

Studies on the Cyliindropsyllidae (Copepoda, Harpacticoida). 1. The status of *Leptastacus laticaudatus* Nicholls

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Leptastacus laticaudatus Nicholls, 1935, commonly found interstitially in fine sands of European boreal waters, is redescribed and figured. As a result, the subspecies names *L. laticaudatus laticaudatus* and *L. laticaudatus intermedius* Kunz, 1938 are nullified. Some variable characters, i.e. caudal rami and structure of the fifth leg, are discussed and the distribution of the species is summarized. The most closely allied species *L. macronyx* (T. Scott, 1892) and *L. spatulisetia* Mielke, 1982 constitute, together with *L. laticaudatus*, the 'macronyx-group'. *L. laticaudatus intermedius sensu* Apostolov, 1973 is considered *species inquirenda*. An amended diagnosis of the genus *Leptastacus* T. Scott, 1906 is presented.

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Introduction

At present the family Cyliindropsyllidae Sars, emend. Lang (Copepoda, Harpacticoida) consists of 17 genera and 111 species based upon adults and considered identifiable. Twenty-one species and six subspecies are assigned to the genus *Leptastacus* T. Scott, 1906, which together with *Arenocaris* Nicholls, 1935, *Paraleptastacus* Wilson, 1932 and *Psammastacus* Nicholls, 1935 forms the subfamily Leptastacinae Lang, 1948.

So far only three species of this world-wide genus have been found in the North Sea: the type species *Leptastacus macronyx* (T. Scott, 1892), *L. laticaudatus* Nicholls, 1935 and a new closely related species (Huys & Kunz, in prep.) identified as *L. minutus* Chappuis, 1954 by Willems *et al.* (1982).

Leptastacus laticaudatus was divided into two subspecies by Kunz (1938), who erected a new form *intermedius*, easily distinguishable by the length of the caudal rami and the structure of the fifth leg in the female.

Many authors reported *L. laticaudatus intermedius* as a dominant interstitial slider in sandy beaches and several subtidal localities. In their study on the benthos communities of the southern North Sea Govaere *et al.* (1980) classified three zones according to their harpacticoid copepod composition: two clearly defined associations, with a transition zone in between. In the open sea (depth >20 m), as well as in the transition zone (10–15 m), *L. laticaudatus intermedius* is a characteristic species forming a *Leptastacus laticaudatus*—*Paramesochra helgolandica* Kunz, 1936 and a *Leptastacus laticaudatus*—*Halecinosoma herdmani* (T. & A. Scott, 1894) association, respectively.

During a study of the meiofauna in the Dutch coastal area I found numerous specimens belonging to what I thought to be the subspecies *intermedius*. After consulting the 'cotype' material of *L. laticaudatus* Nicholls, 1935 (Cannon A. M. Norman collection) deposited in the British Museum (Natural History) and studying the vari-

ability within populations from several localities along the Dutch, Belgian and French coasts, I conclude that the two subspecies are identical. In this paper a detailed redescription and the range distribution of the species is given.

Material and methods

The original type material of *L. laticaudatus* apparently no longer exists. Other specimens, termed 'cotypes' by Norman, were given to Norman by the nominal author of the species, but were not designated types as defined by the International Code of Zoological Nomenclature. However, these 'cotypes' represent the only existing individuals recognized by Nicholls as belonging to this species and are extremely valuable for this reason. These spirit preserved specimens (several males and females) are deposited in the British Museum (Natural History), London, under no. 1936.2.24.13–16 and were collected at the type locality (Balloch Bay, Isle of Cumbrae). In consequence, they can be considered as topotypes.

Additional information has been obtained from numerous male and female specimens collected from different subtidal localities in the Belgian and Dutch coastal areas and from an intertidal site in the Pas-de-Calais (Pointe de Riden), France.

The specimens are fixed in 7% formalin and preserved in 70% alcohol containing a drop of glycerin. Before dissection the habitus was drawn and measurements of body length were made. The specimens were dissected in lactic acid and mounted in polyvinyl lactophenol on Cobb slides. All figures have been prepared using a camera lucida. Abbreviations used in the text and figures are: *PI–P6* = first to sixth legs. The terminology and presentation of the setal formulae are adopted from Lang (1948). The terms *pars incisiva*, *lacinia mobilis* and *pars molaris* are omitted in the description of the mandible (see Mielke 1984).

Systematics

Family Cyliindropsyllidae

Genus *Leptastacus* T. Scott, 1906

Amended diagnosis

Body slender, cylindrical. Rostrum elongated (rounded in *L. aberrans dichutoensis* Mielke, 1985), well defined at base. Antennula seven-segmented in female, first segment shorter than second one, furnished with aesthetasc

on fourth and seventh segments; haplocer in male. Antenna with allobasis; exopodite small, unisegmented with two (a third lateral seta occurs in *L. aberrans dichatoensis*) distal setae. Mandible with well developed praecoxa (corpus mandibulae); endopodite defined, one- or two-segmented; exopodite wanting. Maxillipede strongly developed with a long spinulose claw accompanied at outer edge with a long slender seta. Exopodite of P1 three-segmented with outer seta on middle segment and three or four setae on distal segment; endopodite two- (three- in *L. aberrans aberrans* Chappuis, 1953 and *L. aberrans dichatoensis*) segmented, first segment with one seta on about middle inner edge. P2–P4 with three-segmented exopodites and two-segmented endopodites. First endopodite segment of P4 without inner seta. Baseoendopodite and exopodite P5 in both sexes forming a common plate, with or without distal processus. Genital double somite not subdivided. Caudal rami variable in length and shape. Sexual dimorphism in antennula, fifth and sixth legs; sometimes in endopodite P3, exceptional in exopodite P2 (*L. laminaserrata* Mielke, 1985); and in genital segmentation. One egg sac.

Type species: *Leptastacus macronyx* (T. Scott, 1892).

Remarks

To those species mentioned by Lang (1948) the following have since been added: *Leptastacus rostratus* Nicholls, 1939, *L. aberrans aberrans* Chappuis, 1953, *L. minutus* Chappuis, 1954, *L. wieseri* Chappuis, 1958, *L. delamarei* Rouch, 1962, *L. constrictus* Lang, 1965, *L. incurvatus incurvatus* Lang, 1965, *L. mozambicus* Wells, 1967, *L. japonicus* Itô, 1968, *L. waltirensis* Rao & Ganapati, 1969, *L. operculatus* Masry, 1970, *L. taurica* Marinov, 1973, *L. jenneri* Lindgren, 1975, *L. naylori* McLachlan & Moore, 1978, *L. dispinosus dispinosus* Mielke, 1982, *L. ctenatus* Mielke, 1982, *L. spatulisetia* Mielke, 1982, *L. dispinosus panamensis* Mielke, 1983, *L. mehuinensis* Mielke, 1985, *L. aberrans dichatoensis* Mielke, 1985, *L. laminaserrata* Mielke, 1985 and *L. incurvatus chilensis* Mielke, 1985.

Leptastacus nicholli Krishnaswamy, 1951, *L. acuticaudatus* Krishnaswamy, 1957 and *L. euryhalinus* Krishnaswamy, 1957 must be redescribed before they can be taken into account (Lang 1965; McLachlan & Moore 1978). McLachlan & Moore (1978) omitted *L. macronyx pontica* Griga, 1963 in their key, yet took *L. laticaudatus intermedius sensu* Apostolov, 1973 into account.

Leptastacus laticaudatus Nicholls, 1935

Leptastacus laticaudatus laticaudatus Nicholls, 1935
Leptastacus laticaudatus intermedius Kunz, 1938 syn.n.

Type locality. Sand at about half-tide in Balloch Bay, Isle of Cumbrae (Nicholls 1935).

Material. (1) Scotland, Balloch Bay, Isle of Cumbrae (locus typicus); collected by A. G. Nicholls; several females and males (= topotypes), deposited (spirit preserved) in the British Museum (Natural History), London, under no. 1936.2.24.13–16.

(2) Off Hoek van Holland: 52°16'4"N, 03°32'14"E (20.06.84), medium sand (Md: 0.330 mm; 0.07% mud), 26 m (5 females, 2 males); 52°05'25"N, 03°29'45"E (19.06.84), fine sand (Md: 0.280 mm; 0.06%

mud), 30.5 m (15 females, 11 males); 52°16'14"N, 03°21'10"E (19.06.84), fine sand (Md: 0.290 mm; 0.13% mud), 31 m (2 females, 4 males); 52°09'48"N, 03°19'55"E (19.06.84), medium sand (Md: 0.440 mm; 0.10% mud), 30 m (6 females); 52°29'02"N, 02°58'57"E (18.06.84), fine sand (Md: 0.284 mm; 0.28% mud), 32 m (5 females, 7 males).

