

AN APPRAISAL OF THE TAXONOMIC POSITION OF *ENHYDROSOMA BUCHHOLZI* (BOECK, 1872), *E. BIFURCAROSTRATUM* SHEN & TAI, 1965, *E. BARNISHI* WELLS, 1967 AND *E. VERVOORTI* FIERS, 1987 WITH DEFINITION OF TWO NEW GENERA (COPEPODA, HARPACTICOIDA, CLETODIDAE).

J. MICHAEL GEE & RONY HUYS

SARSIA



GEE, J. MICHAEL & RONY HUYS 1996 10 15. An appraisal of the taxonomic position of *Enhydrosoma buchholzi* (BOECK, 1872), *E. bifurcarostratum* SHEN & TAI, 1965, *E. barnishi* WELLS, 1967 and *E. vervoorti* FIERS, 1987 with definition of two new genera (Copepoda, Harpacticoida, Cletodidae). – *Sarsia* 81:161-191. Bergen. ISSN 0036-4827.

Some morphological features of *Enhydrosoma buchholzi* (BOECK, 1872), *E. barnishi* WELLS, 1967 and *E. vervoorti* FIERS, 1987 are redescribed in detail. It is shown that, in the structure of the antenna, maxillule and the form of sexual dimorphism on the P3 endopod, these species, along with *E. bifurcarostratum* SHEN & TAI, 1965 and a new species from Thailand have greater affinities with the genus *Cletodes* BRADY, 1872 than with *Enhydrosoma* BOECK, 1872. However, they cannot be included in the genus *Cletodes* because they display a more primitive setal formula on P3 and P4 exopod and apomorphic character states on the antennary endopod and P5 of both sexes. Consequently, *E. buchholzi* from north-west Europe (and Canada) is assigned to the genus *Strongylacron* gen. nov. and becomes the type species by monotypy. The other four species from the Indian Ocean and South China Sea can be clearly distinguished from *Strongylacron* by the structure of the rostrum. They are assigned to the genus *Schizacron* gen. nov. as *S. barnishi* (WELLS, 1967) comb. nov., designated as the type species, *S. bifurcarostratus* (SHEN & TAI, 1965) comb. nov., *S. vervoorti* (FIERS, 1987) comb. nov. and *S. intermedius* sp. nov. A key to species of *Schizacron* is provided.

J. Michael Gee, Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, England. – *Rony Huys, Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, England.*

KEYWORDS: Taxonomy; Harpacticoida; *Enhydrosoma*; *Strongylacron*; *Schizacron*.

INTRODUCTION

In the same paper that BOECK (1872) established the genus *Enhydrosoma*, he also very briefly described in old Danish but did not figure, a new species, *Cletodes Buchholzii* BOECK, 1872 from Haugesund, Norway. Presumably, the specific name was in honour of his contemporary, a German zoologist by the name of Dr Reinhold Buchholz. SARS (1909) confirmed that, in his opinion, this species belonged in the genus *Cletodes* BRADY, 1872 and gave an excellent redescription and drawings of the female based on a single specimen found at Risør on the south coast of Norway. However, for no apparent reason, other than that he misread the original name, SARS called this species *C. buchholtzi*. This subsequent incorrect spelling of the specific name has been used in all references to this species since 1909. The correct form of the specific name should be *E. buchholzi* in accordance with Article 31(a)(ii) of the International Code of Zoological Nomen-

clature, 3rd Edition. WILLEY (1929) found specimens in New Brunswick, Canada, which he maintained agreed in all details with SARS' (1909) description of *C. buchholzi*. On the basis of this material he briefly described and figured the P3 endopod and fifth leg of the male.

LANG (1936) published a revision of the Cletodidae SARS in which he argued that the differences between *Cletodes* and *Enhydrosoma* outlined by SARS (1909), with respect to the mouthparts and P5, were inconsistent. After removing certain species of *Cletodes* to new genera, he maintained that the only reliable distinction between these two genera was in the form and setation of the distal segments of P3 and P4 exopod: *Cletodes* having an elongate segment bearing four setae/spines and *Enhydrosoma* a short segment bearing five setae/spines. As a result of this, LANG (1936) transferred *C. buchholzi*, *C. curvirostre* T. SCOTT, 1894, *C. perplexa* T. SCOTT, 1899, *C. sarsi* T. SCOTT, 1904 and *C. latipes* A. SCOTT, 1909 to the genus *Enhydrosoma*. This generic concept is also the one outlined in LANG'S

(1948) monograph, except that *E. perplexa* was removed to a new genus *Acrenhydrosoma* LANG, 1944, and has subsequently been followed to the present day. At the familial level it became increasingly evident that the Cletodidae *sensu* LANG, 1948 was a polyphyletic assemblage. POR (1986) attempted a first revision by removing many genera from the Cletodidae to four new families and to the Canthocamptidae. It is the Cletodidae *sensu* POR, 1986 that we adopt here.

In a paper reviewing our present state of knowledge of the genus *Enhydrosoma*, to which many new species have been added since 1948, GEE (1994) suggested that LANG's (1948) interpretation of the taxonomic position of *E. buchholzi* and *E. curvirostre* was almost certainly erroneous. These two species, along with three other, more recently described species, *E. bifurcarostratum* SHEN & TAI, 1965, *E. barnishi* WELLS, 1967 and *E. vervoorti* FIERS, 1987 were allocated to the *buchholzi*-species group which is more closely related to certain species of *Cletodes* than to *E. curticauda* BOECK, 1872, the type species of *Enhydrosoma*. GEE (1994) based this view on phylogenetically significant differences in the rostrum, antenna, maxillule, and the sexual dimorphism on the male P3 endopod. He also pointed out that *E. curvirostre sensu* SARS (1909) is almost certainly different from T. SCOTT's (1894) original description, and from a cursory examination of material to hand, appeared to have all the features of a *Cletodes* except for the characteristic elongate exopod segments of the swimming legs. The remaining four species of the *buchholzi*-group possess apomorphies on the antennary endopod and fifth leg which clearly distinguish them from the genus *Cletodes*.

For this paper we have re-examined material of *E. buchholzi*, *E. barnishi* and *E. vervoorti* and new material from the Ranong mangrove forest of western Thailand. We redescribe those characters poorly covered in original descriptions and establish two new genera, one to accommodate *E. buchholzi* and one to contain the remaining species.

METHODS

Before dissection the habitus was drawn and body length measurements were made from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactophenol or lactic acid, the parts individually mounted in lactophenol under coverslips subsequently sealed with Bioseal or Glyceel. All drawings were prepared using a camera lucida on a Nikon Optiphot 20 or Zeiss Axioskop 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.

Females were prepared for scanning electron microscopy. Specimens were dehydrated through graded acetone, critical point dried, mounted on stubs, sputter-coated with gold-palladium, and examined with a Hitachi S-800 scanning electron microscope (working distance: 5).

SYSTEMATICS

Family Cletodidae T. Scott, 1904 *sensu* POR (1986)

Genus *Strongylacron* gen. nov.

Cletodes BRADY, 1872 (partim): BOECK (1872), SARS (1909); *Enhydrosoma* BOECK, 1872 (partim): LANG (1936, 1948).

Diagnosis. Cletodidae. Body with slightly chitinized cuticle covered with minute denticles; without sub-cuticular struts; sensillar socles on posterior border of somites small. Female genital field with separate gonopores each covered by vestigial P6 with one seta. Anal somite partially divided; operculum semi-circular with minutely dentate posterior margin. Caudal rami only very slightly dimorphic, cylindrical, twice (female) to three (male) times longer than broad, with tube pores medially and distally on outer margin. Setae I, II and VII in proximal third of ramus, seta III at distal outer margin.

Rostrum well developed, not defined at base, not noticeably recurved dorsally; well defined chitinous ridges dorso-laterally, anterior margin broadly rounded between frontal pair of sensilla and heavily fringed with fine setules. Antennule short, stout, 5-segmented in female; in male 6-segmented, subchirocer, with patch of long setules on segment 4. Antennary allobasis with two well developed pinnate setae on abexopodal margin; exopod a minute segment with one seta; endopod with two stout spines and a small seta sub-distally on posterior face and distal margin with five non-geniculate spines, a small seta fused to base of inner spine, and a tube pore. Anterior surface of labrum with central row of spinules, a raised tuft of setules, and two tube pores. Mandibular coxa broad and robust, palp 1-segmented with five setae. Maxillular arthrite of praecoxa with a large pinnate seta on inner margin; coxal endite distinct with two elements, exopod and endopod completely incorporated into basis forming palp with ten elements. Maxilla with two syncoxal endites each with three elements; allobasal endite with a fused spine, three setae, and a tube pore; endopod represented by two setae not fused at base. Maxillipedal syncoxa with a large pinnate seta on outer distal margin; basis oval, twice as long as broad, no seta on palmar margin; endopod represented by a claw with one small accessory seta.

P1-P4 exopods 3-segmented, segments only two times longer than broad, exp-3 with 4,4,5,5 setae/spines respec-

tively; P1 exp-3 with posterior tube pore; P2-P4 exp-3 with tube pore at base of distal outer spine; male P3 exp-3 with additional tube pore near base of segment; endopods 2-segmented except male P3 which is 3-segmented with recurved apophysis on enp-2 and two setae on enp-3. Female P5 distinctly U-shaped, with endopodal lobe reaching to distal margin of exopod, latter indistinctly separate; baseoendopod with a tube pore on ventral surface; endopodal lobe with three well developed setae and two tube pores at base of proximal seta; exopod with three well developed setae and a tube pore on distal margin. Male P5 baseoendopod incorporated in cuticle of somite (although basal tube pore present) with only tips of endopodal lobe, exopod and basal peduncle in evidence at posterior margin of somite; endopodal lobe with two well developed setae and two tube pores near distal margin; exopod with surface (tube?) pore, one small naked seta and two well developed pinnate setae. Male P6 asymmetrical, unarmed.

Females with one egg-sac, males with one spermatophore.

Type and only species. *Strongylacron buchholzi* (Boeck, 1872) comb. nov.

Etymology. The genus name is derived from the Greek 'strongylos', meaning rounded, and 'akros', meaning tip, and refers to the shape of the rostrum. Gender: masculine.

Strongylacron buchholzi (BOECK, 1872) comb. nov.

Material examined. (1) 10 females (1 dissected onto 3 slides, urosome only of 2 specimens mounted on slides) and 2 males (1 dissected onto 3 slides) collected by J.M. Gee from intertidal mudflats in the Fal Estuary, Cornwall, UK (NHM reg. nos 1996.1-12); (2) 4 females and 1 male collected by J.M. Gee from intertidal mudflats in the Tamar estuary, Devon, UK (NHM reg. nos 1996.13-17); (3) 15 females and 3 males (in alcohol) collected by R. Hamond from algae on mud, Bluejacket Creek Stepping-Stones, Morston marshes, Norfolk, UK (NHM reg. nos 1992.708-717); (4) 5 females and 1 male collected by R. Hamond from amongst weeds, stones and mussels on the flats at the western end of Blakeney harbour, Norfolk, UK and retained in his personal collection.

Female. Body (Fig. 1A). Length 0.50 - 0.81 mm (mean 0.67 mm, n = 15), semi-cylindrical, tapering posteriorly, without clear distinction between prosome and urosome, extensible with large arthrothial membranes between somites. Somites well defined but not heavily chitinized, without sub-cuticular ridges but with surface densely covered with minute denticles (Fig. 7A). Cephalothorax with a few pores and sensilla, posterior dorsal and lateral border smooth but with 14 minute socles each bearing a sensillum,

ventro-lateral border with fringe of fine hairs and three marginal sensilla on each side. Free prosomites and anterior urosomite with approximately 14 sensillum-bearing socles and row of minute setules on dorsal and lateral posterior border; ventro-lateral border with a marginal sensillum on each side. Genital double-somite with more or less complete median subcuticular ridge with eight socles; posterior border with row of hair-like setules and eight socles; one large socle on each side in subdistal lateroventral position, all socles with sensillum. Urosomites 4-5 with hair-like setules on posterior border, former with six small (dorsally and laterally) and two large (lateroventrally) sensillum-bearing socles; latter without any small socles and two large lateroventral socles without sensilla. Anal somite (Fig. 2A) partially divided medially; with two small lateral socles without sensilla and a small sensillum-bearing socle either side of operculum. Operculum semi-circular with minutely dentate margin and ventral fringe of hairs.

Rostrum (Fig. 1B) well developed, fused to cephalothorax, tapering anteriorly, not noticeably recurved dorsally; well defined chitinous ridges dorso-laterally (Fig. 7B); anterior margin broadly rounded between a pair of sensilla and densely fringed with fine setules; a median tube pore on ventral surface.

Caudal rami (Fig. 2A) more or less rectangular (about twice as long as maximum width), slightly convergent, with two tube pores near median and distal outer margin which bears a fringe of fine setules ventrally. Lateral setae I and II and dorsal, pinnate seta VII implanted in proximal third of ramus; setae III implanted at distal outer corner of ramus; seta IV small, fused at base to well developed, spinulose seta V, seta VI unipinnate.

Genital field [Fig. 7C; fig. 9C in GEE (1994)]. Genital apertures completely separate, each closed off by operculum derived from vestigial P6 bearing one pinnate seta. Copulatory pore with two openings located in common median depression, leading to paired copulatory ducts. Shape of seminal receptacles unknown. Pair of composite tube pores with three tubes situated between copulatory pore and gonopores.

Antennule (Fig. 2C). Short, stout, 5-segmented. Segment 1 with three rows of spinules on anterior margin and one spinulose spine. Segment 2 with six pinnate and three naked setae. Segment 3 with three pinnate setae and four naked setae, one of which is fused basally to aesthetasc. Segment 4 small, with one seta. Segment 5 with 11 setae (five anterior, five posterior, one distal), distal of which is fused at base to an aesthetasc.

Antenna (Fig. 1C). Coxa well developed. Allobasis with two well developed pinnate setae on abexopodal margin. Exopod a minute segment with one strongly pinnate seta. Endopod with two rows of spinules on anterior margin and a hyaline frill around inner distal margin; two stout

spines and a tiny seta sub-distally on posterior face and distal margin with six elements (a small outer spine, four strong pectinate non-geniculate spines and a small seta fused to base of inner spine) and a tube pore adjacent to the small seta (Fig. 8A).

Labrum (Fig. 3A). Anterior surface with two median tube pores, several rows of setules and a raised median tuft of long spinules near apex. Posterior surface with central row of spinules and a clump of setules.

Mandible (Fig. 3B). Coxa broad and robust, gnathobase with three large recurved teeth and a short stout pinnate seta at outer distal corner. Palp (Fig. 8B) well developed; exopod and endopod fused to basis but still recognizable, each bearing one seta, basis with three setae.

Maxillule (Fig. 4A). Arthrite of praecoxa with two large tube setae on anterior surface and a large pinnate spine on inner margin; distal margin with six short, recurved spines and a pinnate seta. Coxa with row of spinules at base; endite with large pinnate spine and slender naked seta on distal margin. Exopod and endopod completely incorporated in basis forming 1-segmented palp with three rows of surface spinules and ten marginal elements (Fig. 8C) (baso-endites represented by two pinnate spines and two naked setae distally, and by two largely naked setae subdistally; rami represented by a naked and a pinnate seta each).

Maxilla (Fig. 4B). Syncoxa largely fused to allobasis; with two endites, each with three elements, i.e. two pinnate spines (one fused to endite) and a naked seta. Allobasal endite drawn out into short claw; with three setae and a tube pore. Endopod represented by two setae not fused at base (Fig. 8D).

Maxilliped (Fig. 5A). Syncoxa with a median spinulate ridge, rows of spinules on inner and outer border and a large pinnate seta on inner distal margin. Basis elongate-oval, with row of spinules near palmar margin but no setae. Endopod represented by a claw with one small accessory seta.

