THE RAFFLES BULLETIN OF ZOOLOGY 1998 **46**(2): 399-418

A REVISION OF THE GENUS *LIMNOCLETODES* BORUTSKY, 1926 (COPEPODA: HARPACTICOIDA: CLETODIDAE) WITH A DESCRIPTION OF A NEW SPECIES FROM SOUTHEAST ASIAN MANGROVE FORESTS

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ABSTRACT. - *Limnocletodes mucronatus*, new species, is described from inter-tidal muddy sediments in mangrove forests in Malaysia and Thailand. It is distinguished from all other species in the genus by the setation of the endopod of P4 and the structure of P5 in the female. Specimens of *Limnocletodes* from India are also re-examined. *L. wellsi* , new species, is established for specimens from southern India without an inner seta on exopod-2 of P4 in both sexes. *L. secundus* Sewell, 1934 is maintained as *species inquirenda* for specimens from central India in which the endopod of P2 and P3 is unusually long. The familial position of *Limnocletodes* is briefly discussed and it is concluded that the genus probably occupies a primitive position in the family Cletodidae T. Scott 1904 sensu stricto. A key to the females of the six species of *Limnocletodes* is provided.

KEYWORDS. - Copepoda, Harpacticoida, Cletodidae, *Limnocletodes*, taxonomy, mangroves.

INTRODUCTION

The genus *Limnocletodes* Borutsky was erected to accommodate a new species, *L. behningi* Borutsky, 1926 found in plankton samples from the lower Volga River. Smirnov (1932) redescribed the species from specimens recovered from sediment, fish stomachs and plankton samples in the River Ural and the Aral Sea and pointed out that Borutsky (1926) had mislabelled the P2 and P4 in his original paper. Sewell (1934) found several females of *Limnocletodes* in the Salt Lakes around Calcutta, north-east India. Comparing these to the description in Borutsky (1926) only, he established *L. secundus* Sewell, 1934 on the basis of differences in setation of P2. Lang (1948), dismissing the presence of an extra seta on the endopod of P2 as of no significance, was doubtful that *L. secundus* was really different from *L. behningi* but could not be sure from the descriptions alone. He decided to maintain them

Received 10 Dec 1997 Accepted 27 Jul 1998

as two species in his monograph because the endopod of P2 and P3 appeared longer in *L. secundus*, and because the specimens were found in northern India rather than the Caspian-Aral basin. Since the publication of Lang's (1948) monograph two further new species of *Limnocletodes* have been described, *L. angustodes* Shen & Tai, 1963 from the Pearl River, Kwangtung Province and *L. oblongatus* Shen & Tai, 1964 from Hainan Island in the same Province of southern China. In addition, the recorded distribution of *L. behningi* has been widened to reach across southern Asia from the western shore of the Black Sea (Por, 1960; Damian-Georgescu, 1970) to eastern China (Shen & Tai, 1962; Shen, 1979).

Wells (1971) figured specimens of *Limnocletodes* recovered from beaches in the Vellar River estuary, Porto Novo, southern India and discussed the taxonomy of the genus. In his specimens, the middle exopod segment of P4 lacked an inner seta in both sexes but he maintained that the swimming leg armature in *L. behningi* was variable and that the only differences between all the species were to be found in lengths of the endopods of the female swimming legs and the structure of the female fifth leg. He was of the opinion that, on its own, the difference between whether the endopod reached the distal margin of the first or second exopod segment was not sufficient to separate species. As the fifth leg of *L. secundus* and his material from Porto Novo came within the range of variation of *L. behningi* illustrated by Smirnov (1932) he synonymized *L. secundus* with *L. behningi* and assigned his own material to the same species. On the basis of fifth leg structure he recognized the distinctness of *L. oblongatus* and thought that the extreme elongation of the endopodal lobe in *L. angustodes* may be sufficient to justify specific status.

Without reference to the paper by Wells (1971), Ranga Reddy & Radhakrishna (1980) redescribed both sexes of *L. secundus* based on new material from freshwater impoundments in central eastern India. They concluded that *L. secundus* differs from *L. behningi* in that the endopod of female P2 did have three setae, the inner seta being small and fine; the endopod of the female P2 and P3 was significantly longer than the proximal two segments of the exopod combined; the exopod of P2 and P3 in the male was more robust and with shorter setae than in the female; and the inner seta on the middle exopod segment of P4 in the male, present in *L. secundus*, was absent in *L. behningi*.

During a recent study of the diversity of benthic copepods in mangrove forests of tidal estuaries in Malaysia and Thailand (Gee & Somerfield, 1997, Somerfield *et al*, 1998), the second most abundant cletodid-like species to be found was a new species of *Limnocletodes*. In this paper, that species is described and the material of Wells (1971) and Ranga Reddy & Radhakrishna (1980) is re-examined. Some observations on the taxonomy of the genus are made and characters relevant to its familial affinities discussed.

METHODS

Habitats sampled. - The bulk of the material was obtained from the Merbok mangrove forest, a partially managed forest of some 5000 hectares surrounding the Sungai Merbok estuary in Kedah Province, north-west Peninsular Malaysia (5° 40′ N, 100° 60′ E). The forest contains about 20 species of mangrove plant (E. Ashton, pers. comm.) but is dominated by tall trees (up to 30m) of *Rhizophora apiculata* Bl. and *Bruguiera parviflora* (Roxb.) W. & A. ex Griff. with some fringing patches or strips of *Rhizophora mucronata* Lamk., *Avicennia officinalis* L. and *Sonneratia caseolaris* (L.) Engl.. Three sites were sampled in the middle reaches of the estuary, where the average salinity was around 25%, and one site in the upper reaches of the estuary, where the average salinity was around 20%. Samples of mud (taken by scraping the surface few mm of mud) and decaying leaves (picked individually) were taken primarily under *R. apiculata* trees between high water neap and high water spring tides where the forest floor is muddy (over 80% silt/clay) and relatively undisturbed with plenty of decaying leaves lying on the mud surface. Some samples were taken under *B. parviflora* trees which were in a slightly more elevated position with respect to the tidal regime, and where the muddy sediment of the forest floor was highly disturbed with an abundance of sesarmid crab burrows interspersed with small areas of undisturbed mud on which decaying leaves were rare.

A few leaf and mud samples were also collected by Dr. Chittima Aryuthaka from the Ranong mangrove forest of Muang District, Thailand, 650km southwest of Bangkok at 9° 50′ N, 98° 35′ E. These were taken in the middle and upper reaches of the Klong Nao, a large shallow tidal creek draining 1200 hectares of mangrove wetland. The dominant tree species are the same as in the Merbok forest and samples were taken under a mature stand of *R. apiculata* trees and in a young successional *R. apiculata* plantation in the vicinity of a tin mining concession.

Systematic procedures. - Animals were fixed in 10%, and preserved in 4%, formalin. Before dissection the habitus was drawn and body length measurements made from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactophenol, the parts individually mounted in lactophenol under cover slips subsequently sealed with Bioseal. All drawings were prepared using a camera lucida on a Nikon Optiphot 20 differential interference contrast microscope. The terminology of the body and appendage morphology follows that of Huys & Boxshall (1991). Abbreviations used in the text and figures are P1-P6 for thoracopods 1-6; exp(enp)-1(-2-3) to denote the proximal (middle, distal) segment of a ramus. Body length was measured from the base of the rostrum to the median posterior border of the anal somite. Unless otherwise stated, P1-P5 has been drawn in anterior view. All type material has been deposited in the Natural History Museum, London.

TAXONOMY

FAMILY CLETODIDAE T. SCOTT, 1904 *SENSU* POR, 1986

Genus *Limnocletodes* Borutsky, 1926
Limnocletodes mucronatus, new species
(Figs. 1-5)

Material examined. - Holotype; female (dissected onto 3 slides) from the Merbok mangrove forest, NHM Reg. No. 1997.1966.