(3) SW Dutch coastal area (off Delta region): 51°36'04"N, 03°35'47"E (06.09.84), medium sand (Md: 0.310 mm; 5.06% mud), 12 m; 51°37'47"N, 03°32'10"E (17.10.84), medium sand (Md: 0.360 mm; 0.77% mud), 6.5 m; 51°40'33"N, 03°30'58"E (01.11.84), medium sand (Md: 0.260 mm; 2.48% mud), 11.2 m; 51°46'18"N, 03°36'49"E (13.11.84), fine sand (Md: 0.230 mm; 1.16% mud), 10 m, extremely abundant.

(4) N of Westerschelde mouth: 51°28'25"N, 03°28'10"E (10.05.83), fine sand (Md: 0.235 mm; 0.39% mud), 7.5 m (3 females, 2 males).

(5) Belgian coastal area: 51°16'32"N, 02°51'08"E (09.80; 07.81), medium sand (Md: 0.330 mm; 1.4% mud), 6.5 m, extremely abundant.

(6) Pas-de-Calais, Pointe de Riden (France): sandy beach (09.09.85), extremely abundant.

Redescription

FEMALE (topotypical neotype). Body length 305–335 μm ($n = 15$; $\bar{x} = 321 \mu\text{m}$) excluding rostrum and caudal rami; 345–380 μm ($n = 15$; $\bar{x} = 374 \mu\text{m}$) including rostrum and caudal rami.

Body (Figs. 1A–C) slender, cylindrical, almost colourless and semi-transparent. Thoracic somites slightly broader than urosome, no distinct separation between anterior and posterior body, anal somite narrowest. Cephalothoracic somite about one and a half times as long as two succeeding somites combined. Genital double somite longest, 1/8 of total body length, indistinctly subdivided by a chitinous stripe laterally. Anal somite shortest. Naupliar eye wanting.

Rostrum (Fig. 1D) well developed, elongated, just exceeding first antennular segment; slightly tapering distally, greatest width at one third distance from the base; not fused with cephalosoma, well defined at base; tip pointing downwards; furnished with a pair of delicate sensillae at one third distance from the tip; integument granulated on surface.

Somatic hyaline frill plain, rather modest, particularly in thoracic somites. All somites and caudal rami dorsally and laterally granulated on surface, urosoma and caudal rami also ventrally granulated.

Cephalic shield rectangular, about 1.5 times as long as greatest width, furnished with seven groups of delicate sensillae. Thoracic somites 1–4 provided with eight (4 dorsal, 2 lateral, 2 ventrolateral), twelve (4 dorsal, 4 dorsolateral, 2 lateral, 2 ventrolateral), ten (6 dorsal, 2 dorsolateral, 2 ventrolateral) and six (4 dorsal, 2 lateral) sensillae, respectively. Third and fourth thoracic somites with mediodorsal porus.

Genital double somite with two median dorsal sensillae, posteriorly with two dorsolateral and two ventrolateral sensillae; anteriorly with one mediodorsal porus. Antepenultimate somite furnished with two dorsal and two ventral sensillae. Penultimate somite without sensillae, posterior edge dorsally provided with minute triangular cuticular thickenings. Anal somite (Figs. 1A, B, 3E, F) less densely granulated than others, furnished with two dorsal sensillae; posterior margin bilobed dorsally, ventrally with diminutive spinules; anal operculum moderately rounded, with minute spinules on hind edge.

Caudal rami (Figs. 1A–C, 2E, F) divergent, 1.71–2.70 ($n = 15$; $\bar{x} = 2.45$) times as long as greatest width; furnished with two arched spinular rows on innermost part of

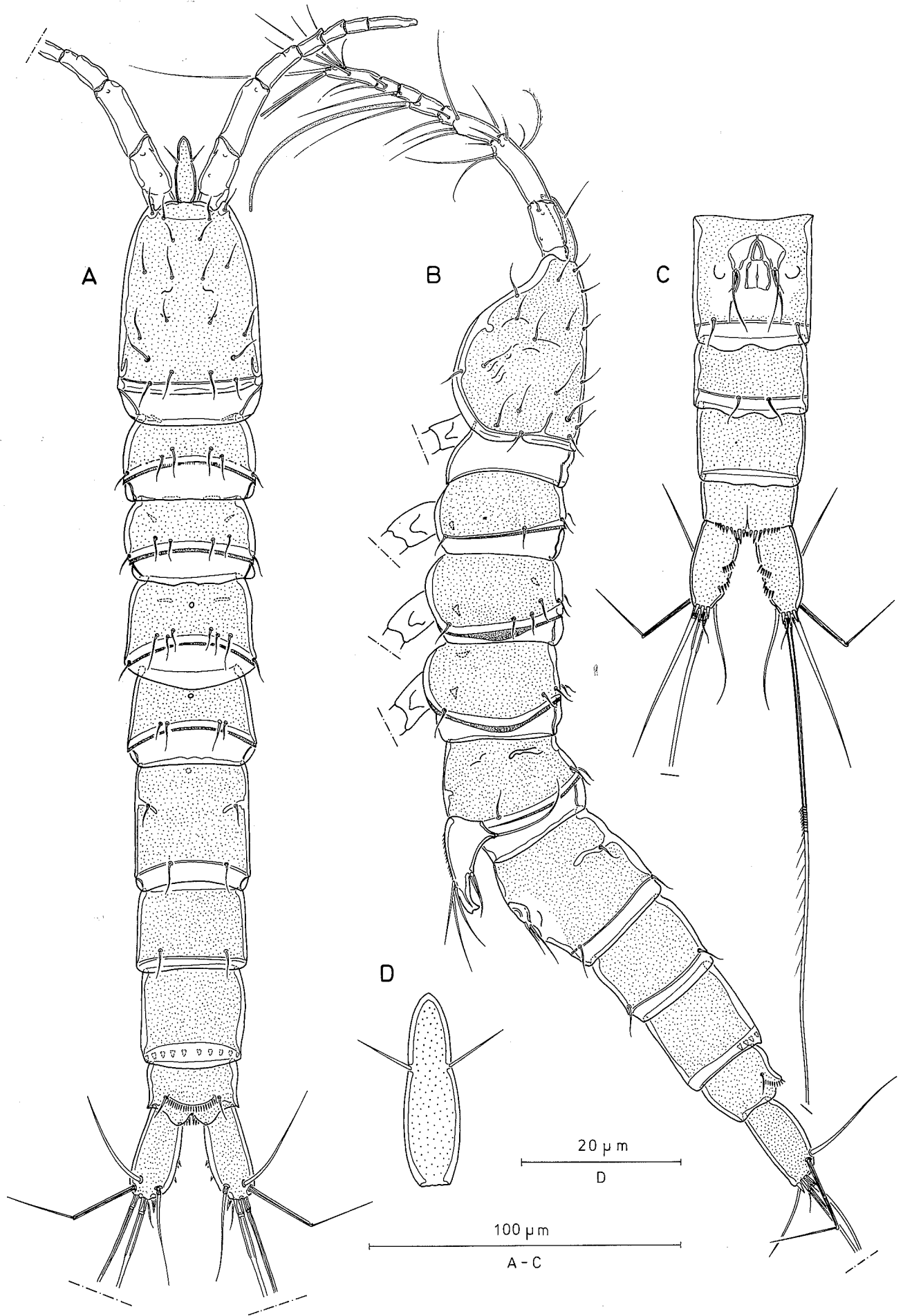


Fig. 1. *Leptastacus laticaudatus* (♀).—A. Habitus, dorsal side.—B. Habitus, lateral side.—C. Abdomen, ventral side.—D. Rostrum.

ventrolateral surface; distal part of ventral edge with some few spinules. Each ramus bears six setae; so-called principal terminal seta strongly developed, length 235–255 μm ($n = 5$; $\bar{x} = 242 \mu\text{m}$), with a delicate accessory seta (setula) on inner proximal corner and a long slender terminal seta outside; three setae arising from the dorsal side of which innermost biarticulated at base and outermost divided into two parts, proximal part styliform and as long as slender distal part.

