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ADENOPLEURELLA, NEW GENUS, *PROCEROPES*, NEW GENUS, *SARSOCLETODES* WILSON (EX LAOPHONTIDAE), AND *MIROSLAVIA* APOSTOLOV (EX CLETODIDAE): REPRESENTATIVES OF A NEW FAMILY (COPEPODA: HARPACTICOIDA)

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ABSTRACT

A new family of harpacticoid copepods, Adenopleurellidae, is proposed to accommodate the genera *Adenopleurella*, new genus, *Sarsocletodes* Wilson, *Miroslavia* Apostolov, and *Proceropes*, new genus. The genus *Sarsocletodes* is removed from the Laophontidae T. Scott on the basis of the reduced nature of leg 1 which cannot be attributed to heterochronic (neotenic) events. *Sarsocletodes secundus* Smirnov is placed in a new genus, *Proceropes*, on account of the primitive P1 and P5, and is considered the most primitive member of the family. *Miroslavia longicaudata* is excluded from the Cletodidae T. Scott and is most closely related to the type genus *Adenopleurella*, new genus, described from the Great Barrier Reef. The family Adenopleurellidae is placed in the superfamily Laophontoidea T. Scott and can be differentiated from the other families by the unique pleural glands, the reduced P1, and the bisetose antennal exopod. There is no relationship with *Platychelipus* Brady, which should be retained in the Laophontidae. A phylogenetic analysis of the adenopleurellid genera is presented.

The genus *Pseudocletodes* was established by G. O. Sars (1920) to accommodate a single species, *P. typicus*, described from deep, coarse, muddy sand at Risør, Norway. However, the name *Pseudocletodes* turned out to be preoccupied, not because of having been used previously for a coleopteran as Nicholls (1941) believed, but because T. and A. Scott (1893) applied it for the unrelated cletodid *P. vararensis*. Lang (1936) coined the substitute name *Pseudoplatychelipus* for *Pseudocletodes*, but it was Wilson (1924) who had already replaced it by *Sarsocletodes*. Since its original description, *S. typicus* has been recorded only sporadically off the Scandinavian coasts (Lang, 1948; Por, 1964, 1965; Drzycimski, 1969) and in the Fladen Ground off Scotland (Wells, 1964). Moore (personal communication) recorded the species in deep muddy sediments off the Isle of Man. A second species, *S. secundus*, was added by Smirnov (1946). Finally, Soyer (1970) mentioned a new species from Banyuls-sur-Mer, but to the author's knowledge the description has never been published. Males were generally not encountered or inadequately described, which added to the difficulties of assessing the affiliations of *Sarsocletodes*. Depending on the authority, the genus was placed either in the Cletodidae (Sars, 1920; Monard, 1927, 1935) or in the Laophontidae (Lang, 1936, 1948). However, it was Nicholls (1941) who was first to suggest a separate family to embrace *Sarsocletodes* and *Platychelipus*, but did not formally establish it.

Recently, Apostolov (1980) described *Miroslavia longicaudata* from the Black Sea and placed it without any further comments in the family Cletodidae. Por (1984) did not include the genus *Miroslavia* in his exploratory analysis of the Langian Cletodidae, but it is clear that there exists an undeniable relationship between *Sarsocletodes* and this Pontic genus. A third closely related genus, collected from the Australian Great Barrier Reef, is described herein. It proved to be impossible to include these genera in any of the existing families without grossly expanding the respective familial diagnoses. Therefore, a new family, Adenopleurellidae, is established to accommodate the type genus *Adenopleurella*, new genus, and its European relatives, *Sarsocletodes* and *Miroslavia*.

Materials and Methods

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

All drawings have been prepared using a camera lucida on a Leitz Dialux 20 interference microscope. The terminology is adopted from Lang (1948, 1965) except for (1) the terms pars incisiva, pars molaris, and lacinia mobilis, which are omitted in the description of the mandibular gnathobase (Mielke, 1984), (2) the segmental composition of the mandible and maxilliped which are followed according to Boxshall (1985: 341–345). The setae of the caudal rami are named and numbered as proposed by Huys (1988). Abbreviations used in the text and figures are: A1, antennula; A2, antenna; P1–P6, first to sixth pereiopods; exp., exopod; enp., endopod; exp(enp)–1(–2, –3), to denote the proximal (middle, distal) segment of a ramus. Specimens were deposited in the Zoological Museum of the University of Bergen, Norway (ZMB).

