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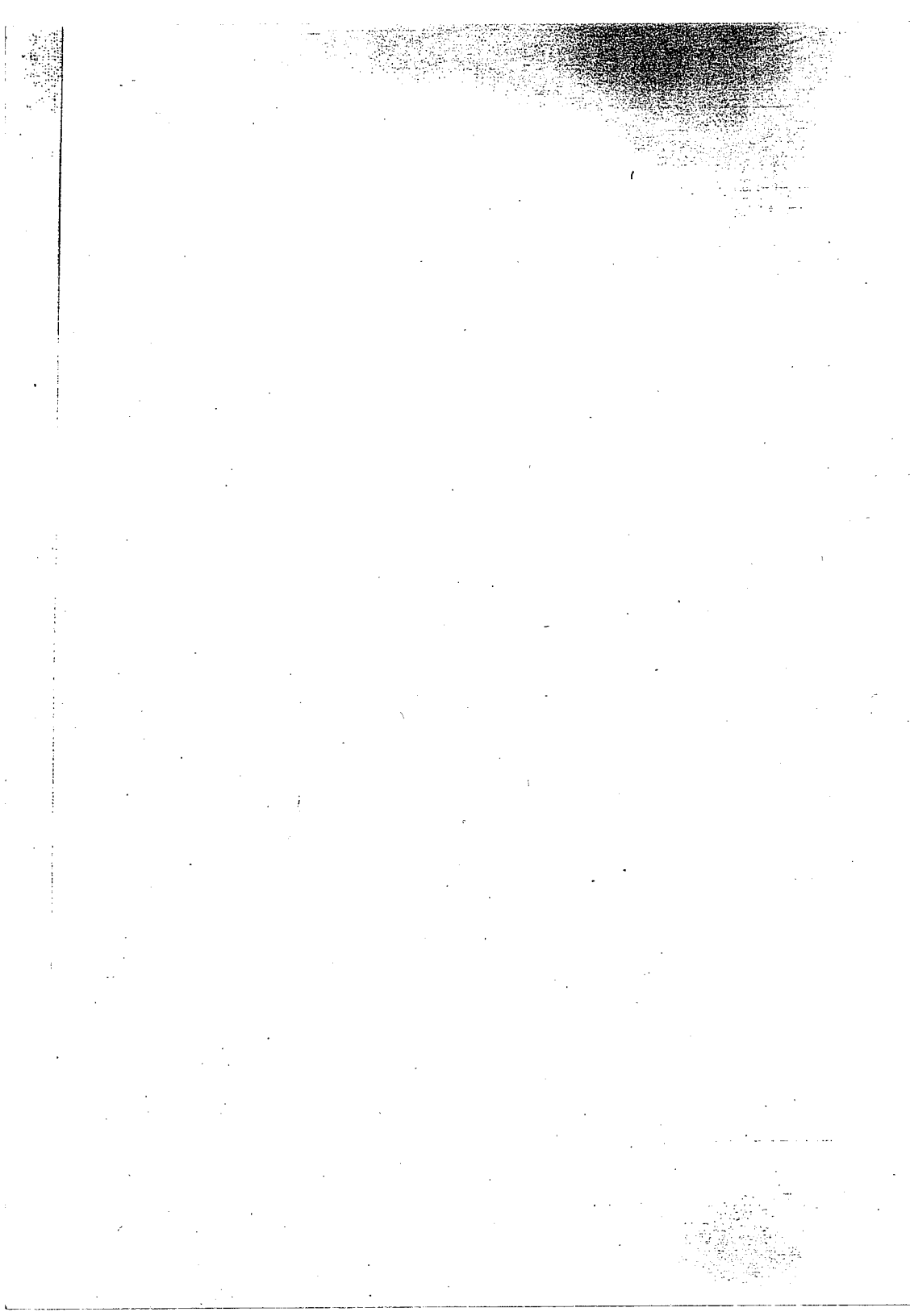
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THE AMPHIATLANTIC DISTRIBUTION  
OF *LEPTASTACUS MACRONYX* (T. SCOTT, 1892)  
(COPEPODA : HARPACTICOIDA) :  
A PARADIGM OF TAXONOMIC CONFUSION  
AND  
A CLADISTIC APPROACH  
TO THE CLASSIFICATION  
OF THE LEPTASTACIDAE LANG, 1948

BY

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## INTRODUCTION

With the development of more effective sampling and extraction techniques in the fifties and sixties, emphasis on discovering, identifying and classifying new meiobenthic taxa became prevalent during this period. Various workers all over the world described many new harpacticoids from a variety of habitats. The start of meiobenthic research in America soon illustrated the particularly common occurrence of amphiatlantic species and transallopatriic species pairs in the meiofauna of both sides of the Atlantic. Virtually identical species on both seaboards of the Atlantic Ocean have been documented for a number of soft-bodied taxa such as interstitial polychaetes (Riser, 1980), turbellarians (Rieger, 1977; Ax & Armonies, 1987, 1990) and gastrotrichs (Ruppert, 1977), and various significant agents or mechanisms have been invoked to explain trans-oceanic dispersal (see Sterrer, 1973; Gerlach, 1977) of these non-crustacean taxa. Logically, the question whether this large scale uniformity can also be detected for marine interstitial crustaceans has to be formulated.

Mystacocarids are only known to live in the interstitial spaces of sandy sediments and individual species can be seen over long distances along continental coastlines (e.g. Hessler, 1972). Although the group is essentially circum-

Atlantic in distribution with most outliers (Chile and Durban) adjacent to the Atlantic, no amphiatlantic species have been found thus far.

Some years ago, a preliminary study was started by the author to test the known global distribution of paramesochrid harpacticoids. Presumed amphiatlantic species distributions could not be supported and instead an extremely high degree of local endemism was found to typify this family. With respect to the *Cylindropsyllidae*, *L. macronyx* (T. Scott, 1892) is perhaps with *Paraleptastacus spinicauda* (T. & A. Scott, 1895) and *Arenopontia subterranea* Kunz, 1937 the most widely distributed interstitial harpacticoid. Compilation of all published records on *L. macronyx* resulted in a typical amphiatlantic distribution which extends to the Mediterranean and Black Sea basin (Fig. 1 ; Table 1). In order to test the currently accepted distribution pattern of *L. macronyx*, material from Massachusetts, South Carolina, Bermuda and the Virgin Islands was compared with specimens from various northwest European localities.

Aroused interest in the interstitial copepod fauna of sandy beaches has almost quadrupled the number of species in the last 20 years, but lack of attention to morphological details, especially in earlier descriptions, caused people to lose sight of relationships and generic boundaries in interstitial

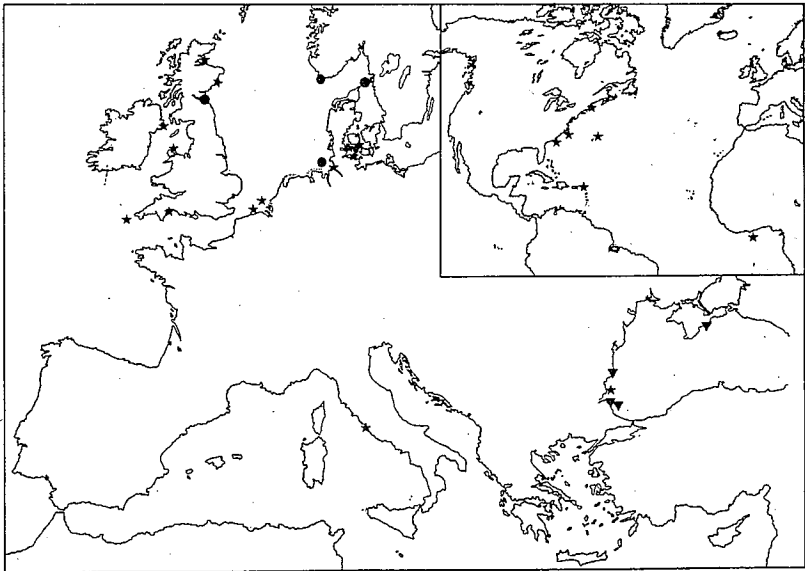


Fig. 1. — Literature records of *Leptastacus macronyx* : Reliable records are indicated by circles ; those related to *L. macronyx* var. *pontica* are indicated by triangles.

families. Within the *Cylindropsyllidae* this problem is particularly apparent in the *Leptastacinae* where some genera such as *Psammastacus* Nicholls, 1935 and *Leptastacus* T. Scott, 1906 already started to serve as taxonomic repositories for loosely related species. The second part of this paper aims at, (1) a redefinition of the diagnoses for the various leptastacid genera, and (2) a reclassification of the *Leptastacidae* by means of a phylogenetic approach.

TABLE I

Distribution records of *L. macronyx* T. Scott based on literature.

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I. *L. macronyx*

Norway : Korshavn, Lindesnaes (Sars, 1911) ;  
 Sweden : Bonden, Bohuslän (Por, 1964 ; Wells *et al.*, 1975) ;  
 Scotland : Cromarty Firth (T. Scott, 1899) ; St. Monans in Firth of Forth (T. Scott, 1892, 1906a) ;  
 River Ythan (Hockin, 1982) ;  
 England : Wales, Anglesey, Red Wharf Bay (Geddes, 1972) ; Devon, River Exe (Wells, 1963a) ;  
 Isles of Scilly : St. Mary's Sound (Norman & T. Scott, 1906), Appletree Bay in Tresco and New  
 Quay in St. Martin's (Wells, 1961, 1970), Peninnis Outer Head (Wells, 1970) ;  
 Northern Ireland : Strangford Harbour (Wells, 1963b) ;  
 Germany : Helgoland (Kunz, 1938 ; Klie, 1950) ; River Elbe estuary (Riemann, 1966) ; Boknis  
 Eck in Eckernförder Bucht (Scheibel, 1976) ; Kieler Förde (Anger & Scheibel, 1976) ; Vesjnaes-  
 Flach and Stoller Grund in Kieler Bucht (Scheibel, 1972, 1973) ; Kieler Bucht (Klie, 1929 ;  
 Kunz, 1935) ;  
 Belgium : Southern Bight (Van Damme & Heip, 1977) ; Kwinte Bank (Claeys, 1979 ; Willems,  
 pers. comm.) ;  
 Bulgaria : Black Sea coast, Nesebur (Marinov, 1971) ;  
 Italy : Lazio, Fregene (Chappuis, 1954a ; Delamare Deboutteville, 1953, 1960) ;  
 Ghana : Accra (Chappuis & Rouch, 1961) ;  
 U.S.A. : South Carolina, Georgetown, North Inlet estuary (Coull & Vernberg, 1975 ; Vernberg  
 & Coull, 1975 ; Coull & Fleeger, 1977 ; Ivester & Coull, 1977 ; Fleeger, 1980 ; Ivester, 1980 ;  
 Montagna *et al.*, 1983 ; Coull, 1985 ; Coull & Dudley, 1985 ; Palmer & Gust, 1985) ; North  
 Carolina, continental shelf from Cape Fear to Cape Hatteras (Coull, 1971a, 1972) ; Massachusetts,  
 Woods Hole, Martha's Vineyard (Wilson, 1932) ;  
 Bermuda : Trunk Island, Baileys Bay and Castle Harbor (Coull, 1968, 1970 ; Coull & Herman,  
 1970) ;  
 Virgin Islands : St. Thomas, Coki Bay (Hartzband & Hummon, 1973) ;

II. *Leptastacus macronyx* var. *pontica* Griga, 1964

- = *Leptastacus rostratus* Nicholls, 1940 ? : Apostolov (1972)
- = *Leptastacus rostratus* Nicholls, 1940 : Apostolov (1973a)
- = *Leptastacus rostratus* subsp. *taurica* Marinov, 1973
- = *Leptastacus taurica* Marinov, 1973 : Geddes (1981), Apostolov & Marinov (1988)

Russia : Black Sea, Eupatoria (Griga, 1962) ;  
 Bulgaria : Varna (Cap Gualata), Michurin, Akhtopol, Izgrevska River (Apostolov, 1970, 1971),  
 Stompolo (Apostolov, 1973a) ; no locality specified (Marinov, 1973)

[This species is not related to the *macronyx*-group and has to be referred to a separate genus *Schizothrix* gen. nov. (see below)].

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## METHODS AND TERMINOLOGY

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England).

All drawings have been prepared using a camera lucida on a Leitz Dialux 20 differential interference contrast microscope. The terminology is adopted from Huys & Boxshall (1991). Abbreviations used in the text are :

P1 - P6	first to sixth thoracopods
exp.	exopod
enp.	endopod
benp.	baseoendopod
exp(enp)-1(-2,-3)	proximal (middle, distal) segment of a ramus

## RESULTS AND DISCUSSION

### 1. A revision of *Leptastacus macronyx* (T. Scott, 1892)

The type species *L. macronyx* will be redescribed *in extenso* first. All subsequent descriptions of species previously confounded with this species will be more concise.

#### *Leptastacus macronyx* (T. Scott, 1892)

(Figs. 2-4)

- 1892 *Tetragoniceps macronyx*, n.sp. : T. Scott, Rep. Fish. Bd. Scotl. 13 : 253-254 ; Pl. X, Figs. 19-28
- 1906 *Leptastacus macronyx* (T. Scott) : T. Scott, Ann. Mag. nat. Hist. : 461-462
- 1911 *Leptastacus macronyx* (T. Scott) : Sars, An Account of the Crustacea of Norway 5 : 417-418 ; Suppl. Pl. XXXX
- 1929 *Leptastacus macronyx* (T. Scott) : Klie, Zool. Jb. 57 : 362
- 1935 *Leptastacus macronyx* (T. Scott) : Kunz, Schr. naturw. v. Schlesw.-Holst. 21 : 87
- 1938 *Leptastacus macronyx* (T. Scott) : Kunz, Kieler Meeresforsch. 2 : 243 ; Abb. 9, Fig. 15
- 1950 *Leptastacus macronyx* (T. Scott) : Klie, Kieler Meeresforsch. 7 : 112
- 1964 *Leptastacus macronyx* (T. Scott) : Por, Cah. Biol. mar. 5 : 237
- 1975 *Leptastacus macronyx* (T. Scott) : Wells *et al.*, Mikrofauna Meeresboden 53 : 15



## TYPE LOCALITY

Off St Monans, Firth of Forth, Scotland ; among dredged material from about 25 m depth ; bottom clean sand.

## MATERIAL EXAMINED

I have not been able to trace Scott's types from St Monans ; the type material of *L. macronyx* apparently does not exist anymore. One vial with specimens from the Firth of Forth and labelled "*Tetragoniceps macronyx*" was found in the Zoologisk Museum, Oslo. These specimens were donated by T. Scott to G. O. Sars. However, inspection revealed that the material belongs to an as yet undescribed species of *Paraleptastacus* Wilson. The re-description is based on the following material :

- Zoologisches Museum, Kiel : Walter Klie collection (reg. no. Cop. 564), 1 ♀ dissected on slide ; from Helgoland, *Amphioxus*-sand, sept. 1928 ;
- Zoologisk Museum, Oslo : G.O. Sars collection (reg. no. F20691), 1 damaged ♀ (anal somite and caudal rami missing) from Korshavn ;
- from Dr. H. Kunz : Bonden/Bohuslän, west coast of Sweden (leg. H. Kunz, 19.08.74) (see Wells *et al.*, 1975 : 15 for collection data) : 1 ♀ dissected on 6 slides.

These 3 females were the only specimens (out of hundreds of other specimens assigned to *L. macronyx* by various authors) that could positively be identified as belonging to Scott's species. Consequently, the detailed morphology of the male remains unknown. Scrutinous comparison of the other material led to the discovery of three other species new to science.

## REDESCRIPTION

*FEMALE*. The exact body length could not be measured since all specimens available were either dissected or incomplete. According to the literature the body length may vary between 500 (Klie, 1929 : 362) and 620  $\mu\text{m}$  (Kunz, 1938 : 243). T. Scott (1892 : 253) gives 540  $\mu\text{m}$  for his specimens. Sars' (1911 : 418) specimens are the largest found (0.7 mm !) ; proportional comparison of the single damaged female from Korshavn suggests that his measurement was wrong.

Body slender, cylindrical, almost colourless and semi-transparent. Thoracic somites slightly broader than abdomen, no distinct separation between prosome and urosome, anal somite narrowest. Cephalothorax about 1.5 times as long

as 2 succeeding somites combined. Genital double somite longest, 1/8 of total body length, indistinctly subdivided by an internal chitinous rib laterally. Anal somite shortest. Nauplius eye not observed.

Rostrum well developed (Fig. 2A), elongated, not exceeding first antennular segment; tapering distally to a fine apex; tip pointing downwards; not fused with cephalothorax; furnished with a pair of delicate sensillae at one third distance from the tip.

Hyaline frill of body somites plain. Integument smooth.

Cephalic shield rectangular, about 1.5 times as long as greatest width. Anal somite with spinules at posterior ventral margin (Fig. 4D); dorsal hind margin with well developed anal operculum furnished with about 10 coarse spinules and flanked by conspicuous spinular row, whose innermost spinules are distinctly larger than the others.

Caudal rami divergent (Fig. 4D), 3.9-4.0 times as long as greatest width. Each ramus with long spinular row on inner ventrolateral margin; distal margin with few spinules ventrally. Armature consisting of six setae (seta I missing); seta V strongly developed, with inner spinous process at about 80  $\mu\text{m}$  distance from the base; seta VI delicate; seta VII bi-articulated at base; seta III composite with proximal part styliform and slightly longer than slender distal part.

Antennule (Fig. 2A) 7-segmented, slender; antennular hyaline frill slightly developed, plain; first segment long with 1 spiniform seta distally; second one longest (measured along anterior margin), approximately 3 times as long as greatest width, distal third with 8 setae, of which 5 are articulated at base; third segment second longest, with 5 setae in distal third; distal outer corner of fourth segment with long aesthetasc (length 112  $\mu\text{m}$ ) and 2 slender setae; fifth and sixth segments with 1 and 2 setae, respectively; seventh segment long and slender, with 9 setae [trifurcate one represents a short aesthetasc (length 35  $\mu\text{m}$ ) confluent at base with 2 bare setae].

Antenna (Fig. 4A). Coxa small, much shorter than wide, unarmed. Allobasis about 4.1 times as long as maximum width; inner margin with 3 spinular rows; original segmentation discernible by slight internal, transverse chitinous rib. Exopod (implanted at 1/8 of the allobasal length) 1-segmented, small, about twice as long as maximum width, slightly tapering distally; furnished with 1 long and 1 short seta apically. Endopod approximately 0.57 times the length of allobasis; distal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is fused at the base with a dwarfed seta and is ornamented with coarse spinules around the geniculation; inner margin with 1 pinnate spine, 1 setule and an oblique spinular row.

Mandible (Fig. 2B). Coxa well developed; gnathobase with 1 thick, unidentate tooth dorsally, several smaller teeth medially and a unipinnate seta at the dorsal corner. Palp 2-segmented; presumably consisting of basis and undivided endopod. Basis a square segment with seta at outer distal corner;

endopod 4 times as long as basis, with a seta arising from a point a third the length of inner margin, and 4 setae arranged around the distal end [the 2 apical setae are fused at the base and were often mistaken for a third segment in previous descriptions (e.g. Mielke, 1982 ; Huys, 1987)].

Maxillula (Fig. 2C). Praecoxa an elongate chitinous segment with anteriorly directed arthrite. Arthrite with 8 claws or spines around the distal margin and 2 juxtaposed setules on the anterior surface. Coxa represented by endite with a pinnate and a naked seta distally ; positioned in between praecoxal arthrite and elongate basis. Basis produced into a single, large, sub-cylindrical endite ; distal armature consisting of 4 slender setae and 1 pinnate spine ; anterior margin spinulose. Endopod and exopod incorporated in the basis and represented by 2 long setae and 1 spinulose seta, respectively.

Maxilla (Fig. 2D). Syncoxa tapering distally, with one spinule on middle outer margin ; with 2 well developed sub-cylindrical endites (derived from the coxa) ; proximal endite shortest, with 2 apical and 1 subterminal short, modified spines ; distal endite with 1 spinulose claw and 1 slender seta distally and 1 short, modified spine subterminally. Allobasis tapering into a strong, recurved claw with 2 setae (1 each on dorsal and ventral side) at base. Endopod well developed, 2-segmented ; proximal segment longest, with 1 outer seta ; distal segment with 3 slender apical setae of which 2 fused at base.

Maxilliped (Fig. 2E). Syncoxa small, with few spinules at inner distal corner. Basis strongly developed, elongated, about 3 times as long as syncoxa ; outer margin with discontinuous spinular row ; middle inner margin with a row of minute spinules. Endopod represented by minute segment bearing a strong long claw, of which distal 2/3 (last third 2-sided) spinulose and a long, slender seta.

Labrum strongly developed ; terminal median part swollen and furnished with numerous long spinules of which anterior ones are more slender than posterior ones ; lateral margins lobate, each provided with lateral rows of minute spinules.

Natatorial legs (Figs. 3A-C, 4B) with 3-segmented exopods ; endopods 2-segmented, always shorter than outer rami except for the endopod of P1. Succeeding legs increasing in length.

Thoracopod 1 (P1) (Fig. 4B). Coxa well developed, with 2 spinular rows on anterior surface. Basis slightly shorter than coxa, with some spinules near articulation with exopod ; inner and outer setae not present. First and second exopodal segments with 1 outer unipinnate spine and several spinules along outer margin. Third exopodal segment with 2 unipinnate spines and 2 geniculate setae, innermost of which longest ; outer margin provided with some spinules. Endopod about 1.35 times as long as exopod. First endopodal segment 1.65 times as long as distal one ; ratio of length to width (measured proximally) 4.1 ; with some minute spinules and 1 pectinate seta on inner margin. Second

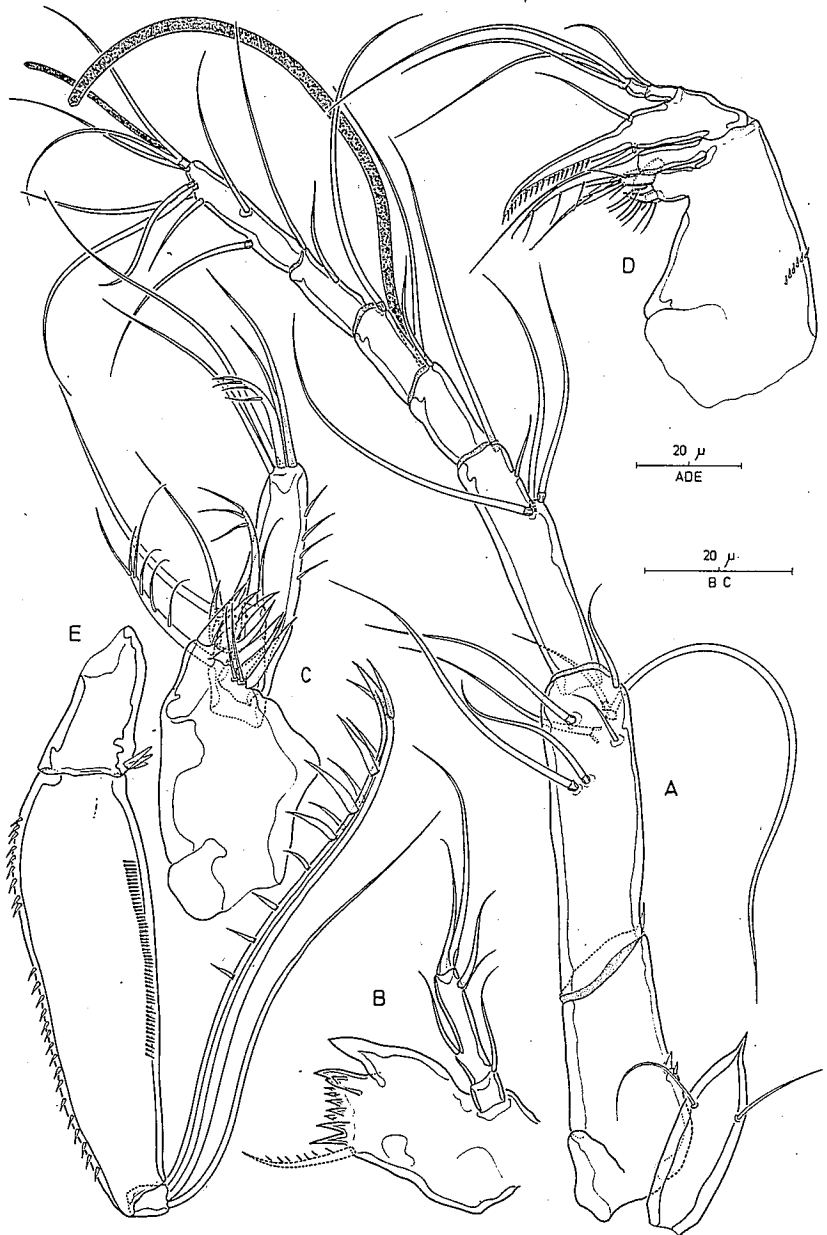


Fig. 2. — *Leptastacus macronyx* (T. Scott, 1892). A. Antennule, ♀; B. Mandible; C. Maxillula; D. Maxilla; E. Maxilliped.

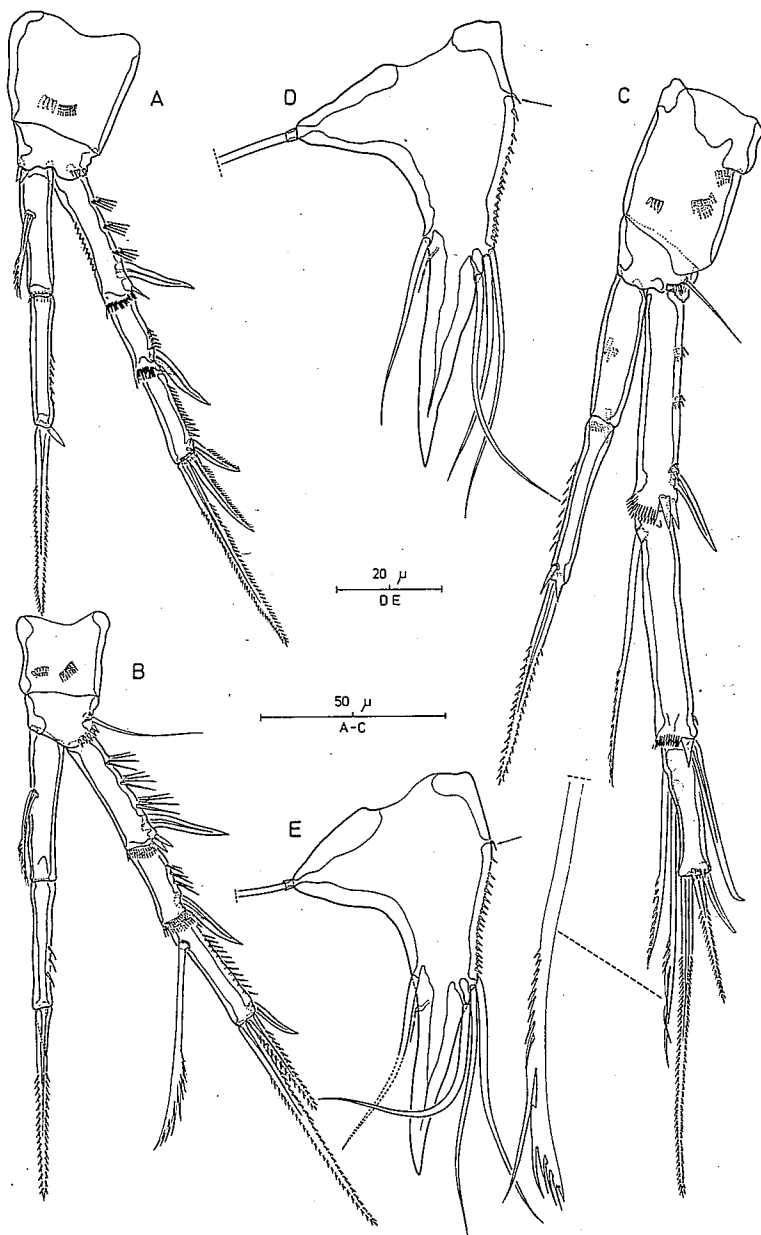


Fig. 3. — *Leptastacus macronyx* (T. Scott, 1892). A. P2; B. P3; C. P4; D. P5, ♀ (Helgoland specimen); E. P5, ♀ (Bohuslän specimen).

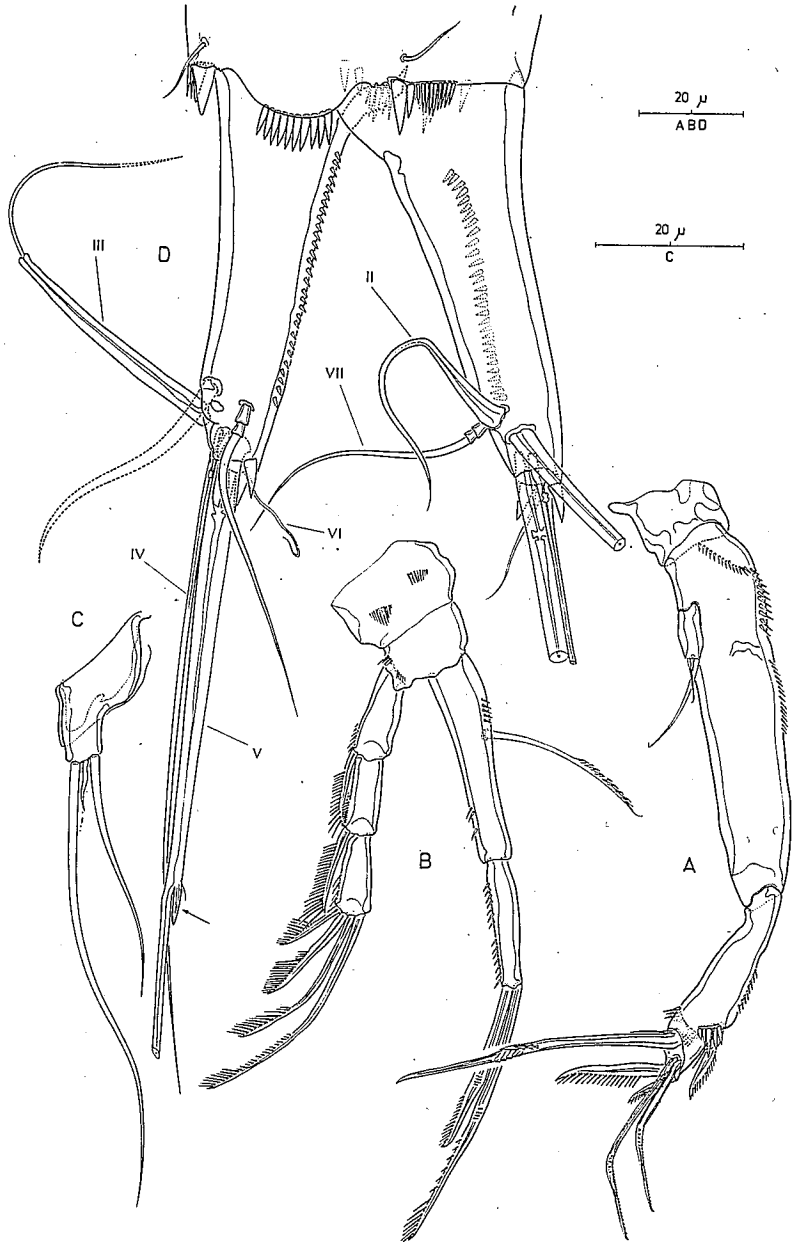


Fig. 4. — *Leptastacus macronyx* (T. Scott, 1892). A. Antenna. B. P1 ; C. P6, ♀ ; D. Caudal rami and anal operculum, laterodorsal view.

endopodal segment more slender than preceding one, with 2 spinular rows along outer margin and 2 geniculate setae distally.

Thoracopods 2-4 (P2-P4) (Figs. 3A-C) with strongly developed coxae. Basis of P3-P4 with outer seta. Inner seta of proximal endopodal segments P2-P3, middle exopodal segment P4 and distal exopodal segment P3-P4 pectinate (see inset Fig. 3C). Proximal endopodal segment P4 without inner seta. Distal endopodal segment of P3 with only 1 well developed spine ; second one presumably represented by small spinous process arising from distal margin (indicated by dotted line in Fig. 3B). Outer exopodal spine of middle segment P4 exceeding third segment and recurved at tip. Inner terminal spine of third exopodal segment P2-P4 not modified. Length : width ratio of P2 endopod 12.0. Length : width ratio of distal endopodal segment P4 9.25.

Seta and spine formulae as follows :

	Exopod	Endopod
P2	0.0.021	1.010
P3	0.0.121	1.010
P4	0.1.221	0.1*10

[\* dwarfed seta]

Thoracopod 5 (P5) (Figs. 3D-E). Exopod and baseoendopod confluent ; represented by a long triangular plate, ending in a spinous distal process. Ratio of length to width (measured proximally) 2.0. Inner margin spinulose ; with 1 vestigial seta proximally (arrowed in Figs. 3D-E) and 3 closely set slender setae midway the margin. Outer margin concave, with 3 setae in total ; proximal one bi-articulated at base and plumose along distal part (= seta derived from basis), second one long and naked, situated at about middle margin and closely set to third vestigial seta (arrowed in Figs. 3D-E).

Thoracopod 6 (P6) represented by a minute non-articulating plate closing off the genital apertures on each side and armed with 1 minute seta flanked by 2 long setae (Fig. 4C).

*MALE.* No specimens were available for study. The information on the male is therefore limited to the original description of T. Scott (1892) which illustrates the antennule and fifth thoracopod only. Sexual dimorphism was not observed on any of the swimming legs, however it is conceivable that the endopod P3 is slightly modified in the male since this is a generic character.

#### VARIABILITY

The only variability detected in the 3 specimens concerns the shape of the fifth legs (Figs. 3D-E). In the P5 of the Bohuslän-specimen the outer

extension bearing the basal seta is slightly shorter. Slight variability is also discernible in the distal process of the leg. In general, intrageneric identification in harpacticoid taxonomy frequently relies heavily on P5 structure. At least in the genus *Leptastacus* this character should be applied with great caution if it represents the only point of difference between two species. Huys (1987) already showed how the shape of the distal process may vary from one specimen to another. It was on the base of such intraspecific differences that the separation of *L. laticaudatus laticaudatus* Nicholls and *L. laticaudatus intermedius* Kunz, 1938 was founded (Huys, 1987).

#### REMARKS

In contrast to *L. laticaudatus* which is widely distributed throughout the Central and Southern North Sea (Huys, 1987), *L. macronyx* displays only a very restricted geographical distribution pattern. Strictly, only 7 records (localities indicated by circles in Fig. 1) are reliable and all are situated in the Central North Sea. At present, the other records from Scotland and Germany have to remain uncertain since other *Leptastacus* species have been reported from these areas. For example, Klie's (1950) material from the Kiel Bay proved upon inspection to be a mixture of two species (see below). Extensive faunistic surveys conducted along the Belgian and Dutch coasts during the last decades have never produced any specimens of *L. macronyx*. It is likely that *L. macronyx* is a typical nordic species and does not penetrate in the Southern Bight, its southernmost record being Helgoland.

#### *Leptastacus kwintei* sp. nov. (Figs. 5-8)

1979 *Leptastacus macronyx* (T. Scott) : Claeys, M.Sc. dissertation : 115, 129

#### TYPE LOCALITY

North Sea, Southern Bight, off Hoek van Holland; 52°09'48" N, 03°19'55" E; collected 19 June 1984 (leg. R. Huys); subtidal sandy sediment (median grain size : 437 µm; 98.6% sand, 1.27% gravel and 0.10% silt), depth 30 m.

#### MATERIAL EXAMINED

— From *locus typicus* : 4 ♀♀, 3 ♂♂ : holotype ♀ (dissected on 3 slides; reg. no. 1992.1099); paratype ♂ (dissected on 3 slides; reg. no. 1992.1100)



and 2 other paratypes (1 ♀, 1 ♂ in alcohol; reg. no. 1992.1101) deposited in The Natural History Museum, London.

- From Dr K. A. Willems: 1 ♀ (dissected on 3 slides), Kwinte Bank; St. SB 5B; 05 September 1978; leg. K. A. Willems [see Vanosmael *et al.* (1982) for locality data].
- From Dr R. L. Herman: 1 ♂ (dissected on 1 slide), mouth of Westerschelde estuary; St. 50A; 07 September 1983; leg. R. L. Herman.

#### DESCRIPTION

**FEMALE.** Body length 445-475  $\mu\text{m}$  ( $n = 3$ ), measured from the tip of the rostrum to the hind margin of the caudal rami.

Body slender, cylindrical, almost colourless and semi-transparent. Thoracic somites slightly broader than abdomen, no distinct separation between prosome and urosome, anal somite narrowest. Cephalothorax about 1.5 times as long as 2 succeeding somites combined. Genital double somite longest, 1/8 of total body length, indistinctly subdivided by an internal chitinous rib laterally. Anal somite shortest. Nauplius eye not observed.

Rostrum well developed, elongated, exceeding first antennular segment; tapering distally; tip pointing downwards; free; with 2 delicate sensillae at one third distance from the tip.

Hyaline frill of body somites plain. Integument smooth.

Cephalic shield rectangular, about 1.5 times as long as greatest width. Anal somite with spinules at posterior ventral margin (Fig. 8A). Anal operculum with about 30 slender spinules (Fig. 8A) and flanked by conspicuous spinular row consisting of coarse inner spinules and fine outer spinules.

Caudal rami (Fig. 8A) divergent, about 3.2-3.3 times as long as maximum width. Each ramus with 1 continuous spinular row on inner ventrolateral margin; distal margin with few coarse spinules ventrally. Armature consisting of six setae (seta I missing); seta V strongly developed, with minute inner spinous process; seta VI delicate; seta VII bi-articulated at base; seta III composite with proximal part styliform and slightly longer than slender distal part.

Antennule (Fig. 5A) 7-segmented, slender; first segment long, with 1 spiniform seta distally; second one longest (measured along anterior margin), approximately 2.5 times as long as greatest width, distal third with 8 setae; third segment second longest, with 5 setae in distal third; distal outer corner of fourth segment with long aesthetasc (length 105  $\mu\text{m}$ ) and 2 slender setae; fifth and sixth segments with 1 and 2 setae, respectively; seventh segment long and slender, with 9 setae [trifurcate one represents an aesthetasc (length 30  $\mu\text{m}$ ) confluent at base with 2 bare setae].

Antenna (Fig. 5B). Coxa small, unarmed. Allobasis about 3.2 times as long as maximum width; inner margin with 2 spinular rows; original segmentation discernible by internal, transverse chitinous rib. Exopod (implanted at 1/5 of the allobasis length) 1-segmented, small, about twice as long as maximum width; with 2 setae apically. Endopod approximately 0.65 times the length of allobasis; distal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is fused at the base with a dwarfed seta and is ornamented with spinules around the geniculation; inner margin with 2 spines, 1 setule and a few spinules.

Mandible (Fig. 5C). Coxa well developed; gnathobase with 1 thick, unidentate tooth dorsally, several smaller teeth medially and a unipinnate seta at the dorsal corner. Palp 1-segmented, about 4 times as long as wide; with 2 setae along the inner margin, 2 apical setae (confluent at the base) and 1 seta and a few spinules along the outer margin.

Maxillula (Fig. 5D). Praecoxa an elongate segment with anteriorly directed arthrite. Arthrite with 8 spines around the distal margin; juxtaposed setules on the anterior surface not observed. Coxal endite with a pinnate and a naked seta distally. Basis produced into a single, large, sub-cylindrical endite; distal armature consisting of 4 slender setae and 1 pinnate spine; anterior margin spinulose in distal third. Endopod and exopod incorporated in the basis and represented by 2 long setae and 1 spinulose seta, respectively.

Maxilla (Fig. 5E). Syncoxa with a spinular row on either inner and outer margin, with 2 endites medially; proximal endite slightly shorter, with 3 short, modified spines; distal endite with 1 spinulose claw and 1 slender seta distally and 1 short, modified spine subterminally. Allobasis tapering into a strong, recurved claw with 2 setae at base. Endopod well developed, 2-segmented; proximal segment longest, with 1 outer seta; distal segment with 3 slender apical setae of which 2 fused at base.

Maxilliped (Fig. 8B). Syncoxa small, with few spinules at inner distal corner. Basis strongly developed, about 2.6 times as long as syncoxa; outer margin with discontinuous spinular row; middle inner margin with a row of fine spinules. Endopod represented by minute segment bearing a strong long claw, of which distal two-thirds (last third 2-sided) spinulose, and a long, slender seta.

Labrum strongly developed; as for type species (see also Huys, 1987: Figs. 3B<sub>1</sub>-B<sub>2</sub>).

Natatorial legs (Figs. 8C, 6A-C) with 3-segmented exopods; endopods 2-segmented, always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

Thoracopod 1 (P1) (Fig. 8C). Coxa strongly developed, no ornamentation observed. Basis distinctly shorter than coxa; inner and outer setae not present. First and second exopodal segments with 1 outer unipinnate spine and several

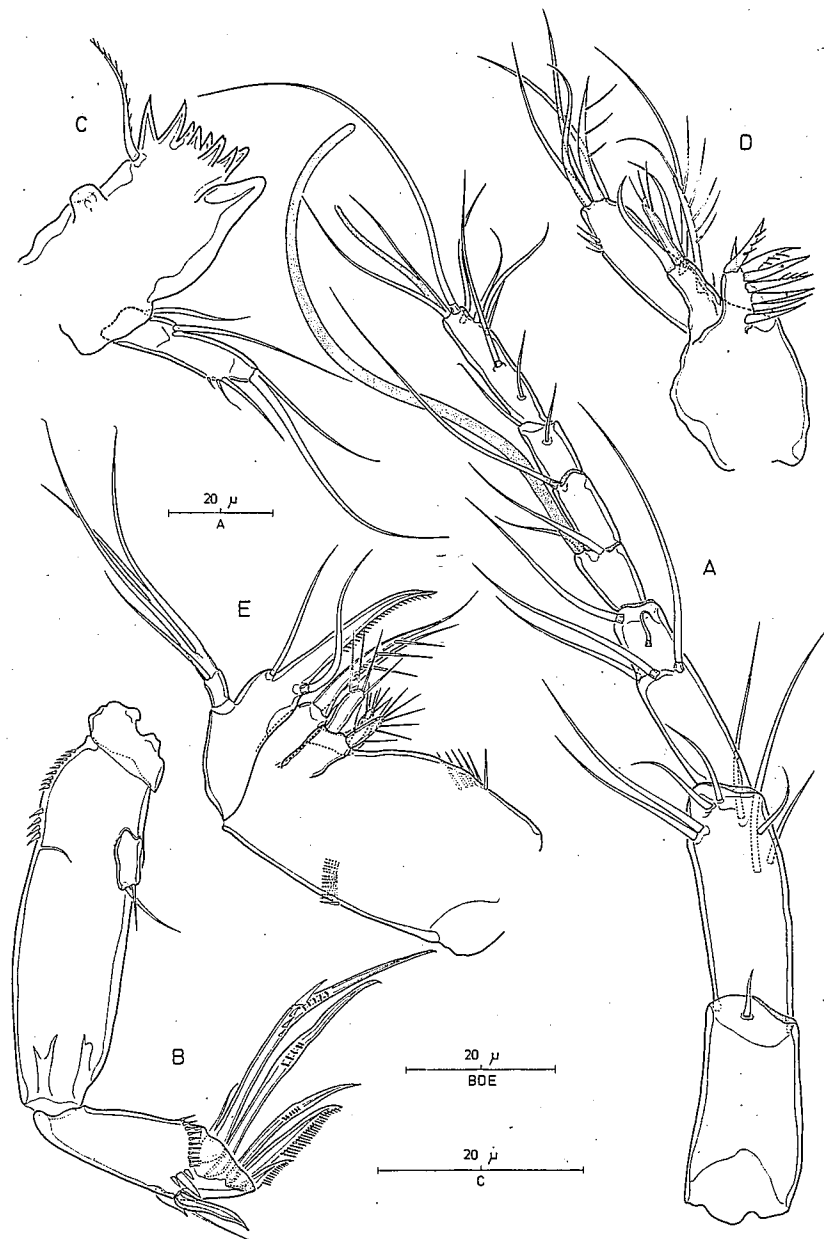


Fig. 5. — *Leptastacus kwintei* sp. nov. A. Antennule, ♀; B. Antenna; C. Mandible; D. Maxillula; E. Maxilla.

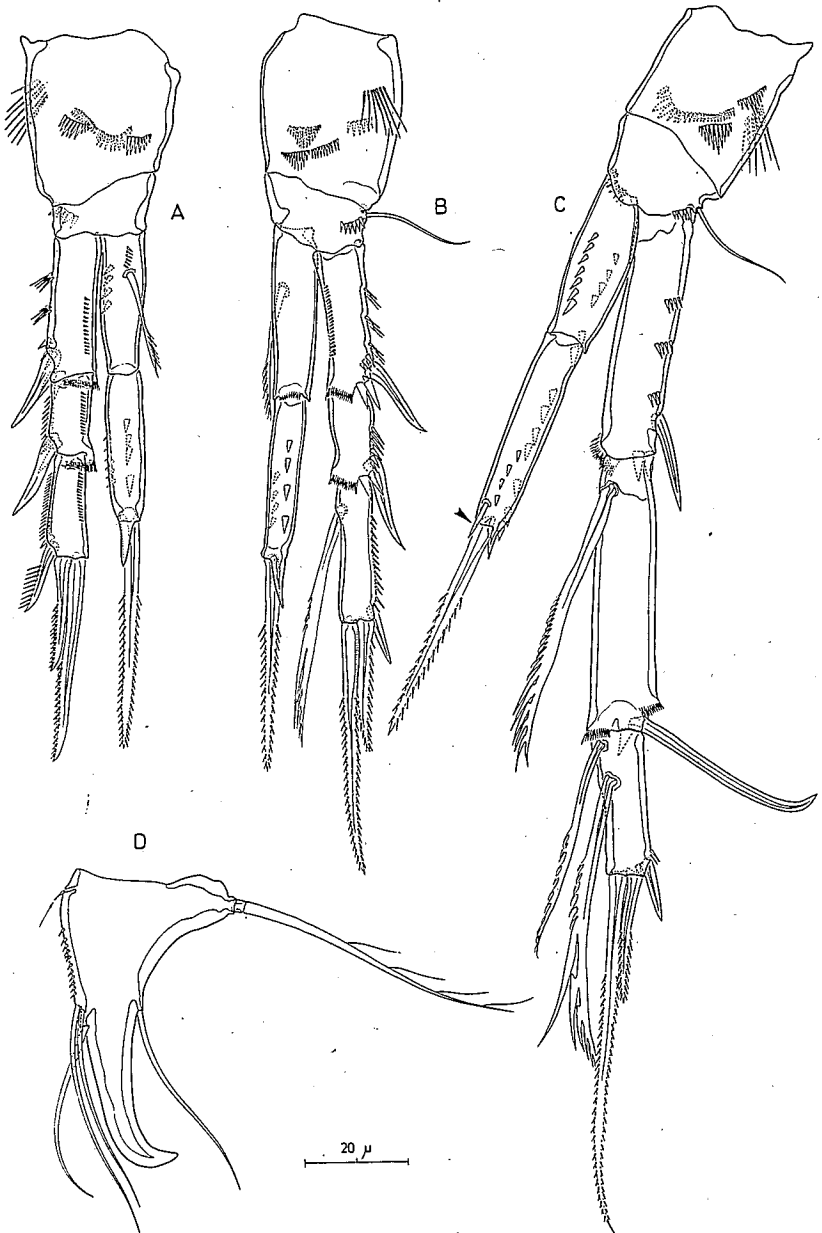


Fig. 6. — *Leptastacus kwintei* sp. nov. A. P2 ; B. P3 ; C. P4 ; D. P5, ♀.

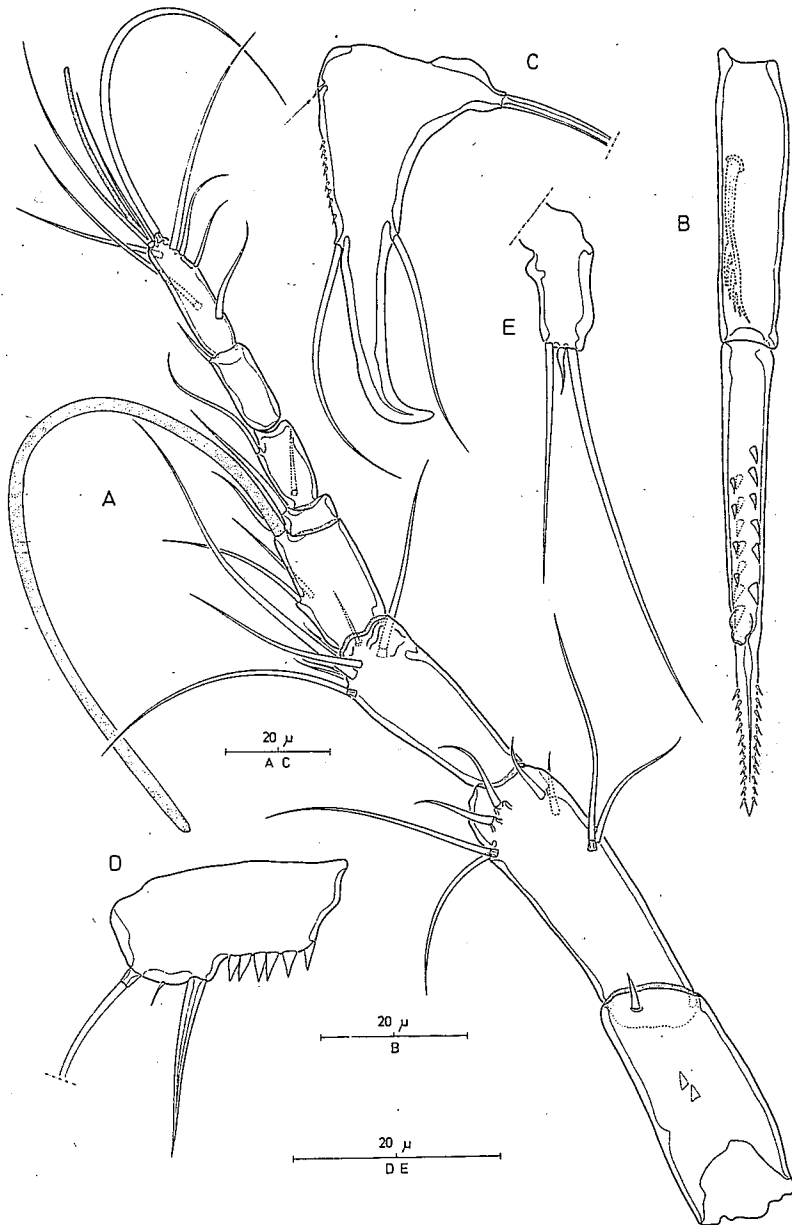


Fig. 7. — *Leptastacus kwintei* sp. nov. A. Antennule, ♂; B. Endopod P3, ♂; C. P5, ♂; D. P6, ♂; E. P6, ♀.

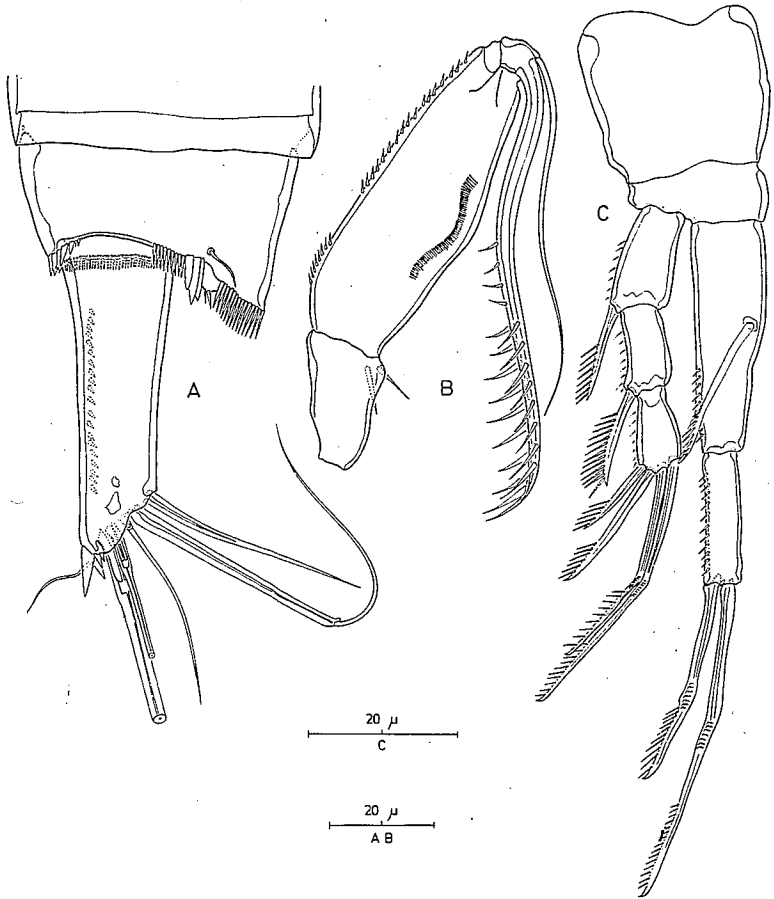


Fig. 8. — *Leptastacus kwintei* sp. nov. A. Anal somite and caudal ramus, lateral view; B. Maxilliped; C. P1.

spinules along outer margin. Third exopodal segment with 2 unipinnate spines, and 2 geniculate setae, innermost of which longest; outer margin with some spinules. Endopod about 1.4 times as long as exopod. First endopodal segment 1.7 times as long as distal one; ratio of length to width (measured proximally) 3.25; with 1 pectinate seta on inner margin and spinules on distal outer margin. Second endopodal segment more slender than preceding one, with continuous spinular row along outer margin and 2 geniculate setae distally.

