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# A REVISION OF *PSAMATHEA* (HARPACTICOIDA : LEPTASTACIDAE) WITH DESCRIPTION OF *P. BRITTANICA* sp. nov.

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COPEPODES  
HARPACTICOIDA  
PSAMATHEA  
*P. BRITTANICA* SP. NOV.  
RÉVISION SYSTÉMATIQUE

RÉSUMÉ. – Le présent travail correspond à la révision d'un genre de Copépodes Harpacticoïdes interstitiels : *Psamathea* Cottarelli & Venanzetti, 1989 (Leptastacidae). L'espèce-type *P. nautarum* est redécrite à partir de nouveaux spécimens récoltés dans la frange infralittorale de la baie de Banyuls-sur-Mer. *Notopontia* (?) sp. *sensu* Bodin (1984) provenant de la Baie de Douarnenez en Bretagne est décrite comme étant la seconde espèce du genre : *P. brittanica* sp. nov. Le problème de la position phylogénétique de *Psamathea* à l'intérieur des Leptastacidae est reconsidéré à la lumière des nouvelles informations obtenues. Les similitudes dans la structure des rames caudales et dans le dimorphisme sexuel des pattes natatoires indiquent une relation particulièrement étroite avec *Paraleptastacus* C.B. Wilson.

COPEPODA  
HARPACTICOIDA  
PSAMATHEA  
*P. BRITTANICA* SP. NOV.  
SYSTEMATICS

ABSTRACT. – The interstitial harpacticoid genus *Psamathea* Cottarelli & Venanzetti, 1989 (Leptastacidae) is revised. The type species *P. nautarum* is redescribed on the basis of new material collected from the shallow subtidal off Banyuls-sur-Mer. *Notopontia* (?) sp. *sensu* Bodin (1984) from the Bay of Douarnenez in Brittany is described as the second species in the genus : *P. brittanica* sp. n. The problematic phylogenetic position of *Psamathea* in the Leptastacidae is re-assessed in the light of the new information available. The resemblance in caudal ramus structure and swimming leg sexual dimorphism favours a sistergroup relationship with *Paraleptastacus* C.B. Wilson.

## INTRODUCTION

In their paper on the Cylindropsyllidae from the circumsardinian isles, Cottarelli & Venanzetti (1989) established three new genera with leptastacid affinities : *Minervella*, *Neopsammastacus* and *Psamathea*. Only the latter has remained monotypic since (Huys, 1992). Cottarelli & Venanzetti (1989) abstained from taking a firm stand in defining the relationships of the type species *P. nautarum* and apparently were unable to allocate it with certainty to any of the cylindropsyllid subfamilies recognized at that time. They pointed out the similarity in morphology and armature of the second to fifth thoracopods between *Psamathea* and the genera related to *Leptastacus* (Leptastacinae *sensu* Lång), yet also recognized a

certain resemblance with *Psammopsyllus* (*Psammopsyllinae sensu* Krishnaswamy) in the structure of the caudal rami. The latter similarity however was regarded as the result of convergence. Using Bodiou & Colomines (1986) generic key to the Cylindropsyllidae it was concluded that *Psamathea* is closest to *Pararenopontia* Bodiou & Colomines, 1986 and *Notopontia* Bodiou, 1977 (Leptopontiinae). Martinez Arbizu & Moura (1994) recently amalgated *Pararenopontia* with *Arenopontia* Kunz, 1937, however, on grounds of insufficient conclusive evidence this act is not accepted by the present authors.

There is little doubt that the relationship with *Pararenopontia* and *Notopontia* as suggested by Cottarelli & Venanzetti (1989) is purely artificial since it is based on a single character, i.e. the 2-segmented exopod of P1. This character was

heavily weighed in Bodiou & Colomines (1986) key, and, with the description of *P. brittanica* sp. nov. presented below, is no longer diagnostic of the genus. The affinity of *Psamathea* to the Leptastacidae is defined unequivocally by the remarkably conservative and unique cephalic feeding appendages displayed by all members of this family (Huys, 1992).

Huys (1992) hinted at a possible relationship between *Psamathea* and *Arenocaris*, because of the shared 2-segmented condition of the P1 exopod in conjunction with the retention of the ancestral number of 4 setae on the distal segment. There is no evidence for the derivation of this condition in these genera, but most likely it originated by fusion of the ancestral middle and distal segments with the additional loss of one armature element, Huys (1992) pointed out that *Psamathea* and *Arenocaris* also share sexual dimorphism on the P4 endopod, but admitted that the homology of these transformations had yet to be revealed since Cottarelli & Venanzetti's (1989) illustrations did not allow a detailed comparison with *Arenocaris*. In his scheme summarizing the phylogenetic relationships within the Leptastacidae, Huys (1992) therefore placed *Psamathea* only provisionally as the sistergroup of *Arenocaris*.

The collection of new material of the type species *P. nautarum* by one of us (JYB) and the discovery of a second species, tentatively identified as *Notopontia* (?) sp. by Bodin (1984), have prompted us to revise the phylogenetic position of *Psamathea*.

## MATERIAL AND METHODS

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium (*P. nautarum*) or glycerinated gelatine with concentrated phenic acid (*P. brittanica* sp. nov.). Preparations were sealed with glyceel (Gurr, BDH Chemicals Ltd, Poole, England). All drawings have been prepared using a camera lucida on a Leitz Diaplan or Dialux 20 microscope equipped with differential interference contrast.

The descriptive terminology applied to segmentation and setation of body appendages is adopted from Huys & Boxshall (1991). Abbreviations used in the text and figures are: P1 – P6, first to sixth thoracopods; exp., exopod; enp., endopod; exp(enp)-1 (-2, -3), to denote the proximal (middle, distal) segment of a ramus.

Specimens are deposited in the collections of the Zoology Department, The Natural History Museum, London.

## SYSTEMATICS

### GENUS *Psamathea* Cottarelli & Venanzetti, 1989

#### *Diagnosis*

Leptastacidae. Rostrum moderately elongate; not clearly demarcated at base. Body somites with pattern of internal chitinous reinforcements. Intersomitic boundaries well defined; hyaline frill weakly developed, slightly striated. Antennary exopod with 2 distal setae. Mandibular palp 2-segmented; seta derived from basis absent. Labrum without frontal recurved process. P1 basis without outer spine/seta. P1 exopod 1- or 2-segmented; if 2-segmented, exp-1 with 1 outer spine, exp-2 with 2 outer spines and 2 distal brush setae. P1 endopod 2-segmented, prehensile; enp-1 2.7 to 3.8 times as long as exopod, without inner seta; enp-2 with 1 unipinnate claw and 1 brush seta. P2-P4 endopods 2-segmented. Armature formula of swimming legs:

	Exopod	Endopod
P1	0.022 or 0.023	0.011
P2	0.0.021	0.010
P3	0.0.121	0.011
P4	0.1.221	0.110

Sexual dimorphism in antennule, P3 endopod (inner subdistal spine reduced and largely incorporated in enp-2), P4 endopod (shorter than in ♀, in particular enp-2 and outer distal spine), P5, P6, and in genital segmentation. P5 uniramous in both sexes; in ♀ with 4 well developed and 2 vestigial setae; in ♂ with 3 well developed and 2 vestigial setae. Male P6 symmetrical or slightly asymmetrical; with 2 setae each. Distal inner corner of caudal ramus produced in dorsally recurved multicuspidate process; each ramus with 6 or 7 setae; setae IV and V not fused at base, none of setae modified.