Swimming legs (Figs 3C; 5B). As described by Sars (1909). P1 exp-3 terminal setae not geniculate; posterior surface of segment with tube pore. P2-P4 with tube pore on basis and near outer margin of exp-3. Setal formula as follows:

	Exopod	Endopod
P1	0.0.022	0.021
P2	0.0.022	0.020
P3	0.0.122	0.021
P4	0.0.122	0.111

P5 (Fig. 3D). Distinctly U-shaped, with endopodal lobe reaching to distal margin of exopod; latter indistinctly separated from baseoendopod. Baseoendopod with patches of spinules and a tube pore on anterior surface and outer pin-

nate seta on a distinct peduncle. Endopodal lobe with row of spinules around distal margin and a double tube pore at base of proximal inner seta; bearing three well developed pinnate setae. Exopod with three rows of spinules on anterior surface, setules along outer margin and a tube pore at base of outer seta, distal margin with three well developed pinnate setae.

Male. As in female except for urosome, caudal rami, antennule, P3, P5, and P6.

Body slightly smaller and more slender than female, length 0.47 - 0.87 mm (mean 0.68 mm, n = 3), urosomites 2-3 separate. Sixth pair of legs (Fig. 6C) asymmetrical; functional gonopore closed off by single plate placed on one side of the body, without setae but ornamented with rows of spinules. Caudal rami (Fig. 2B) slightly broader than in female and with more pronounced ventral ridge.

Antennule (Fig. 6A, B) 6-segmented, subchirocer with segment 4 markedly swollen. Segment 1 with patch of setules and rows of spinules on anterior margin and one pinnate seta. Segment 2 with patch of hairs and nine setae. Segment 3 with patch of hairs on surface and of long setules on distal margin, with nine setae. Segment 4 with patch of robust setules near palmar margin which bears 11 setae and an aesthetasc. Segment 5 with one seta and a tube pore. Segment 6 with nine setae and an aesthetasc which is fused at base to two of the setae.

P3 (Fig. 5C). Exp-3 with an extra tube pore proximally on anterior face (arrowed in Fig. 5C). Endopod 3-segmented; enp-2 inner distal margin produced into recurved apophysis with a small tooth on inner medial margin; enp-3 with two setae on distal margin.

P5 (Fig. 4C). Baseoendopod completely absorbed into somitic cuticle (although basal tube pore present) with only distal portions of endopodal lobe, exopod and basal peduncle in evidence around posterior margin of somite. Endopodal lobe with row of coarse spinules and a double tube pore near distal margin which bears two well developed pinnate setae. Exopod with surface (tube?) pore, one small naked seta and two well developed pinnate setae. Basal peduncle with pinnate seta.

Remarks. There has been no morphological re-examination of *S. buchholzi* since that of Sars (1909) and the male has never been described from within the same geographic area (NW Europe) as the type locality (Haugesund on the west coast of Norway between Bergen and Stavanger). Willey (1929) briefly described the male P3 and P5 of specimens found in New Brunswick, Canada. However, there is absolutely no doubt that the specimens described above belong to the same species described by

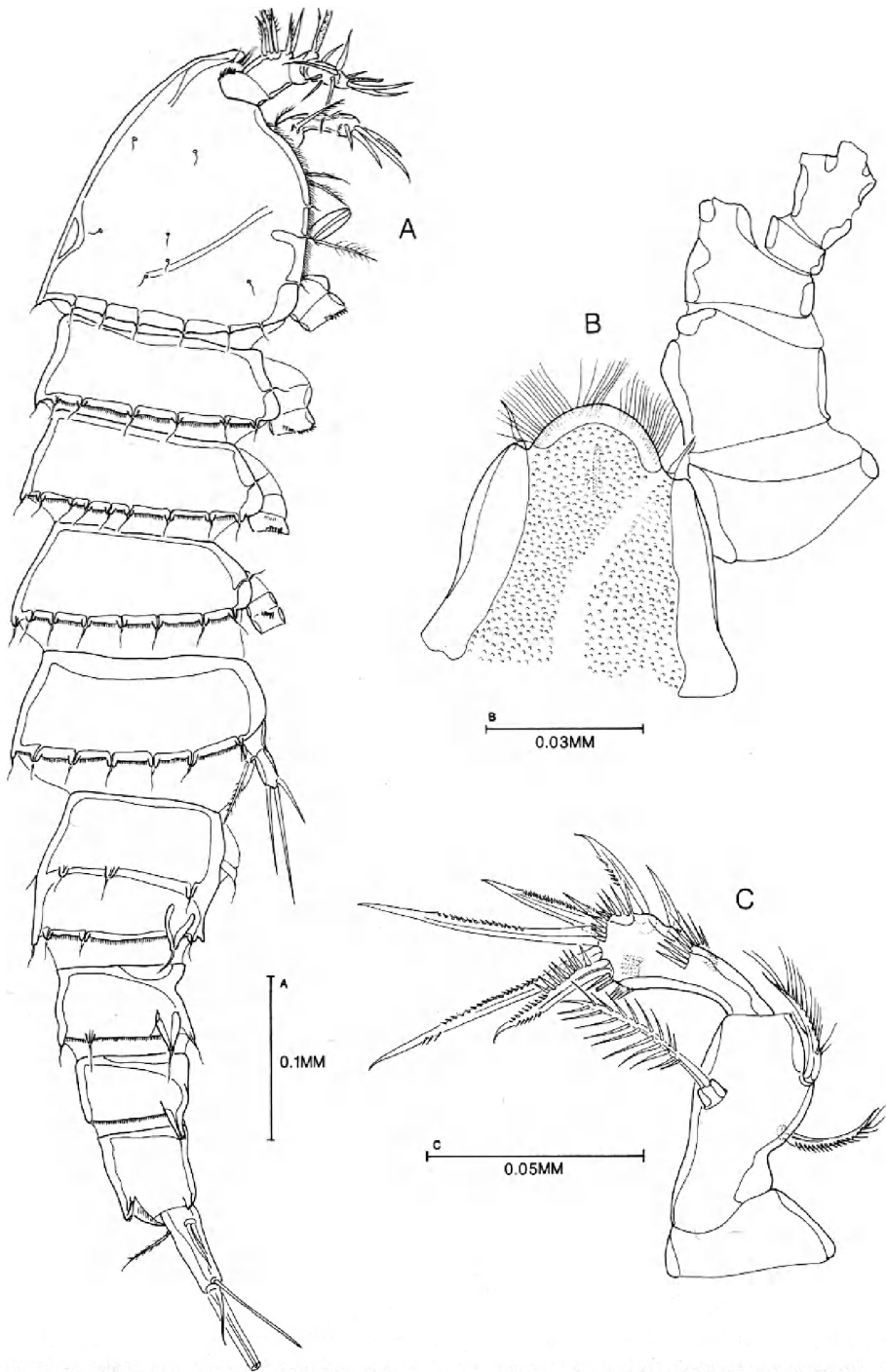


Fig. 1. *Strongylacron buchholzi* (BOECK, 1872) comb. nov. A. Female body, right lateral view. B. Rostrum and female right antennule [armature omitted], dorsal view. C. Left antenna.

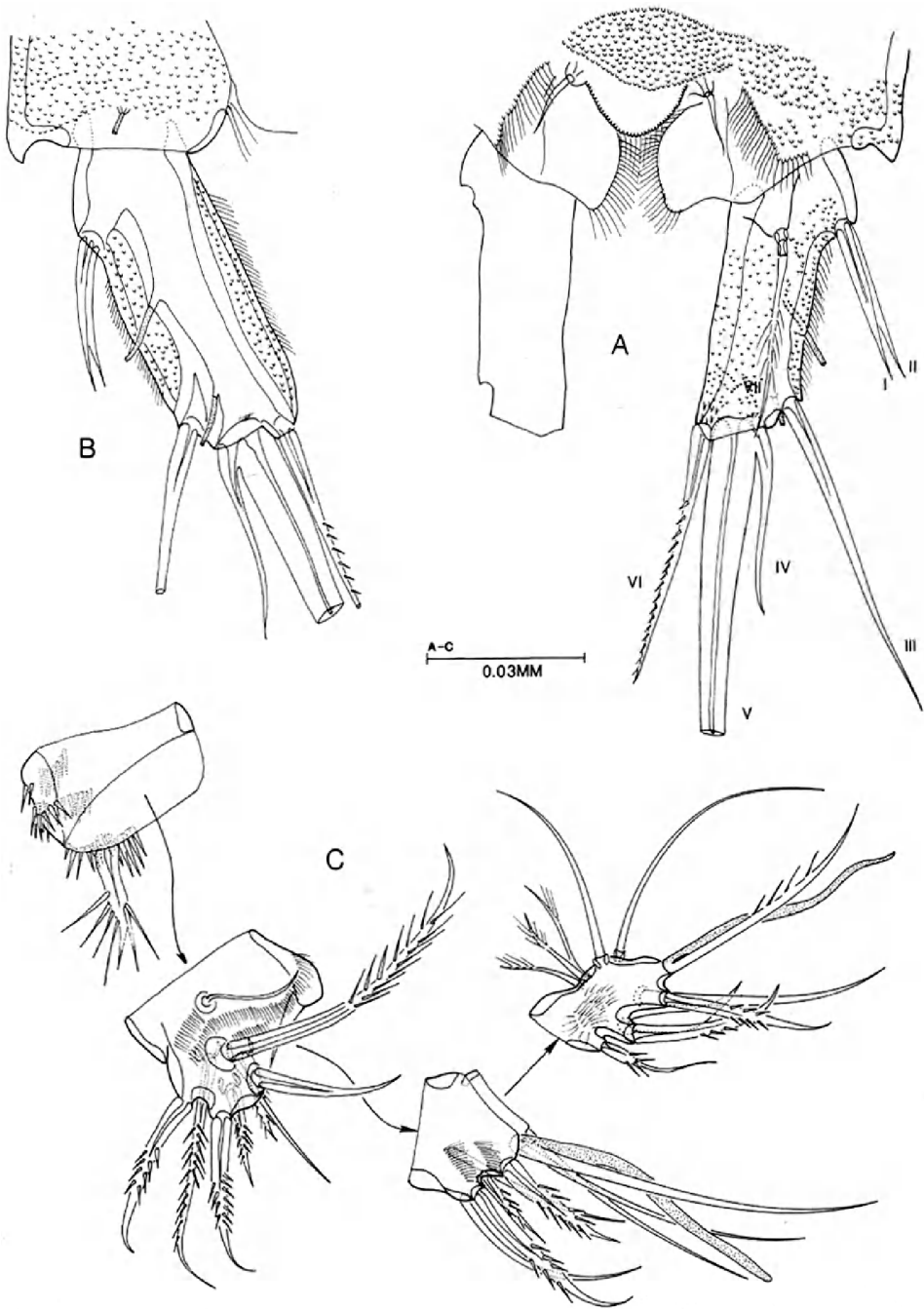


Fig. 2. *Strongylacron buchholzi* (BOECK, 1872) comb. nov. A. Female anal operculum and right caudal ramus, dorsal view. B. Male left caudal ramus, ventral view. C. Female left antennule, disarticulated.

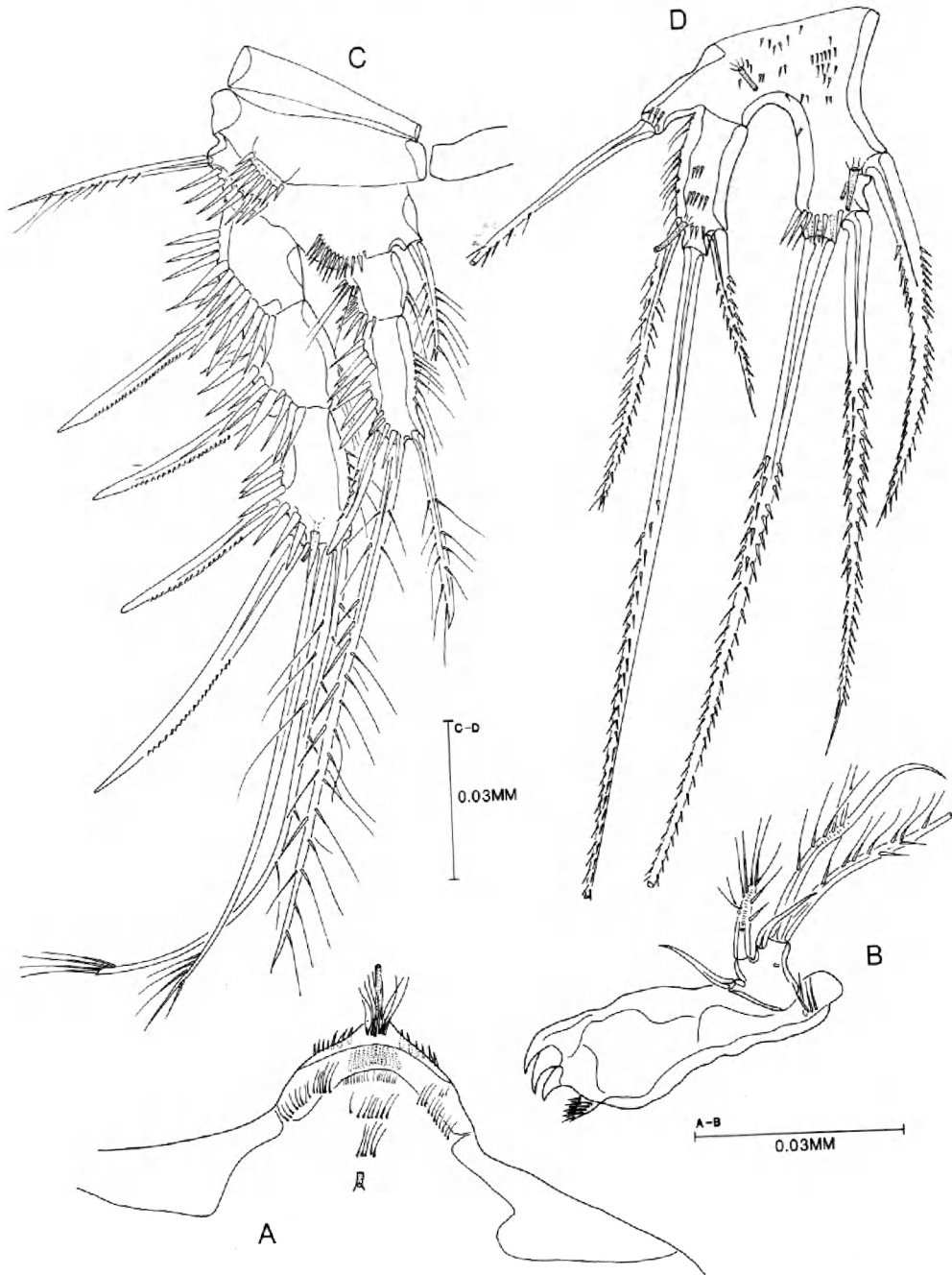


Fig. 3. *Strongylacron buchholzi* (BOECK, 1872) comb. nov. A. Labrum, ventral. B. Mandible. C. P1, anterior view. D. Female P5, anterior view.