Antennula (Fig. 2A). Seven-segmented, slender; antennular hyaline frill slightly developed, plain; first segment long with one bare spiniform seta near distal end; second one longest, approximately 2.5 times as long as greatest diameter, furnished in distal third with eight (1 plumose) setae, of which four are geniculate at base; third segment second longest, partially subdivided at two-thirds the length, provided with five setae in distal third; anterior edge of fourth segment furnished with a long thick aesthetasc (length 62.5 μm) and a short slender seta on outer edge; fifth and sixth segments shortest, furnished with one and two bare setae, respectively; last segment long and slender, provided with ten setae, of which four are geniculate [trifurcate one represents a short aesthetasc (length 20.5 μm) which is confluent at base with two bare setae].

Antenna (Fig. 3A). Coxa small, much shorter than width, bare. Allobasis about 3.2 times as long as maximum width, much longer than endopodite, anterior margin spinulose and forming a transverse chitinous stripe opposite the base of the exopodite. Exopodite (implanted one third the segment length from the proximal margin) one-segmented, small, more than three times as long as greatest width, slightly tapering distally; furnished with one long slender seta and one short spiniform seta at distal end. Endopodite approximately two-thirds length of allobasis; anterior margin furnished subdistally with two spines (of which the distal-most is bifid and curved at tip and accompanied by some spinules and a setula at base) and one row of minute spinules on surface just inside the spines; posterior margin with two spinules; distal edge furnished with a short and a long curved spine, both spinulose along anterior edges, and three geniculate setae, the posterior one with a long spinule along middle part and a short straight setula arising from subproximal end. Antennal hyaline frill around proximal articulation of allobasis not observed.

Mandible (Fig. 2B). Praecoxa (corpus mandibulae) well developed, about 2.1 times as long as width; distal margin (cutting edge) with one, thick, unidentate spine, one smaller spine, seven small teeth and one slender unilaterally spinulose seta on the dorsal side. Palp three-segmented. Coxa-basis almost square, furnished with a one-sided plumose seta on inner subdistal corner. Endopodite two-segmented; proximal segment approximately 3 times as long as greatest width, with a seta arising from a point a third the length of inner edge and one subterminal short setula; second segment square, diminutive, terminating in two setae of different lengths which are confluent at base.

Maxillula (Fig. 2C). Praecoxa thickly chitinous along outer edge. Arthrite of praecoxa furnished with seven claws or spines, of which three are pectinate along inner edge; parallel setae on anterior surface not observed.

Coxa rather moderate, with one spinulated claw and one bare slender seta on inner end. Basis sub-cylindrical, distal end furnished with two long slender setae, confluent at base, one slightly arched claw, spinulose along distal half and two shorter bare setae of different lengths; apical half of ventral edge spinulose. Exopodite a little knob with two strong setae of different lengths. Endopodite represented as a one-sided spinulose seta on a small protuberance.

Maxilla (Figs. 2D1, D2). Syncoxa tapering distally, with one spinule on middle outer edge, furnished with two well developed sub-cylindrical endites. Proximal endite shortest, slightly bending ventrally, with one apical and two subterminal short spinulose setae. Distal endite furnished with one terminal claw, spinulose on subdistal edge, and one slender seta on distal end; middle inner edge with one short spinulose seta. Distally, basis tapering into a strong, recurved claw with several delicate dorsal spinules and with two biarticulated setae (one each on dorsal and ventral side) at base. Endopodite well developed, two-segmented; proximal segment longest, with one bare seta on subdistal outer corner; distal segment with three slender apical setae of different lengths, of which two fused at base.

Maxillipede (Fig. 2E). Basis thickened distally, approximately 1.4 times as long as greatest width, furnished with some spinules on subdistal inner edge. Endopodite two-segmented. First segment strongly developed, elongated, about 2.6 times as long as basis; outer edge partially spinulose, middle inner edge furnished with an arched row of minute spinules. Distal endopodite segment small, forming into a strong long claw, of which distal two-thirds (last third two-sided) spinulose and accompanied at base with a long bare slender seta.

Labrum (Figs. 3B1, B2). Well developed; terminal median part convex and furnished with two series of six long spinules of which anterior ones are more slender than posterior ones; lateral edges lobate, each provided with two lateral rows of four minute spinules.

Natatorial legs (P1–P4) (Figs. 4A–D) with three-segmented exopodites; endopodites two-segmented, always shorter than outer rami except for the endopodite of P1. Appendicular hyaline frill restricted to the second to fourth legs, in particular to the first two segments (podomeres) of the exopodite; generally strongly developed, fully incised broad subulate (*sensu* Moore 1976), present chiefly around inner parts of proximal articulations. Succeeding legs increasing in length.

P1 (Fig. 4A). Coxa well developed, outer edge convex, furnished with an arched row of diminutive spinules on anterior surface in distal half. Basis shorter than coxa, with some spinules in proximal part near outer edge and a few distal ones near first endopodite segment; inner and outer setae not present. First exopodite segment longest, thickening distally, furnished with one outer unilaterally spinulose spine at subdistal corner. Second exopodite segment as long as third, with one outer unilaterally spinulose spine subdistally and several spinules along outer margin. Third segment with one short seta at outer subdistal corner, one outer one-sided spinulose spine and two apical geniculate setae, innermost of which longest; outer margin provided with some spinules. Endopodite

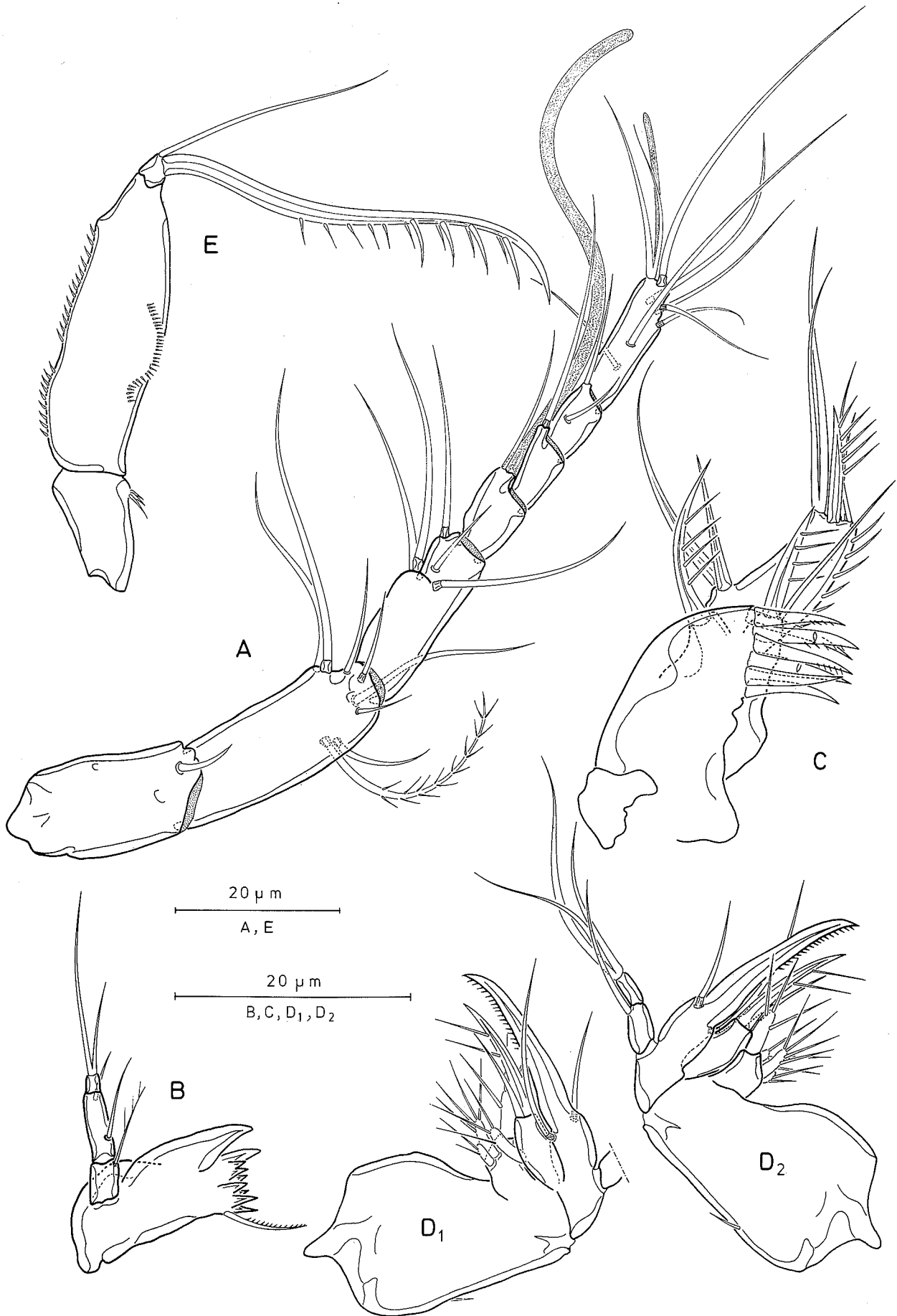


Fig. 2. *Leptastacus laticaudatus* (♀).—A. Antennula.—B. Mandible.—C. Maxillula.—D1. Maxilla, anterior view.—D2. Maxilla, posterior view.—E. Maxillipede.