*Type species.* *Psamathea nautarum* Cottarelli & Venanzetti, 1989 [by monotypy]

*Other species.* *P. brittanica* sp. nov.

## DESCRIPTIONS

*Psamathea nautarum* Cottarelli & Venanzetti, 1989

Original description. Cottarelli & Venanzetti (1989): 223-228, Figs 20-21.

Type locality. 1 m depth; Punta Martin, Isola S. Pietro, Arcipelago de La Maddalena (Italy).

Material examined. One ♀ (dissected on 5 slides) and 1 ♂ (in alcohol); off Banyuls-sur-Mer, Stn 1B, 5m depth; coll. J.-Y. Bodiou; deposited

in the Natural History Museum under reg. nos. 1996. 21-22.

## Redescription

### FEMALE

Total body length measured from anterior tip of rostrum to rear margin of caudal rami: 290  $\mu$ m.

Body (Fig. 1A) slender, cylindrical, vermiform, almost colorless; intersomitic membranes strongly developed. Pleural areas of cephalothorax weakly developed so that cephalic appendages are clearly exposed in lateral aspect (Fig. 3A); hyaline frill reduced, plain. Free thoracic and abdominal somites with weakly developed hyaline frill, not incised and slightly striated. Integument weakly chitinised, smooth externally, internally with pattern of elongate cuticular reinforcements dorsally on thoracic somites and both dorsally and ventrally on abdominal somites (Figs 1A-C; 5A-B). No distinct separation between prosome and urosome. Genital double-somite about as long as wide (Figs 1A; 5A-B); no trace of original subdivision discernible; with genital apertures located in posterior half, each covered by operculum derived from sixth legs, bearing 2 vestigial setae (Figs 1E; 5B); copulatory pore located midventrally near posterior margin of genital double-somite, connected via long copulatory duct with receptacles (Fig. 1E). Anal somite narrowest; anal operculum rounded, moderately developed, smooth (Fig. 1B).

Caudal rami (Figs 1B; 5A-B) slightly divergent, about twice as long as maximum width (measured in dorsal aspect); distinctly constricted in distal third. Inner margin with small dorsal spur anterior to base of seta VII (Fig. 1B). Posterior margin produced into dorsally recurved, tricuspidate spinous process (Fig. 1B-C). Outer margin with 2 slit-like pores (Fig. 1C). Armature consisting of 7 setae; seta I minute, located in between smooth setae II and III; setae IV and V not fused basally, slightly displaced laterally, with fracture planes near base; seta VI short and bare; seta VII bi-articulated at base and sparsely plumose.

Rostrum (Fig. 2A) well developed, not clearly demarcated from cephalothorax; located subapically; moderately elongate with distinctly expanded lateral margins in proximal half; with pair of sensilla laterally and subapical pore ventrally.

Antennule (Fig. 2A) moderately slender, 7-segmented; surrounded at base by small sclerite located at posterior margin of first segment; segment 1 widest and shortest, with 1 vestigial seta ventrally and 1 pore dorsally; segment 2

longest, with 1 plumose and 8 bare setae (3 being very short) and secretory pore near ventral anterior margin; segment 3 with 1 short and 4 well developed setae; segment 4 with 1 anterior seta and produced ventrally into subcylindrical pedestal bearing basally fused seta and aesthetasc (43  $\mu$ m); segment 5 with 1 seta; segment 6 with 1 anterior and 1 ventrodorsal seta; segment 7 with 1 seta anteriorly, 6 setae posteriorly and acrothek distally. Apical acrothek consisting of 2 long setae fused basally to slender aesthetasc (31  $\mu$ m).

Antenna (Fig. 2B-C). Coxa represented by small sclerite without ornamentation. Basis and proximal endopod segment completely fused forming elongate allobasis with spinules along abexopodal margin. Exopod minute, with 2 short setae apically. Endopod with 2 spinular rows on anterior surface (Fig. 2B) and 1 spinular row on posterior surface (Fig. 2C); lateral margin with 2 small spines; apical armature consisting of 2 unipinnate spines, 2 geniculate setae and 1 geniculate spine provided with strong spinules halfway its length and fused basally to vestigial seta.

Labrum (Fig. 3A, D, F) trilobate, moderately developed; frontal lobe without hook-like spinous process but with median row of long spinules; lateral lobes with patch of short spinules; posterior lateral margins with tiny spinules (Fig. 3D).

Mandible reduced (Figs 2A-B; 3A, D). Gnathobase with 2 large, multicusped teeth ventrally and series of spinules dorsally. Palp 1-segmented, with 1 lateral and 3 apical setae.

Paragnaths (Fig. 3D) represented by paired rounded lobes with tiny spinules medially. Paired spinulose swellings discernible posterior to paragnaths (Fig. 3D).

Maxillule (Fig. 2F). Praecoxa with well developed arthrite bearing 5 strong pinnate spines and 1 short seta. Coxa with 2 setae. Basis represented by elongate segment with total of 5 setae apically. Exopod and endopod entirely incorporated in basis; represented by 1 and 3 basally fused setae, respectively.

Maxilla (Fig. 2G) with 2 endites on syncoxa; proximal endite with 3 stumpy spines bearing long radiating spinules; distal endite with 1 stumpy spine with long spinules, 1 pinnate claw and 1 bare seta. Allobasis drawn out into long pinnate claw with 2 accessory setae. Endopod elongate, 2-segmented; proximal segment with 1 lateral seta; distal segment with 3 basally fused setae.

Maxilliped (Fig. 2H). Syncoxa with bare seta. Basis large; outer margin distinctly convex and provided with spinules. Endopod represented by long sigmoid claw bearing long spinules and accompanied at base by slender seta.