Paratypes; 24 females (1 dissected onto 3 slides) and 23 males (2, each dissected onto 3 slides) from the Merbok mangrove forest, NHM Reg. Nos 1997.1967-2014 and 2 females from the Ranong mangrove forest, NHM Reg. Nos 1997.2015-2016.

Description. - Female. - Body (Fig. 1) extensible, with pronounced arthrodial membranes. Length 0.28-0.40mm (mean = 0.32mm, n = 11), maximum width at posterior margin of cephalothorax, tapering posteriorly, without clear distinction between prosome and urosome. In dorsal view, cephalothorax tapering anteriorly with a few pores, sensilla and ridges as in Fig. 1A; lateral margins, with distinct angle medially, fringed with micro-setules (Fig. 1B);

posterior margin dentate, with eight, small, sensillum-bearing socles and four rounded chitinous extensions crowned with micro-setules (Fig. 1C). Posterior border of free-prosomites similar to cephalothorax but with 8:8:6 micro-setular extensions on P2-P3-P4-bearing somites respectively. Urosomites with dorsal (urosomites-4 and -5) and lateral median (all urosomites) rows of fine spinules; dorsal and lateral posterior margins (except anal somite) with row of fine teeth overlain by dense row of setules (Fig. 1D), also with four sensillum-bearing socles and four chitinous extensions with micro-setules on each somite except preanal and anal; ventral posterior margin of urosomites-3 to -6 with row of fine spinules (Fig. 2A,C). Urosomites-2 and -3 completely fused to form genital double somite, line of fusion marked on dorsal and lateral (but not ventral) surface by ornamentation similar to that described above for posterior border. Operculum (Figs. 1A, 2B), semi-circular with finely dentate margin and sub-opercular hairs; bordered by two sensillum-bearing socles. Caudal rami only slightly longer than wide with row of setules on ventral distal margin (Fig. 2B); setae I-III moderately well-developed, with a few spinules at base, inserted on outer margin in distal third of ramus; seta IV very well developed, one third length of terminal seta V, both minutely pinnate in distal half; seta VI naked; dorsal tri-articulate seta VII inserted near distal margin of ramus.

Rostrum (Figs. 1A, 2E) fused to cephalothorax, triangular, with pair of sensilla near tip and pore on ventral surface.

Antennule (Fig. 2D-E) short, stout, 4-segmented; segment 1 with two rows of spinules on outer margin; segment 3 with large aesthetasc (fused at base to one seta) at outer distal corner; distal segment without aesthetasc on distal margin. All setae smooth except for three pectinate setae on distal segment. Setal formula as follows: 1-[1], 2-[8], 3-[8+a], 4-[11].

Antenna (Fig. 3A-B). Syncoxa with row of spinules. Allobasis with one pinnate seta and group of setules on abexopodal margin. Exopod 1-segmented with three pinnate setae (one lateral and two distal) and a marginal row of spinules. Endopod with row of stout spinules on outer margin and small spinules near inner distal margin which also bears a dentate hyaline frill; subdistal armature consists of two slender spines and a minute seta; distal armature comprises two slender naked spines and three geniculate setae, inner one pinnate in distal half .

Mandible (Fig. 3C). Syncoxa stout, gnathobase bearing three strong bicuspid and one unicuspid teeth and a pinnate seta at inner distal corner. Palp 1-segmented with six naked setae (one exopodal; three endopodal and two basal).

Maxillule (Fig. 3D). Praecoxa with two rows of spinules, arthrite with 7 elements on distal margin and no surface setae. Coxal endite with two naked setae. Rami incorporated into basis which bears nine setae (two exopodal, three endopodal, one on subdistal basal endite and three on distal basal endite).

Maxilla (Fig. 3E). Syncoxa with row of spinules on outer margin and three endites on inner margin; proximal endite represented only by a tube seta; middle and distal endites well developed with three elements (one pinnate and two naked setae) on distal margin; allobasal endite with a fused naked claw and two naked setae at its base; endopod represented by two naked setae not fused at base.

Maxilliped (Fig. 2F). Syncoxa with two rows of spinules on face; two small setae (one pinnate) at inner distal corner. Basis short, oval with row of spinules near inner margin. Endopod represented by a curved, pinnate claw (much longer than basis), with one small accessory seta.

P1 (Fig. 3F). Praecoxa without ornamentation. Coxa with row of setules on inner margin and row of spinules medially on anterior face and on outer margin. Basis with inner pinnate spine and outer pinnate seta; row of setules on inner margin; row of spinules at base of inner spine, medially on anterior face and distal margin. Exopod 3-segmented, each segment with row of setules on inner margin and spinules on outer margin; exp-3 with two short pinnate setae (without pinnule comb at tip) on distal margin and two pinnate spines on outer margin. Endopod 2-segmented and equal in length to exopod; both segments with row of setules on inner margin and spinules on outer margin; enp-2 much more slender, and slightly longer than enp-1 which only reaches distal margin of exp-1; enp-1 with pinnate seta on inner margin; enp-2 with terminal pinnate seta and outer pinnate spine.

P2-P4 (Figs. 3G, 4A, 5A). Exopods 3-segmented, endopods 2-segmented; enp-1 a small segment but enp-2 long and slender, equal in length to exopod-1 in P2 and P3. Protopod and rami ornamented as in P1 except that praecoxa with row of spinules; basis without inner spine, outer seta naked and increasing in length from P2-P4; exp-1 with curved row of spinules on anterior face; exp-1 and exp-2 with dentate hyaline frill. Setal formula of swimming legs as follows:

	Exopod	Endopod
P1	0:0:022	1:011
P2	0:1:022	0:011
P3	0:1:022	0:011 (3-segmented)
P4	0:1:022	0:011 (0:021)

(Figures in parentheses denote male condition)

P5 (Fig. 4B-C). Limbs on each side not fused medially, baseoendopod and exopod separate. Baseoendopod with row of setules on inner margin; on outer margin a long articulating peduncle bearing a naked seta; and, near outer border, a conical chitinous projection with a pore at tip. Endopodal lobe enormously extended into a mucroniform process with a flagellum at tip and many rows of small spinules all round distal portion; inner margin bears three small pinnate setae and a hyaline tube pore closely associated with the distal seta. Exopod a small vase-shaped segment, with a median row of long setules across anterior face, and two pinnate setae, of equal length, on distal margin.

Genital field (Fig. 2A). Vestigial P6s, each bearing one lateral naked seta, fused medially to form anterior flap of genital slit. Small copulatory pore well posterior to genital slit, with a simple duct leading to a central seminal receptacle. Presence or absence of paired tube pores between copulatory pore and genital slit unconfirmed due to dirt covering this region in both preparations. Single egg-sac attaches to genital slit.

Male. - As in female except for urosome, antennule, P3 and P4 endopods, P5 and P6.

Body shorter than female, 0.23 - 0.30mm (mean = 0.25mm, n = 10), and more slender; urosomites-2 and -3 not fused.

Antennule (Figs. 4F, 5B), indistinctly 6-segmented, chirocer, with major articulation between segments 5 and 6. Segment 1 with two rows of spinules; segment 4 minute; segment 5 with strong chitinous tooth on inner margin and large aesthetasc fused at base to one seta. Distal segment hook-shaped, with two modified tube setae proximally but no aesthetasc on distal margin. Setal formula as follows: 1-[1], 2-[9], 3-[9], 4-[2], 5-[10+2 spines + a], 6-[10 + 2 tube setae].

P3 (Fig. 4D). Protopod and exopod as in female. Endopod 3-segmented; proximal segment small with setules on inner margin; middle segment with setules on inner margin and spinules and setules on outer margin, and a slightly curved apophysis at inner distal margin; distal segment small with setules on inner margin, one large pinnate seta on distal margin and a tube pore on anterior face.