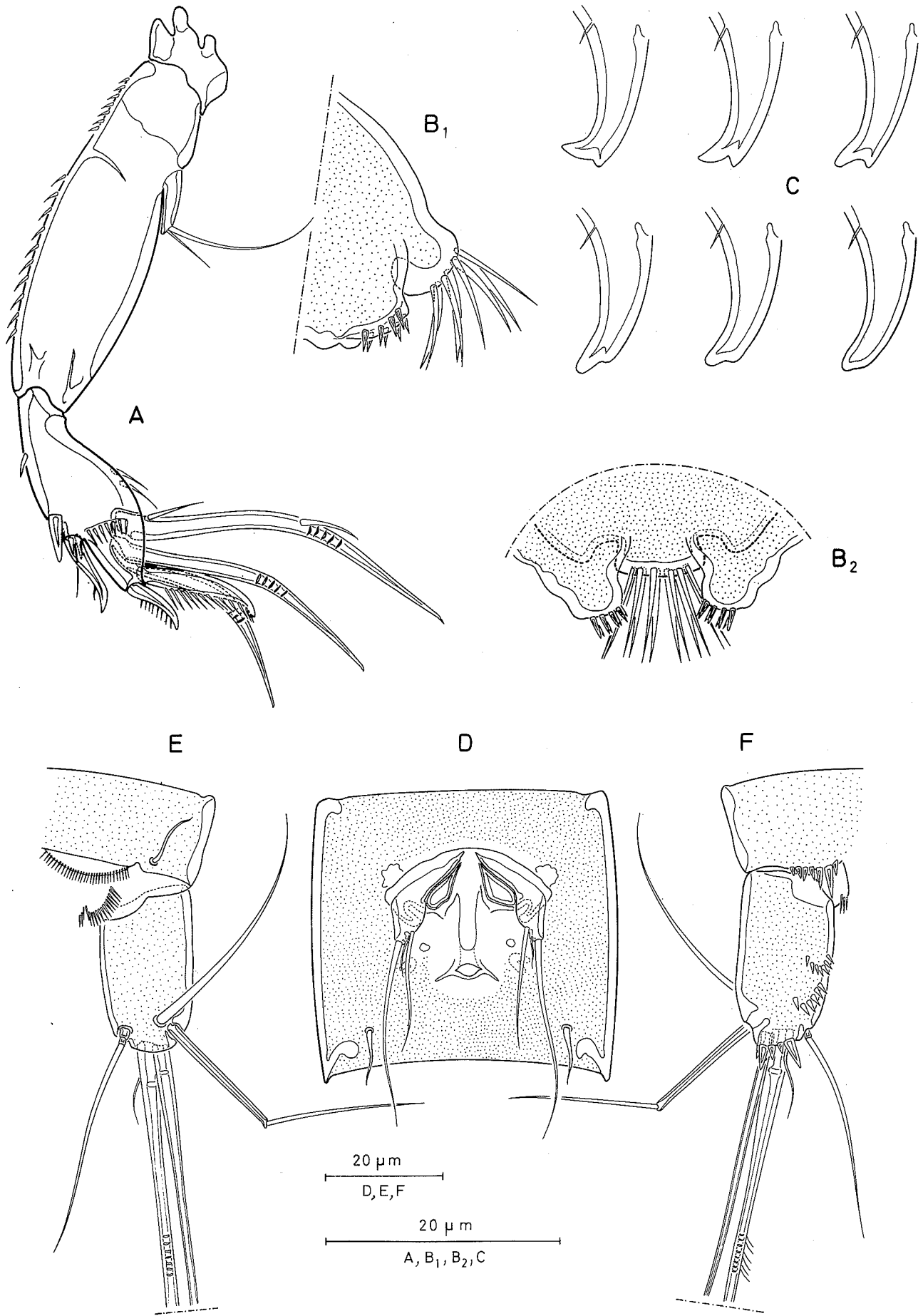


Fig. 3. *Leptastacus laticaudatus* (♀).—A. Antenna.—B1. Labrum, lateral view.—B2. Labrum, anterior view.—C. Variability distal process P5.—D. Genital complex with P6.—E. Caudal ramus, dorsal view.—F. Caudal ramus, ventral view.

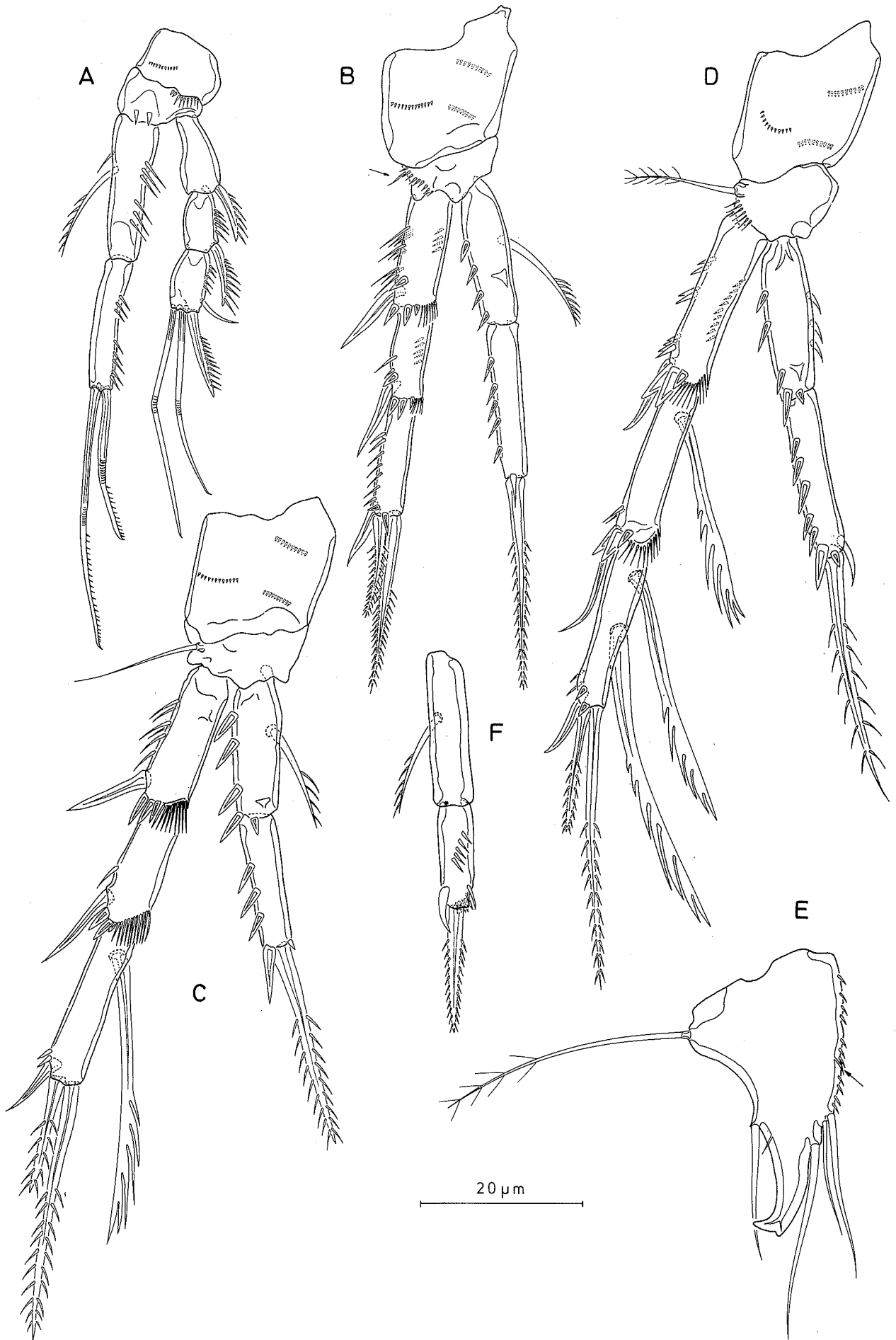


Fig. 4. *Leptastacus laticaudatus*—A. P1 (♀).—B. P2 (♀).—C. P3 (♀).—D. P4 (♀).—E. P5 (♀).—F. Endopodite P3 (♂).

about 1.4 times as long as exopodite. First endopodite segment slightly longer than distal one and exceeding first two segments of exopodite combined; furnished with two groups of long spinules along outer edge, a spinule and one apically pectinate seta on about middle inner edge. Second segment more slender than preceding one, provided with short spinules along outer margin and two apical geniculate setae, inner one of which longer than outer.