P1 (Fig. 4A). Intercoxal sclerite transversely elongated. Praecoxa represented by minute sclerite

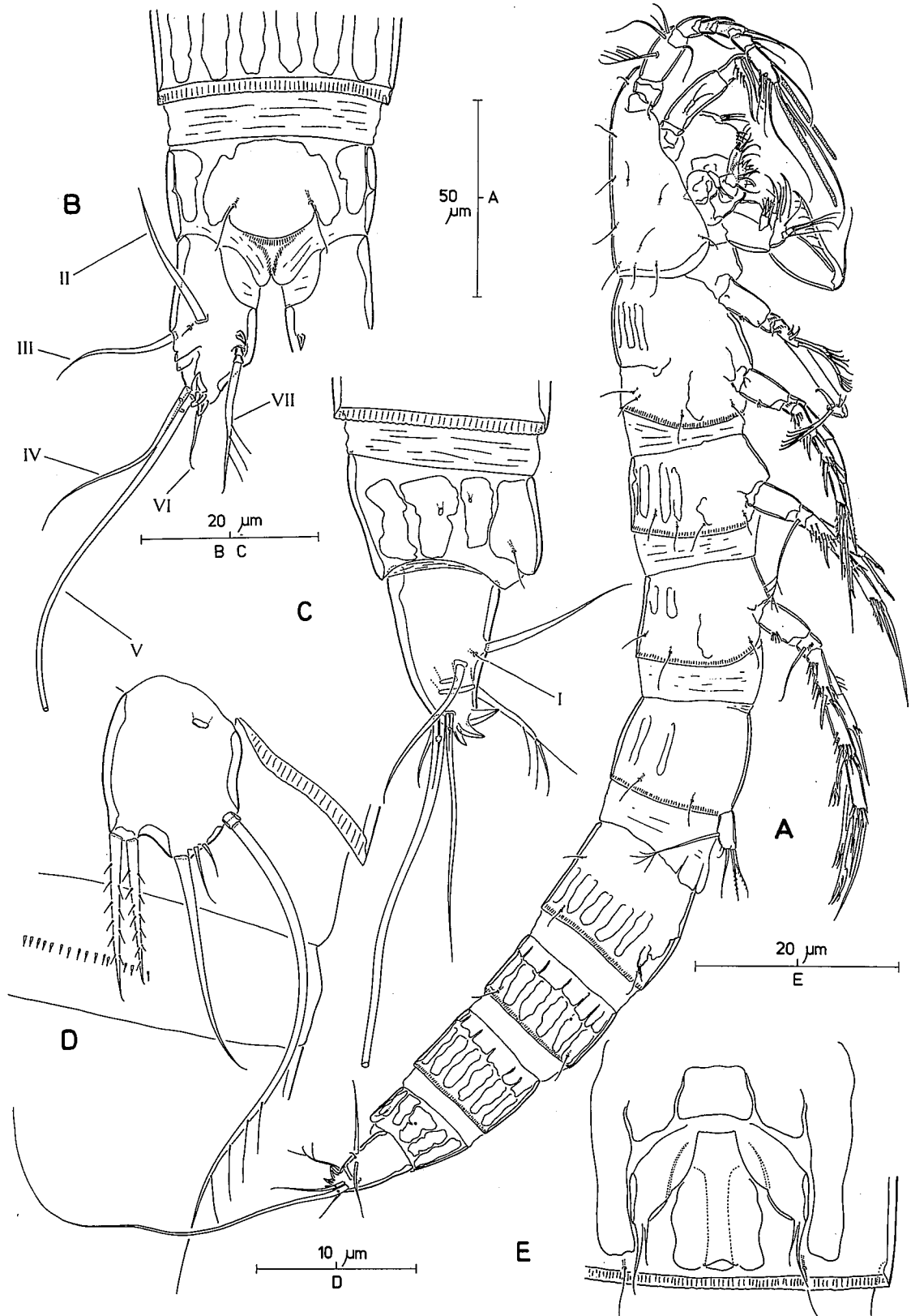


Fig. 1. – *Psamathea nautarum* Cottarelli & Venanzetti, 1989 (♀). A. Habitus, lateral; B. Anal somite and left caudal ramus, dorsal; C. Same, lateral; D. P5, anterior; E. Genital field.

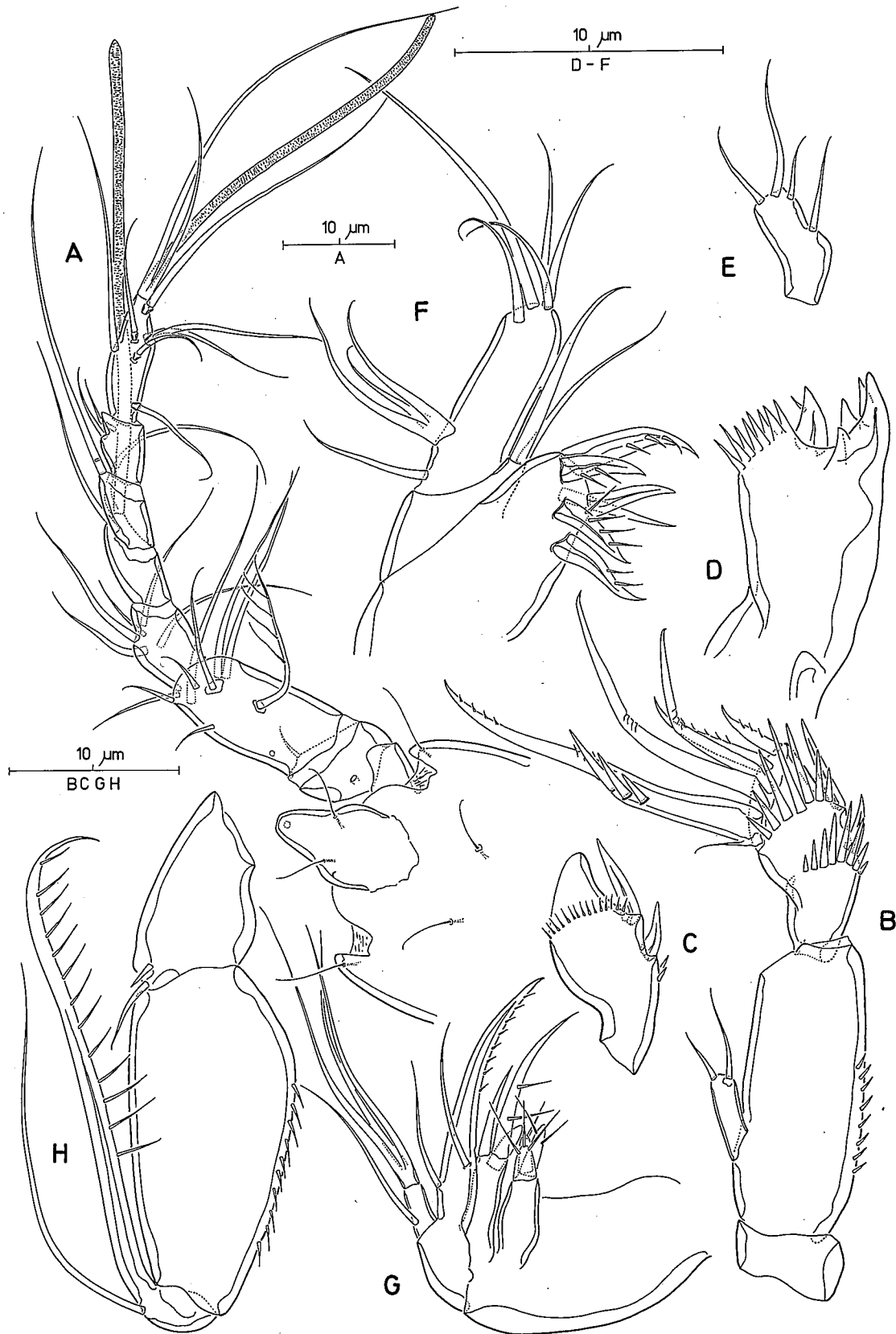


Fig. 2. - *Psamathea nautarum* Cottarelli & Venanzetti, 1989 (♀). A. Rostrum and antennule, dorsal; B. Antenna, outer lateral view; C. Antennary endopod, inner lateral view [distal armature omitted]; D. Mandibular gnathobase; E. Mandibular palp; F. Maxillule; G. Maxilla; H. Maxilliped.