Adenopleurellidae, new family

Cletodidae (partim).
Laophontidae (partim).

Diagnosis.—Body slightly depressed, maximum width measured at posterior border of cephalothorax. First pedigerous somite fused to cephalosoma. Cephalothorax with 2 pairs of globular glands near ventral margin of cephalic shield and with another pair of dorsal glands close to hind margin. Thoracic (except P4–bearing somite) and abdominal somites each with one pair of similar glands laterally (female genital double somite with 2 pairs). Posterior margin of body somites spinular both dorsally and dorsolaterally. Rostrum not completely defined at base, fused medially; with 2 sensilla and middorsal tube-pore. Female genital double somite without internal chitinous rib ventrally; original segmentation marked by dorsal ornamentation and by lateral constriction. Anal operculum well developed; pseudoperculum absent. Caudal rami with 7 setae. Sexual dimorphism in antennula, endopod P3 (outer seta of enp–2 modified into an apophysis; 3-segmented), probably endopod P4 (inner apical seta of enp–2 elongated), P5, P6, and in genital segmentation.

Antennula short, with outer spinous process on segment II; setae either pinnate or bare; 4-segmented in female, with aesthetasc on segment III; 7-segmented and modified in male with geniculation between segments IV and V, and with long aesthetasc on segment IV. Antenna with allobasis bearing 1 abexopodal seta and bisetose, unisegmented exopod; endopod with 6 distal elements and 2 spines plus 1 seta laterally. Labrum undivided, with few ornamentation elements. Mandible with unisegmented palp; endopod represented by distal process with 3 setae; exopod absent. Paragnaths well developed, slightly ornamented lobes with pair of unornamented secondary lobes in between. Maxillule with both rami incorporated into basis; exopod with 1 seta; endopod with 3 setae; basal endites fused (proximal one absent); no epipodite. Maxillary syncoxa with 3 endites, precoxal endite vestigial (with 1 seta); endopod unisegmented, with 2 elements. Maxilliped with syncoxa bearing 1 seta; basis asetose; endopod unisegmented with 1 minute seta and 1 long claw.

P1 with well-developed 3-segmented protopod; basis with inner spine located at inner margin and not on anterior surface; exopod 2-segmented, distal segment with 4 spines (innermost spine geniculate); endopod not prehensile, either (1) 1-segmented with 1 pinnate spine and 1 minute seta, or (2) subdivided in long, asetose, proximal segment and short distal segment with 1 pinnate spine and 1 minute seta. P2–P4 with 3-segmented exopods and 2-segmented endopods; spine and seta formulae as follows:

	Exopod	Endopod
P2	0.1.12[2–3]	0.220
P3	0.1.22[2–3]	0.[1–2]21
P4	0.1.22[2–3]	0.121

Female fifth pair of legs not fused medially, sometimes fused to ventral wall of supporting somite; exopod and baseoendopod separate or fused; exopod with 3 or 4 setae; endopodal lobe well developed or vestigial, with 2 or 3 setae; basal seta standing on strongly developed setophore partly covered by pleurotergite of somite bearing P5. Male fifth pair of legs fused with ventral wall of somite; endopodal lobe vestigial or absent, with 1 or 2 setae; exopod with 4 setae (*Sarsocletodes, Proceropes,* new genus); basal seta standing on long setophore.

Female gonopores fused to form W-shaped genital slit covered on both sides by vestigial P6 bearing 2 or 3 elements; copulatory pore well developed, located in median depression; 2 pairs of secretory pores associated with genital complex. One egg sac.

Male P6 nonarticulating, fused medially; slightly asymmetrical, with 2 setae each. Reproductive system asymmetrical with only 1 (either right or left) gonopore functional, releasing 1 spermatophore at a time.

Marine, free-living.

Type Genus.—*Adenopleurella,* new genus.

Other Genera.—*Sarsocletodes* Wilson, 1924; *Miroslavia* Apostolov, 1980; *Proceropes,* new genus.