Thoracopods 2-4 (P2-P4) (Figs. 6A-C) with strongly developed coxae which are heavily ornamented on both anterior and posterior surfaces. Basis of P3-P4 with outer seta. Inner seta of proximal endopodal segments P2-P3, middle exopodal segment P4 and distal exopodal segment P3-P4 pectinate. Proximal endopodal segment P4 without inner seta. Distal endopodal segment of P3 with only 1 well developed spine; second one presumably represented by small spinous process arising from distal margin. Outer exopodal spine of middle segment P4 exceeding third segment, recurved at tip. Inner terminal spine of third exopodal segment P2-P4 not modified. Length: width ratio of P2 endopod 8.6. Length: width ratio of distal endopodal segment P4 5.0.

Seta and spine formulae as follows:

	Exopod	Endopod
P2	0.0.021	1.010
P3	0.0.121	1.010
P4	0.1.221	0.1*10

[\* dwarfed seta]

Thoracopod 5 (P5) (Fig. 6D). Exopod and baseoendopod confluent; represented by a triangular plate, ending in a spinous distal process recurved at tip. Ratio of length to width (measured proximally) 2.0. Inner margin spinulose; with 1 vestigial seta proximally (arrowed in Fig. 6D) and 3 closely set slender setae midway the margin. Outer margin distinctly concave, with 2 setae in total; basal seta bi-articulated at base and plumose along distal half, second one long and naked, situated at about middle margin; vestigial seta absent.

Thoracopod 6 (P6) represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 1 minute seta flanked by 2 long setae (Fig. 7E).

*MALE*. Body length including rostrum and caudal rami: 415-450  $\mu$ m. General body shape, colour, ornamentation and sensillar pattern as in female. Sexual dimorphism in antennule, third, fifth and sixth thoracopods and in genital segmentation.

Antennule (Fig. 7A) 8-segmented, slender; haplocer; geniculation located between segments 6 and 7. First segment as in the female; second segment longest, approximately 3 times as long as wide, with 8 setae in distal third; third segment incorporating small ancestral segment XIII (see Huys & Boxshall, 1991), with 8 setae in total; fourth segment with 2 slender setae at about middle anterior margin, and with an aesthetasc (length: 145  $\mu\text{m}$ ) and a slender seta at the antero-distal corner; fifth segment small, with 1 seta; sixth and seventh segments with 2 and 1 seta(e), respectively; terminal segment with 9 setae and apical trifurcate seta being made up of a slender short aesthetasc (length 37  $\mu\text{m}$ ) and 2 setae.

Third thoracopod (P3) (Fig. 7B). Protopod and exopod as in female. Endopod 2-segmented; distal segment with 3 spinular rows and produced into bipinnate process (homologous to distal seta in female) distally and smaller secondary, lobate process at the anterior surface (presumably homologous to the spinous process found in the female).

Fifth thoracopod (P5) (Fig. 7D). Baseoendopod and exopod confluent, forming elongate triangular plate ending in a distal spinous process recurved at tip. Inner margin spinulose in proximal half, furnished with vestigial seta proximally and with slender seta at about midway. Outer margin with 2 setae, proximalmost (basal seta) bi-articulated at base and plumose along inner distal margin, second one situated at about half the length, vestigial seta absent.

Sixth thoracopod (P6) (Fig. 7D) represented by a rectangular plate and furnished with 3 setae; outermost (basal) seta longest and plumose along inner distal margin, middle one vestigial, inner one slender and bare; inner distal margin with row of coarse spinules.

#### VARIABILITY

No variability was observed among the specimens under study.

#### ETYMOLOGY

The species is named after the area where it was first discovered about 15 years ago, the Kwinte Bank off the Belgian coast.

#### REMARKS

The new species is reminiscent of *L. uncinatus* Cottarelli & Venanzetti, 1989 in the shape of the fifth legs in both sexes, but differs substantially in the length: width ratio of the caudal rami and the ornamentation of the anal operculum. The same characters can be applied to differentiate *L. kwintei* from



*L. macronyx* in addition to other features such as the length : width ratio of the proximal endopodal segment of P1, the endopod of P2 and the distal exopodal segment of P4. *L. kwintei* is restricted to the Southern Bight.

***Leptastacus coulli* sp. nov.**

(Figs. 9-12)

- 1932 *Leptastacus macronyx* (T. Scott) : C.B. Wilson, Bull. U.S. natn. Mus. 158 : 253-254, Fig. 166
- 1975 *Leptastacus macronyx* (T. Scott) : Coull & Vernberg, Mar. Biol. 32 : 290-292, Figs. 2, 4
- 1975 *Leptastacus macronyx* (T. Scott) : Vernberg & Coull, Cah. Biol. mar. 16 : 727, Fig. 5
- 1977 *Leptastacus macronyx* (T. Scott) : Coull & Fleegeer, Ecology 58 : 1137, 1141
- 1977 *Leptastacus macronyx* (T. Scott) : Ivester & Coull, Mikrofauna Meeresboden 61 : 141, Fig. 2
- 1980 *Leptastacus macronyx* (T. Scott) : Fleegeer, Estuar. coast. mar. Sci. 10 : 117
- 1980 *Leptastacus macronyx* (T. Scott) : Ivester, Bull. mar. Sci 30 : 637-642, Fig. 3, Tables 2, 4-5
- 1983 *Leptastacus macronyx* (T. Scott) : Montagna *et al.*, Estuar. cstl Shelf Sci. 17 : 387, Fig. 5c, Table 3
- 1985 *Leptastacus macronyx* (T. Scott) : Coull, Mar. Estuaries 8 : 88, 90, Table 1
- 1985 *Leptastacus macronyx* (T. Scott) : Coull & Dudley, Mar. Ecol. Prog. Ser. 24 : 220-224, 226-227, Figs. 2, 7, Tables 1, 2, 4
- 1985 *Leptastacus macronyx* (T. Scott) : Palmer & Gust, J. mar. Res. 43 : 202, Table 5

TYPE LOCALITY

North Inlet, South Carolina, U.S.A. ; 79° 10' W, 35° 20' N ; subtidal sand, 1 m below MLW.

MATERIAL EXAMINED

- From Prof. Dr B. C. Coull : 11 ♀♀, 6 ♂♂ (*locus typicus* ; leg. B.C. Coull ; collection date not specified) : holotype ♀ (dissected on 7 slides ; reg. no. 1992.1102), paratype ♂ (dissected on 7 slides ; reg. no. 1992.1103) and

4 other paratypes (2 ♀♀, 2 ♂♂ in alcohol; reg. no. 1992.1104) deposited in The Natural History Museum, London.

- National Museum of Natural History (Smithsonian Institution), Washington, D.C.: 1 ♀, 1 ♂ (alcohol preserved); Katama Bay, Martha's Vineyard, Woods Hole; from sand washings, 15 August 1927; leg. C. B. Wilson; reg. no. 63913.

#### DESCRIPTION

*FEMALE.* Body length 340-360  $\mu\text{m}$  ( $n = 6$ ), measured from the tip of the rostrum to the hind margin of the caudal rami.

Body slender, cylindrical, almost colourless and semi-transparent. Thoracic somites slightly broader than abdomen, no distinct separation between prosome and urosome, anal somite narrowest. Cephalothorax about 1.5 times as long as 2 succeeding somites combined. Genital double somite longest, 1/8 of total body length, indistinctly subdivided by an internal chitinous rib laterally. Anal somite shortest. Nauplius eye not observed.

Rostrum well developed, elongated, exceeding first antennular segment; tapering distally; tip pointing downwards; defined at the base; furnished with 2 delicate sensillae at one third distance from the tip.

Hyaline frill of body somites plain. Integument pitted.

Cephalic shield rectangular, about 1.5 times as long as greatest width. Anal somite with spinules at posterior ventral margin (Fig. 9C); outermost spinules coarsest. Anal operculum minutely denticulate (Fig. 9B) and flanked by 1 coarse spinule on either side.

Caudal rami divergent (Figs. 9B-C), about twice as long as maximum width. Each ramus with 2 spinular rows on inner ventrolateral margin; distal margin with few coarse spinules ventrally. Armature consisting of six setae (seta I missing); seta V strongly developed, without inner spinous process; seta VI delicate; seta VII bi-articulated at base; seta III composite with proximal part styliform and slightly longer than slender distal part.

Antennule (Fig. 10A) 7-segmented, slender; first segment long, with 1 spiniform seta distally and few spinules medially; second one longest (measured along anterior margin), approximately 3.1 times as long as greatest width, distal third with 8 setae, of which 5 are articulated at base; third segment second longest, with 5 setae in distal third, of which 3 are articulated; distal outer corner of fourth segment with long aesthetasc (length 55  $\mu\text{m}$ ) and 2 slender setae; fifth and sixth segments with 1 and 2 setae, respectively; seventh segment long and slender, with 9 setae [trifurcate one represents an aesthetasc (length 37  $\mu\text{m}$ ) confluent at base with 2 bare setae].

Antenna (Fig. 10B). Coxa small, unarmed. Allobasis about 2.8 times as long as maximum width; inner margin with 2 spinular rows; original

segmentation discernible by internal, transverse chitinous rib. Exopod (implanted at 1/5 of the allobasis length) 1-segmented, small, about 3 times as long as maximum width; with 1 long and 1 short seta apically. Endopod approximately 0.6 times the length of allobasis; distal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is fused at the base with a dwarfed seta and is ornamented with spinules around the geniculation; inner margin with 1 pinnate spine, 1 setule and an oblique spinular row.

Mandible (Fig. 10C). Coxa well developed; gnathobase with 1 thick, unidentate tooth dorsally, several smaller teeth medially and a unipinnate seta at the dorsal corner. Palp 2-segmented. Basis a rectangular segment with 1 seta at outer distal corner; endopod 2.3 times as long as basis, with a seta arising from a point a third the length of inner margin, and 1 subapical and 2 apical (confluent at the base) setae.

Maxillula (Fig. 10D). Praecoxa an elongate chitinous segment with anteriorly directed arthrite. Arthrite with 8 spines around the distal margin and 2 juxtaposed setules on the anterior surface. Coxal endite with a pinnate and a naked seta distally. Basis produced into a single, large, sub-cylindrical endite; distal armature consisting of 4 slender setae and 1 pinnate spine; anterior margin setulose. Endopod and exopod incorporated in the basis and represented by 2 long setae and 1 spinulose seta, respectively.

Maxilla (Fig. 10E). Syncoxa tapering distally, with one spinular row on middle outer margin and 2 endites medially; proximal endite shortest, with 1 apical and 2 subterminal short, modified spines; distal endite with 1 spinulose claw and 1 slender seta distally and 1 short, modified spine subterminally. Allobasis tapering into a strong, recurved claw with 2 setae at base. Endopod well developed, 2-segmented; proximal segment longest, with 1 outer seta; distal segment with 3 slender apical setae of which 2 fused at base.

Maxilliped (Fig. 9D). Syncoxa small, with few spinules at inner distal corner. Basis strongly developed, about 3 times as long as syncoxa; outer margin with discontinuous spinular row; middle inner margin with a short row of denticles. Endopod represented by minute segment bearing a strong long claw, of which distal two-thirds (last third 2-sided) spinulose, and a long, slender seta.

Labrum strongly developed; as for type species (see also Huys, 1987: Figs. 3B<sub>1</sub>-B<sub>2</sub>).

Natatorial legs (Figs. 11A-D) with 3-segmented exopods; endopods 2-segmented, always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

Thoracopod 1 (P1) (Fig. 11A). Coxa well developed, no ornamentation observed. Basis slightly shorter than coxa, with some spinules on outer margin; inner and outer setae not present. First and second exopodal segments with 1 outer unipinnate spine and several spinules along outer margin. Third

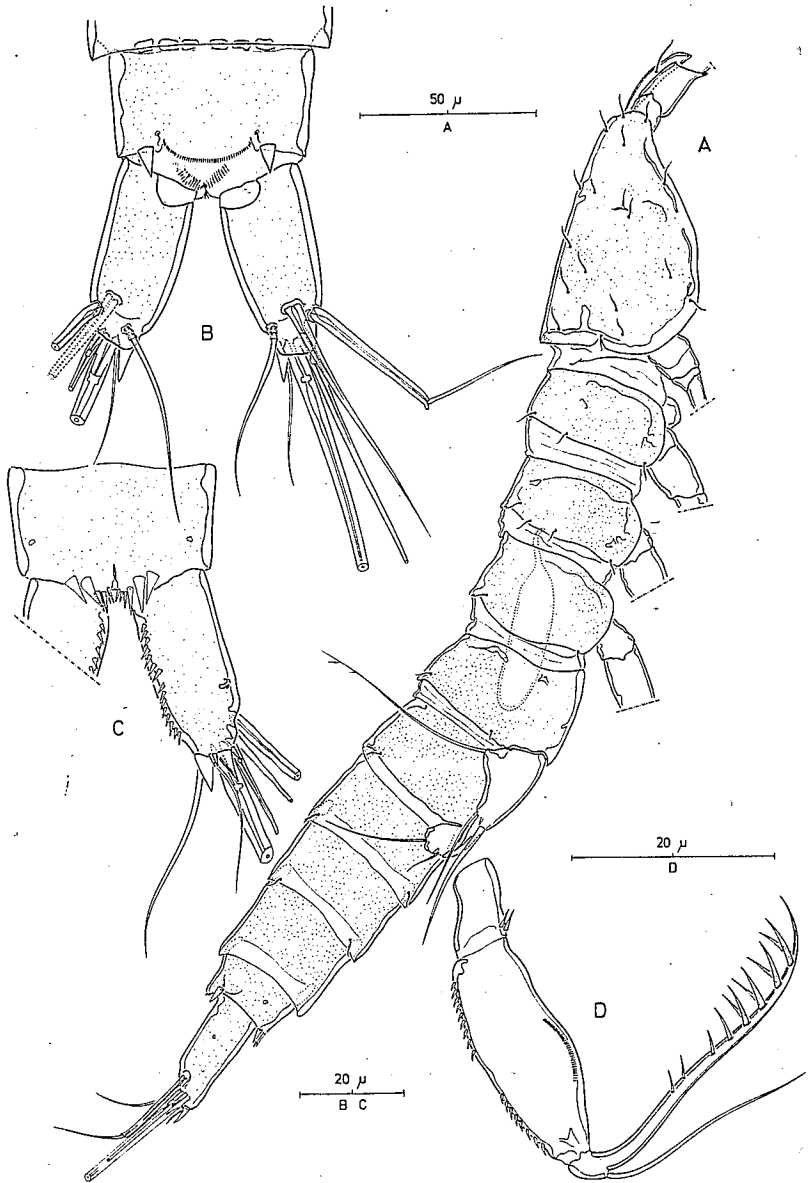


Fig. 9. — *Leptastacus coulli* sp. nov. A. Habitus ♂, lateral view; B. Anal somite and caudal rami, dorsal view; C. Same (right caudal ramus omitted), ventral view; D. Maxilliped.

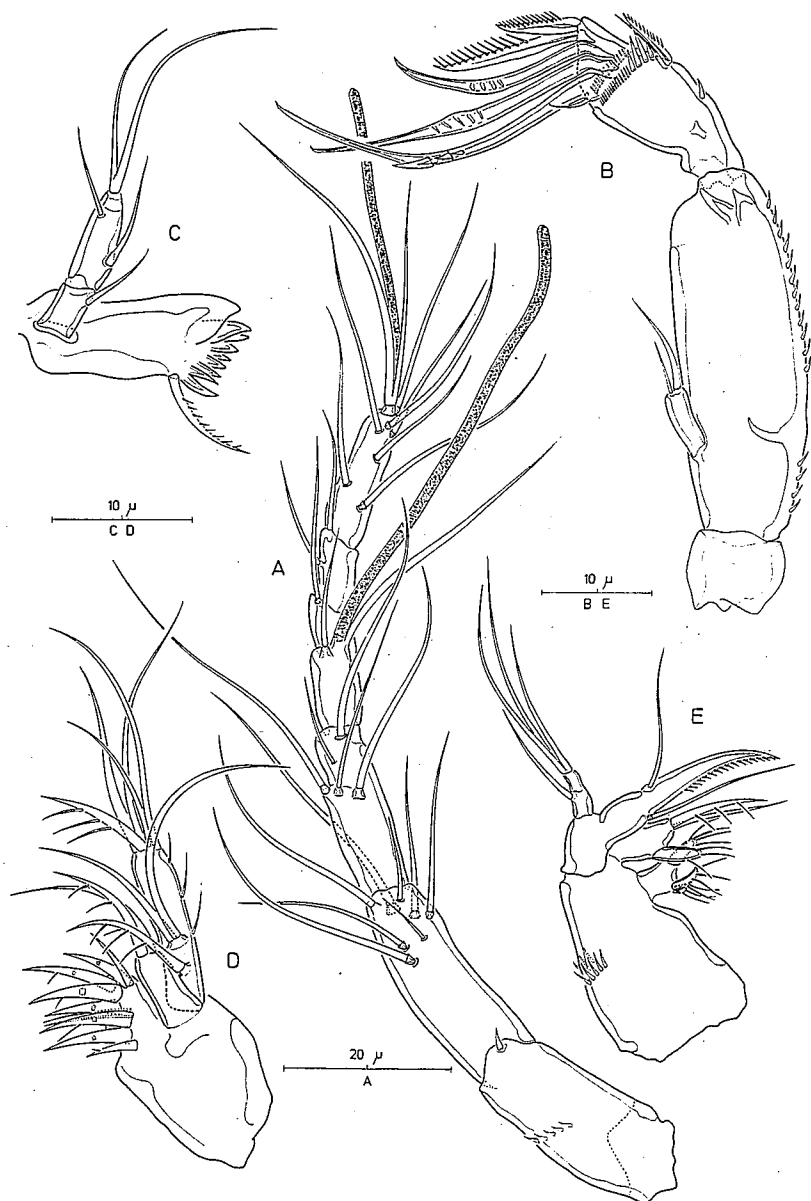


Fig. 10. — *Leptastacus coulli* sp. nov. A. Antennule ; B. Antenna ; C. Mandible ; D. Maxillula ; E. Maxilla.

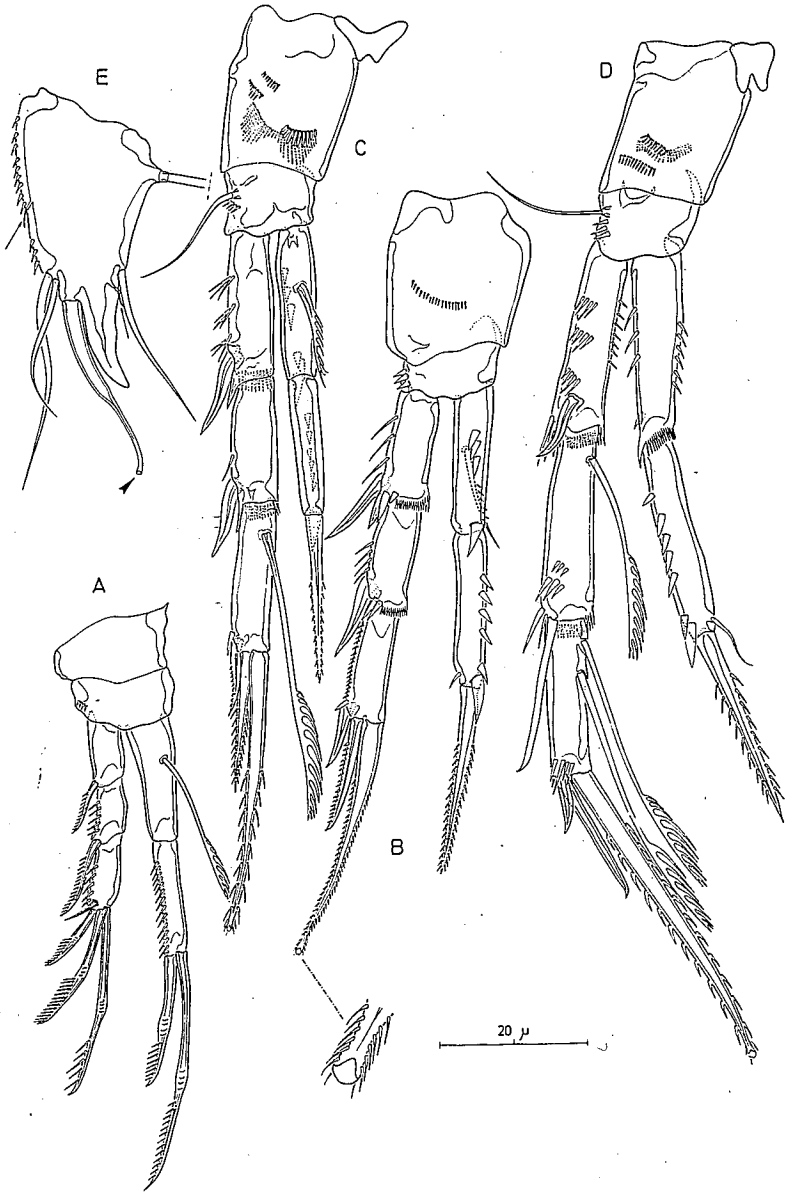


Fig. 11. — *Leptastacus coulli* sp. nov. A. P1 ; B. P2 ; C. P3 ; D. P4 ; E. P5, ♀.

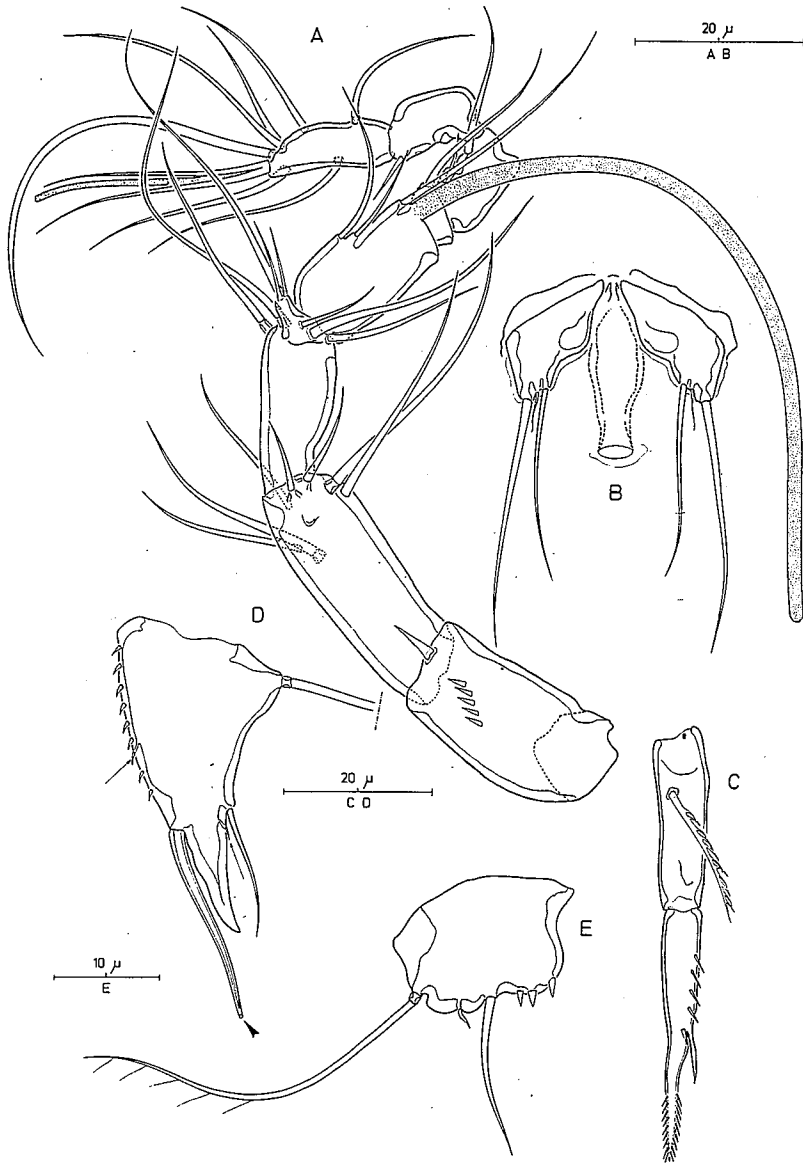


Fig. 12. — *Leptastacus coulli* sp. nov. A. Antennule, ♂; B. Genital complex, ♀; C. Endopod P3, ♂; D. P5, ♂; E. P6, ♂.

exopodal segment with 1 bare (?) and 1 unipinnate spine, and 2 geniculate setae, innermost of which longest; outer margin with some spinules. Endopod about 1.23 times as long as exopod. First endopodal segment as long as distal one; ratio of length to width (measured proximally) 2.85; with 1 pectinate seta on inner margin. Second endopodal segment more slender than preceding one, with continuous spinular row along outer margin and 2 geniculate setae distally.

Thoracopods 2-4 (P2-P4) (Figs. 11B-D) with strongly developed coxae. Basis of P3-P4 with outer seta. Inner seta of proximal endopodal segments P2-P3, middle exopodal segment P4 and distal exopodal segment P3-P4 pectinate. Proximal endopodal segment P4 without inner seta. Distal endopodal segment of P3 with only 1 well developed spine; second one presumably represented by small spinous process arising from distal margin (indicated by dotted line in Fig. 11C). Outer exopodal spine of middle segment P4 not exceeding third segment, recurved at tip. Inner terminal spine of third exopodal segment P2-P4 swollen and spatulate at the tip (see inset Fig. 11B). Length: width ratio of P2 endopod 8.1. Length: width ratio of distal endopodal segment P4 5.6.

Seta and spine formulae as follows:

	Exopod	Endopod
P2	0.0.021	1.010
P3	0.0.121	1.010
P4	0.1.221	0.1*10

[\* dwarfed seta]

Thoracopod 5 (P5) (Fig. 11E). Exopod and baseoendopod confluent; represented by a triangular plate, ending in a spinous distal process slightly bent apically. Ratio of length to width (measured proximally) 1.6. Inner margin spinulose; with 1 vestigial seta proximally (arrowed in Fig. 11E) and 3 closely set slender setae midway the margin; the distalmost of these setae is swollen in the proximal half and spatulate at the tip (arrowed in Fig. 11E). Outer margin slightly concave, with 3 setae in total; basal seta bi-articulated at base and plumose along distal half, second one long and naked, situated at about middle margin and closely set to third vestigial seta (arrowed in Fig. 11E).

Thoracopod 6 (P6) represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 1 minute seta flanked by 2 long setae (Fig. 12B). Copulatory pore large.

*MALE.* Body length including rostrum and caudal rami: 325  $\mu$ m. General body shape, colour, ornamentation and sensillar pattern as in female (Fig. 9A). Sexual dimorphism in antennule, third, fifth and sixth thoracopods and in genital segmentation.



Antennule (Fig. 12A) 8-segmented, slender; haplocer; geniculation located between segments 6 and 7. First segment as in the female; second segment longest, approximately 2.6 times as long as wide, with 7 setae in distal third; third segment incorporating small ancestral segment XIII (see Huys & Boxshall, 1991), with 8 setae in total; fourth segment with 2 slender setae at about middle anterior margin, and with an aesthetasc (length: 84  $\mu\text{m}$ ) and a slender seta at the antero-distal corner; fifth segment small, with 1 seta; anterior margin of sixth segment thickly chitinous, with 2 setae; anterior margin of seventh segment with 2 concave chitinous formations and 1 at antero-distal corner; terminal segment with 9 setae with apical trifurcate seta made up of a slender short aesthetasc (length 28  $\mu\text{m}$ ) and 2 setae.

Third thoracopod (P3) (Fig. 12C). Protopod and exopod as in female. Endopod slightly more robust in appearance; distal segment produced into bipinnate process (homologous to distal seta in female) distally and smaller secondary process at the anterior surface (presumably homologous to the spinous process found in the female).

Fifth thoracopod (P5) (Fig. 12D). Baseoendopod and exopod confluent, forming elongate triangular plate ending in a distal spinous process pointing slightly outwards. Inner margin spinulose, furnished at 1/3 the length with vestigial seta and at 2/3 the length with long swollen seta which is spatulate at the tip. Outer margin with 3 setae, proximalmost (basal seta) bi-articulated at base and plumose along inner distal margin, second one situated at about 3/5 the length, third one vestigial and closely set to preceding one.

Sixth thoracopod (P6) (Fig. 12E) represented by a rectangular plate, slightly concave along the inner margin and furnished with 3 setae; outermost (basal) seta longest and plumose along inner distal margin, middle one vestigial, inner one slender and bare; inner distal margin with few spinules.

Spermatophore (Fig. 9A); length about 50  $\mu\text{m}$ .

#### VARIABILITY

In some specimens (3 ♀♀, 1 ♂) the outer margin of the distal endopodal segment P1 showed 2 spinular rows rather than a single continuous row. The inner distal margin of the male sixth legs may have a variable number of spinules.

#### ETYMOLOGY

In honour of Prof. Dr Bruce Coull (Belle W. Baruch Institute, South Carolina) distinguished for his numerous experimental and in-depth analyses of the meiofauna at the type locality for nearly 20 years.

## REMARKS

The present description of *L. coulli* agrees with Wilson's (1932) illustrations given for the *L. macronyx* material collected from Martha's Vineyard. It was mainly this publication and lack of attention to the original descriptions that have misled Coull and co-workers. Re-examination of Wilson's material did not reveal any discrepancies (even not in body length though Wilson states 450-550  $\mu\text{m}$ ) with the specimens from South Carolina upon which the foregoing description is based. Hence, one can safely state that *L. coulli* displays an almost continuous distribution along the Atlantic seaboard of the United States from Woods Hole in the north to at least Georgetown in the south. *L. coulli* is the dominant sand site species in the North Inlet estuary (Coull & Dudley, 1985). The records from the North Carolina continental shelf (Coull, 1971a, 1972) are unconfirmed.

*L. coulli* belongs to the group of species (*L. spatuliseta* Mielke, 1982; *L. pygmaeus* sp. nov) that exhibits modified setae on the distal exopodal segment of the P2 to P4, and on the fifth legs. The inner terminal seta is distinctly swollen and tapers to a spatulate tip. SEM has revealed that these setae possess a small pore at the apex and the swollen nature of these appendages suggests that they may release secretory substances. Such "tubular setae" were also found on the caudal rami in various other leptastacid genera (*Arenocaris*, *Psammastacus*, ...), but only in the genera *Leptastacus* and *Arenocaris* they are present on the swimming legs.

*L. coulli* can be differentiated from *L. spatuliseta* by the shorter caudal rami, the presence of a coarse spinule on either side of the anal operculum, and the shape of the fifth legs. The North American species (340-360  $\mu\text{m}$ ) is also distinctly smaller than the animals from the Galapagos (490-500  $\mu\text{m}$ ). The major differences between *L. coulli* and *L. pygmaeus* sp. nov. are found in the anal operculum, the shape of the distal process on the fifth legs and body length.

***Leptastacus pygmaeus* sp. nov.**

(Figs. 13-15)

1977 *Leptastacus macronyx* (T. Scott) : Van Damme & Heip, Mathematisch Model Noordzee 7 : 40

## TYPE LOCALITY

North Sea, Southern Bight, off Hoek van Holland; 52°16'29" N, 03°32'14" E; collected 19 June 1984 (leg. R. Huys); subtidal sandy sediment (median grain size : 331  $\mu\text{m}$ ; 99.9% sand and 0.07% silt), depth 26 m.

## MATERIAL EXAMINED

- From *locus typicus*: 3 ♀♀, 5 ♂♂; holotype ♀ (dissected on 7 slides; reg. no. 1992.1105), paratype ♂ (dissected on 7 slides; reg. no. 1992.1106) and 2 other paratypes (1 ♀, 1 ♂ in alcohol; reg. no. 1992.1107) deposited in The Natural History Museum, London.
- North Sea, Southern Bight, off Hoek van Holland; 52°16'15.5" N, 03°21'10" E; collected 19 June 1984 (leg. R. Huys); subtidal sandy sediment (median grain size: 292 µm; 99.87% sand and 0.13% silt), depth 31 m: 1 ♀, 1 ♂.
- From Dr D. Van Damme: 3 slide preparations labelled *L. macronyx*; North Sea, Southern Bight, no other locality data specified.

## DESCRIPTION

**FEMALE.** Body length 245-255 µm (n = 3), measured from the tip of the rostrum to the hind margin of the caudal rami.

Body slender, cylindrical, almost colourless and semi-transparent. Thoracic somites slightly broader than abdomen, no distinct separation between prosome and urosome, anal somite narrowest. Cephalothorax about twice as long as 2 succeeding somites combined. Genital double somite longest, 1/8 of total body length, indistinctly subdivided by an internal chitinous rib laterally. Anal somite shortest. Nauplius eye not observed.

Rostrum well developed, elongated, exceeding first antennular segment; tapering distally; tip pointing downwards; defined at the base; furnished with 2 delicate sensillae at one third distance from the tip.

Hyaline frill of body somites plain. Integument pitted.

Cephalic shield rectangular, about 1.5 times as long as greatest width. Anal somite with spinules at posterior ventral margin (Fig. 13C); outermost spinules coarsest. Anal operculum minutely denticulate (Fig. 13B), not flanked by other spinules.

Caudal rami divergent (Figs. 13B-C), about twice as long as maximum width. Each ramus with 1 spinular row on inner ventrolateral margin; distal margin with few coarse spinules ventrally. Armature consisting of six setae (seta I missing); seta V strongly developed, without inner spinous process; seta VI delicate; seta VII bi-articulated at base; seta III composite with proximal part styliform and slightly longer than slender distal part.

Antennules through maxillipeds as in *L. coulli*.

Natatorial legs (Figs. 14A-D) with 3-segmented exopods; endopods 2-segmented, always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

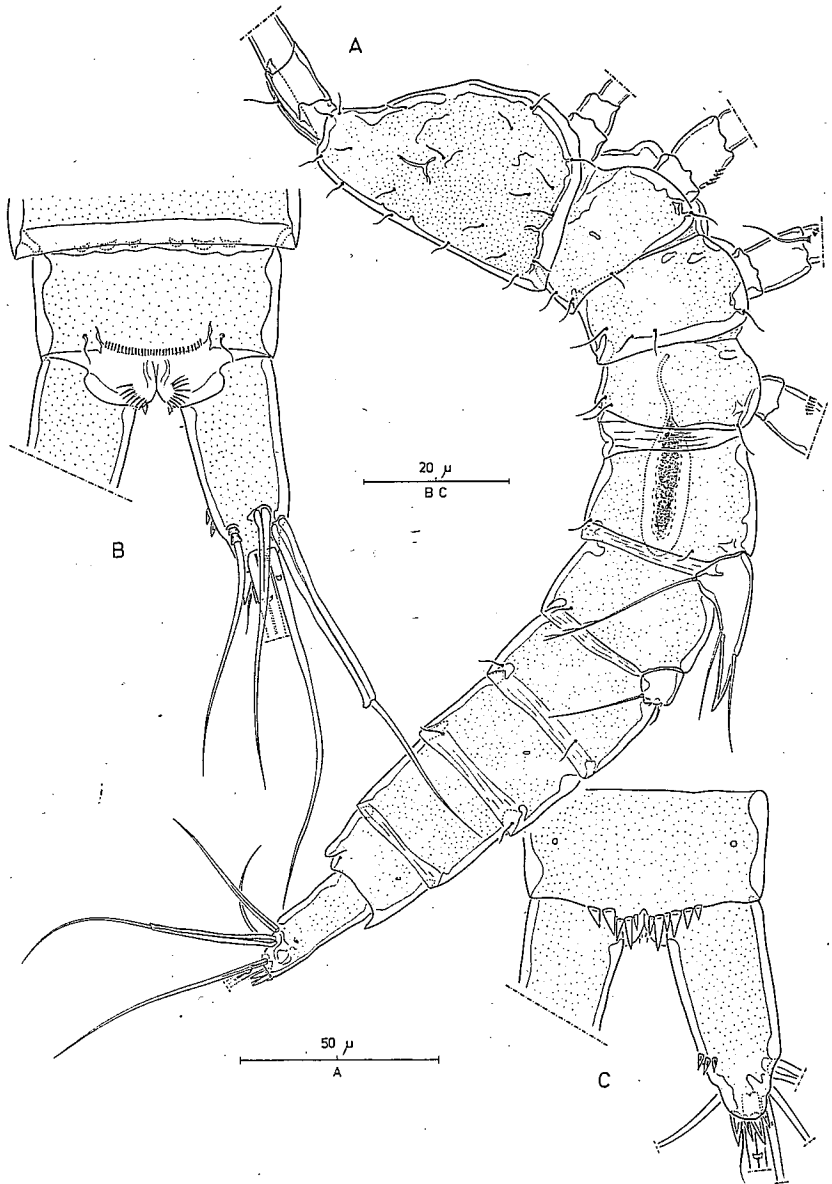


Fig. 13. — *Leptastacus pygmaeus* sp. nov. A. Habitus ♂, lateral view ; B. Anal somite and right caudal ramus, dorsal view ; C. Anal somite and left caudal ramus, ventral view.

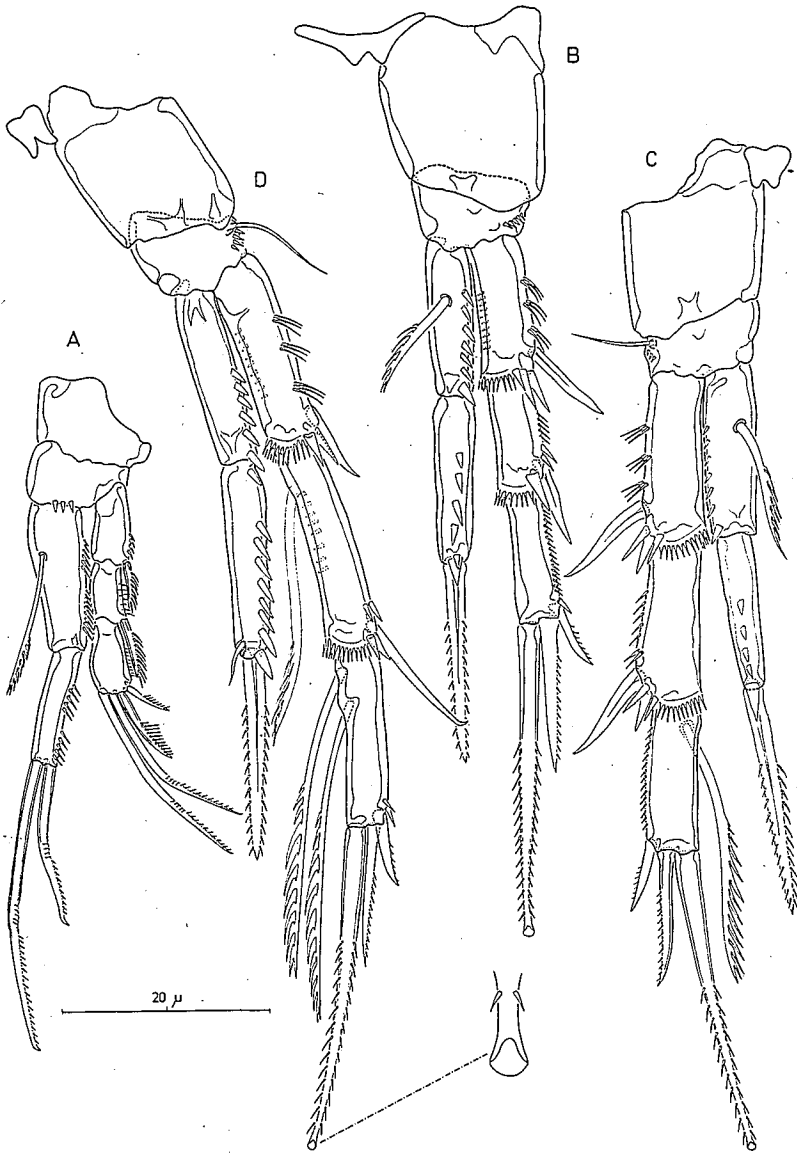


Fig. 14. — *Leptastacus pygmaeus* sp. nov. A. P1. ; B. P2 ; C. P3 ; D. P4.

Thoracopod 1 (P1) (Fig. 14A). Coxa well developed, no ornamentation observed. Basis slightly shorter than coxa, with some spinules near articulation with endopod; inner and outer setae not present. First and second exopodal segments with 1 outer unipinnate spine and several spinules along outer margin. Third exopodal segment with 2 unipinnate spines, and 2 geniculate setae, innermost of which longest; outer margin with some spinules. Endopod about 1.25 times as long as exopod. First endopodal segment 1.24 times as long as distal one; ratio of length to width (measured proximally) 2.75; with 1 pectinate seta on inner margin and 2 spinular rows on outer margin. Second endopodal segment more slender than preceding one, with 2 spinular rows along outer margin and 2 geniculate setae distally.

Thoracopods 2-4 (P2-P4) (Figs. 14B-D) with strongly developed coxae. Basis of P3-P4 with outer seta. Inner seta of proximal endopodal segments P2-P3 and distal exopodal segment P3-P4 pectinate. Proximal endopodal segment P4 without inner seta. Distal endopodal segment of P3 with only 1 well developed spine; second one presumably represented by small spinous process arising from distal margin. Outer exopodal spine of middle segment P4 not exceeding third segment, recurved at tip. Inner terminal spine of third exopodal segment P2-P4 swollen and spatulate at the tip (see inset Fig. 14D). Length : width ratio of P2 endopod 8.6. Length : width ratio of distal endopodal segment P4 4.9.

Seta and spine formulae as follows :

	Exopod	Endopod
P2	0.0.021	1.010
P3	0.0.121	1.010
P4	0.1.221	0.1*10

[\* dwarfed seta]

Thoracopod 5 (P5) (Fig. 15B). Exopod and baseendopod confluent; represented by a triangular plate, ending in a spinous distal process slightly bent apically. Ratio of length to width (measured proximally) 1.9 - 2.0. Inner margin spinulose; with 1 vestigial seta proximally (arrowed in Fig. 15A) and 3 closely set slender setae midway the margin; the distalmost of these setae is spatulate at the tip (arrowed in Fig. 15A). Outer margin slightly concave, with 3 setae in total; basal seta bi-articulated at base and plumose along distal half, second one long and naked, situated at about middle margin and closely set to third vestigial seta (arrowed in Fig. 15A).

Thoracopod 6 (P6) represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 1 minute seta flanked by 2 long setae.

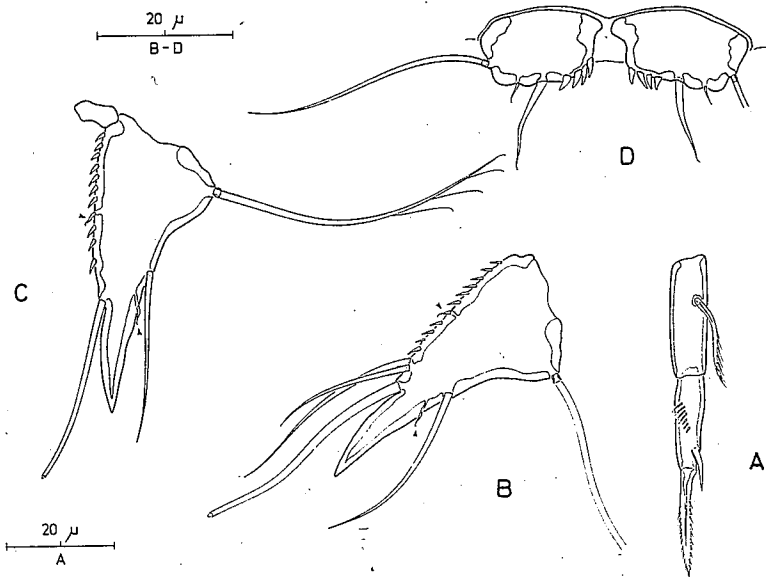


Fig. 15. — *Leptastacus pygmaeus* sp. nov. A. Endopod P3, ♂; B. P5, ♀; C. P5, ♂; D. P6, ♂.

**MALE.** Body length including rostrum and caudal rami: 235  $\mu\text{m}$ . General body shape, colour, ornamentation and sensillar pattern as in female (Fig. 13A). Sexual dimorphism in antennule, third, fifth and sixth thoracopods and in genital segmentation.

Antennule as in *L. coulli*.

Third thoracopod (P3) (Fig. 15A). Protopod and exopod as in female. Endopod 2-segmented; distal segment produced into bipinnate process (homologous to distal seta in female) distally and smaller secondary process at the anterior surface (presumably homologous to the spinous process found in the female).

Fifth thoracopod (P5) (Fig. 15C). Baseoendopod and exopod confluent, forming elongate triangular plate ending in a distal spinous process pointing slightly outwards. Inner margin spinulose, furnished at 1/3 the length with vestigial seta and at 2/3 the length with long seta which is spatulate at the tip. Outer margin with 3 setae, proximalmost (basal seta) bi-articulated at base and plumose along inner distal margin, second one situated at about midway, third one vestigial and closely set to preceding one.

Sixth thoracopod (P6) (Fig. 15D) represented by a rectangular plate, slightly concave along the inner margin and furnished with 3 setae; outermost

(basal) seta longest and plumose along inner distal margin, middle one vestigial, inner one slender and bare; inner distal margin with few coarse spinules.

Spermatophore (Fig. 13A); length about 50  $\mu\text{m}$ .

#### VARIABILITY

Slight variability was noticed in the number of spinules on the male sixth legs.

#### ETYMOLOGY

The species name is derived from the Latin *pygmaei*, meaning dwarf and refers to the small body size.

#### REMARKS

*L. pygmaeus* is the smallest representative of the genus. A recent survey of the North Sea meiobenthos has shown it to be a common species in the Southern Bight. It was often found to co-occur with *L. laicaudatus*. *L. coulli* and *L. pygmaeus* are obviously very closely related (see above). Their differences have already been discussed under *L. coulli*.

#### ***Leptastacus corsicaensis* sp. nov.**

(Figs. 16-19)

#### TYPE LOCALITY

Bay of Calvi, Corsica, Mediterranean; in washings of *Posidonia oceanica* (L.) Delile, taken by SCUBA diving at 4 m depth; leg. C. Héip & L. Thielemans; May 1985.

#### MATERIAL EXAMINED

From *locus typicus*: 2 ♀♀ and 1 ♂; holotype ♀ (dissected on 7 slides; reg. no. 1992.1108), paratype ♂ (dissected on 7 slides; reg. no. 1992.1109) and 1 other paratype (♂ in alcohol; reg. no. 1992.1110) deposited in The Natural History Museum, London.

#### DESCRIPTION

**FEMALE.** Body length 780  $\mu\text{m}$ , measured from the tip of the rostrum to the hind margin of the caudal rami.



Body slender, cylindrical, almost colourless and semi-transparent. Thoracic somites slightly broader than abdomen, no distinct separation between prosome and urosome, anal somite narrowest. Cephalothorax slightly longer than 2 succeeding somites combined. Genital double somite longest, 1/8 of total body length, indistinctly subdivided by an internal chitinous rib laterally. Anal somite shortest. Nauplius eye not observed.

Rostrum well developed (Fig. 17A), elongated, not exceeding first antennular segment; tapering distally; tip pointing downwards; defined at the base; furnished with 2 delicate sensillae at one third distance from the tip.

Hyaline frill of body somites plain. Integument smooth.

Cephalic shield rectangular, about 1.5 times as long as greatest width. Anal somite with spinules at posterior ventral margin (Fig. 19B); outermost spinules coarsest. Anal operculum with numerous spinules decreasing in size abaxially (Fig. 19A) and flanked by conspicuous spinular row consisting of large spinules decreasing in size abaxially.

Caudal rami divergent (Fig. 19A-B), about 7.5 times as long as maximum width. Each ramus with continuous spinular row on inner ventrolateral margin; distal margin with few coarse spinules ventrally. Armature consisting of six setae (seta I missing); seta V strongly developed, with inner spinous process; seta VI delicate; seta VII bi-articulated at base; seta III composite with proximal part styliform and slightly longer than slender distal part.

Antennule (Fig. 17A) 7-segmented, slender; first segment long, with 1 spiniform seta distally and few spinules medially; second one longest (measured along anterior margin), approximately 3 times as long as greatest width, distal third with 8 setae; third segment second longest, with 5 setae in distal third, of which 3 are articulated at the base; anterodistal corner of fourth segment with long aesthetasc (length 100  $\mu\text{m}$ ) and 2 slender setae; fifth and sixth segments with 1 and 2 setae, respectively; seventh segment long and slender, with 9 setae [trifurcate one represents an aesthetasc (length 36  $\mu\text{m}$ ) confluent at base with 2 bare setae].

Antenna. Coxa with 1 spinule. Allobasis about 4.2 times as long as maximum width; inner margin with 3 spinular rows; original segmentation no longer discernible. Exopod (implanted at 1/5 of the allobasis length) 1-segmented, small, less than twice as long as maximum width; with 2 long setae apically. Endopod approximately 0.6 times the length of allobasis; distal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is fused at the base with a dwarfed seta and is ornamented with spinules around the geniculation; inner margin with 2 spines, 1 setule and a few spinules.

Mandible (Fig. 17B). Coxa well developed; gnathobase with 1 thick, unidentate tooth dorsally, several smaller, multicusped teeth medially and a unipinnate seta at the dorsal corner. Palp 2-segmented. Basis a rectangular segment with 2 confluent setae; endopod 1.75 times as long as basis, with

a seta arising from a point  $1/4$  the length of inner margin, and 2 subapical and 2 apical (confluent at the base) setae.

Maxillula (Fig. 17C). Praecoxa an elongate chitinous segment with anteriorly directed arthrite. Arthrite with 8 spines around the distal margin and 2 juxtaposed setules on the anterior surface. Coxal endite with a pinnate and a naked seta distally. Basis produced into a single, large, sub-cylindrical endite; distal armature consisting of 4 slender setae and 1 pinnate spine; anterior margin setulose. Endopod and exopod incorporated in the basis and represented by 2 long setae and 1 spinulose seta, respectively.

Maxilla. Syncoxa tapering distally, with spinular row on either medial and outer margin, and 2 medial endites; proximal endite shortest, with 1 apical and 2 subterminal short, modified spines; distal endite with 1 spinulose claw and 1 slender seta distally and 1 short, modified spine subterminally. Allobasis tapering into a strong, recurved claw with 2 (+ 1 vestigial) setae at base. Endopod well developed, 2-segmented; proximal segment longest, with 1 outer seta; distal segment with 3 slender apical setae of which 2 fused at base.

Maxilliped. Syncoxa small, with few spinules at inner distal corner. Basis strongly developed, about 3 times as long as syncoxa; outer margin with discontinuous spinular row; middle inner margin with a short row of slender spinules. Endopod represented by minute segment bearing a strong long claw, of which distal two-thirds (last third 2-sided) spinulose, and a long, slender seta.

Labrum strongly developed; as for type species (see also Huys, 1987: Figs. 3B<sub>1</sub>-B<sub>2</sub>).

Nataforial legs (Figs. 18A-D) with 3-segmented exopods; endopods 2-segmented, always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

Thoracopod 1 (P1) (Fig. 18A). Coxa well developed, with 3 spinular rows. Basis slightly shorter than coxa, with some spinules on outer margin; inner and outer setae not present. First and second exopodal segments with 1 outer unipinnate spine and several spinules along outer margin. Third exopodal segment with 2 unipinnate spines, and 2 geniculate setae, innermost of which longest. Endopod about 1.35 times as long as exopod. First endopodal segment 1.85 times as long as distal one; ratio of length to width (measured proximally) 4.2; with 1 pectinate seta on inner margin and few spinules on both inner and outer margins. Second endopodal segment more slender than proximal one, with 2 spinular rows along outer margin and 2 geniculate setae distally.