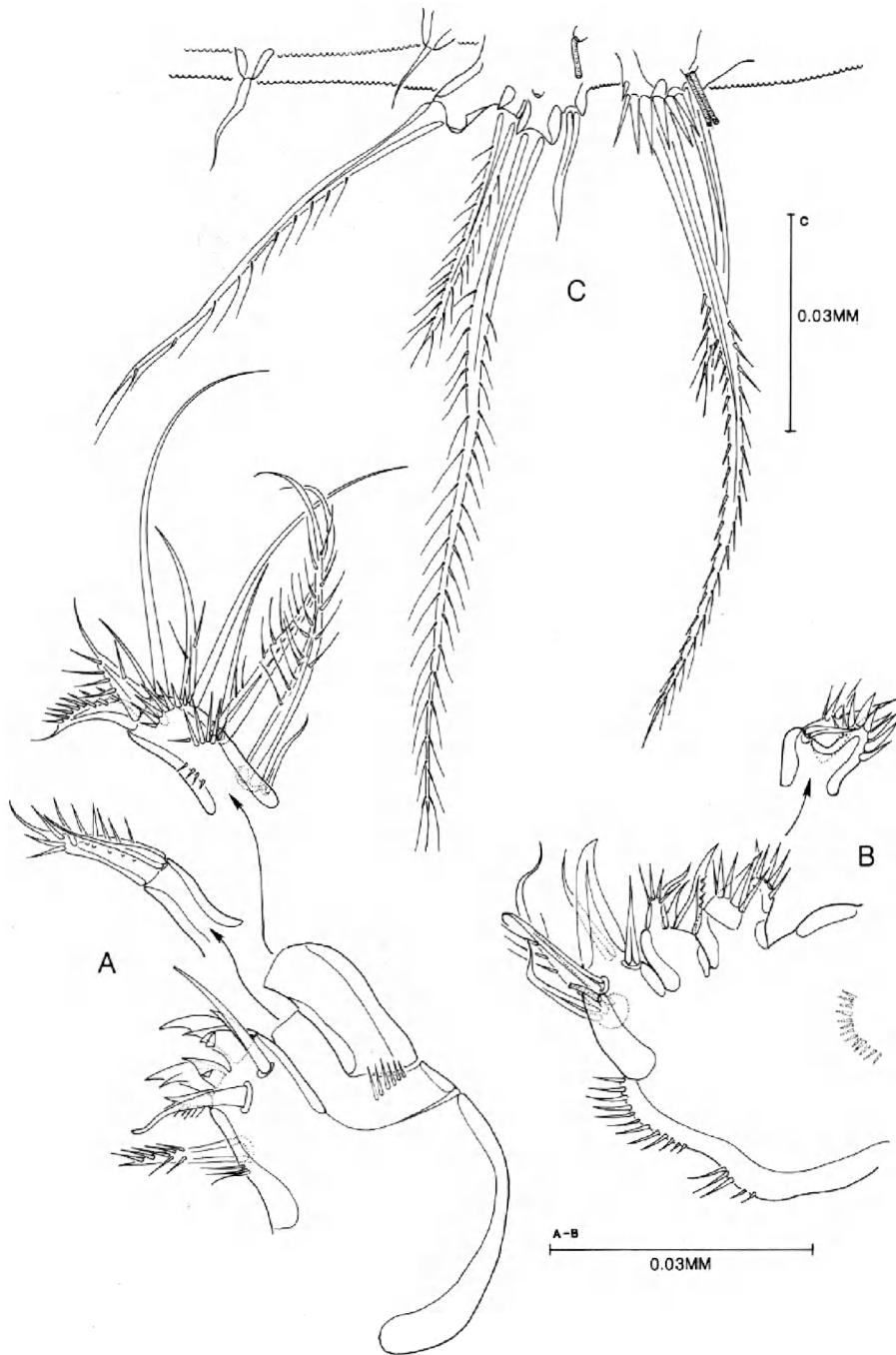


Fig. 4. *Strongylacron buchholzi* (BOECK, 1872) comb. nov. A. Maxillule, with coxal and basal endites disarticulated. B. Maxilla, also showing inner syncoxal endite from opposite side. C. Male P5, anterior view.

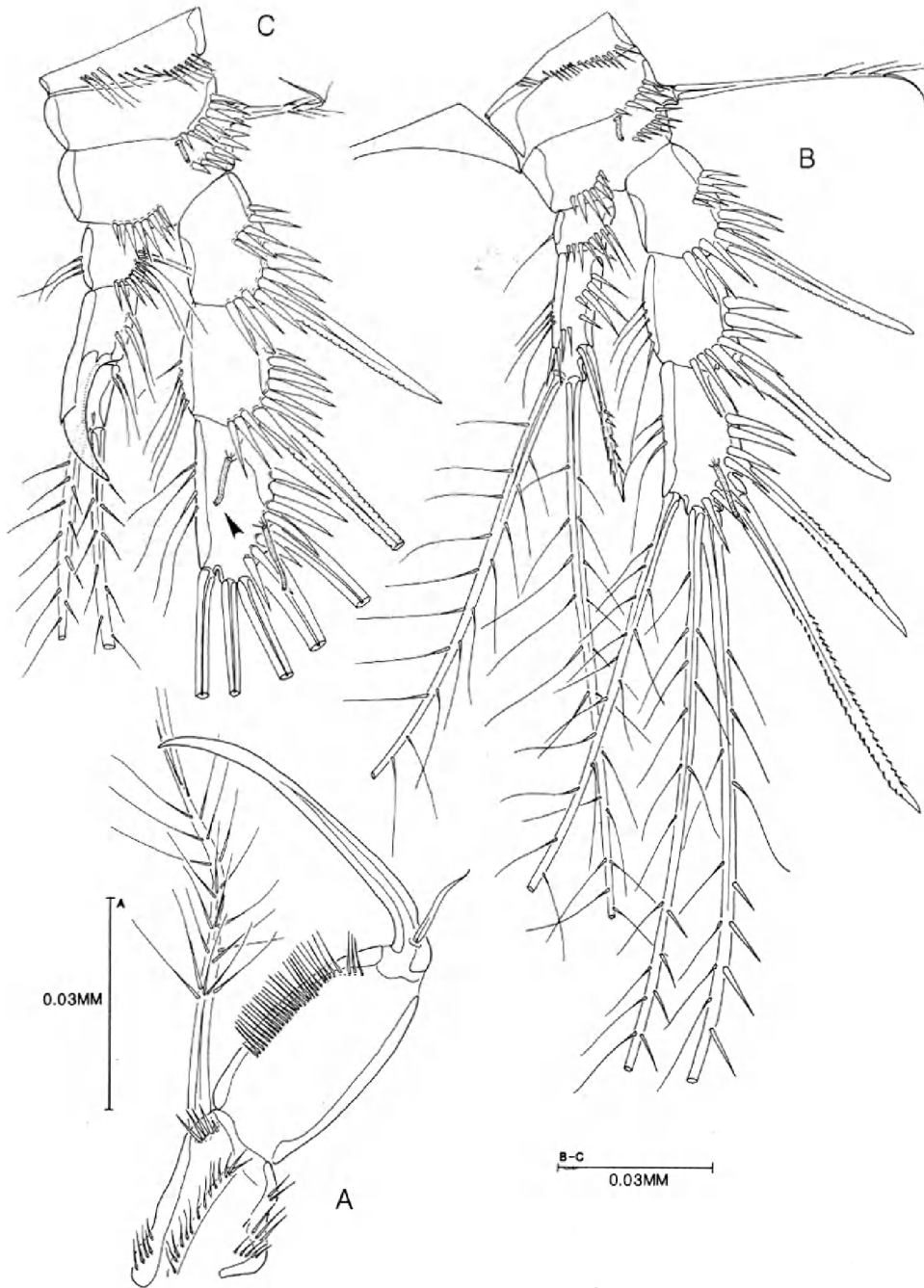


Fig. 5. *Strongylacron buchholzi* (BOECK, 1872) comb. nov. A. Left maxilliped. B. Female P3, setae cut off at half their full length, anterior view. C. Male P3, setae cut off arbitrarily [sexually dimorphic tube pore arrowed], anterior view.

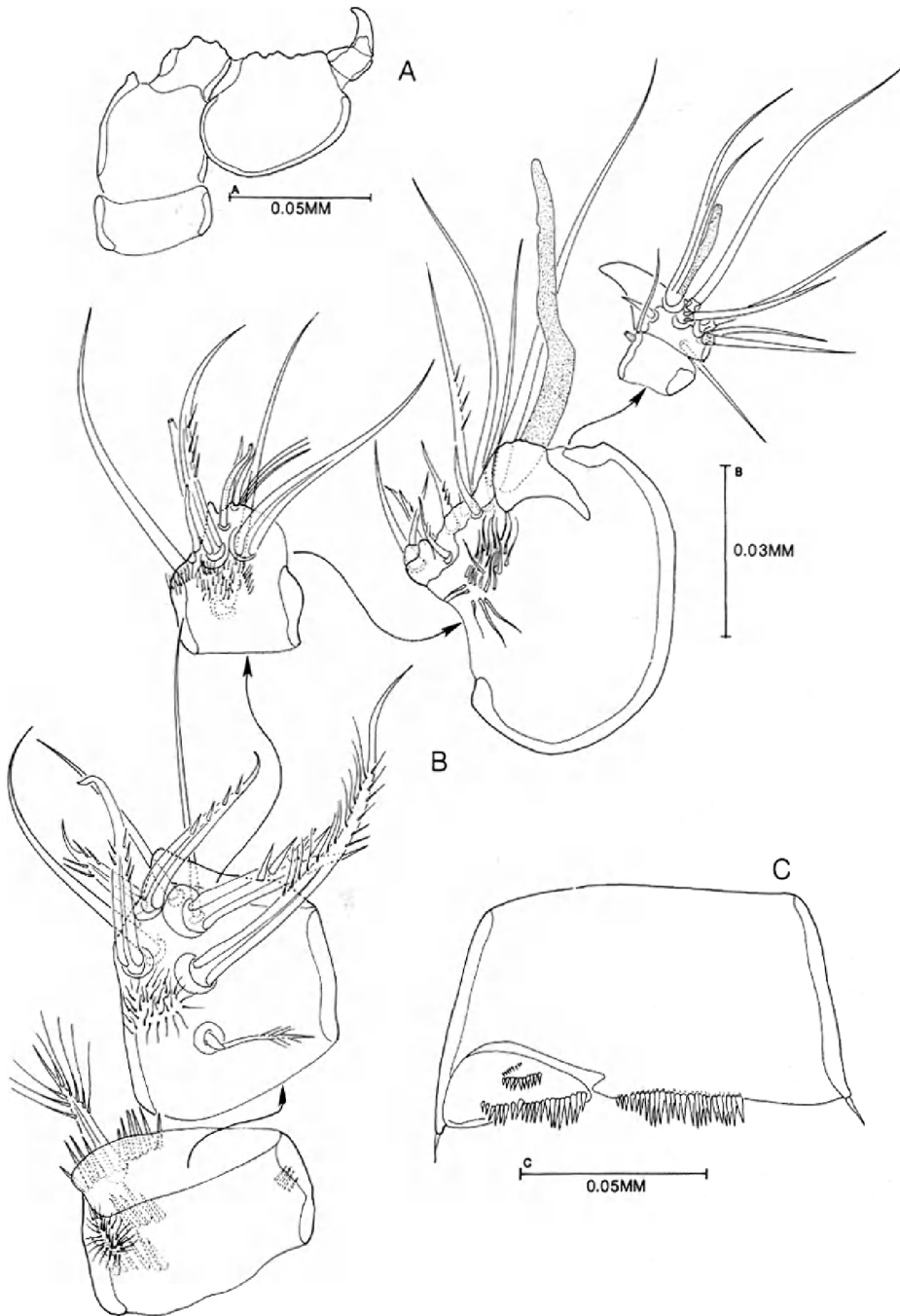


Fig. 6. *Strongylacron buchholzi* (Boeck, 1872) comb. nov. A. Male right antennule, outline of segments only. B. Male antennule, disarticulated. C. Male P6, ventral.

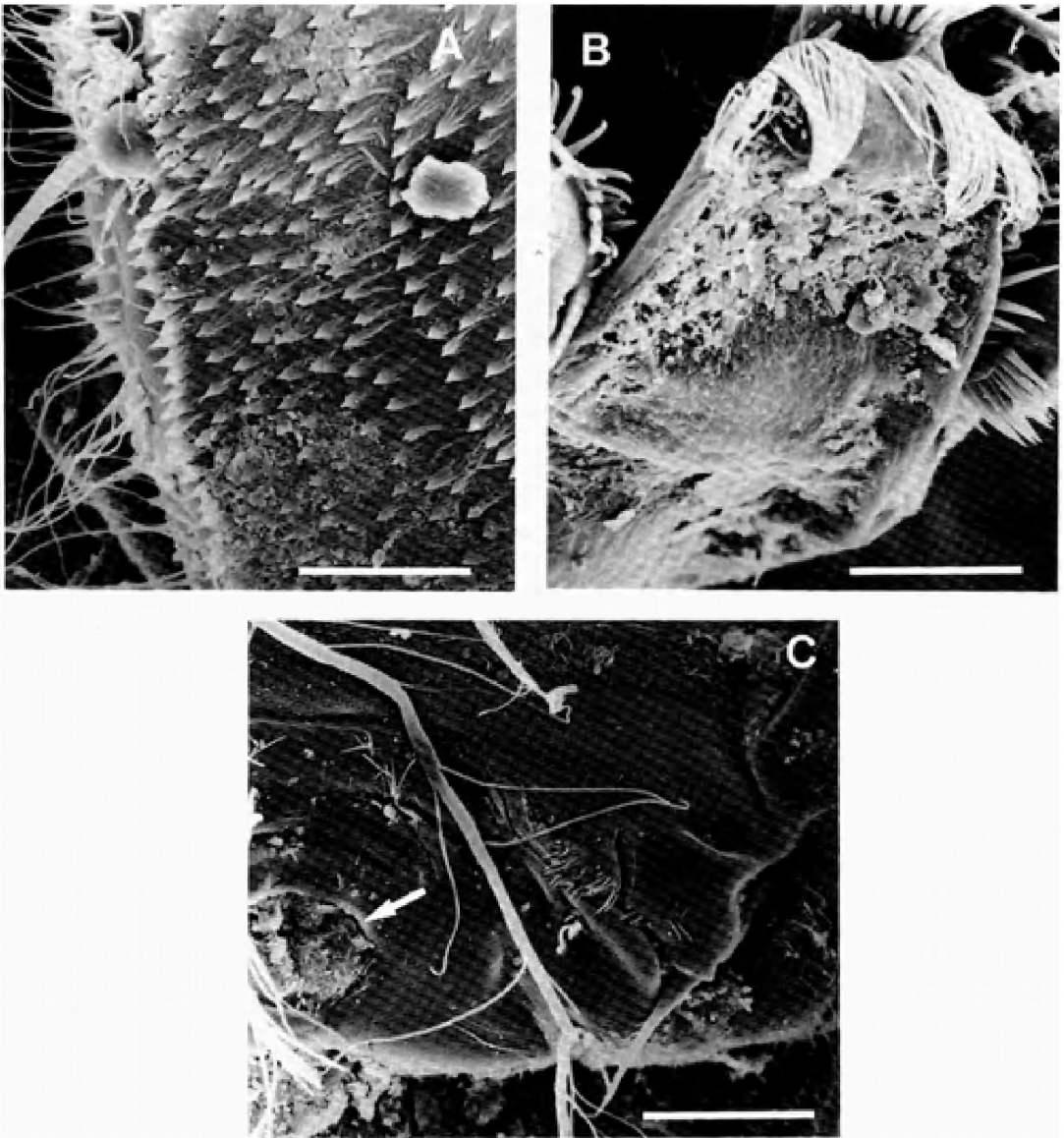


Fig. 7. *Strongylacron buchholzi* (BOECK, 1872) comb. nov. SEM micrographs. A. Portion of the posterior margin of a prosomite showing the denticulate nature of the cuticle and marginal setules. B. Rostrum, dorsal view showing the lateral ridges. C. Female genital field showing copulatory pore (arrowed) and the vestigial P6 with one seta covering the gonopore. Scale bars: A = 7.5 μm , B-C = 15 μm .

SARS (1909) as *Cletodes buchholzi*. For its time, SARS' description is remarkably accurate and the main differences between that and the present study are found only in the fine structure of the cephalosomic appendages and the distribution of tube pores on the swimming legs and caudal rami.