P4 (Fig. 5C). Protopod and exopod as in female. Endopod 2-segmented; enp-2 somewhat stouter than in female, bearing two short stout pinnate setae on distal margin and a small pinnate spine at outer distal corner.

P5 (Fig. 4E). Limbs on each side apparently not fused medially but each almost completely absorbed into somatic cuticle with only the tip of the basal peduncle (bearing outer seta), baseoendopod and exopod visible. Endopodal lobe of baseoendopod none -existent, latter with one tube pore and one pore without tube, and bearing two stout spines with a digitate tip. Exopod with row of spinules and two setae equal in length, one stout and pinnate, one fine and naked.

P6 not discernable as a separate structure (Fig. 4E). Single spermatophore slender with a long neck.

Etymology. - The specific name is derived from *mucro(nis)*, Latin for a sharp point (or a sword), and refers to the structure of the endopodal lobe of the female P5.

***Limnocletodes wellsi*, new species**

(Fig. 6A-B)

Limnocletodes behningi Borutsky *sensu* Wells (1971, p.516).

Material examined. - Holotype; female dissected onto three slides NHM Reg. No. 1997.2017.

Paratypes; 4 females and prosome only of 1 male, NHM Reg. Nos 1997.2018-2022. Collected in 1966 by A. D. McIntyre from the Vellar River estuary, Porto Novo, Madras, India and deposited in NHM by J.B.J. Wells.

This material was originally illustrated, but not formally described, by Wells (1971).

Description. - Female. - Body as in *L. mucronatus*, except that posterior border of somites without micro-setule bearing protruberances.

Antennule, antenna, mouthparts, genital field and caudal ramus as described for *L. mucronatus*.

P1 endopod longer than exopod. P2 endopod-2 slightly oval in shape exactly as drawn in Wells (1971), equal in length to exp-1 and with spinules at inner distal corner.

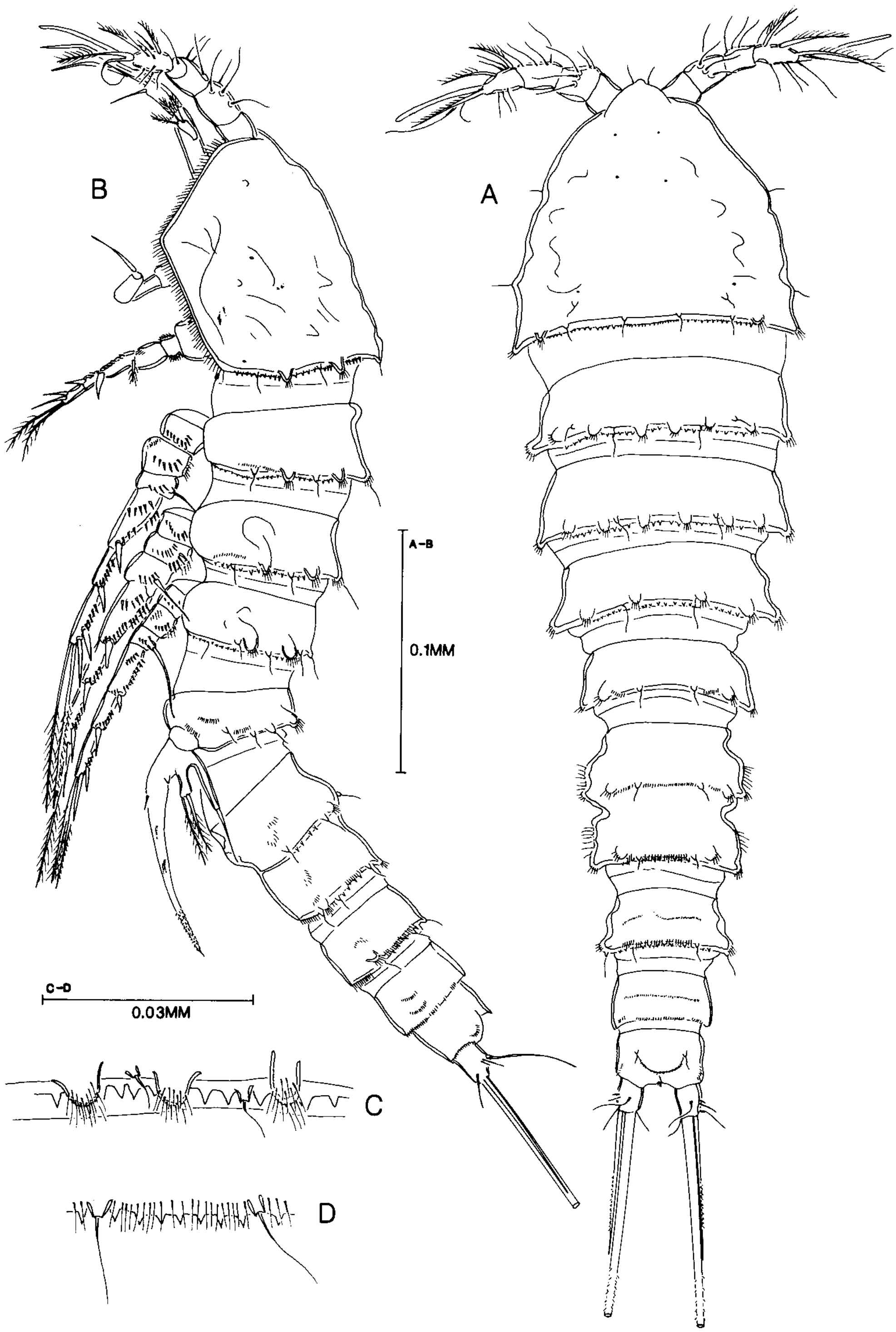

Fig. 1. *Limnocletodes mucronatus*, new species. Female holotype habitus A, dorsal view; B. lateral view: C, dorsal posterior border of P2-bearing somite; D, dorsal posterior border of genital double-somite.