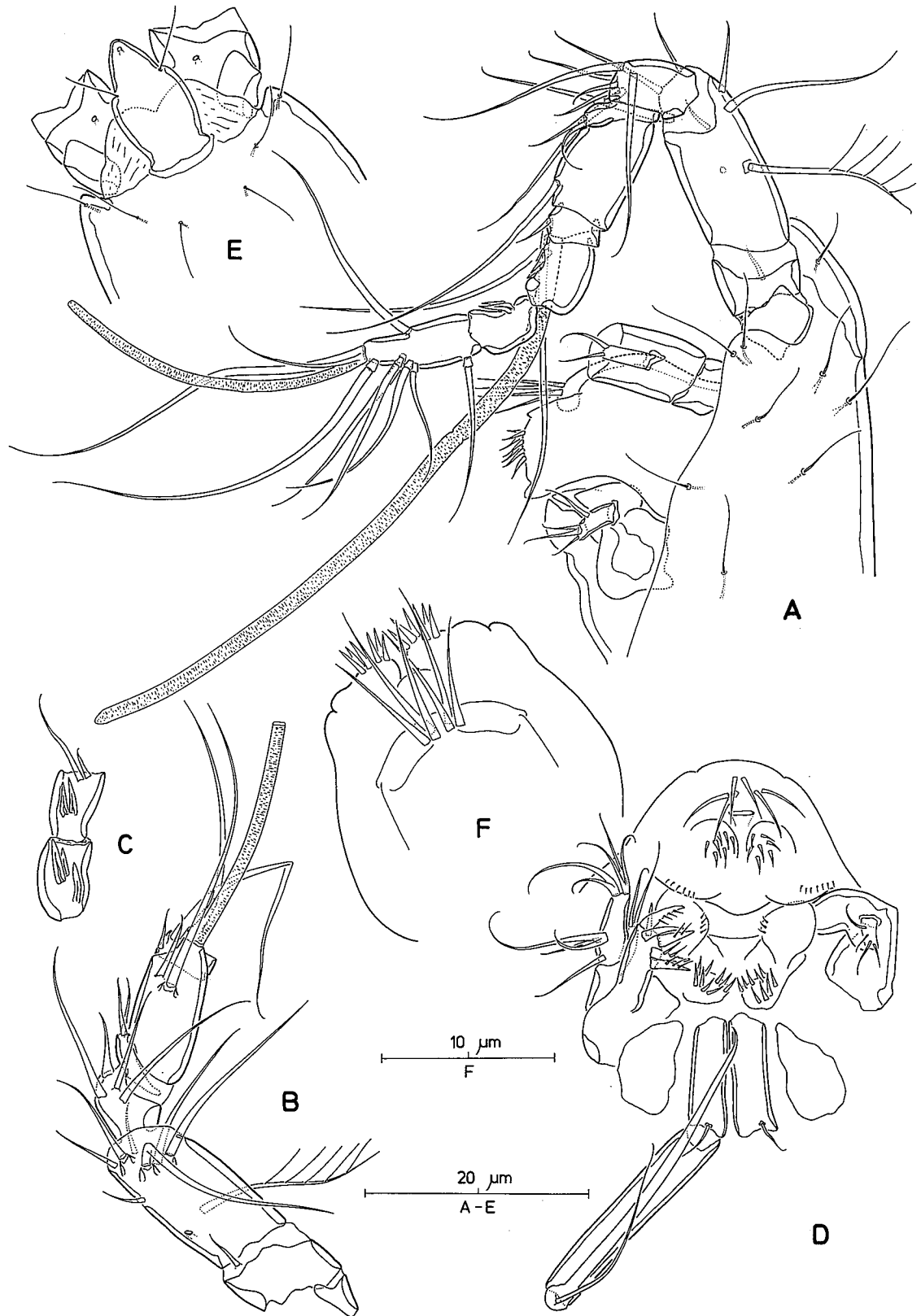


Fig. 3. – *Psamathea nautarum* Cottarelli & Venanzetti, 1989 (♂). A. Cephalothorax, anterior half, lateral view [antennary endopod omitted]; B. Antennular segments 1-6, ventral; C. Antennular segments 7-8, ventral; D. Oral area, showing labrum and paragnaths [maxillae omitted]; E. Rostrum and bases of antennules, dorsal; F. Labrum, anterior.