Within Europe, *S. buchholzi* appears to have a restricted distribution. It has been recorded only from southern Scandinavia (BOECK 1872; SARS 1909; LANG 1936), the western Baltic (KLIE 1929; KUNZ 1935), the Isle of Anglesey, north Wales (GEDDES 1972), the east coast of Ireland (O'RIORDAN 1971), the south coast of England from East

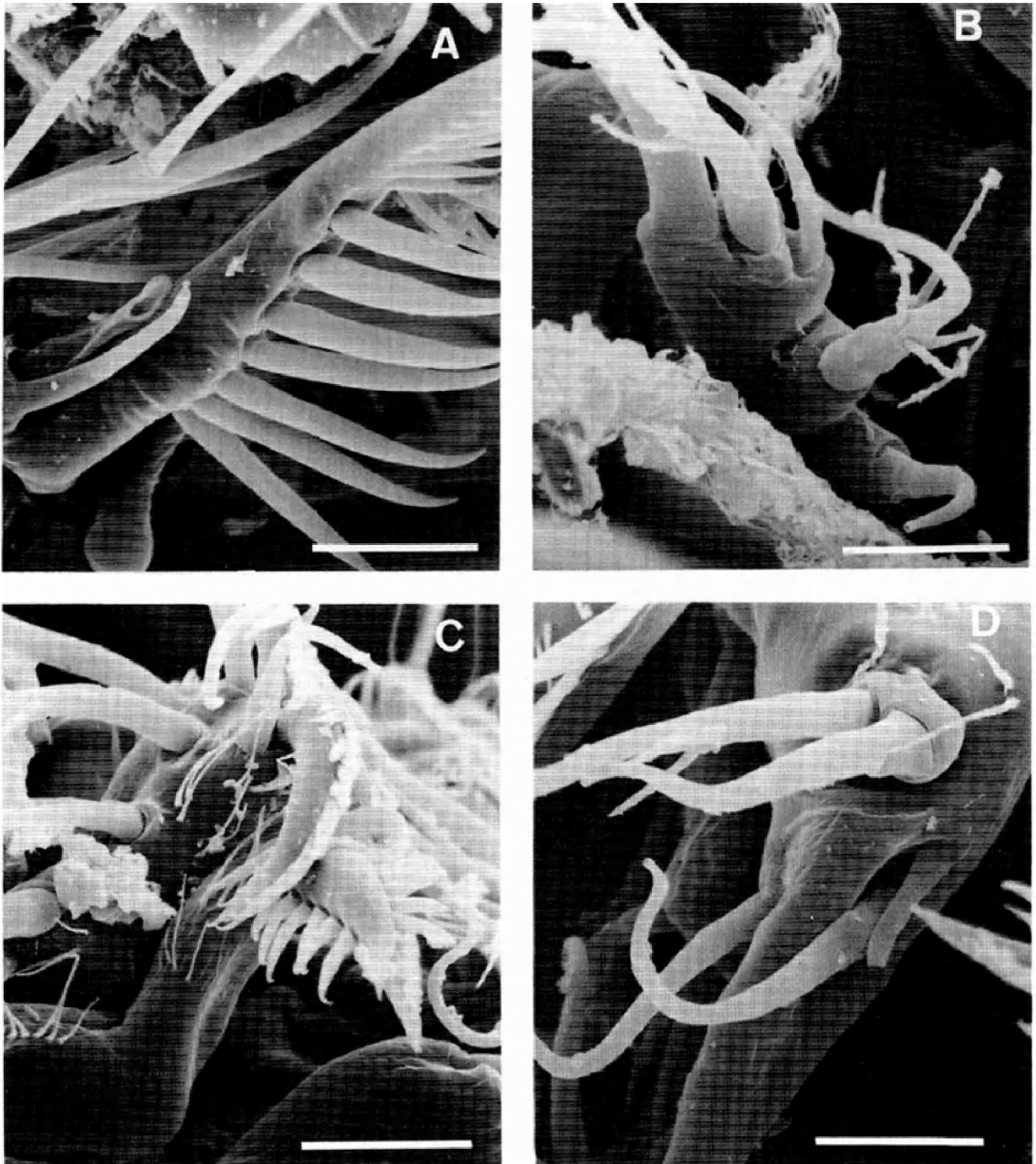


Fig. 8. *Strongylacron buchholzi* (BOECK, 1872) comb. nov. SEM micrographs. A. Antenna, showing the inner spine on the distal margin and the fused seta and tube pore at its base. B. Mandibular palp. C. Maxillule, coxal and basal endites. D. Maxilla, allobasal endite and endopod. Scale bars: 4.3 μ m.

Anglia to Cornwall (EL MAGHRABY & PERKINS 1956; WELLS 1963; BARNETT 1968; WARWICK & GEE 1984; present paper), and on the west coast of France at La Rochelle (BODIN 1971, 1972). As far as we know, it has not been recorded

from the Norwegian west coast north of the type locality, or northern Britain and does not appear to occur in the Mediterranean. In any one locality the species is rather rare, very few specimens being recorded from any one sample.

It occurs from the intertidal down to about 20 m, in mud or muddy sand sediments with high organic content, usually around the mouths of estuaries (although it appears intolerant of salinities much lower than about 25 ‰). Outside this area there are only two records of *S. buchholzi*, both from North America. WILLEY (1929) recorded two specimens from St. Andrews, New Brunswick on intertidal mudflats in the Bay of Fundy. COULL (1971) recorded one female from 30 m depth in muddy sand off Beaufort, North Carolina but this record must be regarded as doubtful (B.C. Coull pers. commn).

Genus *Schizacron* gen. nov.

Enhydrosoma BOECK, 1872 (partim); SHEN & TAI (1965), WELLS (1967), FIERS (1987).

Diagnosis. Cletodidae. Body semi-cylindrical, without clear distinction between prosome and urosome, heavily chitinized, without subcuticular ridges but surface covered with minute tubercles; somites other than preanal and anal somite with large, sensillum-bearing, socles on posterior margin. Female genital field with separate gonopores each covered by vestigial P6 with one seta. Anal somite partially divided, bearing well developed operculum with a smooth posterior margin. Caudal rami more or less cylindrical, two to three (female) or three to five (male) times longer than wide, with two tube pores on lateral outer margin; setae I, II and VII implanted in proximal fifth of ramus, seta III implanted at distal outer margin.

Rostrum not defined at base, strongly developed and recurved dorsally, markedly bifid anteriorly between pair of sensilla. Antennule short, stout, 5-segmented in female; in male indistinctly 7-segmented, subchirocer, with patch of spinules on segment 5. Antennary allobasis with two well developed pinnate setae on abexopodal margin; exopod a minute segment with one seta; endopod with two stout spines and a seta sub-distally on posterior face and distal margin with five non-geniculate spines, a small seta fused to base of inner spine and a tube pore. Anterior surface of labrum with a raised tuft of setules and one very long tube pore. Mandibular coxa robust, palp 1-segmented with four or five setae. Maxillulary arthrite of praecoxa with large pinnate seta on inner margin; coxal endite distinct with two elements, exopod and endopod completely incorporated in basis forming palp with ten elements. Maxilla with two syncoxal endites each with three elements; allobasal endite with a fused spine, three setae, and a tube pore; endopod represented by two setae not fused at base. Maxillipedal syncoxa with a large pinnate seta on outer distal margin; basis oval, twice as long as broad, no seta on palmar margin; endopod represented by a claw with one small accessory seta.

P1-P4 exopods 3-segmented, segments at most twice as long as broad, exp-3 with 4,4,5,5 setae/spines respectively; P1 exp-3 with posterior tube pore; P2-P4 exp-3 with tube pore at base of distal outer spine, and male P3 exp-3 with a tube pore near base of segment; endopods 2-segmented except P3 in male which is 3-segmented with recurved apophysis on enp-2 and two setae on enp-3. Female P5 distinctly U-shaped, with endopodal lobe reaching to distal margin of exopod, latter fused to baseoendopod; baseoendopod with a tube pore on outer surface; endopodal lobe with three well developed setae and two tube pores at base of proximal seta; exopod with three setae and a tube pore on distal margin. Male P5 baseoendopod incorporated in somitic cuticle (although basal tube pore present) with only tips of endopodal lobe, exopod, and basal peduncle in evidence at posterior margin of somite; endopodal lobe with two well developed setae and two tube pores near distal margin; exopod with surface (tube?) pore, and two or three setae, with only terminal seta well developed. Male P6 asymmetrical, unarmed.

Type species. *Schizacron barnishi* (WELLS, 1967) comb. nov.

Other species. *S. bifurcarostratus* (SHEN & TAI, 1965) comb. nov.; *S. vervoorti* (FIERS, 1987) comb. nov.; *S. intermedius* sp. nov.

Etymology. The generic name is derived from the Greek 'schizein', meaning to cleave, and 'akros', meaning tip, and refers to the bifid nature of the rostrum. Gender: masculine.

Schizacron barnishi (WELLS, 1967) comb. nov.

Enhydrosoma barnishi WELLS, 1967.

Material examined. Holotype female dissected onto 1 slide containing the P2, P3, P4, P5 and remaining urosome (NHM Reg. No. 1967.8.4.98); paratype female and male mounted *in toto* on slides (NHM Reg. Nos. 1967.8.4.99-100); paratype female preserved in spirit (subsequently dissected on 9 slides by R. Huys) (NHM Reg. No. 1967.8.4.101). All collected by Dr J.B.J. Wells from detritus sand plus grass at Saco on Inhaca Island, Lourenço Marques, Mozambique.

Female. Body (Fig. 9). Length 0.54 mm (paratype) to 0.67 mm (holotype), semi-cylindrical, tapering posteriorly, without clear distinction between prosome and urosome. Somites well defined, heavily chitinized, without subcuticular ridges but surface covered with minute tubercles. Cephalothorax, free prosomites and urosomites 1-4

with large socles on posterior margin each bearing a large lanceolate sensillum; ten on cephalothorax, 14 on free prosomites and first urosomite, eight on genital double-somite and six on urosomite-4. Genital double-somite with median dorsal subcuticular ridge with six socles. Penultimate and anal somite with two socles without sensilla. Anal somite (Fig. 10A) partially divided, dorsal surface with a small sensillum-bearing socle at either side of a well developed operculum with a smooth posterior margin and setules on its ventral surface.

Rostrum (Fig. 10B, C) not defined at base, very robust in lateral view, with strongly dorsally recurved, markedly bifid tip bearing a fringe of setules ventrally and laterally, a pair of trifid sensilla on dorsolateral margin and a tube pore medially on ventral surface.

Caudal rami (Fig. 10A) more or less rectangular, almost three times longer than maximum width and covered with fine setules on dorsal and lateral surface; slightly recurved proximally in the holotype (Fig. 10A) but this is an artefact caused by the mounting of the specimen, normal shape is as for the male (Fig. 13B). Lateral setae I-II and dorsal, triarticulate seta VII implanted in proximal fifth of ramus; bipinnate seta III implanted at distal outer margin; small seta IV fused at base to well developed seta V; seta VI unipinnate.

Genital field (Fig. 13A) with separate gonopores covered by vestigial P6s bearing one pinnate seta. Copulatory pore situated between gonopores with a single opening at the base of a depression leading to paired seminal ducts and small seminal receptacles. A double tube pore just posterior to each gonopore.

Antennule short, 5-segmented, as in *S. buchholzi*.

Antenna (Fig. 10D) as in *S. buchholzi*.

Mandible. Coxa robust but with minute gnathobase bearing one large and three small teeth and a pinnate seta (WELLS 1967). Palp (Fig. 11A) well developed, 1-segmented with four setae (one representing each of exopod and endopod and two on basis).

Maxillule (Fig. 11B). Praecoxal arthrite with nine elements: marginal teeth large (three spiniform, one rounded), other elements; three naked and two pinnate setae. Coxal endite with one naked and one bipinnate seta. Palp with total of ten elements: exopod represented by short seta and enlarged pinnate seta; endopod represented by two setae; remaining six elements (two pinnate, four naked setae) derived from basis.

Maxilla (Fig. 11C) as in *S. buchholzi* except that armature elements on syncoxal endites more slender.

Maxilliped (Fig. 11D) as in *S. buchholzi* except that syncoxa with only one small row of setules.

P1 (Fig. 12A). As in *S. buchholzi* except that inner terminal seta of enp-2 more than half as long as outer terminal seta.

P2-P4 (Fig. 12B-D). As in *S. buchholzi*. The tube pore on exp-3 is much more difficult to discern than in *S. buchholzi* but is present. Setal formula as follows:

	Exopod	Endopod
P1	0.0.022	0.021
P2	0.0.022	0.020
P3	0.0.122	0.021
P4	0.0.122	0.111

P5 (Fig. 10E). Distinctly U-shaped, with endopodal lobe as long as exopod and ornamented as in *S. buchholzi*. Endopodal lobe with three pectinate setae somewhat shorter than in *S. buchholzi*. Exopod completely fused to baseoendopod, with three setae, inner seta small and naked, outer seta small and weakly pinnate.

Male. As in female except in urosome (urosomites 2 and 3 not fused), antennule, P3, P5, and P6. The male paratype is a squashed whole mount but according to WELLS (1967) the body length and ornamentation is as for the female except for a possible reduction in the number of sensilla on the posterior border of urosomite-2.

Antennule indistinctly 7-segmented, subchirocer, similar to *S. buchholzi*.

P3 (Fig. 13C). Major features as in *S. buchholzi* including the presence of a small tooth on the outer margin of the recurved apophysis on enp-2. However, the presence of a sexually dimorphic tube pore on exp-3 could not be confirmed in the whole mounted paratype.

P5. (Fig. 13D). Baseoendopod absorbed into somatic cuticle with only the endopodal lobe, exopodal lobe, and baseoendopod outer peduncle projecting slightly from the posterior margin of the somite. The presence of tube pores could not be detected in the whole mount, otherwise endopodal lobe as in *S. buchholzi*. Exopodal lobe bearing only two setae, a long pinnate distal seta and a short naked outer seta.

P6 (Fig. 13E) a single asymmetrical plate, without setae but with rows of spinules.

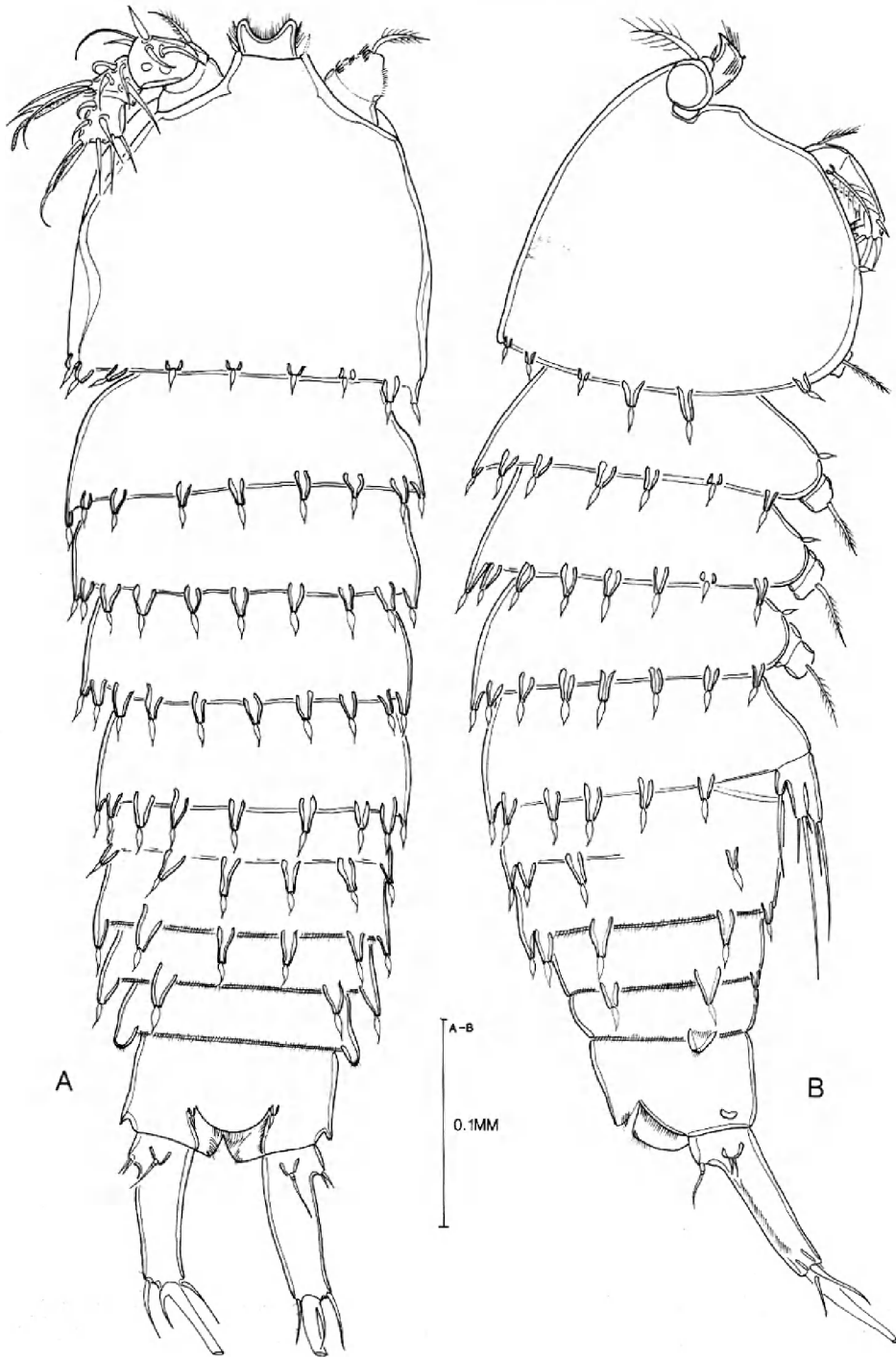


Fig. 9. *Schizacron barnishi* (WELLS, 1967) comb. nov. Female Body, A. Dorsal view. B. Right lateral view.