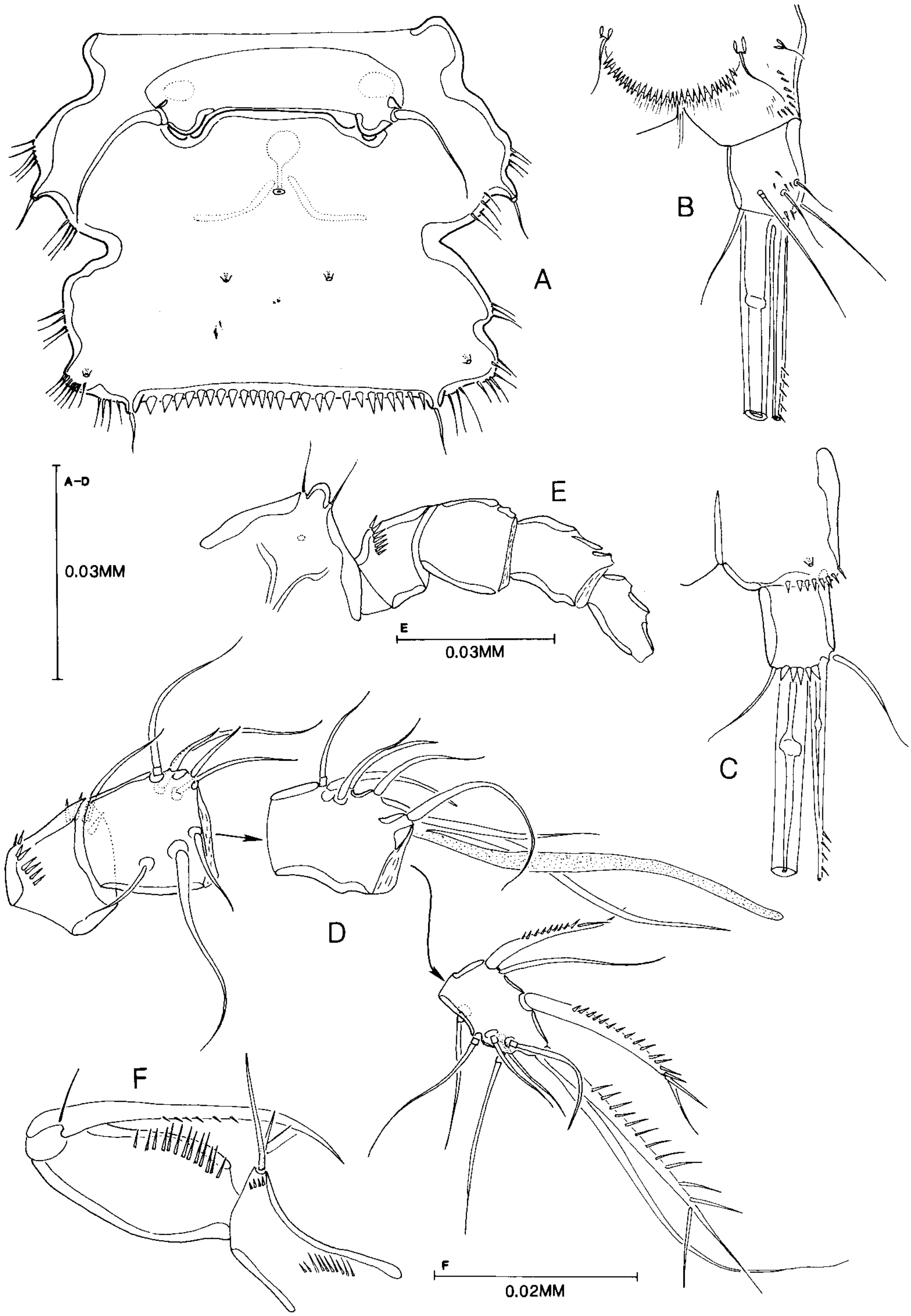

Fig. 2. *Limnocletodes mucronatus*, new species. Female holotype A, genital double somite, ventral view; B. operculum and caudal ramus, dorsal view; C, caudal ramus, ventral view; D, antennule, distarticulated, dorsal view; E, rostrum and segmentation of antennule, dorsal view; F. maxilliped.

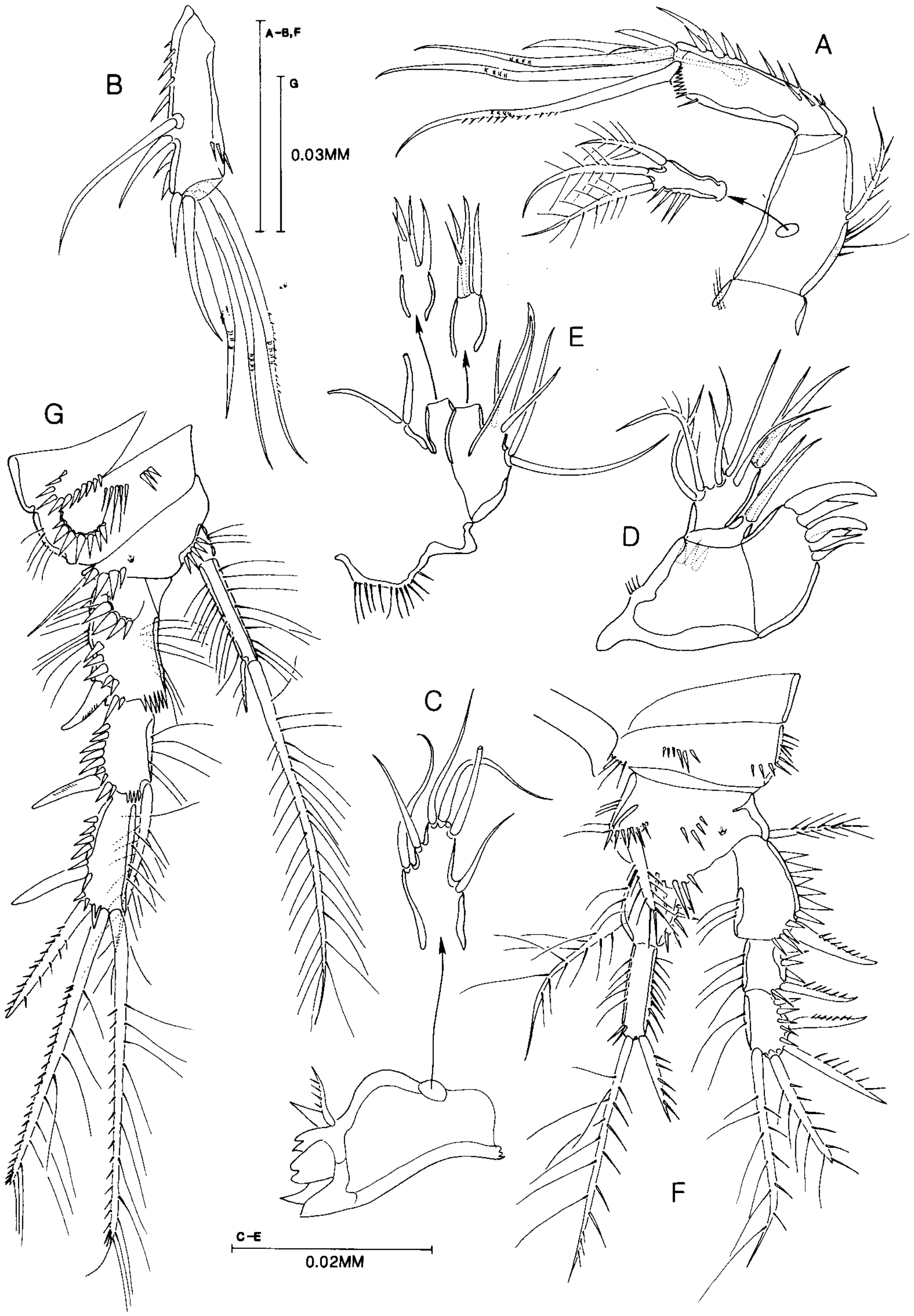

Fig. 3. *Limnocletodes mucronatus*, new species. Female holotype A, Antenna, anterior view; B, antennal endopod, posterior view; C, mandible; D, maxillule; E, maxilla; F, P1; G, P2.

