from deep-sea sediments. Helgoland Marine Research 64: 223–255.

Ferrari, F. D. & V. N. Ivanenko (2008). The identity of protopodal segments and the ramus of maxilla 2 of copepods (Copepoda). Crustaceana 81 (7): 823–835.

George, K. H. (2004). Description of two new species of *Bodinia*, a new genus incertae sedis in Argestidae Por, 1986 (Copepoda, Harpacticoida), with reflections on argestid colonization of the Great Meteor Seamount plateau. Organisms, Diversity & Evolution 4: 241–264.

— (2008). *Argestes angolaensis* sp. Nov. (Copepoda: Harpacticoida: Argestidae) from the Angola Basin (Southeast Atlantic), and the phylogenetic characterization of the taxon *Argestes* Sars, including the redescription of *A. mollis* Sars, 1910, and *A. reductus* (Itô, 1983). Zootaxa 1866: 223–262.

George, K. H. & H. K. Schminke (2003). *Isthmiocaris longitelson* gen. et sp. nov., a strongly derived harpacticoid (Copepoda) from the Magellan region, and its systematic affinities to certain "canthocamptid" taxa. Journal of the Crustacean Society 23: 119–130.

Hicks, G. R. F. & B. C. Coull (1983). The ecology of marine meiobenthic harpacticoid copepods. Oceanography and Marine Biology, Annual Review 21: 67–175.

Huys, R. (1996). Superornatiremidae fam.nov. (Copepoda: Harpacticoida): An enigmatic family from North Atlantic anchialine caves. Scientia Marina 60: 497–542.

Huys, R. & G. A. Boxshall (1991). Copepod Evolution. The Ray Society, London, 468 pp.

Huys, R. & S. Conroy-Dalton (1997). Discovery of hydrothermal vent Tantulocarida on a new genus of Argestidae (Copepoda: Harpacticoida). Cahiers de Biologie Marine 38, 235–249.

Itô, T. (1983). Harpacticoid copepods from the Pacific abyssal off Mindanao. II. Cerviniidae (cont.), Thalestridae, and Ameiridae. Publications of Seto Marine Biology Laboratory 28 (1/4), 151–254.

Lang, K. (1948). Monographie der Harpacticiden. Otto Koeltz Science Publishers, Königstein (reprint 1975), 1683 pp.

— (1965). Copepoda Harpacticoida from the Californian pacific coast. K. svenska vetensk. akad. Handl. 10: 1–566.

Menzel, L. (2011). First records of copepodid stages, sexual dimorphism and intraspecific variability of *Mesocletodes* Sars, 1909 (Copepoda: Harpacticoida: Argestidae) including the description of a new species from various deep-sea regions. Zookeys 96: 39–80.

— (in press). A new species of *Eurycletodes* Sars, 1909 (Copepoda, Harpacticoida, Argestidae) from the southern hemisphere including remarks on the phylogeny of and within the genus. Helgoland Mar. Res.

Menzel, L. & K. H. George (2009). Description of four new species of *Mesocletodes* Sars, 1909 (Copepoda, Harpacticoida, Argestidae) and redescription of *Mesocletodes robustus* Por, 1965 from the South Atlantic, including remarks on the *Mesocletodes abyssicola*-group. Zootaxa 2096: 214–256.

Mielke, W. (1984). Some remarks on the mandible of the Harpacticoida (Copepoda). Crustaceana 46: 257–260.

Noodt, W. (1971). Ecology of the Copepoda. Smithsonian Contributions to Zoology 76: 97–102.

Por, F. D. (1979). The Copepoda of Di Zahav Pool (gulf of Elat, Red Sea). Crustaceana 37: 13–30.

— (1986). A re-evaluation of the family Cletodidae Sars, Lang (Copepoda, Harpacticoida). Syllogeus 58, 420–425.

Rose, A., S. Seifried, E. Willen, K. H. George, G. Veit-Köhler, K. Bröhldick, J. Drewes, G. Moura, P. Martínez Arbizu & H. K. Schminke, (2005) A method for comparing within-core alpha-diversity values from repeated multicorer samplings, shown for abyssal Harpacticoida (Crustacea: Copepoda) from the Angola Basin. Organisms, Diversity & Evolution 5 (suppl. 1), 3–17.

Sars, G. O. (1910) Copepoda Harpacticoida. Parts XXIX & XXX. Tachidiidae (concluded), Metidae, Balaenophilidae, supplement (part). An Account of the Crustacea of Norway, with short descriptions and figures of all the species. Bergen Museum, Bergen 5, 337–368, pls. 225–230, suppl. pls. 1–10.

Schminke, H. K. (1976). The ubiquitous telson and the deceptive furca. Crustaceana 30: 292–299.

Scott, T. (1902). VIII.– Notes on gatherings of Crustacea collected by the fishery steamer "Garland", and the steam trawlers "Star of Peace" and "Star of Hope", of Aberdeen, during the year 1901. Twentieth Annual Report of the Fishery Board for Scotland III: 447–485, 25 plates.