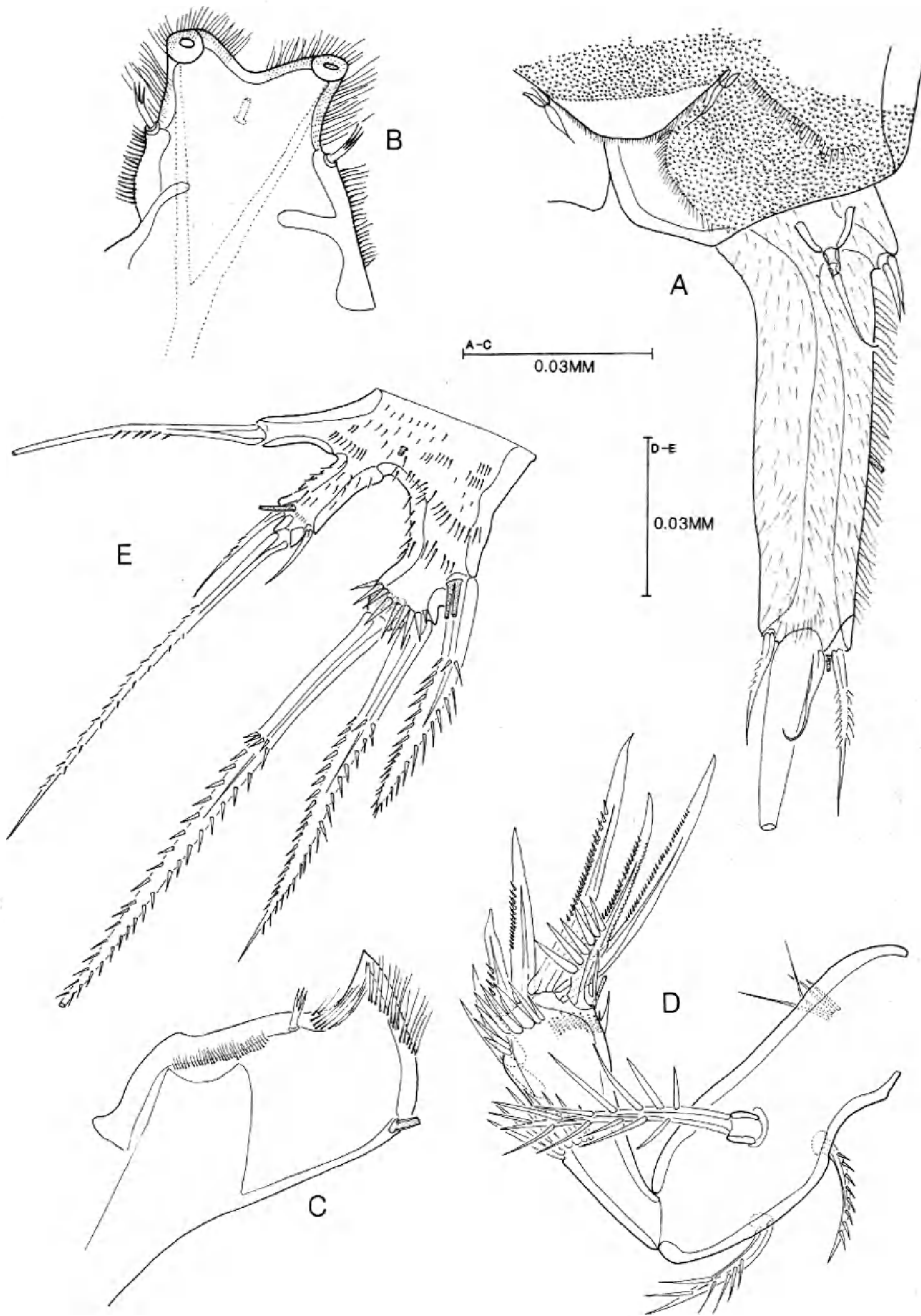


Fig. 10. *Schizacron barnishi* (WELLS, 1967) comb. nov. A. Female operculum and right caudal ramus, dorsal view. B. Rostrum, dorsal view. C. Rostrum, lateral view. D. Right antenna. E. Female P5, anterior view.

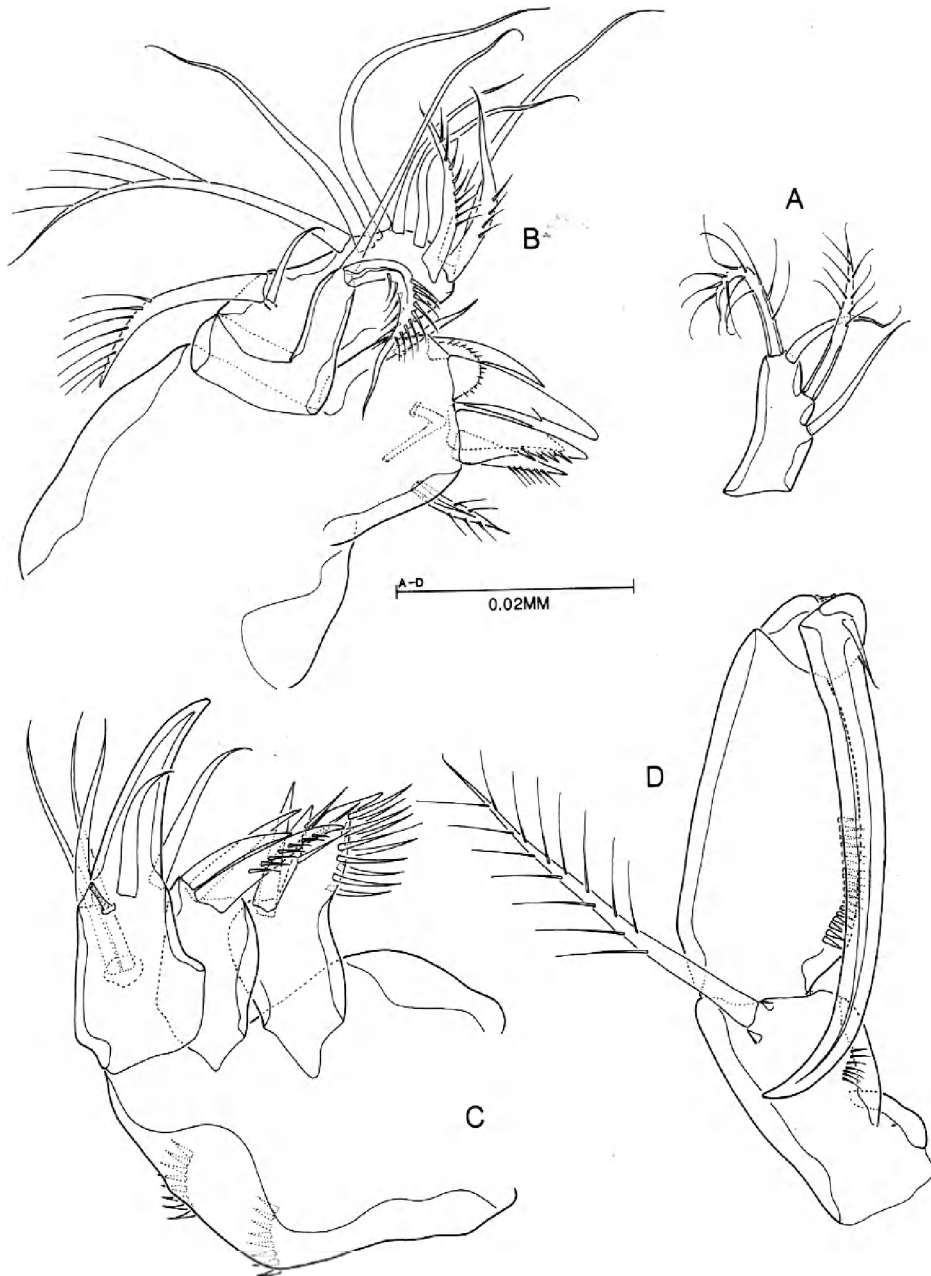


Fig. 11. *Schizacron barnishi* (WELLS, 1967) comb. nov. A. Mandibular palp. B. Maxillule. C. Maxilla. D. Maxilliped.

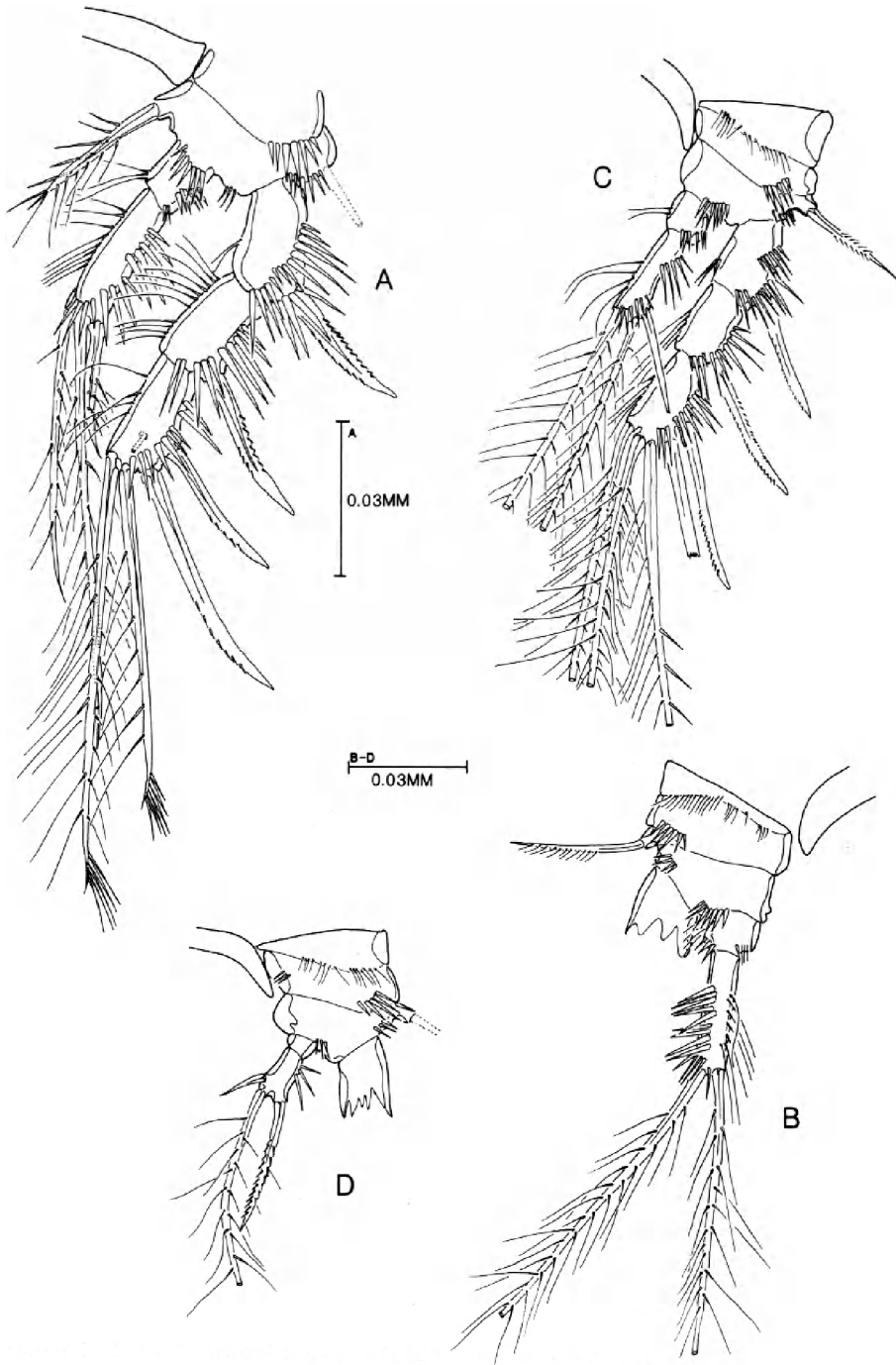


Fig. 12. *Schizacron barnishi* (WELLS, 1967) comb. nov. Anterior view of A. P1. B. P2 endopod. C. Female P3. D. P4 endopod.