Thoracopods 2-4 (P2-P4) (Figs. 18B-D) with strongly developed coxae which are richly ornamented on both anterior and posterior surfaces. Basis of P3-P4 with outer seta. Inner seta of proximal endopodal segments P2-P4 absent; those of middle exopodal segment P4 and distal exopodal segment P3-P4 pectinate. Distal endopodal segment of P3 with only 1 well developed

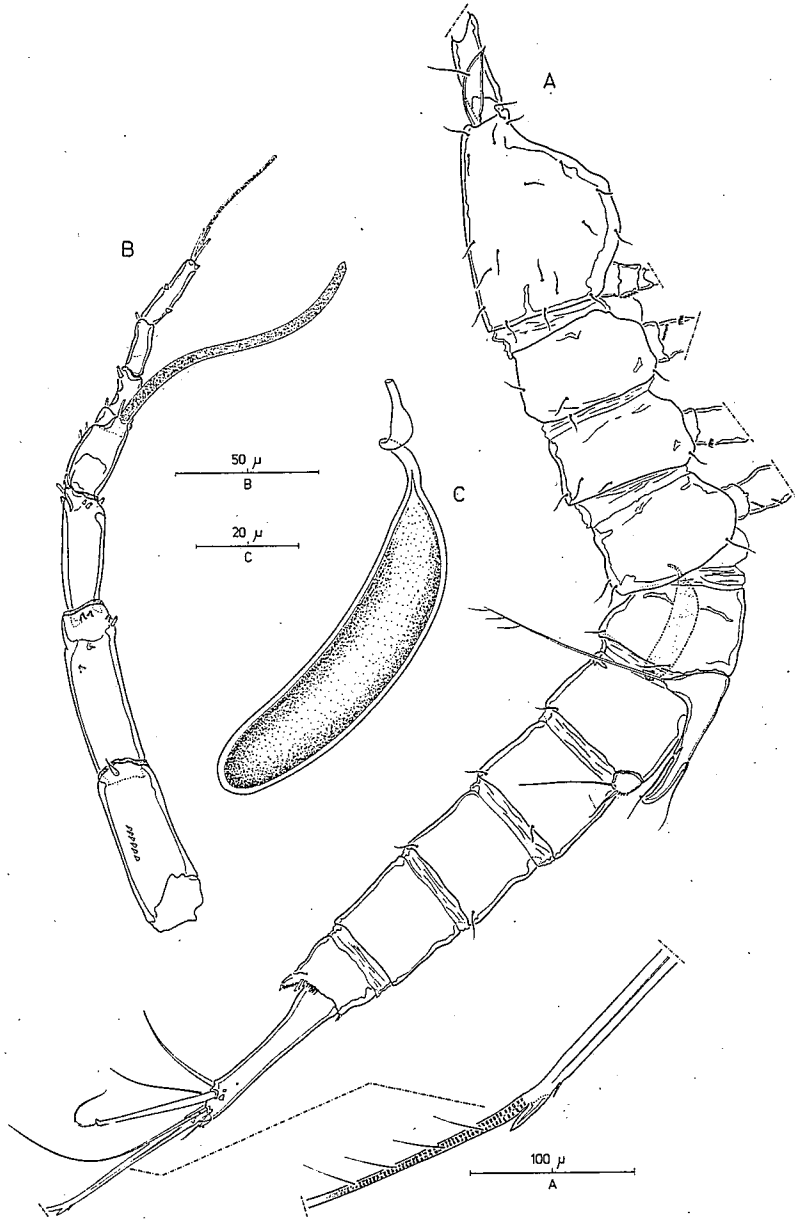


Fig. 16. — *Leptastacus corsicaensis* sp. nov. A. Habitus ♂, lateral view; B. Antennule, ♂ (only implantation sites of setae illustrated); C. Spermatophore.



Fig. 17. — *Leptastacus corsicaensis* sp. nov. A. Antennule; B. Mandible; C. Maxillula; D. Genital complex, ♀.

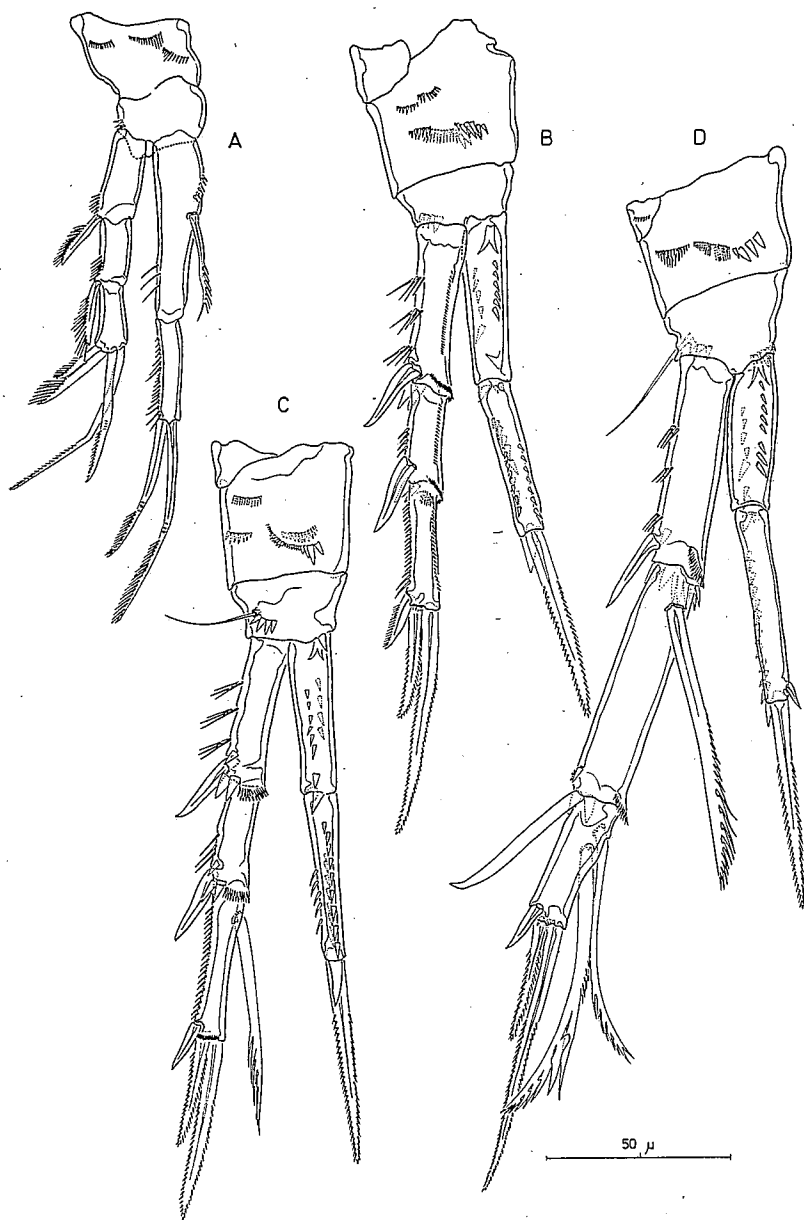


Fig. 18. — *Leptastacus corsicaensis* sp. nov. A. P1 ; B. P2 ; C. P3 ; D. P4.

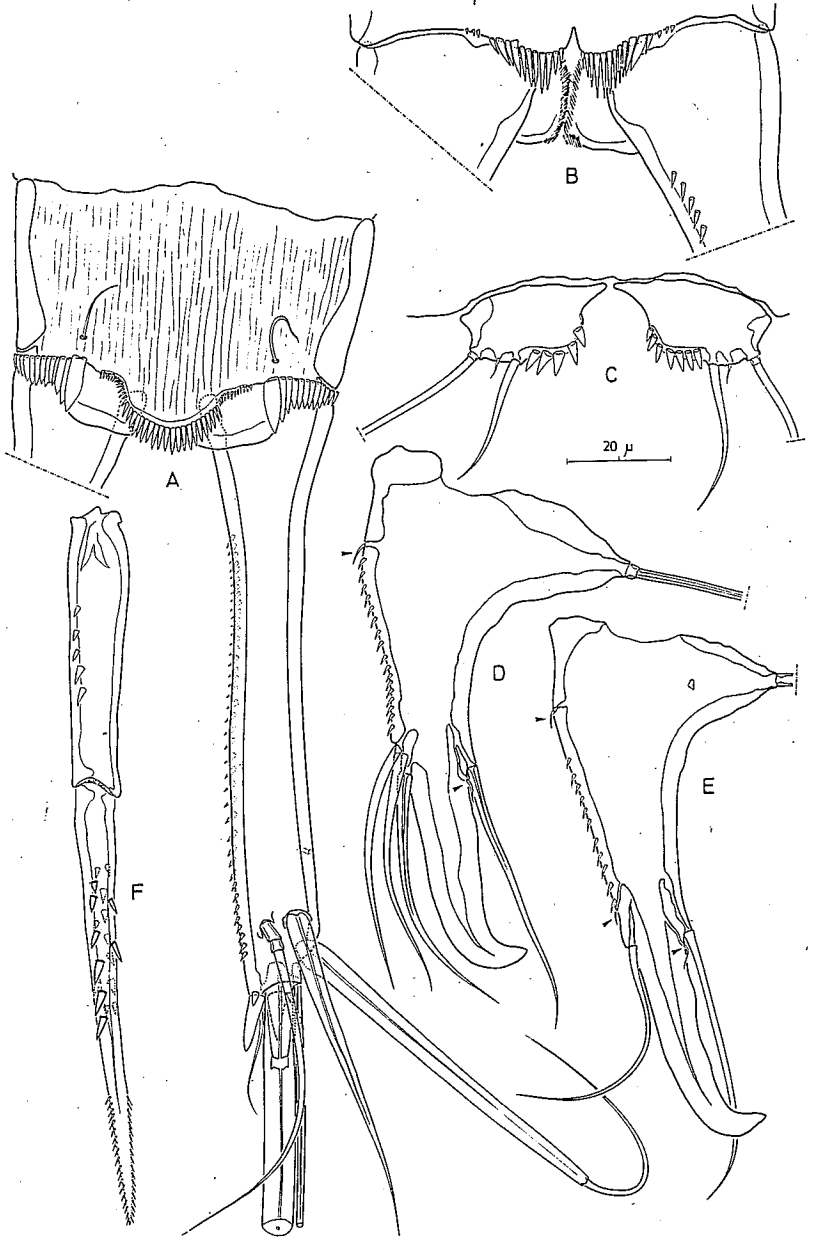


Fig. 19. — *Leptastacus corsicaensis* sp. nov. A. Anal somite and right caudal ramus, dorsal view; B. Rear margin of anal somite, ventral view; C. P6, ♂; D. P5, ♀; E. P5, ♂.

spine; second one presumably represented by small spinous process arising from distal margin. Outer exopodal spine of middle segment P4 exceeding third segment, recurved at tip. Inner terminal spine of third exopodal segment P2-P4 not modified. Length : width ratio of P2 endopod 10.9. Length : width ratio of distal endopodal segment P4 7.5.

Seta and spine formulae as follows :

	Exopod	Endopod
P2	0.0.021	1.010
P3	0.0.121	1.010
P4	0.1.221	0.1*10

[\* dwarfed seta]

Thoracopod 5 (P5) (Fig. 19D). Exopod and baseoendopod confluent; represented by a triangular plate, ending in a spinous distal process recurved at tip. Ratio of length to width (measured proximally) 1.8. Inner margin spinulose; with 1 vestigial seta proximally (arrowed in Fig. 19D) and 3 closely set slender setae midway the margin. Outer margin concave, with 3 setae in total; basal seta bi-articulated at base and plumose along distal half, second one long and naked, situated at about middle margin and closely set to third vestigial seta (arrowed in Fig. 19D).

Thoracopod 6 (P6) represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 1 minute seta flanked by 2 long setae (Fig. 17D). Copulatory pore large.

*MALE.* Body length including rostrum and caudal rami : 745  $\mu$ m. General body shape, colour, ornamentation and sensillar pattern as in female (Fig. 16A). Sexual dimorphism in antennule, third, fifth and sixth thoracopods and in genital segmentation.

Antennule (Fig. 16B) 8-segmented, slender; haplocer; geniculation located between segments 6 and 7. Armature pattern as for other species. Second segment longest, approximately 3.5 times as long as wide; fourth segment with 2 slender setae at about middle anterior margin, and with an aesthetasc (length : 98  $\mu$ m) and a slender seta at the antero-distal corner; terminal segment with 9 setae with apical trifurcate seta made up of a slender short aesthetasc (length 45  $\mu$ m) and 2 setae.

Third thoracopod (P3) (Fig. 19F). Protopod and exopod as in female. Endopod 2-segmented; distal segment ornamented with numerous spinules and produced into bipinnate process (homologous to distal seta in female) distally; no secondary process at the anterior surface (presumably homologous to the spinous process found in the female).

Fifth thoracopod (P5) (Fig. 19E). Baseoendopod and exopod confluent, forming elongate triangular plate ending in a distal spinous process recurved

at the tip. Inner margin spinulose, furnished at  $1/6$  the length with vestigial seta and with a second vestigial and 1 slender long seta at about midway the margin. Outer margin with 3 setae, proximalmost (basal seta) bi-articulated at base and plumose along inner distal margin, second one situated at about  $3/5$  the length, third one vestigial and closely set to preceding one.

Sixth thoracopod (P6) (Fig. 19C) represented by a rectangular plate, slightly concave along the inner margin and furnished with 3 setae; outermost (basal) seta longest and plumose along inner distal margin, middle one vestigial, inner one slender and bare; inner distal margin with a variable number of coarse spinules.

Spermatophore (Fig. 16C); length about 90  $\mu\text{m}$ .

#### VARIABILITY

Except for the spinulation on the male sixth thoracopods, no variability was noticed.

#### ETYMOLOGY

The species is named after Corsica.

#### REMARKS

*L. corsicaensis* shows clearcut differences with all other species of the genus. The L : W ratio of the caudal rami (7.5) is by far the highest found among the species currently allocated to the genus *Leptastacus* as it is re-defined in this paper. The species is also unique by the loss of the inner seta on the proximal endopodal segments of P2-P3. *L. corsicaensis* shows a certain resemblance in fifth leg structure with *L. uncinatus*, also described from the Mediterranean, however the new species is about twice as large as the Sardinian specimens.

#### Other material

##### I. Scilly Islands — University of London Sub-Aqua Club Expedition

Wells' material from the Scilly Islands (2 ♂♂, 2 ♀♀; reg. no. 1967.10.31.63) without doubt belongs to *Leptastacus laticaudatus*. Wells was probably misled by the shape of the distal process of the P5 which is completely rounded in his material rather than foot-shaped. However, Huys (1987) already pointed out the high variability found for this character.



## II. Klie's (1950) collections from Helgoland and Kiel Bay

Klie's collection at the Zoologisches Museum, Kiel includes 3 vials labelled *L. macronyx* (reg. nos Cop. 1916, Cop. 1922 and Cop. 2034). This material corresponds to his 1950 study conducted in the Kiel Bay and around Helgoland. The single female from Helgoland (St. I: S1) was dissected (Cop. 564) and belongs to *L. macronyx* (see above). All the other specimens (preserved in glycerin) were collected in the Kiel Bay (Gulstaf Flach and Vijsnäs Flach) and represent a mixture of *L. laticaudatus* and a second new species closely related to *L. rostrata* Nicholls, 1940. The *rostrata*-group will be raised to full generic status (see section 2.5. : *Schizothrix* gen. nov.).

## III. Coull's (1968, 1970) specimens from Bermuda

The material (8 ♀♀, 4 ♂♂) collected in Bermuda by Coull (his Castle Harbor Shallow site) and sent to me for re-examination does not correspond to *L. macronyx* nor to *L. coulli* but shows close similarities to *L. jenneri* Lindgren, 1975 which does not belong to the *macronyx*-group. Similarly, the 5 female specimens found among the material collected by Dr E. Gnaiger (University of Vienna) from Tucker's Town Beach represent a distinct species which is currently under study.

IV. *Leptastacus macronyx* from the Virgin Islands

The record of Hartzband & Hummon (1973) from Coki Bay, St Thomas (Virgin Islands) is in all probability wrong. It is unlikely that *L. macronyx* would display such a disjunct distribution pattern. The single damaged male from Nazareth Bay (18° 18.3' N, 64° 52.6' W; 2 m depth; median grain-size 730 µm; January 1970), St. Thomas listed as *Leptastacus* sp. in Coull (1971b) represents a distinct species but is in a too bad condition to be described accurately.

V. *Leptastacus macronyx* from Ghana (Chappuis & Rouch, 1961)

The only African record of *L. macronyx* is provided by Chappuis & Rouch (1961). The 2 female specimens collected from a sandy beach in the bay of Accra, Ghana clearly belong to a different species. Chappuis & Rouch (1961) list many "petites différences" with Scott's (1892) and Sars' (1911) descriptions, not the least the general structure of the caudal rami, and the setation of the second, third and fifth thoracopods. The authors abstained from establishing a new subspecies but even their concise description provides sufficient evidence that they were dealing with a species not related to the *macronyx*-group. A comparison of the Ghanese material with Mielke's (1982) excellent description of *L. dispinosus*-Mielke, 1982 from the Galapagos reveals a close resemblance in the caudal rami, the anal somite ornamentation and the fifth legs. The absence of the inner seta on the proximal endopodal segment

of P2 and P3 is another point of similarity. There is no doubt that Chappuis & Rouch' (1961) specimens belong to the *dispinosus*-group; this species complex will be elevated to generic rank (see section 2.5: *Belemnopontia* gen. nov.).

VI. *L. macronyx* and *L. macronyx* var. *pontica* Griga, 1964 from the Black Sea

The taxonomy of the Black Sea *Leptastacus* species is utterly confusing. Apostolov & Marinov (1988) list 3 species in their catalogue: *L. macronyx*, *L. laticaudatus* Nicholls f. *intermedius* Kunz, 1938 and *Leptastacus taurica* (Marinov, 1973)<sup>1</sup>.

Both Marinov (1971) and Apostolov & Marinov (1988) give illustrations of what they consider to be *L. macronyx*. Marinov's poor drawings give only the barest minimum of information to allow inclusion of his specimens in the genus *Leptastacus*, and make reliable identification virtually impossible. Apostolov and Marinov (1988) considerably fueled the taxonomic confusion by combining illustrations taken from Sars (1911) and original drawings (male fifth leg). It is therefore impossible to evaluate their identification and pending new material from the Bulgarian coast becomes available, we have to regard their records as doubtful.

The history of *L. taurica* (Marinov, 1973) starts with Griga's (1964) description of *L. macronyx* var. *pontica*. Griga's illustrations of the caudal rami and the endopod of P3 (distal segment with 2 setae) already suggests that the species does not belong to the *macronyx*-group as defined by Huys (1987). The same species was also recorded by Apostolov (1970, 1971). In his catalogue of the Black Sea harpacticoids (1972), Apostolov synonymised Griga's species with *L. rostratus* Nicholls, 1940? and apparently listed it a second time under *L. macronyx*. Marinov (1973) also synonymised *L. macronyx* var. *pontica*, however, with a new subspecies which he described as *L. rostratus* Nicholls subsp. *taurica* n. subsp. Finally Geddes (1981) raised the latter subspecies to *L. taurica* Marinov, 1973. From this sequence of nomenclatorial events it is clear that the latter species name has no right of existence. Marinov (1973) unjustly treated Griga's subspecies as a senior synonym, and therefore the correct name should be *Leptastacus ponticus* Griga, 1964. This species will be allocated to the new genus *Schizothrix* gen. nov. (see section 2.5.)

The status of *L. laticaudatus* Nicholls f. *intermedius* Kunz, 1938 was already discussed by Huys (1987).

### Zoogeographical considerations

The present revision of *L. macronyx* proves its alleged amphi-atlantic distribution to be erroneous. This pattern mainly resulted from lack of attention

<sup>1</sup> Apostolov & Marinov (1988) erroneously cited the author's name in parentheses.

to structural details, yet also from the ignorance of the unexpected diversity generated by multiple speciation events in interstitial habitats. *L. macronyx* is not a Pan Atlantic species, and a survey of the North Sea meiobenthic harpacticoids showed that it is distributed only in a limited area of the North Sea. This is far from an amphi-oceanic distribution and the question arises whether such restricted geographical patterns correlate well with other interstitial copepods. Wells' (1986) following statement is relevant to this question: "Interstitial species, however, tend to show a higher degree of local endemism (76%) than primarily epibenthic or phytal species (63% and 68% respectively). None are truly cosmopolitan, though a few do have a rather wide distribution."

*L. macronyx* is not an isolated case; the literature on interstitial harpacticoids abounds with examples of presumed amphi-Atlantic species. In the Leptastacidae, for example, a similar controversy exists over the distribution of *Paraleptastacus spinicauda* and *P. holsaticus* on both sides of the Atlantic. Whybrew (1986) demonstrated that *P. holsaticus* from Lake Pontchartrain, Louisiana is a morphologically distinct species, clearly different from the European populations. Similarly, he showed that *P. spinicauda* is remarkably constant in most of its morphological characteristics and that it can co-exist with a number of other congeners at the same locality. As a result of his revision, Whybrew (1986) allocated Nicholls' (1935) specimens of *P. spinicauda* from Kames Bay to *P. kliei* and Mielke's (1975) material from the Isle of Sylt to *P. espinulatus*; he further described Moore's material of *P. spinicauda* from the Isle of Man under the new species *P. monensis* Whybrew, 1986. Whybrew did not examine American populations of *P. spinicauda*, but specimens from South Carolina (leg. B. C. Coull) donated to the present author proved upon inspection to belong to a different species.

The only truly amphi-Atlantic leptastacid is *L. rostratus* Nicholls, 1940 originally described from the shores of the St Lawrence River in Canada (Nicholls, 1940) and recently found near Tromsø, Norway (Geddes, 1981). Re-examination of Nicholls' type material (2 ♀♀ in alcohol) deposited in The Natural History Museum (reg. no. 1940.5.1.71-2) revealed no differences with Geddes' description. However, both are high latitude populations and as such the barrier separating them is much smaller than the width of the Atlantic Ocean. It should be emphasised that *L. rostratus* does not represent a genuine interstitial species since it is twice the size (1.5 mm!) of any other member of the family. Presumably it displays a circumpolar distribution pattern similar to that of certain interstitial Plathelminthes (Ax & Armonies, 1990).

American populations of interstitial harpacticoids are often considered subspecies of the European ones. This is apparent for the Paramesochridae with species such as *Paramesochra helgolandica galapagoensis* Mielke, 1984; *Diarthrodella parorbiculata pacifica* Mielke, 1984; and *Kliopsyllus constrictus pacificus* Mielke, 1984. Clearly, this attitude results from failure of comparing

the material with the original description, either because type material was no longer available, or the description itself did not provide the necessary detail. Comparison of Mielke's (1984a, b) excellent descriptions with North Sea specimens revealed many differences that extend far beyond the degree of intra-specific variation and would provide sufficient evidence to warrant Mielke's taxa specific rank. Therefore it is highly recommended to consult the type collection or topotypes first rather than just presenting a new forma, subspecies or morphotype.

Transallopatic species pairs on both sides of the Atlantic give strong support to Sterrer's (1973) Continental Drift hypothesis for the dispersal and speciation of meiofauna. Within the genus *Leptastacus* the *spatuliset*a-group represents such a transallopatic species group, encompassing three closely related species, *L. pygmaeus* (North Sea), *L. spatuliset*a (Galapagos) and *L. coulli* (North America). Sterrer's hypothesis (1973) would suggest extremely slow speciation (100-200 mill. years) (see Westheide & Rieger, 1987; Westheide, 1987). However, new evidence has been accumulated suggesting a "Thule land bridge" between Europe and North America much later than the time of formation of the Northern Atlantic. This trans-Atlantic bridge presumably reached across Scotland, the Faroes and Iceland to Greenland and broke up at the end of the Eocene (McKenna, 1972) or even still existed at the transition of the Pliocene to Pleistocene (Strauch, 1983). It implies that the divergence of the European (*pygmaeus*) and American species (stem species of *coulli* and *spatuliset*a) from the ancestral stock could have happened only a few million years ago. Ax & Schmidt (1973) suggested a similar maximal time available to the interstitial species for the colonisation of the sandy beaches of the Galapagos. This scenario of speciation would conform to the slight morphological differences found between *L. coulli* and *L. spatuliset*a since their separation from the North American stem species perhaps dates back to only 2 mill. years ago. As for many meiobenthic organisms, however, this scenario does not explain how the oceanic gap between the Galapagos and Central America could have been bridged.

## 2. A cladistic approach to the classification of the Leptastacidae Lang, 1948

### 2.1. HISTORY

According to Lang's (1948) monograph, three subfamilies can be recognised in the Cylindropsyllidae: the nominate subfamily Cylindropsyllinae Sars, the Leptastacinae and the Leptopontiinae. The discovery of *Sewellina reducta* prompted Krishnaswamy (1956) to establish the Psammopsyllinae.

Prior to Lang's revision, the genus *Leptastacus* had been invariably linked to the Canthocamptidae. This is not surprising since the latter family has always

been a taxonomic repository for loosely related genera drawn from different evolutionary lineages. Various authors failed to frame any precise family diagnosis which would unite the utterly diverse array of genera referred to. Sars (1911) assigned about 30 genera to the Canthocamptidae and briefly pointed to possible affinities with other families. Particularly, he reckoned a close relationship between *Leptastacus*, *Evansia* Scott (= *Evansula* Scott), *Pteropsyllus* Scott, *Tetragoniceps* Brady and *Phyllopodopsyllus* Scott, suggesting that they might better be combined in a separate family which "... in some respects would seem to approach that of the *Cylindropsyllidae*". This opinion was not adopted by Monard (1927) whose system displayed a perplexing artificiality. Monard satisfactorily isolated a new family, Ameiridae, from the Canthocamptidae but divided the remaining 26 genera into two groups, marine and freshwater. The marine series included *Leptastacus*, but also genera of the "modern" Cletodidae (*Leimia* Willey, *Hemimesochra* Sars, *Cletomesochra* Sars [= *Heteropsyllus* Scott]), Ameiridae (*Leptomesochra* Sars), Paramesochridae (*Leptopsyllus* Scott, *Paramesochra* Scott) and Tetragonicipitidae (*Tetragoniceps*, *Phyllopodopsyllus*, *Pteropsyllus*). Chappuis (1929), being influenced by Monard's (1927) division, established the subfamily Canthocamptinae to include the freshwater series, but did not diagnose it. He further recognised the extreme difficulties in laying down the precise limits of the marine subgroup, however, Pesta (1932) in adopting Chappuis' systematic arrangement, coined the name Halocanthocamptinae for the division containing the marine genera.

Gurney (1932) attempted to combine what he considered to be the best features of the previous systems and this approach generated six evolutionary series. Gurney abstained from proposing family or subfamily names but considered the series to be natural. He proposed the *Evansula* series for the three Scottian genera *Evansula*, *Leptopontia* and *Leptastacus*, however, simultaneously pointed to the uncertainty about the latter's position because of the peculiar structure of the mouth-parts.

In 1944 Lang arranged the *Cylindropsyllidae* into three series (Reihen) according to the structure of the maxilliped, the first leg and the nature of the sexual dimorphism. For the first time *Leptastacus* was considered to be part of a separate lineage, the *Leptastacus*-Reihe, containing also the newly described genera *Paraleptastacus* Wilson, *Psammastacus* Nicholls and *Arenocaris* Nicholls. Lang eventually abandoned the Reihe-concept in his monograph (1948) and elevated the series to subfamily rank. Lang's concept of the *Cylindropsyllidae* allowed for the recognition of distinct lineages within the family but the subsequent discovery of new types foreshadowed that some of them were less closely related than previously believed. Lang (1948 : 1214) himself had to admit that the three lineages must have been diverged very early in the evolution of the family. Inspection of the family diagnosis indicates that the three subfamilies are united merely on the base of shared plesiomorphic

features and that synapomorphies sustaining common ancestry are lacking altogether. The few advanced characters (e.g. antennary allobasis, maxillula without defined rami, ...) listed in the diagnosis are commonplace in other interstitial families and might be owed to convergence.

## 2.2. UPGRADING OF THE LEPTASTACINAE TO FAMILY RANK

A survey of the various leptastacinid genera shows that :

(1) Leptastacinae are extremely conservative morphologically. Examination of the cephalic appendages revealed an astounding similarity in armature and ornamentation among the 14 genera recognised in this paper. Slight deviations are found only in the antennary exopod, the mandibular palp and the maxillipedal syncoxa. Mesopsammic copepods usually become adapted to the interstitial habitat by miniaturization or by the adoption of vermiformity and gradual reduction of the swimming legs P2-P4 (cf. Paramesochridae, Cyclopininae). In the Leptastacinae, however, except for *Arenocaris bifida* Nicholls, 1935, all other representatives exhibit a remarkable consistency in natatory leg segmentation. This structural uniformity is in marked contrast to the plethora of morphological adaptations illustrated by the other subfamilies of the Cylindropsyllidae.

(2) Leptastacinae have unique cephalic appendages (Figs. 20A-B : *L. corsicaensis*) which are fully exposed in lateral aspect. Perhaps the most conspicuous feature of the leptastacinid cephalothorax is the massive, spiny labrum. It is a slightly posteriorly directed, extremely swollen expansion of the ventral cephalic surface, extending from behind the antennules. The labrum is basically tripartite with its steep anterior face leading to the median lobe which is ornamented with long, radiating spinules. The lateral portions are triangular lobes bearing posteriorly directed spinules and closing off the lateral margins of the preoral food chamber. The labrum possesses labral glands and paired dilator muscles which are concentrated in the voluminous proximal part. Contraction of these labral muscles may enlarge the preoral food chamber and perhaps the large oesophagus. The paragnaths are small lobes whose integument is continuous with the posterior wall of the preoral chamber. Their ornamentation consists of tiny, anteriorly directed spinules.

The maxillulae are unique within the harpacticoid realm because of the rotated praecoxal endite (arthrite). Unlike other harpacticoids, the angle at which the praecoxa and the remainder of the protopod are fused directs the arthrite anteriorly rather than medially. In lateral aspect (Fig. 20) the basis, coxa and arthrite can be observed in an overlapping sequence. The basis consists of an elongated segment in which the vestigial exopod (1 seta) and endopod (2 setae) are incorporated.

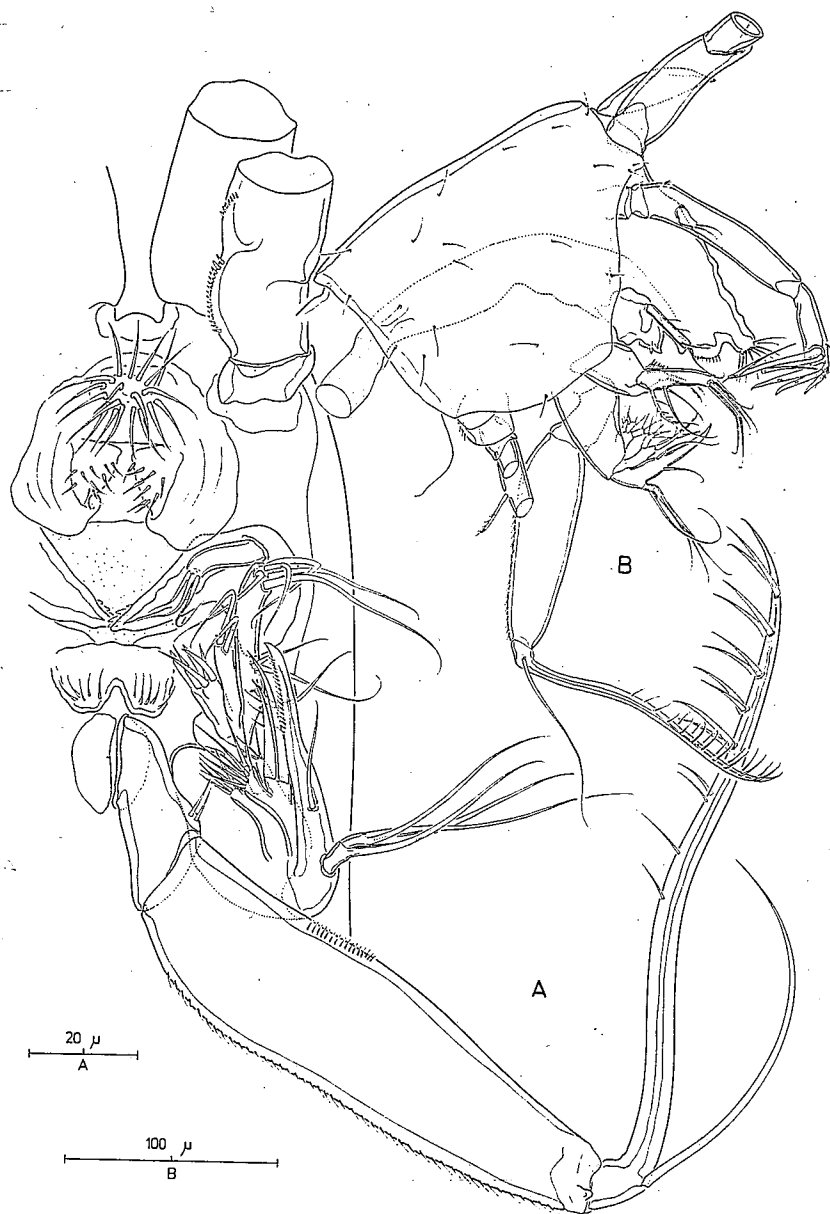


Fig. 20. — *Leptastacus corsicaensis* sp. nov. A. Ventral view of cephalic appendages showing relative positions. B. Same, lateral view.

The maxillae are very distinctive because of their elongated endopod and the conspicuous modified spines on the syncoxal endites (3 on proximal endite ; 1 on distal endite). Like the preceding limb, the endites are anteriorly directed towards the preoral chamber.

The maxillipeds of the Leptastacinae are without doubt the most powerful limbs involved in food manipulation. They comprise a syncoxa, a large basis and an undivided endopod bearing a long, bipinnate claw which is slightly sigmoid and accompanied by a long, slender seta. The maxillipedal syncoxae meet at the ventral midline and articulate with the cephalothorax immediately behind the paragnaths, however, anterior to the head-syncoxa joints of the maxillae. A wide range of movements is possible at the head-syncoxa joint but the protopod and the endopodal claw are anteriorly directed.

The peculiar arrangement and relative position of the respective appendages is in all probability related to the feeding strategy of the Leptastacinae. Live observations on *Paraleptastacus espinulatus* Nicholls, 1935 and *Arenocaris bifida* showed the presence of large glands which fill the anterior two-thirds of the caudal rami. These glands often display a dark colouration in live specimens (see also Krishnaswamy, 1957 : 99 and Wells & Rao, 1987 : 158). Similar paired reservoirs were observed in the anal somite and might even extend anteriorly in half of the penultimate somite. Both glands are connected via thin-walled ducts with distinct pores (evidently used to discharge the secretion) located on the lateral sides of the anal somite and the caudal rami. In the majority of the specimens long transparent strands were seen attached at the posterior end of the urosome and the caudal rami, although the exact attachment sites could not be determined. After being artificially dislodged these strands were stained histochemically to test for acid mucopolysaccharides (mucin) (Humason, 1979). A positive reaction with PAS and Alcian Blue was obtained. When crawling between the sand grains the animal at regular intervals stops swimming for a short period lasting between 5 and 15 sec. During this interval the urosome is flexed downward and forward at the prosome-urosome junction, bringing the caudal rami to lie in direct contact with the mouth parts and the maxillipeds. Meanwhile the antennae, maxillae and particularly the maxillipeds operate at a higher rate and seem to manipulate and draw the distal part of the mucus strands into the preoral food chamber. During this phase the labral muscles and the peristalsis of the foregut also operate at a higher frequency. Except for a few diatom remnants, inspection of the gut lumen revealed only an unidentifiable amorphous mass. However, interference contrast microscopy of various strands showed that high numbers of rod-shaped bacteria, small diatoms and unidentifiable debris were trapped on the mucus. Hicks & Grahame (1979) suggested that mucopolysaccharides may act as a rich and very rapidly decomposable organic substrate for colonization by marine prokaryotes. The use of mucus derived from pharyngeal and caudal



glands in "gardening" microflora has already been hypothesized for nematodes (Riemann & Schrage, 1978 ; Warwick, 1981) and thalestrid harpacticoids (Hicks & Grahame, 1979). It is likely that mucus-trap feeding may produce at least a secondary food-source for leptastacinid copepods since their preoral chamber and associated limbs are pre-adapted for handling large amounts of mucus. In another interstitial harpacticoid, *Cylindropsyllus laevis* Brady, 1880, the structure of the mouthparts and particularly the labrum (Huys, 1988a : Fig. 6C) are designed for rasping off diatoms from sand grains rather than for manipulating a mucilage food bolus.

There can be little doubt that the Leptastacinae deserve full family status. The current knowledge of the familial interrelationships in the Harpacticoida is insufficient to make judgements on the possible outgroup of the Leptastacidae. In addition, ontogenetic studies are scarce and often lack detail. The only reliable study of the naupliar development of Leptastacidae (Dahms, 1990) does not provide any important insights as to relationships. The nauplii of *Paraleptastacus brevicaudatus* Wilson, 1932 display many features which are not known from any other family thus far. A particular character present at the N II stage was also found in some freshwater Canthocamptidae and a single representative of the Parastenocarididae. The unique facies of the cephalothorax and its appendages is regarded as sufficient evidence for the monophyletic status of the Leptastacidae. A close relationship to any of the other constituent subfamilies of the Cylindropsyllidae is unlikely for a variety of reasons, not the least the differences encountered in the gross morphology of leg 1, the sexual dimorphism of the swimming legs and the female genital apparatus. It has to be remarked that the Cylindropsyllidae remains a polyphyletic group, even after excluding the Leptastacidae.

### 2.3. FAMILY DIAGNOSIS

Subclass	COPEPODA Milne Edwards, 1840
Infraclass	NEOCOPEPODA Huys & Boxshall, 1991
Superorder	PODOPLEA Giesbrecht, 1882
Order	HARPACTICOIDA Sars, 1903
Family	<b>LEPTASTACIDAE</b> Lang, 1948 <b>grad. nov.</b> syn. : <i>Leptastacus-Reihe</i> Lang, 1944

### DIAGNOSIS

Body slender, cylindrical. First pedigerous somite fused to cephalosome. Rostrum triangular or elongated, completely defined at the base. Female genital double-somite without external trace of original segmentation. Anal operculum well developed, rounded or with bifid process ; pseudoperculum absent. Caudal rami (sub)cylindrical, with 7 setae (V well developed, I vestigial or absent).

Sexual dimorphism in antennule, endopod P3 (enp-2 slightly modified or modified into apophysis; 2-segmented), P5, P6, and in genital segmentation; sometimes also in exopod P2, exopod P3, both rami of P4 and caudal rami.

Antennule slender, without projections; except for long plumose seta on segment 2 all setae naked; 7-segmented in female, with aesthetasc on segments 4 and 7; 8-segmented and modified (segment 4 slightly swollen, 2 segments distal to geniculation) in male with geniculation between segments 6 and 7 and with aesthetasc on segments 4 and 8; homology of male antennular segmentation: I, II-VIII, IX-XIII, XIV-XVII, XVIII, XIX-XX, XXI-XXII, XXIII-XXVIII. Antenna with allobasis (or basis and enp-1 incompletely fused) bearing unisegmented exopod with 1-3 setae; endopod with 6 distal elements (2 spines, 3 geniculate setae + 1 setule) and 1-2 spines (+ sometimes 1 setule) laterally. Labrum tripartite, extremely swollen and ventrally directed. Mandible with uniramous palp consisting of basis and 1-segmented endopod. Maxillule with rotated, anteriorly directed arthrite; coxal endite bisetose; unisetose exopod and bisetose endopod incorporated in basis bearing a single endite with 5 setae/spines. Maxillary syncoxa with 2 endites, proximal endite with 3 transformed spines, distal endite with 1 transformed and 2 simple spines; endopod elongated, 2-segmented, with 4 setae (1 on enp-1; 3 on enp-2). Maxilliped with syncoxa bearing 0-1 seta; basis asetose; endopod unisegmented with 1 long, sigmoid, bisetose claw and 1 slender seta.

P1 without outer seta or inner spine on basis; exopod 1- to 3-segmented; when 3-segmented: exp-2 without inner seta, exp-3 with 1-2 spines and 2 geniculate setae; endopod 3- or 2-segmented with elongated enp-1 bearing inner seta and short enp-2 (asetose) and enp-3 (2 geniculate setae); when 2-segmented enp-2 and enp-1 fused. P2-P4 with 3-segmented exopods and 2-segmented endopods (endopod P2-P3 of *Arenocaris* 1-segmented); spine- and seta formulae as follows:

	Exopod	Endopod
P2	0.0.[0-1]2[1-2]	[0-1].01[0-1]
P3	0.0.[0-1]2[1-2]	[0-1].01[0-1]
P4	0.[0-1].[1-2]2[1-2]	0.[0-1]10

Fifth pair of legs in both sexes not fused medially, usually defined at the base; exopod (max. 4 setae) and baseoendopod (max. 2 setae) separate or fused;

Female gonopores separate and each covered laterally by vestigial P6 bearing 1-3 setae; copulatory pore of moderate size. One egg-sac.

Male P6 at least slightly asymmetrical, with 1-3 setae each. Male grasping terminal setae of female's caudal rami during precopulatory phase.

Marine, freeliving.

## TYPE GENUS

*Leptastacus* T. Scott, 1906

## OTHER GENERA

*Paraleptastacus* Wilson, 1932 ; *Arenocaris* Nicholls, 1935 ; *Psammastacus* Nicholls, 1935 ; *Arenotopa* Chappuis & Rouch, 1960 ; *Minervella* Cottarelli & Venanzetti, 1989 ; *Neopsammastacus* Cottarelli & Venanzetti, 1989 ; *Psamathea* Cottarelli & Venanzetti, 1989 ; *Afroleptastacus* gen. nov. ; *Archileptastacus* gen. nov. ; *Belemnopontia* gen. nov. ; *Cerconeotes* gen. nov. ; *Membranastacus* gen. nov. ; *Schizothrix* gen. nov. ; *Sextonis* gen. nov.

## LEPTASTACIDAE INCERTAE SEDIS

*Leptastacus christelleae* Bodiou & Colomines, 1989

*Leptastacus naylori* McLachlan & Moore, 1978 (partim)

*Psammastacus acuticaudatus* Krishnaswamy, 1957

## 2.4. IMPORTANT EVOLUTIONARY TRENDS WITHIN THE LEPTASTACIDAE

As pointed out above, the gradual adaptation to life in the interstitial environment did not generate many morphological changes in the cephalic appendages and the swimming legs of the Leptastacidae. In contrast to the prosome, two interesting evolutionary trends are found in appendages of the urosome. The first involves the gradual reduction of the fifth leg, the second is related to the caudal rami and provides a good example of the detail that is necessary for accurate determination of homology. In addition, attention will be paid to the different kinds of sexual dimorphism within the family.

2.4.1. *Fifth thoracopod*

The maximum number of setae found on the P5 in any leptastacid is seven. These setae are numbered *a* to *g* in Fig. 21A and Fig. 24A. The ancestral state of the leptastacid fifth legs is illustrated by both sexes of *Paraleptastacus*. In most representatives of the latter (cf. *P. moorei* Whybrew, 1986 ; Figs. 24A-B) it consists of a biramous limb with a bisetose baseoendopod (setae *a* — *b*), and a tetrasetose exopod (setae *c* — *f*). The basal seta (*g*) is biarticulated at the base and stands at the outer distal corner of the baseoendopod. This primitive condition (Fig. 21 : state A) is further also found in both sexes of *Arenocaris reducta* and in females of *A. bifida* (Figs. 28C ; 31D).

The most common modification found in the family is the fusion of the exopod and the baseoendopod in both sexes (Fig. 21 : state B). The possession

of a uniramous P5 is regarded as a synapomorphy for the lineage grouping all leptastacid genera other than *Paraleptastacus*, *Arenocaris* and *Archileptastacus* gen. nov.<sup>2</sup> In the most primitive genera of this lineage such as *Sextonis* gen. nov. (see *Leptastacus laminaserrata* Mielke, 1985: Abb. 6C) all 7 setae are retained on a distinctly bilobed P5. Both exopod and baseoendopod are discernible as separate lobe-like extensions of the distal margin of the limb (Fig. 21: state B). The evolutionary reduction of these extensions has produced two types of fifth legs in which the fate of the exopod and the baseoendopod can be identified only by virtue of the setation elements *a* to *g*.

The first of these types is commonly found among the genera *Minervella*, *Neopsammastacus* and *Arenotopa* and represents a rectangular or (more typical) rounded plate bearing up to 7 setae along the distal margin (Fig. 43D).

The second type is more distinctive by its triangular shape caused by the formation of a distal spinous process, and is found in the genera related to *Leptastacus*. Identification of the homologies with the original exopodal and baseoendopodal lobes is difficult because of the apical extension distorting the setation pattern and because some of the setation elements are extremely reduced and for that reason frequently overlooked (see e.g. Fig. 3D). However, assessment of these homologies can be facilitated by taking into account ontogenetic evidence. Examination of the postembryonic development of the P5 in both sexes of *L. pygmaeus* (Fig. 22) revealed that the distal process is first formed in the copepodid IV stage. It is also showed that the setae located on either side of this process do not reflect the original baseoendopodal-exopodal pattern. Using the setae in the adult as reference points, it can be deduced that the distal process is a derivative from the limb portion homologous to the offset exopod in *Paraleptastacus*. More precisely, the projection is formed between setae *d* and *e* (Figs. 21, 22). The spatulate "tubular" setae of the *spatuliset*a-species group of *Leptastacus* gives support to this interpretation. Comparison of the fifth thoracopod with the P2 to P4 shows that the spatulate seta *d* is exopodal in origin (Figs. 11B-E), implying that the distal process in the fifth leg is flanked by exopodal setae only and does not coincide with the endopod-exopod boundary.

Scrutinous examination of the triangular P5 in the *Leptastacus*-group (= *Leptastacus*, *Schizothrix* gen. nov., *Belemnopontia* gen. nov., *Cerconeotes* gen. nov. and *Psammastacus*) revealed a clear evolutionary trend of gradual reduction and loss of various setation elements, ultimately leading to the strongly reduced trisetose lamella of *Psammastacus*, in which the triangular outline is no longer identifiable (Figs. 33D-E). The starting point in this morphocline

<sup>2</sup> *Archileptastacus* gen. nov. (Fig. 24C) also has a uniramous fifth leg but too many other characters point to an early divergence from the rest of the Leptastacidae and suggest that the uniramous P5 was acquired convergently earlier in the evolution of the family (see below).

is illustrated by *Leptastacus* and *Schizothrix* gen. nov. In the females all setae are identifiable but *a* and *e* are already vestigial (Fig. 21 : state C). The next step is the loss of one of the 3 setae (presumably *c*) typically grouped in a cluster along the inner margin in the previous genera (*Belemnopontia* gen. nov. ; Fig. 21 : state D). In *Cerconeotes* gen. nov. the vestigial setae *a* and *e* are lost as well (Fig. 21 : state E) retaining a total number of 4 setae. One of these setae is then lost in *Psammastacus*, but it is impossible to decide which elements were retained on this heavily reduced leg.

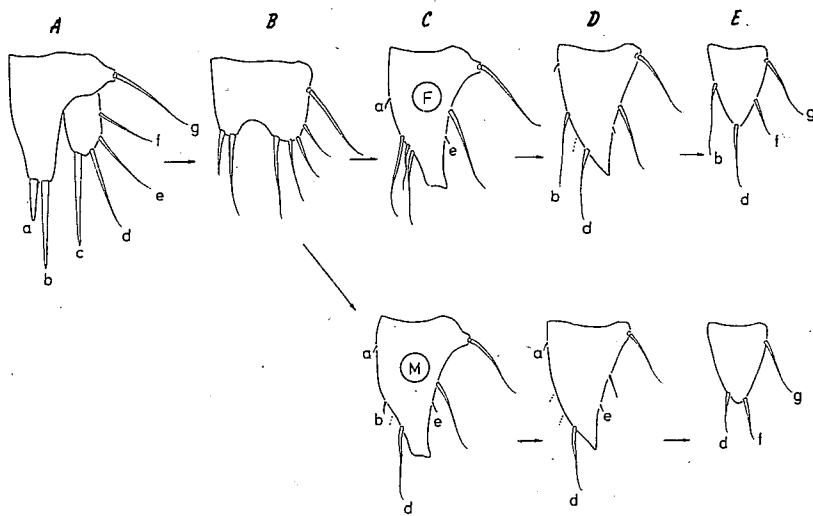


Fig. 21. — Evolutionary trends in P5 structure. A. Ancestral condition (*Paraleptastacus*); B. Bilobed condition (*Sextonis*); C. *Leptastacus*-condition; D. *Belemnopontia*-condition; E. *Cerconeotes*-condition (F : ♀, M : ♂). [For explanation see text.]

A similar trend is found in the males. In *Leptastacus* and *Schizothrix* gen. nov. setae *a*, *b* and *e* are vestigial and seta *c* is lost (Fig. 21 : state C). The same configuration is present in *Belemnopontia* gen. nov. except for the vestigial seta *b* which is lost (Fig. 21 : state D). The other vestigial setae (*a* and *e*) will finally be lost as well in *Cerconeotes* gen. nov. (Fig. 21 : state E). The remaining 3 setae are presumably homologous in *Cerconeotes* gen. nov. and *Psammastacus*. The evolutionary trend summarized in Fig. 21 excludes a neotenic origin for the reduced fifth legs in *Psammastacus* and *Cerconeotes*, however, gives support to the hypothesis that they are the ultimate product of a gradual reduction process.

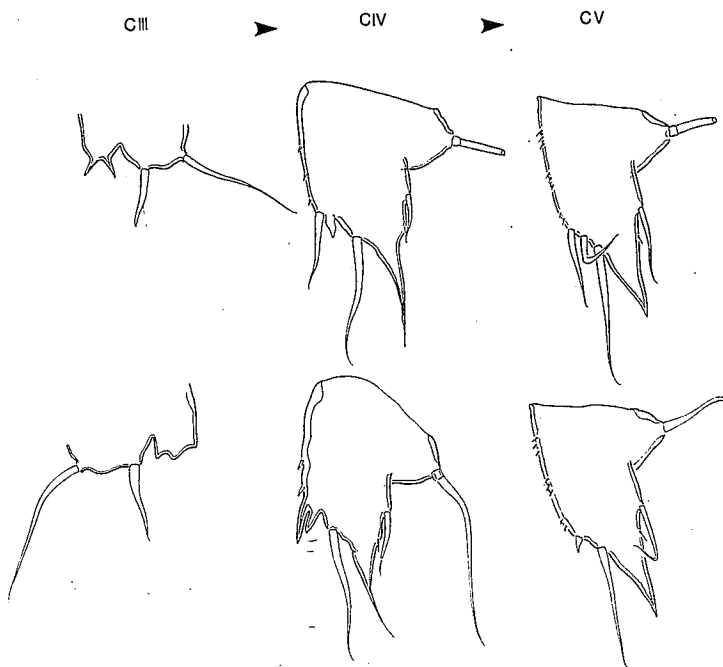


Fig. 22. — Postembryonic development of fifth leg in both sexes of *L. pygmaeus*. Upper row : ♀ ; lower row, ♂ (CIII-V : copepodid stages).

#### 2.4.2. Caudal rami

In their most generalised form the caudal rami are cylindrical in shape and rectangular in dorsal aspect. Each ramus bears 7 setae. The terminology used to denote the caudal setae follows that proposed by Huys (1988b) for the generalised paramesochrid caudal ramus. It was found that this terminology is applicable to all copepods (Huys & Boxshall, 1991) : anterolateral accessory seta (I), anterolateral seta (II), posterolateral seta (III), outer terminal seta (IV), inner terminal (or "principal") seta (V), terminal accessory seta (VI) and dorsal seta (VII).

The ancestral condition of the caudal ramus and the various modifications occurring in the family are summarized in Fig. 23. Primitively the dorsal seta is located near the inner margin of the ramus and setae IV-V are fully separate and display predesigned fracture planes. Applying this configuration (A) as a starting point a number of transformations (B - I) can be described :

(B) Retention of the ancestral condition except for seta III which is composite ; it consists of a rigid, proximal styliform portion which articulates with

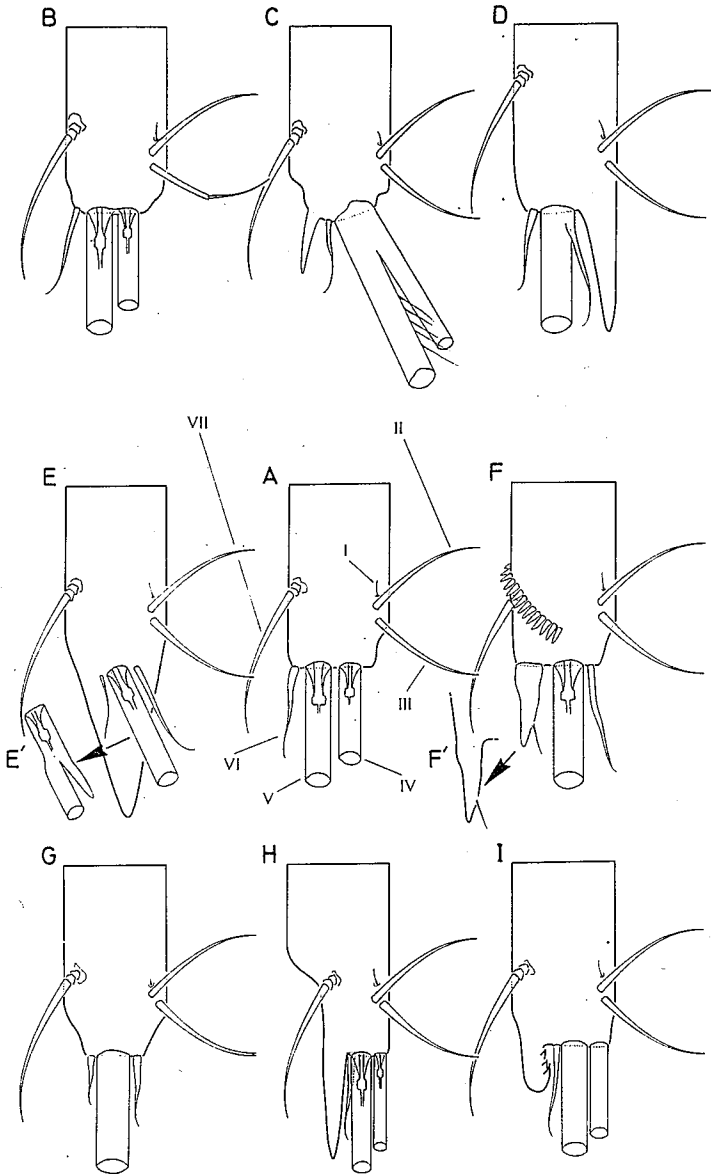


Fig. 23. — Comparison of caudal ramus structures in the Leptastacidae. A. Ancestral condition; B. *Leptastacus*; C. *Cerconeotes-Psammostacus*; D. *Archileptastacus*; E. *Belemnopontia*; E'. *Schizothrix*; F. *Arenotopa-Minervella-Neopsammostacus-Sextonis*; F'. *Sextonis incurvatus chilensis*; G. *Arenocaris*; H. *Paraleptastacus*; I. *Psamathea*.

a flagellate, distal part (e.g. Fig. 9B); setae IV and V are unmodified, but slightly fused at the base (*Leptastacus*).