P2 (Fig. 4B). Coxa strongly developed, twice as long as that of P1, ornamented with one and two arched rows of diminutive spinules on anterior and posterior surface, respectively. Basis small, with an oblique row of spinules near outer edge and one bare setula near junction with coxa. Exopodite approximately 1/10 longer than endopodite. First exopodite segment thickest one, with three sets of fine slender spinules along outer edge, a strong bare spine at subdistal outer corner and several strong spinules at distal end. Second segment shortest, ornamented almost as in first one. Third segment longer and more slender than preceding ones, spinulose along outer margin, furnished with one bare strong spine at subdistal corner and two apically two-sided setae, innermost of which longest, at distal end. First endopodite segment somewhat shorter and thicker than distal one, spinulose along outer margin, furnished with one apically pectinate seta on about middle inner edge. Second segment provided distally with a short spinule and one long seta, spinulose along both margins.

P3 (Fig. 4C). Coxa ornamented almost as in P2. Basis much shorter than coxa, unadorned except for a long slender bare seta on a small protuberance near outer margin. All exopodite segments at least partially spinulose along outer margin. First two segments each furnished with one strong bare spine at subdistal outer corner and some spinules distally. Third segment longest with one apically serrate long seta at subproximal inner corner, one short bare spine with a few spinules at its base at subdistal outer corner and two bilaterally spinulose setae of different lengths at distal end. Endopodite as long as first two exopodite segments combined. First segment furnished with strong spinules along outer margin and one apically pectinate short seta at about middle of inner edge. Second segment somewhat more slender and longer than proximal segment, spinulose along inner margin and furnished distally with a strong spinule and one bilaterally spinulose seta.

P4 (Fig. 4D). Coxa ornamented almost as in P2. Basis longer than that of preceding leg and furnished with an oblique spinular row on anterior surface near outer edge and one apically plumose seta on a small protuberance at subproximal outer corner. Exopodite approximately 1.5 times as long as endopodite. First segment furnished with one bare spine and some strong spinules at subdistal outer corner, spinulose along outer margin. Second segment slightly longer than other ones, with one apically serrate long seta on subproximal inner edge and a long bare seta accompanied with several strong spinules basally, at subdistal outer corner. Third segment slightly tapering distally; furnished with two apically serrate long setae on inner edge; one bare short spine and some minute spinules at subdistal outer corner; distal margin furnished with two

bilaterally spinulose setae, the inner one of which longer than the outer one. First endopodite segment devoid of spines or setae, but with inner and outer edges spinulose. Distal segment slender and somewhat longer than proximal segment, spinulose along outer edge, furnished with one spinulose seta on distal margin and one short spiniform seta at inner subdistal corner.

Setal formula.

	Exopodite	Endopodite
P1	(0.0.022)	(1.020)
P2	(0.0.021)	(1.010)
P3	(0.0.121)	(1.010)
P4	(0.1.221)	(0.110)

P5 (Fig. 4E). Exopodite and baseendopodite confluent; represented by a long triangular plate, ending in a slightly outwards directed bifid foot-shaped distal process. Inner edge spinulose, chitinous rim separated into two parts by a small pit at which a spiniform projection is situated (dwarfed seta?); furnished with three setae in total at about two-thirds the length, distal-most long and slender, preceding two shorter. Outer margin concave, with two setae in total, proximal-most biarticulated at base and plumose along distal part, second one situated at about middle edge, bare and shorter than preceding one; distal half of chitinous rim at about 1/5 the length divided into two parts by a small pit at which a spiniform projection arises (dwarfed seta?).

Genital complex (as shown in Fig. 3D). P6 small, represented by a minute triangular plate attaching on outer part of genital area, distally not fused with genital double somite, furnished with three setae in total, distal-most long and slender, preceding one subdistal and setula-like, proximal-most slender yet shorter than distal one.

MALE. Body a little shorter and less slender than in female. Body length 295–317 μm ($n = 15$; $\bar{x} = 305 \mu\text{m}$) excluding rostrum and caudal rami; 332–370 μm ($n = 15$; $\bar{x} = 365 \mu\text{m}$) including rostrum and caudal rami. General body shape, colour, ornamentation and sensillar pattern as in female. Sexual dimorphism in antennula, third, fifth and sixth leg and genital segmentation (Fig. 5B).

Antennula (Fig. 5A). Eight-segmented, slender; haplocer; antennular hyaline frill weakly developed, plain. First segment second longest, with one bare spiniform seta near distal end. Second segment longest, approximately 2.3 times as long as wide, furnished in distal third with seven setae, of which one is biarticulated at base and plumose along distal margin. Third segment partially subdivided into two parts transversely, provided in distal part with four bare setae, of which three are geniculate at base and the other setule-like. Fourth segment furnished with two slender setae at about middle outer edge and at the outer distal corner with a long, well developed aesthetasc (length 64 μm) which has a short seta at its base. Fifth segment diminutive, with one slender seta biarticulated at base. Outer margin of sixth segment slightly convex, thickly chitinous, furnished with one short subterminal seta. Outer margin of seventh segment with two concave chitinous formations (haplocer apparatus) and one slender seta at distal corner. Terminal segment more slender than preceding ones; furnished with eleven setae; the two subproximally on the inner margin are basally