Remarks.—Although the male is unknown at present, the author preferred to select the new genus *Adenopleurella* as type of the family, because of its name which refers to the most striking and diagnostic feature of the family, i.e., the presence of peculiar globular glands in the pleural area of the body somites. Despite being the oldest genus, *Sarsocletodes* was not chosen because the name refers to the genus *Cletodes* Brady and the family Cletodidae has no direct relationships with the family Adenopleurellidae, not even in its widest sense. The genus *Miroslavia* is inadequately described, and, moreover, the male is unknown.

Adenopleurella, new genus

Diagnosis.—Adenopleurellidae. Posterolateral corners of genital double somite and free urosomites I and II laterally expanded and produced in backwardly directed process. Caudal rami about 1.3 times as long as wide. Rostrum triangular, narrowing anteriorly to rounded tip. Antennula armed with numerous pinnate setae and spines; segment IV distinctly shorter than segment III; spinous process on segment II moderately developed. Antennal exopod very small, square segment with 1 long and 1 short seta; allobasis with short abexopodal spine. Labrum with minute denticles medially. Exp–2 P1 with 4 short spines. Endopod P1 1-segmented, short, as long as exp–1; armed with 1 minute seta and 1 strong bipinnate spine. Exp–3 P2–P4 with 2 outer spines. Enp–1 P2–P4 decreasing in size posteriorly, with enp–1,2 P2 of about same length and enp–1 P4 nearly square. Enp–2 P3 with 2 inner setae. Female P5 fused to ventral wall of supporting somite; rami fused; endopodal lobe vestigial with 2 short spines; exopod small lobe with 3 setae. Female P6 small protuberance with 2 minute setae; anterior pair of secretory tube-pores close to copulatory pore. Male unknown. Monotypic.

Type Species.—*Adenopleurella brevipes,* new species.

Etymology.—The generic name is derived from the Greek *aden,* meaning gland, and *pleura,* meaning side, and refers to the paired globular glands found in the pleurites of the body somites.

Gender.—feminine.

Adenopleurella brevipes, new species

Material Examined.—One female taken at 35 m depth near Yonge Reef during Belgian Great Barrier Reef Expedition; sandy sediment; collected by Prof. Dr. A. Coomans (29 August 1967); dissected and mounted on 4 slides; deposited in the ZMB under No. 66532.

Description of Female (Figs. 1A–C, 2A,B, 3A–H, 4A–G).—Total body length 465 μm from tip of rostrum to posterior margin of caudal rami. Maximum width 135 μm measured at posterior margin of cephalothorax. Rostrum (Fig. 3E) triangular, 1.5 times broader than long, slightly deflexed (Fig. 1A), acutely tapering to narrow rounded apex, ornamented laterally with pair of tiny setules, standing on minute tubercles, and mid-dorsal tube-pore. Body (Figs. 1A, 2A, B) covered with minute denticles both laterally and dorsally. Epimeral areas of cephalothorax (Fig. 1A) not particularly produced ventrally; ventrolateral margins of cephalic shield furnished with 2 clusters of hairs and 2 moderately sized, globular glands; dorsal surface with 2 similar, but smaller glands near posterior margin, but without large pores on dorsal midline; hind margin not spinulose but with minute protuberances bearing tiny setules. Pleurotergites of thoracic somites bearing P2–P4 narrow; hind margin finely spinulose with long hairs dorsally, and ventrolateral margin coarsely spinulose and without hairs; small, paired lateral glands present on somites bearing P2 and P3 but absent on following somite. Glands of somite bearing P5 somewhat larger; rear margin spinulose dorsally and laterally, lateroventral ornamentation consisting of spinules (Fig. 4C). Last thoracic somite and first abdominal somite completely fused and forming bilaterally constricted genital double somite (Figs. 1A, B, 2A, B); original segmentation also marked by dorsal ornamentation consisting of spinules and setules; thoracic (anterior) half with 2 small glands; abdominal (posterior) half of genital double somite and following 2 urosomites with 2 large, lateral glands located in laterally expanded and backwardly