(C) In this case the most important change involves the proximal fusion of setae IV and V and the reduction of the fracture planes. This condition is a good example of how virtually the same modification can be brought about by different developmental processes.

It might be regarded as a result of heterochrony since ontogenetically setae IV and V are derived from a single long, bifurcated seta present in copepodid I. From copepodid II onwards these setae become separate and fracture planes develop only in the later instars. This developmental sequence is widespread among Harpacticoida (see discussion in Dahms & Bergmans, 1988). The bifurcated seta can be retained in later instars (and eventually in the adult) by delaying the separation of setae IV and V with one or several moults. Evidence for such a neotenic event in *Cerconeotes* gen. nov. is provided by examination of copepodid V stages of *C. mozambicus* (Wells, 1967) comb. nov. (Fig. 49D).

The second developmental process is provided by inspection of copepodid V instars of *Psammastacus confluens* Nicholls, 1935. In this genus the fusion of setae IV and V in the adult cannot be attributed to heterochrony since these elements are already separated in the preceding stage (Fig. 35D). Here the "bifurcated seta" represents a developmental novelty acquired at the final moult. In both cases the fused setae are laterally directed and seta V is tubular (spatulate at the tip).

(D) A spinous process is developed in this ramus; it is derived from a posterior outgrowth of the outer posterolateral corner and none of the setae are involved in the formation. Setae IV and VI are reduced with seta IV fused to seta V (neoteny?) (*Archileptastacus* gen. nov.).

(E) The terminal setae keep their relative positions but the posterior margin of the ramus is produced into a slightly recurved process so that the setae IV-VI are now sited dorsally. Seta IV is reduced (*Belemnopontia* gen. nov.).

(E') This is a further modification in which seta V is furcated; a short lateral process is present along the outer margin of this seta (Figs. 24D-D') (*Schizothrix* gen. nov.).

(F) This type involves the development of an oblique spinular row on the dorsomedial surface, the reduction of seta IV (no fracture plane) and particularly the transformation of the accessory terminal seta into a spiniform, articulating element (Figs. 36A, E; 43A; 46B) which at a later stage (F') can become incorporated in the distal inner corner of the ramus (*Sextonis* gen. nov., *Neopsammastacus*, *Arenotopa*, *Minervella*, *Afroleptastacus* gen. nov., *Membranastacus* gen. nov.).

(G) The *Arenocaris*-type does not show any projections or thorns. The ramus distinctly tapers in the distal third and setae IV and VI are reduced; seta III is spatulate at the tip (Fig. 25E).



(H) In *Paraleptastacus* the distal process is homologous to a posterior outgrowth of the inner distal corner. The full complement of setae is retained and neither reductions nor migrations have taken place (Figs. 24E-F).

(I) This modification is reminiscent of the preceding one in showing a process at exactly the same position, however, the nature of the process proper is different; it is tricuspidate and recurved dorsally (*Psamathea*).

In the past only little attention has been paid to the homologies of the caudal rami when new species were compared with existing descriptions. The caudal ramus has been invariably cited as being "... acutely produced ..." without explicitly making reference to the structures involved in the modification. In some descriptions it is even virtually impossible to trace which transformation has taken place (e.g. Krishnaswamy's (1957) Fig. 22 of *Psammastacus acuticaudatus*). The presence of an acutely produced caudal ramus nevertheless has frequently been used as a diagnostic character. This is exemplified by the numerous species names alluding to this character: *spinicauda*, *spini-caudatus*, *acuticaudatus*, *dyadacantha*, ... This has contributed considerably to the taxonomic confusion in the Leptastacidae and eventually led to vague generic boundaries. Seven of the ten different caudal ramus transformations are found in the genus *Leptastacus* as it stands at present. Various modifications are not unique to the genus and are shared with one or several other leptastacinid genera. For example, type E is found in *L. laminaserrata* and *L. mehuinensis* Mielke, but also in all representatives of *Arenotopa*, *Minervella* and *Neopsammastacus*. Type C is found both in *Psammastacus confluens* and *L. jenneri* Lindgren, 1975.

#### 2.4.3. Sexual dimorphism

Sexual dimorphism can be encountered in the antennules, P2 to P6 and the caudal rami, but only the modifications of the swimming legs P2 - P4 will be discussed here.

##### *Exopod of P2*

Distinct sexual dimorphism on this ramus is restricted to a single species of the genus *Schizothrix* gen. nov. The male of *S. laminaserrata* (Mielke, 1985) comb. nov. displays a serrate extension on the inner distal corner of the middle exopodal segment. This structure is interpreted here as a secondary novelty originated within the genus *Sextonis* gen. nov. and has therefore no significance for intergeneric relationships. In species of *Paraleptastacus* the outer distal spine of enp-2 is occasionally reduced in the males.

##### *Exopod of P3*

Only the males of *Minervella* possess a modified exopod P3. All three exopodal segments are modified and each of the intersegmentary joints is

capable of extensive posterior flexure, directing distal segments almost at a right angle (Figs. 40A, 42B). Both the proximal and middle segments are swollen (Fig. 42C) and their hyaline frills alternate in position. Flexure of the middle segment is achieved by a strong retractor muscle originating proximally at a transverse chitinous rim of the proximal segment and inserting distally at a well developed condyle of the middle segment (Fig. 42B).

#### *Endopod of P3*

This is the basic type of swimming leg dimorphism found in the family. Virtually all members show a transformation of the distal endopodal segment of leg 3. In general, it is the subdistal seta or spine (often anterior in position) that is modified and additional modification can occur when the distal armature element and the segment itself are involved as well.

In *Paraleptastacus* (Mielke, 1975 ; Whybrew, 1986) and *Sextonis* gen. nov. (*S. mehuinensis* (Mielke, 1985) comb. nov. ; *S. chilensis* (Mielke, 1985) comb. nov.) the distal seta is reduced in length and the subdistal element is modified into a small (articulating) apophysis. This modification presumably represents the ancestral state in the family.

In the females of *Belemnopontia* gen. nov., *Schizothrix* gen. nov., *Cerco-neotes* comb. nov. and *Psammastacus* the subdistal seta is fused to the segment. This seta has frequently been overlooked since it is often anteriorly displaced (cf. *S. rostratus* : Nicholls (1940) vs. Geddes (1981)). In the males of these genera this seta is modified into a barbed, slightly sigmoid process arising from the anterior surface of the segment (Figs. 34D, 48D).

The modification found in *Psamathea* differs from all others because of the combination of the reduction in size of the distal segment, and the apparent total loss of the subdistal spine. The homologies between both sexes are difficult to assess without re-examination of the type material.

The subdistal seta is strongly reduced in the females of *Leptastacus*. It is found as a small spinous process at the anterior margin (e.g. Fig. 14C). In the males it is replaced by a minute spinous or knob-like process or might be lost altogether (*L. corsicaensis*); the distal seta is fused to the segment in all species.

A number of genera have lost the subdistal seta in the female and this has led to a series of different modifications. In most *Arenotopa* species the entire distal segment is involved in the formation of a spinous appendage at whose outer margin the small distal seta inserts (Fig. 36B). Both Chappuis & Rouch (1960) and Cottarelli (1977) figured the distal endopodal segment as a pectinate appendage without seta. It is conceivable that they have misinterpreted the small spinules found in *A. erasmusi* (Fig. 36B) and have overlooked the tiny seta. In males of *Minervella* and *Neopsammastacus* the distal segment is considerably reduced in length, forming a recurved apophysis ; the distal seta arises from the outer margin (Fig. 42D).

Some Leptastacidae have been reported to lack sexual dimorphism on the endopod P3. This loss appears to be real in *Arenocaris*, *Afroleptastacus* gen. nov., *Archileptastacus* gen. nov. and *Sextonis laminaserrata* comb. nov. but might be due to inaccuracies in the description in other species such as *L. christelleae* Bodiou & Colomines, 1989 and *L. naylori* McLachlan & Moore, 1978.

#### *Exopod of P4*

*Afroleptastacus* gen. nov. is the only genus that displays transformations of the male P4 exopod. The sexual dimorphism is not extensive since it is confined to the distal armature elements which are elongated in the male. In *Arenotopa* males the exopod appears to be more slender than in the females.

#### *Endopod of P4*

Modifications of this ramus include the most elaborate ones found in the family. In male *Arenotopa* the first endopodal segment is elongate and possesses fewer spinules than in the female. The distal segment is highly modified and medially directed. Allometric growth of the distal part has distorted the original implantation pattern of the 2 distal setae. One seta is sited along the outer margin at about 1/3 distance from the tip whereas the other one inserts along the inner margin near the apex of the segment (cf. Wells & Rao, 1987 : Fig. 131g).

A similar, not homologous, medially directed endopod is found in male *Arenocaris* (Fig. 25A), but no allometric growth has occurred here so that the distal setae (of which the inner one is modified into a claw) have not moved away from their original position. It is possible that the modification in *Psamathea* is homologous to the *Arenocaris* condition but a re-examination of *P. nautarum* Cottarelli & Venanzetti, 1989 is necessary before this interpretation can be corroborated.

A different kind of sexual dimorphism is observed in *Psammastacus* (Fig. 34F). The modification involves the loss of most of the ornamentation on the segments and on the distal spine, and the formation of a spinous process along the inner margin.

Finally, in *Paraleptastacus* males the inner distal spine can be reduced in size.

## 2.5. GENERIC DIAGNOSES

The family Leptastacidae currently includes 8 genera (Lang, 1948 ; Chapuis & Rouch, 1960 ; Cottarelli & Venanzetti, 1989). Particularly *Leptastacus* and *Psammastacus* are in an urgent need of revision. Both are polyphyletic assemblages and their redefinition in the following account will result in the

establishment of 7 new genera, representing different lineages in the evolution of the family.

GENUS **Leptastacus** T. Scott, 1906b

syn. : *Tetragoniceps* Brady, 1880 (partim) : Norman & T. Scott (1906), T. Scott (1892, 1899)

HISTORY

At present 30 species and subspecies have been referred to the genus *Leptastacus* on the basis of the uniramous P5 in both sexes and the 3-segmented exopods and 2-segmented endopods in P1 to P4. In addition, the present re-examination of *L. macronyx* has added 4 more species. The bulk of these species was referred to *Leptastacus* because they did not fit to any of the remaining genera recognised by Lang (1948) : *Paraleptastacus* (P5 biramous), *Arenocaris* (endopod P2-P3 1-segmented), *Psammastacus/Arenotopa* (exopod P1 1-segmented). The recent establishment (Cottarelli & Venanzetti, 1989) of 3 new genera (*Minervella*, *Neopsammastacus*, *Psamathea*) did not affect the generic boundaries of *Leptastacus*. With the description of numerous new species during the last decade, it became apparent that the current taxonomic concept of the genus *Leptastacus* is no longer tenable and that the genus comprises different evolutionary lineages. Huys (1987) hinted at the need of splitting up *Leptastacus* when he defined the *macronyx* species-group. Bodiou & Colomines' (1989) suggestion to divide the genus according to the presence or absence of a terminal chitinous process on the fifth leg is oversimplified and should be abandoned.

DIAGNOSIS

Leptastacidae. Rostrum elongated. Urosomites with plain hyaline frill. Antennary exopod with 2 distal setae. Mandibular palp (sometimes indistinctly) 2-segmented ; basis with 1 or 2 setae. Labrum without frontal spinous process. P1 exopod 3-segmented ; exp-3 with 4 setae/spines. P1 endopod 2-segmented, not prehensile. P2-P4 endopod 2-segmented. Anterior spine of enp-2 P3 incorporated into segment and represented by vestigial spinous process. Outer spine of exp-2 P4 elongated and curved. Spine and seta formulae as follows :

	Exopod	Endopod
P2	0.0.021	[0-1].010
P3	0.0.121	[0-1].010 <sup>3</sup>
P4	0.1.221	0.1*10

[\* dwarfed seta]

<sup>3</sup> Cottarelli & Venanzetti (1989) figured 2 setae on the distal endopod segment of *L. uncinatus*, resulting in a formula 1.011. The outer short element (which is figured on the inner margin

Slight sexual dimorphism on endopod P3 (enp-2) represented by small inner process subdistally; distal spine often fused to segment. P5 uniramous in both sexes; triangular and produced distally; in female with 5 well developed setae (setae *a* and *e* vestigial or absent); in male with 3 well developed setae (setae *a-c* and *e* vestigial or absent). Male P6 symmetrical or slightly asymmetrical, with 3 setae. Caudal ramus not acutely produced distally; seta III composite.

#### TYPE SPECIES

*L. macronyx* (T. Scott, 1892) T. Scott, 1906b (by monotypy): This species is also the type species of the family.

syn.: *Tetragoniceps macronyx* T. Scott, 1892

#### OTHER SPECIES

*L. laticaudatus* Nicholls, 1935

syn.: *L. laticaudatus intermedius* Kunz, 1937: Huys (1987)

*L. spatuliseta* Mielke, 1982

*L. uncinatus* Cottarelli & Venanzetti, 1989

*L. coulli* sp. nov.

*L. kwintei* sp. nov.

*L. corsicaensis* sp. nov.

*L. pygmaeus* sp. nov.

#### SPECIES INQUIRENDAE

*L. laticaudatus intermedius* Kunz, 1937 *sensu* Apostolov (1973b), Apostolov & Marinov (1988): Huys (1987)

*L. minutus* Chappuis, 1954b

*L. wieseri* Chappuis, 1958

#### MATERIAL EXAMINED

- *L. laticaudatus*: see list in Huys (1987: 156);
- *L. spatuliseta*: from Prof. Dr A. Coomans: 1 ♀ collected in front of marine laboratory in Bahía Academy, Isla Santa Cruz, Galápagos; 18 February 1988; leg. A. Coomans;
- other material: see section 1.

in the male!) is presumably either a long spinule or the spinous process found in other members of the genus. The alleged sexual dimorphism (absence of inner seta on enp-1 P3 and enp-3 and enp-2 P4) described in this species is extremely unlikely and needs confirmation.

## REMARKS

This genus is now restricted to the *macronyx*-group as defined by Huys (1987) and can be readily distinguished on the base of the composite seta III of the caudal rami. This seta was not illustrated in Chappuis' descriptions (1954b, 1958) of *L. minutus* and *L. wieseri*, but the triangular shape of the fifth legs and the rectangular, not acutely produced caudal rami provide sufficient evidence for their inclusion in the genus. Chappuis' poorly rendered illustrations, however, make reliable identification virtually impossible and the type material is apparently lost (Rouch, *in litt.*). Therefore both *L. minutus* and *L. wieseri* cannot be treated as anything more than *species inquirendae* until topotypes are available.

*L. spatuliseta*, *L. coulli* and *L. pygmaeus* represent a distinct species complex within the genus. It is characterised by spatulate setae on the exopods of P2 to P4 and on the fifth legs, and by the pitted integument of the body somites.

A simple key to this genus cannot easily be constructed. Identification is best achieved by comparing the respective descriptions (Mielke, 1982; Huys, 1987; Cöttarelli & Venanzetti, 1989; present account) and the salient features of the various species compiled in Table 2.

## RELATIONSHIPS

The genus *Leptastacus* represents the earliest offshoot of the lineage that adopted the triangular, uniramous fifth leg. This lineage further includes *Schizothrix* gen. nov., *Belemnopontia* gen. nov., *Cerconeotes* gen. nov. and by inference *Psammastacus*. As in *Schizothrix* gen. nov. the genus *Leptastacus* retains the full complement of armature elements on the P5. The genus can be readily distinguished from the others by the following diagnostic autapomorphies: (i) the composite seta III on the caudal rami, (ii) the presence of only 1 well developed seta on the distal endopodal segment of P3 (the second one being represented by a small non-articulating spinous process), and (iii) the elongated, recurved outer spine on the middle exopodal segment of P4.

## GENUS

**Paraleptastacus** Wilson, 1932

- syn. : *Mesochra* T. & A. Scott, 1895 (partim) : Gager (1923), T. Scott (1895, 1900, 1906a), T. & A. Scott (1895)  
*Leptastacus* T. Scott, 1892 (partim) : Jakubisiak (1930), Klie (1929, 1934), Kunz (1935), Monard (1935), Pesta (1927, 1932), Remane (1933), Schäfer (1936a-b)

TABLE 2

Salient features of *Leptastacus* species.

	<i>macroryx</i> (T. Scott)	<i>kwintei</i> sp. nov.	<i>coulti</i> sp. nov.	<i>pygmaeus</i> sp. nov.
Body length ♀ (µm)	500-620	445-475	340-360	245-255
Body length ♂ (µm)	?	415-450	325	235
Integument	smooth	smooth	pitted	pitted
Anal operculum	ca. 10 coarse spinules flanked by spinular row	ca. 20-30 fine spinules flanked by spinular row	minutely denticulate flanked by 1 coarse spinule	minutely denticulate not flanked by spinules
Caudal ramus : L : W	3.9-4.0	3.2-3.3	2.0	2.0
P1 L : W	1.65	1.7	1.0	1.24
P1 L : W (proximal)	4.1	3.25	2.85	2.75
P2-P3 exp-1 inner seta	+	+	+	+
P2-P4 exp-3, inner terminal seta	not modified	not modified	swollen, spatulate	swollen, spatulate
endopod P2 L : W	12.0	8.6	8.1	8.6
P4 exp-2 L : W	9.25	5.0	5.6	4.9
P4 exp-2, outer spine	> exp3	> exp-3	= exp-3	< exp-3
P5 distal process	almost straight	recurved at tip	slightly bent distally	straight
P5 L : W (proximal)	2.0	2.0	1.6	2.2
secondary process ♂ endopod P3	?	knob-like	spinous	spinous

TABLE 2 (continued)  
Salient features of *Lepiastacus* species.

	<i>corsicaensis</i> sp. nov.	<i>laticaudatus</i> Nicholls	<i>spatulisetia</i> Mielke	<i>uncinatus</i> Cottarelli & Venanzetti
Body length ♀ (µm)	780	345-380	490-500	415
Body length ♂ (µm)	745	332-370	?	370
Integument	smooth	smooth	pitted	smooth
Anal operculum	long spinules decreasing in length abaxially	minutely denticulate	minutely denticulate	short spinules
	not flanked by spinules	not flanked by spinules	flanked by spinular row	flanked by spinules
Caudal ramus : L : W	7.5	1.7-2.7	3.3	2.3
P1 L enp-1 : L enp-2	1.85	1.1	1.2	1
P1 enp-1, L : W (proximal)	4.2	3.25	4.2	2.2
P2-P3 enp-1 inner seta	-	+	+	+
P2-P4 exp-3, inner terminal seta	not modified	swollen, spatulate	not modified	not modified
endopod P2 L : W	10.9	7.0	8.6	8.2
P4 enp-2 L : W	7.5	4.6	5.8	5
P4 exp-2, outer spine	> exp3	< exp-3	= exp-3	< exp-3
P5 distal process	recurved at tip	(typically) foot-shaped	recurved at tip	recurved at tip
P5 L : W (proximal)	1.8	1.7	2.7	1.6
secondary process ♂ endopod P3	absent	spinous	?	spinous



## DIAGNOSIS

Leptastacidae. Rostrum triangular. Hyaline frill of urosomites well developed, consisting of rectangular lappets. Antennary exopod with 2 distal setae. Mandibular palp 1-or 2-segmented; basis with 1 seta. Labrum without frontal spinous process. P1 exopod 3-segmented; exp-3 with 4 setae/spines. P1 endopod 2-segmented, not prehensile. P2-P4 endopod 2-segmented. Spine and seta formulae as follows:

	Exopod	Endopod
P2	0.0.022	1.010-1]
P3	0.0.122	[0-1].011
P4	0.1.[1-2]22	0.110

Slight sexual dimorphism on endopod P2-P4. P5 biramous in both sexes (male exopod occasionally fused to baseoendopod); baseoendopod with 2 setae; exopod with 2-4 setae. Male P6 with 3 (occasionally 2) setae, asymmetrical. Distal inner corner of caudal ramus acutely produced; none of setae modified except for bifid seta VII.

## TYPE SPECIES

*P. brevicaudatus* Wilson, 1932<sup>4</sup>

## OTHER SPECIES

*P. spinicauda* (T. & A. Scott, 1895) Nicholls, 1935

syn.: *Mesochra spinicauda* T. & A. Scott, 1895

*M. spinicaudata* T. & A. Scott, 1895: T. Scott (1895: *lapsus calami*)

*Leptastacus spinicauda* (T. & A. Scott, 1895) Sars, 1911

*L. spinicaudatus* (T. & A. Scott, 1895): Pesta (1927: *lapsus calami*)

*P. kliei* (Gagern, 1923) Kunz, 1937

syn.: *Mesochra spinicauda* var. *kliei* Gagern, 1923

*Leptastacus spinicaudatus* var. s. subsp. *kliei* (Gagern, 1923)  
Jakubisiak, 1930

*Paraleptastacus spinicauda* s. *spinicaudatus* var. *kliei* (Gagern, 1923) Lang, 1936

<sup>4</sup> Apostolov & Marinov (1989: 284) erroneously mention *P. spinicauda* (T. & A. Scott, 1895) as the type species.

- P. spinicaudus* (T. & A. Scott, 1895) *sensu* Nicholls (1935 : *lapsus calami*)  
*P. espinulatus* Nicholls, 1935 *sensu* Scheibel (1972)  
*P. katamensis* Wilson, 1932  
*P. espinulatus* Nicholls, 1935  
 syn. : *P. spinicauda* (T. & A. Scott, 1895) *sensu* Mielke (1975, 1976)  
*P. holsaticus* Kunz, 1937  
*P. laurenticus* Nicholls, 1940  
*P. longicaudatus* Nicholls, 1940  
*P. triseta* Noodt, 1954  
 syn. : *P. spinicauda triseta* Noodt, 1954  
*P. spinicauda trisetosa* Serban & Eitel-Lang, 1957  
*P. ponticus* Apostolov, 1969  
*P. unisetosus* Itô, 1972  
*P. supralitoralis* Mielke, 1975  
*P. monensis* Whybrew, 1986  
 syn. : *P. spinicauda* (T. & A. Scott, 1895) *sensu* Moore (1975)  
*P. wilsoni* Whybrew, 1986  
*P. moorei* Whybrew, 1986  
 syn. : *P. holsaticus* Kunz, 1937 *sensu* Moore (1975)  
*P. holsaticus moorei* Whybrew, 1986

#### SPECIES INQUIRENDAE

- P. spinicauda bisetosus* Jakubisiak, 1938  
*P. ammodytensis* Carvalho, 1952  
*P. caspicus* Stërba, 1973

#### MATERIAL EXAMINED

- *P. espinulatus* : numerous specimens : North Sea, Southern Bight, off Hoek van Holland ; 52°16'29" N, 03°32'14" E ; collected 19 June 1984 (leg. R. Huys) ; subtidal sandy sediment (median grain size : 331 µm ; 99.9% sand and 0.07% silt), depth 26 m ;  
 — *P. spinicauda* : 5 ♀♀, 3 ♂♂ : North Sea, Southern Bight, off Hoek van Holland ; 52°02'30" N, 03°25'00" E ; collected 09 July 1986 (leg. R. Huys) ; subtidal sandy sediment (median grain size : 360 µm ; 99.32% sand and 0.68% silt) ;  
 — *P. moorei* : 4 ♀♀, 1 ♂ : North Sea, Southern Bight, off Hoek van Holland ; 52°16'14" N, 03°21'10" E ; collected 09 July 1986 (leg. R. Huys) ; subtidal sandy sediment (median grain size : 339 µm ; 98.37% sand and 1.63% silt).

## REMARKS

The genus *Paraleptastacus* is perhaps the least well known of the family despite the many contributions to its taxonomy. This state of affairs is mainly due to two reasons: (i) the repeated failure to distinguish *P. holsaticus*, *P. espinulatus* and *P. spinicauda*, and (ii) the confused picture that exists about the populations of the Black Sea basin. The partial redescriptions or additional descriptions of new varieties did not solve the problem but added instead new names to the already extensive list of synonyms of *P. spinicauda* (see Moore, 1975: 503). The major turning point in this accumulative process came in 1986 when Whybrew published his revision of the genus. Whybrew's detailed comparative study was largely based on type material or topotypes which enabled him to start from scratch.

Mielke (1975) and Moore (1975) almost simultaneously (re)described several species from beaches of the Isle of Sylt and the Isle of Man, respectively. Whybrew's analysis (hinted at in an addendum of his 1984 paper) showed that at least some of their redescriptions did not coincide with the original type description and expressed also some doubts about Nicholls' (1935) identification of *P. spinicauda* from the Isle of Cumbrae, Scotland. As a result he re-allocated the respective populations as follows:

NICHOLLS (1935)	MOORE (1975)	MIELKE (1975)	WHYBREW (1986)
<i>espinulatus</i> <i>spinicaudus</i>	<i>espinulatus</i>  <i>spinicauda</i> <i>holsaticus</i>	<i>spinicauda</i>   <i>holsaticus</i> <i>supralitoralis</i>	<i>espinulatus</i> <i>kliei</i> <i>monensis</i> <i>holsaticus moorei</i> <i>spinicauda</i> <i>supralitoralis</i>

Whybrew (1986: 26) suggested to consider tentatively Moore's specimens of *P. holsaticus* as a distinct subspecies *P. holsaticus moorei* because of striking differences in the hyaline frill, the caudal rami and the sexual dimorphism on the swimming legs. Additional discrepancies with Kunz' (1937) original description are listed by Moore (1975) for the exopod of P4 (distal inner seta of exp-3 absent) and the body length. Whybrew (1986) was unable to examine material but closer inspection of specimens from the Southern Bight by the present author could confirm these differences and provide sufficient grounds for assigning Moore's material the level of species: *P. moorei* grad. nov.

Lang (1948) suggested that Nicholls' (1935) specimens of *P. spinicaudus* might belong to *P. holsaticus* but Moore (1975) regarded Nicholls' identification as valid given the large pool of variability encountered in the Manx populations of *P. spinicauda*. Whybrew's inspection of Nicholls' original material kept in the Natural History Museum, London proved both interpretations to be wrong,

showing instead that they belong to *P. kliei*. The latter species was reinstated by Whybrew after Lang (1948) and Moore (1975) had synonymized it with *P. spinicauda*. Lang's decision to regard *P. kliei* an invalid species was based on the presence of numerous transitional forms in some Swedish localities, however Whybrew attributes this variability to the co-occurrence of several species.

*P. monensis* was proposed by Whybrew (1986) for the Manx specimens of *P. espinulatus* described and illustrated by Moore (1975). Distinct differences between the two species are found in the relative lengths of the armature elements on the fifth legs and the armature of the male P6.

As for the genus *Leptastacus*, the taxonomy of Black Sea *Paraleptastacus* is extremely intricate. Various species and subspecies have been reported from this area (Jakubisiak, 1938; Noodt, 1954; Serban & Eitel-Lang, 1957; Apostolov, 1969) but subsequent lumping and synonymising have reduced this number to two (Apostolov & Marinov, 1988): *P. spinicauda* and *P. holsaticus*. Moore (1975) even states that all *Paraleptastacus* described from the Black Sea should be relegated to at most subspecies of *P. spinicauda*. These are: *P. spinicauda* var. *bisetosus* Jakubisiak, 1938; *P. spinicauda trisetata* Noodt, 1954; *P. spinicauda trisetosa* Serban & Eitel-Lang, 1957; *P. ponticus* Apostolov, 1969; as well as *P. caspicus* Stërba, 1973 described from the Caspian Sea.

Only the female P5, the maxilliped and the caudal rami were illustrated in the original description of *P. spinicauda* var. *bisetosus*. However, Lang (1948) considered the bisetose exopod on the fifth leg as good evidence for elevating this variety to species level, and this opinion was followed by Whybrew (1986). Serban (1959) believed that the exopod might show slight variability in the number of setae, and on the base of this statement Apostolov (1973b) subsequently relegated *P. spinicauda* var. *bisetosus* to a synonym of *P. spinicauda trisetosa* though the former name takes precedence. There is, however, no evidence for such variability and therefore Jakubisiak's subspecies should stand as Moore (1975) and Whybrew (1986) suggested. Jakubisiak's (1938) description is grossly incomplete and it is likely that he missed one of the minute armature elements on the exopod of the fifth leg. In view of the insufficient knowledge, *P. spinicauda bisetosus* is ranked here as *species inquirenda*.

*P. spinicauda trisetata*, described from a low salinity habitat in Turkey (Noodt, 1954), differs from all other species reported at that time by the presence of 3 setae on the exopod of P5. Both *P. spinicauda trisetosa* and *P. ponticus* exhibit the same character, but were described (Serban & Eitel-Lang, 1957; Apostolov, 1969) without reference to Noodt's paper. Apostolov (1973b) first synonymised the latter two species before Moore (1975) listed them as junior synonyms of *P. spinicauda trisetata*. Whybrew (1986) corroborated this view when he redescribed and upgraded *P. spinicauda trisetata* to species level.

The taxonomic picture of the genus in the Black Sea summarized in Apostolov & Marinov's (1988) recent catalogue is absolutely confusing. The

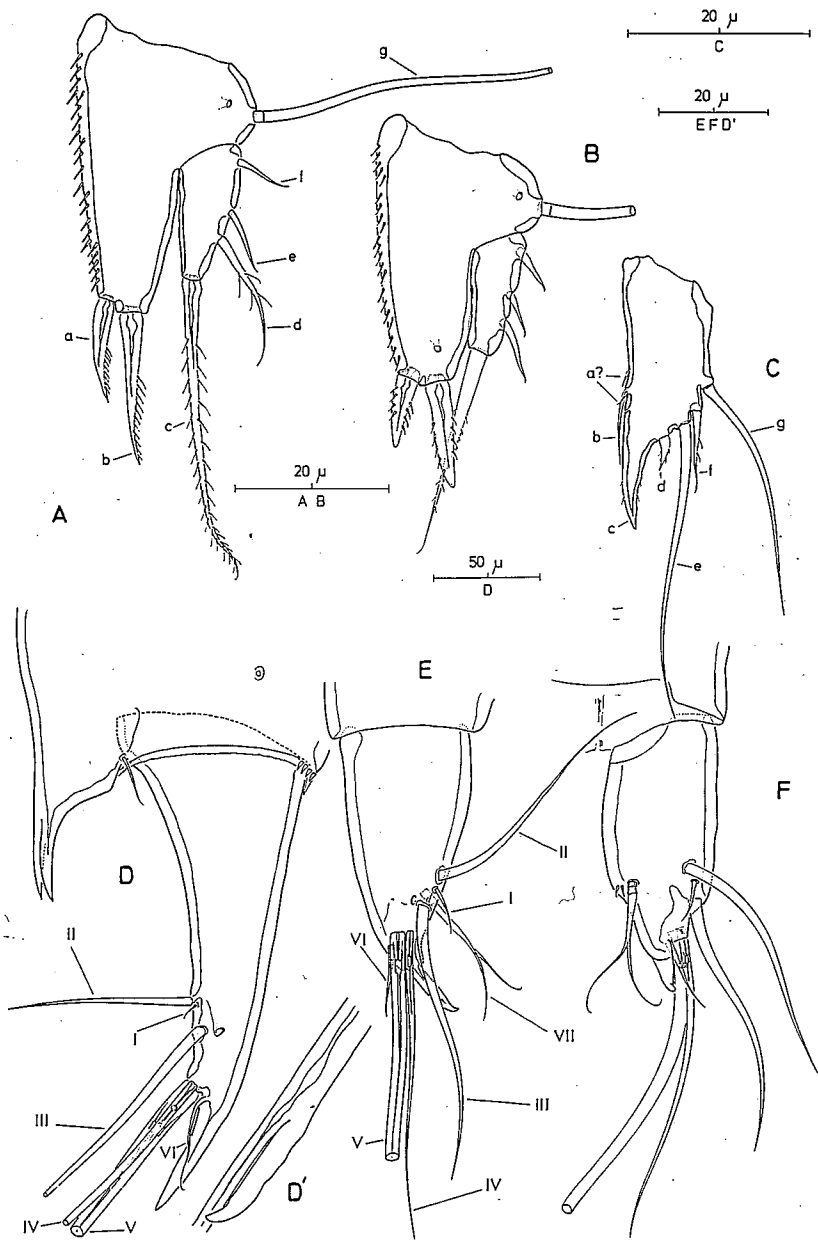


Fig. 24. — *Paraleptastacus moorei* Whybrew, 1986. A. P5 of ♀; B. P5 of ♂; E. Caudal ramus, lateral view; F. Same, dorsal view; *Archileptastacus dichatoensis* (Mielke, 1985) comb. nov., C. P5 of ♀; *Schizothrix rostratus* (Nicholls, 1940) comb. nov., D. Anal somite and caudal ramus, lateral view (seta VII not drawn); D'. detail of furcated seta V. [C redrawn after Mielke (1987)].

setal formula given for *P. spinicauda* does not coincide with the West European material and furthermore disagrees with the illustrations given. These illustrations are different from the earlier figures prepared by Apostolov for *P. ponticus* (1969b) or *P. spinicauda trisetosa* (1973), yet represent a combination of reproduced drawings taken from Mielke's (1975) description of *P. spinicauda* from the Isle of Sylt (= *P. espinulatus*) and Moore's description of *P. spinicauda* from the Isle of Man (= *P. monensis*). Similarly they used Mielke's setal formula given for *P. holsaticus* (= *P. spinicauda*) and reproduced his illustration of the caudal rami and Kunz' (1937) drawings of the antenna and the male P5, though the latter was mentioned as the female P5. Needless to say that Apostolov & Marinov's records and Apostolov's (1971) earlier record of *P. holsaticus* have to be considered extremely doubtful.

*P. caspicus* from the Caspian Sea resembles *P. trisetata* in most aspects but differs primarily in the presence of an inner seta on the proximal endopodal segment of P3. Surprisingly, this seta was not illustrated in the male third leg. Whybrew (1986) therefore suggested that Stěrba (1973) might have confounded males and females of different species. Moore (1975) noticed that this particular seta may or may not be present in the populations of *P. spinicauda* of the Isle of Man and on this ground ranked *P. caspicus* as a junior synonym of *P. spinicauda trisetata*. In view of the lack of topotype material and taking into account the differences encountered in the male sixth legs, Moore's decision is considered premature and instead *P. caspicus* should be regarded *species inquirenda*.

Whybrew (1986) suggested to withdraw *P. ammodiense* Carvalho, 1952 from the genus and to consider it at best *species incertae sedis* in the Cylindropsyllidae. This was based on the unique segmentation of the first leg (both rami 2-segmented) described but not figured in the original description. Carvalho's description is extremely fragmentary in various other aspects, however the illustrations of the maxilliped, the setation of P3-P4 and the caudal rami warrants inclusion in the genus *Paraleptastacus* as Moore (1975) suggested before. Several atypical features such as the long rostrum and the extra somite boundaries undoubtedly are wrong and perhaps result from excessive squashing of the slide preparations. The long first antennular segment is also highly unusual and it is conceivable that Carvalho has combined this segment with the well developed pedestal that supports the antennule. Pending a complete redescription *P. ammodiense* has to be considered *species inquirenda*.

*P. (?) incertus* Chappuis & Delamare-Deboutteville, 1956 does not belong to *Paraleptastacus* nor to the Leptastacidae, however should be placed among the Ameiridae most likely within the genus *Pseudoleptomesochrella* Lang, 1965 (see Moore, 1975 ; Petkovski, 1976).

Whybrew (1986) divided the genus into two species groups, the *spinicauda*-group and the *kliei*-group according to whether the inner seta of the proximal

endopodal segment of P3 is present or absent, respectively. This division was further supported by two other characters, the length of the seminal receptacle and the structure of the hyaline frill on the third abdominal somite in the male. Re-examination has proved the latter two characters to be of no value for discriminating species groups within the genus.

Whybrew's interpretation of the female genital complex is utterly misleading and incorrect. His illustration Abb. 3B results from intentionally superimposing internal and external structures. The paired structures indicated by "V" (Vulva, Eiablageporus) are not the gonopores through which the eggs are released. They rather represent large secretory pores connected with underlying glands, and are found in several other genera (Figs. 43C, 49E). This misinterpretation led Whybrew to suggest that Lang's (1948) statement that the female gonopores are always covered by opercula derived from the sixth legs could not be generalised. The interpretation of the seminal receptacle and of the copulatory pore is also incorrect. Whybrew's opening "BP" (Begattungs-porus) is an internal sclerotised structure marking the anterior end of the copulatory duct. The real copulatory pore is positioned at about the posterior margin of his structure "RST", but was apparently overlooked. His division of the seminal receptacle into an anterior thick-walled ("RSD") and a posterior thin-walled ("RST") zone is inadequate because they are both part of a continuous, voluminous copulatory duct. The receptacle itself is partly located beneath this duct. The so-called "fertilisation ducts" indicated by "D" are in fact the exposed parts of the genital apertures.

With regard to the hyaline frill Whybrew (1986) recognised two types, the bipartite and the tripartite frill. The latter type was considered to be typical for the *spinicauda*-group and consists of an anterior spinular row, a series of rectangular membranous lappets and dubious paired structures called "... tatzenförmigen Verdickungen mit klauenartig ansitzenden Dörnchenreihen". Re-examination revealed that the thickenings are the paired median insertion sites of the ventral longitudinal trunk muscles. The tendon of each of these muscles was mistaken for the minute spinules drawn by Whybrew (1986). The anterior spinular row represents internal striated structures of the posterior margin of the somite.

The separation between both species-groups on the basis of the inner seta of enp-1 P3 is nevertheless considered valid and is applied in the species key below.

#### Key to the species of *Paraleptastacus* Wilson

1. Enp. P1 twice as long as exp ..... *laurenticus* Nicholls, 1940.  
Enp. P1 at most 1.2 times as long as exp ..... 2.
2. Enp-1 P3 without inner seta ..... 3.  
Enp-1 P3 with inner seta ..... 6.

3. Exp. P5 with 3 setae/spines ..... *trisetata* Noodt, 1954.  
Exp. P5 with 4 setae/spines ..... 4.
4. Enp-2 P2 ♀ with 1 distal seta ; enp-2 P3 ♂ 0.8 times the length of enp-1 ..... *espinulatus* Nicholls, 1935.  
Enp-2 P2 ♀ with 2 distal setae ; enp-2 P3 ♂ at most half the length of enp-1 ..... 5.
5. Distal exopodal seta (seta *c*) of P5 ♀ 1.3 times the length of seta *d* ; in P5 ♂ seta *c* distinctly shorter than seta *d*, and inner baseoendopodal spine (*a*) shorter than outer one (*b*) ..... *kliei* (Gagern, 1923).  
Distal exopodal seta (seta *c*) of P5 ♀ twice the length of seta *d* ; in P5 ♂ seta *c* distinctly longer than seta *d*, and inner baseoendopodal spine (*a*) longer than outer one (*b*) ..... *wilsoni* Whybrew, 1986.
6. Exp-3 P4 with 1 inner seta ..... 7.  
Exp-3 P4 with 2 inner setae ..... 9.
7. Exp-3 without inner seta ..... *brevicaudatus* C.B. Wilson, 1932.  
Exp-3 with inner seta ..... 8.
8. Distal margin of exopod P5 not exceeding endopodal lobe .....  
..... *moorei* Whybrew, 1986.  
Exopod P5 at least reaching to distal margin of benp. ....  
..... *unisetosus* Itô, 1972.
9. Outer baseoendopodal spine of P5 ♀ at least 1.5 times the length of inner one ; P6 ♂ with 2 spines and 1 seta ..... *spinicauda* (T. & A. Scott, 1895).  
Inner baseoendopodal spine of P5 ♀ at least 1.6 times the length of outer one ; P6 ♂ with 3 setae ..... *katamensis* C.B. Wilson, 1932.  
Inner baseoendopodal spine of P5 ♀ slightly shorter than or as long as outer spine ; P6 ♂ with 2 setae and 1 spine (or 1 seta and 1 spine) ..... 10.
10. Ventral posterior border of anal somite with 2 strong thorns flanked by minute ones ; P6 ♂ with 1 seta and 1 spine .... *supralitoralis* Mielke, 1975.  
Ventral posterior border of anal somite with minute spinules only ; P6 ♂ with 2 setae and 1 spine ..... 11.
11. Enp-2 of P3-P4 ♀ with 1 well developed and 1 minute seta ; seta *c* of exp. P5 ♂ shorter than seta *d* ..... *longicaudatus* Nicholls, 1940.  
Enp-2 of P3-P4 ♀ with 2 well developed setae ; seta *c* the longest seta of exp. P5 ♂ ..... 12.
12. Caudal ramus with narrow terminal spinous process ; enp. P4 longer than exp-(1,2) combined ..... *monensis* Whybrew, 1986.  
Caudal ramus with broad terminal spinous process ; enp. P4 shorter than exp-(1,2) combined ..... *holsaticus* Kunz, 1937.

#### RELATIONSHIPS

Various characters indicate the primitive position of the genus such as the ancestral setation and segmentation of the fifth legs (Figs. 24A-B). It is



also the only genus that has retained the proximal outer spine on the distal exopodal segment of P2 to P4 and the outer seta on the distal endopodal segment of P2. The genus can be distinguished on the base of the modification of the caudal rami, involving the formation of a posteriorly directed spinous process at the inner distal corner (Figs. 24E-F) and the presence of a lappeted hyaline frill on the majority of the urosomites. The latter character evolved also convergently in *Minervella*, *Arenocaris* and *Neopsammastacus*.

GENUS **Arenocaris** Nicholls, 1935

#### HISTORY

The genus remained monotypic since the description of its type species *A. bifida* from Kames Bay, Isle of Cumbrae (Nicholls, 1935). Lang's (1965) statement that *Psammoleptastacus orientalis* Krishnaswamy, 1957 belongs to *Arenocaris* should be considered a slip of the pen. The numerous deficiencies contained by Krishnaswamy's description raise severe doubts about its affinity to any of the subfamilies of the Cylindropsyllidae. Its present allocation to *Arenopontia* Kunz, 1937 (see Bodin, 1988) should therefore be seriously questioned.

#### DIAGNOSIS

Leptastacidae. Rostrum elongated. Abdominal somites with well developed hyaline frill consisting of rectangular lappets. Antennary exopod with 2 distal setae. Mandibular palp 1-segmented; seta of ancestral basis present. Labrum without frontal spinous process. P1 exopod 2-segmented; exp-1 with 1 outer spine; exp-2 with 3 or 4 setae/spines. P1 endopod 2-segmented, not prehensile; enp-2 with 2 spatulate setae. P2-P3 endopod 1-segmented; P4 endopod 2-segmented; inner distal spine of exp-3 P2-P4 spatulate. Spine and seta formulae as follows:

	Exopod	Endopod
P2	0.0.021	010
P3	0.0.121	010
P4	0.[0-1].[1-2]21	0.110

Sexual dimorphism on endopod P4. P5 biramous in both sexes; baseoendopod with 2 setae in female and 1-2 setae in male; exopod with 4 setae. Male P6 with 3 setae, asymmetrical. Caudal ramus sometimes sexually dimorphic, not acutely produced distally; seta III spatulate at tip; seta IV reduced.

## TYPE SPECIES

*A. bifida* Nicholls, 1935 (by monotypy)

*Redescription*  
(Figs. 25 - 29)

*FEMALE.* Body length 530-620  $\mu\text{m}$  ( $n = 8$ ), measured from the tip of the rostrum to the hind margin of the caudal rami.

Body slender (Fig. 25A), cylindrical, vermiform, almost colourless; boundaries and articulations between thoracic somites weakly developed, cephalothorax and second pedigerous somite (P2) fused dorsally (Fig. 25A). Integument smooth, weakly chitinised. Hyaline frill of abdominal somites well developed, consisting of rectangular lappets. Abdominal somites also with rectangular cuticular thickenings (Fig. 25C). Cephalothorax rectangular, slightly narrower than thoracic somites; no distinct separation between prosome and urosome, anal somite narrowest. Genital double-somite longer than wide, with genital apertures located at about midway the segment; no trace of original subdivision discernible (Figs. 25A; 27E). Anal somite with tiny spinules near ventral posterior margin (Fig. 27B).

Caudal rami divergent (Figs. 25A; 27D), about 2.5 times as long as maximum width. Armature consisting of 7 setae; seta III strongly developed and tubular at the tip; seta V long and slightly plumose, fused at the base with seta IV; seta VI reduced; seta VII bi-articulated at base. Ventral surface with spinular-row near inner margin.

Rostrum (Fig. 29A) free at the base; elongated, about 2.6 times as long as maximum width, exceeding first antennular segment. Nauplius eye not observed.

Antennule 7-segmented, slender; with aesthetasc on segment IV.

Antenna (Fig. 29B). Coxa small, unarmed. Allobasis about 3 times as long as maximum width; inner margin with 2 spinular rows; original segmentation marked by small transverse chitinous rib. Exopod 1-segmented, with 2 apical setae. Distal endopodal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is swollen at the base, fused with a dwarfed seta and is ornamented with spinules around the geniculation; inner endopodal margin with 1 spine covered by a spinular row.

Mandibular palp 1-segmented (Fig. 29C) but inner seta of ancestral proximal segment (basis) retained; with 2 inner setae, 1 outer seta and 2 apical setae which are fused at the base.

Maxillula and maxilla as for the family.

Maxilliped (Fig. 29D) with long bare seta on syncoxa; basis without ornamentation.

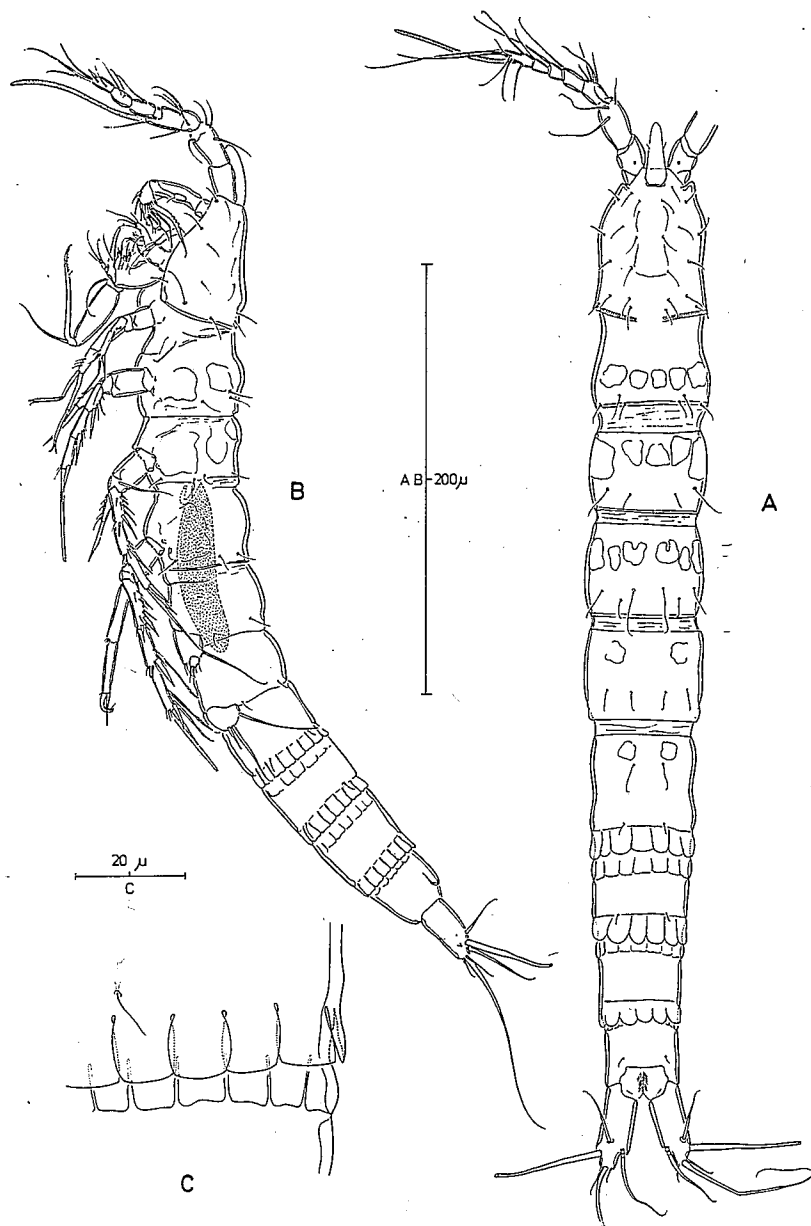


Fig. 25. — *Arenocaris bifida* Nicholls, 1935. A. Habitus ♀, dorsal view; B. Habitus ♂, lateral view; C. Hyaline frill of urosomite.

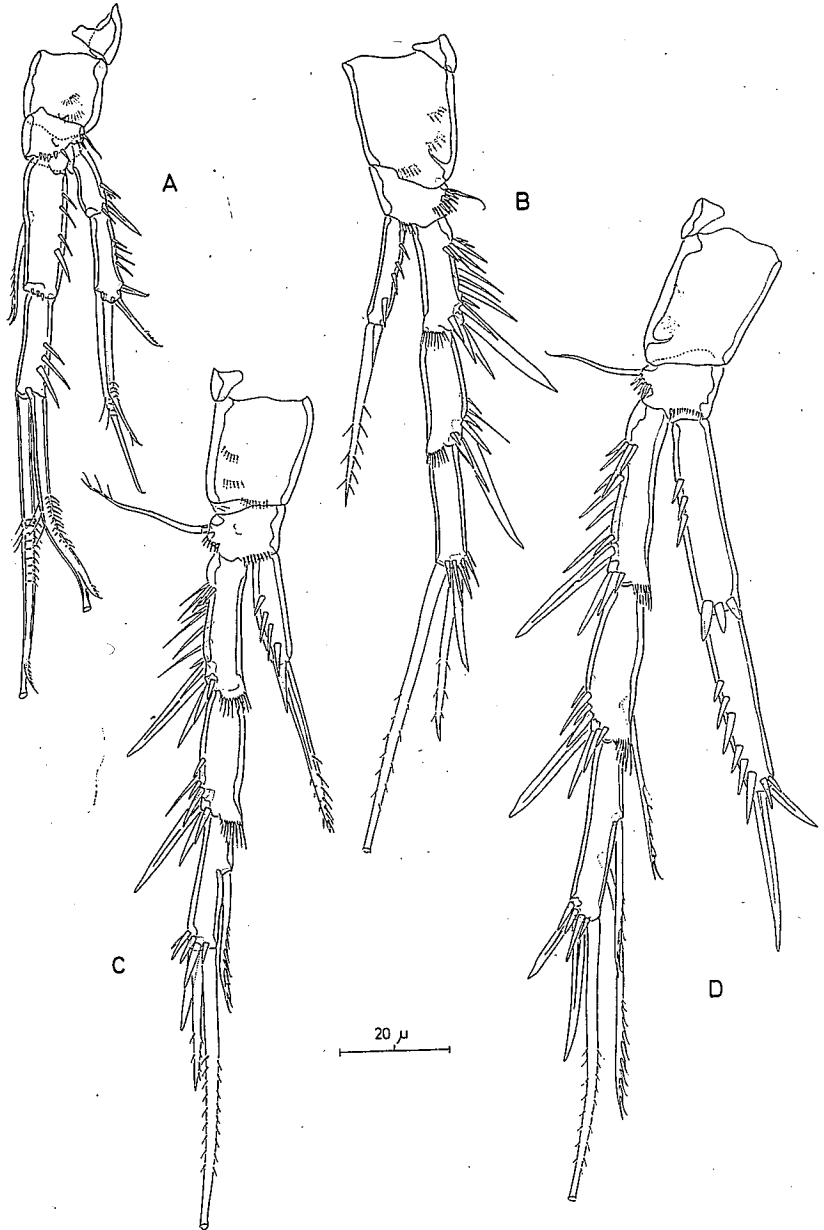


Fig. 26. — *Arenocaris bifida* Nicholls, 1935. Female. A. P1 ; B. P2 ; C. P3 ; D. P4.