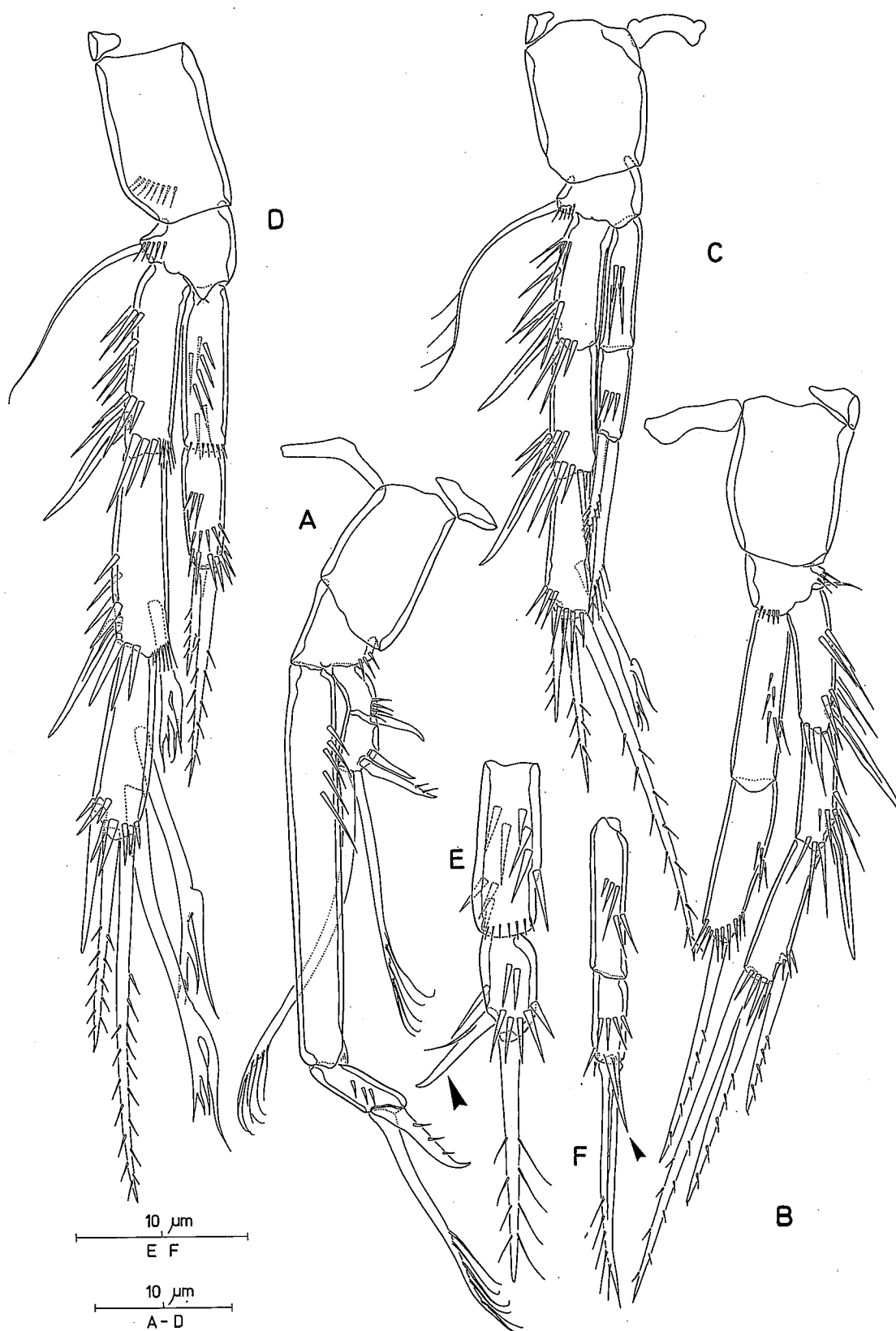


Fig. 4. - *Psamathea nautarum* Cottarelli & Venanzetti, 1989. A. P1 (♀), anterior; B. P2 (♀), anterior; C. P3 (♀), anterior; D. P4 (♀), anterior; E. P4 endopod (♂) [modified spine arrowed]; F. P3 endopod (♂) [modified spine arrowed].



rite. Coxa elongated along longitudinal (dorso-ventral) axis, without ornamentation. Basis without outer or inner seta, but with few spinules at outer subdistal corner. Exopod indistinctly 2-segmented; enp-1 and enp-2 separated by superficial suture line on anterior surface only; exp-1 with outer spine; exp-2 with 2 outer spines and 2 brush-setae apically. Endopod 2-segmented, prehensile; enp-1 elongate, 5.6 times as long as enp-2, without inner seta but with long spinules along proximal outer margin; enp-2 2.3 times as long as wide, with anterior pinnate claw and posterior brush-seta.

P2-P4 (Fig. 4B-D) with 3-segmented exopods and 2-segmented endopods. Praecoxae represented by small sclerite. Outer seta of basis long and slender in P3-P4, strongly reduced in P2. Endopod P3-P4 shorter than exp-1 and exp-2 combined, longer in P2. Inner setae of P3-P4 pectinate.

P5 (Figs 1D; 5B) with completely fused exopod and baseoendopod; represented by oval plate; inner corner with 2 well developed pinnate setae, outer margin with long plumose seta, 2 vestigial and 1 moderately developed seta; with secretory pore on anterior surface.

Genital field (Fig. 1E) located in posterior half of double-somite. Genital apertures paired, covered each by small operculum with 2 vestigial setae derived from P6. Copulatory pore located near ventral rear margin of double-somite, leading via short copulatory duct to paired seminal receptacles.

#### MALE

Total body length measured from anterior tip of rostrum to posterior margin of caudal rami: 300  $\mu\text{m}$ . Urosome (Fig. 5C) with internal pattern of cuticular reinforcements as in  $\text{♀}$ .

Rostrum (Fig. 3E) as in  $\text{♀}$  but demarcated at base by superficial suture.

Antennule (Fig. 3A-C) 9-segmented, haplocer, geniculation between segments 7 and 8. Segment 1 surrounded at base by small sclerite, with dorsal secretory pore (Fig. 3E) and ventral seta. Segment 2 with 1 plumose and 7 bare setae. Segment 3 with 6 setae. Segment 4 represented by U-shaped sclerite with 2 setae. Segment 5 with 2 setae laterally, produced distally into small process bearing basally fused seta and aesthetasc (length 60  $\mu\text{m}$ ). Segment 6 with vestigial seta laterally and long seta distally. Segment 7 with 3 modified elements (Fig. 3C). Segment 8 with 2 short setae and 2 modified elements (Fig. 3C). Segment 9 with 1 seta anteriorly, 6 setae posteriorly and an apical trithec consisting of 2 setae fused basally to aesthetasc (length 26  $\mu\text{m}$ ).

P3 endopod (Fig. 4F). Subdistal spine of enp-2 fused to segment and forming spinous process.

P4 endopod (Fig. 4E) considerably shorter than in  $\text{♀}$ ; outer spine modified, bifid and outwardly directed.

P5 (Fig. 5D) small; exopod and baseoendopod completely fused; inner corner with short pinnate spine, outer margin with pinnate seta, 2 vestigial setae and long plumose seta; anterior surface with secretory pore.

Sixth pair of legs (Fig. 5D) slightly asymmetrical; each with inner pinnate spine and outer plumose seta. P6-bearing somite with transverse spinular row ventrally.

Spermatophore (Fig. 5C) elongate; length 25  $\mu\text{m}$ .

#### Distribution

Italy: Isola S. Pietro, Arcipelago de La Maddalena;

France: Banyuls-sur-Mer.

#### *Psamathea britannica* sp. nov.

Synonym. *Notopontia* (?) sp. *sensu* Bodin (1984).

*Type locality.* Bay of Douarnenez, Finistère (Brittany), France; 48°10'N, 4°30'W; 22 m depth, coarse sand (median grain size 300  $\mu\text{m}$ ) with < 1% silt/clay content.

Paratypes localities: beaches of Kersaint and Brignongan, Finistère (Brittany).

*Material examined.* Holotype  $\text{♀}$  (dissected on 3 slides; reg. no. 1996.23) 2 paratypes  $\text{♀♀}$  dissected on 3 slides each, 1 paratype  $\text{♂}$  dissected on 4 slides; coll. Ph. Bodin, 29 June 1977, SCUBA-diving. Two paratypes (1  $\text{♀}$ , 1  $\text{♂}$ ) deposited in The Natural History Museum under reg. nos. 1996.24-25; 1 paratype  $\text{♀}$  retained in personal collection of Dr Ph. Bodin.

*Description.* The description is necessarily based on mounted specimens which were routinely dissected in the course of ecological work. Consequently, not all structural details could be satisfactorily illustrated with the material available.