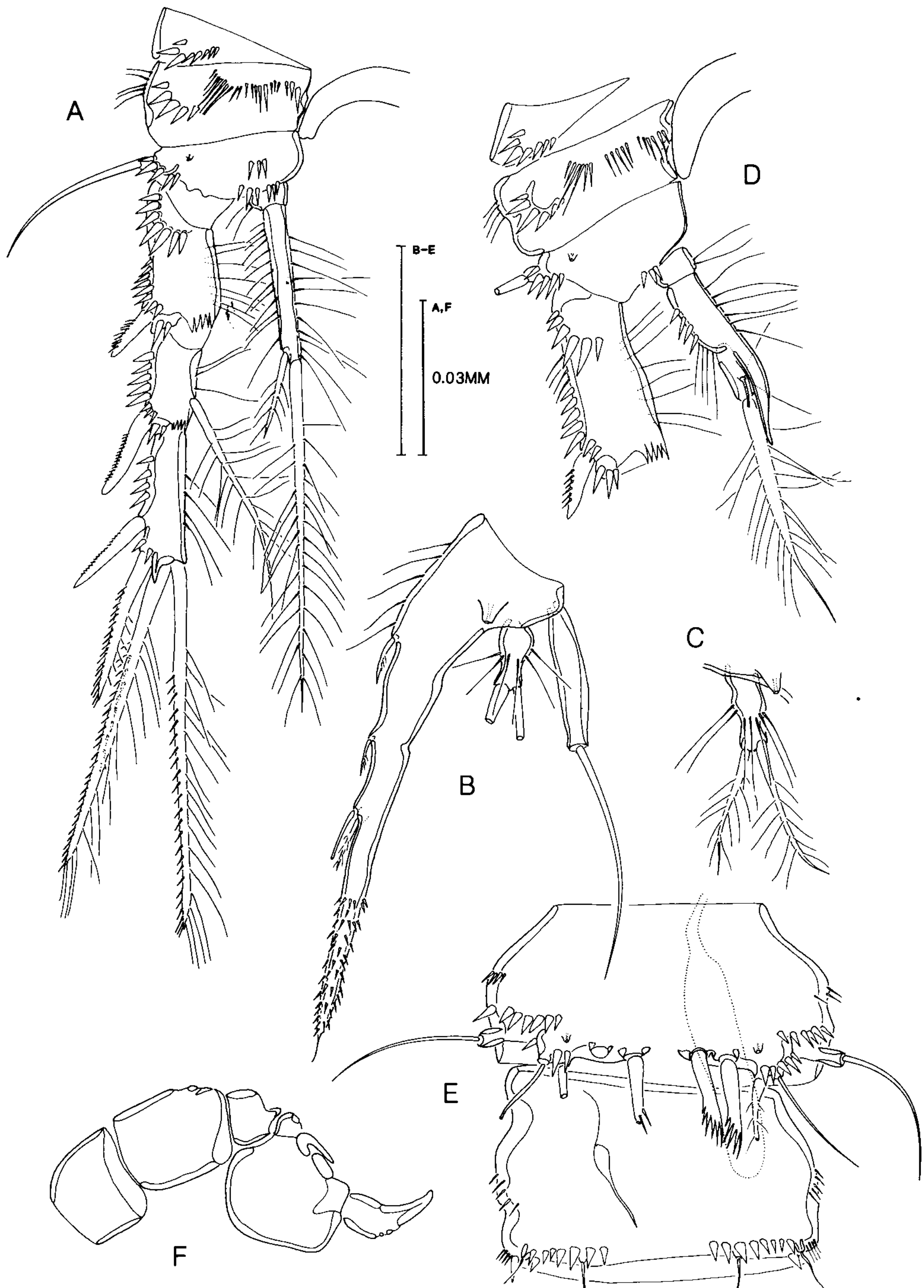

Fig. 4. *Limnocletodes mucronatus*, new species. Female holotype A, P3; B, P5; C. P5 exopod of a paratype. Male paratype D, P3 protopod, exp-1 and endopod; E, Urosomites-1 and-2, ventral view; F, segmentation of antennule.

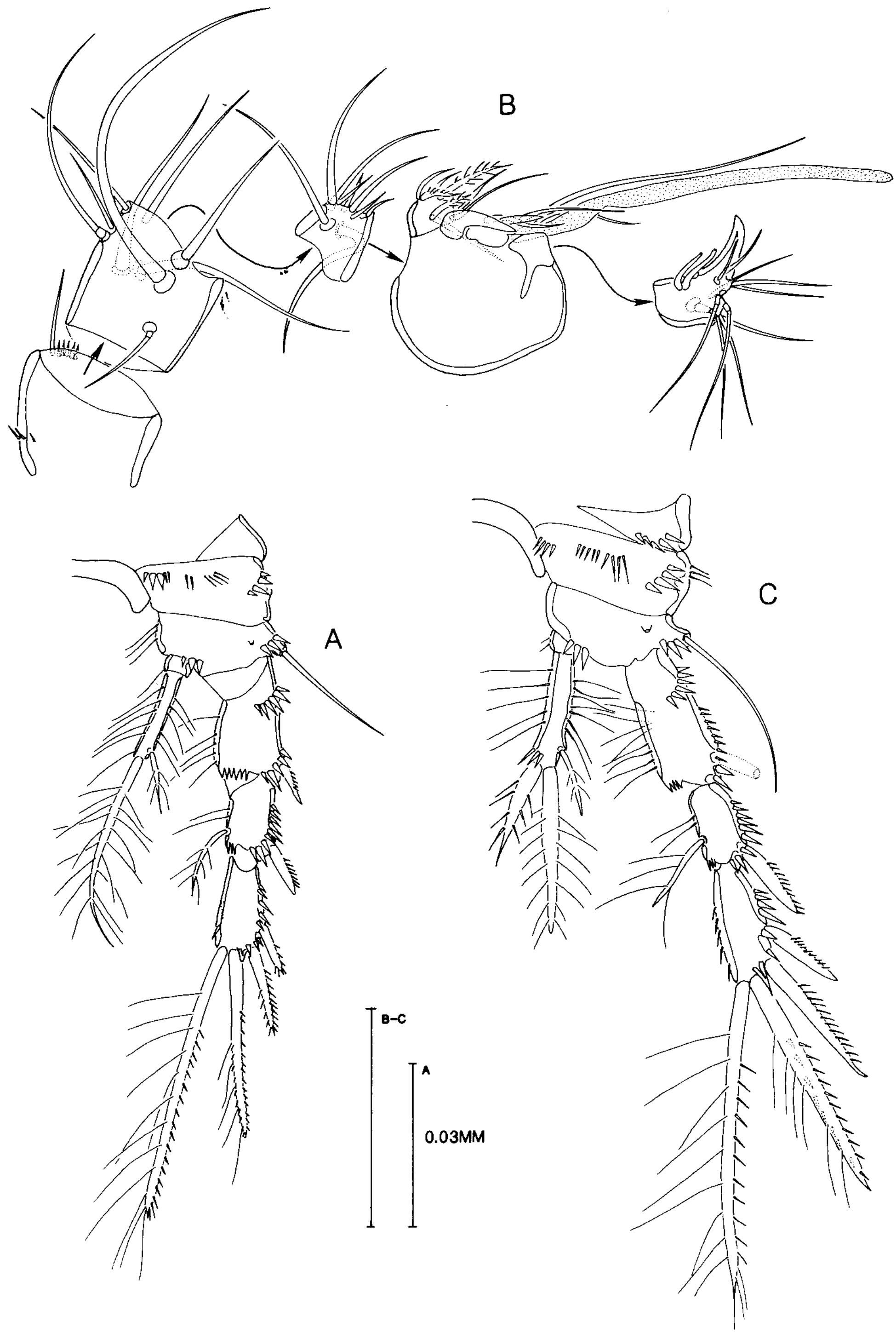

Fig. 5. *Limnocletodes mucronatus*, new species. Female holotype A, P4. Male paratype B, antennule, distarticulated, C, P4.

P3 endopod reaches to midpoint of exp-2, enp-2 equal in length to exp-1, with three well developed setae. P4 (fig. 6A) exp-2 without inner seta. Setal formula of swimming legs as follows:

	Exopod	Endopod
P1	0:0:022	1:011
P2	0:1:022	0:011
P3	0:1:022	0:111 (3-segmented)
P4	0:0:022	0:111

(Figures in parentheses denote male condition)

P5 (Fig. 6B). As figured in Wells (1971) except that on anterior face of baseoendopod is a row of short, stout spinules and the triangular protruberance bears a terminal pore; lateral margin bears two pinnate spines proximally and a small seta with an associated tube pore distally; apical seta pinnate. Exopod with a row of long setules across anterior face and setae on distal margin unequal in length.

Male. - The urosome is missing from the one male specimen examined. Sexual dimorphism in antennule, P3, P4 endopod (and presumably P5 and genital somite).

Antennule as in *L. mucronatus* .

P2 very damaged, endopods missing from specimen but Wells (1971) does not indicate any differences between the sexes.

P3 exopod distal two segments slightly stouter than in female as are two terminal setae on exp-3, endopod exactly as illustrated for *L. mucronatus.*

P4 exopod as in female, enp-2 stouter and setae shorter than in female (as illustrated by Wells, 1971).

P5 not available, but almost certainly as illustrated for *L. mucronatus.*

Etymology. - The specific name is in honour of J.B.J. Wells who first described these specimens.