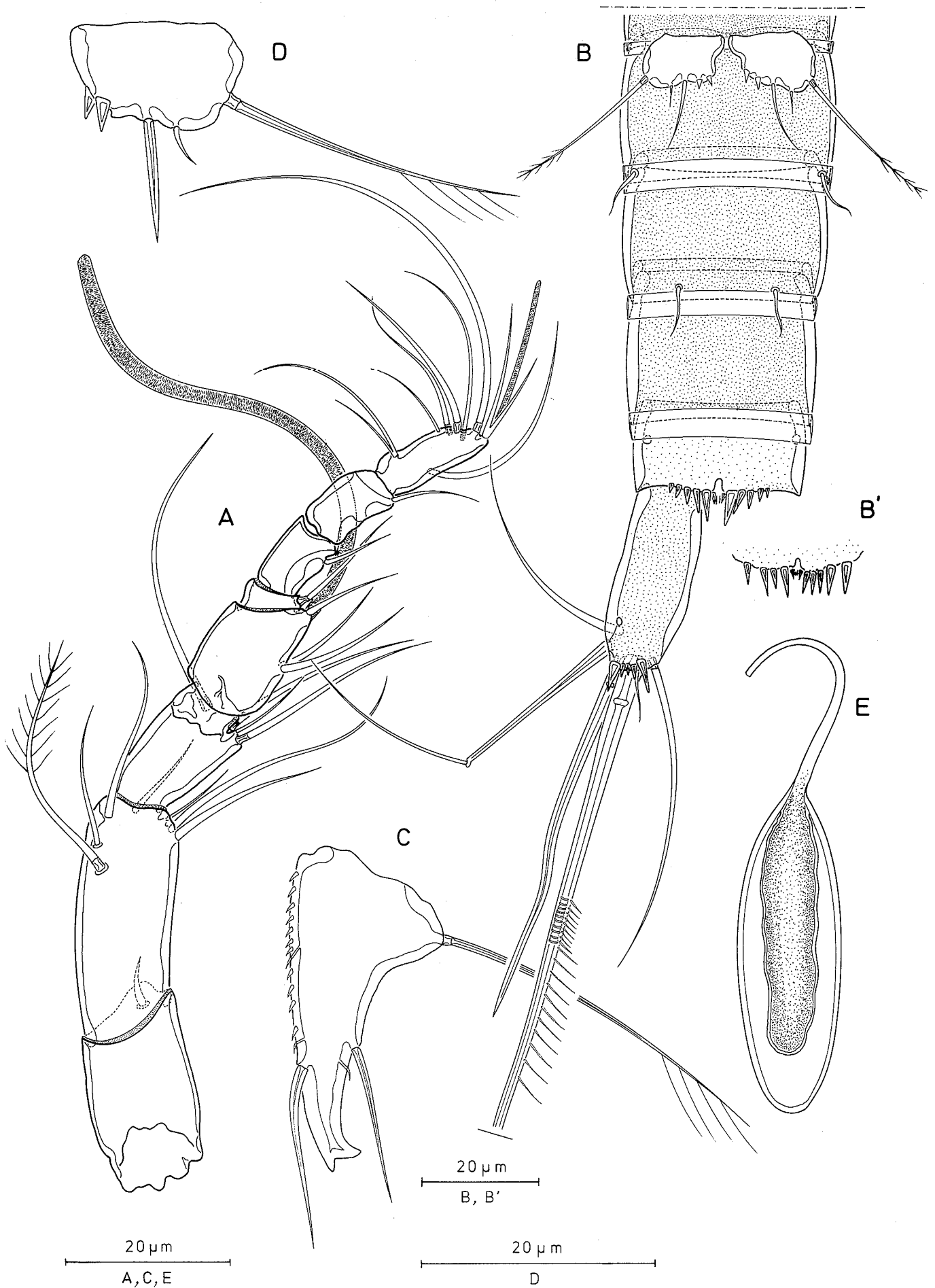


Fig. 5. *Leptastacus laticaudatus* (δ).—A. Antennula.—B. Abdomen, ventral view.—B'. Distal spine of anal somite of other specimen.—C. P5.—D. P6.—E. Spermatophore.

confluent; four of the terminal setae are geniculate at base and the trifurcate seta on the outer distal corner is made up of a slender short aesthetasc (length 20 μm), which is confluent at its base with two bare setae of different lengths.

Leg 5 (Fig. 5C). Baseoendopodite and exopodite confluent, forming elongate triangular plate ending in a bifid foot-shaped distal processus pointing slightly outwards. Inner chitinous margin spinulose, subdivided into three parts by two small pits at which a spiniform projection arises; furnished at two-thirds the length with one slender bare seta. Outer margin furnished with two setae, proximal-most geniculate at base and plumose along inner distal margin, second one situated at about two-thirds the length, bare; distal part of chitinous rim subdivided by a small pit which is provided with a spiniform structure (dwarfed seta?).

Leg 6 (Figs. 5B, D). Represented by a rectangular plate with thickly chitinous margin and three setae, outermost well developed and plumose along inner distal margin, succeeding one spiniform and curved, third one straight and bare; inner distal edge provided with two spinules.

Spermatophore (as shown in Fig. 5E). Length about 50 μm .

Variability

A number of differences in various structures were found between the twenty females and fifteen males which were studied.

(1) The length:width ratio of the caudal rami in males and females ranged from 1.71 to 2.70 ($n = 15$; $\bar{x} = 2.45$); even between both rami differences could be noticed in a few specimens (Figs. 1A, C, 3E, F, 5B).

(2) The number and shape of ventral spinules on the distal edge of the caudal rami is somewhat variable (Figs. 1C, 3F, 5B).

(3) The number and shape of ventral spinules on the distal edge of the anal somite shows moderate variability (Figs. 1C, 3F, 5B, B').

(4) The shape of the distal processus of P5 is fairly variable in females and males and ranges from foot-shaped to almost completely rounded (Figs. 3C, 4E, 5C).

(5) The inner distal edge of male P6 is provided with either 2 or 3 spinules.

Distribution

Records of Leptastacus laticaudatus Nicholls. Scotland: Balloch Bay, Isle of Cumbrae (Nicholls 1935). England: Devon, River Exe estuary (Wells 1963a), Cornwall, Whitsand Bay (Harris 1972), Isle of Man (Moore 1979). Germany: Kiel Bay (Scheibel & Noodt 1975). The Netherlands: off Hoek van Holland, N of Westerschelde mouth, offshore Delta region (Huys, unpubl.). Belgium: Sluice Dock, Ostend (Thielemans & Heip 1984); Westerschelde estuary (Van Damme *et al.* 1984), North Sea coastal zone (Govaere *et al.* 1980; Willems 1981). France: Pas-de-Calais, Pointe de Riden (Huys unpubl.), Bassin d'Arcachon (Renaud-Debyser 1963).

Records of Leptastacus laticaudatus intermedius Kunz. Sweden: Skagerak, Hällö (Por 1964a). England: Isles of Scilly, Tresco, St. Martin's (Wells 1961, 1970); North Wales, Tal-y-Foel (Geddes 1972). Northern Ireland: Strangford Harbour (Wells 1963b). Germany: Helgoland (Kunz 1938), Kiel Bay (Scheibel 1973, 1976; Anger & Scheibel 1976). Belgium: Kwinte Bank (North Sea) (Willems *et al.* 1982). France: Douarnenez Bay (Bodin 1984); Charente Maritime (Bodin 1976, 1977); Bassin d'Arcachon, Arguin (Renaud-Debyser & Salvat 1963); Banyuls-sur-Mer (Soyer 1970; Bodiou & Soyer 1973); Marseille (Nodot 1978). ?Rumania: Black Sea coast (Por 1964b).

Records of Leptastacus laticaudatus laticaudatus Nicholls. ?U.S.A.: North Carolina continental shelf (Coull 1971).

Discussion

The erection of the new subspecies *Leptastacus laticaudatus intermedius* by Kunz (1938) was based on four minor differences with Nicholls' description and drawings of *L. laticaudatus s. str.*: (1) as in *L. macronyx*, three setae occur on inner edge of the female P5, instead of two in the form *laticaudatus*; (2) the caudal rami are about three times as long as the greatest width, instead of approximately two times; (3) as in *L. macronyx*, the inner seta on the first endopodite segment of P2 and P3 is longer than in the form *laticaudatus*; (4) there is a difference in body length.

The high variability in the length of the caudal rami and total body length within a single population invalidates the use of these characters in defining a new taxon, even at the subspecies level. That the inner seta of the proximal endopodite segment of P2–P3 is longer in the forma *intermedius* is probably incorrect, since all specimens examined, even those of the Norman collection (=topotypes), possess considerably longer setae than those figured in Nicholls (1935). With respect to earlier drawings and descriptions, which are often poor, descriptive expressions such as "comparatively . . . , longer than . . . , smaller than . . .", etc. should be avoided, since they cannot be correctly interpreted out of context, i.e. without comparison with the related species. The setation of leg 5 in the female seems to be the only valid difference between the two varieties. For that reason, McLachlan & Moore (1978) incorporate this differentiating character in their key to the females of *Leptastacus*, contrary to Lang (1965) who used the length:width ratio of the caudal rami. It is clear that a part of Lang's keys (1948, 1965) was based on Nicholls' drawings and descriptions, which are only reproduced, without inspection of the type material.

As Kunz (1938) himself pointed out in his original description, the third inner seta of the fifth leg, which is usually very small and difficult to observe, could have been overlooked by Nicholls (1935). Examination of the 'cotype' material of Balloch Bay confirmed this hypothesis. Finally, Kunz' statement "Das 5. Bein des Männchens ist wie bei der Hauptart gebaut" must be incorrect (cf. difference of P5 in *L. dispinosus dispinosus* and *L. dispinosus panamensis*).

It is apparent from these remarks that both subspecies are identical and in consequence the names *L. laticaudatus laticaudatus* and *L. laticaudatus intermedius* have to be rejected. In fact, Kunz (1938) just presented some amendments to Nicholls' (1935) description rather than described a distinct subspecies.

Since in the original description the small spiniform seta on the distal endopodite segment of leg 4 was mistaken for a spinule, the formula of setae and spines presented in Lindgren (1975) has to be corrected. Moreover, following McLachlan & Moore (1978) the redescribed *L. laticaudatus* keys out to *L. rostratus rostratus* Nicholls, 1939 (= *L. rostratus*, see Geddes 1981) because of the presence of an inner seta on the proximal segment of the endopodite P2–P3, two setae on the terminal segment of

the endopodite P4, the long distal processus of the fifth leg and the presence of one seta on the distal endopodite segment of P3.