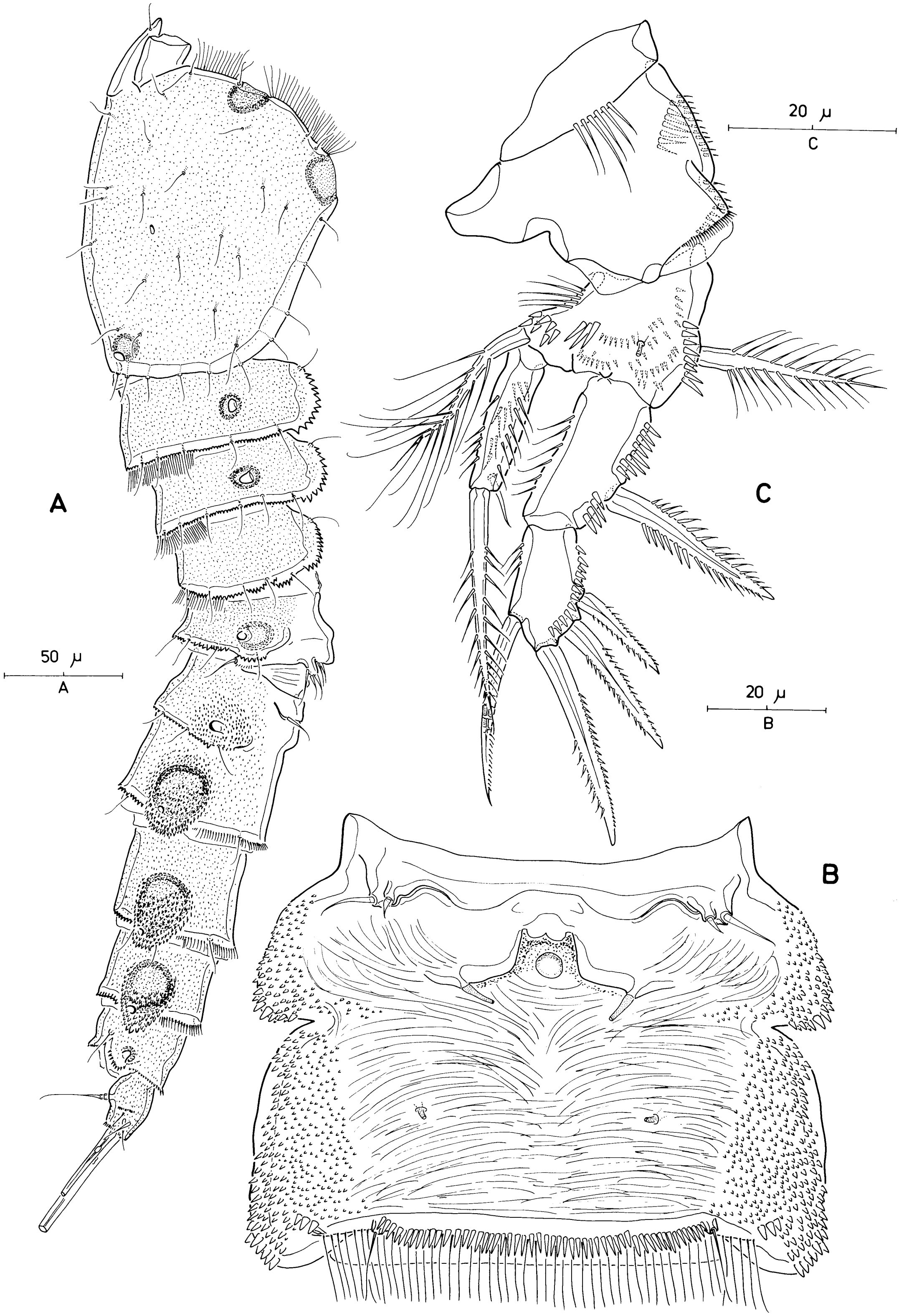