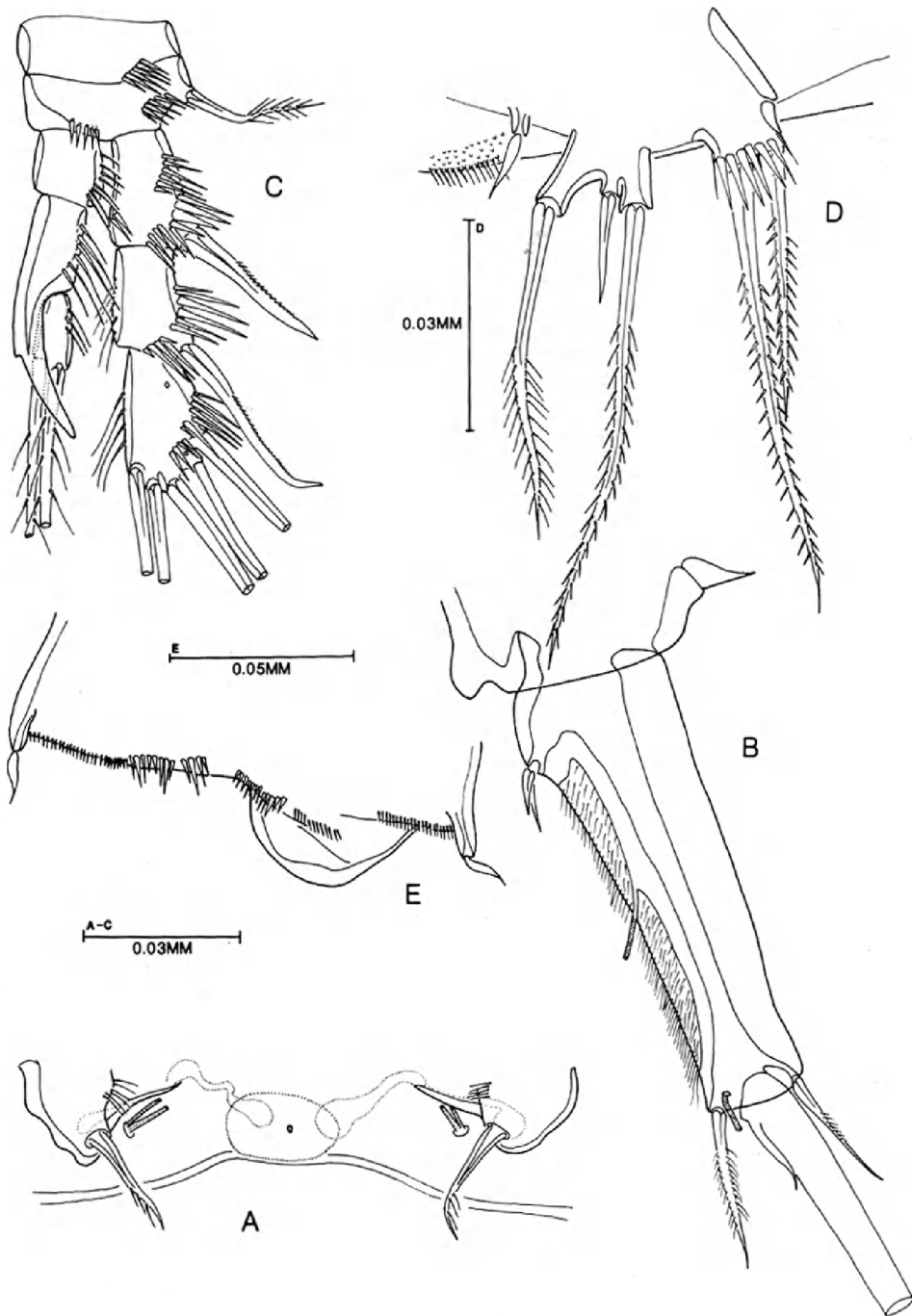


Fig. 13. *Schizacron barnishi* (WELLS, 1967) comb. nov. A. Female genital field. B. Male right caudal ramus, ventral view. C. Male P3, anterior view. D. Right male P5, anterior view. E. Male P6, ventral.

Schizacron vervoorti (FIERS, 1987) comb. nov.

Enhydrosoma vervoorti FIERS, 1987

Material examined. Holotype male mounted on 3 slides, Leiden Reg. No. RMNH Cop. 803a-c. Collected by Dr A. Choudhury, 1981, from Sagar Island, Hooghly River estuary, south of Calcutta, India. Fiers also deposited 1 male paratype preserved in spirit (Reg. No. RMNH Cop. 803), however, upon scrutinous inspection the vial supposed to contain this specimen proved empty.

Female. Unknown.

Male. The following description is confined to those characters which were either not covered or require re-interpretation from that given in the description of FIERS (1987).

Rostrum (Fig. 14A) large, strongly developed; distinctly recurved dorsally and deeply bifid apically; with two sensilla implanted dorsolaterally, one median tube pore ventrally, and tiny spinules anteriorly at frontal surface.

Antennule indistinctly 7-segmented as in *S. intermedius* sp. nov. (see below).

Antenna (Fig. 14B). Abexopodal margin of allobasis with unipinnate seta proximally, and setulose spine surrounded by long setules distally. Exopod represented by minute segment bearing strong setulose spine. Endopod with row of very long spinules halfway along the segment and row of smaller coarse spinules near distal margin; lateral armature consisting of two pinnate spines and one small seta (positioned between distal lateral spine and coarse spinule row); distal armature consisting of five non-geniculate spines, the outermost one bearing long spinules in proximal third, provided with tubular extension and fused at base to vestigial seta; a tube pore present at outer distal corner.

Mandible (Fig. 14C). Palp represented by short segment with two short naked, and two long pinnate, setae.

Maxillule (Fig. 15A). Palp with ten elements in total, all with tubular extensions; exopod represented by short naked and long pinnate seta; endopod represented by two long setae; basal armature consisting of four naked setae and two unipinnate spines.

Maxilla (Fig. 15B). Syncoxa with two bulbous endites along inner margin and two spinular rows along outer margin; proximal endite with one tube seta, one tube spine with large spinules and one stubby element fused to endite and provided with long spinules; distal endite with one tube seta, one pinnate spine and one tube spine fused to endite and provided with few long spinules. Allobasis represented by short claw-like endite; additional armature consisting of four tube setae (two probably representing endopod), one tube pore and one unipinnate spine.

Maxilliped as in Fig. 15C.

Swimming legs. P1 (Fig. 14D). Basis with plumose outer seta and pinnate inner spine. Exp-3 with posterior tube pore near distal margin; armature consisting of proximal bipinnate spine, distal scarcely pinnate spine and two plumose setae apically provided with strong spinules along outer subdistal margin. Enp-2 with outer spine being distinctly longer than segment. P2 exp-3 (Fig. 14E) with anterior secretory tube pore located between proximal and distal outer spines. P3 (Fig. 15D) exp-3 with two secretory tube pores on anterior surface. Apophysis on enp-2 minutely dentate along outer margin. P4 endopod (Fig. 14F) with enp-2 about five times as long as enp-1.

P5 (Fig. 15E) completely fused to and largely integrated in somite. Endopodal lobe short but discrete; with double tube pore, four large spinules and two setae (outer one longest and pinnate, inner one short and bare). Exopodal lobe with tube pore and three setae (outer one uniplumose, middle one very long and pinnate, inner one short and bare). Basal setophore large and swollen, bearing enlarged outer seta.

Caudal ramus (Fig. 15F) long and slender, about 3.7 times as long as maximum width (measured at proximal margin), about eight times as long as width measured halfway the ramus; covered with minute spinules. Setae I-II closely set and spiniform; seta III pinnate; setae IV and V fused, V strongly developed and minutely denticulate, IV naked; seta VI distinct and naked; seta VII tri-articulate at base and located anteriorly near setae I-II. Ventral surface with two secretory tube pores; posterior margin with row of fine spinules.

Fig. 14. *Schizacron vervoorti* (FIERS, 1987) comb. nov. Male. A. Rostrum, left lateral view. B. Right antenna. C. Mandibular palp. D. P1, anterior view. E. P2 exp-3, anterior view. F. P4 endopod, anterior view. →





Schizacron intermedius sp. nov.

Material examined. Holotype male (dissected onto 5 slides) collected from muddy sediment in the Ranong mangrove forest, western Thailand by Dr C. Aryuthaka, NHM reg. no. 1996.18. Paratypes: 1 adult male and 1 copepodid V male, preserved in spirit, collected from the same place as the holotype, NHM reg. no. 1996.19-20.

Male. As in generic diagnosis except for following features.

Body (Fig. 16A) length 0.451 mm. Pair of dorsolateral, sensillum-bearing socles on free prosomites and anterior four urosomites very well developed, others small; total of 14 on cephalothorax, 12 on free prosomites, ten on urosomite-1, eight on urosomites 2-3, six on urosomite-4, urosomites 5-6 with two small, lateral socles without sensilla. Cuticle more or less covered with minute tubercles; prosomites and anterior urosomites with two or three rows of slightly larger denticles (Fig. 16C). Male P6 ornamented as in Fig. 16C. Caudal rami (Fig. 16B) four times longer than wide with a row of minute setules ventrally on distal margin.

Rostrum (Figs 16A; 17A, D) strongly developed, dorsally recurved, and widely bifid distally (T-shaped); with two short sensilla laterally and long tube pore midventrally; branches with ventral patch of fine spinules.

Antennule (Fig. 17A-C, E) indistinctly 7-segmented, subchirocer; geniculation between segments 5 and 6. Segment 1 surrounded at base by large membranous area (Fig. 17D-E) and well developed sclerite (Fig. 17A); with several spinular rows as in Fig. 17A-B; with one spinulose spine at anterior distal corner. Segment 2 with four rows of fine setules (Fig. 17B) and nine armature elements (Fig. 17A-B): three pinnate spines, four naked tube setae, one large bi-articulate pinnate seta and one short plumose seta located in circular cup (Fig. 17E). Segment 3 with eight tube setae. Segment 4 minute, represented by small sclerite with two short setae and spinule row. Segment 5 with spinular patch on dorsal surface; armature consisting of 12 unmodified setae (one of which fused to large aesthetasc) and two modified elements (one rosetta-like, one spiniform with ridges). Segment 6 with one minute spinule-like element and one seta. Distal segment hook-shaped, with aesthetasc fused basally to two setae, five plumose and two naked setae.

Antenna, maxilla and maxilliped as in *S. vervoorti*.

Labrum (Fig. 18A) well developed, broad; with spinules around ventral distal margin; anterior face with two patches of fine spinules laterally, and a raised tuft of long setules and a very long tube pore medially.

Mandibular palp (Fig. 18B) short; armature consisting of two naked and three pinnate setae.

Maxillule (Fig. 18C-E). Praecoxal arthrite with nine elements: marginal teeth large and densely pinnate (two spiniform, one rounded), other elements four naked and two pinnate setae. Coxal endite with one slender seta and one pinnate spine. Palp with total of ten elements: exopod represented by short seta and enlarged pinnate seta; endopod represented by two setae; remaining six elements (one pinnate spine, one pinnate seta, four naked setae) derived from basis.

Swimming legs. P1 (Fig. 19A). Exp-3 with tube pore on posterior surface. Enp-2 with two setae and an outer spine; inner distal seta two-thirds length of outer distal seta. P3 (Fig. 19B) exp-3 apparently without tube pore at base of distal outer spine but dimorphic tube pore near base of segment present. Recurved apophysis on enp-2 without ornamentation. P4 endopod (Fig. 19C) only as long as exp-1, with three elements: one small, naked inner seta, one pinnate distal seta and one well developed outer naked seta. Setal formula as for *S. barnishi*.

P5 (Fig. 19D). Endopodal lobe clearly identifiable, projecting from posterior margin of somite with a row of setules near distal/outer margin and two tube pores on inner margin, bearing two strong, pinnate setae. Exopod with long tube issuing from pore; three elements on distal margin: a short naked inner seta, a short weakly pinnate outer seta and a well developed, naked, terminal seta.

Remarks. *S. barnishi* has never been recorded since its discovery on Inhaca Island, Mozambique. It is in the appendages of the cephalothorax, the P3, P5 and the distribution of tube pores that the above description of *S. barnishi* differs from, or supplements, that of WELLS (1967). The interpretation of the structure of the rostrum by WELLS (1967), as truncated distally with a bifid chitinous shelf beneath, is erroneous, probably caused by distortion of the structure on mounting. The position of the pair of sensilla and the ventral tube pore shows that the rostrum is a single, very strongly developed structure, unusually deep dorso-ventrally (Fig. 10C). The antennary exopod is represented by a small segment, not just a seta and there are six distal and three subdistal elements on the endopod. The structure of the praecoxal arthrite of the maxillule is not as illustrated by WELLS (1967) and there are ten elements (not eight) on the basis. The maxilla has the usual three elements (not two) on the syncoxal endites and the allobasal endite has three setae in addition to the two representing

← Fig. 15. *Schizacron vervoorti* (FIERS, 1987) comb. nov. Male. A. Maxillulary palp. B. Maxilla (elements of distal syncoxal endite cut, shown in B'). C. Right maxilliped. D. P3, anterior view. E. P5, anterior view. F. Right caudal ramus, ventral view.

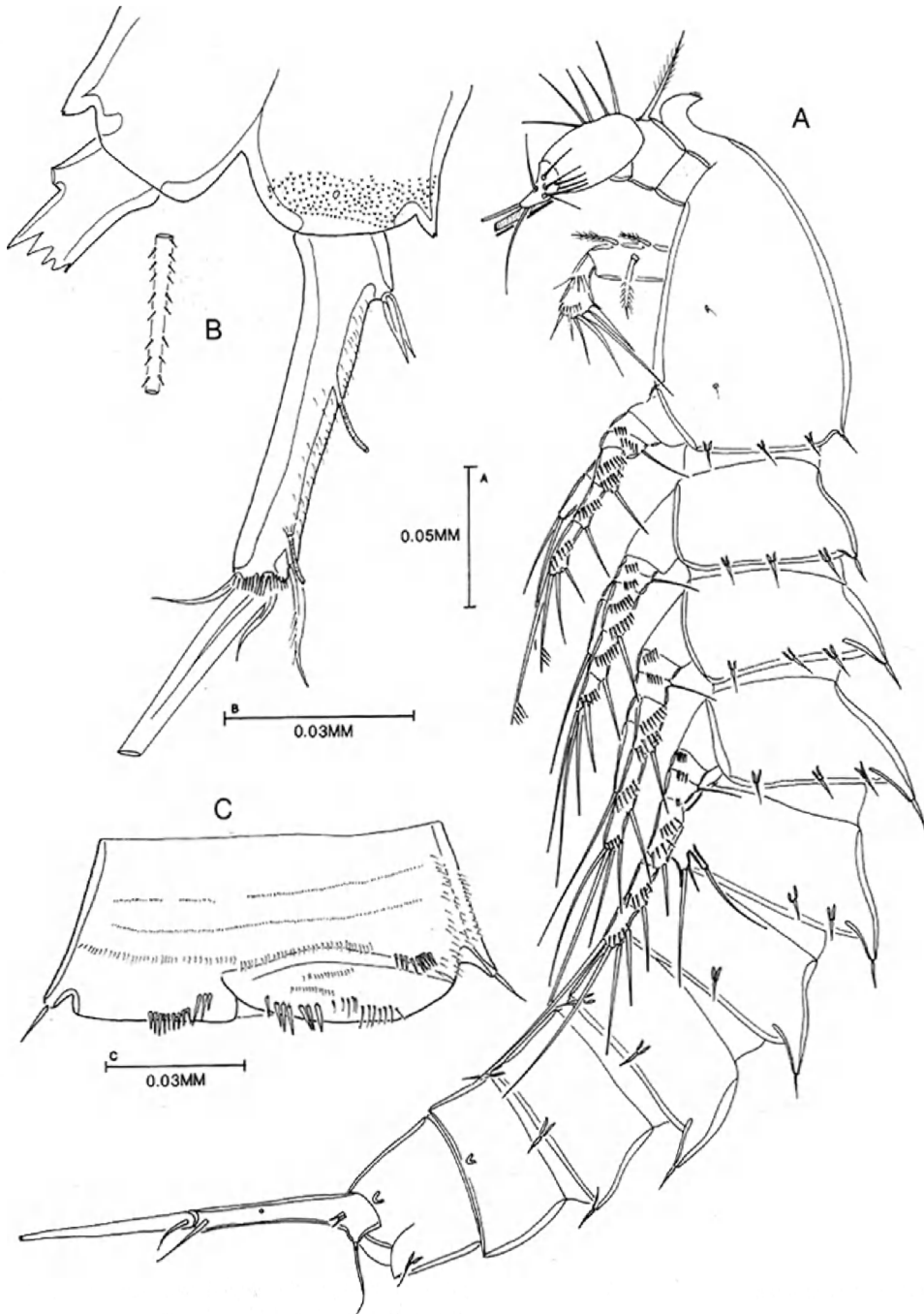
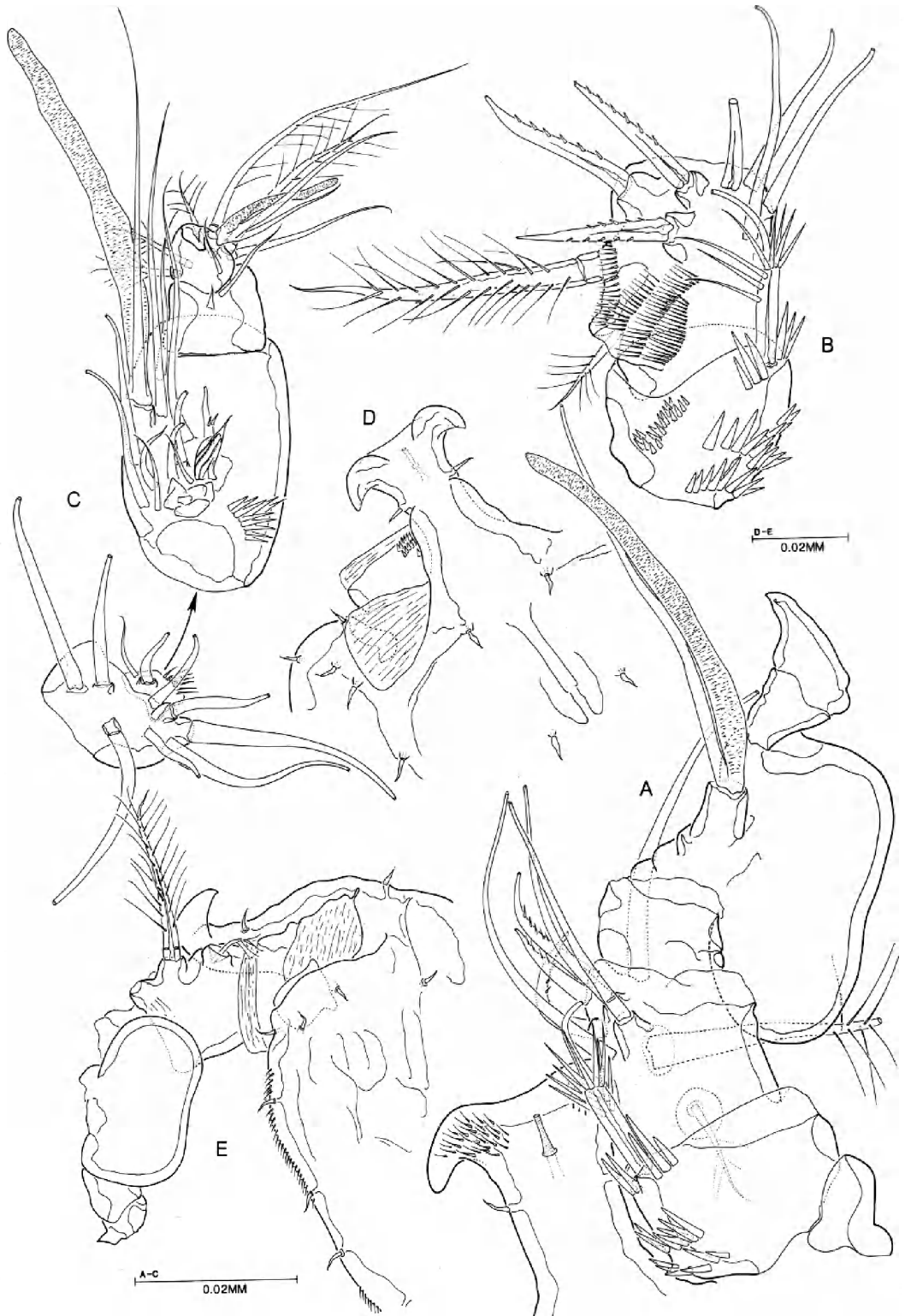