Seifried, S. (2003) Phylogeny of Harpacticoida (Copepoda): Revision of "Maxillipedasphalea" and Exanechentera. Cuvillier Verlag Göttingen, 259 pp.

Smirnov, S. (1946). New species of Copepoda Harpacticoida from the Arctic Ocean (en Russe, resumée en anglais). Trudy dreif. expedition glavsevmov. Ledokolskaja par "Sedov" 3: 231–263.

Soyer, J. (1964). Copépodes Harpacticoïdes de l'étage bathyal de la région de Banyuls-sur-Mer: III. Le genre *Fultonia* T Scott, genre nouveau pour la Méditerranée. Vie Milieu 15: 95–103.

— (1966). Copépodes Harpacticoïdes de Banyuls-sur-Mer: 3. Quelques formes du coralligène. Vie Milieu 17: 303–344.

— (1971). Bionomie benthique du plateau continental de la côte catalane francaise. III. Les peuplements de Copépodes Harpacticoïdes (Crustacea). Vie Milieu 21: 337–511.

Wells, J. B. J. (2007). An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). Zootaxa 1568: 1–872.

Appendix
List of morphological characters used for the phylogenetic analysis of Argestinae Por subfam. nov.

Of characters 1–38, the apomorphic conditions are described. **1**, marks the apomorphic, **0**, plesiomorphic state as discussed in the text. Abbreviations: ***F. hi.***, *Fultonia hirsuta*; ***F. ga.***, *F. gascognensis*; ***F. wi.***, *F. wilhelmsenae* sp. nov.; ***F. bo.***, *F. bougisi*; ***Arg.***, *Argestes*; ***Ame.***, Ameiridae (outgroup). Bold numbers point to possible convergences; n.a., not applicable.

No.	Apomorphic condition of respective characters	*F. hi.*	*F. ga.*	*F. wi.*	*F. bo.*	*Arg.*	**Ame.**
1	Body densely covered with small cuticular spinules	1	1(?)	1	1(?)	1	0
2	A1 with very strong seta terminally on 6th segment in female	1	1	1	1	1	0
3	Dorsal thoracic sensilla remarkably elongate	1	1	1	1	1	0
4	Furcal setae I, II, III, VI rat-tailed	0	0	0	0	1	
5	Thoracic sensilla arising from long cylindrical tubercles	0	0	0	0	1	
6	P1 exp outer spines with subterminal tubular extensions	0	0	0	0	1	
7	A2 with allobasis	0	**1**	**1**	0	**1**	
8	Md gnathobase transformed into single grinding mortar	1(?)	1	1	1	0	
9	Md gnathobase ventrally with strong toothed spine	1(?)	1	1	1	0	
10	Mxp syncoxa with 1 seta, 1 seta lost	1	1	1	1	0	
11	Mxp claw with only few but long pinnae st distal half	1	1	1	1	0	
12	P1 enp with 2 segments, 1 segment lost	1	1	1	1	0	
13	P2-P4 enps remarkably shortened	1	1	1	1	0	
14	P2-P4 enps3 with at most 4 setae, 1 inner seta lost	1	1	1	1	0	
15	P5 benp with 1 seta only, 1 seta lost	1	1	1	1	0	
16	Female A1 second segment elongate	1	0	0	0	0	
17	Mx distal endite with 1 seta fused to segment	1	0	0	0	0	
18	P1 enp2 with 3 setae, inner seta lost	1	0	0	0	n.a.	
19	P3 exp3 with 7 setae, 1 inner seta lost	1	0	0	0	0	
20	P3 enp3 with 3 setae, inner seta lost	1	0	0	0	n.a.	
21	P4 enp3 with 3 setae, inner seta lost	1	0	0	0	n.a.	
22	Md palp exp with 2 setae, 2 setae lost	?	1	0	0	0	
23	Mx: 1 claw-like seta fused with basis	0	**1**	0	0	**1**	
24	P4 exp3 additional outer seta	0	1	0	0	0	
25	Md gnathobase ventrally with second spine	0	0	1	0	0	
26	Mx proximal endite remarkably swollen	0	0	1	0	0	
27	Md palp enp 1 terminal seta lost	?	0	0	1	0	
28	Md palp basal setae set widely apart	?	0	0	1	0	
29	P1 inner basal seta strong, longer than enp	0	0	0	1	0	
	Incongruent characters						
30	Md palp basis curved	?	1	1	1	0	
31	Mx basis 3 setae (1 seta lost)	0	1	1	1	0	
32	Mx enp lost, represented by 2 setae only	1	1	1	0	0	
33	Female A1 with 7 segments instead of 8	0	**1**	**1**	0	**1**	
34	Mxp claw denticles strong	0	1	1	0	0	
35	Mx distal endite with 2 setae; 1 seta lost	1	0	0	1	0	
36	P1 enp1 inner seta lost	1	0	1	0	0	
37	P2 enp3 with 3 setae, inner seta lost	1	1	0	0	0	
38	Md palp exp remarkably elongate	?	1	0	1	0	