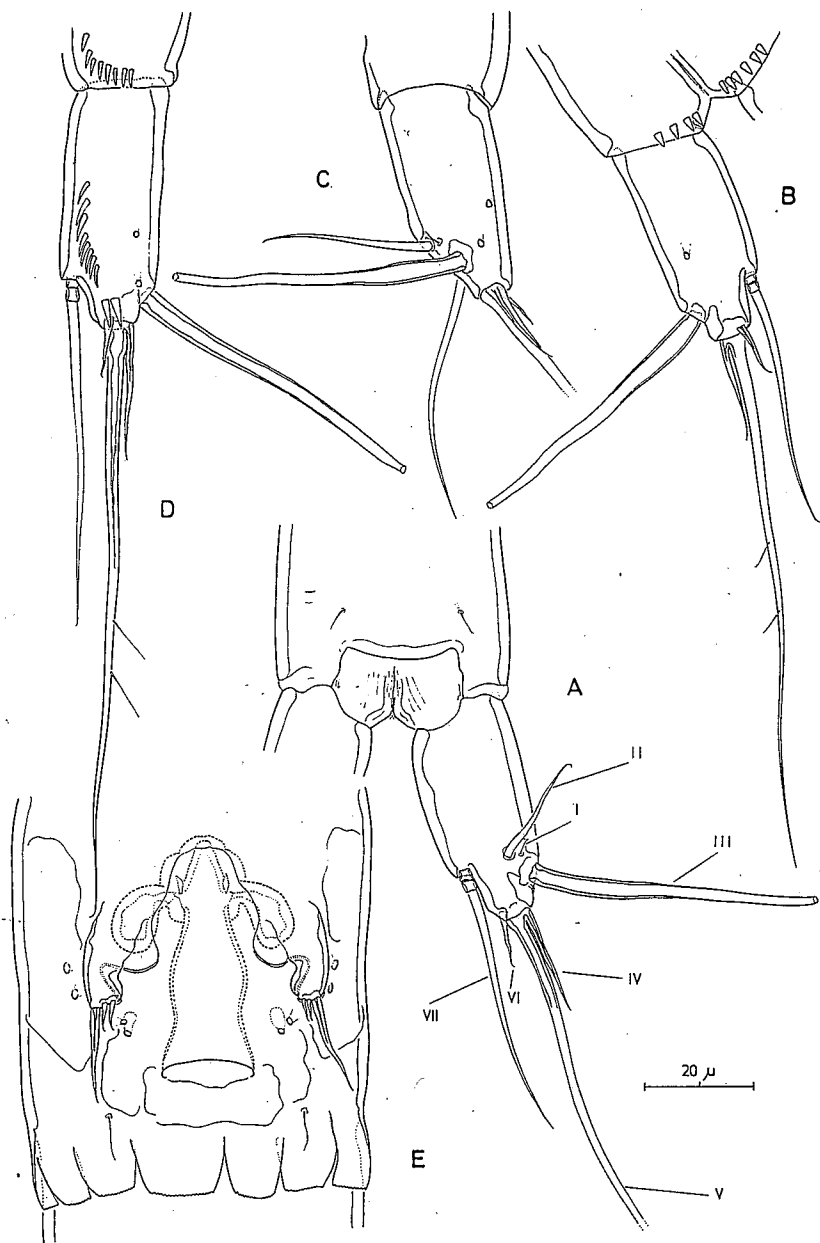


Fig. 27. — *Arenocaris bifida* Nicholls, 1935. A. Caudal ramus ♂, dorsal view; B. Same, ventral view; C. Same, lateral view; D. Caudal ramus ♀, ventral view; E. Genital double-somite ♀, ventral view.

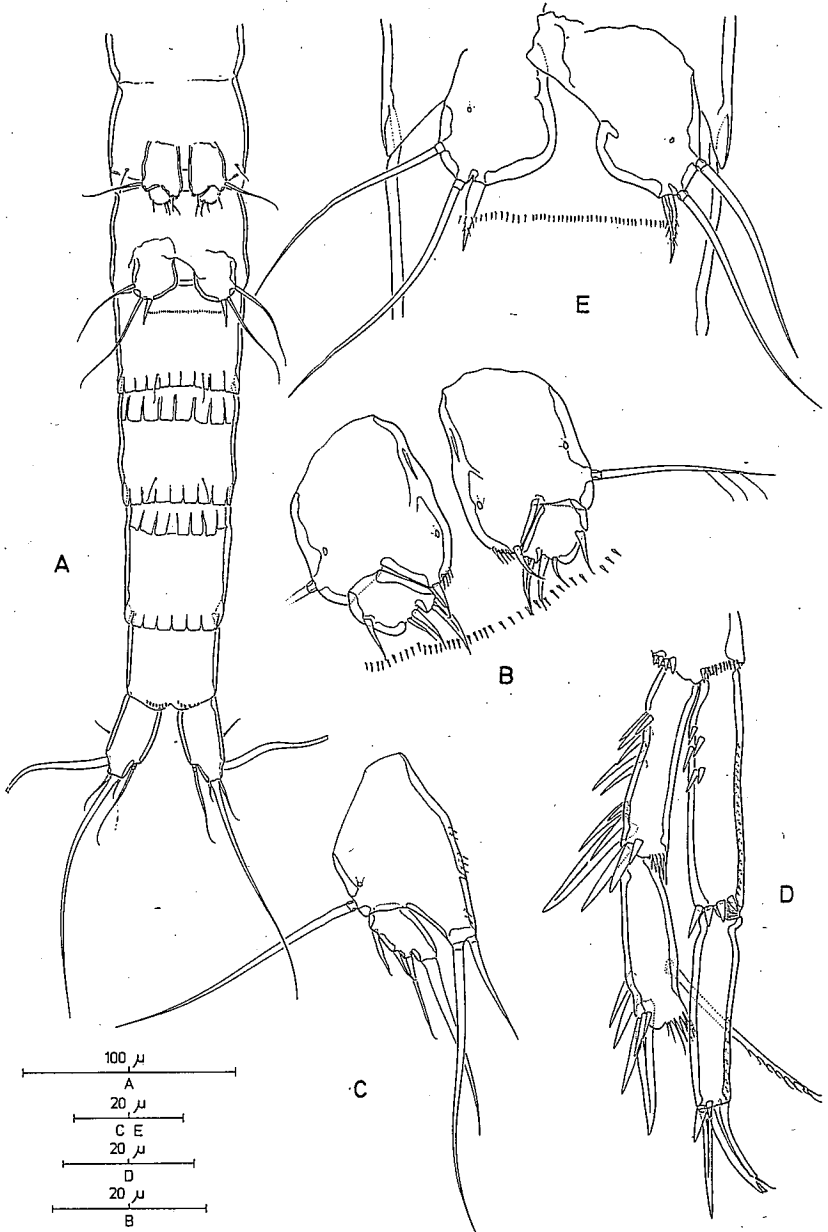


Fig. 28. — *Arenocaris bifida* Nicholls, 1935. A. Urosome ♂, ventral view; B. P5 ♂; C. P5 ♀; D. P4 ♂ (exp-3 omitted); E. P6 ♂.

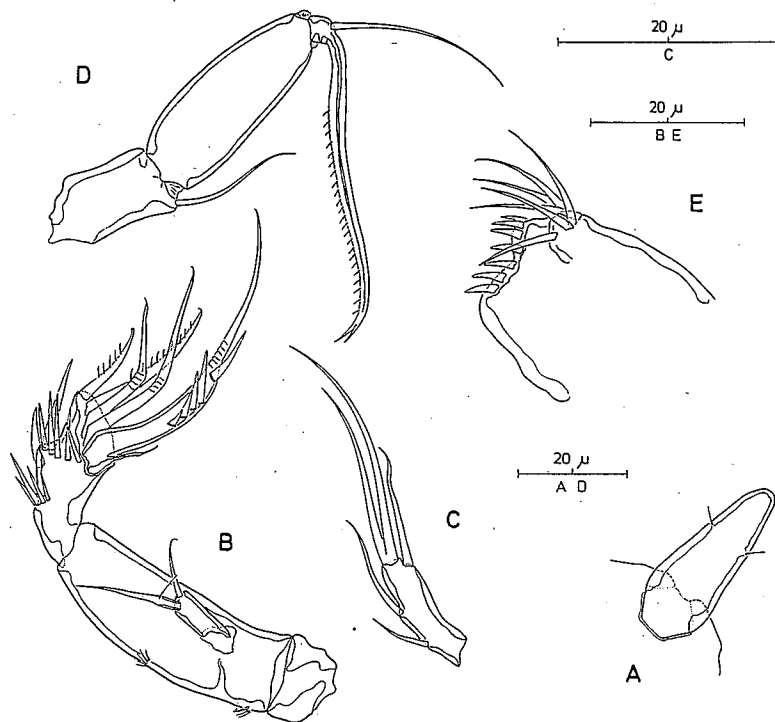


Fig. 29. — *Arenocaris bifida* Nicholls, 1935. A. Rostrum ; B. Antenna ; C. Mandibular palp ; D. Maxilliped ; E. Labrum, lateral view.

Labrum (Fig. 29E) strongly developed ; ornamentation consisting of median group of long spinules arranged around swelling of anterior face, and of smaller spinules located at distal margin of labrum ; frontal, dorsally projected, spinous process absent.

Natatorial legs (Figs. 26A-D) with 3-segmented exopods (except for P1) ; endopods 1-segmented (P2-P3) or 2-segmented (P1, P4), always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

Thoracopod 1 (P1) (Fig. 26A). Coxa strongly developed, with 2 spinular rows on posterior surface. Basis distinctly shorter than coxa ; outer seta present ; distal anterior margin with spinules. Exopod 2-segmented ; proximal segment with 1 spine and few spinules along outer margin ; distal segment longer, with 2 geniculate setae, 1 pinnate spine and 1 bare spine, and ornamentation consisting of spinules along the outer margin. First endopodal segment 1.3 times as long as distal one ; with 1 short pectinate seta midway inner margin and

few spinules along both distal and outer margins. Second endopodal segment with few large spinules along outer margin and 2 geniculate setae distally; distal portion of geniculate setae produced in subterminal funnel and pinnate recurved apex.

Thoracopods 2-4 (P2-P4) (Figs. 26B-D) with strongly developed coxae ornamented at posterior surfaces with 2 or 3 spinular rows. Basis with short (P2) or long (P3-P4) outer seta. Inner seta of middle exopodal segment P4 and distal exopodal segment P3-P4 pectinate. Inner terminal spine of distal exopodal segment P2-P4 thin-walled and tubular at the tip. Distal endopodal segment of P3 with 1 distal bipinnate seta only. Outer exopodal spine of middle segment P4 neither elongate nor recurved at tip.

Seta and spine formulae as follows :

	Exopod	Endopod
P2	0.0.021	010
P3	0.0.121	010
P4	0.1.221	0.110

Thoracopod 5 (P5) (Fig. 28C) biramous. Baseoendopod with well developed endopodal lobe bearing 2 distal setae; outer basal seta long; with 2 secretory pores on anterior surface and few spinules along inner margin. Exopod with long terminal seta and 3 smaller ones along the outer margin.

Thoracopod 6 (P6) represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 1 long and 2 short setae (Fig. 27E). Copulatory pore large, located near posterior margin of genital double somite and flanked by 4 secretory pores.

*MALE.* Body length including rostrum and caudal rami : 515-530  $\mu\text{m}$  ( $n = 5$ ). General body shape, colour, ornamentation and sensillar pattern as in female (Fig. 25B). Sexual dimorphism in antennule, fourth to sixth thoracopods, caudal rami and in genital segmentation (Fig. 28A). Genital somite (P6) and first abdominal somite with ventral transverse row of diminutive spinules (largely covered by P5 and P6, respectively) (Figs. 28A, B, E).

Antennule 8-segmented, slender; haplocer; geniculation located between segments 6 and 7; with aesthetasc on segment 4.

Fourth thoracopod (P4) (Fig. 28D). Protopod and exopod as in female. Endopod 2-segmented; proximal segment much shorter than proximal and middle exopodal segments combined, with long row of tiny spinules along the inner margin; distal segment without ornamentation along the outer margin but with tiny spinules along the distal inner margin, distal margin with short outer spine (reduced in comparison with female homologue) and short inner claw which is medially directed, provided with a bifid apex and a subapical



flagellate process. Articulation between endopodal segments specialised ; allowing for considerable inward flexure of the distal ramus portion.

Fifth thoracopod (P5) (Figs. 28B) small, biramous. Baseoendopod with weakly developed endopodal lobe bearing a small outer seta and some minute spinules at the inner distal corner. Exopod a small subcircular plate with 4 small setae, the distal one arising from an apical process.

Sixth thoracopods (P6) (Figs. 28E) asymmetrical. One member represented by small articulating plate with 1 spine and 2 long setae ; other member with same armature but larger and fused to supporting somite ; dextral and sinistral configurations present in material examined.

Caudal ramus (Figs. 27A-C) shorter than in the female ; ventral spinular row absent.

#### OTHER SPECIES

*A. reducta* sp. nov.

#### *Description* (Figs. 30 - 31)

The following description is based on a single male specimen which unfortunately was routinely dissected before habitus drawings could be made. Only the differences with *A. bifida* will be listed.

**MALE.** Body length 400  $\mu$ m, measured from the tip of the rostrum to the hind margin of the caudal rami. Anal somite without ornamentation near ventral posterior margin (Fig. 31A).

Caudal rami slightly divergent (Figs. 31A, 31B), about 1.75 times as long as maximum width. Setae IV and V not fused. Ventral surface without spinular row near inner margin.

Rostrum (Fig. 31C) about 3.2 times as long as maximum width.

Natatorial legs (Figs. 30A-D) with 3-segmented exopods (except for P1) ; endopods 1-segmented (P2-P3) or 2-segmented (P1, P4), always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

Thoracopod 1 (P1) (Fig. 30A). Coxa with 1 spinular row on posterior surface. Basis distinctly shorter than coxa ; outer seta present ; distal anterior margin with spinules. Exopod 2-segmented ; proximal segment with 1 spine and spinular row along outer margin ; distal segment spinulose along outer margin, with 2 geniculate setae and 1 bare spine. First endopodal segment 1.5 times as long as distal one ; with 1 short pectinate seta midway inner margin and few spinules along both distal and outer margins. Second endopodal segment with few slender spinules along outer margin and 2 geniculate setae distally ; distal portion of outer geniculate seta produced in subterminal funnel and pinnate recurved apex.

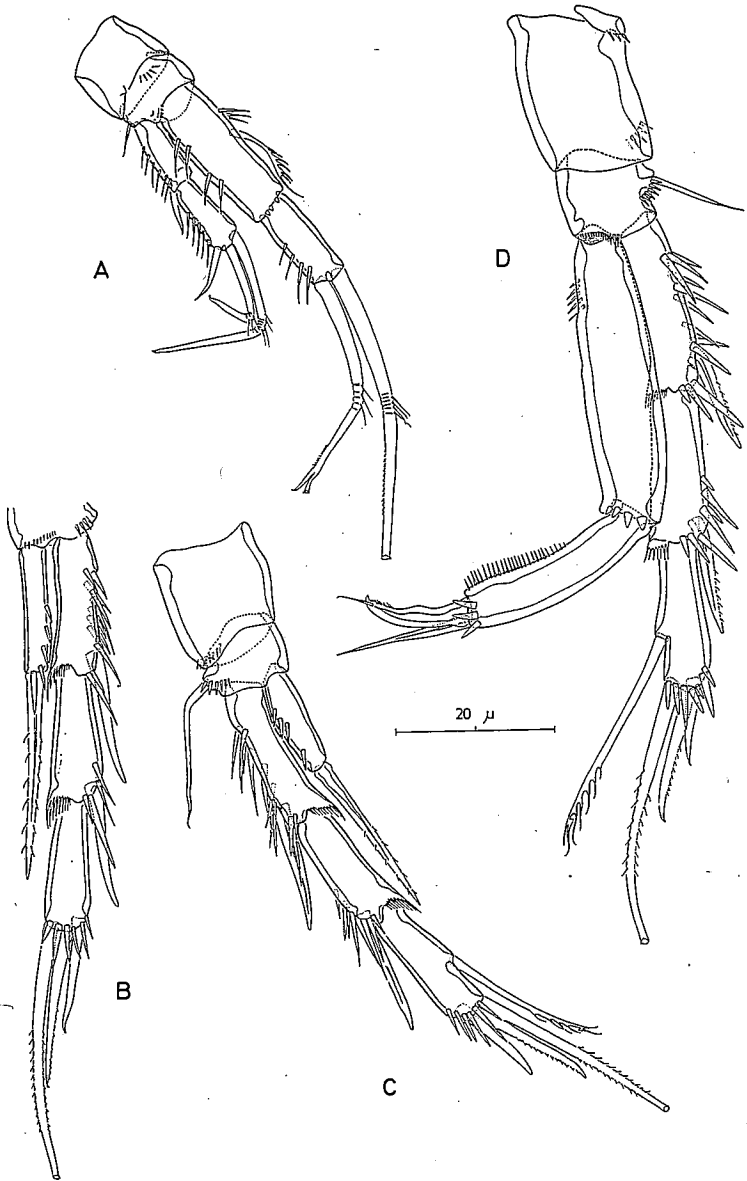


Fig. 30. — *Arenocaris reducta* sp. nov. Male. A. P1 ; B. P2 ; C. P3 ; D. P4.

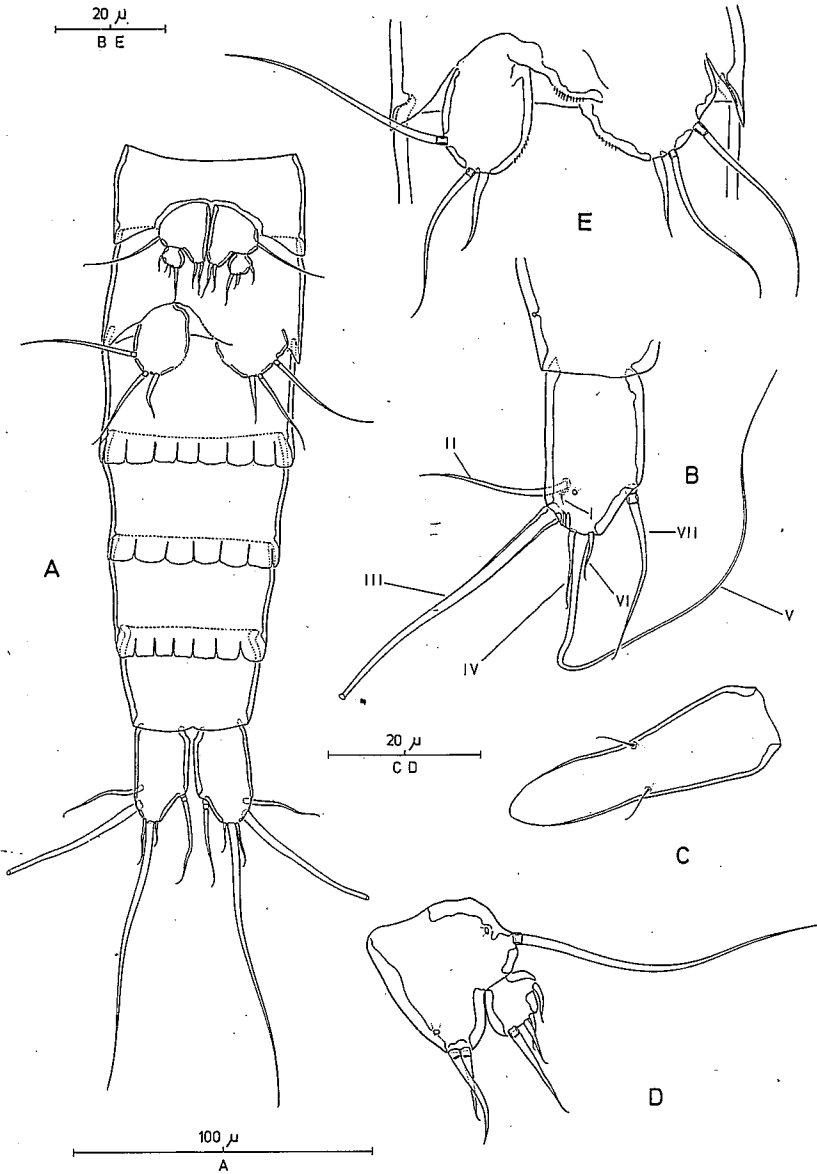


Fig. 31. — *Arenocaris reducta* sp. nov. A. Urosome ♂, ventral view; B. Caudal ramus ♂, ventral view; C. Rostrum; D. P5 ♂; E. P6 ♂.

Thoracopods 2-4 (P2-P4) (Figs. 30B-D) with strongly developed coxae ornamented at posterior surfaces with 1 spinular row. Basis with short (P2) or long (P3-P4) outer seta. Inner seta of distal exopodal segment P3-P4 pectinate. Inner terminal spine of distal exopodal segment P2-P4 thin-walled and tubular at the tip. Distal endopodal segment of P3 with 1 distal bipinnate seta only. Outer exopodal spine of middle segment P4 neither elongate nor recurved at tip.

Seta and spine formulae as follows :

	Exopod	Endopod
P2	0.0.021	010
P3	0.0.121	010
P4	0.0.121	0.110

Fourth thoracopod (P4) (Fig. 30D) with modified 2-segmented endopod. Proximal segment almost as long as proximal and middle exopodal segments combined ; with few short spinules along proximal inner margin ; distal segment medially directed, with comb of tiny spinules along the distal inner margin and a short outer spine plus a short inner claw (provided with a pinnate apex and a subapical flagellate process) distally.

Fifth thoracopod (P5) (Figs. 31D) small, biramous. Baseoendopod with weakly developed endopodal lobe bearing 2 small setae. Exopod a small sub-circular plate with 4 small setae.

Sixth thoracopods (P6) (Figs. 31E) asymmetrical ; with 1 spine and 2 long setae each ; inner margin of articulating plate with tiny spinules, other member with 2 sets of spinules along the inner margin.

#### ETYMOLOGY

The species name refers to the reduced armature of the distal exopodal segment of P1 and the middle and distal exopodal segments of P4.

#### MATERIAL EXAMINED

- *A. bifida* : 17 ♀♀, 12 ♂♂ : North Sea, Southern Bight, dumping area for TiO<sub>2</sub>-acid wastes ; 52°02'00" N, 03°13'30" E ; collected 09 July 1986 (leg. N. Smol) ; subtidal sandy sediment (median grain size : 343 µm ; 95.6% sand, 0.8% silt and 3.6% gravel) ;
- *A. reducta* : 1 ♂ (holotype) : North Sea, Southern Bight, dumping area for TiO<sub>2</sub>-acid wastes ; 52°21'03" N, 03°18'26" E ; collected 23 July 1987 (leg. N. Smol) ; subtidal sandy sediment (median grain size : 275 µm ;

100% sand); dissected on 1 slide and deposited in the Natural History Museum, London (reg. no. 1992.1111).

#### REMARKS

Nicholls' small illustrations of *A. bifida* are fairly accurate by contemporary standards and agree well with the present redescription except for the structure of the male fifth leg and the sexual dimorphism of the caudal rami which was overlooked. Sexual dimorphism of the caudal rami is rarely found within the Leptastacidae. Only *Psammastacus* shows a different kind of sexual dimorphism on these appendages. The spinular row on the female caudal ramus of *A. bifida* was not figured by Mielke (1975) presumably because it was examined in dorsal aspect. Nicholls (1935) derived the species name from the bifid distal ends of the endopodal setae of the first leg. Careful examination of these geniculate setae revealed the true nature of the bifid apex (Fig. 26A). Each of them represents a tubular seta with a subapical funnel-shaped process, suggesting that they may play a secretory role. Such a function may also be performed by the "ordinary" tubular setae found on the exopods of P2 to P4 and on the caudal rami.

The rectangular-lappeted hyaline frill of the abdominal somites is a distinctive generic character. A similar hyaline frill was also observed in *Paraleptastacus* and *Minervella*, but in these genera the frill is found around the genital somite as well (Fig. 40A). The rectangular cuticular thickenings are not associated with the hyaline frill. They are found in many other Leptastacidae (see e.g. McLachlan & Moore, 1978: Fig. 6A) and are interpreted here as mere internal structures of the integument.

The major differences between both species are encountered in the setal formula of P1 and P4, the male fifth legs and the caudal rami.

#### RELATIONSHIPS

*Arenocaris* displays a mosaic of primitive features, such as the relatively unmodified fifth legs and the retention of the syncoxal seta of the maxilliped, and various advanced character states including the sexual dimorphism of the P4 endopod and the unisegmented endopods of P2 and P3. The biramous fifth legs suggests that *Arenocaris* diverged relatively early in the evolution of the family since this character is shared only with *Paraleptastacus*. It is, however, postulated that it splitted off at a later stage than the latter genus because of the loss of the proximal outer spine on the distal exopodal segment of P2 to P4 and of the outer distal seta on the distal endopodal segment of P2. *Arenocaris* exhibits numerous autapomorphies including the tubular setae on the various thoracopods and the caudal rami, the segmentation of

the P1 exopod and of the endopods P2-P3, the sexual dimorphism of the caudal rami and the loss of sexual dimorphism on the P3 endopod. Conversely, the sistergroup relationships of *Arenocaris* remain largely unresolved. A likely candidate for the immediate outgroup position is probably *Psamathea* (see below).

## GENUS

**Psammastacus** Nicholls, 1935

## HISTORY

The taxonomic history of the genus is intricate due to the progressive addition of newly discovered species displaying various degrees of sexual dimorphism on the swimming legs. The genus *Psammastacus* was originally established (Nicholls, 1935) to accommodate two closely related species from a sandy beach of the Isle of Cumbrae, Scotland: *P. confluens* Nicholls, 1935 and *P. brevicaudatus* Nicholls, 1935. A third new species from Madras, *P. acuticaudatus* was added by Krishnaswamy (1957), but the description lacks the details necessary to allow inclusion in the genus.

In 1960 Chappuis & Rouch proposed a new genus *Arenotopa* which was similar to *Psammastacus* in the segmentation of the P1 to P4 and in the exact configuration of the fifth legs, but differed clearly in the presence of sexual dimorphism on the endopod of P3 and P4. Chappuis & Rouch (1960) attached great importance to these structures since such copulatory modifications were not reported in the previous species. The discovery of *P. perplexus* Wells & Clark, 1965 casted some doubt on the validity of the distinction between both genera because the latter species exhibited restricted sexual dimorphism on the P3 endopod. Wells & Clark (1965) interpreted the relatively simple transformation of this ramus as being a morphometric reduction (as found in many interstitial harpacticoids) rather than a functional appendage involved in copulation. They abstained therefore from erecting a new genus and tentatively allocated the new species to *Psammastacus*. With the discovery of *P. remanei* Noodt, 1964 and *P. spinicauda* Wells, 1967, one of the authors (Wells, 1967) revised his earlier opinion and synonymised *Arenotopa* with *Psammastacus*.

Both Rao & Ganapati (1969) and Cottarelli (1977) made new contributions to the taxonomy of the genus *Psammastacus* (or *Arenotopa*) but did not consider the relevant literature. Rao & Ganapati (1969) described *P. spinicaudatus* without making reference to the species descriptions postdating Krishnaswamy (1957), whilst Cottarelli (1977) added a second species *A. rossii* to the genus *Arenotopa* apparently being unaware of the controversy fueled by Wells & Clark (1965) and Wells (1967). McLachlan & Moore (1978) on the other hand continued to use *Psammastacus* in its broadest sense when they described the *Arenotopa*-like species *P. erasmusi* McLachlan & Moore, 1978.

Both Wells & Rao (1987) and Cottarelli & Venanzetti (1989) independently reinstated *Arenotopa*. The latter authors did not only resurrect the genus but further divided *Psammastacus* into two separate genera. According to Cottarelli & Venanzetti (1989) only Nicholls' species *P. confluens* and *P. brevicaudatus* should be retained in *Psammastacus* whilst the remaining species *P. acuticaudatus*, *P. remanei*, *P. spinicauda*, *P. spinicaudatus* and, with some reservations, *P. perplexus* should be allocated to the new genus *Neopsammastacus* Cottarelli & Venanzetti, 1989. Wells & Rao (1987) argued that females of *Arenotopa* and *Psammastacus* are impossible to separate in the current state of knowledge.

Re-examination of the type-material of *P. confluens*, *P. brevicaudatus*, *P. perplexus* and *P. spinicauda* has revealed new insights in the taxonomy of the genus. As a result the various species might be allocated as documented in Table 3.

#### DIAGNOSIS

Leptastacidae. Integument weakly chitinised, intersomitic boundaries not well defined, hyaline frill rudimentary. Rostrum elongated. Antennary exopod small, with 1 distal seta. Mandibular palp 2-segmented; basis without seta. Labrum without frontal, dorsally projected spinous process. P1 exopod 1-segmented; with 1 lateral spine and 3 terminal setae/spines. P1 endopod 2-segmented, not prehensile. P2-P4 endopod 2-segmented. Outer spine of exp-1 P4 absent. Spine and seta formulae as follows:

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.011
P4	0.1.121	0.010

Sexual dimorphism on endopod P3 (subdistal seta enp-2 modified into barbed, sigmoid process) and P4 (enp-2 with spinous process along inner margin). P5 uniramous and minute in both sexes; with 3 setae. Male P6 with 1 seta. Caudal ramus not acutely produced distally, slight sexual dimorphism; setae IV and V distinctly fused at their bases and laterally directed; seta V tubular.

#### TYPE SPECIES

*P. confluens* Nicholls, 1935 (by subsequent designation: Apostolov & Marinov, 1989)

syn.: *P. brevicaudatus* Nicholls, 1935 syn. nov.

TABLE 3

Allocation of *Psammastacus* species according to Wells & Rao (1987),  
Cottarelli & Venanzetti (1989) and the present account.

<p>A. Wells &amp; Rao (1987)</p> <p><i>Psammastacus</i> Nicholls, 1935</p>	<p>type species : <i>confluens</i> Nicholls, 1935 <i>brevicaudatus</i> Nicholls, 1935 <i>acuticaudatus</i> Krishnaswamy, 1957 <i>remanei</i> Noodt, 1964 <i>perplexus</i> Wells &amp; Clark, 1965 <i>spinicauda</i> Wells, 1967 <i>spinicaudatus</i> Rao &amp; Ganapati, 1969</p>
<p>B. Cottarelli &amp; Venanzetti (1989)</p> <p><i>Psammastacus</i> Nicholls, 1935</p> <p><i>Neopsammastacus</i> Cottarelli &amp; Venanzetti, 1989</p> <p>[<i>Minervella</i> Cottarelli &amp; Venanzetti, 1989]</p>	<p>type species : <i>confluens</i> Nicholls, 1935 <i>brevicaudatus</i> Nicholls, 1935</p> <p>type species : <i>spinicauda</i> (Wells, 1967)</p> <p><i>acuticaudatus</i> (Krishnaswamy, 1957) <i>remanei</i> (Noodt, 1964) <i>spinicaudatus</i> (Rao &amp; Ganapati, 1969) provisionally : <i>perplexus</i> (Wells &amp; Clark, 1965)</p> <p>[type species : <i>baccettii</i> Cottarelli &amp; Venanzetti, 1989]</p>
<p>C. Present account</p> <p><i>Psammastacus</i> Nicholls, 1935</p> <p><i>Neopsammastacus</i> Cottarelli &amp; Venanzetti, 1989</p> <p><i>Minervella</i> Cottarelli &amp; Venanzetti, 1989</p> <p><i>Afroleptastacus</i> gen. nov.</p> <p><i>Membranastacus</i> gen. nov.</p> <p>Leptastacidae <i>incertae sedis</i> :</p>	<p>type species : <i>confluens</i> Nicholls, 1935 (syn. <i>brevicaudatus</i> Nicholls, 1935 syn. nov.)</p> <p>type species : <i>spinicauda</i> (Wells, 1967) [partim]</p> <p><i>spinicaudatus</i> (Rao &amp; Ganapati, 1969)</p> <p>type species : <i>baccettii</i> Cottarelli &amp; Venanzetti, 1989</p> <p><i>perplexa</i> (Wells &amp; Clark, 1965) comb. nov.</p> <p>type species : <i>clandestinus</i> sp. nov. (syn. <i>spinicauda</i> Wells, 1967 [partim])</p> <p><i>remanei</i> (Noodt, 1964) comb. nov.</p> <p>type species : <i>inopinatus</i> sp. nov. (syn. <i>spinicauda</i> Wells, 1967 [partim])</p> <p><i>Psammastacus acuticaudatus</i> Krishnaswamy, 1957</p>



*Redescription*  
(Figs. 32 - 35)

**FEMALE.** Body length 480-500  $\mu\text{m}$  ( $n = 5$ ), measured from the tip of the rostrum to the hind margin of the caudal rami.

Body slender (Figs. 32A-B), cylindrical, vermiform, almost colourless; somitic boundaries weakly developed, functional articulations between somites almost completely reduced. Integument smooth, weakly chitinised, hyaline frill of body somites vestigial. Cephalothorax rectangular, slightly narrower than thoracic somites; no distinct separation between prosome and urosome, anal somite narrowest. Genital double-somite short compared to other genera, with genital apertures located in distal half near posterior margin; no trace of original subdivision discernible (Fig. 32C).

Caudal rami divergent (Figs. 32B; 35A-B), about 1.5 times as long as maximum width. Armature consisting of 7 setae; seta V tubular at the tip, fused at base with seta IV; seta VI moderately developed; seta VII bi-articulated at base.

Rostrum (Fig. 32B) well developed, elongated, exceeding first antennular segment, free at base. Nauplius eye not observed.

Antennule 7-segmented, slender; with aesthetasc on segment IV.

Antenna (Fig. 34A). Coxa small, unarmed. Allobasis about 2.2 times as long as maximum width; inner margin with 2 spinular rows; original segmentation not discernible. Exopod 1-segmented, small; with 1 apical seta. Distal endopodal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is swollen at the base, fused with a dwarfed seta and is ornamented with spinules around the geniculation; inner endopodal margin with 1 spine covered by a few spinules.

Mandibular palp 2-segmented (Fig. 34B); basis without seta; distal segment with 1 seta on inner and 1 seta on outer margin and 2 setae distally.

Maxillula, maxilla and maxilliped as for the family.

Labrum strongly developed; *Leptastacus*-type; without frontal, dorsally projected, spinous process.

Natatorial legs (Figs. 33A-C, E) with 3-segmented exopods (except for P1); endopods 2-segmented, always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

Thoracopod 1 (P1) (Fig. 33A). Coxa strongly developed, with 1 spinular row. Basis distinctly shorter than coxa; inner and outer setae not present; no ornamentation. Exopod 1-segmented; outer margin spinulose and with 1 bare spine; distal margin with 1 unipinnate spine and 2 geniculate setae, innermost of which longest. First endopodal segment 1.35 times as long as distal one; with 1 short pectinate seta on inner margin and few spinules on both inner and outer margins. Second endopodal segment with 2 spinular rows along outer margin and 2 geniculate setae distally.

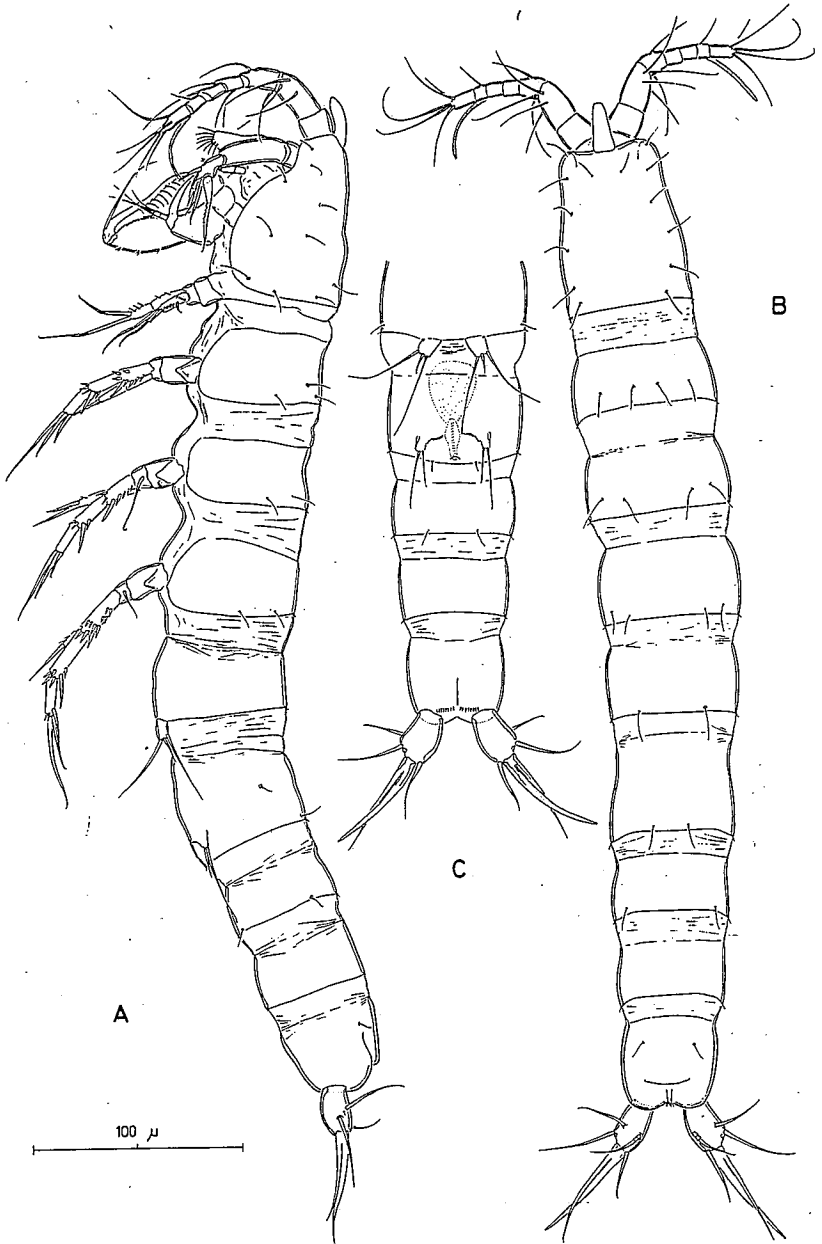


Fig. 32. — *Psammastacus confluens* Nicholls, 1935. A. ♀ habitus, lateral; B. Same, dorsal view; C. Urosome ♀, ventral view.

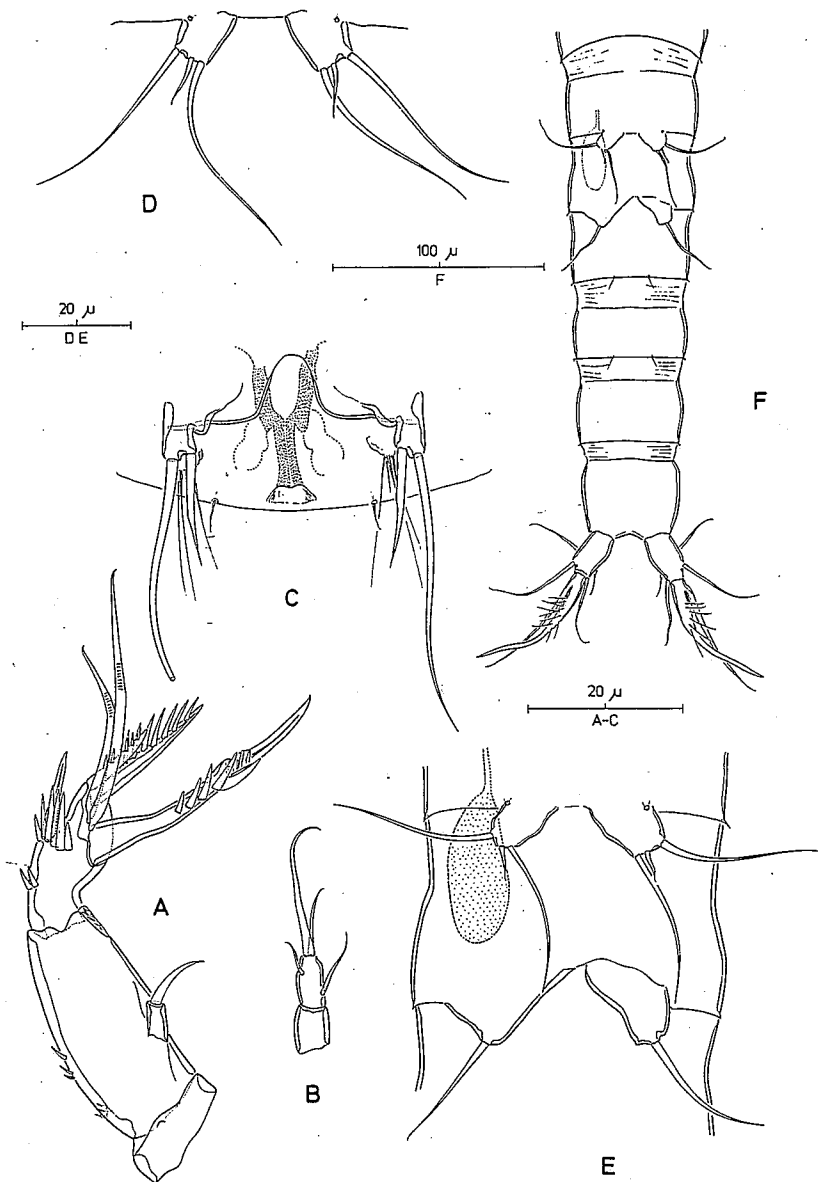


Fig. 33. — *Psammastacus confluens* Nicholls, 1935. A. P1; B. P2; C. P3; D. Endopod P3, ♂; E. P4; F. Endopod P4, ♂. (Arrows in D and F indicate outer margin).

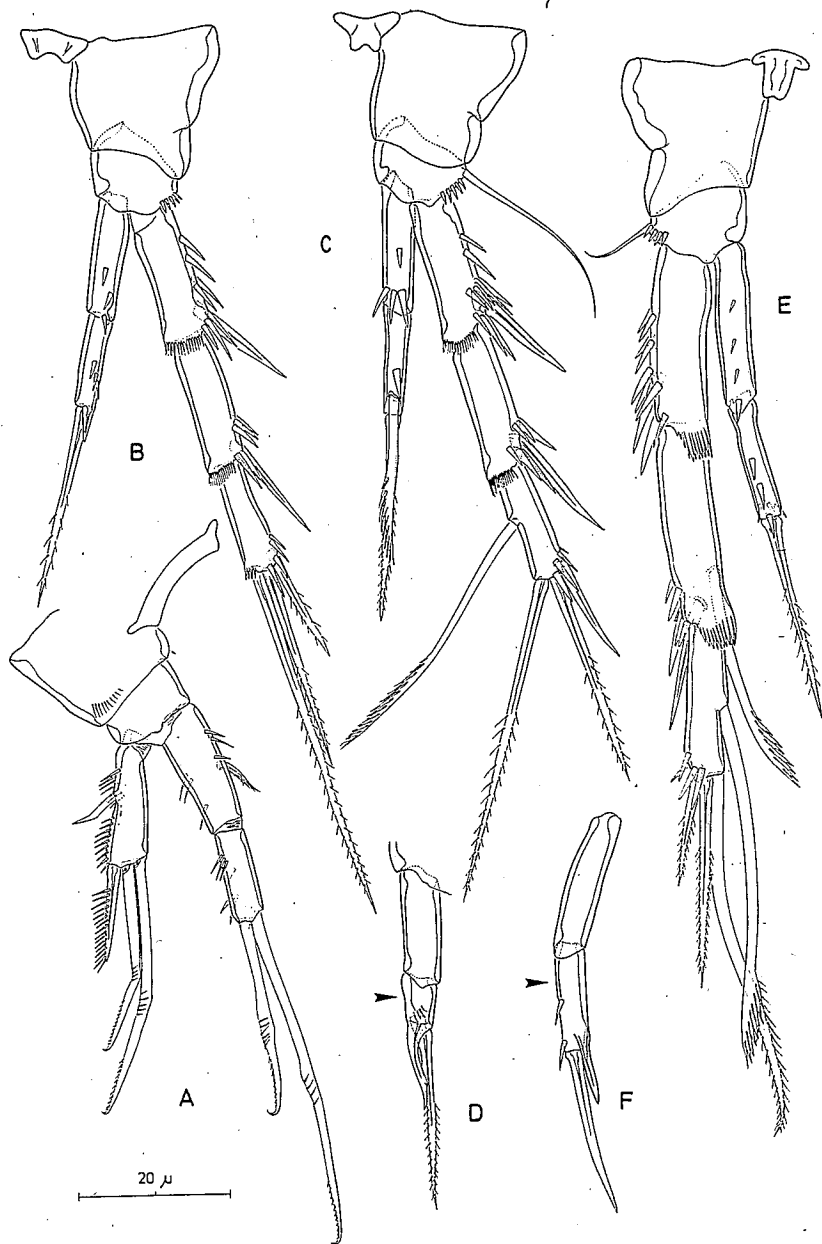


Fig. 34. — *Psammastacus confluens* Nicholls, 1935. A. Antenna ; B. Mandibular palp ; C. Genital complex, ♀ ; D. P5, ♀ ; E. P5 and P6, ♂ ; F. Urosome ♂, ventral view.

Thoracopods 2-4 (P2-P4) (Figs. 33B, C, E) with strongly developed coxae which are presumably not ornamented on both anterior and posterior surfaces. Basis of P3-P4 with outer seta. Inner seta of middle exopodal segment P4 and distal exopodal segment P3-P4 pectinate. Proximal exopodal segment P4 without outer seta. Distal endopodal segment of P3 with 1 subterminal serrate seta and 1 distal bipinnate seta. Outer exopodal spine of middle segment P4 neither elongate nor recurved at tip.

Seta and spine formulae as follows :

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.011
P4	0.1.121	0.010

Thoracopod 5 (P5) (Fig. 34D) fused to supporting somite. Exopod and baseoendopod confluent ; represented by a small plate with 3 setae, middle one being shortest.

Thoracopod 6 (P6) represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 2 long setae (Fig. 34C). A few long spinules were observed on either side of the large copulatory pore which is located near the posterior margin of the genital double-somite.

*MALE.* Body length including rostrum and caudal rami : 475-485  $\mu\text{m}$  ( $n = 3$ ). General body shape, colour, ornamentation and sensillar pattern as in female. Sexual dimorphism in antennule, third to sixth thoracopods, caudal rami and in genital segmentation (Fig. 34F).

Antennule 8-segmented, slender ; haplocer ; geniculation located between segments 6 and 7 ; with aesthetasc on segment 4.

Third thoracopod (P3) (Fig. 33D). Protopod and exopod as in female. Endopod 2-segmented ; proximal segment without spinular ornamentation ; distal segment with 1 bipinnate seta and produced into distal, sigmoid process (homologous to subterminal seta in female) bearing small barb along inner margin.

Fourth thoracopod (P4) (Fig. 33F). Protopod and exopod as in female. Endopod 2-segmented ; no spinules discernible on proximal segment ; distal segment with bare spine distally and spinous process at the inner subdistal corner.

Fifth thoracopod (P5) (Figs. 34E-F) fused to supporting somite. Exopod and baseoendopod confluent ; represented by a small plate with 3 setae, middle one being shortest.

Sixth thoracopods (P6) (Figs. 34E-F) asymmetrical. One member represented by small articulating plate with 1 seta ; other member fused to supporting

somite and represented by small lobe with 1 seta; sinistral and dextral configurations present in material.

Caudal ramus (Figs. 34F, 35C) slightly more slender than in the female; seta expanded proximally and furnished with long setules in proximal half; seta VI longer than in female.

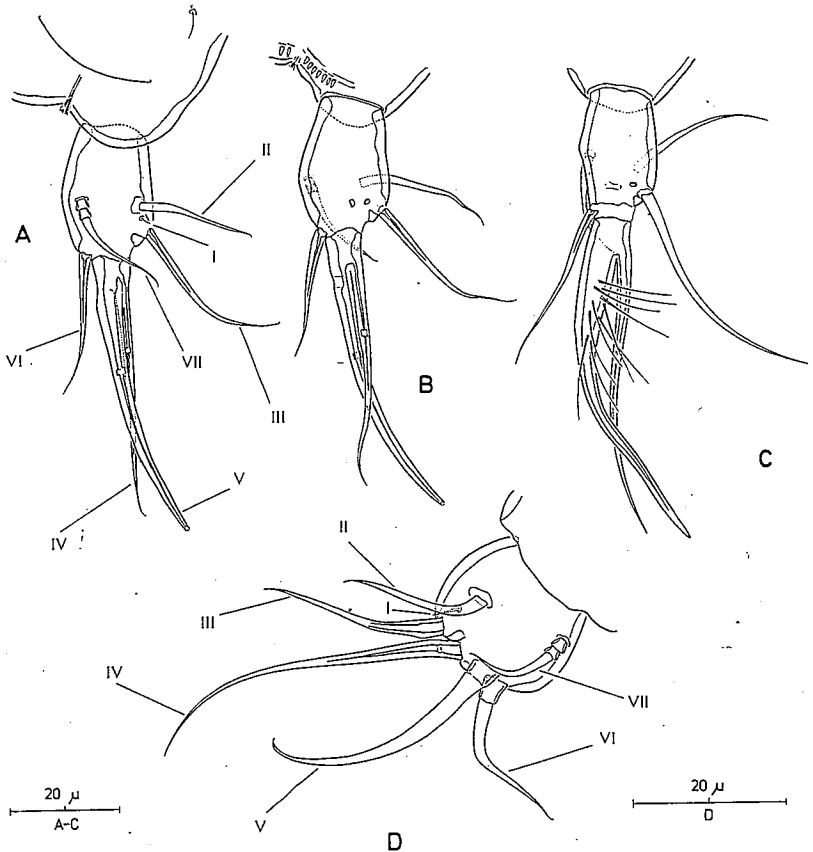


Fig. 35. — *Psammastacus confluens* Nicholls, 1935. A. Caudal ramus ♀, dorsal view; B. Same, lateral view; C. Caudal ramus ♂, ventral view; D. Caudal ramus of copepodid V, dorsal view.

*SPECIES INQUIRENDAE*

*P. confluens* Nicholls, 1935 *sensu* Chappuis (1954a)

*P. confluens* Nicholls, 1935 *sensu* Apostolov (1977), Apostolov & Marinov (1989)

## MATERIAL EXAMINED

- *P. confluens*: The Natural History Museum, reg. no. 1936.2.24.17-22; 5 ♀♀ and 5 ♂♂ in alcohol, 1 ♀ dissected on 6 slides, 1 ♂ dissected on 5 slides; Kames Bay, Millport, Isle of Cumbrae; leg. A.G. Nicholls; status not specified (presumably syntypes);
- *P. brevicaudatus*: The Natural History Museum, reg. nos 1947.12.1.4 and 1936.2.24.23-26; about 100 specimens preserved in alcohol in 2 vials; Kames Bay, Millport, Isle of Cumbrae; leg. A.G. Nicholls; syntypes.

## REMARKS

Nicholls' (1935) description of *P. brevicaudatus* based on specimens from Kames Bay, Millport leaves little doubt that he was dealing with immature specimens and the apparent lack of males in his sample might be attributed to this. The 6-segmented antennule and the segmentation of the urosome (with the very small "genital double somite") shown in the original illustrations indicate that Nicholls had examined a copepodid V stage rather than an adult. Inspection of the paratypes corroborates this interpretation and, in addition, revealed that they belong to *P. confluens*. This is not surprising since they were collected from the same locality. The differences mentioned by Nicholls for the mandibular palp setation and swimming leg armature are based on inaccuracies or are due to the immature condition of the specimens. His statement on the egg-sac is definitely wrong since the material contained only juveniles. The conspicuous difference in the caudal ramus is worth considering (Fig. 35D). Apart from the shape (cf. name), there is a distinct difference in the condition of setae IV and V. In the copepodid V stage these setae are free at the base, their separation being pronounced by individual socles, whereas in the adults they are confluent at the base. This indicates that the fusion of setae IV and V cannot be interpreted as the result of a heterochronic event since it is known that these setae are still fused in the early copepodids of most harpacticoids. The pattern displayed in *P. confluens* is in marked contrast with the developmental process found in *Cerconeotes*. Here the fused condition in the adult is the result of neoteny (see observations on *C. mozambicus* and section 2.4.2.).

Chappuis (1954a) states that his two female specimens from Algeria agree in all details with Nicholls' description, however, his illustration of the fifth leg shows only 2 setae. Similarly, it is impossible to allocate Apostolov's (1977) male to *P. confluens*. His drawings of the Black Sea specimen lack sufficient detail and moreover the first exopodal segment of P4 shows an outer spine (which perhaps might have been mistaken for a long spinule). In the current state of knowledge both Chappuis' and Apostolov's material can be considered only *species inquirendae* in the genus.

#### RELATIONSHIPS

Cottarelli & Venanzetti (1989) discussed the differences between *Psammastacus*, *Neopsammastacus*, *Arenotopa* and *Minervella*. This comparison was based on relatively few characters: setation of the antennary exopod, segmentation of the mandibular palp and presence of sexual dimorphism on P2-P4. According to these authors both *Psammastacus* and *Neopsammastacus* lack male modifications on the swimming legs and have a 2-segmented mandibular palp though the latter character remained partially unconfirmed in their analysis. This leaves the presence of either 1 or 2 setae on the antennary exopod as the only character for distinguishing the two genera. A comparison of *Psammastacus* as it is defined herein with the other species previously allocated to this genus proved Cottarelli & Venanzetti's (1989) decision to separate *P. confluens* and *P. brevicaudatus* from the remainder of species to be valid, yet on different grounds. The genus *Neopsammastacus* as it was diagnosed by these authors, however, cannot be accepted since it turned out to represent a paraphyletic group (see below). Their statement that both *Psammastacus* and *Neoleptastacus* lack sexual dimorphism is also erroneous but was founded on previous observations that failed to detect such male modifications on the swimming legs (Nicholls, 1935; Krishnaswamy, 1957; Wells, 1967; Rao & Ganapati, 1969).

*Psammastacus* belongs to the group of genera comprising *Cerconeotes*, *Schizothrix* and *Belemnopontia*. Members of this group show a particular type of sexual dimorphism on the endopod of P3, i.e. the presence of a barbed process on the outer distal corner of the distal endopodal segment. This process is found in for example *C. mozambicus* (Fig. 48D), *Schizothrix* sp. (from the Belgian coast) and *B. dispinosus panamensis* (Mielke, 1983: Abb. 6C). It is homologous with the subterminal serrate seta sited at the anterior surface (and for that reason sometimes overlooked) of the distal segment in the female. Its derivation is different from the recurved process found in other genera related to *Minervella* where it represents an elaboration of the distal margin of the segment (cf. the anterior seta is lost in these genera).