Fig. 16. *Schizacron intermedius* sp. nov. Male. A. Body, left lateral view. B. Left caudal ramus, ventral view. C. Genital somite, ventral view.

Fig. 17. *Schizacron intermedius* sp. nov. Male. A. Rostrum and left antennule, ventral view [armature elements of segments 2-7 omitted]. B. Antennular segments 1-2, anterior view. C. Antennular segments 3-7, anterior view [disarticulated between segments 4 and 5]. D. Rostrum, dorsal view. E. Anterior part of cephalothorax showing rostrum and antennule [armature omitted], lateral view. →



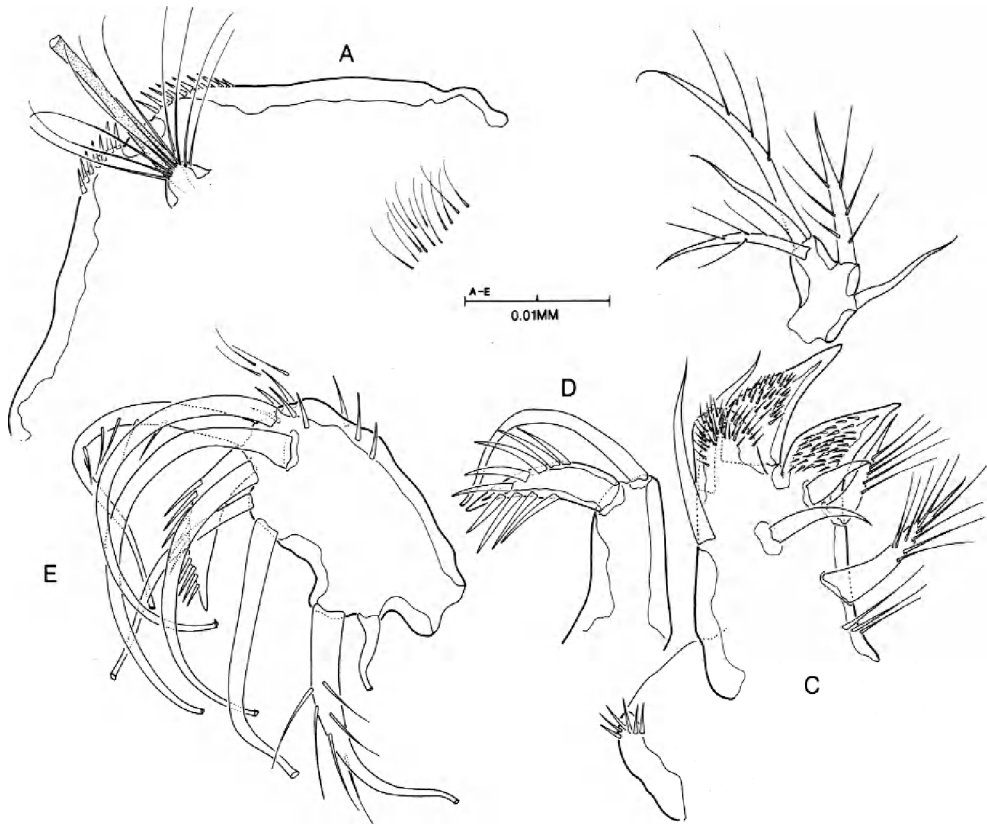


Fig. 18. *Schizacron intermedius* sp. nov. Male. A. Labrum, anterior view. B. Mandibular palp. C. Maxillary praecoxa with arthritis. D. Maxillule, coxal endite. E. Maxillule, palp.

the endopod. Further, there is no inner seta on enp-1 of P2-P3 as described and figured by WELLS (1967). The presence of these setae was always suspect as no other ctenophore, except *Barbaracletodes carola* BECKER, NOODT & SCHRIEVER, 1979 (and this genus must be regarded as *incertae sedis* in the Ctenophoridae), has a seta on enp-1 of the swimming legs. WELLS' (1967) interpretation of the structure of the male P5, with a normally developed baseoendopod as in the female, is also erroneous and the P5 basis is absorbed in the somatic cuticle as in the other species in this group. *S. barnishi* can be distinguished from other *Schizacron* species by (1) the regular size of the socles and the very lanceolate form of the sensilla on the posterior margin of the somites, and (2) the presence of only two setae on the male P5 exopod.

S. bifurcarostratus is unique within this genus in that the P4 endopod only has two setae, and from the figure and setal formula given in SHEN & TAI (1965) and SHEN (1979) it is the larger, outer seta, rather than the small in-

ner seta, which is lost. The presence of only two setae on this ramus is unusual in species included in the genus *Enhydrosoma*. Prior to the paper of GEE (1994), this condition was found only in *E. baruchi* COULL, 1975, *E. longicauda* MARINOV & APOSTOLOV, 1983, and in the group of species removed to the genus *Kollerua* GEE, 1994. Although it is possible that one seta could have been lost during dissection, SHEN & TAI (1965) based their description on four specimens (two females and two males). It is unlikely that accidental loss of a seta would have occurred in all four specimens and so this condition must be regarded as genuine in *S. bifurcarostratus*. FIERS (1987) also noted that the inner distal seta on the P1 endopod of *S. bifurcarostratus* was unusually short compared to the other closely related species. There is no information on the mouthparts of this species and it has not been recorded since its discovery in the delta of the Pearl River in South China.

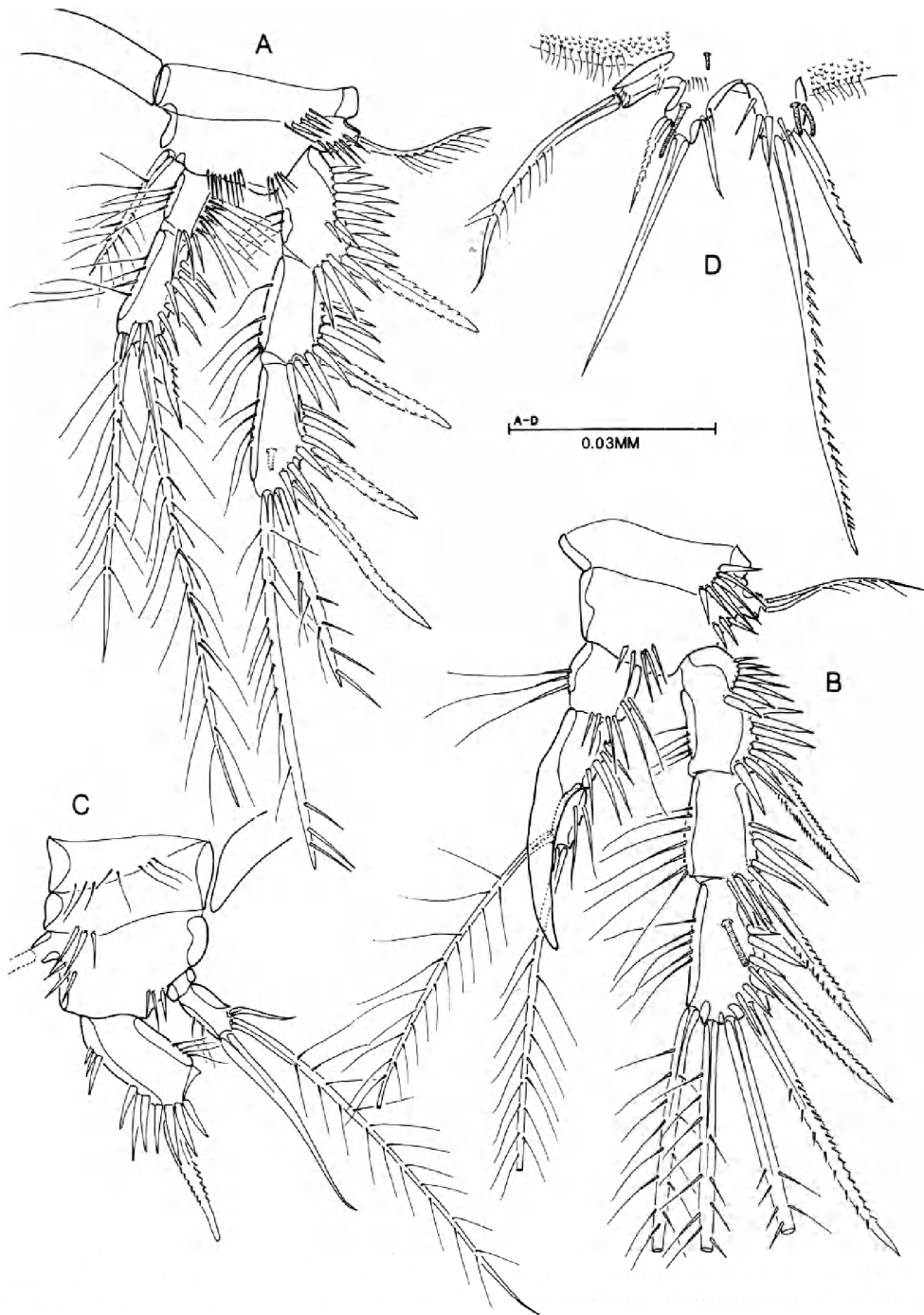


Fig. 19. *Schizacron intermedius* sp. nov. Male. Anterior view of A. P1. B. P3. C. P4 endopod. D. P5.

There are a number of unexpected features on the appendages of the cephalothorax of *S. vervoorti* as illustrated by FIERs (1987) which can all be attributed to inaccuracies in the original description: (1) the male antennule is indistinctly 7-segmented and subchirocer rather than 5-segmented and chirocer (cf. compare with *S. intermedius*); (2) the maxillary palp displays two pinnate and four naked elements around the distal margin, rather than three pinnate spines and two naked setae; (3) the maxillary allobasis has five elements in addition to the fused spine rather than four (i.e. the anterior pinnate spine was overlooked) and the elements on the proximal endite of the syncoxa are of a different form; (4) as pointed out already by HUYS & BOXSHALL (1991), the outer seta on the P1 protopod arises from the basis and not from the coxa as described and figured by FIERs (1987). However, according to the author, it is in the structure of the male P5 that *S. vervoorti* differs mostly from its congeners. In the original description the endopodal lobe of the P5 is not differentiated from the somite margin but its position is marked by the presence of three setae, having an additional small inner seta compared to the other species. Re-examination (Fig. 15E) proved this additional seta to be a strong spinule forming part of a spinular row found on the distal margin of the endopodal lobe in *Strongylacron* and other species of *Schizacron* [see Figs 4C; 13D; 19D; and SHEN & TAI (1965, fig. 56)]. Similarly, FIERs (1987) illustrates the P5 exopod with four setae whereas only three are present in the other species. Four (or five) setae on the male P5 exopod are found in *Stylicletodes* and some species of *Cletodes* but these numbers are very rare in species previously attributed to *Enhydrosoma*, being found only in *E. baruchi* and *E. stylicaudatus* WILLEY, 1935 (which FIERs 1996 has removed to the genus *Stylicletodes*). Re-examination showed that the supernumerary inner seta is in fact the dislodged distal half of the outer seta (which is illustrated as short but is in fact twice the size) which has floated during the mounting process to the inner margin of the exopodal lobe, thereby obscuring the double tube pore found in this position. *S. vervoorti* has not been recorded other than from the type locality in the estuary of the Hooghly River, Sagar Island, south of Calcutta (northeast India) and the females are unknown at present.

S. intermedius, recovered from the Ranong mangrove forest in western Thailand, is clearly more closely related to *S. bifurcarostratus* and *S. vervoorti* than to *S. barnishi* from the form of the socles on the body and a male P5 exopod with three setae. However, it cannot be allocated to either species. In the setation of the legs it is similar to *S. vervoorti* but in the structure of the male P5 it is similar to *S. bifurcarostratus*, assuming that SHEN & TAI (1965) mistook a setule on the endopodal lobe for a small seta. The shape of the rostrum is also similar to that illustrated for *S. bifurcarostratus*, with a wide-spread bifid tip giving

the rostrum almost a T-shape, as opposed to the Y-shaped bifid tip in *S. vervoorti*. Further, the proportions of the male caudal ramus are intermediate between *S. bifurcarostratus* and *S. vervoorti*. Finally *S. intermedius* is the only species in the genus that has retained five setae on the mandibular palp, a condition also found in *S. buchholzi*. It is for these reasons that the Thai material has been assigned to a new species.

KEY TO SPECIES OF *SCHIZACRON*.

1. Socles on posterior border of body somites more or less equal in size and bearing distinctly lanceolate sensilla. Male P5 exopod with two setae *S. barnishi* (WELLS, 1967)
- Dorso-lateral socles on prosomites and anterior urosomites much larger than others, sensilla only slightly lanceolate. Male P5 exopod with three setae 2
2. P4 endopod with two setae *S. bifurcarostratus* (SHEN & TAI, 1965)
- P4 endopod with three setae 3
3. Male rostrum distinctly Y-shaped at tip. Mandibular palp with four setae. P5 endopodal lobe minute, outer seta of exopod much longer than inner seta. Caudal ramus 7-8 times longer than broad *S. vervoorti* (FIERs, 1987)
- Male rostrum almost T-shaped. Mandibular palp with five setae. P5 endopodal lobe distinct, outer seta of exopod about as long as inner seta. Caudal ramus four times longer than broad *S. intermedius* sp. nov.