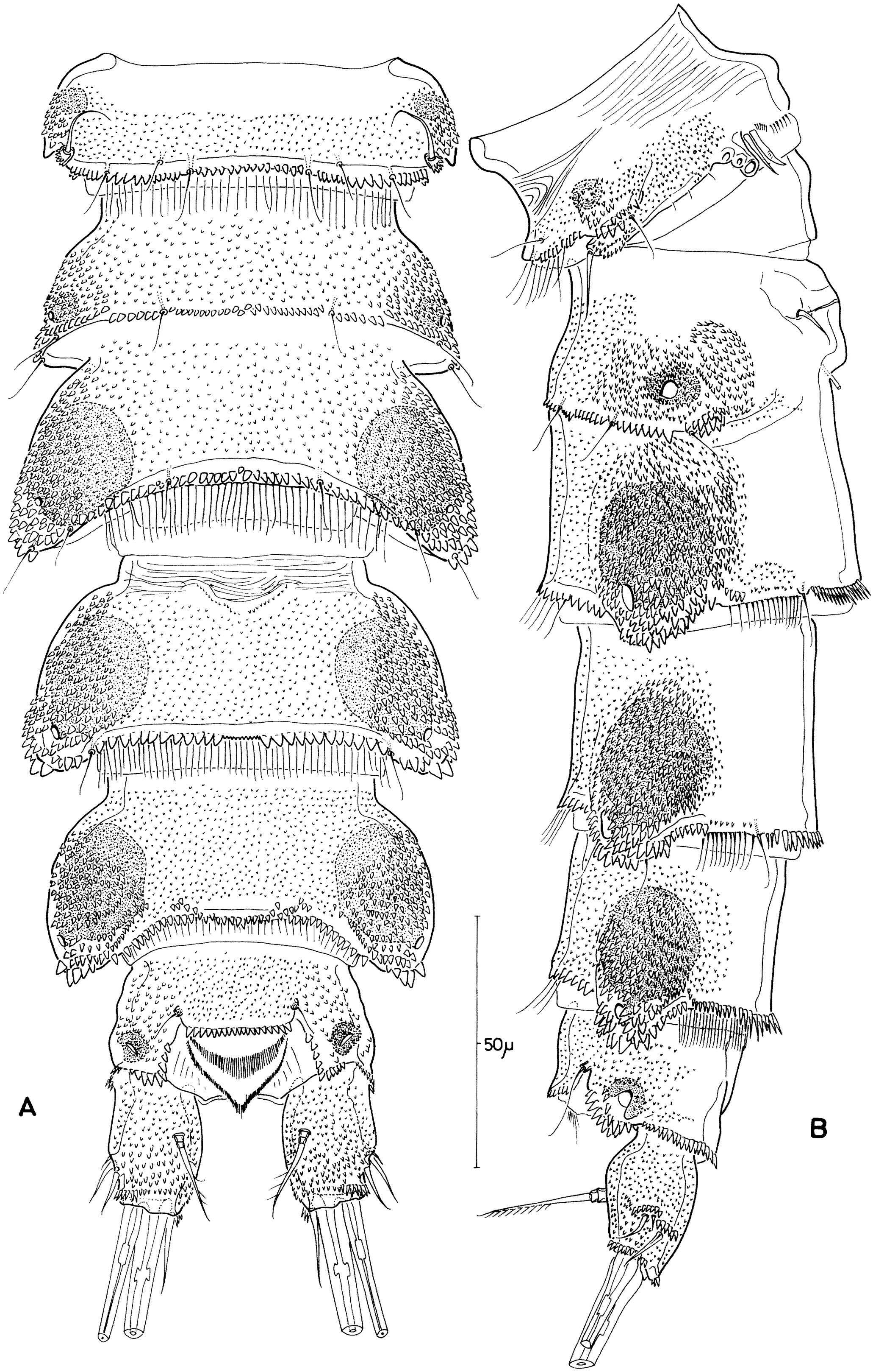