Within its lineage *Psammastacus* represents the most advanced genus. This is perhaps best exemplified by the accumulation of morphological reductions in the antenna, mandible, P1, P5 and P6, each of them in itself representing the most apomorphous character state found in the family. The simplifications in body plan have also affected the exoskeletal properties of the animals, their integument being very weakly chitinised and the intersomitic boundaries and articulations strongly reduced. The adoption of vermiformity is also found in other interstitial families such as the Paramesochridae (*Apodopsyllus* Kunz, 1962; *Leptopsyllus* T. Scott, 1894) and marks the final phase in a gradual adaptation to the interstitial habitat. *Psammastacus* is most closely related to *Belemnopontia* and *Cerconeotes*, because of the loss of the inner seta on the proximal endopodal segment of P2 and P3, the loss of the proximal inner seta on the distal exopodal segment of P4, the reduction of the mandibular palp and reductions in the fifth legs. Comparison with *Cerconeotes* suggests a sistergroup relationship with this genus. Evidence for this affinity is found in the caudal rami though the shared basal fusion of setae IV and V is a product of convergence. However, *Cerconeotes* and *Psammastacus* are unique within the family by the presence of a tubular inner terminal seta (V). They are also the only genera that have a maximum of 2 setae on the male sixth legs, although in *Psammastacus* this reduction proceeded to the 1 seta-condition, and show a synapomorphic state for the 5th thoracopod in both sexes, i.e. the loss of setae *a* and *e* (see section 2.4.1.).

The configuration of the exopod of P1 in *Psammastacus* is reminiscent of the condition found in *Minervella*, *Arenotopa*, etc. (Figs. 34A, 41A) but this is interpreted here as a result of convergence. The latter genera (and all other species previously assigned to *Psammastacus*) belong to a lineage defined by — amongst other characters — the modification of seta VI and the presence of an oblique spinular row on the caudal ramus. These characters are very conservative within this lineage but are not observed in *Psammastacus* nor in any of its closest relatives. The P1 exopod of the sistertaxon *Cerconeotes* presents additional evidence for a convergent evolution of the *Psammastacus* condition, since the outer terminal spine is already lost here (Fig. 48A).

The discovery of an intermediate genus with a 2-segmented exopod and 3 elements on the distal segment would then perfectly bridge the morphological gap between both genera. The loss of the outer seta on exp-3 of the P1 is regarded as a synapomorphy linking *Cerconeotes* and *Psammastacus*.

There are numerous unique autapomorphies for *Psammastacus*, including the sexual dimorphism on the endopod of P4 and on the caudal rami, the unisetose condition of the antennary endopod and of the male sixth legs, the fusion of setae IV and V on the caudal rami and the extreme reduction of the fifth legs in both sexes.

## GENUS

*Arenotopa* Chappuis & Rouch, 1960

syn. : *Psammastacus* Nicholls, 1935 (partim) : Wells (1967), McLachlan & Moore (1978), Bodin (1979, 1988)

## HISTORY

After a long history of alternating synonymisation and reinstatement, it appears that the separate status of the genus *Arenotopa* is finally accepted (Bodiou & Colomines, 1986 ; Wells & Rao, 1987 ; Cottarelli & Venanzetti, 1989).

## DIAGNOSIS

Leptastacidae. Rostrum elongated triangular. Hyaline frill of urosomites reduced, plain. Antennary exopod with 2 distal setae. Mandibular palp unconfirmed. Labrum without frontal recurved process. P1 exopod 1-segmented ; with 1 lateral spine and 3 terminal setae/spines. P1 endopod 2-segmented, not prehensile. P2-P4 endopod 2-segmented. Spine and seta formulae as follows :

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.[0-1]21	0.010
P4	0.1.[1-2]21	0.110

Strong sexual dimorphism on endopod P3 and endopod (and probably exopod) P4. P5 uniramous in both sexes ; in female with 4-5 setae ; in male with 3-4 setae. Male P6 with 3 setae, middle one vestigial. Caudal ramus not acutely produced distally ; seta VI short and spiniform ; dorsomedial surface of each ramus with oblique spinular row ; dorsal hind margin with movable recurved spinule.

## TYPE SPECIES

*A. ghanai* Chappuis & Rouch, 1960 (by monotypy)

## OTHER SPECIES

*A. rossii* Cottarelli, 1977

*A. erasmusi* (McLachlan & Moore, 1978) Wells & Rao, 1987  
syn. : *Psammastacus erasmusi* McLachlan & Moore, 1978

*A. dyadacantha* Wells & Rao, 1987

## MATERIAL EXAMINED

- *A. erasmusi*: South African Museum, holotype ♀ (reg. no. SAM-A15717), allotype ♂ (reg. no. SAM-A15718) and 7 paratype ♀♀ (SAM-A15719); all specimens are whole mounts in polyvinyl lactophenol; Sunday's River beach, Algoa Bay, South Africa; low tide level, medium sand (leg. A. McLachlan & J. P. Furstenberg);
- the type material of *A. ghanai* is lost (Rouch, *in litt.*); requests to borrow *A. rossii* and *A. dyadacantha* failed.

## RELATIONSHIPS

The genus *Arenotopa* is unique within the family because of the atypical sexual dimorphism on the P3 and P4 (see Figs. 36B-D). The various species can be arranged along an evolutionary gradient according to the degree of modification exhibited on these limbs. *A. dyadacantha* is the least modified and *ghanai-rossii* the most advanced ones; *A. erasmusi* occupies an intermediate position. It is postulated that *Arenotopa* is most closely related to the new genus *Afroleptastacus* (see below).

GENUS **Neopsammastacus** Cottarelli & Venanzetti, 1989

syn.: *Psammastacus* Nicholls, 1935 (partim): Krishnaswamy (1957), Wells (1967), Rao & Ganapati (1969), Wells & Rao (1987)

## HISTORY

The taxonomy of *Neopsammastacus* is utterly confusing. The reason for the taxonomic imbroglio created by Cottarelli & Venanzetti (1989) is twofold.

First, the genus *Neopsammastacus* was merely proposed to receive all *Psammastacus* species that could no longer fit the revised generic diagnosis as it was presented by Cottarelli & Venanzetti. At best the genus can be considered an artificial repository for species which individually were urgently in need of revision. The few generic characters presented are either plesiomorphic (antennary exopod with 2 setae), unconfirmed (mandibular palp 2-segmented) or not diagnostic (P2 - P4 without sexual dimorphism).

Second, Cottarelli & Venanzetti (1989) unintentionally fueled the confusion by selecting *P. spinicauda* Wells, 1967 as the type species. Inspection of the paratypes revealed that Wells (1967) had examined an amalgamate of 3 species whose major differentiating characters are:

- Species A (6 ♀♀, 4 ♂♂): hyaline frill of urosomites rectangular-lappeted; labrum with dorsal recurved process; endopod P3 with sexual dimorphism;

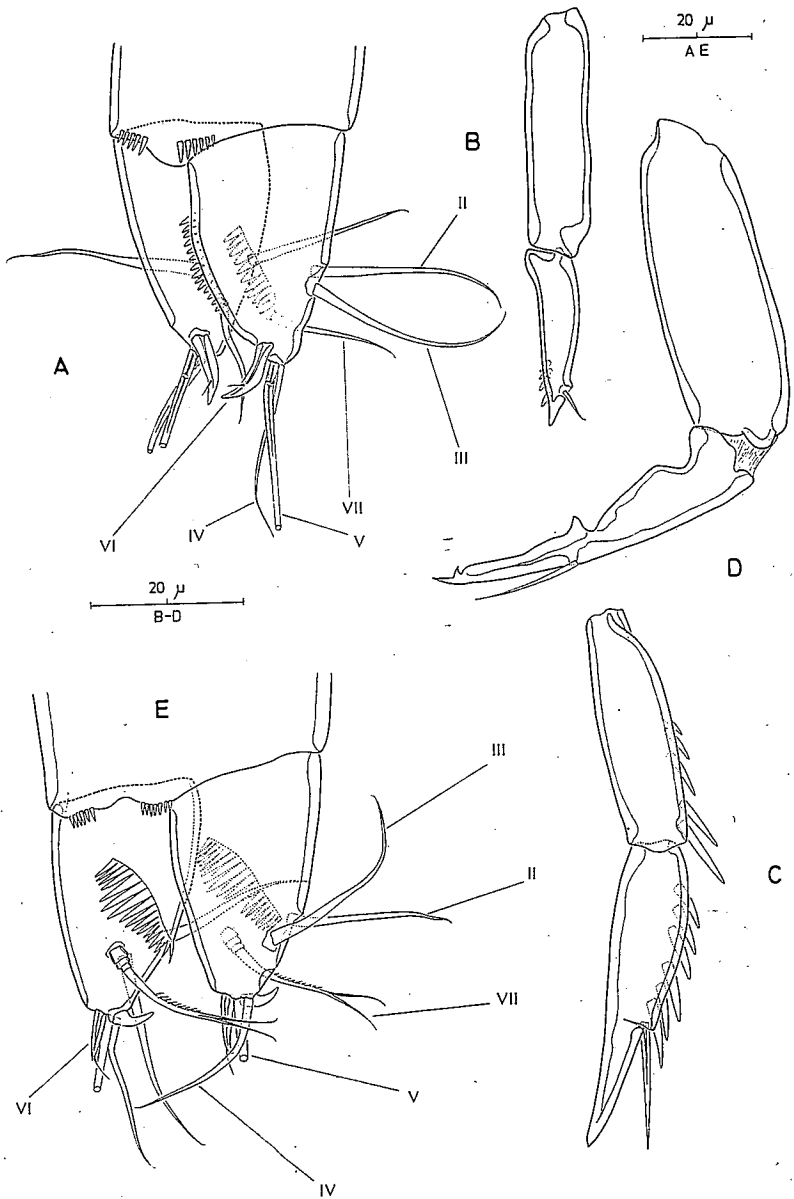


Fig. 36. — *Sextonis naylori* (McLachlan & Moore, 1978) comb. nov., A. Caudal rami, ventrolateral view; *Arenotopa erasmusi* (McLachlan & Moore, 1978), B. Endopod P3, ♂; C. Endopod P4, ♀; D. Endopod P4, ♂; E. Caudal rami, ventrolateral view.

exopod P4 without sexual dimorphism ; fifth legs with 7 setae in both sexes ; ventral hind margin of anal somite with large spinules decreasing in size towards the lateral part ; inner dorsal surface of caudal ramus with strong spinules ;

— Species B (4 ♀♀, 1 ♂) : hyaline frill of urosomites reduced, plain ; labrum with dorsal recurved process ; endopod P3 with sexual dimorphism ; exopod P4 without sexual dimorphism ; fifth legs with 6 setae in ♀ and 5 setae in ♂ ; ventral hind margin of anal somite with few small spinules of equal size ; inner dorsal surface of caudal ramus with almost hyaline spinules ;

— Species C (2 ♀♀, 1 ♂) : hyaline frill of urosomites reduced, plain ; labrum without dorsal recurved process ; endopod P3 without sexual dimorphism ; exopod P4 with sexual dimorphism ; fifth legs with 7 setae in ♀ and 5 setae in ♂ ; ventral hind margin of anal somite with few small spinules of about equal size ; inner dorsal surface of caudal ramus with almost hyaline spinules.

Wells (1967) remarked that the combination of ornamentation of the anal somite and the caudal rami was always consistent, however, he did not test the possibility that this might have been caused by two or more intermingled species. His combination (a) + (a) agrees with species A but both species B and C display the (b) + (b) ornamentation pattern. Clearly, more characters have to be considered before a conclusion can be reached about the real identity of *P. spinicauda*. This procedure is hindered in the absence of the holotype which never has been deposited in the Natural History Museum, London (S.H. Halsey, pers. comm.) and which is in all probability lost.

Comparison of the three species distinguished among the "paratypes" of *P. spinicauda* revealed that Wells' illustrations of the P3, the fifth legs of both sexes and the male sixth legs were taken from specimens belonging to species B. According to Wells' description *P. spinicauda* possesses a deeply divided hyaline frill on the abdominal somites and a frontal spinous process on the labrum. The combination of these characters is displayed only by species A, however this species shows a distinct transformation of the male endopod P3. Wells' statement that *P. spinicauda* lacks any trace of sexual dimorphism on the swimming legs is erroneous since all three species show male modifications on these appendages. Presumably this statement was based on observations of either species B or species C since only slight dimorphism is developed here. The foregoing illustrates that the actual description was based on at least two species. In the absence of a holotype this is regarded as an "exceptional circumstance" (ICZN Art. 75(b)) allowing the designation of a neotype which is essential for solving this complex nomenclatorial problem.

Since the majority of Wells' (1967) drawings were based on species A, it is herein formally identified as *Neopsammastacus spinicauda* (Wells, 1967) and redescribed *in extenso* below. Species B and C do not belong to *Neopsammastacus* but will be designated as type species of two new genera, *Membranastacus* gen. nov. and *Afroleptastacus* gen. nov., respectively (see below).

## DIAGNOSIS

Leptastacidae. Rostrum triangular with rounded apex. Hyaline frill of urosomites rectangular-lappeted. Antennary exopod with 2 distal setae. Mandibular palp 2-segmented; basis with 1 seta. Labrum with frontal recurved process. P1 exopod 1-segmented; with 1 lateral spine and 3 terminal setae/spines. P1 endopod 2-segmented, not prehensile. P2-P4 endopod 2-segmented. Spine and seta formulae as follows:

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.011
P4	0.1.221	0.110

Sexual dimorphism on endopod P3 (reduction of distal segment and formation of recurved process). P5 uniramous and with 7 setae in both sexes. Male P6 with 3 well developed setae. Caudal ramus not acutely produced distally; seta VI short and spiniform; dorsomedial surface of each ramus with oblique spinular row.

## TYPE SPECIES

*N. spinicauda* (Wells, 1967) Cottarelli & Venanzetti, 1989  
syn.: *Psammastacus spinicaudus* Wells, 1967 (partim)<sup>5</sup>

*Redescription*  
(Figs. 37 - 39)

**FEMALE.** Body length 440-480  $\mu\text{m}$  ( $n = 4$ ), measured from the tip of the rostrum to the hind margin of the caudal rami.

Body slender, cylindrical, almost colourless; intersomitic boundaries well developed (Fig. 37A). Integument smooth, moderately chitinised. Hyaline frill of cephalothorax and somites bearing P2 to P5 striated (Figs. 37A, C), of genital double somite and 2 following somites broadly lappeted (Figs. 37A, B). Cephalothorax tapering anteriorly, no distinct difference in width between cephalothorax and free body somites; no distinct separation between prosome and urosome, anal somite narrowest. Genital double-somite longer than wide, with genital apertures located in anterior half (Fig. 37F); no trace of original subdivision.

Anal somite with strong spinules at midventral hindmargin, decreasing in size to the lateral part (Fig. 39B).

<sup>5</sup> The species name was originally misspelled and should be *spinicauda*.

Caudal rami slightly divergent (Figs. 39A-C), about 2.2 times as long as maximum width, distinctly tapering posteriorly, with concave medial margin. Armature consisting of 7 setae; seta V strongly developed and together with small seta IV arising from common cylindrical socle; seta VI strongly spiniform; seta VII bi-articulated at base and pinnate. Dorsal inner margin of ramus with oblique spinular row consisting of strongly chitinised spinules which are largest in the middle of the row (Fig. 39A); ventral inner margin with few tiny spinules (Fig. 39B).

Rostrum (Fig. 37E) well developed, triangular with rounded anterior margin; exceeding first antennular segment, free at base. Nauplius eye not observed.

Antennule 7-segmented, slender; with aesthetasc on segment IV.

Antenna (Fig. 37D). Coxa small, unarmed. Allobasis about 2.9 times as long as maximum width; original segmentation not discernible. Exopod 1-segmented, small; with 2 apical setae. Distal endopodal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is swollen at the base, fused with a dwarfed seta and ornamented with spinules around the geniculation; inner endopodal margin with 2 spines covered by a few spinules.

Mandibular palp 2-segmented (Fig. 37D); basis with 1 seta; distal segment with 1 inner seta, 1 outer seta and 2 apical confluent setae.

Labrum strongly developed (Figs. 37A, D); with frontal dorsally projected spinous process covered with long spinules proximally, and flanked by lobes with smaller spinules.

Maxillula, maxilla and maxilliped as for the family.

Natatorial legs (Figs. 38A-D) with 3-segmented exopods (except for P1); endopods 2-segmented, always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

Thoracopod 1 (P1) (Fig. 38A). Coxa strongly developed, without ornamentation. Basis distinctly shorter than coxa; inner and outer setae not present; no ornamentation. Exopod 1-segmented; outer margin spinulose and with 1 bare spine; distal margin with 1 unipinnate spine and 2 geniculate setae, innermost of which longest. First endopodal segment about as long as distal one; with 1 short pectinate seta on inner margin and few spinules along outer margin. Second endopodal segment with 2 spinular rows along outer margin and 2 geniculate setae distally.

Thoracopods 2-4 (P2-P4) (Figs. 38B-D) with strongly developed coxae; not ornamented. Basis of P3-P4 with outer seta. Inner setae of middle exopodal segment P4 and of distal exopodal segment P3-P4 pectinate. Distal endopodal segment of P3 with 1 distal bipinnate seta and 1 subapical short spine. Outer exopodal spine of proximal and middle segments P4 neither elongate nor recurved at tip.

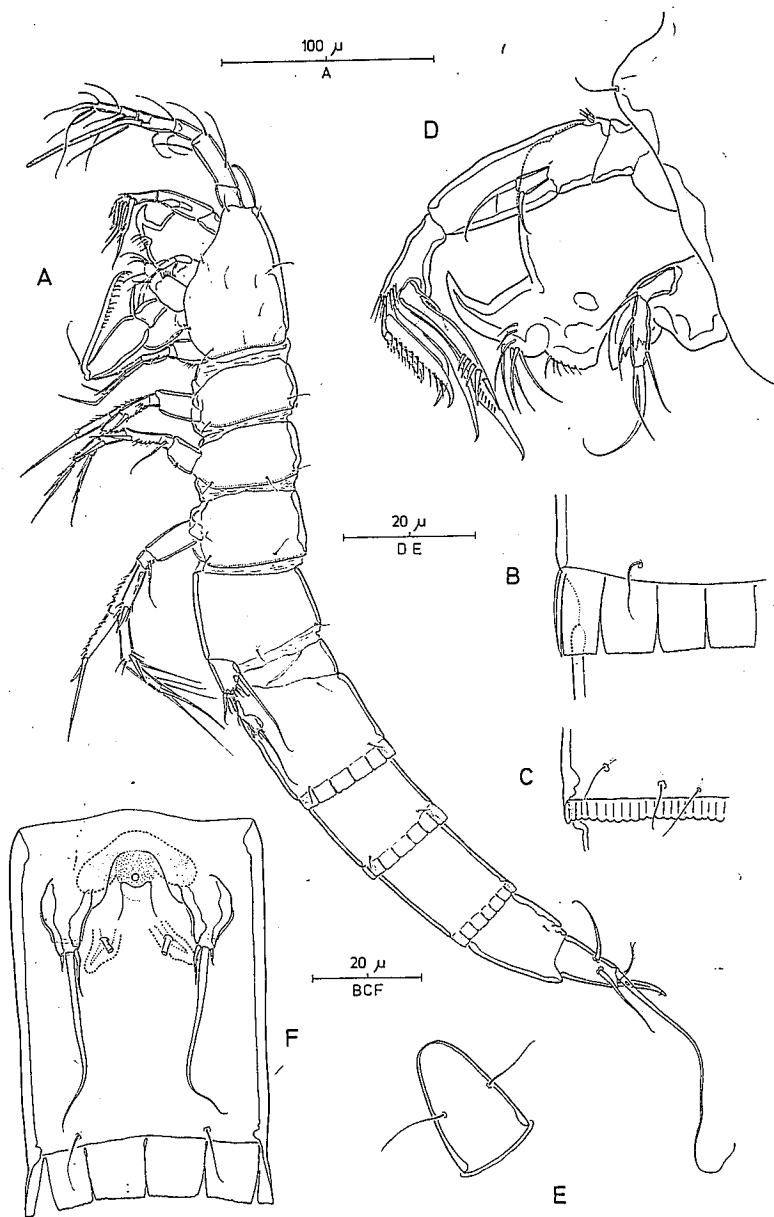


Fig. 37. — *Neopsammastacus spinicauda* (Wells, 1967). A. Habitus ♀, lateral view; B. Hyaline frill of genital double-somite; C. Hyaline frill of P4-bearing somite; D. Antenna, labrum and mandibular palp, lateral view; E. Rostrum; F. Genital double-somite, ventral view.



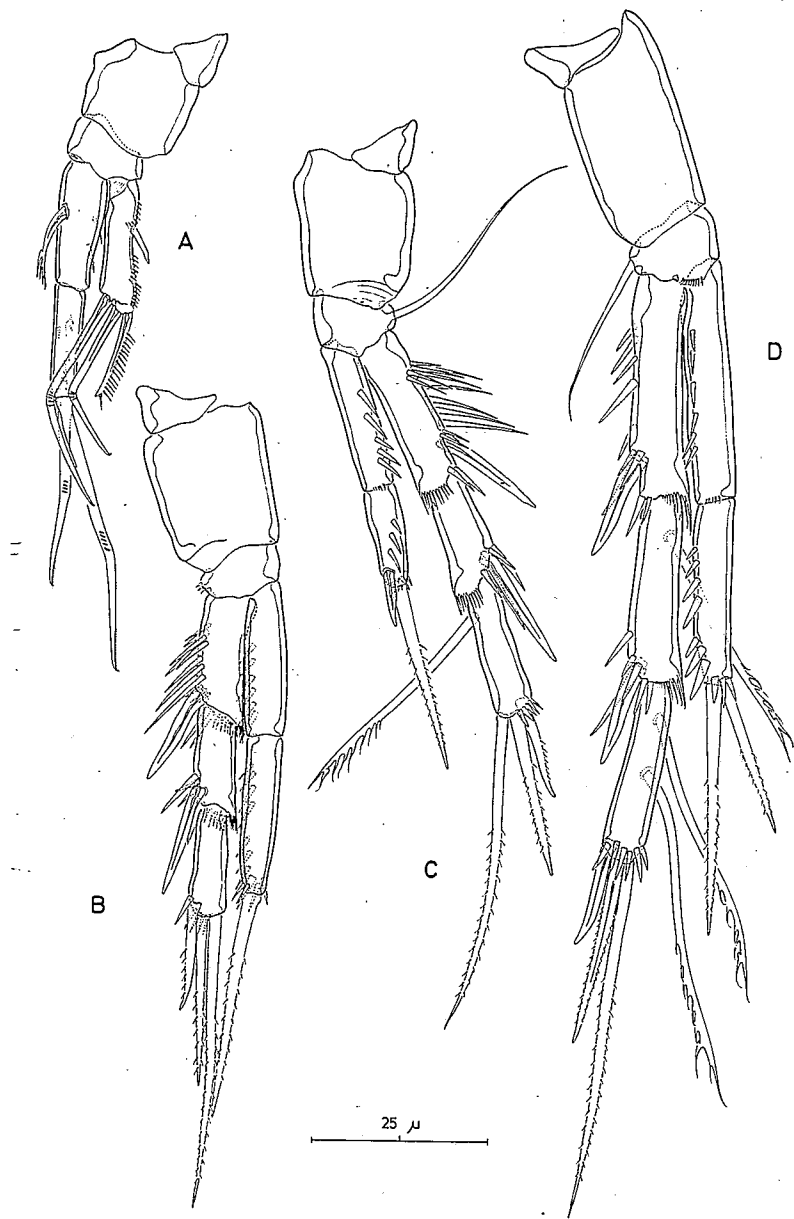


Fig. 38. — *Neopsammastacus spinicauda* (Wells, 1967). Female. A. P1; B. P2; C. P3; D. P4.

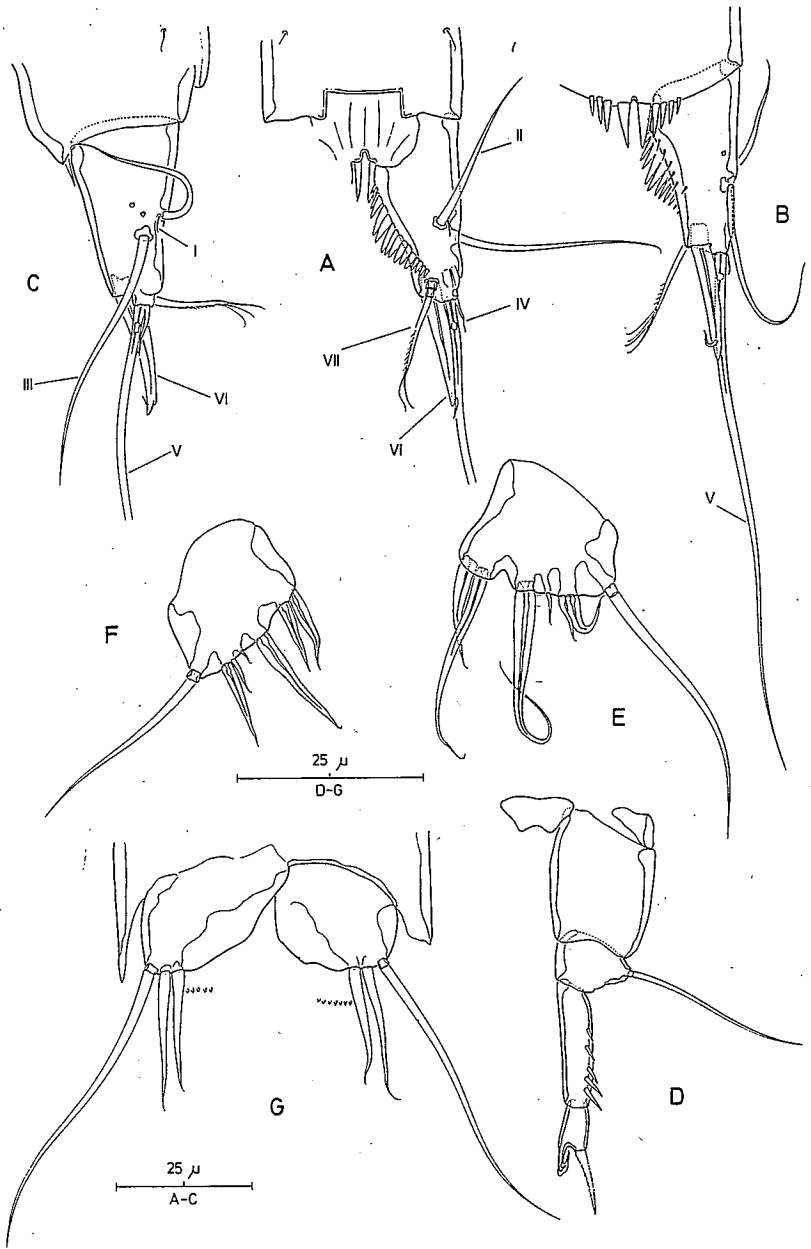


Fig. 39. — *Neopsammastacus spinicauda* (Wells, 1967). A. Caudal ramus, dorsal view; B. Same, ventral view; C. Same, lateral view; D. Endopod P3, ♂; E. P5, ♀; F. P5, ♂; G. P6, ♂.

Seta and spine formulae as follows :

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.011
P4	0.1.221	0.110

Thoracopod 5 (P5) (Fig. 39E) with exopod and baseoendopod confluent ; represented by a slightly bilobed plate with 7 setae ; exopodal setae *d* and *e* reduced in size.

Thoracopod 6 (P6) represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 1 long seta flanked by 2 vestigial setae (Fig. 37F). Two large secretory tube pores are discernible on either side of the ventral midline ; copulatory pore small.

*MALE.* Body length including rostrum and caudal rami : 415  $\mu$ m. General body shape, colour, ornamentation and sensillar pattern as in female. Sexual dimorphism in antennule, P3 endopod, P5, P6, and in genital segmentation.

Antennule 8-segmented, slender ; haplocer ; geniculation located between segments 6 and 7 ; with aesthetasc on segment 4.

Third thoracopod (P3) (Fig. 39D). Protopod and exopod as in female. Endopod 2-segmented ; proximal segment as in the female ; distal segment reduced, modified into a recurved spinous process bearing a short bipinnate seta (homologous to bipinnate spine in female).

Fifth thoracopod (P5) (Fig. 39F) with exopod and baseoendopod confluent ; represented by a rectangular plate with 7 setae in total ; exopodal setae *d* and *e* vestigial.

Sixth thoracopods (P6) (Fig. 39G) slightly asymmetrical, each with 3 well developed setae.

#### OTHER SPECIES

*N. spinicaudatus* (Rao & Ganapati, 1969) Cottarelli & Venanzetti, 1989  
syn. : *Psammastacus spinicaudatus* Rao & Ganapati, 1969

#### MATERIAL EXAMINED

— *N. spinicauda* : The Natural History Museum, reg. no. 1967.8.4.88 ; paratypes (1 ♀ dissected on 6 slides ; 5 ♀♀ and 2 ♂♂ preserved in alcohol) ; a neotype (♀ in alcohol) is selected and registered under no. 1992.1112 ; Ilha dos Portuguesos (Elephant Isle), Inhaca Island, Mozambique ; clean sand from beach ; September 1963 ; leg. J. B. J. Wells.

## REMARKS

Comparison with the type material showed that the distal exopod segment of the female P3 had been accidentally rotated in Wells' slide preparations so the inner margin seta (in his Fig. 64C) appeared to be on the outer margin. A similar explanation applies for the exopod P1 shown in his Fig. 64A.

Wells & Rao (1987) did not give information about the state of the labrum in *P. spinicaudatus*. The gross morphology of the female genital complex, the caudal rami, the anal somite and the P1 to P4 however suggest that the species belongs to *Neopsammastacus*. A detailed account of the sexual dimorphism on the swimming legs and of the fifth legs remains necessary. The confluent fifth legs of the male are extremely unusual within the family and require re-examination.

## RELATIONSHIPS

Unlike Wells' (1967) and Cottarelli & Venanzetti's (1989) opinion, there exists no direct relationship between *N. spinicauda* and *P. acuticaudatus* (= *Leptastacidae incertae sedis*), *P. remanei* (= *Afroleptastacus*) or *P. perplexus* (= *Minervella*).

The undeniable relationship between *Neopsammastacus*, *Minervella* and *Membranastacus* is indicated by the shared presence of the frontal labral process and the modifications of the male P3 endopod, both of which represent unique features within the family. However, the relationships within this genus-group are less clear in the current state of knowledge. Several characters suggest that *Neopsammastacus* represents the most primitive genus of the trio, e.g. the retention of the ancestral armature on the fifth legs of both sexes, the presence of 2 spines on the distal endopodal segment of the female P3, and primitive condition of the female sixth legs. A *Neopsammastacus*-*Minervella* sistergroup relationship is favoured by (i) the rectangular lappeted hyaline frill and (ii) the advanced condition of the sexual dimorphism on the P3 endopod. Support for a close relationship between *Membranastacus* and *Minervella* is gained through comparison of the female fifth legs (loss of 1 baseoendopodal seta), the male fifth legs (reduction of armature) and the female genital complex (P6 reduced to vestigial seta). In view of this scarce information it is best to treat this 3-genera-clade as an unresolved trichotomy (Fig. 53).

## GENUS

*Minervella* Cottarelli & Venanzetti, 1989

Syn. : *Psammastacus* Nicholls, 1935 (partim) : Wells & Clark (1965)

## HISTORY

The genus *Minervella* was only recently established by Cottarelli & Venanzetti (1989) for a new species *M. baccettii*. The existence of this genus was already foreshadowed by Wells & Clark (1965) when they described *Psammastacus perplexus* but abstained from formally establishing it because at that time only relatively few species were known in the genus *Psammastacus*. Wells & Clark (1965) thought that the proposal of this genus for *P. perplexus* could be a possible way out of the dilemma created by the fundamentally different sexual dimorphism displayed by *Arenotopa* and the presumed complete absence of sexual dimorphism in *Psammastacus*. It is therefore surprising that Cottarelli & Venanzetti (1989) tried to force *P. perplexus* within the generic boundaries of *Neopsammastacus* because it was primarily the discovery of *M. baccettii* that prompted them to rearrange the genus *Psammastacus* and to propose the genus *Minervella*. One possible reason for this misunderstanding may lie in the partly inadequate original description of *P. perplexa* though the unique sexual dimorphism on the endopod of P3 was illustrated by Wells & Clark.

A detailed redescription of *M. perplexa* comb. nov. is given below.

## DIAGNOSIS

Leptastacidae. Somites posterior to P5-bearing somite with broadly lappeted hyaline frill. Rostrum elongated, triangular. Antennary exopod with 2 distal setae. Labrum with frontal, dorsally projected, spinous process. Mandibular palp 2-segmented. P1 exopod 1-segmented; with 1 lateral spine and 3 terminal setae/spines. P1 endopod 2-segmented, not prehensile. P2-P4 endopod 2-segmented. Spine and seta formulae as follows:

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.01(0-?1)
P4	0.1.221	0.110

Strong sexual dimorphism on endopod P3. P5 uniramous in both sexes; in female with 5 setae; in male with 4 setae. Male P6 with 3 setae. Caudal ramus not acutely produced distally; seta VI spiniform; dorsomedial surface of each ramus with oblique spinular row. Spermatophore very large.

## TYPE SPECIES

*M. baccettii* Cottarelli & Venanzetti, 1989 (by monotypy)

## OTHER SPECIES

*M. perplexa* (Wells & Clark, 1965) comb. nov.

syn. : *Psammastacus perplexus* Wells & Clark, 1965

*Redescription*

(Figs. 40 - 43)

**FEMALE.** Body length 625  $\mu\text{m}$ , measured from the tip of the rostrum to the hind margin of the caudal rami.

Body slender, cylindrical, almost colourless; intersomitic boundaries well developed. Integument smooth, moderately chitinised. Hyaline frill of cephalothorax and somites bearing P2 to P5 striated (Figs. 40A-B), of genital double-somite and 2 following somites broadly lappeted (Figs. 40A, C; 43C). Cephalothorax tapering anteriorly, no distinct difference in width between cephalothorax and free body somites; no distinct separation between prosome and urosome, anal somite narrowest. Genital double-somite longer than wide, with genital apertures located in anterior half; no trace of original subdivision (Fig. 43C).

Caudal rami parallel (Figs. 43A-B), about 2.4 times as long as maximum width. Armature consisting of 6 setae (seta I absent); seta V strongly developed and together with small seta IV arising from common cylindrical socle; seta VI strongly spiniform; seta VII bi-articulated at base and bifid; dorsal inner margin of ramus with oblique spinular row.

Rostrum (Fig. 40E) well developed, elongated triangular, exceeding first antennular segment, free at base. Nauplius eye not observed.

Antennule 7-segmented, slender; with aesthetasc on segment IV.

Antenna (Fig. 40E). Coxa small, unarmed. Allobasis about 2.7 times as long as maximum width; original segmentation not discernible. Exopod 1-segmented, small; with 2 apical setae. Distal endopodal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is swollen at the base, fused with a dwarfed seta and ornamented with spinules around the geniculation; inner endopodal margin with 2 spines covered by a few spinules.

Mandibular palp 2-segmented (Fig. 42E); basis with 1 seta; distal segment with 1 proximal seta, 2 subterminal confluent setae and 2 apical confluent setae.

Labrum strongly developed (Figs. 40D-E); with frontal, dorsally projected, spinous process covered with long spinules proximally, and flanked by lobes with smaller spinules.

Maxillula, maxilla and maxilliped as for the family.

Natatorial legs (Figs. 41A-C, 42A) with 3-segmented exopods (except for P1); endopods 2-segmented, always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

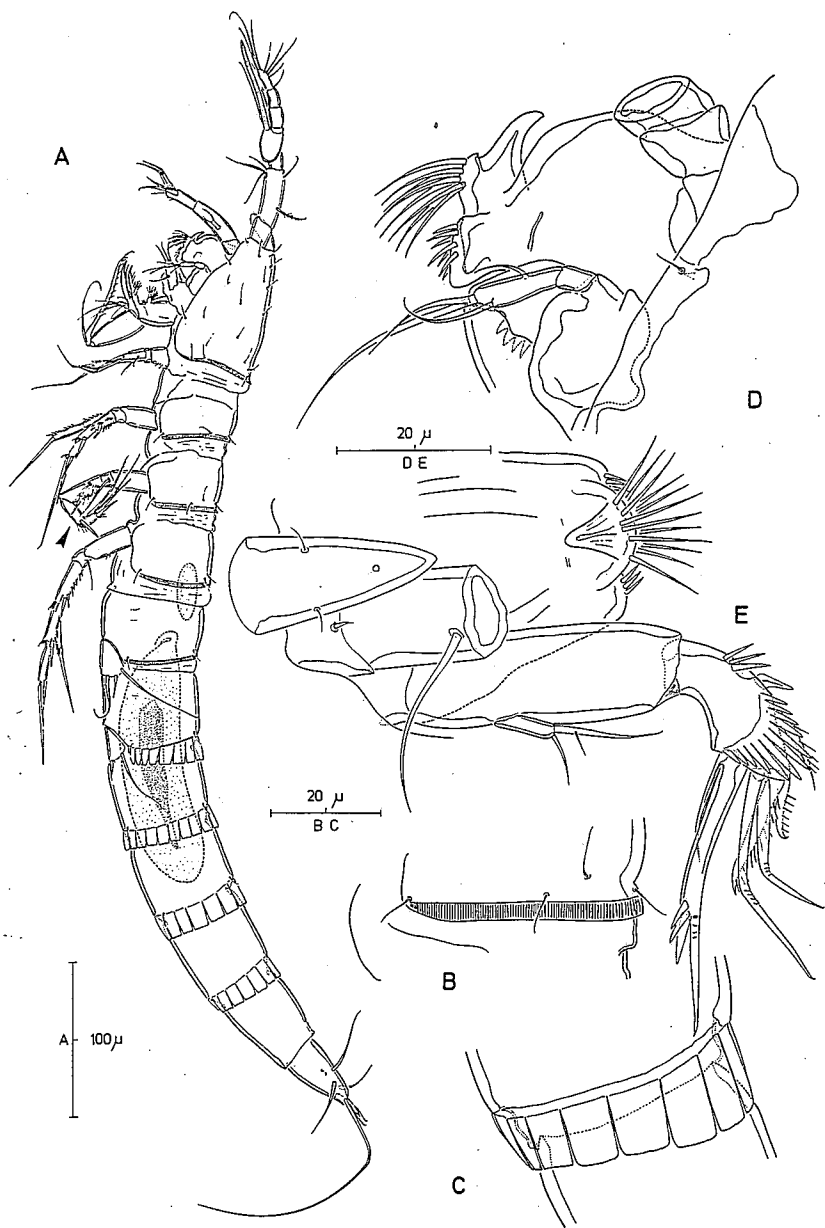


Fig. 40. — *Minervella perplexa* (Wells & Clark, 1965) comb. nov., A. Habitus ♂, lateral view (modified exopod of P3 arrowed); B. Hyaline frill of P3-bearing somite, lateral view; C. Hyaline frill of penultimate somite, lateral view; D. Labrum and mandible, lateral view; E. Rostrum, antenna and labrum, frontal view.

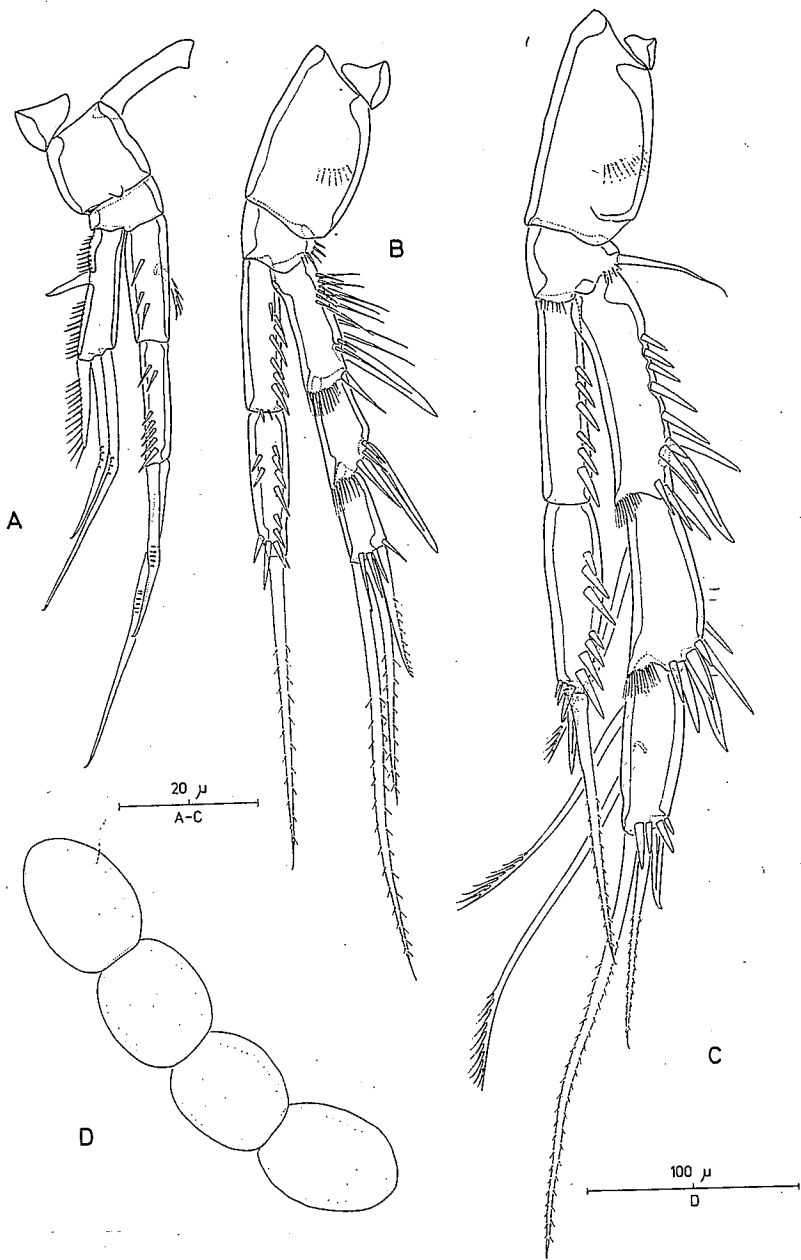


Fig. 41. — *Minervella perplexa* (Wells & Clark, 1965) comb. nov., A. P1; B. P2; C. P4; D. Egg-sac.



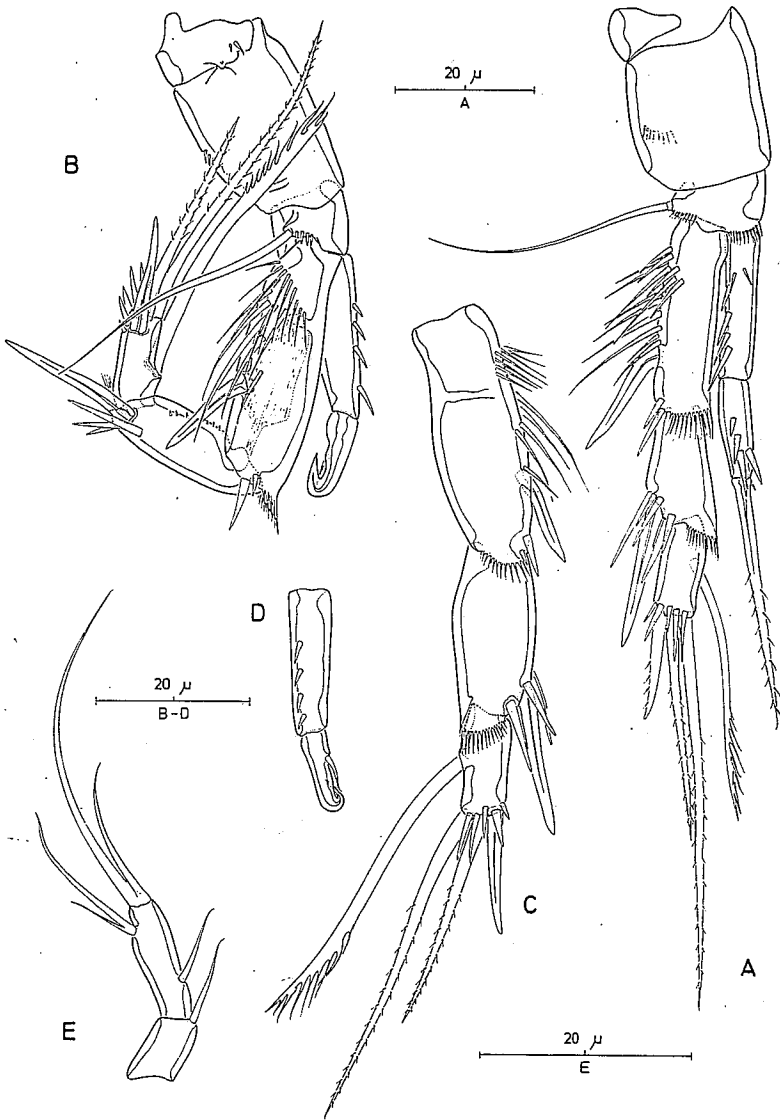


Fig. 42. — *Minervella perplexa* (Wells & Clark, 1965) comb. nov., A. P3, ♀; B. P3, ♂, lateral view; C. Exopod of ♂ P3, in stretched position, anterior view; D. Endopod P3, ♂; E. Mandibular palp.

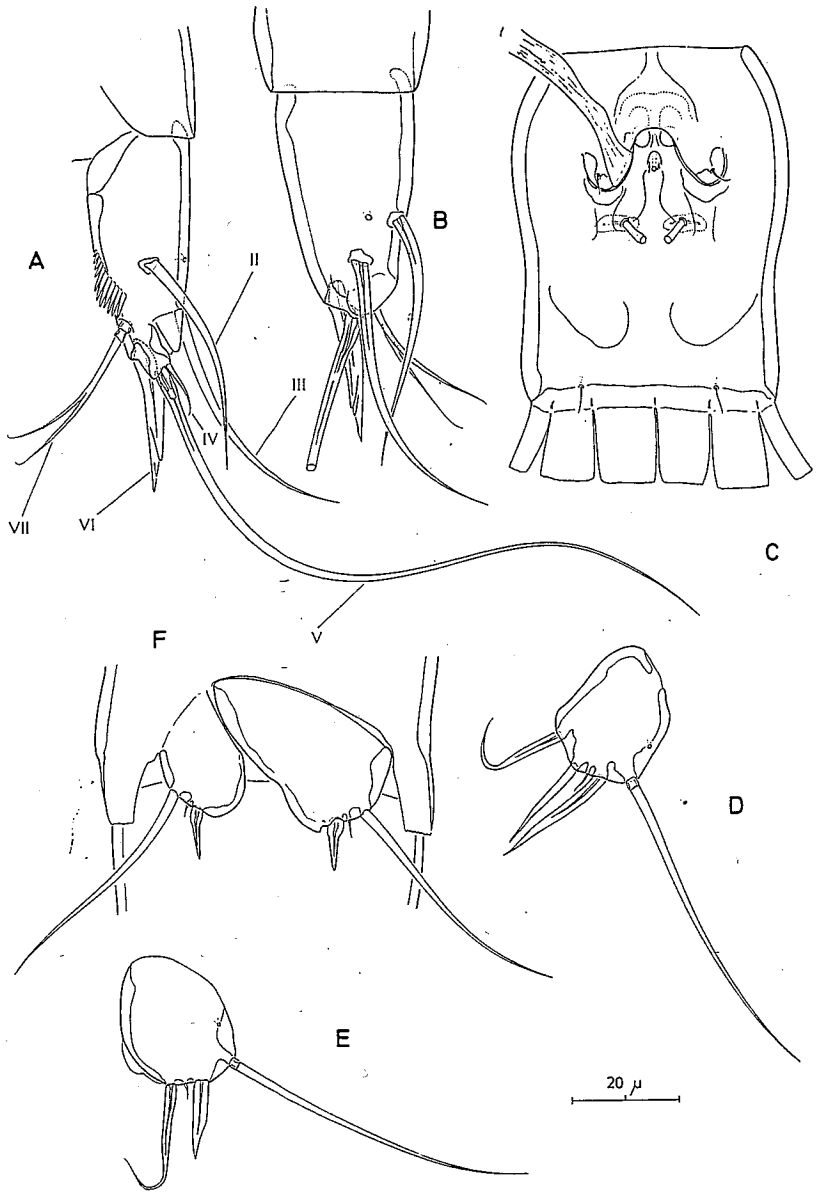


Fig. 43. — *Minervella perplexa* (Wells & Clark, 1965) comb. nov., A. Caudal ramus, dorsal view; B. Caudal ramus, lateral view; C. Genital double somite, ♀, ventral view; D. P5, ♀; E. P5, ♂; F. P6, ♂.

Thoracopod 1 (P1) (Fig. 41A). Coxa strongly developed, without ornamentation. Basis distinctly shorter than coxa; inner and outer setae not present; no ornamentation. Exopod 1-segmented; outer margin spinulose and with 1 bare spine; distal margin with 1 unipinnate spine and 2 geniculate setae, innermost of which longest. First endopodal segment about as long as distal one; with 1 short pectinate seta on inner margin and few spinules along outer margin. Second endopodal segment with 2 spinular rows along outer margin and 2 geniculate setae distally.

Thoracopods 2-4 (P2-P4) (Figs. 41B-C, 42A) with strongly developed coxae ornamented with spinular row on posterior surface. Basis of P3-P4 with outer seta. Inner setae of middle exopodal segment P4 and of distal exopodal segment P3-P4 pectinate. Distal endopodal segment of P3 with 1 distal bipinnate seta. Outer exopodal spine of proximal and middle segments P4 neither elongate nor recurved at tip.

Seta and spine formulae as follows :

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.010
P4	0.1.221	0.110

Thoracopod 5 (P5) (Fig. 43D) with exopod and baseoendopod confluent; represented by a subcircular plate with 5 setae, middle one being minute.

Thoracopod 6 (P6) represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 1 tiny seta (Fig. 43C). Two large secretory tube pores are discernible on either side of the ventral midline; copulatory pore small.

Egg-sac typically with 4 eggs arranged in a row (Fig. 41D).

**MALE.** Body length including rostrum and caudal rami: 615  $\mu\text{m}$ . General body shape (Fig. 40A), colour, ornamentation and sensillar pattern as in female. Sexual dimorphism in antennule, third thoracopod (both rami), P5, P6, and in genital segmentation (Fig. 40A).

Antennule 8-segmented, slender; haplocer; geniculation located between segments 6 and 7; with aesthetasc on segment 4.

Third thoracopod (P3) (Figs. 40A, 42B-D). Protopod as in female. Exopod with robust, swollen proximal and middle segments; inner pectinate seta of distal segment also swollen; hyaline frill between proximal and middle segments restricted to outer margin; exopod acting as prehensile ramus. Endopod 2-segmented; proximal segment shorter than in the female; distal segment reduced, modified into a recurved spinous process bearing a small lateral seta (homologous to bipinnate spine in female).

Fifth thoracopod (P5) (Fig. 43E) with exopod and baseoendopod confluent; represented by a subcircular plate with 1 vestigial seta, 2 well developed setae and 1 spine.

Sixth thoracopods (P6) (Fig. 43F) strongly asymmetrical. One member represented by large articulating plate bearing inner spine, middle vestigial seta and outer long seta; other member with same armature but smaller and fused to supporting somite; sinistral and dextral configurations present in material.

#### MATERIAL EXAMINED

— *M. perplexa*: The Natural History Museum, reg. no. 1964.12.1.4; paratypes (1 ♀, 2 ♂♂); Peniche, Portugal; littoral sand; 27 July 1964; leg. J. B. J. Wells.

#### REMARKS

There is no doubt that *P. perplexus* should belong to *Minervella*. In fact both species can be differentiated only on the base of the length: width ratio of the caudal rami and the armature of the fifth legs in both sexes which show 2 vestigial setae in the type species rather than a single dwarfed element in *M. perplexa*. It must be admitted, however, that a careful comparison is hindered by some doubtful observations made by Cottarelli & Venanzetti (1989). The lappeted hyaline frill of the abdominal somites was almost certainly overlooked in *M. baccettii*, and the sexual dimorphism noticed for the exopod of P2 and P3 is extremely difficult to assess in the absence of topotype material. The differences in armature between both sexes are likely to be the result of misinterpreting ornamentation elements (e.g. large spinules) as genuine setae or spines. This might explain the odd setal formula presented on p. 191 which actually should be identical to the one given for *M. perplexa*, except for perhaps the second short element observed on the distal endopod segment of the female third leg. The presence of this extra seta in *M. baccettii* might represent an additional differentiating character at the species level.

#### RELATIONSHIPS

*Minervella* is the only genus that exhibits sexual dimorphism on both rami of the third thoracopod. The male modification of the exopod of P3 is a unique autapomorphy for the genus and represents also the only type of sexual dimorphism for this ramus in the entire family (see section 2.4.3.). The transformed exopod was first recognised by Cottarelli & Venanzetti (1989) and used as a diagnostic generic character. The sexual dimorphism of the endopod of P3 involving the reduction of the distal seta and the formation

of a recurved apophysis is also displayed by *Neopsammastacus* and *Membranastacus* gen. nov. Another synapomorphic character favouring a close relationship between these genera is the highly distinctive frontal process on the labrum. The combination of the unisegmented exopod of P1 and the modified caudal rami (type F) is shared with *Neopsammastacus*, *Arenotopa*, *Membranastacus* and *Afroleptastacus*.

GENUS *Psamathea* Cottarelli & Venanzetti, 1989

#### DIAGNOSIS

Leptastacidae. Rostrum elongated. Intersomitic boundaries well defined; hyaline frill plain. Antennary exopod with 2 distal setae. Mandibular palp 2-segmented; basis with 1 seta. Labrum without frontal recurved process. P1 exopod 2-segmented; exp-1 with 1 outer spine, exp-2 with 4 setae/spines. P1 endopod 2-segmented, prehensile; inner seta of enp-1 lacking (?); enp-2 with 1 claw and 1 geniculate seta. P2-P4 endopod 2-segmented. Spine and seta formulae as follows:

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.011
P4	0.1.221	0.110

Sexual dimorphism on endopod P3-P4. P5 uniramous in both sexes; in female with 4 well developed and 2 vestigial setae; in male with 3 well developed and 2 vestigial setae. Male P6 with 2 setae. Distal inner corner of caudal ramus produced in dorsally recurved tricuspidate process; none of setae modified.