#### FEMALE

Total body length unknown but is, based on urosome measurements, expected to range between 300 and 400  $\mu\text{m}$ .

Urosome slender, cylindrical, almost colourless; intersomitic boundaries well developed. Integument smooth, moderately chitinised. Hyaline frill of urosomites reduced to narrow, slightly striated membrane (Fig. 6B). Anal somite about 2.5 times as long as average width. Genital double-somite wider than long, with genital apertures located in anterior half; no trace of original subdivision except for paired dorsal sensilla.

Caudal rami slightly divergent (Fig. 6B), about 1.75 times as long as maximum width; distinctly

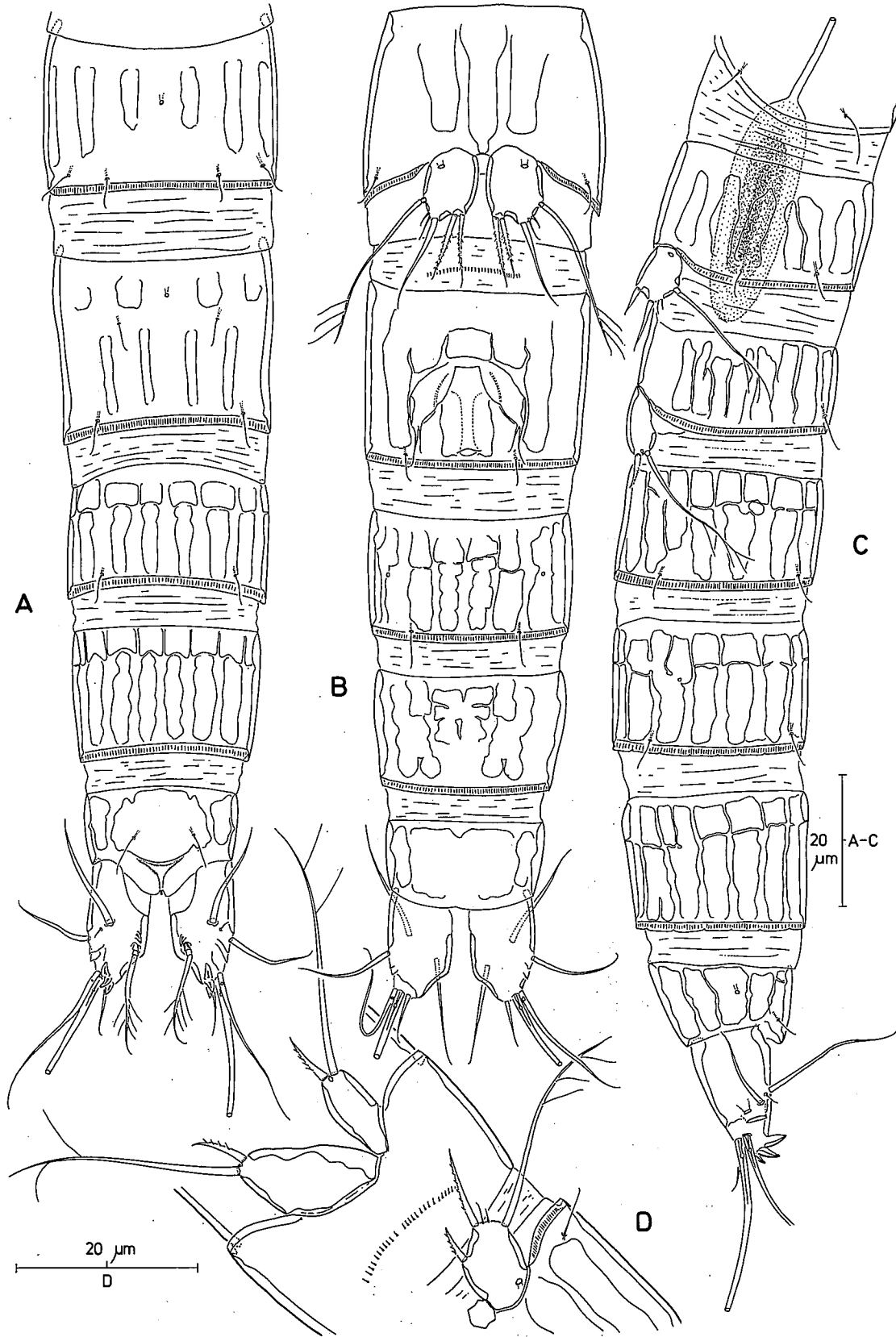


Fig. 5. — *Psamathea nautarum* Cottarelli & Venanzetti, 1989. A. Urosome (♀), dorsal; B. Same, ventral; C. Urosome (♂), lateral; D. P5 and P6 (♂), ventral.