With respect to the distal processus of P5 in both sexes, it should be mentioned that the typical foot-shape is not always as strongly pronounced as figured in the original description or in the usual keys (Lang 1948, 1965; McLachlan & Moore 1978). As shown in Fig. 3C, this so-called diagnostic character can display a rather high variability within a population and even in a single specimen, ranging from perfectly foot-shaped to almost rounded at the tip (in which the original bifid base structure is still recognizable). In his description of *L. laticaudatus intermedius* Kunz (1938, p. 241, abb. 9, fig. 16) figured a female P5 which clearly shows a transitional form between the two extremes mentioned above. Though over 70% of the studied specimens showed the typical foot-shaped distal processus, this character must be used with caution in constructing species keys.

In his paper dealing with the harpacticoid copepods of the Black Sea, Apostolov (1973) gives drawings of specimens which he ascribes to *L. laticaudatus intermedius*. Because of the difference in P5, which is produced distally into a non-foot-shaped short processus with rounded tip, the identification is questioned by McLachlan & Moore (1978), however, they included this Black Sea form in their key as *L. laticaudatus intermedius sensu* Apostolov 1973. It is clear that the shape of P5 fits into the range of variability in *L. laticaudatus*, but Apostolov's specimens clearly differ from the latter in the setation of the swimming legs: i.e. distal exopodite segment P1 with three setae, one inner seta on distal exopodite segment P4, one terminal seta on distal endopodite segment P4, basis of P2 with long outer seta. It is impossible to give an adequate diagnosis of this probably new species, since several morphological details are not figured nor is the material available. I therefore propose to consider Apostolov's form as *species inquirenda* until collection of new material permits a thorough redescription. In his study of the Levantine and Pontic Harpacticoida, Por (1964b, p. 52) found *L. laticaudatus* dominant in the Rumanian coastal zone (at 67 m depth in pure mud). These specimens probably belong to Apostolov's form.

Mielke (1982) stressed the great similarity between *L. laticaudatus*, *L. macronyx* and *L. spatulisetata*. In fact, these three species and eight new ones proposed by Huys (in prep.) and Huys & Kunz (in prep.) agree in several characters and constitute a separate species group within the genus *Leptastacus*. This 'macronyx-group' is defined by the following characters: first leg with four setae on distal exopodite segment; sexual dimorphism in endopodite P3; P4 furnished with two inner setae on distal exopodite segment and two setae (of which one is small) on second endopodite segment; P5 produced distally in male as well as female into a long processus, furnished in female with two setae on outer edge and three setae on inner edge, furnished in male with one inner seta; P6 in both sexes with three setae, of which one is diminutive; caudal rami not distally produced into spiniform projection, outermost dorsal seta bi-articulated with proximal part styliform and distal part slender and directed forwards.

The same setation of the first to fourth leg is only found in *L. macronyx*, *L. spatulisetata* and *L. ctenatus*. The latter species differs mainly in the structure of the caudal rami, several mouthparts and the long endopodite of leg 4. *Leptastacus spatulisetata* agrees with *L. laticaudatus* in the structure of the antennula, mandibular palp, maxillula, maxilla and maxillipede, but differs in the presence of a spatuliform seta on the distal exopodite segment P2-P4 and the inner edge of leg 5. The length of the caudal rami, the spiniform distal processus of the fifth leg and the presence of a seta on the maxillipede basis differentiate *L. macronyx* from *L. laticaudatus*. The idea of a close relationship between *L. naylori* and *L. laticaudatus*, thought to exist on the basis of setation (McLachlan & Moore 1978), cannot be maintained, since these species differ very much in other respects (distal processus of P5 absent, caudal rami distally produced into a spiniform projection, structure of the mouthparts).

The only previous diagnosis of the genus *Leptastacus* was made by Lang in 1948 and was based on two species. Since then 21 new species and 6 subspecies have been described world wide. Except for *L. minutus*, *L. wieseri*, *L. operculatus* and *L. taurica*, all other species are characterized by a one-segmented antennal exopodite furnished with two terminal setae. I believe this is a generic diagnostic character; in all exceptions the antenna is either poorly described or not figured at all. Even *L. laticaudatus* and *L. macronyx* (Huys & Kunz, in prep.) were originally described with a single seta on the exopodite and in consequence this character was adopted by Lang (1948), but both species in fact possess two terminal setae, the second one sometimes being very difficult to distinguish (Fig. 3A; see also *L. ctenatus*; Mielke 1982).

The fused baseoendopodite and exopodite of leg 5 are not always produced distally into a long processus. *Leptastacus aberrans aberrans*, *L. wieseri*, *L. delamarei*, *L. constrictus*, *L. incurvatus incurvatus*, *L. incurvatus chilensis*, *L. mozambicus*, *L. japonicus*, *L. waltirensis*, *L. operculatus*, *L. jenneri*, *L. naylori*, *L. laminaserrata* and *L. mehuinensis* do not have a distinct distal processus on leg 5 in either the female or the male.

Finally, since the discovery of *L. aberrans aberrans* by Chappuis (1953), the two-segmented endopodite in leg 1 is no longer a uniform character for the genus. Recently Mielke (1985) described *L. aberrans dichatoensis* from central Chile.

According to Lang (1948) no sexual dimorphism occurs in P2 and the P3 of genera belonging to the subfamily Leptastacinae Lang 1948. At present one can state that at least in the genera *Leptastacus* and *Paraleptastacus* Wilson, 1932 [e.g. see *P. espinulatus* Nicholls, 1935 (= *P. spinicauda* (T. & A. Scott, 1895) in Mielke 1975) and *P. spinicauda* (= *P. holsaticus* Kunz, 1937 in Mielke 1975)] sexual dimorphism has been found, i.e. in the endopodite of P3. In the genus *Leptastacus* this sexual dimorphism is either strongly developed (e.g. *L. dispinosus dispinosus*, *L. jenneri*), or slightly developed (e.g. *L. laticaudatus*) or completely absent (e.g. *L. incurvatus incurvatus*). Recently, Mielke (1985) found a unique species along the beaches of central Chile. Indeed, *L. laminaserrata* differs from all other described *Leptastacus* species by sexual dimorphism in the exopodite of P2 (cf. name).