Limnocletodes secundus Sewell, 1934

(Figs. 6C-7D)

Material examined. - 4 complete and 1 partial female (1 female dissected by JMG onto 3 slides and P2-P4 of partial female dissected onto 1 slide) and 2 whole and one partial male (1 male dissected by JMG onto 3 slides) NHM Reg. Nos 1980.387-396. Collected and presented by Y. Radhakrishna from Lake Kolleru and the reservoir on the Nagarjuna University campus, Guntar, Andra Pradesh, eastern India.

This material was originally described and figured by Ranga Reddy & Radhakrishna (1980).

Description. - Female. - Body as in *L. wellsi.* Antennule, antenna, mandible, maxillule, maxilla and maxilliped exactly as described for *L. mucronatus.* Antennal exopod of one side in one dissected specimen aberrant, with only two setae (one distal seta failed to develop).

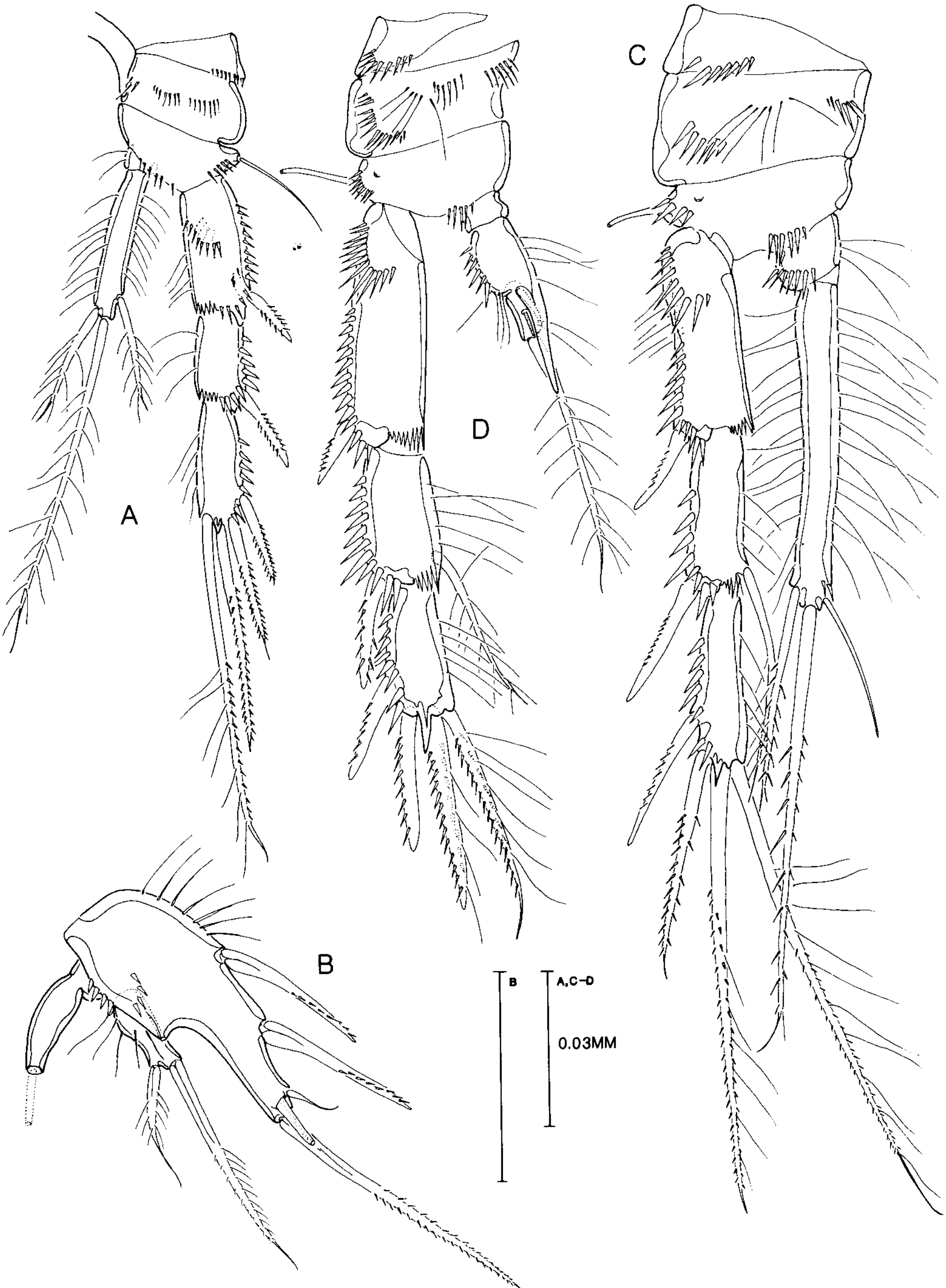

Fig. 6. *Limnocletodes wellsi*, new species. Female holotype A, P4; B, P5. *Limnocletodes secundus* Sewell sp. inq. C, female P3; D, male P3.

P1 endopod longer than exopod. P2 (Fig. 7A) enp-2 long and slender, 1.5 times longer than exp-1 and reaching distal margin of exp-2; lateral margins with long setules over most of length but with distinct groups of spinules in distal portion; armed with one long pinnate seta on distal margin and one shorter pinnate seta at distal outer corner.

P3 (Fig. 6C). Endopod as in P2 except that enp-2 without spinules on outer distal margin and a well developed naked seta at inner distal corner. P4 exp-2 with inner seta.