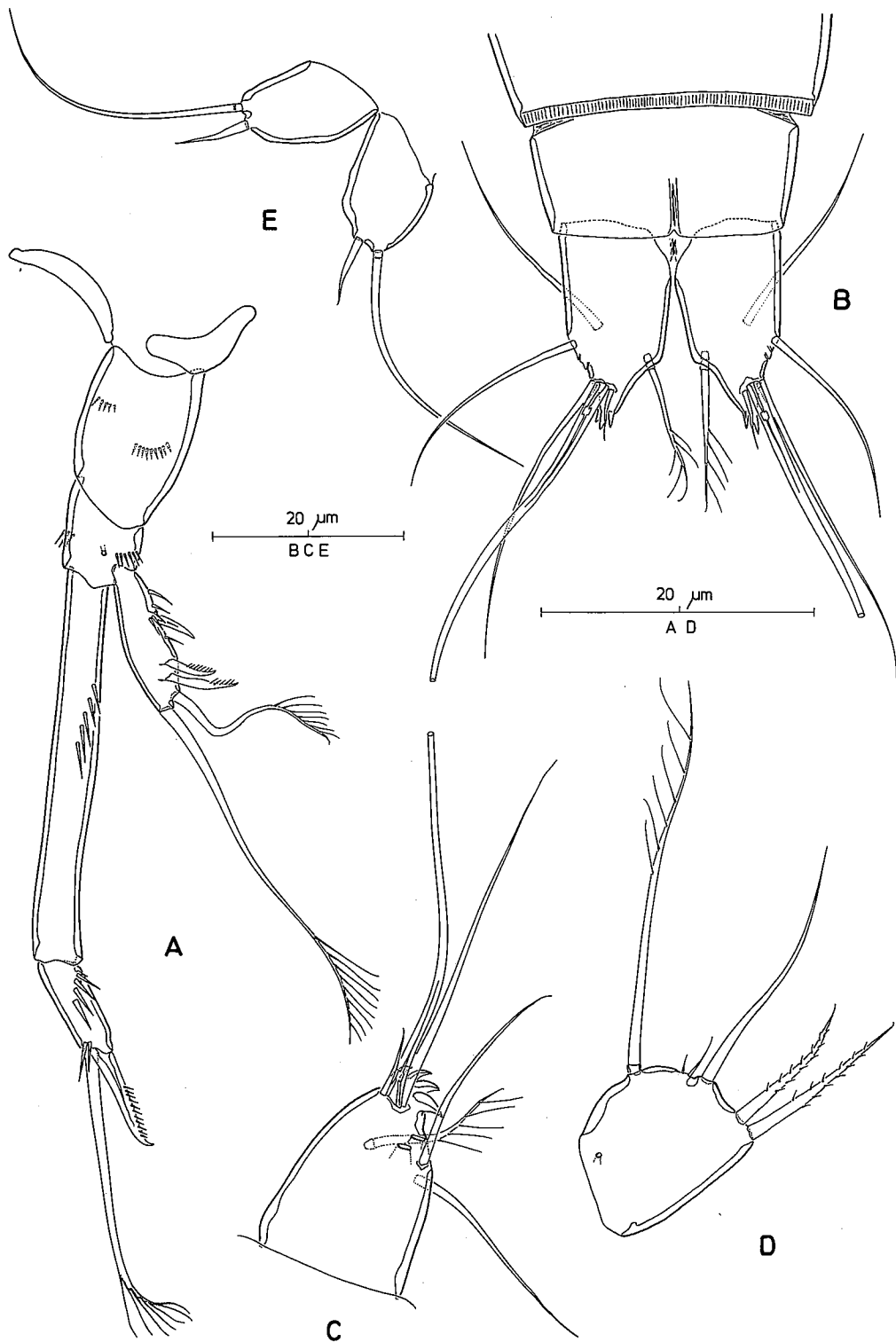


Fig. 6. – *Psamathea brittanica* n. sp. A. P1 (♀), anterior; B. Anal somite and caudal rami (♀), ventral; C. Right caudal ramus (♀), lateral; D. P5 (♀), anterior; E. Sixth pair of legs (♂).

tapering in distal third, inner distal corner forming conspicuous quadricuspidate process with individual cusps slightly recurved and directed dorsally (Fig. 6C). Armature consisting of 6 setae; seta V very long, not fused at base with well developed seta IV; seta VI vestigial; seta VII bi-articulated at base and plumose at the tip. Lateral margin with 2 slit-like pores between insertion sites of setae III and IV.

Rostrum well developed, triangular, slightly exceeding first antennular segment, defined at base.

Antennule to maxillipeds as in type species.

P1 – P4 (Figs 6A, 7A-B, F) with 3-segmented exopods (except for P1); endopods 2-segmented, always shorter than outer rami except for endopod P1. Successive legs increasing in length.

P1 (Fig. 6A). Coxa well developed, about 1.5 times longer than wide, with 2 spinular rows on posterior surface. Basis distinctly shorter than coxa; inner and outer setae absent; with spinules at the outer corner and inner margin and pore on anterior surface. Exopod represented by elongate segment, swollen in posterior half, about 4 times as long as wide; outer margin spinulose, with 1 bare spine (derived from exp-1) and 2 unipinnate spines; distal margin with 2 brush setae, inner one longest. Endopod 2-segmented, prehensile: enp-1 about 6.6 times as long as enp-2, without inner seta, with short spinular row at middle outer margin; enp-2 about 3 times as long as wide, with 1 spinular row along outer margin and few spinules, anterior pinnate claw and slender posterior brush seta distally.

P2-P4 with strongly developed, unornamented coxae. Basis of P3-P4 with outer seta. Inner setae of P4 exp-2 and P3-P4 exp-3 pectinate, unusually short on P4 exp-2 (Fig. 7D). P3 enp-2 with short anterior and long posterior seta, both distally uniserrate. Outer spine of P4 exp-1 or exp-2 neither elongate nor recurved at tip (Fig. 7D). Seta and spine formulae as for genus.

P5 (Fig. 6D) with exopod and baseoendopod confluent; represented by a subquadrate plate with 6 setae, exopodal armature represented by 1 long inner seta and 2 accessory vestigial ones, baseoendopodal setae well developed, pinnate.

P6 represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 2 vestigial setae. Two small secretory pores are discernible on either side of the ventral midline; copulatory pore small.

#### MALE

Antennule and P5 as in type species.

P3 (Fig. 7C). Protopod and exopod as in ♀. Endopod with both enp-1 and enp-2 shorter than in ♀; anterior seta of enp-2 vestigial and incorporated in segment, distal seta with serrate tip.

P4 (Fig. 7D-E). Protopod and exopod as in ♀. Endopod with both segments slightly shorter than in ♀; enp-1 without spinules around distal margin; distal setae of enp-2 with shorter spinules and inner one distinctly shorter than in ♀.

Sixth legs (Fig. 6E) symmetrical; each leg with short inner spine and long outer seta.

*Etymology.* The name refers to Brittany, the type locality.

*Distribution.* Known only from the type locality. One of us (Ph. B) has collected additional material on the beaches of Kersaint and Brignogan on the north coast of Brittany.

#### DISCUSSION

Representatives of *Psamathea* are amongst the smallest Leptastacidae known and species discrimination can only be achieved by using sophisticated techniques such as differential interference microscopy. In addition, the conservative nature in mouthpart and swimming leg morphology as found in many other leptastacid genera further hampers species identification. Both species can be distinguished on the basis of the following characters:

	<i>nautarum</i>	<i>britannica</i> sp. nov.
P1 exopod	2-segmented	1-segmented
Caudal ramus distal process	tricuspidate	quaticuspidate
Caudal ramus L : W	2.3	1.75
P4♂ length enp-1 : enp-2	2.25	1.7

There are a number of differences between the type description of *P. nautarum* and our observations based on specimens from Banyuls, however the majority of these can be attributed to deficiencies in Cottarelli & Venanzetti's (1989) illustrations rather than to variation displayed by geographically separated populations. The Sardinian specimens are slightly larger (♀ : 370 µm, ♂ : 380 µm) and appear to have longer caudal rami in dorsal aspect, however, when viewed laterally the rami look exactly like in the Banyuls specimens. The absence of the dorsal spur and seta I on the caudal rami, and the concave anal operculum (instead of rounded) are almost certainly erroneous observations resulting from excessive squashing of the mounted urosome.