Fig. 1. *Adenopleurella brevipes,* new genus, new species. A, habitus, female, lateral view; B, genital double somite of female, ventral view; C, P1, anterior view.


A
50µ
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directed extensions of pleural areas. Ventral surface of genital double somite and all following somites with fine cuticular lamellae arranged in more or less symmetrical pattern, and with small spinules interspersed with long hairs along hind margin (Figs. 2B, 4D). Anal somite (Figs. 2A, B, 4B) with spinulose operculum flanked by 2 tiny sensilla standing on small tubercle; with numerous minute spinules around rear margin; paired dorsolateral glands small. Caudal rami (Figs. 2A, B, 4B) short, about 1.6 times as long as maximum width; with 7 setae: I minute, II–IV short, VII tri-articulated at base, IV and VI longest and pinnate.

Antennula (Fig. 4A) 4-segmented, short. Segment I with several patches of spinules; segment II with moderately developed, spinous, outer process and numerous denticles; segment III with fine spinules along outer margin, distinctly longer than segment IV. Spine and seta ornamentation: I–1; II–[2 bare + 6 pinnate]; III–[3 bare + 6 pinnate + aesthetasc]; IV–[(7 + 3) bare, + 2 pinnate].

Antenna (Fig. 3A) with coxa not ornamented; allobasis with coarse spinules proximally and pinnate abexopodal spine not exceeding distal margin; exopod almost square, with 1 long, pinnate and 1 short, smooth seta; endopodal ornamentation as in *Sarsocletodes*.

Labrum (Fig. 3F) simple muscular lobe with numerous denticles medially, lateral margins expanded.

Mandible (Fig. 3B) with well-developed gnathobase bearing several cuspidate teeth and bifid, recurved spine; palp subcylindrical, sigmoid: basis with 2 patches of spinules and 1 plumose spine, endopod represented by 3 apical setae, exopod absent.

Paragnaths (Fig. 3D) well developed and heavily ornamented; with paired, large, secondary lobes medially.

Maxillula (Fig. 3C) with well-developed arthrite armed with 6 terminal spines, 2 inner setae and 1 outer seta; coxa with spinular row and 2 curved spines on its endite; basis with one endite (=distal one) bearing 2 setae and 1 claw; rami incorporated into basis, endopod represented by 3 setae, exopod small lobe with 1 seta.

Maxilla (Fig. 3G) with 3 endites on syncoxa; proximal (precoxal) endite small, with 1 seta, coxal endites with 3 pinnate spines each; basis produced into clawlike endite with 2 claws and 1 seta; endopod 1-segmented with 2 well-developed spines.

Maxilliped (Fig. 3H) with 1 seta on syncoxa; basis asetose, with 2 inner spinular rows and 2 sets of spinules along outer margin; endopod with 1 setule and 1 long claw serrate along distal half.

Thoracopods with wide intercoxal sclerites and well-developed precoxae. Leg 1 (Fig. 1C) with large coxa, produced adaxially in proximal half, and with spinular rows around outer margin; basis with plumose seta on inner margin and with strong, plumose spine standing on outer margin; exp–1 with 1 bipinnate spine, exp–2 with 4 short spines (3 bipinnate, 1 geniculate); endopod shorter than exp–1, with 1 long, bipinnate spine and 1 setule.

P2–P4 (Fig. 4E–G) with spinules around outer margin of precoxa and coxa; basis with tube-pore on anterior surface, with long spinules on inner margin, and with outer short, setophore bearing plumose (P2) or smooth (P2–P4) seta. Length of enp–1 decreasing in length in anteroposterior direction. Spine and seta formulae as follows:

	Exopod	Endopod
P2	0.1.122	0.220
P3	0.1.222	0.221
P4	0.1.222	0.121

Fifth pair of legs (Figs. 1A, 2B, 4C) laterally displaced, reduced, fused to supporting somite, rami entirely incorporated in basis. Baseoendopod forming long spinulose setophore with basal seta; endopodal lobe almost absent, with 1 short seta and 1 geniculate spine; exopod short process with (based on scars) 3 setae.