#### TYPE AND ONLY SPECIES

*P. nautarum* Cottarelli & Venanzetti, 1989 (by monotypy)

#### MATERIAL EXAMINED

None.

#### RELATIONSHIPS

Cottarelli & Venanzetti (1989) obviously had difficulties in tracking down the relationships of *P. nautarum* since they were unable to assign it to any of the four subfamilies defined in the *Cylindropsyllidae*. Using Bodiou

& Colomines' (1986) key they concluded that *Psamathea* is closest to *Pararenopontia* Bodiou & Colomines, 1986 and *Notopontia* Bodiou, 1977. They further stressed the similarity in morphology and armature of the second to fifth thoracopods between *Psamathea* and *Leptastacus* plus related genera. Finally a certain resemblance with *Psammopsyllus* was recognised in the structure of the caudal rami, but according to the authors this should be owed to convergence.

It is evident that the relationship with *Pararenopontia* and *Notopontia* is purely artificial since it is based on a single character, i.e. the 2-segmented exopod of P1, that was heavily weighed in Bodiou & Colomines' key. The morphology of the cephalic feeding structures and of the thoracopods leave no doubt about the leptastacid affinity of *Psamathea*. The elongated prehensile P1 endopod is an unusual character within the family and is further only exhibited by *Paraleptastacus laurenticus*. However, this should rather be regarded as being a product of convergent evolution. There are a few features that might point to a possible sistergroup relationship between *Psamathea* and *Arenocaris*. Both genera display the 2-segmented condition for the exopod P1 with an ancestral number of 4 setae on the distal segment. There is no evidence for the derivation of this condition but most likely it is originated by fusion of the ancestral middle and distal segments with 1 armature element been lost. *Psamathea* and *Arenocaris* also share sexual dimorphism on the P4 endopod, but the homology of these transformations has yet to be revealed. It should be stressed that Cottarelli & Venanzetti's (1989) illustrations do not allow a detailed comparison with *Arenocaris* and thus the position of *Psamathea* in Fig. 53 is merely tentative until the material is available for an in-depth study.

The genus can be defined by the following autapomorphies: (i) prehensile endopod (extreme elongation of enp-1), (ii) sexual dimorphism of endopod P3 (involving reduction of distal segment and loss of subapical seta), (iii) uniramous fifth legs in both sexes, and (iv) tricuspidate dorsal process of caudal rami.

#### GENUS

#### *Afroleptastacus* gen. nov.

syn.: *Psammastacus* Nicholls, 1935 (partim): Noodt (1954), Wells (1967).

#### DIAGNOSIS

Leptastacidae. Rostrum triangular. Hyaline frill of urosomites reduced, plain. Antennary exopod with 2 distal setae. Mandibular palp 2-segmented; basis with 1 seta. Labrum without frontal recurved process. P1 exopod

1-segmented ; with 1 lateral spine and 3 terminal setae/spines. P1 endopod 2-segmented, not prehensile. P2-P4 endopod 2-segmented. Spine and seta formulae as follows :

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.010
P4	0.1.221	0.110

Sexual dimorphism on exopod P4. P5 uniramous in both sexes ; in female bilobed with 7 setae ; in male subcircular with 5 setae. Male P6 with 3 setae, middle one vestigial. Caudal ramus not acutely produced distally ; seta VI short and spiniform ; dorsomedial surface of each ramus with oblique spinular row ; dorsal hind margin with movable recurved spinule.

#### TYPE SPECIES

*A. clandestinus* sp. nov.

syn. : *Psammastacus spinicauda* Wells, 1967 (partim)

#### Description

(Figs. 44 - 46)

**FEMALE.** Body length 465  $\mu\text{m}$ , measured from the tip of the rostrum to the hind margin of the caudal rami.

Body slender, cylindrical, almost colourless ; intersomitic boundaries well developed. Integument smooth, moderately chitinised. Hyaline frill of cephalothorax and body somites reduced to narrow membrane. Cephalothorax tapering anteriorly, no distinct difference in width between cephalothorax and free body somites ; no distinct separation between prosome and urosome, anal somite narrowest. Genital double-somite wider than long, with genital apertures located in anterior half ; no trace of original subdivision (Fig. 46E).

Caudal rami parallel (Figs. 46A-C), about 2.3 times as long as maximum width. Armature consisting of 7 setae ; seta V strongly developed and fused at base with well developed seta IV ; seta VI thorn-like ; seta VII bi-articulated at base and plumose at the tip ; dorsal inner margin of ramus with oblique spinular row consisting of hyaline spinules ; dorsal hind margin with small recurved spinule (Fig. 46A, B).

Rostrum (Fig. 46H) well developed, triangular, exceeding first antennular segment, free at base. Nauplius eye not observed.

Antennule 7-segmented, slender ; with aesthetasc on segment IV.

Antenna (Fig. 46G). Coxa small, unarmed. Allobasis about 2.9 times as long as maximum width ; original segmentation not discernible. Exopod

1-segmented, small; with 2 apical setae. Distal endopodal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is swollen at the base, fused with a dwarfed seta and ornamented with spinules around the geniculation; inner endopodal margin with 2 spines covered by a few spinules.

Mandibular palp 2-segmented (Fig. 46F); basis with 1 seta; distal segment with 1 inner seta, 2 subterminal confluent setae along the outer margin and 2 apical confluent setae.

Labrum strongly developed (Figs. 46G), swollen; without frontal, dorsally projected, spinous process, but with lateral spiny lobes flanking median group of longer spinules.

Maxillula, maxilla and maxilliped as for the family.

Natatorial legs (Figs. 45A-D) with 3-segmented exopods (except for P1); endopods 2-segmented, always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

Thoracopod 1 (P1) (Fig. 45A). Coxa strongly developed, without ornamentation. Basis distinctly shorter than coxa; inner and outer setae not present; with spinules at the outer corner. Exopod 1-segmented; outer margin spinulose and with 1 bare spine; distal margin with 1 unipinnate spine and 2 geniculate setae, innermost of which longest. First endopodal segment about as long as distal one; with 1 short pectinate seta on inner margin and few spinules along outer margin. Second endopodal segment with 2 spinular rows along outer margin and 2 geniculate setae distally.

Thoracopods 2-4 (P2-P4) (Figs. 45B-D) with strongly developed, unornamented coxae. Basis of P3-P4 with outer seta. Inner setae of middle exopodal segment P4 and of distal exopodal segment P3-P4 pectinate. Distal endopodal segment of P3 with 1 distal bipinnate seta. Outer exopodal spine of proximal and middle segments P4 neither elongate nor recurved at tip.

Seta and spine formulae as follows:

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.010
P4	0.1.221	0.110

Thoracopod 5 (P5) (Fig. 46D) with exopod and baseoendopod confluent; represented by a bilobed plate with 7 setae, exopodal setae *d* and *e* vestigial, baseoendopodal seta *a* swollen and hyaline.

Thoracopod 6 (P6) represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 1 long seta (Fig. 46E). Two small secretory pores are discernible on either side of the ventral midline; copulatory pore small.



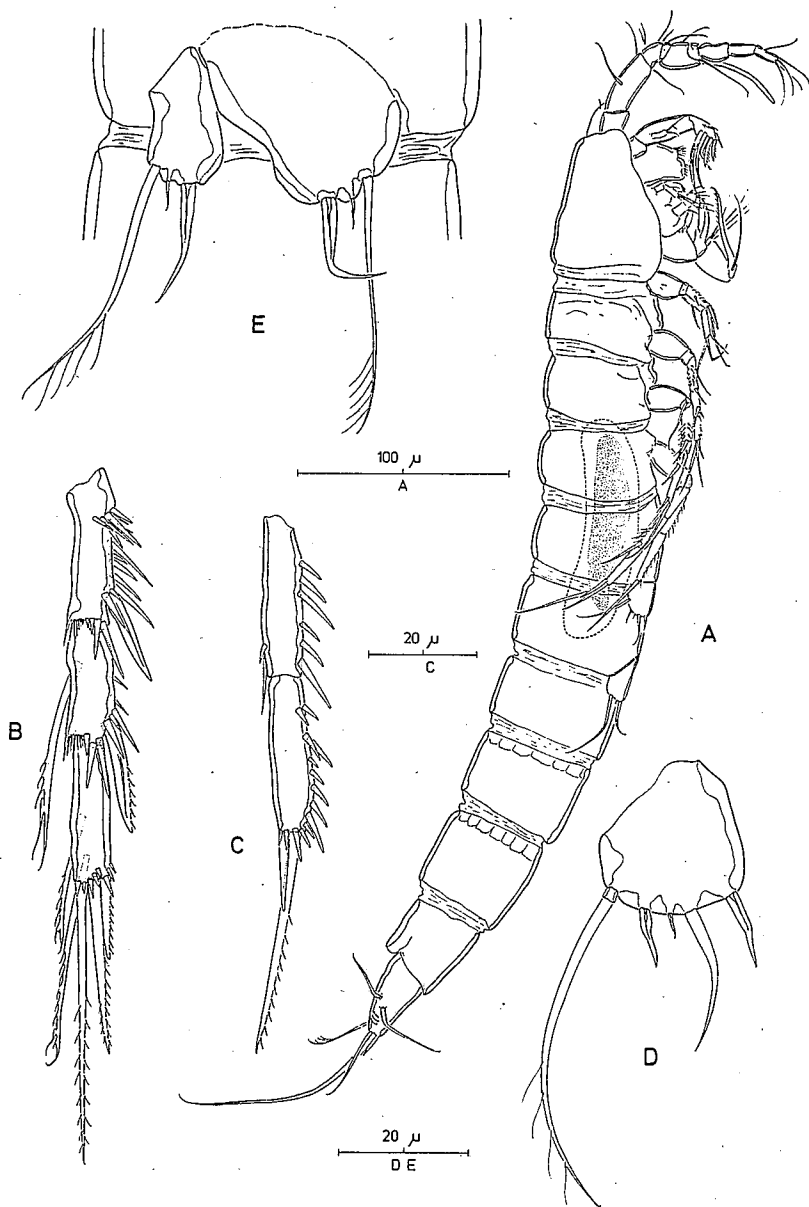


Fig. 44. — *Afroleptastacus clandestinus* gen. et sp. nov., A. Habitus ♂, lateral view; B. P4 exopod, ♂; C. P4 endopod, ♂; D. P5, ♂; E. P6, ♂.

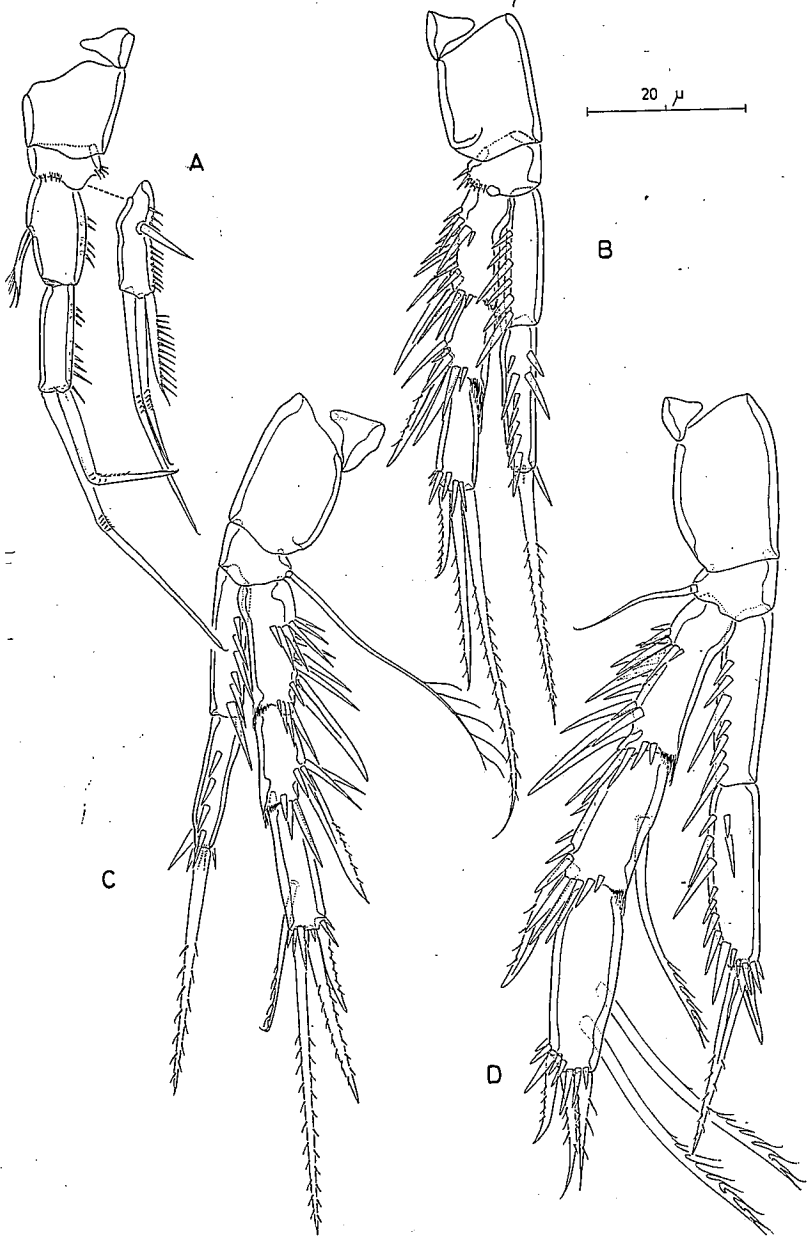


Fig. 45. — *Afroleptastacus clandestinus* gen. et sp. nov. Female. A. P1 with disarticulated exopod; B. P2; C. P3; D. P4.

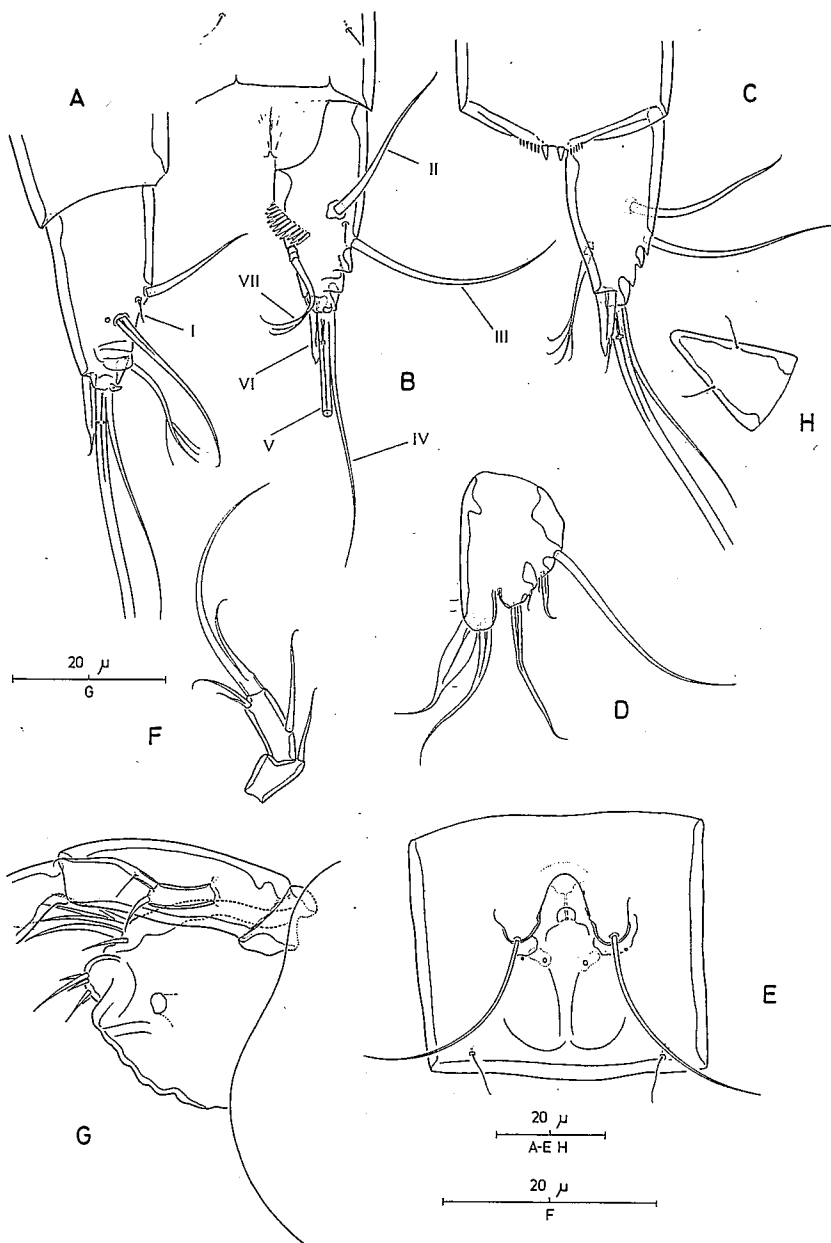


Fig. 46. — *Afroleptastacus clandestinus* gen. et sp. nov., A. Caudal ramus, lateral view; B. Same, dorsal view; C. Same, ventral view; D. P5, ♀; E. Genital complex and sixth legs, ♀; F. Mandibular palp; G. Antennary allobasis (including exopod) and labrum, lateral view.

*MALE*. Body length including rostrum and caudal rami : 450  $\mu$ m. General body shape, colour, ornamentation and sensillar pattern as in female (Fig. 44A). Sexual dimorphism in antennule, exopod P4, P5, P6, and in genital segmentation (Fig. 44A).

Antennule 8-segmented, slender ; haplocer ; geniculation located between segments 6 and 7 ; with aesthetasc on segment 4.

Fourth thoracopod (P4) (Figs. 44B, C). Protopod as in female. Exopod more slender than in female, with distal setae distinctly elongated. Endopod as in female except for distal spine which is slightly longer in male.

Fifth thoracopod (P5) (Fig. 44D) with exopod and baseoendopod confluent ; represented by a subcircular plate with 5 setae in total of which one is vestigial.

Sixth thoracopods (P6) (Fig. 44E) strongly asymmetrical. One member represented by large articulating plate bearing inner spine, middle vestigial seta and outer long seta ; other member with same armature but smaller and fused to supporting somite.

#### ETYMOLOGY

The generic name is derived from the Latin *Afer*, meaning African, and *Leptastacus* and refers to its distribution along the African continent (gender : masculine). The Latin species name *clandestinus* (= hidden) refers to its chance discovery among the type material of another species.

#### OTHER SPECIES

*A. remanei* (Noodt, 1954) comb. nov.  
syn. : *Psammastacus remanei* Noodt, 1954

#### MATERIAL EXAMINED

— *A. clandestinus* : The Natural History Museum ; found among paratype material of *Psammastacus spinicauda* (reg. no. 1967.8.4.88) ; holotype ♀ (dissected on 6 slides, reg. no. 1992.1113) and 2 paratypes (1 ♀ in alcohol, reg. no. 1992.1115 ; 1 ♂ dissected on 4 slides, reg. no. 1992.1114) ; Ilha dos Portuguesos (Elephant Isle), Inhaca Island, Mozambique ; clean sand from beach ; September 1963 ; leg. J. B. J. Wells.

#### REMARKS

Noodt's (1954) illustrations of *P. remanei* were primarily based on the male (since he had some reservations about the maturity of the single female),

however, the little information presented on the female is of major significance in resolving the species' position. Noodt mentioned that the female agreed in most respects with the male except for the P3 and the P4 which were more robust than in the male and had shorter spines and setae. This statement and his drawing of the male P4 are in accordance with the sexual dimorphism displayed by *A. clandestinus* on the P4 exopod. The major differences in both descriptions are found in the structure of the caudal rami and the fifth legs. It is however conceivable that Noodt (1954) overlooked the oblique spinular row of the caudal rami since this structure is rather transparent in *A. clandestinus*. Similarly, the innermost baseoendopodal spine of the female fifth leg is missing in his illustration (though an insertion space is available), however, this element is extremely hyaline and flaccid and thus hardly discernible without interference contrast microscopy. The other discrepancies in fifth leg structure appear to reflect merely small inaccuracies, in particular with respect to the tiny, vestigial setae of the exopod.

#### RELATIONSHIPS

Four other genera share the combination of a unisegmented exopod P1 and a caudal ramus with modified seta VI: *Neopsammastacus*, *Membranstacus*, *Minervella* and *Arenotopa*. The first three genera form a natural group and the sexual dimorphism of the P3 and the frontal labral process serve to separate them from both *Afroleptastacus* and *Arenotopa*. It is interesting to examine the detailed caudal rami morphology of the latter genera. *A. clandestinus* shows a dorsally recurved, movable spinous element at the posterior margin near the common articulation of seta IV and V. This movable spinule cannot be homologised with any of the seven ramal setae and is thus a novel ornamentation element. Inspection of *Arenotopa erasmusi* revealed a similar, however larger, element in exactly the same position (Fig. 36E) and Wells & Rao's (1987) illustration of the caudal ramus of *A. dyadacantha* (Fig. 130d) suggests an identical structure. This articulating spinule has not been found in any of the other genera and is thus regarded as a synapomorphy for *Arenotopa* and *Afroleptastacus*. Additional evidence for this sistergroup relationship is provided by the structure of the genital complex (a single long seta; cf. Wells & Rao, 1987: Fig. 130b) and the setation of the male sixth leg (middle seta vestigial). It is possible that the sexual dimorphism on the exopod P4 is not unique to *Afroleptastacus* since at least some *Arenotopa* species (Cottarelli, 1977) display a similar modification, however this requires re-examination. The loss of sexual dimorphism on the third thoracopod is an autapomorphy for *Afroleptastacus*.

## GENUS

**Archileptastacus** gen. nov.

Syn. : *Leptastacus* T. Scott, 1906 (partim) : Chappuis (1954a), Kunz (1974), Mielke (1985, 1987)

## HISTORY

Lang (1965) already mentioned that *Leptastacus aberrans* Chappuis, 1954a differed from all other members of the family because of the 3-segmented endopod of the first thoracopod. He nevertheless kept the species in *Leptastacus* because of the gross resemblance "... in all other aspects ...", yet presumably he was unable to evaluate critically the other appendages due to the very imperfect original description. Bodiou & Colomines (1989) upgraded *L. aberrans dichatoensis* Mielke, 1985 to full species rank. As a result of this comparative study both species are referred to a new genus *Archileptastacus*. Supporting evidence for this act is mainly provided by Mielke's (1985, 1987) excellent illustrations.

## DIAGNOSIS

Leptastacidae. Rostrum triangular, rounded anteriorly. Hyaline frill of urosomites well developed, plain. Antenna with separate basis and endopod ; exopod with 1 lateral and 2 distal setae. Mandibular palp 2-segmented ; basis with 1 seta. Labrum without frontal spinous process. P1 exopod 3-segmented ; exp-3 with 4 setae/spines. P1 endopod 3-segmented, enp-2 without setae ; not prehensile. P2-P4 endopod 2-segmented. Spine and seta formulae as follows :

	Exopod	Endopod
P2	0.[0-2]1.[?0-1]21	0.010
P3	0.0.121	0.010
P4	0.0.121	0.010

Presumably no sexual dimorphism on P2-P4. P5 uniramous in both sexes ; produced distally ; in female with 5 well developed setae (seta *a* vestigial or absent ; seta *c* modified and forming strong apical process) ; in male with 5 well developed setae (setae *a* and *b* vestigial or absent). Distal outer corner acutely produced posteriorly ; none of setae modified.

## TYPE SPECIES

*A. dichatoensis* (Mielke, 1985) comb. nov.

syn. : *Leptastacus aberrans dichatoensis* Mielke, 1985

*Leptastacus dichatoensis* Mielke, 1985 : Bodiou & Colomines (1989)

## OTHER SPECIES

*A. aberrans* (Chappuis, 1954a) comb. nov.

syn. : *Leptastacus aberrans* Chappuis, 1954a

## ETYMOLOGY:

The generic name is derived from the Greek prefix *archi-*, meaning first in time and alludes to the primitive position in the family (gender : masculine).

## MATERIAL EXAMINED

None.

## RELATIONSHIPS

*Archileptastacus* is without doubt the most primitive taxon of the family. The early divergence of the genus is indicated by retention of several plesiomorphic character states found in the antenna and in the first and second thoracopods. In *A. dichatoensis* the antennary basis and first endopodal segment are separated by a weak suture line, and the articulation between the two segments is still discernible at the inner margin (Mielke, 1985 : Abb. 15B). A distinct basis was also reported but not illustrated in the concise description of *A. aberrans* (Chappuis, 1954a : 271). In all other Leptastacidae the basis and the proximal endopodal segment are completely fused to form an antennary allobasis. *Archileptastacus* is also the only genus that has retained the maximum setation (1 lateral, 2 apical setae) on the antennary exopod. The lateral seta is lost in all other members of the family, leaving a bisetose segment (unisetose in *Psammastacus*). Perhaps the most characteristic limb of the genus is the first thoracopod, displaying the ancestral 3-segmented condition of the endopod. Using the spinular rows on the various segments as the reference points, it can be deduced that the 2-segmented state in the other genera arose through fusion of the middle and distal endopodal segments. *Archileptastacus* is the only genus that has retained the inner seta on the distal exopodal segment of leg 2 (Mielke, 1985 ; Kunz, 1974). This seta was not observed by Chappuis

(1954a) but this might be attributed to the very imperfect description. Kunz (1974) also reported an inner seta on the middle exopodal segment of leg 2. This observation has to be confirmed since the retention of this armature element would represent a unique plesiomorphy within the family.

There are numerous apomorphies for *Archileptastacus*, most of them unique to this genus. The endopods of P2 to P4 show a marked reduction in the armature, resulting in a consistent 0.010 formula. The inner seta on the middle exopodal segment of P4 is also lost. The caudal ramus shows a unique modification. In contrast to the other genera with backwardly produced caudal rami, the spinous process is derived from a posterior outgrowth of the outer posterolateral corner. None of the ramal setae take part in the formation of the attenuation. Setae IV and VI are reduced.

The triangular, anteriorly rounded rostrum is atypical and differs clearly from the prevailing elongated rostrum found in all other genera. The polarity of this character is difficult to assess, but the rounded shape is interpreted here as the advanced state since it is rarely found among harpacticoids.

The fifth legs superficially resemble those of *Leptastacus* and related genera because of the fused exopod and baseopod and of the presence of a distal spinous process. However, the distal process of the P5 in *A. dichatoensis* is not homologous to the process of *Leptastacus* where it represents an elaboration of the distal exopodal margin. The precise homology of this structure in *Archileptastacus* is revealed by comparison with *A. aberrans* (Chappuis, 1954a; Kunz, 1974) where all armature elements are still free. In *A. dichatoensis* the thorn-like seta *c* (of the fused exopod) is incorporated in the limb, resulting in a distal, pinnate projection (Fig. 24C). The homology of the distal process in *Leptastacus* and allies was already discussed in section 2.4.1. The endopodal seta *a* is lost or at most vestigial in all species.

#### GENUS

#### **Belemnopontia gen. nov.**

syn. : *Leptastacus* T. Scott, 1906 (partim) : Krishnaswamy (1957), Mielke (1982, 1983)

#### DIAGNOSIS

Leptastacidae. Urosomites with plain hyaline frill (?). Rostrum elongated. Antennary exopod with 2 distal setae. Mandibular palp 2-segmented; basis without seta, distal segment with 4 setae. Labrum without frontal process. P1 exopod 3-segmented; exp-3 with 4 setae/spines. P1 endopod 2-segmented, not prehensile. P2-P4 endopod 2-segmented. Outer spine of exp-1 P4 elongated and curved. Spine and seta formulae as follows :



	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.011
P4	0.1.121	0.110

Slight sexual dimorphism on endopod P3. P5 uniramous; triangular and produced distally; in female with 4 well developed setae (setae *a* and *e* vestigial, seta *c* absent); in male with 2-3 well developed setae (setae *a*, *e* and sometimes *f* vestigial, setae *b* and *c* absent). Male P6 with 3 setae. Caudal ramus acutely produced distally; none of setae modified.

#### TYPE SPECIES

*B. dispinosa* (Mielke, 1982) comb. nov.

syn. : *Leptastacus dispinosus* Mielke, 1982

*Leptastacus dispinosus dispinosus* Mielke, 1982 : Mielke (1983)

#### OTHER SPECIES

*B. panamensis* (Mielke, 1983) comb. nov.

syn. : *Leptastacus dispinosus panamensis* Mielke, 1983

#### SPECIES INQUIRENDAE

*B. acuticaudatus* (Krishnaswamy, 1957) comb. nov.

syn. : *Leptastacus acuticaudatus* Krishnaswamy, 1957

*Leptastacus macronyx* (T. Scott) *sensu* Chappuis & Rouch (1961)

#### ETYMOLOGY

The generic name is derived from the Greek *belemnon*, meaning spear or dart, and *pontos*, meaning sea, and refers to the acutely produced caudal rami (gender : feminine).

#### MATERIAL EXAMINED

None.

#### REMARKS

Mielke's (1982, 1983) subspecies of *L. dispinosus* are here elevated to full species rank. Apart from being smaller, the Panamese specimens differ distinctly from the nominate subspecies in the relative proportions of the endopodal

segments of leg 1 and the male leg 3, the apex of the fifth legs in both sexes and the shape and ornamentation of the caudal rami.

The close similarity between *L. dispinosus* and Chappuis & Rouch' (1961) Ghanese material of *L. macronyx* was already discussed in section 1.

The spine and seta formulae of the swimming legs, the gross morphology of the fifth legs and the type of sexual dimorphism on the P3 endopod leave little doubt about the affinity of *L. acuticaudatus*. Krishnaswamy's (1957) description, however, is of little assistance in differentiating the species from its congeners, and thus *L. acuticaudatus* should remain a *species inquirenda*. According to the text the species description was based on males only, yet it is unknown where Krishnaswamy's drawing of the genital complex is derived from.

#### RELATIONSHIPS

The new genus is established to accommodate former *Leptastacus* species that share an intermediate position between the *rostratus*-group (= *Schizothrix* gen. nov.) and the genera *Cerconeotes* and *Psammastacus*. These four genera represent the monophyletic sistergroup of *Leptastacus* and share the outer spine of exp-1 P4 which is elongated and recurved at the tip, the barbed spinous process on the distal segment of the ♂ P3 endopod, and the posteriorly produced caudal rami which have a dorsally recurved process. The similarity in caudal ramus structure between *Belemnopontia* and *Schizothrix* is striking and already Krishnaswamy (1957) used this character to relate *L. acuticaudatus* to *L. rostratus*. It is unlikely, however, that this indicates a sistergroup relationship between these two genera because there is ontogenetic evidence that *Cerconeotes* possesses the same type of caudal ramus, however, being already in a state of reduction.

*Belemnopontia* is obviously closely related with *Cerconeotes* and *Psammastacus* as is exemplified by the following synapomorphies: (i) loss of inner seta on proximal endopodal segment of P2-P3, (ii) loss of proximal inner seta on exp-3 P4, (iii) loss of seta *c* in female fifth leg and of seta *b* in male fifth leg, (iv) reduction in mandibular palp setation (loss basal seta; distal segment with 4 setae). The presence of two strong spinules at the ventral posterior margin of the anal somite is a unique feature. No information is available on the female genital complex and the hyaline frill of the body somites.

#### GENUS

#### *Cerconeotes* gen. nov.

Syn.: *Leptastacus* T. Scott, 1906 (partim): Krishnaswamy (1951, 1957), Lang (1965), Wells (1967), Itô (1968), Rao & Ganapati (1969), Lindgren (1975), Masry (1970), Mielke (1983)

## DIAGNOSIS

Leptastacidae. Urosomites with plain hyaline frill. Rostrum elongated. Mandibular palp 2-segmented; basis without seta; distal segment with 4 setae. Labrum without frontal process. Antennary exopod with 2 distal setae. P1 exopod 3-segmented; exp-3 with 3 terminal setae/spines. P1 endopod 2-segmented, not prehensile. P2-P4 endopod 2-segmented. Outer spine of exp-1 P4 elongated and curved. Spine and seta formulae as follows:

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.011
P4	0.1.121	0.110

Sexual dimorphism on endopod P3. P5 uniramous and minute in both sexes; triangular and slightly produced distally; with 4 or 3 (occasionally 2) setae. Male P6 with 2 setae. Caudal ramus not acutely produced distally but constricted subdistally; setae IV and V distinctly fused at their bases and laterally directed; seta V strong and plumose.

## TYPE SPECIES

*C. mozambicus* (Wells, 1967) comb. nov.  
syn. : *Leptastacus mozambicus* Wells, 1967

*Redescription*  
(Figs. 47 - 49)

**FEMALE.** Body length 435-450  $\mu\text{m}$  ( $n = 4$ ), measured from the tip of the rostrum to the hind margin of the caudal rami.

Body slender (Figs. 47A-B), cylindrical, yellowish; intersomitic boundaries well defined. Integument smooth, moderately chitinised, hyaline frill of body somites vestigial. Cephalothorax tapering anteriorly; only slight differences in width between cephalothorax and free body somites; anal somite narrowest, with small spinules on ventral posterior border (Fig. 49F); no distinct separation between prosome and urosome. Genital double-somite wider than long; with genital apertures located halfway (Fig. 49E); no trace of original subdivision.

Caudal rami slightly divergent (Figs. 47A; 49A-B), about 2.3 times as long as maximum width; with inner distal corner extending into dorsally recurved spinous process. Armature consisting of 6 setae (seta I absent); seta II spiniform; seta V tubular at the tip, fused at base with seta IV; seta VI long; seta VII bi-articulated at base.

Rostrum well developed (Fig. 47A), elongated, not exceeding first antennary segment, free at base. Nauplius eye not observed.

Antennule 7-segmented, slender; with aesthetasc on segment IV,

Antennary exopod 1-segmented, with 2 apical setae.

Mandibular palp 2-segmented; basis without seta; distal segment with 1 seta on inner and 1 seta on outer margin and 2 setae distally.

Maxillula, maxilla and maxilliped as for the family.

Labrum strongly developed; *Leptastacus*-type; without frontal dorsally projected spinous process.

Natatorial legs (Figs. 48A-C, E) with 3-segmented exopods; endopods 2-segmented, always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

Thoracopod 1 (P1) (Fig. 48A). Coxa strongly developed, without spinular rows. Basis distinctly shorter than coxa; inner and outer setae not present; no ornamentation. Exopod 3-segmented; outer margin of proximal and middle exopodal segments spinulose and with 1 unipinnate spine each; distal segment with 1 unipinnate spine and 2 geniculate setae, innermost of which longest. First endopodal segment 1.1 times as long as distal one; with 1 short pectinate seta on inner margin and few spinules along outer margin. Second endopodal segment with 2 spinular rows along outer margin and 2 geniculate setae distally.

Thoracopods 2-4 (P2-P4) (Figs. 48B-C, E) with strongly developed coxae which are not ornamented on both anterior and posterior surfaces. Basis of P3-P4 with outer seta. Inner seta of middle exopodal segment P4 and distal exopodal segment P3-P4 pectinate. Proximal exopodal segment P4 with recurved spine. Distal endopodal segment of P3 with 1 subterminal serrate seta and 1 distal bipinnate seta. Outer exopodal spine of middle segment P4 neither elongate nor recurved at tip.

Seta and spine formulae as follows:

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.110
P4	0.1.121	0.110

Thoracopod 5 (P5) (Fig. 49G) with exopod and baseoendopod confluent; represented by a small bilobed plate with 4 setae, apical one inserted subterminally.

Thoracopod 6 (P6) represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 1 long and 1 short seta (Fig. 49E). Copulatory pore located in distal half of genital double-somite.

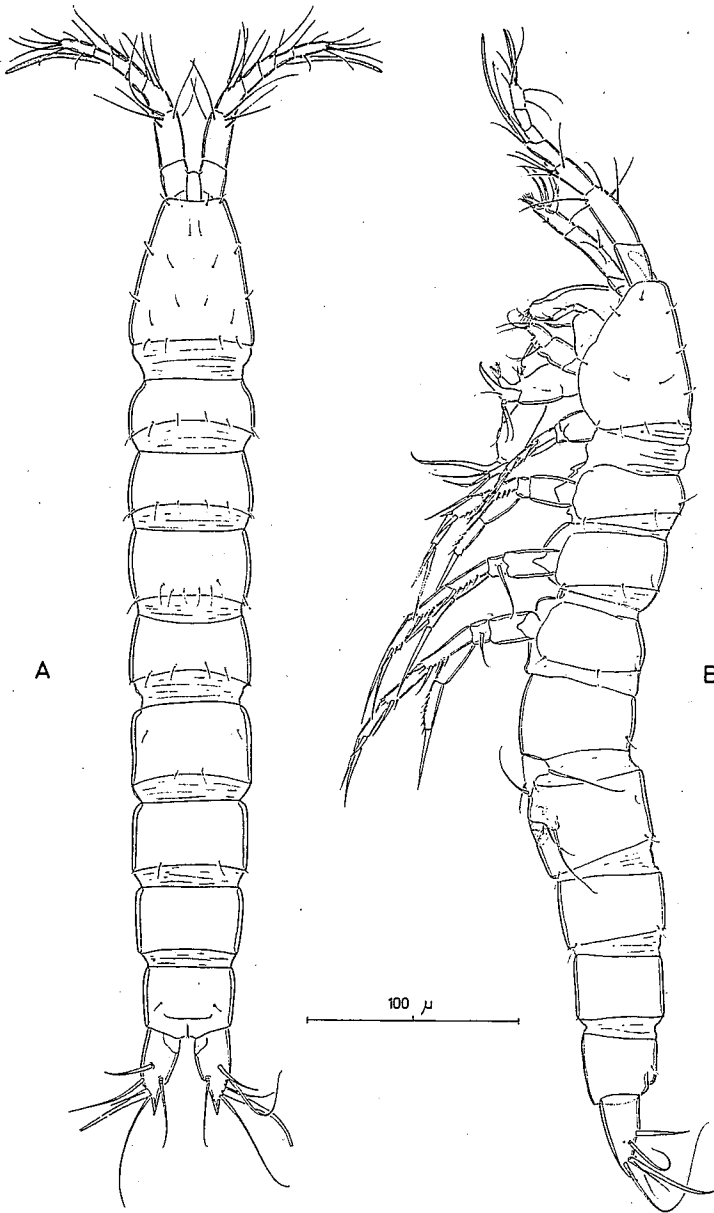


Fig. 47. — *Cerconeotes mozambicus* (Wells, 1967) comb. nov., A. Habitus ♀, dorsal view; B. Same, lateral view.

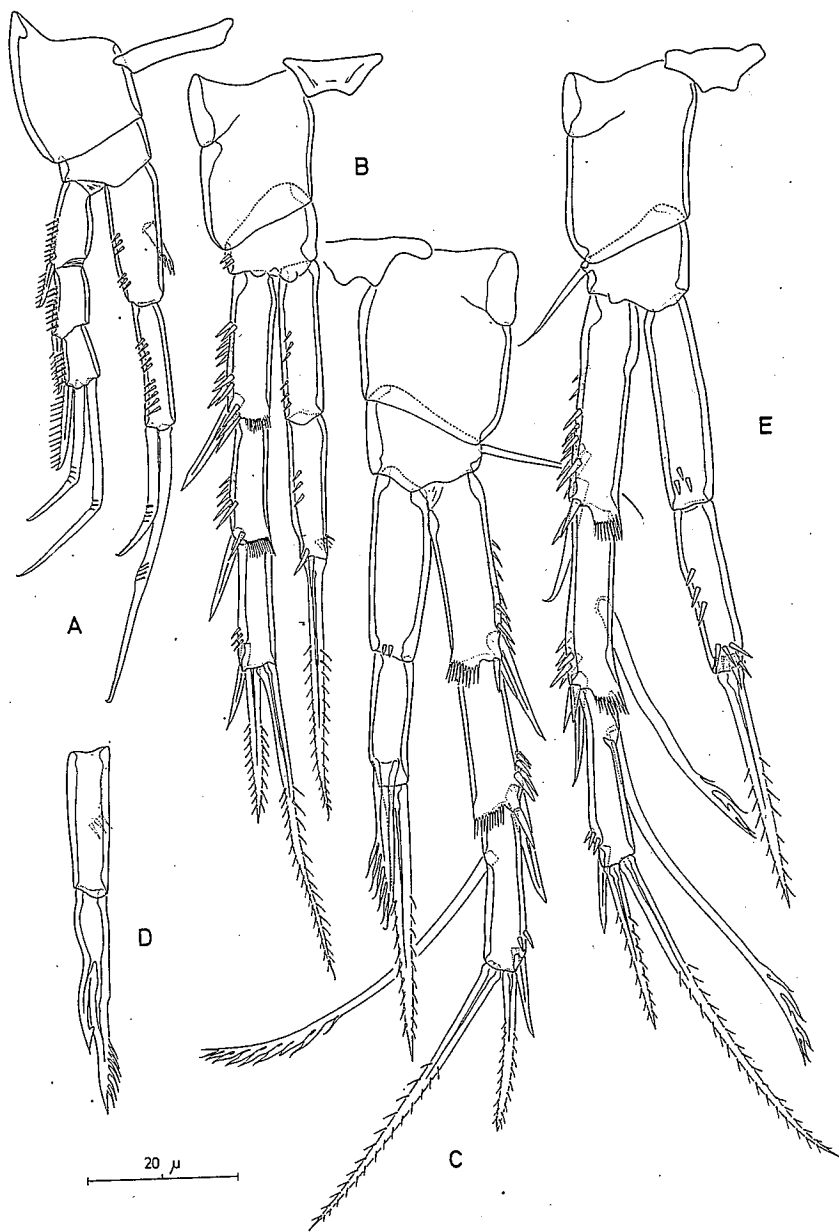


Fig. 48. — *Cerconeotes mozambicus* (Wells, 1967) comb. nov., A. P1; B. P2; C. P3; D. ♂ endopod P3; E. P4.

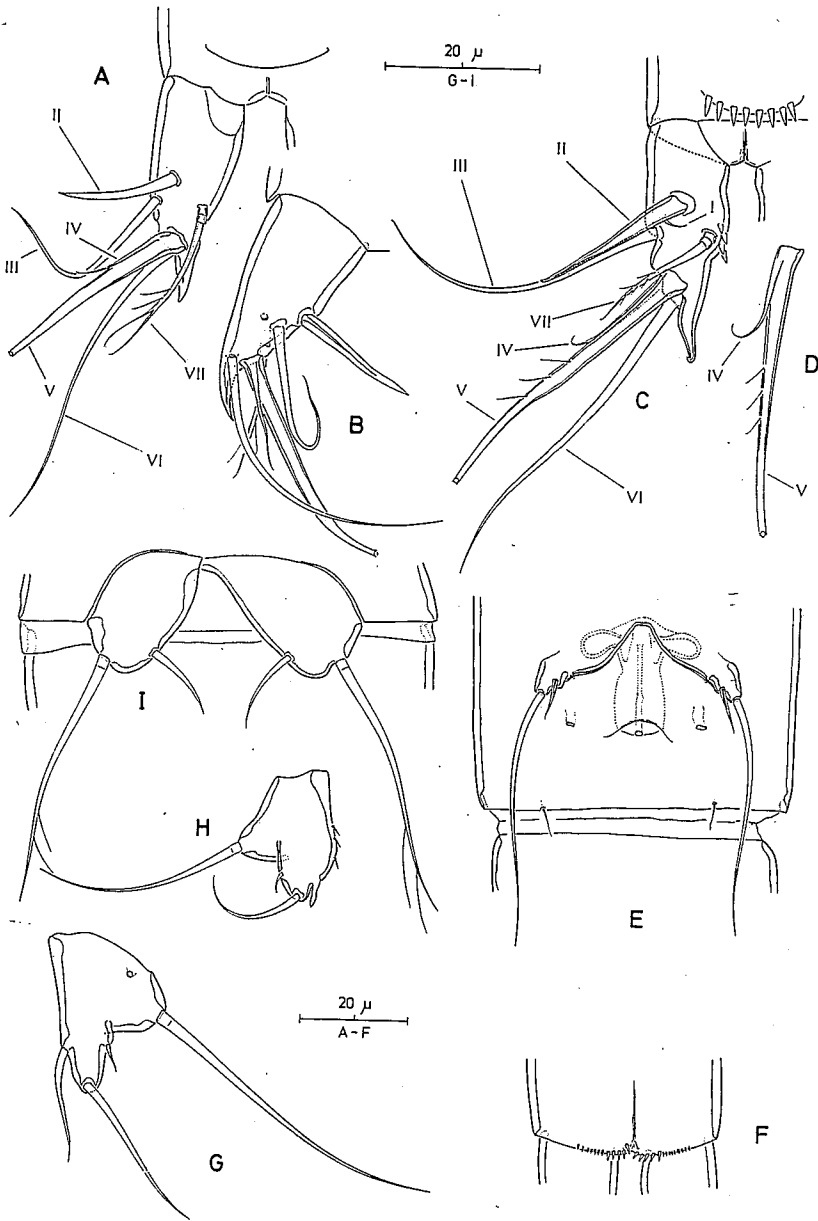


Fig. 49. — *Cerconeotes mozambicus* (Wells, 1967) comb. nov., A. Caudal ramus, dorsal view; B. Same, lateral view; C. Caudal ramus of copepodid V, dorsal view; D. Same, fused seta IV and V; E. Genital complex and P6, ♀; F. Posterior border of anal somite; ventral view; G. P5, ♀; H. P5, ♂; I. P6, ♂.

*MALE*. Body length including rostrum and caudal rami : 420  $\mu\text{m}$  ( $n = 2$ ). General body shape, colour, ornamentation and sensillar pattern as in female. Sexual dimorphism in antennule, endopod P3, fifth and sixth thoracopods, and in genital segmentation.

Antennule 8-segmented, slender ; haplocer ; geniculation located between segments 6 and 7 ; with aesthetasc on segment 4.

Third thoracopod (P3) (Fig. 48D). Protopod and exopod as in female. Endopod 2-segmented ; proximal segment with 1 spinular row ; distal segment with 1 unipinnate seta fused to the segment and with distal spinous process (homologous to subterminal seta in female) bearing small barb along inner margin.

Fifth thoracopod (P5) (Fig. 49H) with exopod and baseoendopod confluent ; represented by a small bilobed plate with hyaline process (vestigial seta ?) and 3 setae, apical one inserted subterminally.

Sixth thoracopods (P6) (Fig. 49I) slightly asymmetrical, with 2 setae each.

#### OTHER SPECIES

- C. constrictus* (Lang, 1965) comb. nov.  
syn. : *Leptastacus constrictus* Lang, 1965
- C. japonicus* (Itô, 1968) comb. nov.  
syn. : *Leptastacus japonicus* Itô, 1968
- C. jenneri* (Lindgren, 1975) comb. nov.  
syn. : *Leptastacus jenneri* Lindgren, 1975

#### SPECIES INQUIRENDAE

- C. nicholli* (Krishnaswamy, 1951) comb. nov.  
syn. : *Leptastacus nicholli* Krishnaswamy, 1951
- C. euryhalinus* (Krishnaswamy, 1957) comb. nov.  
syn. : *Leptastacus euryhalinus* Krishnaswamy, 1957
- C. waltirensis* (Rao & Ganapati, 1969) comb. nov.  
syn. : *Leptastacus waltirensis* Rao & Ganapati, 1969
- C. operculatus* (Masry, 1970) comb. nov.  
syn. : *Leptastacus operculatus* Masry, 1970

#### ETYMOLOGY

The generic name is derived from the Greek *kerkos*, meaning tail and *neotês*, meaning youth, and refers to the possible neotenic origin of the caudal rami (gender : masculine).



## MATERIAL EXAMINED

- *C. mozambicus*: The Natural History Museum, reg. no. 1967.8.4.91; paratypes consisting of 5 ♀♀ (4 in alcohol, 1 on 6 slides), 2 ♂♂ (1 in alcohol, 1 on 6 slides), 1 Cop. V; Saco da Inhaca and Ponta Torres, Inhaca Island, Mozambique; detritus sand and clean sand from beach; September 1963; leg. J. B. J. Wells.

## REMARKS

There are several deficiencies in the description of *L. operculatus*. In addition to the anal operculum, Masry (1970) attached much importance to minor characters such as the presence of sensilla on the rostrum and the slenderness of the antennules in order to differentiate it from *C. constrictus*. On the other hand he failed to provide adequate illustrations of the male endopod of P3 and the anal operculum and caudal rami in dorsal aspect which are vital in clearing up unequivocally the relationships of the species. The absence of an inner seta on the proximal endopodal segment of P1 is unquestionably wrong, however the setation of the exopod of this limb points to a relationship with *Cerconeotes*. This affinity is substantiated by the shape of the fifth leg and the setation of the male P6. A re-examination of this species is nevertheless preferable. The species is included in the key below because the large anal operculum is a unique character within the family.

Lang's (1965) statement that the distal exopodal segment of P1 in *C. constrictus* bears 4 setae, is undoubtedly wrong and is presumably the result of misinterpreting one of the spinules generally found along the outer margin of this segment. In all other aspects it is very closely related to *C. japonicus*. Re-examination of the Californian and Japanese material might reveal them to be synonymous since the difference is based on a few subtle characters only (see key).

Krishnaswamy's (1951) illustrations of *L. nichollsi* are grossly inadequate as is exemplified by for instance the drawing of the fourth leg which shows 2 outer spines on the middle exopodal segment. The setal formula of the first leg, the absence of inner setae on the endopods and exopods of P2 to P4, the shape and setation of the P5 and general outline of the caudal rami, however, leave no doubt that *L. nichollsi* should be placed in *Cerconeotes*. Reliable identification based on Krishnaswamy's (1951) description is impossible and pending this the species can at best be considered *species inquirenda* in the genus. The same remark applies for his later description (Krishnaswamy, 1957) of *L. euryhalinus*. I concur with Wells' (1967) opinion that there is a close relationship between *C. mozambicus* and the latter species. The large difference in body size (*L. euryhalinus* is nearly 3 times as long) however rules

out the possibility that both species are identical as Wells (1967) suggested, provided that Krishnaswamy's measurements were correct. The poor illustrations of *L. euryhalinus* fit with the generic diagnosis of *Cerconeotes*, but a detailed redescription without discrepancies between the text and figures is necessary before it can be included in the key given below. Pending this it should remain *species inquirenda* in the genus.

The third species described from Indian waters (Rao & Ganapati, 1969), *L. waltirensis*, may also be allocated to the genus *Cerconeotes*. Unfortunately, Rao & Ganapati's (1969) description and minute drawings do not meet the standard necessary for detailed comparison. The key below illustrates the detail that is required for species differentiation.

#### Key to the species of *Cerconeotes*

1. Proximal half of caudal rami concealed beneath anal operculum .....  
..... *C. operculatus* (Masry, 1970).  
Anal operculum weakly developed ..... 2.
2. Female fifth leg with 3 setae in total ..... *C. jenneri* (Lindgren, 1975).  
Female fifth leg with 4 setae in total ..... 3.
3. Fifth legs with distinct distal and lateral lobes in both sexes .....  
..... *C. mozambicus* (Wells, 1967).  
Fifth legs triangular in both sexes ..... 4.
4. L : W caudal ramus 2.5 ; female fifth leg with distal spinule .....  
..... *C. japonicus* (Itô, 1968).  
L : W caudal ramus 2.0 ; female fifth leg with distal setule .....  
..... *C. constrictus* (Lang, 1965).

#### RELATIONSHIPS

Mielke (1983) was the first to point out the long recurved spine on the first exopodal segment of P4 of *C. jenneri*. The shape and dimensions of this spine were often neglected in earlier descriptions as illustrated by the original description of *C. jenneri* (Lindgren, 1975). The actual size of this spine was figured on one side in *S. operculatus* by Masry (1970 : Fig. 11-52). The recurved shape of this armature element is typical for the genera *Schizothrix* (Mielke, 1982 : Abb. 9C), *Belemnopontia* (Mielke, 1982 : Abb. 13B) and *Cerconeotes* and constitutes a synapomorphy for this group. It is postulated that this spine showed the same condition before it was secondarily lost in *Psammastacus* since other unique synapomorphies are shared between these four genera (cf. sexual dimorphism). The caudal ramus of *Cerconeotes* shows a posterior process which is derived from an extension of the distal margin (see also

copepodid V; Fig. 49D). Since this process is often dorsally projected it may be mistaken for an articulating spinule when viewed in dorsal aspect (see Mielke, 1983 : Abb. 4B ; Wells, 1967 : Fig. 63A). Such an extension is shared with *Schizothrix* and *Belemnopontia* where it is extensively developed. It is suggested that this process is another apomorphy grouping the four genera mentioned above, and that it is in a state of reduction in *Cerconeotes* since it is absent in its immediate sistergroup. The loss of the inner setae on the proximal endopodal segments of P2 and P3, and of the proximal inner seta of the distal exopodal segment of P4 is shared with *Psammastacus* and *Belemnopontia*. Examination of a copepodid V showed that setae IV and V are fused (Figs. 49C-D) and as such provides evidence for the neotenic origin of this character state in the adult.

## GENUS

***Membranastacus* gen. nov.**

syn. : *Psammastacus* Nicholls, 1935 (partim) : Wells (1967).