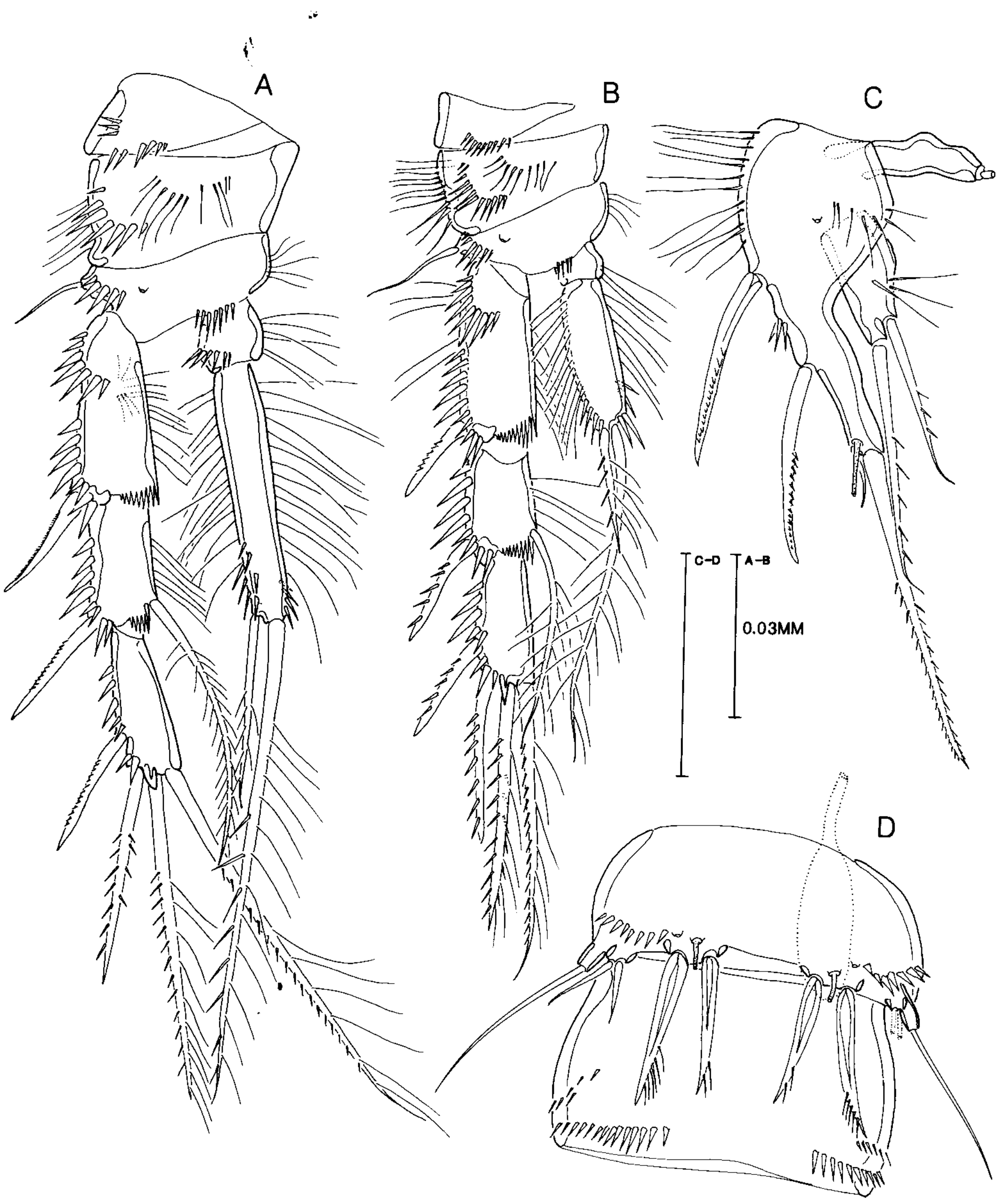

Fig. 7. *Limnocletodes secundus* Sewell sp. inq.. A, female P2; B, male P2; C, female P5; D, male urosomites-1 and -2, ventral view.

Setal formula of swimming legs as follows:

	Exopod	Endopod
P1	0:0:022	1:011
P2	0:1:022	0:011
P3	0:1:022	0:111 (3-segmented)
P4	0:1:022	0:111

(Figures in parentheses denote male condition)

P5 (Fig. 7C). As described by Ranga Reddy & Radhnakrishna (1980) but with the following additional features: a pore and a row of setules on anterior face of baseoendopod near outer margin (note that pore not borne on conical protruberance as described for *L. mucronatus*); a group of spinules on inner margin of endopodal lobe between two well developed setae; a small naked seta and a tube pore on distal inner margin of endopodal lobe; a row of long setules across anterior face of exopod.

Male. - As in female except for urosome, antennule, P2, P3, P4 endopod, P5 and P6.

Body ornamented as in female. Antennule as described for *L. mucronatus*.

P2 (Fig. 7B) exp-2 and exp-3 slightly stouter than in female and distal setae on exp-3 only twice as long as segment (cf. to three times as long as segment in female). Enp-2 distinctly shorter than in female, whole endopod only reaching distal margin of exp-1. Spinules at inner distal corner of enp-2 longer than in female.

P3 (Fig. 6D) exp-1 longer than in female and exp-2-3 shorter and stouter; ratio of length of distal setae to segment on exp-3 same as for P2. Endopod distinctly dimorphic, exactly as described for *L. mucronatus*.

P4 endopod-2 stouter than in female with shorter more robust setae.

P5 and P6 (Fig. 7D) as described for *L. mucronatus* except that setae of P5 exopod shorter and both appear naked.

DISCUSSION

Wells (1971) is correct in his assertion that the structure of the female P5 is of great significance in the taxonomy of *Limnocletodes* but, in addition to the degree of elongation of the endopodal lobe, significance should also be attached to the form of the armature elements. The female P5 of *L. mucronatus* is unique within the genus in that the apical seta has fused to the endopodal lobe to form a mucroniform process and all three setae on the lateral margin of the lobe are very small (Fig. 4B). In the genus there is a clear evolutionary sequence in P5 structure from *L. oblongatus* with a rectangular baseoendopod bearing four well-developed spines of equal length on the distal margin (see Shen & Tai, 1964, fig. 82); through *L. behningi* where the endopodal lobe has elongated under the outer spine so that the other three elements become lateral on the inner margin and the distal inner spine is reduced to a small seta with an accompanying tube pore (as in Figs 6B, 7C); and *L. angustodes* where the endopodal lobe is even more elongate and one of the proximal spines on the inner margin has either been lost (see Shen & Tai, 1963, fig. 53 and Kikuchi & Dai, 1993, fig. 4G) or reduced to a minute seta; culminating in *L. mucronatus* with the fused distal spine and all the inner setae minute. No such differentiation has taken place in the male P5 which is more or less identical in all species in the genus.

However, the assertion by Wells (1971) that differences in swimming leg armature are unimportant in the taxonomy of this genus and merely expressions of variability within *L. behningi* is incorrect. *L. mucronatus* is unique within the genus in the presence of only two setae on P4 enp-2 in the female, with the well developed inner seta found in all other species being absent. This is not an aberration of the dissected specimens but is the condition in all the adult specimens collected from Merbok and Ranong. However, what is most peculiar, is that the male P4 endopod bears three short setae on enp-2, thus being structurally identical to that of the male of all other species.

The female P3 enp-2 of *L. mucronatus* also bears only two setae. This condition has been reported also for *L. angustodes* (in Shen & Tai, 1963, Kikuchi & Dai, 1993) and *L. oblongatus* (in Shen & Tai, 1964) but the situation in *L. behningi* is more confusing. In the original descriptions and figures of Borutsky (1926) and Smirnov (1932) and in Damian-Geogescu (1970) the distal inner seta on P3 enp-2 appears to be a minute element (which could be equated with a spinule - see below) but in descriptions of *L. behningi* in Shen & Tai (1962, fig. 38) and Shen (1979, fig. 162) this element is absent. In all the Indian material I have examined there is a well developed distal inner seta on P3 enp-2 (see Fig. 6C), much bigger than that illustrated in Ranga Reddy & Radhakrishna (1980, fig. 13) but similar in size to that illustrated in Wells (1971, fig. 30). The sexual dimorphism of the male P3 endopod (Figs 4D, 6D), is constant throughout the genus but in *L. behningi* and the Indian material there is also a slight difference in proportional length of the segments and terminal setae in the male P3 exopod.

The P1 and P2 enp-2 in all species of *Limnocletodes* has two setae. Sewell (1934) and Ranga Reddy & Radhakrishna (1980) both maintained that *L. secundus* was distinguished from *L. behningi* by the presence of a small inner seta on P2 enp-2. However, an examination of the latter author's material shows that there is a group of spinules (particularly large in the male) but no seta in this position (Fig. 7A-B).

The setation of the P1-P4 exopods in all *Limnocletodes* is as shown here for *L. mucronatus*, except for the material of Wells (1971) from southern India, in which the P4 exp-2 in both sexes definitely lacks an inner seta. Although this author states that the condition is unique within the family he attached no significance to it, believing rather that *L. behningi* has a variable setal formula. However, apart from the doubt about the setation of P3 enp-2 mentioned above, the setal arrangements of the swimming legs, within a species, appear to be constant. Consequently, the condition of the P4 endopod in Wells' (1971) material is sufficient justification for regarding this as a separate species, named herein as *L. wellsi* new species

With respect to the specific status of *L. secundus*, the situation cannot be properly resolved without careful re-examination of material of *L. behningi* from the type and other localities. In addition to the supposed difference in the setation of P2 enp-2 (which is shown above to be spurious), Ranga Reddy & Radhakrishna (1980) maintain that the P4 exp-2 of male *L. behningi* lacks an inner seta which is present in *L. secundus*. There is no convincing evidence in the descriptions of *L. behningi* for this statement as Borutsky (1926), Smirnov (1932) and Shen & Tai (1962) all say that the structure of the P4 exopod is the same in both sexes and clearly illustrate a seta on this segment in the female. However, Smirnov's (1932) fig. 20 of the male P4 exopod does not clearly show a seta on this segment, but there are some vague lines which could certainly represent a broken seta. Thus, apart from the longer P2 and P3 endopods in the female (and proportionally much shorter P2 endopod in the male), and the prominent distal inner seta on P3 enp-2, I can find no other significant differences between the material of Ranga Reddy & Radhakrishna (1980) and the descriptions of *L. behningi*. However, because of the reported wide distribution of *L. behningi* across southern Asia in isolated bodies of water, there is potential for the existence of sibling species with significant genetic divergence but little morphological expression (Todaro et al., 1996). Therefore, it is recommended that *L. secundus* is retained as a *species inquirenda* rather than subsuming it as a synonym of *L. behningi*. Similarly it is also possible that, upon re-examination, the material described by Shen & Tai (1962) and Shen (1979) may prove to be a separate species.