Various setae were overlooked in the original description of the appendages of the cephalothorax such as on the antennules of both sexes, the mandibular palp, the maxillule and maxilla, and the maxillipedal syncoxa. The P1 exopod was illustrated as distinctly 2-segmented by Cottarelli

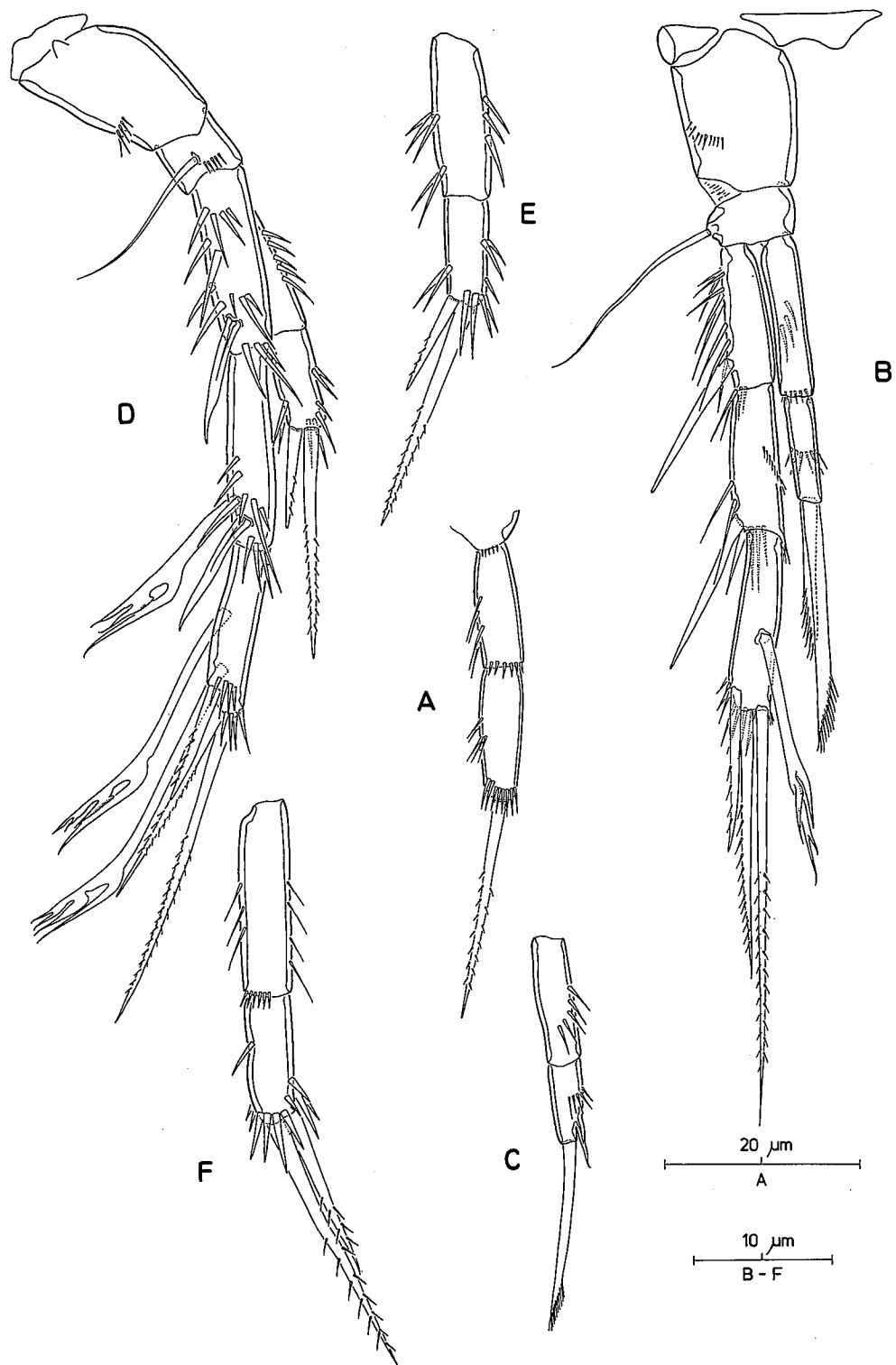


Fig. 7. – *Psamathea brittanica* n. sp. A. P2 endopod (♀), anterior; B. P3 (♀), posterior; C. P3 endopod (♂), anterior; D. P4 (♂), lateral; E. P4 endopod (♂), anterior; F. P4 endopod (♀), anterior,

& Venanzetti (1989), however, examination of the French material revealed that this subdivision is superficial and expressed at the anterior surface only. The authors also overlooked the brush-like structure of the long setae on both rami of the P1. Cottarelli & Venanzetti (1989) figure an outer seta on the basis of P1 and P2 in the type species, whereas this seta is definitely absent in both legs in *P. brittanica* and in the P1 in *P. nautarum*. It is conceivable that Cottarelli and Venanzetti naturally presumed this seta to be present on all legs even if they failed to observe it on P1 and P2. This would explain the unusually great length of this element in their Fig. 21 b-c. A discrepancy is also found in the setal formula of the male P4 endopod which is given as 0.120 rather than 0.110 as in the female. Comparison with our observations suggests that Cottarelli & Venanzetti have misinterpreted the marginal spinule (the only one drawn of the spinular row) as a supplementary armature element. The alleged sexual dimorphism on the P3 exopod is unreal since it is based solely on the pectinate inner seta which has clearly not been viewed from the same angle in males and females.

The present examination of both known species of *Psamathea* has provided two new facts of high phylogenetic significance. First, comparison of the caudal ramus of *Psamathea* and *Paraleptastacus* reveals that the multicuspidate process in the former is the positional homologue of the inner dorsally recurved process in the latter. The tri- or quadricuspidate process can be regarded as an elaboration of the spinous process. The general shape of the caudal rami in both genera is also similar, showing a marked constriction in the distal third. Unlike most other genera setae IV and V are not basally fused, however, this is probably a symplesiomorphy. The relative position, shape and length of the 6 major setae is identical, the only difference being the dorsal seta VII which is distally plumose in *Psamathea* and bifid in *Paraleptastacus*.

Second, the sexual dimorphism expressed on the P4 endopod of *Psamathea* and *Areocaris* is fundamentally different. In *Areocaris* the entire endopod functions as a copulatory appendage that is capable of extensive inward (adaxial) flexing at the [enp-1]-[enp-2] joint (Huys, 1992). The inner distal element of enp-2 is transformed into a curved claw with flagellate tip. In *Psamathea* the sexual dimorphism is less well developed and involves slight size reductions of the two endopodal segments, and more important, of the distal inner seta of enp-2. While the latter reduction might appear insignificant, it is remarkable that the same kind of modification is also displayed in a variety of degrees in the species of *Paraleptastacus*. These two characters taken in conjunction provide evidence for a *Paraleptastacus*-*Psamathea*

sistergroup relationship. However, *Paraleptastacus* is plesiomorphic in many character states and, apart from the inner seta on P2 exp-3 (retained only in *Archileptastacus*), displays the most primitive swimming leg setal formula in the family. Conversely, *Psamathea* has undergone several reductions in setal counts but can be defined by the following autapomorphies: (1) prehensile P1 endopod, involving the extreme elongation of enp-1, and the modification of the anterior outer element into a unipinnate claw; this character is unusual within the family and has evolved only once more in a distinct lineage within the genus *Paraleptastacus* (cf. Nicholls, 1939); (2) the presence of "brush" setae on both exopod and endopod of P1; such setae have also been recorded in a number of other families such as the Rhizothricidae; (3) uniramous fifth legs in both sexes, (4) the reduction in armature of the male sixth legs, and (5) the multicuspidate dorsal process on the caudal rami.

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