DISCUSSION

In a review of the characters of possible phylogenetic significance within the genus *Enhydrosoma*, GEE (1994) concluded that, apart from the structure of the P5, female genital field and male sexual dimorphism, the most important characters were to be found in the appendages of the cephalosome, particularly the antenna, mandible, maxillule and maxilla. Description and illustration of these appendages in most of the early, and not a few of the later, papers are either inaccurate or non-existent. Thus a re-examination of the structure of even well established species is an essential step in assessing their taxonomic status based on phylogenetic grounds. A detailed comparison of the above descriptions with that of the type species given in GEE (1994) leads to the conclusion that these species cannot be included in the same genus as *Enhydrosoma curticauda* and in many respects are more closely related to the genus *Cletodes*.

Firstly, this view is based on two robust apomorphies shared by the above species and *Cletodes*. (A) FIERs (1996) presented ample evidence that the primitive condition of

the antennary exopod within the Cletodidae is a broad segment bearing three setae (present in copepodid I of *E. lacunae*, in the adult of at least some species of *Acrenhydrosoma* and as a malformation in one specimen of *E. curticauda*). A broad segment bearing two well developed setae is the condition of this appendage in the adults of most cletodid genera. However, in all species of *Cletodes*, in *E. curvirostre* and the five species dealt with here, the antennary exopod is a small cylindrical segment bearing one seta; (B) The form of the sexual dimorphism found in the P3 endopod is distinctly different in *Cletodes*, *E. curvirostre* and the species described above, to that found in *E. curticauda*. In the latter species the male P3 endopod is as in the female (2-segmented with 021 elements) except that the outer spine is enlarged, fused to the somite and slightly differently ornamented. In the former group, the male P3 endopod is 3-segmented, enp-2 having a large apophysis at the outer/anterior distal margin and enp-3 with a maximum of two setae.

GEE (1994), in a preliminary discussion of the likely homology of the segmentation and armature of this ramus in the male, suggested that the 3-segmented condition was a secondary development from an originally 2-segmented ramus. FIERS (1996) however, argued that the 3-segmented condition of the male endopod in cletodids is the plesiomorphic condition and a 2-segmented endopod is apomorphic. He based this view on the fact that species with a 3-segmented endopod possess the most primitive chaetotaxy on the mouthparts and swimming legs and that whatever outgroup is chosen, in the study of character state transformation in cletodids, a 3-segmented endopod in the male is the norm. In our opinion, neither of these arguments is valid. Firstly, the display of primitive chaetotaxy does not preclude the possession of other, more advanced characters, viz. the structure of the antennary exopod which is the most advanced in the family. Secondly, it is well known (FERRARI 1993) that, in normal harpacticoid development, the distal segment is the *first* to develop and subsequent segments are normally added proximally. Therefore in taxa with a 2-segmented ramus it is the proximal segment which is missing. In the males of Cletodidae, Orthopsyllidae and Laophontidae there is ontogenetic evidence (FIERS 1991, 1996; HUYS 1990) to show that, in a 3-segmented endopod, the distal segment is the *last* to develop by the process of budding off (at some stage during development) of the portion of the second segment distal to the outer spine. Thus, the 3-segmented condition in the male P3 endopod in cletodids is *not* homologous to the 3-segmented ramus in most harpacticoid families but is a derived (apomorphic) state from an originally 2-segmented ramus (plesiomorphic). It should be noted however, that the absence of sexual dimorphism (i.e. only a 2-segmented endopod) in some species of *Cletodes* (and in *Monocletodes* LANG, 1936 and *Interkletodes* FIERS, 1987)

is the result of a secondary loss of sexual dimorphism and is not the plesiomorphic condition.

The homology (and therefore, phylogenetic significance) of the apophysis on male P3 enp-2 in cletodids however, is more difficult to determine. HUYS (1990) showed that, in Orthopsyllidae and other families of the Laophontoidea, such an apophysis is homologous to the outer spine of the distal endopod segment in the female and is *never* present in the male if it is absent in the female. In those species of cletodid where an outer spine is present on enp-2 of the female, the evidence suggests that it forms the outer element on enp-2 in a 2-segmented male endopod (e.g. *E. curticauda*) and, if not actually lost in the final moult, must at least be incorporated into the apophysis on enp-2 in a 3-segmented male endopod (e.g. *S. buchholzi*, *Cletodes macrura* FIERS, 1991). However, an apophysis is present in some cletodids with a 3-segmented endopod (e.g. *Cletodes tenuipes* T. SCOTT, 1896; *E. baruchi*) or a 2-segmented endopod [e.g. *Kolleria radakrishnai* (RANGA REDDY, 1977)] when, as far as we know, it is not present in any development stage. In these cases, the apophysis must be derived from an outgrowth of the segment cuticle. Thus the apophysis on male P3 enp-2 in the species dealt with here may, or may not, be homologous to the apophysis in *E. curticauda*. However, the 3-segmented condition of the ramus is certainly an apomorphy which would exclude *S. buchholzi* and associated species from the genus *Enhydrosoma*.

Secondly, *E. curticauda* exhibits a number of autapomorphies which are not shared by the species dealt with in this paper. (A) segment 4 of the male antennule bears a columnar pad which represents a modified armature element, whereas at approximately the same site a patch of long setules or spinules is found in species of *Schizacron* and *Strongylacron*; (B) although the rostrum of *E. curticauda* is distinctly bifid, the bifid structure is derived from processes formed *posterior* to the pair of rostral sensilla whereas in all other cletodids with a bifid rostrum the bifid structure arises *anterior* of the pair of sensilla; (C) there are no setae on the abexopodal margin of the antennary allobasis whereas the plesiomorphic condition within the family is two setae on the antennary allobasis; (D) in the present group of species and in *Cletodes* there are two spines and a seta subdistally on the antennary endopod. In *E. curticauda* and other species of *Enhydrosoma* the seta has been lost at this location; (E) the maxillary basis (in which the exopod and endopod are almost always incorporated forming a 1-segmented palp) primitively has a maximum of 11 setae (exopod, endopod and basal endites represented by 2, 2 and 7 elements, respectively). In the species dealt with above this number is reduced to ten (i.e. one basal seta being lost) but in *E. curticauda* (and other species presently allocated to the genus *Enhydrosoma*) there are, at most, six setae on

the basis (exopod, endopod and basal endites represented by 1, 1, and 4 setae, respectively); (F) primitively the allobasal endite of the maxilla bears a fused spine and three setae and the endopod is represented by two setae not fused at the base. In *E. curticauda* and other *Enhydrosoma* species there is a maximum of two setae and a fused spine in addition to the two setae representing the endopod which are fused at the base; (G) in *E. curticauda* the female genital apparatus has a common genital antrum (gonopores fused medially forming genital slit) whereas in the species described above the female gonopores are separate, which is generally regarded as the more primitive condition. However, *E. curticauda* also appears to be unique within the Cletodidae in having two setae on the vestigial sixth legs compared to at most one in all other cletodids; (H) it would appear that the two tube pores near the ventral outer margin of the caudal ramus (illustrated in Figs 2A; 10A; 15F; 16B) may be almost universal in cletodids but they have been lost in *E. curticauda*.

It is clear from the foregoing discussion that the species dealt with in this paper cannot be included in the genus *Enhydrosoma*. Apart from the fact that they have a more primitive setal formula on P3-P4 exp-3 than *Cletodes* these species also have at least two autapomorphies which exclude them from the latter: (A) The form of the distal elements on the antennary endopod. In all cletodids for which the condition has been verified the armature consists of two geniculate setae, three spines, a small seta fused to the base of the outer spine and a tube pore. In the species dealt with in this paper, the full complement of elements is present but the two geniculate setae are replaced by two pectinate non-geniculate spines; (B) The form of the P5 in both sexes of *Schizacron* and *Strongylacron* is unique within the Cletodidae, being distinctly U-shaped in the female (with the endopodal lobe of the baseopod and the exopod well separated and equal in length) and in the male the baseopod is completely absorbed into the somitic cuticle; (C) The markedly proximal insertion site for seta VII on the caudal ramus in these species (Fig. 2A), compared to the usual median position of this seta in *Cletodes* may also be an apomorphy for this group; (D) Similarly, the presence of a sexually dimorphic tube pore on P3 exp-3 in the male (Fig. 5C) may also be of significance. Such a tube-pore is not present in the male of *E. curticauda* but the condition in all other cletodids is unknown as these pores have not been reported, probably because they are not easy to see even under interference phase contrast illumination and are virtually invisible under normal bright field. GEE & FLEEGER (1990) have indicated that similar sexually dimorphic tube pores may have some significance in the phylogeny of the Diosaccidae.

Thus, it is evident that the species under consideration here, form a well defined group within the family Cletodidae. Within this monophyletic clade, *S. buchholzi*

clearly occupies an isolated and primitive position. It is clear that the rostrum of the latter (normally developed, rounded anterior margin, not dorsally recurved) is very different from that of the species allocated to *Schizacron* (powerfully developed, particularly in dorso-ventral thickness, strongly bifid and dorsally recurved - suggesting that it has a role in burrowing activity). Bifid rostra are relatively common in cletodids but the polarity and phylogenetic significance of these are not always clear. In this case, however, it is conceivable that the bifid rostrum is derived from the *buchholzi*-condition as is evidenced by the relative position of the ventral setular fringes, the lateral sensilla and the midventral tube pore. Added to this, is the biogeographic evidence of a wide separation in distribution of *S. buchholzi*, found only in the north Atlantic area in north-west Europe and Canada, and the remaining species which are all from the Indian and western Pacific Oceans.

ACKNOWLEDGEMENTS

The authors wish to thank Dr R. Hamond (Morston, Norfolk) and Prof. Dr W. Vervoort (Nationaal Natuurhistorisch Museum, Leiden) for the loan of type, and other material. We also acknowledge that the material from the Ranong mangrove forest was collected by Dr C. Aryuthaka (Kasetsart University, Bangkok) under the DoE Darwin Initiative for the Survival of Species project on Biodiversity in S.E. Asian Mangrove Ecosystems.

REFERENCES

- Barnett, P.R.O. 1968. Distribution and ecology of harpacticoid copepods of an intertidal mudflat. – *Internationale Revue der gesamten Hydrobiologie* 53:177-209.
- Bodin, P. 1971. Copépodes Harpacticoides marins des environs de La Rochelle. 3. - Espèces de la zone intertidale de Fouras-Nord. – *Téthys* 3:841-864.
- 1972. Copépodes Harpacticoides marins des environs de La Rochelle. IV. - Espèces de la zone intertidale des Nauteries. – *Téthys* 4:651-682.
- Boeck, A. 1872. Nye Slægter og Arter af SaltvandsCopepoder. – *Forhandlinger i Videnskabselskabet i Kristiania* 1872:35-60.
- Coull, B.C. 1971. Meiobenthic Harpacticoida (Crustacea, Copepoda) from the North Carolina continental shelf. – *Cahiers de Biologie Marine* 12:195-237.
- El Maghraby, A.M. & E. J. Perkins 1956. Additions to the marine fauna of Whitstable. – *Annals and Magazine of Natural History* Ser. 12(9):481-496.
- Ferrari, F.D. 1993. Exceptions to the rule of development that anterior is older among serially homologous segments of postmaxillipedal legs in copepods. – *Journal of Crustacean Biology* 13:763-768
- Fiers, F. 1987. *Enhydrosoma vervoorti* spec. nov., a new harpacticoid copepod from India (Harpacticoida: Cletodidae). – *Zoologische Mededelingen* 61(20):295-302.

- 1991. Three new harpacticoid copepods from the Santa Maria Basin off the Californian Pacific coast (Copepoda, Harpacticoida). – *Beaufortia* 42:13-47.
- 1996. Redescription of *Enhydrosoma lacunae* JAKUBISIAK, 1933 (Copepoda, Harpacticoida); with comments on the *Enhydrosoma* species reported from West Atlantic localities, and a discussion of cletodid development. – *Sarsia* 81:1-27.
- Geddes, D.C. 1972. The Copepoda Harpacticoida of Anglesey and the North Wales coast. – *Naturalist, Hull* 921:61-76.
- Gee, J.M. 1994. Towards a revision of *Enhydrosoma* BOECK, 1872 (Harpacticoida: Cletodidae *sensu* Por); a re-examination of the type species, *E. curticauda* BOECK, 1872, and the establishment of *Kollerua* gen. nov. – *Sarsia* 79:83-107.
- Gee, J.M. & J.W. Fleeger 1990. *Haloschizopera apprisea*, a new species of harpacticoid copepod from Alaska, and some observations on sexual dimorphism in the family Diosaccidae. – *Transactions of the American Microscopical Society* 109:282-299.
- Huys, R. 1990. Amsterdam Expedition to the West Indian Islands. Report No. 64, A new family of harpacticoid copepods and an analysis of the phylogenetic relationships within the Laophontoidea T. Scott. – *Bijdragen tot de Dierkunde* 60:79-120.
- Huys, R. & G.A. Boxshall 1991. *Copepod evolution*. – Ray Society No. 159. London. 468pp.
- Klie, W. 1929. Die Copepoda Harpacticoida der südlichen und westlichen Ostsee mit besonderer Berücksichtigung der Sandfauna der Kieler Hafen. – *Zoologische Jahrbücher für Systematik* 57:329-386.
- Kunz, H. 1935. Zur Oekologie der Copepoden Schleswig-Holsteins und der Kieler Bucht. *Schriften des Naturwissenschaftlichen Vereins für Schleswig-Holstein* 21:84-132.
- Lang, K. 1936. Die Familie der Cletodidae Sars, 1909. – *Zoologische Jahrbücher für Systematik* 68:445-480.
- 1948. *Monographie der Harpacticiden*, I: 1-896, figs. 1-361; II: 897-1682, figs. 362-607, maps 1-378. Håkan Ohlsson, Lund.
- O’Riordan, C.E. 1971. Meiobenthic Harpacticoida on the east coast of Ireland. – *Proceedings of the Royal Irish Academy* (B)71(14):191-210.
- Por, F.D. 1986. A re-evaluation of the family Cletodidae Sars, Lang. (Copepoda, Harpacticoida). Pp. 420-425 in: Schriever, G., H.K. Schminke & C.-t. Shih (Eds). Proceedings of the Second International Conference on Copepoda, Ottawa, Canada, 13-17th August, 1984, *Syllogeus* 58.
- Sars, G.O. 1909. *An Account of the Crustacea of Norway, with short descriptions and figures of all the species*, 5: *Copepoda Harpacticoida*. – Bergen Museum, Bergen. 449 pp.
- Scott, T. 1894. Additions to the fauna of the Firth of Forth. – *12th Annual Report of the Fisheries Board for Scotland, Part III*:231-271.
- Shen C.-j. 1979. *Freshwater Copepoda*. – *Fauna Sinica, Crustacea*: i-xiv, 1-450 [In Chinese].
- Shen C.-j. & A.-y. Tai 1965. Descriptions of six new species of freshwater copepods chiefly from the Pearl River delta, South China. – *Acta zootaxonomica* 2:126-140.
- Warwick, R.M. & J.M. Gee 1984. Community structure of estuarine meiobenthos. – *Marine Ecology Progress Series* 18:97-111.
- Wells, J.B.J. 1963. Copepoda from the littoral region of the estuary of the River Exe (Devon, England). – *Crustaceana* 5:10-26.
- 1967. The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. – *Transactions of the Royal Society of Edinburgh* 67(7):189-358.
- Willey, A. 1929. Notes on the distribution of free-living Copepoda in Canadian waters. Part II. Some intertidal harpacticoids from St. Andrews, New Brunswick. – *Contributions to Canadian Biology n. ser.* 4(33):527-539.

Accepted 15 June 1996.