## DIAGNOSIS

Leptastacidae. Cephalothorax and thoracic somites bearing P2-P4 with dorsal "nuchal organ". Rostrum triangular. Hyaline frill of urosomites reduced, plain. Antennary exopod with 2 distal setae. Mandibular palp 2-segmented ; basis with 1 seta. Labrum with frontal recurved process. P1 exopod 1-segmented ; with 1 lateral spine and 3 terminal setae/spines. P1 endopod 2-segmented, not prehensile. P2-P4 endopod 2-segmented. Spine and seta formulae as follows :

	Exopod	Endopod
P2	0.0.021.	0.010
P3	0.0.121	0.010
P4	0.1.221	0.110

Sexual dimorphism on endopod P3 (distal segment reduced in size and with blunt lateral process). P5 uniramous in both sexes ; in female with 6 setae ; in male with 5 setae. Male P6 with 3 well developed setae. Caudal ramus not acutely produced distally ; seta VI short and spiniform ; dorsomedial surface of each ramus with oblique spinular row.

## TYPE AND ONLY SPECIES

*M. inopinatus* sp. nov.

syn. : *Psammastacus spinicauda* Wells, 1967 (partim)

*Description*  
(Figs. 50 - 52)

**FEMALE.** Body length 520-535  $\mu\text{m}$  ( $n = 3$ ), measured from the tip of the rostrum to the hind margin of the caudal rami.

Body slender, cylindrical, almost colourless; intersomitic boundaries well developed. Integument smooth, moderately chitinised. Dorsal cephalic shield with elongated membranous plate, slightly constricted at about midway. Thoracic somites bearing P2 to P4 also with dorsal membranous plate. Hyaline frill of cephalothorax and body somites reduced to narrow membrane. Cephalothorax slightly tapering anteriorly, no distinct difference in width between cephalothorax and free body somites; no distinct separation between prosome and urosome, anal somite narrowest. Genital double-somite about as long as wide, with genital apertures located in anterior half; no trace of original subdivision (Fig. 52A). Ventral posterior margin of anal somite with some tiny spinules (equal in size).

Caudal rami parallel (Figs. 50B-D), about 2.1 times as long as maximum width. Armature consisting of 7 setae; seta V strongly developed, very long and arising with seta IV from common cylindrical socle; seta VI thorn-like; seta VII bi-articulated at base, pinnate and bifid at the tip; dorsal inner margin of ramus with oblique spinular row consisting of hyaline spinules.

Rostrum (Fig. 52G) well developed, triangular, exceeding first antennular segment, free at base. Nauplius eye not observed.

Antennule 7-segmented, slender; with aesthetasc on segment IV.

Antenna (Fig. 50E). Coxa small, unarmed. Allobasis about 2.9 times as long as maximum width; original segmentation not discernible. Exopod 1-segmented, small; with 2 apical setae. Distal endopodal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is swollen at the base, fused with a dwarfed seta and ornamented with spinules around the geniculation; inner endopodal margin with 2 spines covered by a few spinules.

Mandibular palp 2-segmented (Fig. 50E); basis with 1 seta; distal segment with 1 inner seta, 2 subterminal confluent setae along the outer margin and 2 apical confluent setae.

Labrum strongly developed (Figs. 50E), swollen; with frontal, dorsally projected, spinous process bearing long spinules and flanked by lateral spiny lobes.

Maxillula, maxilla and maxilliped as for the family.

Natatorial legs (Figs. 51A-D) with 3-segmented exopods (except for P1) ; endopods 2-segmented, always shorter than outer rami except for endopod P1. Succeeding legs increasing in length.

Thoracopod 1 (P1) (Fig. 51A). Coxa strongly developed, with spinular row on posterior surface. Basis distinctly shorter than coxa ; inner and outer setae not present ; with spinules at the outer corner. Exopod 1-segmented ; outer margin spinulose and with 1 bare spine ; distal margin with 1 unipinnate spine and 2 geniculate setae, innermost of which longest. First endopodal segment about as long as distal one ; with 1 short pectinate seta on inner margin and few spinules along outer margin. Second endopodal segment with 2 spinular rows along outer margin and 2 geniculate setae distally.

Thoracopods 2-4 (P2-P4) (Figs. 51B-D) with strongly developed coxae, each with 1 spinular row on posterior surface. Basis of P3-P4 with outer seta. Inner setae of middle exopodal segment P4 and of distal exopodal segment P3-P4 pectinate. Distal endopodal segment of P3 with 1 distal bipinnate seta. Outer exopodal spine of proximal and middle segments P4 neither elongate nor recurved at tip.

Seta and spine formulae as follows :

	Exopod	Endopod
P2	0.0.021	0.010
P3	0.0.121	0.010
P4	0.1.221	0.110

Thoracopod 5 (P5) (Fig. 52B) with exopod and baseoendopod confluent ; represented by a subcircular plate with 6 setae, exopodal setae *d* and *e* vestigial.

Thoracopod 6 (P6) represented by a minute non-articulating plate on either side, closing off the genital apertures and armed with 1 vestigial seta (Fig. 52C). Two large secretory tube pores are discernible on either side of the ventral midline ; copulatory pore small.

**MALE.** Body length including rostrum and caudal rami : 505  $\mu$ m. General body shape (Fig. 50A), colour, ornamentation and sensillar pattern as in female. Sexual dimorphism in antennule, endopod P3, P5, P6, and in genital segmentation (Fig. 50A).

Antennule 8-segmented, slender ; haplocer ; geniculation located between segments 6 and 7 ; with aesthetasc on segment 4.

Third thoracopod (P3) (Figs. 52D). Protopod and exopod as in female. Endopod 2-segmented ; proximal segment without surface ornamentation ; distal segment strongly reduced in size, with blunt, slightly curved inner process.

Fifth thoracopod (P5) (Fig. 52E) with exopod and baseoendopod confluent ; represented by a subcircular plate with 5 setae in total of which one is vestigial.

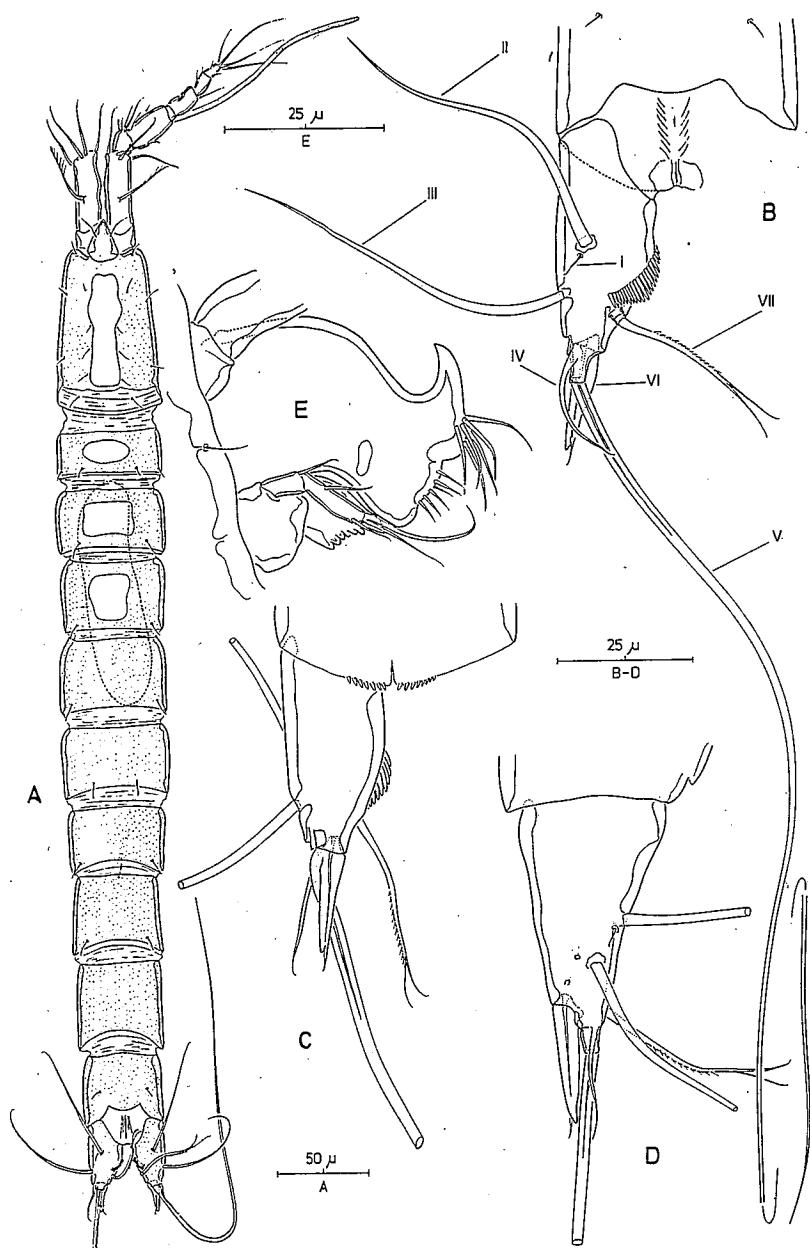


Fig. 50. — *Membranastacus inopinatus* gen. et sp. nov., A. Habitus ♂, dorsal view; B. Caudal ramus, dorsal view; C. Same, ventral view; D. Same, lateral view; E. Labrum and mandibular palp, lateral view.

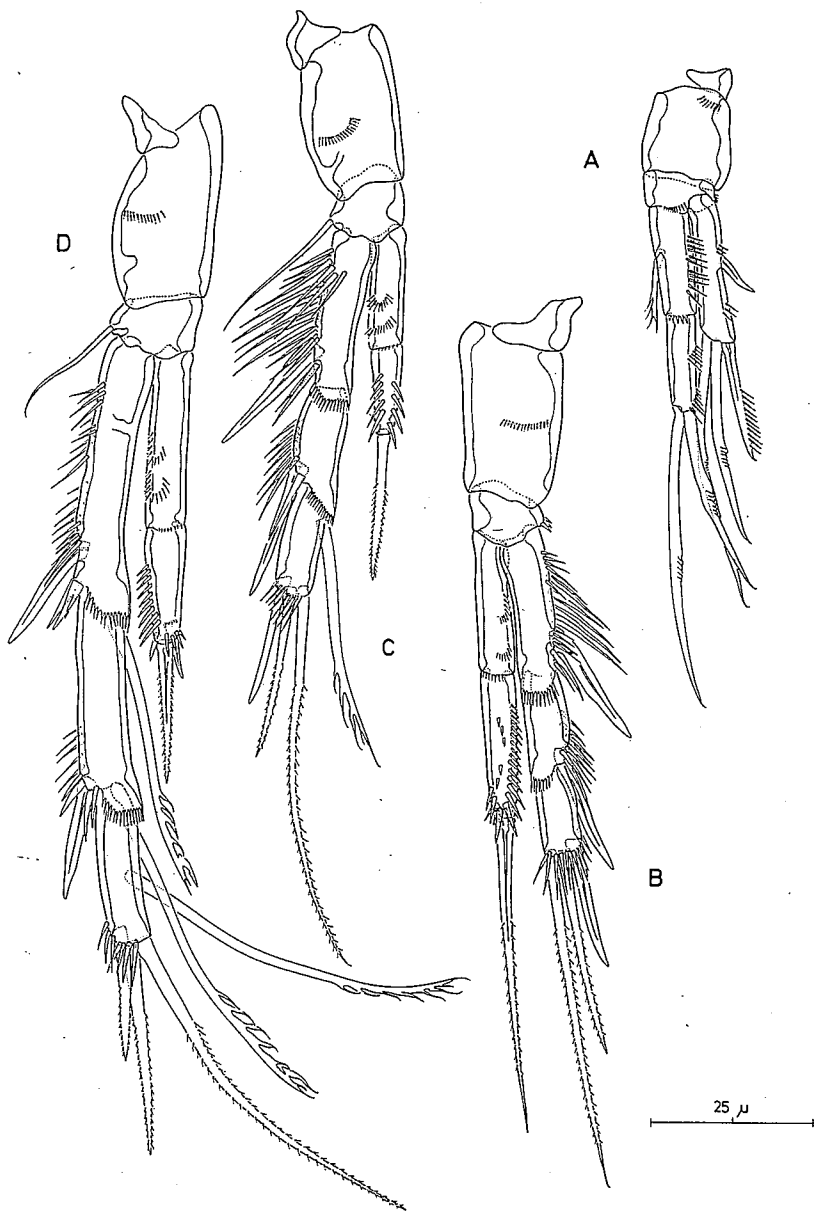


Fig. 51. — *Membranastacus inopinatus* gen. et sp. nov. Female. A. P1 ; B. P2 ; C. P3 ; D. P4.

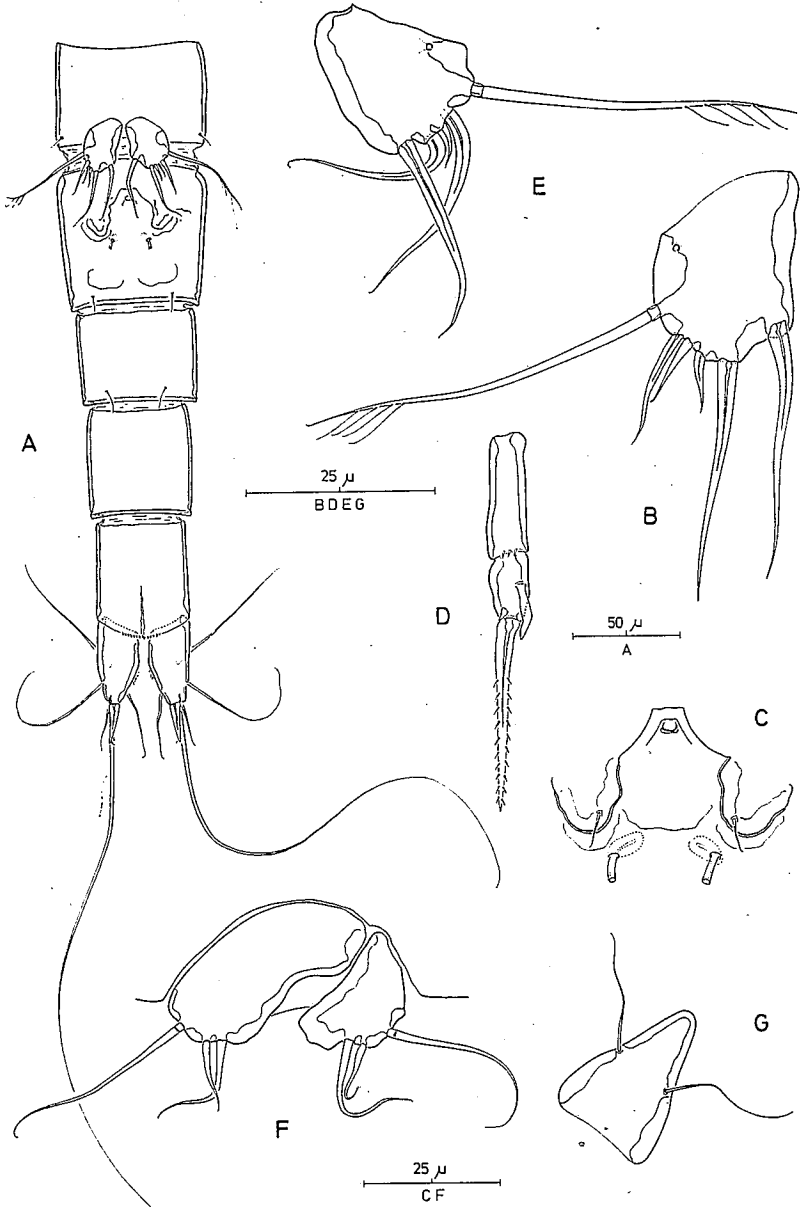


Fig. 52. — *Membranastacus inopinatus* gen. et sp. nov., A. Urosome of ♀, ventral view; B. P5, ♀; C. Genital apertures, ♀; D. Endopod P3, ♂; E. P5, ♂; F. P6, ♂; G. Rostrum.



Sixth thoracopods (P6) (Fig. 52F) strongly asymmetrical. One member represented by large articulating plate bearing 3 well developed setae; other member with same armature but smaller and fused to supporting somite.

#### ETYMOLOGY

The generic name is derived from the Latin *membrana*, meaning membrane, and *astacus*, which is part of the family name, and refers to the membraneous dorsal structures ("nuchal organs") on the cephalothorax and first thoracic somites (gender: masculine). The Latin species name *inopinatus* (= surprising) alludes to its unexpected discovery during inspection of the types of *P. spinicauda*.

#### MATERIAL EXAMINED

— *M. inopinatus*: The Natural History Museum; found among paratype material of *Psammastacus spinicauda* (reg. no. 1967.8.4.88); holotype ♀ (dissected on 6 slides, reg. no. 1992.1116) and 4 paratypes (3 ♀♀ in alcohol, reg. no. 1992.1118; 1 ♂ dissected on 6 slides, reg. no. 1992.1117); Ilha dos Portuguesos (Elephant Isle), Inhaca Island, Mozambique; clean sand from beach; September 1963; leg. J. B. J. Wells.

#### REMARKS

The relationships of *Membranastacus* were already discussed under the closely related genera *Minervella* and *Neopsammastacus*. It can be differentiated from these genera primarily on the presence of dorsal "nuchal organs" on the cephalothorax and first thoracic somites. These structures are widespread in freshwater harpacticoids (e.g. Parastenocarididae, Canthocamptidae, some Cletodidae) or species that occur in brackish water (Tachidiidae) but were not observed before in leptastacid copepods. The absence of sexual dimorphism on the P3 exopod also serves to distinguish the new genus from *Minervella*.

#### GENUS

*Schizothrix* gen. nov.

syn.: *Leptastacus* T. Scott, 1906 (partim): Nicholls (1940); Griga (1964), Marinov (1973), Geddes (1981), Mielke (1982)

#### DIAGNOSIS

Leptastacidae. Rostrum elongated. Urosomites with plain hyaline frill. Mandibular palp 2-segmented; basis with 1 seta. Antennary exopod with 2 distal setae. Labrum without frontal process. P1 exopod 3-segmented; exp-3

with 4 setae/spines. P1 endopod 2-segmented, not prehensile. P2-P4 endopod 2-segmented. Outer spine of exp-1 P4 elongated and curved. Spine and seta formulae as follows :

	Exopod	Endopod
P2	0.0.021	1.010
P3	0.0.121	1.010
P4	0.1.221	0.110

Slight sexual dimorphism on endopod P3. P5 uniramous ; triangular and produced distally ; in female with 5 well developed setae (setae *a* and *e* vestigial or absent) ; in male with 3 well developed setae (setae *a-c* and *e* vestigial or absent). Male P6 with 3 setae. Anal operculum with spinous processes. Caudal ramus acutely produced distally ; seta V furcated.

#### TYPE SPECIES

*S. ctenata* (Mielke, 1982) comb. nov.  
syn. : *Leptastacus ctenatus* Mielke, 1982

#### OTHER SPECIES

*S. rostrata* (Nicholls, 1940) comb. nov.  
syn. : *Leptastacus rostratus* Nicholls, 1940  
*S. pontica* (Griga, 1964) comb. nov.  
syn. : *Leptastacus macronyx* var. *pontica* Griga, 1964  
*Leptastacus rostratus* Nicholls, 1940 ? : Apostolov (1972)  
*Leptastacus rostratus* Nicholls, 1940 : Apostolov (1973a)  
*Leptastacus rostratus* Nicholls subsp. *taurica* Marinov, 1973  
*Leptastacus taurica* Marinov, 1973 : Geddes (1981), Apostolov & Marinov (1988)

#### ETYMOLOGY

The generic name is derived from the Greek *schizoo*, meaning to split, and *trichos*, *thrix*, meaning hair, and refers to the furcate seta V on the caudal ramus (gender : feminine).

#### MATERIAL EXAMINED

Paratypes (2 ♀♀) of *S. rostrata* kept in The Natural History Museum (reg. no. 1940.5.1.71-2). Observations on male morphology were based on *Schizothrix* sp. A from the Kwinte Bank, Belgian North Sea coast.

## REMARKS

Re-examination of the paratypes of *S. rostrata* has removed the only point of difference found between Geddes' (1981) material from the island of Grindøy and Nicholls' (1940) types from the St. Lawrence River. Geddes' (1981) suspicion that the smaller subdistal spine on the distal endopodal segment of leg 3 might have been obscured by the larger distal one in Nicholls' slide preparation proved to be correct.

The confusing taxonomic history of *S. pontica* was already discussed in section 1.

Key to the species of *Schizothrix*

1. Anal operculum with posteriorly directed bifid process ; total body length of ♀ about 1520 μ ..... *S. rostrata* (Nicholls, 1940).  
Anal operculum with a number of small spinules ; total body length of ♀ less than 800 μ ..... 2.
2. Anal operculum with about 4 spinules ; length : width (measured at proximal margin) 3.7 ; enp-1 P1 0.78 times as long as exopod and 1.45 times as long as enp-2 ..... *S. pontica* (Griga, 1964).  
Anal operculum with 10-12 spinules ; length : width (measured at proximal margin) 4.4 ; enp-1 P1 0.95 times as long as exopod and 1.90 times as long as enp-2 ..... *S. ctenata* (Mielke, 1982).

## RELATIONSHIPS

*Schizothrix* is the most primitive member of a genus group (*Belemnopontia*, *Psammastacus*, *Cerconeotes*) that displays the following synapomorphies : (i) outer spine of exp-1 P4 elongated and recurved at tip, (ii) caudal ramus with acutely produced, dorsally recurved process (type E). No published information is available on male *Schizothrix*, but observations of male specimens of an as yet undescribed species from the Belgian coast revealed the presence of a barbed spinous process on the distal endopodal segment of P3. This transformation constitutes another synapomorphic character for the genus group mentioned above. There was no difference in male P5 morphology between *Leptastacus* and the undescribed *Schizothrix* species. A unique apomorphy for the genus is the bifurcated seta V of the caudal ramus (Figs. 24D, D').

## GENUS

*Sextonis* gen. nov.

syn. : *Leptastacus* T. Scott, 1906 (partim) : Rouch (1962), Lang (1965), McLachlan & Moore

## DIAGNOSIS

Leptastacidae. Rostrum elongated. Hyaline frill of urosomites reduced, striated. Antennary exopod with 2 distal setae. Mandibular palp 2-segmented; basis with 1 seta. labrum without frontal recurved process. P1 exopod 3-segmented; exp-3 with 4 setae/spines. P1 endopod 2-segmented, not prehensile; long setae on exp-3 and enp-2 swollen and blunt. P2-P4 endopod 2-segmented. Spine and seta formulae as follows :

	Exopod	Endopod
P2	0.0.021	[0-1].010
P3	0.0.121	[0-1].01[0-1]
P4	0.1.221	0.110

Slight sexual dimorphism in endopod P3 (sometimes exopod P2). P5 uniramous in both sexes; bilobed; in female with 4-5 well developed setae on outer lobe and 2 (occasionally 1) setae on inner lobe; in male with 3-5 setae on outer lobe and 1 (occasionally 2) seta(e) on inner lobe or equivalent site (if not pronounced). Male P6 with 3 setae. Caudal ramus not acutely produced distally; seta VI short and spiniform, occasionally incorporated into ramus; dorsomedial surface of each ramus with oblique spinular row.

## TYPE SPECIES

- S. mehuinensis* (Mielke, 1985) comb. nov.  
syn. : *Leptastacus mehuinensis* Mielke, 1985

## OTHER SPECIES

- S. incurvatus* (Lang, 1965) comb. nov.  
syn. : *Leptastacus incurvatus* Lang, 1965  
*S. chilensis* (Mielke, 1985) comb. nov.  
syn. : *Leptastacus incurvatus chilensis* Mielke, 1985  
*Leptastacus chilensis* Mielke, 1985 : Bodiou & Colomines (1989)  
*S. laminaserratus* (Mielke, 1985) comb. nov.  
syn. : *Leptastacus laminaserrata* Mielke, 1985

## SPECIES INQUIRENDAE

- S. delamarei* (Rouch, 1962) comb. nov.  
syn. : *Leptastacus delamarei* Rouch, 1962  
*S. naylori* (McLachlan & Moore, 1978) comb. nov.  
syn. : *Leptastacus naylori* McLachlan & Moore, 1978 (partim)

## ETYMOLOGY

The generic name is derived from the Latin *sex*tus, meaning sixth, and *onis*, meaning dagger, and refers to the modified seta VI on the caudal ramus (gender : masculine).

## MATERIAL EXAMINED

— *S. naylori*: South African Museum, holotype ♀ (reg. no. SAM-A15713), allotype ♂ (reg. no. SAM-A15716) and 1 paratype ♀ (SAM-A15714); all specimens are whole mounts in polyvinyl lactophenol; Sunday's River beach (25°53' E, 33°43' S), Algoa Bay, South Africa; fine sand (leg. A. McLachlan & J. P. Furstenberg)

## REMARKS

Rouch' (1962) concise description leaves little doubt about the affinity of *L. delamarei*. The segmentation of the first leg, the setation of the female fifth leg (though presumably incomplete) and the male P6, and the spini-form seta VI of the caudal ramus indicate the species' relationships to the other members of *Sextonis*. There are, however, several inaccuracies in Rouch' illustrations (e.g. the male P5) and most likely the sexual dimorphism on the male P3 endopod has been overlooked. The presence of several other species along the beaches of South America hinders reliable identification of *L. delamarei* and urges a detailed redescription. Thus, the species is tentatively ranked *species inquirenda*.

The paratype male (reg. no. SAM-A15715) of *Leptastacus naylori* proved upon examination to belong to a different species. The bad condition of the slide preparation makes it impossible to redescribe the specimen adequately or to assign it with certainty to an existing genus, though certain characters indicate that its affinities may lie with *Minervella*. Similarities with the latter genus include the deeply subdivided hyaline frill of the urosomites, the frontal dorsally directed process on the labrum, the 1-segmented exopod of P1 and the presence of sexual dimorphism on the endopod of P3. Closer inspection also revealed that McLachlan & Moore's (1978) illustrations of the male fifth and sixth legs of *L. naylori* were based on this specimen. Unfortunately, the condition of the allotype male did not permit a redescription of these appendages nor of the possible modifications on the P3 endopod. For these reasons *L. naylori* has to be considered *species inquirenda* within the genus *Sextonis*.

Bodiou & Colomines (1989) upgraded Mielke's (1985) subspecies *L. incurvatus chilensis* to full species level on the base of the absence of the inner seta on the middle exopodal segment of P3. Mielke (1985) already doubted

the presence of this seta in the Lang's (1965) nominate species since the inner distal part of the hyaline frill can be misinterpreted as an additional armature element. No other species of Leptastacidae exhibits a seta on this segment and it is likely that Kunz' (1974) observation of the inner seta on the middle exopodal segment of leg 2 in *A. aberrans* was due to such a misinterpretation. The discovery of the male of *L. incurvatus chilensis* and re-examination of the male paratypes of *L. incurvatus incurvatus* shed more light on the relationships of both species (Mielke, 1987). The differences found in the male P5 and the caudal rami (but not described precisely) suggested to Mielke that both the Californian and the Chilean populations represented distinct species, however, this status was not formally recognised. In view of the new information supplied by Mielke (1987) it is preferable to maintain Bodiou & Colomines' (1989) elevation to species level.

#### Key to the species of *Sextonis*

1. Enp-1 P2 without inner seta ..... *S. mehuinensis* (Mielke, 1985).  
Enp-1 P2 with inner seta ..... 2.
2. Enp-1 P3 without inner seta ; enp-2 P3 with 1 seta .....  
..... *S. laminaserratus* (Mielke, 1985).  
Enp-1 P3 with inner seta ; enp-2 P3 with 2 setae ..... 3.
3. P5 of ♂ with 7 setae ..... *S. incurvatus* (Lang, 1965).  
P5 of ♂ with 5 setae ..... *S. chilensis* (Mielke, 1985).

#### RELATIONSHIPS

This genus is perhaps still the most heterogeneous one of the family. Unquestionably, it occupies a position near the base of the lineage that is characterised by the spiniform seta VI and the dorsomedial oblique spinular row of the caudal ramus. This lineage leads to the advanced genera *Afroleptastacus*, *Arenotopa*, *Membranastacus*, *Neopsammastacus* and *Minervella* which all display a unisegmented P1 exopod. If we accept this character as a synapomorphy linking these 5 genera, all other species (whether or not they belong to a single genus *Sextonis*) must have been diverged at an earlier stage in the evolution because they have a 3-segmented exopod. The discovery of an intermediate with a 2-segmented exopod might provide evidence for this hypothesis. The heterogeneity of the genus *Sextonis* is illustrated by its diagnosis since almost every species shows one or other unique feature. For example, it accommodates the only species that display sexual dimorphism on the P2 exopod (*S. laminaserratus*) or have the seta VI incorporated in the caudal ramus (*S. incurvatus*, *S. chilensis*). Gross variation exists in the setal formula of the swimming legs and in setation of the fifth legs in both sexes. Apart

from the modified setae on the first thoracopod no distinct apomorphies could be detected. This assemblage of species will require more detailed investigation in the future. In spite of this unknown information the present taxonomic concept of *Sextonis* is regarded more valuable in defining relationships than the repository *Leptastacus sensu lato* whose species were incorporated before.

#### *Leptastacidae incertae sedis*

##### *Leptastacus christelleae* Bodiou & Colomines, 1989

The atypical setal formula of *L. christelleae* is, unless it is inadequate, an unsurmountable obstacle to allow inclusion of the species in the genus *Sextonis*. The authors most likely overlooked the pectinate setae on the distal exopodal segment of thoracopods 3 and 4. Their illustration of the caudal ramus is undoubtedly wrong. Their statement that each ramus bears 8 setae (seta I not taken into account!) is suspicious and presumably arose by misinterpreting the bifid dorsal seta VII and the subapical flagellate process of seta VI. The spinule observed along the inner margin might be part of the oblique spinular row which was overlooked altogether. Requests to borrow the types failed.

##### *Leptastacus naylori* McLachlan & Moore, 1978 (partim : paratype ♂ SAM-A15715)

See under *Sextonis*.

##### *Psammastacus acuticaudatus* Krishnaswamy, 1957

Cottarelli & Venanzetti (1989) referred this species to *Neopsammastacus* on account of the bisetose antennary exopod, the 2-segmented mandibular palp and the complete absence of sexual dimorphism on P2 to P4. Krishnaswamy's (1957) illustrations do not provide the barest minimum of information to allow confirmation of the latter two characters. The unisegmented P1 exopod and the spinous caudal rami suggest that *P. acuticaudatus* most likely belongs to the *Minervella* genus-group which further includes also *Membranastacus* and *Neopsammastacus*. The lack of information about the fifth legs and swimming leg dimorphism, however, does not permit a more precise allocation.

## 2.6. ANALYSIS (Fig. 53)

A study of all the limbs and the caudal rami of representatives of all ten copepod orders (Huys & Boxshall, 1991) revealed that setation patterns are highly conservative evolutionary and as such might provide an important

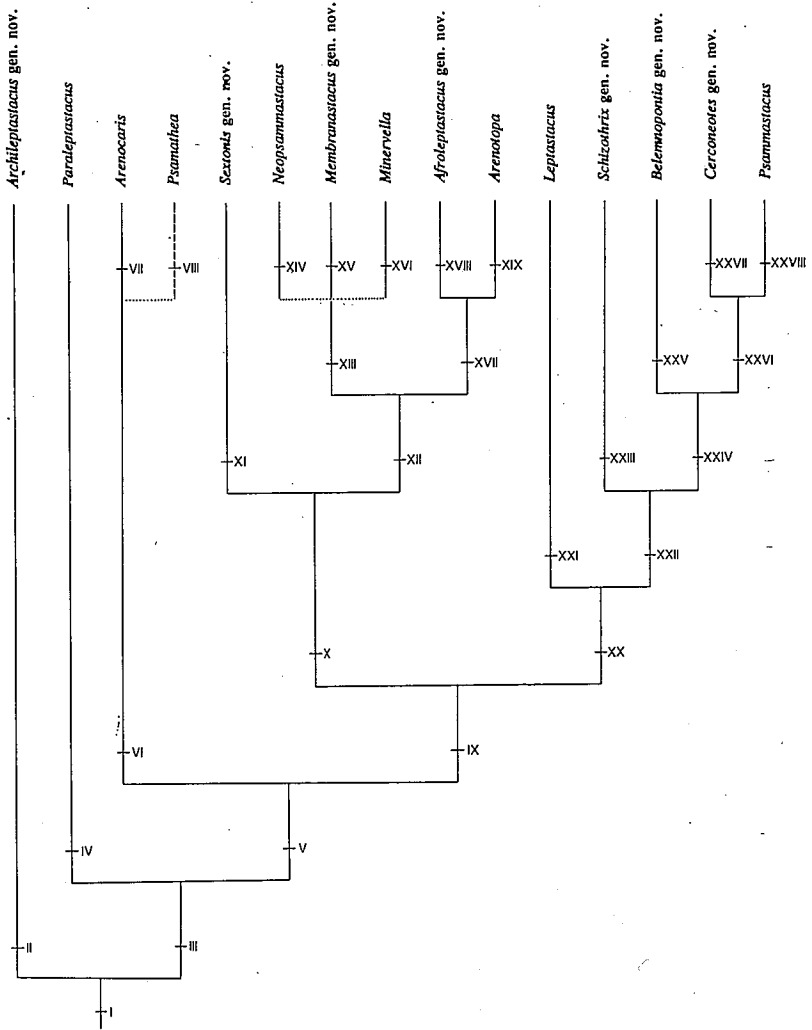


Fig. 53. — Cladogram depicting the phylogenetic relationships within the Leptastacidae.  
 [Explanation in the text].



tool in assessing phylogenetic relationships. Boxshall & Huys (1992) argued strongly for a rigorous application of the principle of homology in any phylogenetic study in order to improve the robustness of the character sets used. Simple setal counts or segment numbers are unusable unless it can be confirmed that the elements involved are homologous. Hence, the apomorphic character states listed below (clades II - XXVIII) should be regarded as the acquired ultimate product of a particular evolutionary process and therefore are expressed as such. It are the transformations (loss, fusion, incorporation) that constitute the actual characters.

The monophyly of the Leptastacidae (clade I) can be unequivocally supported by (1) the tripartite, spinous labrum, (2) the rotation and anterior direction of the maxillary arthrite, (3) the design of the maxilla including the transformed spines on the syncoxal endites and secondarily elongated endopod, and (4) the position and structure of the maxilliped, including its sigmoid, bipinnate claw accompanied by the slender seta. The exact primitive state of the swimming leg sexual dimorphism is difficult to assess but it is postulated that the ancestor possessed a slight transformation on the distal endopodal segment of P3 (involving the subapical seta). Among the 15 genera considered here *Archileptastacus* without doubt represents the earliest offshoot in the family. *Paraleptastacus* and *Arenocaris* are the next genera to diverge early whereas the bulk of the leptastacid genera can be grouped in two clades. These groups are mainly defined by the structure of the caudal rami and the fifth legs, respectively. The various clades depicted in Fig. 53 and denoted by Roman numerals can be defined by the following synapomorphies :

- II :       — reduction of endopodal armature P2-P4 to single distal seta on enp-2 ;  
           — loss of inner seta on exp-2 P4 ;  
           — transformation of caudal rami involving reduction of setae IV and VI and development of posteriorly directed, spinous process arising from distal outer corner of ramus (type D) ;  
           — fusion of exopod and baseoendopod of P5 in both sexes ; exopodal seta *c* thorn-like and fused to supporting segment ; endopodal seta *a* vestigial or absent ;
- III :       — P1 endopod 2-segmented (fusion of enp-2 and enp-3) ;  
           — basis and proximal endopod segment of antenna fused to allobasis ;  
           — A2 exopod bisetose (loss of lateral seta) ;  
           — loss of inner seta on exp-3 P2 ;
- IV :       — transformation of caudal rami involving development of posteriorly directed process homologous to the inner distal corner of the ramus (type H) ;  
           — rectangular lappeted hyaline frill of urosomites ;

- V : — loss of proximal outer spine on exp-3 P2-P4 ;  
— loss of distal outer seta on enp-2 P2 ;
- VI : — P1 exopod 2-segmented (fusion of exp-2 and exp-3) ;  
— ? sexual dimorphism of P4 (medially directed endopod with distal claw and spine) ;
- VII : — loss sexual dimorphism on endopod P3 ;  
— inner distal spine of exp-3 P2-P4 tubular ;  
— endopod P2-P3 1-segmented (presumably loss of enp-1) ;  
— transformation of caudal rami involving reduction of setae IV and VI, seta III tubular (type G) ;  
— sexual dimorphism of caudal rami (loss of spinular row in ♂) ;
- VIII : — prehensile endopod P1 ; extreme elongation of enp-1 ;  
— fusion of P5 rami ; reduction or loss of exopodal setae *d-f* ;  
— transformation of caudal rami involving the development of a dorsal tricuspidate process (type I) ;  
— sexual dimorphism of endopod P3 involving reduction of distal segment and loss of subapical seta ;
- IX : — fusion of P5 rami in both sexes ; ancestral armature pattern retained
- X : — transformation of caudal rami involving the development of an oblique spinular row on the dorsomedial surface, modification of seta VI (spiniform) and partial reduction of seta IV (loss fracture planes) (type F) ;
- XI : — P1 with modified (blunt, swollen) geniculate setae on endopod (inner one of enp-2) and exopod (distal two of exp-3) ;
- XII : — P1 exopod 1-segmented ; armature consisting of 1 lateral and 3 terminal setae/spines ;
- XIII : — labrum with frontal, dorsally recurved process ;  
— sexual dimorphism on endopod P3 involving reduction of distal segment and formation of recurved apophysis ;
- XIV : — ventral hind margin of anal somite with strong armature ;  
— elaboration of dorsomedial spinular row on caudal rami ;
- XV : — cephalothorax and thoracic somites bearing P2-P4 with dorsal "nuchal organs ;
- XVI : — sexual dimorphism on exopod P3 ;
- XVII : — dorsal hind margin of caudal rami with movable recurved spinule ;  
— sexual dimorphism on exopod P4 involving elongation of distal spines in male ;  
— genital complex in female with 1 long seta on each side ;  
— male P6 with middle seta vestigial ;
- XVIII : — loss of sexual dimorphism on endopod P3 ;

- XIX : — development of extreme sexual dimorphism on P4 endopod (elongation of enp-2) ;  
— reduction of P5 armature in both sexes ;
- XX : — transformation of P5 in both sexes involving formation of median, distal process between exopodal setae *d* and *e* ; reduction of setae *a* and *e* in female ; reduction of setae *a*, *b* and *e* and loss of seta *c* in male ;  
— basal fusion of subdistal seta enp-2 P3 ;
- XXI : — outer spine of exp-2 P4 elongated and recurved at tip ;  
— transformation of caudal ramus involving development of composite seta III comprising rigid, proximal part and flagellate distal part (type B) ;  
— reduction of anterior spine enp-2 P3 to minute non-articulating spinous process ;
- XXII : — outer spine of exp-1 P4 elongated and recurved at tip ;  
— barbed process on male enp-2 P3 ;  
— caudal ramus with acutely produced, dorsally recurved process (type E) ;
- XXIII : — furcated seta V of caudal ramus (type E) ;
- XXIV : — loss of inner seta on proximal endopodal segment of P2-P3 ;  
— loss of proximal inner seta on exp-3 P4 ;  
— P5 : loss of seta *c* in female and of seta *b* in male ;  
— reduction in mandibular palp (loss basal seta ; distal segment with 4 setae) ;
- XXV : — ventral hind margin of anal somite with 2 strong spinules ;
- XXVI : — distal exopodal segment of P1 with 3 setae/spines ;  
— loss of setae *a* and *e* in P5 of both sexes ;  
— seta V of caudal rami tubular ;  
— male P6 with 2 setae ;  
— loss of subapical seta exp-3 P4 ;
- XXVII : — heterochronic development of caudal rami ;
- XXVIII : — exopod P1 1-segmented ; with 1 outer and 3 distal spines/setae ;  
— fusion of seta IV and V of caudal rami ;  
— loss of dorsally recurved process of caudal ramus ;  
— loss of outer spine exp-1 P4 ;  
— extreme reduction of P5 in both sexes ; incorporation in somite.

### 3. A key to the genera of the Leptastacidae

The upgrading of the Leptastacinae to family rank and the revision of the ill-defined genera *Leptastacus*, *Psammastacus* and *Neopsammastacus* have made Cottarelli & Venanzetti's (1989) key to the genera of the *Cylindropsyllidae*

out of date. Therefore a new generic key, applicable to both sexes, is proposed incorporating the seven new genera resulting from the present account.

1. P1 endopod 3-segmented ; exp-3 P2 with inner seta ; exp-2 P4 without inner seta ; antennary exopod with 3 setae ..... *Archileptastacus* gen. nov.  
P1 endopod 2-segmented ; exp-3 P2 without inner seta ; exp-2 P4 with inner seta ; antennary exopod with 1-2 setae ..... 2.
2. P5 biramous in both sexes ..... 3.  
P5 with exopod and baseoendopod fused in both sexes ..... 4.
3. P1 exopod 3-segmented ; endopod P2-P4 2-segmented ; exp-3 P2-P4 with 2 outer spines ..... *Paraleptastacus*.  
P1 exopod 2-segmented ; endopod P2-P3 1-segmented, endopod P4 3-segmented ; exp-3 P2-P4 with 1 outer spine ..... *Arenocaris*.
4. P1 endopod prehensile ..... *Psamathea*.  
P1 endopod not prehensile ..... 5.
5. Caudal ramus with spiniform seta VI ; dorsomedial surface with oblique spinular row ..... 6.  
Dorsomedial surface of caudal ramus without conspicuous spinular row ; seta VI not modified ..... 11
6. P1 exopod 3-segmented ..... *Sextonis* gen. nov.  
P1 exopod 1-segmented ..... 7.
7. Cephalothorax and thoracic somites bearing P2-P4 with dorsal "nuchal organ" ..... *Membranastacus* gen. nov.  
No nuchal organs present ..... 8.
8. Labrum with frontal, dorsally projected process ..... 9.  
Labrum without such process ..... 10.
9. Exopod P3 with sexual dimorphism ; P5 with 5-6 setae in ♀, with 4-5 setae in ♂ ..... *Minervella*.  
Exopod P3 without sexual dimorphism ; P5 with 7 setae in both sexes ..... *Neopsammastacus*.
10. No distinct sexual dimorphism on endopod P3-P4 ; P5 with 7 setae in ♀ ..... *Afroleptastacus* gen. nov.  
Endopod P3-P4 with strong sexual dimorphism ; P5 with 4-5 setae in ♀ ..... *Arenotopa*.
11. Exopod P1 3-segmented ..... 12.  
Exopod P1 1-segmented ..... *Psammastacus*.
12. Caudal ramus with composite seta III ..... *Leptastacus*.  
Caudal ramus with seta III not being composite ..... 13.
13. Exp-3 P1 with 3 setae/spines ; setae IV and V of caudal ramus fused .....  
..... *Cerconeotes* gen. nov.  
Exp-3 P1 with 4 setae/spines ; setae IV and V not fused ..... 14.
14. Enp-1 P2-P3 with inner seta ; exp-3 P3 without inner seta ; caudal

- ramus with seta V furcated ; anal operculum with spinous processes .....  
 ..... *Schizothrix* gen. nov.  
 Enp-1 P2-P3 without inner seta ; exp-3 P3 with inner seta ; caudal ramus  
 with normal seta V ; anal operculum without distinct processes .....  
 ..... *Belemnopontia* gen. nov.

ADDENDUM : List of species and genera (species in bold are type species ;  
 \* indicate *species inquirendae*).

*Leptastacus* T. Scott, 1906

- L. macronyx** (T. Scott, 1892) T. Scott, 1906  
*L. laticaudatus* Nicholls, 1935  
*L. spatuliseta* Mielke, 1982  
*L. uncinatus* Cottarelli & Venanzetti, 1989  
*L. coulli* sp. nov.  
*L. kwineii* sp. nov.  
*L. corsicaensis* sp. nov.  
*L. pygmaeus* sp. nov.  
 \* *L. laticaudatus intermedius* Kunz, 1937 *sensu* Apostolov (1973)  
 \* *L. minutus* Chappuis, 1954  
 \* *L. wieseri* Chappuis, 1958

*Paraleptastacus* Wilson, 1932

- P. brevicaudatus** Wilson, 1932  
*P. spinicauda* (T. & A. Scott, 1895) Nicholls, 1935  
*P. kliei* (Gagern, 1923) Kunz, 1937  
*P. katamensis* Wilson, 1932  
*P. espinulatus* Nicholls, 1935  
*P. holsaticus* Kunz, 1937  
*P. bisetosus* Jakubisiak, 1938  
*P. laurenticus* Nicholls, 1940  
*P. longicaudatus* Nicholls, 1940  
*P. triseta* Noodt, 1954  
*P. unisetosus* Itô, 1972  
*P. supralitoralis* Mielke, 1975  
*P. monensis* Whybrew, 1986  
*P. moorei* Whybrew, 1986  
*P. wilsoni* Whybrew, 1986  
 \* *P. spinicauda bisetosus* Jakubisiak, 1938  
 \* *P. ammodytensis* Carvalho, 1952  
 \* *P. caspicus* Stërba, 1973

*Arenocaris* Nicholls, 1935**A. bifida** Nicholls, 1935*A. reducta* sp. nov.*Psammastacus* Nicholls, 1935**P. confluens** Nicholls, 1935\* *P. confluens* Nicholls, 1935 *sensu* Chappuis (1954)\* *P. confluens* Nicholls, 1935 *sensu* Apostolov (1977)*Arenotopa* Chappuis & Rouch, 1960**A. ghanai** Chappuis & Rouch, 1960*A. rossii* Cottarelli, 1977*A. erasmusi* (McLachlan & Moore, 1978) Wells & Rao, 1987*A. dyadacantha* Wells & Rao, 1987*Minervella* Cottarelli & Venanzetti, 1989**M. baccettii** Cottarelli & Venanzetti, 1989*M. perplexa* (Wells & Clark, 1965) comb. nov.*Neopsammastacus* Cottarelli & Venanzetti, 1989**N. spinicauda** (Wells, 1967) Cottarelli & Venanzetti, 1989*N. spinicaudatus* (Rao & Ganapati, 1969) Cottarelli & Venanzetti, 1989*Psamathea* Cottarelli & Venanzetti, 1989**P. nautarum** Cottarelli & Venanzetti, 1989*Afroleptastacus* gen. nov.**A. clandestinus** sp. nov.*A. remanei* (Noodt, 1954) comb. nov.*Archileptastacus* gen. nov.**A. dichatoensis** (Mielke, 1985) comb. nov.*A. aberrans* (Chappuis, 1954) comb. nov.*Belemnopontia* gen. nov.**B. dispinosa** (Mielke, 1982) comb. nov.*B. panamensis* (Mielke, 1983) comb. nov.\* *B. acuticaudatus* (Krishnaswamy, 1957) comb. nov.\* *Leptastacus macronyx* (T. Scott) *sensu* Chappuis & Rouch (1961)*Cerconeotes* gen. nov.**C. mozambicus** (Wells, 1967) comb. nov.*C. constrictus* (Lang, 1965) comb. nov.

*C. japonicus* (Itô, 1968) comb. nov.

*C. jenneri* (Lindgren, 1975) comb. nov.

\* *C. nicholli* (Krishnaswamy, 1951) comb. nov.

\* *C. euryhalinus* (Krishnaswamy, 1957) comb. nov.

\* *C. waltirensis* (Rao & Ganapati, 1969) comb. nov.

\* *C. operculatus* (Masry, 1970) comb. nov.

*Membranastacus* gen. nov.

**M. inopinatus** sp. nov.

*Schizothrix* gen. nov.

**S. ctenata** (Mielke, 1982) comb. nov.

*S. rostrata* (Nicholls, 1940) comb. nov.

*S. pontica* (Griga, 1964) comb. nov.

*Sextonis* gen. nov.

**S. mehuinensis** (Mielke, 1985) comb. nov.

*S. incurvatus* (Lang, 1965) comb. nov.

*S. chilensis* (Mielke, 1985) comb. nov.

*S. laminaserratus* (Mielke, 1985) comb. nov.

\* *S. delamarei* (Rouch, 1962) comb. nov.

\* *S. naylori* (McLachlan & Moore, 1978) comb. nov. (partim)

Leptastacidae incertae sedis

*Leptastacus christelleae* Bodiou & Colomines, 1989

*Leptastacus naylori* McLachlan & Moore, 1978 (partim : paratype ♂)

*Psammastacus acuticaudatus* Krishnaswamy, 1957♀

## ABSTRACT

The presumed amphiatlantic distribution of *Leptastacus macronyx* is reviewed on the base of material from South Carolina, Bermuda, the Virgin Islands, the Scilly Islands, the German Bight and the Skagerak. As a result, three new species are described which were previously confounded with the type species. *L. coulli* sp. nov. occurs along the Atlantic seaboard of the United States. Both *L. kwintei* sp. nov. and *L. pygmaeus* sp. nov. are common species in the Southern Bight where *L. macronyx* is not found. Only four literature records of *L. macronyx* are considered as valid. It is postulated that the species displays a very restricted distribution pattern in the Central North Sea, covering the Skagerak and the German Bight in the east and the Scottish coast in the west. Another closely related species *L. corsicaensis* sp. nov. is described

from the Mediterranean. The amphiatlantic distribution patterns of some other interstitial harpacticoids are briefly discussed.

The highly distinctive cephalic appendages are discussed and interpreted in the light of possible feeding mechanisms (gardening) based on live observations of *Paraleptastacus espinulatus* Nicholls and *Arenocaris bifida* Nicholls. The unique design of these limbs is regarded as sufficient evidence for upgrading the Leptastacinae to full family status. There is no direct relationship with any of the other subfamilies of the Cylindropsyllidae. The primary evolutionary trends related to the structure of the fifth legs, the modifications of the caudal rami and the sexual dimorphism of the swimming legs are discussed in detail.

A phylogenetic analysis of the Leptastacidae is presented and as a result 7 new genera are established. The taxonomic history of each of the 15 genera is reviewed and updated generic diagnoses are given. Both *Leptastacus* T. Scott and *Psammastacus* Nicholls are polyphyletic assemblages. The genus *Leptastacus* is revised and includes now only the *macronyx*-group. Five other natural groups could be distinguished inside the genus and these are given the rank of genera: *Archileptastacus* gen. nov. (*L. dichatoensis* Mielke, *L. aberrans* Chappuis), *Sextonis* gen. nov. (*L. mehuinensis* Mielke, *L. incurvatus* Lang, *L. chilensis* Mielke, *L. laminaserrata* Mielke, *L. delamarei* Rouch, *L. naylori* McLachlan & Moore), *Belemnopontia* gen. nov. (*L. dispinosus dispinosus* Mielke, *L. dispinosus panamensis* Mielke, *L. acuticaudatus* Krishnaswamy), *Schizothrix* gen. nov. (*L. ctenatus* Mielke, *L. rostratus* Nicholls, *L. macronyx* var. *pontica* Griga) and *Cerconeotes* gen. nov. (*L. mozambicus* Wells, *L. constrictus* Lang, *L. japonicus* Itô, *L. jenneri* Lindgren, *L. nichollsi* Krishnaswamy, *L. euryhalinus* Krishnaswamy, *L. waltirensis* Rao & Ganapati, *L. operculatus* Masry).

Species keys are given for *Cerconeotes*, *Paraleptastacus*, *Schizothrix* and *Sextonis*. Complete redescriptions are presented for *Arenocaris bifida*, *Psammastacus confluens* Nicholls, *P. perplexus* Wells & Clark, *Neopsammastacus spinicauda* (Wells) and *Leptastacus mozambicus*. Additional information is illustrated for *Arenotopa erasmusi* McLachlan & Moore, *Paraleptastacus moorei* Whybrew, *Schizothrix rostratus* and *Sextonis naylori*. A new species of *Arenocaris* is described from the North Sea: *A. reducta*.

An attempt is made to revise *Neopsammastacus* Cottarelli & Venanzetti. The paratype material of the type species *N. spinicauda* proved upon re-examination to consist of an amalgamate of three species belonging to different genera: *N. spinicauda*, *Membranastacus inopinatus* gen. et sp. nov. and *Afroleptastacus clandestinus* gen. et sp. nov. The latter genus also serves to include *Psammastacus remanei* Noodt. *Psammastacus perplexus*, previously placed in *Neopsammastacus* is removed to *Minervella* Cottarelli & Venanzetti. Only the type species *N. spinicauda* and *N. spinicaudatus* (Rao & Ganapati) are retained in *Neopsammastacus*.



*Psammastacus brevicaudatus* Nicholls is founded on copepodid stages of *P. confluens* Nicholls. *Leptastacus christelleae* Bodiou & Colomines, *Psammastacus acuticaudatus* Krishnaswamy and the male paratype of *L. naylori* are ranked *species incertae sedis* within the family.

The phylogenetic relationships within the family are summarized in a cladogram. *Archileptastacus* gen. nov. represents the earliest offshoot in the evolution of the family. The majority of the other genera is grouped in two lineages according to the structure of the caudal rami and the transformations of the fifth legs.

An updated key to the genera of the Leptastacidae is presented.

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## NOTE ADDED IN PROOF

Due to security regulations imposed during the Gulf War, the type material of *Leptastacus operculatus* Masry, 1970 held in the collections of the Hebrew University of Jerusalem, became accessible for re-examination not until this paper had gone to press. Masry (1970) reported to have found one female and one male but inspection of the latter proved both types to be female. In the absence of the male and in the light of the discovery of unique characters that were overlooked in the original description, it is best to tentatively consider *L. operculatus* a *species incertae sedis* within the family rather than to provisionally rank it *species inquirenda* in the genus *Cerconeotes* as suggested earlier in this study. A complete redescription of the species will be published elsewhere.



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