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References

- Anger, K. & Scheibel, W. 1976. Die benthische Copepodenfauna in einem ufernahen Verschmützungsgebiet der westlichen Ostsee.—*Helgoländer wiss. Meeresunters.* 28: 19–30.
- Apostolov, A. 1973. Sur divers Harpacticoides (Copépodes) de la Mer Noire.—*Zool. Anz.* 190: 88–110.
- Bodin, P. 1976. Les copépodes harpacticoides (Crustacea) des côtes charentaises (Atlantique). Données écologiques et biologiques sur les espèces principales.—*Bull. Mus. natn. Hist. nat., Paris* (sér. 3) 29: 1–45.
- Bodin, P. 1977. Les peuplements de copépodes harpacticoides (Crustacea) des sédiments meubles de la zone intertidale des côtes charentaises (Atlantique).—*Mém. Mus. natn. Hist. nat., Paris* 104: 1–120.
- Bodin, P. 1984. Densité de la méiofaune et peuplements de copépodes harpacticoides en Baie de Douarnenez (Finistère).—*Annls Inst. océanogr.*, Paris 60: 5–17.
- Bodiou, J.-Y. & Soyer, J. 1973. Sur les harpacticoides (Crustacea, Copepoda) des sables grossiers et fins graviers de la région de Banyuls-sur-Mer.—*Rapp. Commn. int. Mer Méditerran.* 21: 657–659.
- Chappuis, P. A. 1953. Harpacticoides psammiques récoltés par C. Delamare Deboutteville en Méditerranée.—*Vie Milieu* 8: 254–276.
- Chappuis, P. A. 1954. Recherches sur les crustacés souterrains. IV.—Copépodes psammiques des plages du Roussillon.—*Archs. Zool. exp. gén.* 91: 35–50.
- Chappuis, P. A. 1958. Harpacticoides psammiques marins des environs de Seattle (Washington, U.S.A.).—*Vie Milieu* 8: 409–422.
- Coull, B. C. 1971. Meiobenthic Harpacticoida (Crustacea, Copepoda) from the North Carolina continental shelf.—*Cah. Biol. mar.* 12: 195–237.
- Geddes, D. C. 1972. The Copepoda Harpacticoida of Anglesey and the North Wales coast.—*Naturalist, Hull* 921: 61–76.
- Geddes, D. C. 1981. On two interstitial marine harpacticoids (Crustacea, Copepoda) from northern Norway.—*Sarsia* 66: 19–24.
- Govaere, J. R., Van Damme, D., Heip, C. & De Coninck, L. A. P. 1980. Benthic communities in the Southern Bight of the North Sea and their use in ecological monitoring.—*Helgoländer wiss. Meeresunters.* 33: 507–521.
- Griga, R. E. 1963. Copepoda of the benthonic biocenoses in the region of Eupatoria of the Black Sea.—*Trudy sevastopol'. biol. Sta.* 15: 101–117 (in Russian).
- Harris, R. P. 1972. Horizontal and vertical distribution of the interstitial harpacticoid copepods of a sandy beach.—*J. mar. biol. Ass. U.K.* 52: 375–387.
- Itô, T. 1968. Descriptions and records of marine harpacticoid copepods from Hokkaido I.—*J. Fac. Sci. Hokkaido Univ.* (ser. 6, Zool.) 16: 369–381.
- Krishnaswamy, S. 1951. Three new species of sand dwelling copepods from the Madras coast.—*Ann. Mag. nat. Hist.* (ser. 12) 4: 273–280.
- Krishnaswamy, S. 1957. Studies on the Copepoda of Madras. Ph.D. dissertation, University of Madras, India.
- Kunz, H. 1938. Zur Kenntnis der Harpacticoiden des Küstengrundwassers der Kieler Förde.—*Kieler Meeresforsch.* 2: 95–115.
- Lang, K. 1948. *Monographie der Harpacticiden*. Håkan Ohlsson, Lund.
- Lang, K. 1965. Copepoda Harpacticoida from the Californian coast.—*K. svenska VetenskAkad. Handl.* 10: 1–560.
- Lindgren, E. W. 1975. Six meiobenthic Harpacticoida (Crustacea) from North Carolina beaches.—*Cah. Biol. mar.* 16: 445–473.
- McLachlan, A. & Moore, C. G. 1978. Three new species of Harpacticoida (Crustacea, Copepoda) from sandy beaches in Algoa Bay, South Africa, with keys to the genera *Arenosetella*, *Hastigerella*, *Leptastacus* and *Psammastacus*.—*Ann. S. Afr. Mus.* 76: 191–211.
- Marinov, T. 1973. Quelques harpacticides psammophiles inconnus pour la bassin de la mer Noire.—*Vie Milieu* 23: 309–326.
- Masry, D. 1970. Ecological study of some sandy beaches along the Israeli Mediterranean coast, with description of the interstitial harpacticoids (Crustacea, Copepoda).—*Cah. Biol. mar.* 11: 229–258.
- Mielke, W. 1975. Systematik der Copepoda eines Sandstrandes der Nordseeinsel Sylt.—*Mikrofauna Meeresboden* 52: 1–134.
- Mielke, W. 1982. Interstitielle Fauna von Galápagos. XXIX. Darcythompsoniidae, Cylindropsyllidae (Harpacticoida).—*Mikrofauna Meeresboden* 87: 1–52.
- Mielke, W. 1983. Zwei *Leptastacus*-Arten aus dem zentralen Teil von Panama (Copepoda, Harpacticoida).—*Spixiana* 6: 291–299.
- Mielke, W. 1984. Some remarks on the mandible of the Harpacticoida (Copepoda).—*Crustaceana* 46: 257–260.
- Mielke, W. 1985. Interstitielle Copepoda aus dem zentralen Landesteil von Chile: Cylindropsyllidae, Laophontidae, Ancorabolidae.—*Microfauna mar.* 2: 181–270.
- Moore, C. G. 1976. The form and significance of the hyaline frill in harpacticoid copepod taxonomy.—*J. nat. Hist.* 10: 451–456.
- Moore, C. G. 1979. Analysis of the associations of meiobenthic Copepoda of the Irish Sea.—*J. mar. biol. Ass. U.K.* 59: 831–849.
- Nicholls, A. G. 1935. Copepods from the interstitial fauna of a sandy beach.—*J. mar. biol. Ass. U.K.* 20: 379–404.
- Nicholls, A. G. 1939. Marine harpacticoids and cyclopids from the shores of the St. Lawrence.—*Fauna Flora laurent.* 2: 241–316.
- Nodot, C. 1978. Cycles biologiques de quelques espèces de copépodes harpacticoides psammiques.—*Téthys* 8: 241–248.
- Por, F. D. 1964a. Les harpacticoides (Copepoda Crustacea) des fonds meubles du Skagerak.—*Cah. Biol. mar.* 5: 233–270.
- Por, F. D. 1964b. A study of the Levantine and Pontic Harpacticoida (Copepoda, Crustacea).—*Zool. Verh., Leiden* 64: 1–128.
- Rao, G. C. & Ganapati, P. N. 1969. Some new interstitial copepods from Waltair coast.—*Proc. Indian Acad. Sci.* 69B: 1–14.
- Renau-Debyser, J. 1963. Recherches écologiques sur la faune interstitielle des sables (Bassin d'Arcachon, île de Bimini, Bahamas).—*Vie Milieu* (Suppl.) 15: 1–157.
- Renau-Debyser, J. & Salvat, B. 1963. Elements de prospérité des sédiments meubles intertidaux et écologie de leurs populations en microfaune et macrofaune.—*Vie Milieu* 14: 463–550.
- Rouch, R. 1962. Harpacticoides (Crustacés Copépodes) d'Amérique du Sud.—*Biologie Amérique Australe* 1: 237–280.
- Scheibel, W. 1973. Quantitativ-ökologische Untersuchungen am uferfernen Mesopsammon in der Kieler Bucht.—*Kieler Meeresforsch.* 24: 58–68.
- Scheibel, W. 1976. Quantitative Untersuchungen am Meiobenthos eines Profils unterschiedlicher Sedimente in der westlicher Ostsee.—*Helgoländer wiss. Meeresunters.* 28: 31–42.
- Scheibel, W. & Noodt, W. 1975. Population densities and characteristics of meiobenthos in different substrates of Kiel Bay.—*Merentutkimuslait. Julk./HavsforskInst. Skr.* 239: 173–178.
- Scott, T. 1892. Additions to the fauna of the Firth of Forth.—*Rep. Fishery Bd Scotl.* 3: 244–272.
- Scott, T. 1906. Notes on British Copepoda: change of names.—*Ann. Mag. nat. Hist.* (ser. 7) 17: 458–466.
- Soyer, J. 1970. Bionomie benthique du plateau continentale de la côte Catalane française. III. Les peuplements de copépodes harpacticoides (Crustacea).—*Vie Milieu* (sér. B) 11: 337–511.
- Thielemans, L. & Heip, C. 1984. The response of a harpacticoid copepod community to sediment disturbance in a semi-enclosed lagoon.—*Hydrobiologia* 118: 127–133.
- Van Damme, D., Heip, C. & Willems, K. A. 1984. Influence of pollution on the harpacticoid copepods of two North Sea estuaries.—*Hydrobiologia* 112: 143–160.
- Wells, J. B. J. 1961. Interstitial copepods from the Isles of Scilly.—*Crustaceana* 2: 262–274.
- Wells, J. B. J. 1963a. Copepoda from the littoral region of the estuary of the River Exe (Devon, England). *Crustaceana* 5: 10–26.
- Wells, J. B. J. 1963b. On some new and rare Crustacea from Northern Ireland.—*Ann. Mag. nat. Hist.* 13: 85–96.
- Wells, J. B. J. 1967. The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique.—*Trans. R. Soc. Edinb.* 67: 189–358.
- Wells, J. B. J. 1970. The marine flora and fauna of the Isles of Scilly. Crustacea: Harpacticoida.—*J. nat. Hist.* 4: 255–268.
- Willems, K. A. 1981. *Boreopontia heipi* n.g., n.sp. An interstitial harpacticoid (Copepoda) from the Southern Bight of the North Sea.—*Biol. Jaarb. Dodonaea* 49: 200–209.
- Willems, K. A., Vincx, M., Claeys, D., Vanosmael, C. & Heip, C. 1982. Meiobenthos of a sublittoral sandbank in the Southern Bight of the North Sea.—*J. mar. biol. Ass. U.K.* 62: 535–548.
- Wilson, C. B. 1932. The copepods of the Woods Hole region, Massachusetts.—*Bull. U.S. natn. Mus.* 158: 1–635.