The genus *Limnocletodes* was assigned to the family Cletodidae by its original author. In his revision of the Cletodidae, Lang (1936) divided the family into four Reihe (series) and grouped *Limnocletodes* in his *Leimia*-Reihe along with *Leimia* Willey and *Cletocamptus* Schmankewitsch. Por (1986) put forward a preliminary revision of the Langian concept of the Cletodidae; established four new families (Paranannopidae, Huntemanniidae, Rhizothricidae and Argestidae); moved a number of genera to Hemimesochrinae, a new sub-family of the Canthocamptidae; regarded a number of genera (among them *Leimia* and *Cletocamptus*) as *incertae sedis* in the Canthocamptidae, pending a revision of that family; and defined the Cletodidae *sensu stricto* to embrace the genera *Cletodes* Brady, *Enhydrosoma* Boeck, *Enhydrosomella* Monard, *Acrenhydrosoma* Lang, *Stylicletodes* Lang, [*Monocletodes* Lang], *Australonannopus* Hamond, *Limnocletodes*, *Barbaracletodes* Becker and *Scintis* Por, at the same time acknowledging that the latter four genera "have a somewhat peripheric position in the family". Since this time six new genera have been described which are included in the family, viz. *Kollerua* Gee, *Strongylacron* Gee & Huys, *Schizacron* Gee & Huys (all three genera to accommodate species previously included in *Enhydrosoma*), *Intercletodes* Fiers, *Triathrix* Gee & Burgess and *Sphingothrix* Fiers.

Australonannopus, *Barbaracletodes* and *Scintis* possess many characters which clearly suggest that they do not belong in the Cletodidae *sensu* Por and are excluded from further consideration here. *Limnocletodes* also has characteristics which are not found in any of the remaining genera listed above. (1) Seta IV of the caudal ramus is very well developed, pinnate and at least one third the length of seta V. (2) The distal segment of the antennule in both sexes lacks an aesthetasc. (3) The inner element on the distal margin of the antennal endopod (arrowed in Fig. 3A-B) is a geniculate seta rather than a stout pectinate spine with a small seta fused to its base. (4) The maxillipedal syncoxa bears two setae as opposed to a maximum of one seta on this limb segment. (5) P1 enp-1 has an inner seta. (6) Sexual dimorphism is present on the endopod of P4 (and occasionally P2) as well as on the endopod of P3. (7) The insertion of a well developed seta on the outer margin of the vestigial P6 on the female genital field.

In addition to the above, *Limnocletodes* possesses the following characteristics which are very rare within the cletodid genera. (8) A 4-segmented female antennule; this has only been reported for *Cletodes reductus* Moore, 1976 and the monotypic genus *Intercletodes*. In all these cases the 4-segmented condition has arisen through the fusion of the two segments distal to the aesthetasc-bearing segment-3. (9). A 1-segmented exopod of the antenna bearing three setae (one lateral and two distal) has also been reported in the adult of *Triathrix* and *Sphingothrix* but Fiers (1996) has shown that it is also present in the copepodid-I stage in the development of some (if not all) cletodids. (10). The presence of three maxillary syncoxal endites, with the inner endite being represented by a seta (Fig. 3E) has been reported previously only in *Cletodes macrura* Fiers, 1991. (11). The presence of four setae on the baseoendopodal lobe of the female P5 is only found in *Stylicletodes* and *Enhydrosoma curvirostre* (T. Scott, 1894) *sensu* Sars (1911) . The general structure of the female P5 in all *Limnocletodes* except *L. oblongatus* is similar to that found in *Acrenhydrosoma* but this may be the result of convergence. (12). The form of the male P5, in which the baseoendopod is completely absorbed into the somatic cuticle is only found in *Strongylacron* and *Schizacron*. (13).The presence of a continuous genital slit forming the opening to the gonopore in the female genital field has only been reported in *Enhydrosoma curticauda*.

Of the above characters, (2),(6), (7) and (8) are regarded as autapomorphies for the genus whereas all the others, except (12), may be interpreted as the plesiomorphic condition in the Cletodidae and are therefore of little use in determining whether *Limnocletodes* should be included in the Cletodidae or in a sister-family (Canthocamptidae?). So far no autapomorphies have been identified for the Cletodidae and this may not be possible until a revision of the Canthocamptidae has been attempted. However, within the group of families exhibiting the same sexual dimorphism on P3 endopod as shown here for *Limnocletodes* (Fig. 3D), the Cletodidae *sensu stricto* might be defined by a combination of the following potential apomorphies. (i) A rostrum fused to the cephalothorax. (ii) An antennule which, in the female, is 4/5-segmented, with the aesthetasc on segment-3 and, in the male, indistinctly 6/7-segmented, chirocer or subchirocer. (iii) An antennal exopod at most 1-segmented with three setae. (iv) A mandible and maxillule without segmented rami. (v) A 3-segmented P1 exopod with a 0:0:022 setal formula. (vi) P2 exp-3 with a 022 setal formula: (vii) P3-P4 exp-3 with at most six armature elements (including only two outer spines): (viii) P1-P4 endopods at most 2-segmented (except male P3), enp-1 without an inner seta and distinctly shorter than enp-2. (ix) An asymetrical, but often indistinguishable, male P6 without armature elements.

Limnocletodes exhibits all these characteristics except for the absense of a seta on P1 enp-1. As stated above, the presence of this seta could be interpreted as the plesiomorphic condition in the family and as it is clear that *Limnocletodes* has extremely close affinities with the Cletodidae, it is proposed that the genus be maintained within that family, at least for the present.

KEY TO FEMALES OF *LIMNOCLETODES*

1. P3 enp-2 with 3 setae; P5 baseoendopodal lobe triangular with 1 terminal seta, inner margin with 2 spines, a minute seta and a tube pore 2
- P3 enp-2 with 2 setae; P5 not exactly as above 4

2. P4 exp-2 without inner seta .... *L. wellsi*, new species
- P4 exp-2 with inner seta 3

3. P2 & P3 enp-2 1.5 times longer than exp-1 .... *L. secundus* Sewell sp. inq.
- P2 & P3 enp-2 equal in length to exp-1 .... *L. behningi* Borutsky

4. P4 enp-2 with 2 setae; P5 baseendopodal lobe a long mucroniform process, with 3 minute setae and a tube pore on inner margin .... *L. mucronatus*, new species
- P4 enp-2 with 3 setae; P5 not as above 5

5. P5 baseoendopodal lobe rectangular with 4 equally well-developed setae .... *L. oblongatus* Shen & Tai

- P5 baseoendopodal lobe attenuated, triangular, with 1 terminal seta, inner margin with 1 spine, a minute seta and a tube pore .... *L. angustodes* Shen & Tai

The lack of structural differences in the P5 and the endopods of P3 and P4 makes the identification of male specimens extremely uncertain at present (except for *L. wellsi* which lacks an inner seta on P4 exp-2.).

ACKNOWLEDGEMENTS

The author wishes to thank the Curator of Crustacea at the Natural History Museum, London, for facilitating the examination of the Indian material in their collections; Dr. Chittima Aryuthaka for collecting the material from Thailand; and Dr. R. Huys for his helpful comments on an earlier draft of the MS. This work forms part of the Plymouth Marine Laboratory Biodiversity Programme and was funded by the DOE Darwin Initiative for the Survival of Species.

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