Genital complex (Fig. 1B) with 1 pair of

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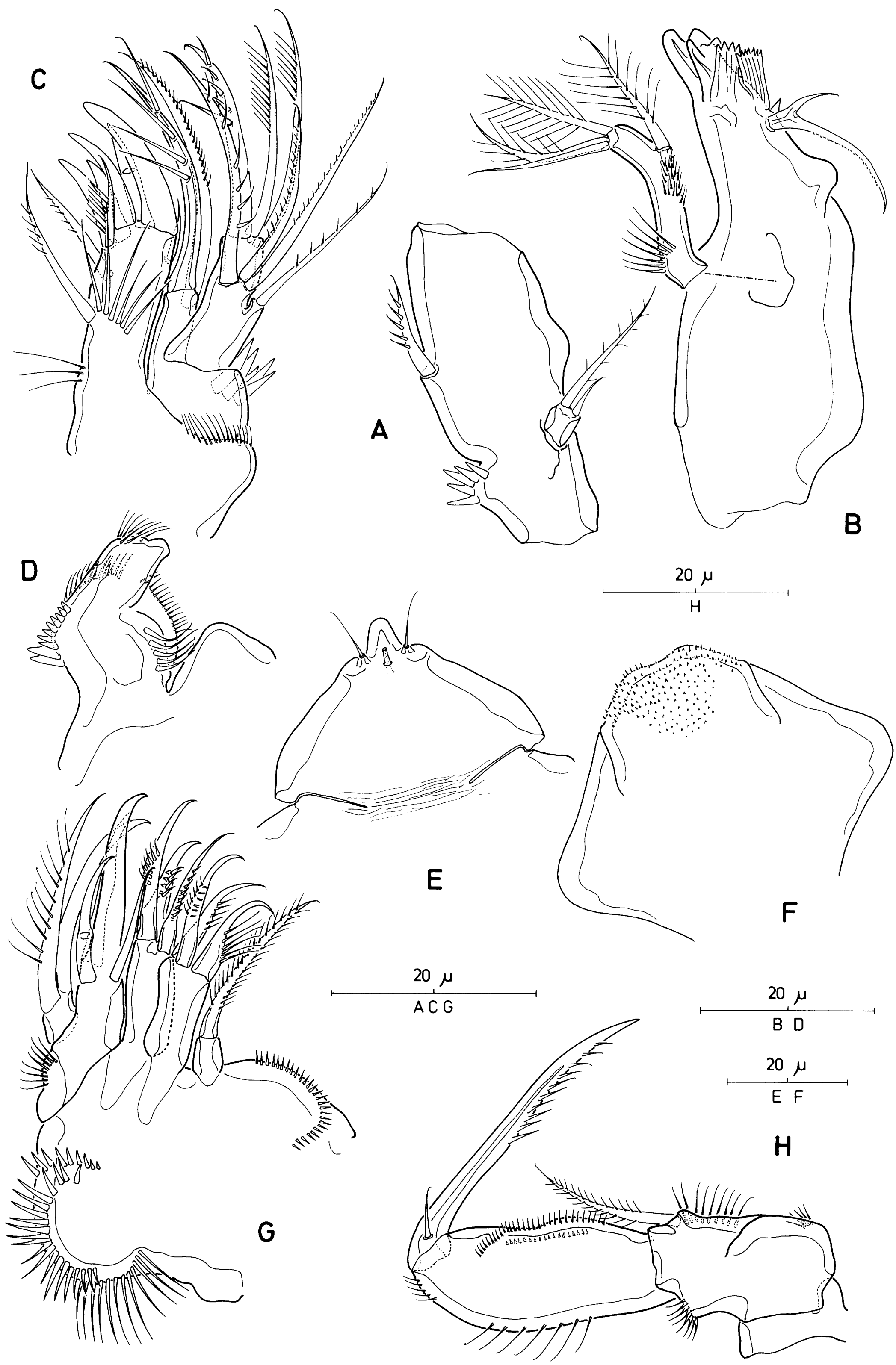
Fig. 2. *Adenopleurella brevipes*, new genus, new species. A, urosome, female, dorsal view; B, urosome, female, lateral view.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secretory tube-pores in posterior half; copulatory pore large, located in median depression with steep anterior face, covered anteriorly by slightly bilobed cuticular eminence, and flanked by 2 long secretory pores. P6 small bilobed protuberance with 2 tiny setae; gonopores fused to median W-shaped slit.

Male.—Unknown.

Etymology.—The species name is derived from the Latin *brevis,* meaning short, and *pes,* meaning leg, and refers to the very short P1 endopod.

Remarks.—*Adenopleurella* is most closely related to *Miroslavia* with which it shares the strongly abbreviated, unisegmented P1 endopod, the presence of only 2 outer spines on exp–3 of P2–P4, the reduced glands in the anal somite, and the short antennal exopod. The new genus can be distinguished from all other genera by the posteriorly directed, pleural extensions of the abdominal somites and by the endopod of P1 which is shorter than the proximal exopod segment. It differs also from all known genera in the reduced nature of the female P5. The baseoendopod and exopod are fused as in *Miroslavia,* but the vestigial endopodal lobe with 2 short (1 geniculate!) setae is unique to *Adenopleurella.*

Genus *Sarsocletodes* Wilson, 1924

Pseudocletodes Sars, 1920, p. 89. nec T. and A. Scott, 1893, p. 239.
Sarsocletodes Wilson, 1924, p. 22.
Pseudocletodes (pro part.) Monard, 1927, p. 170; 1935, p. 83.
Pseudoplatychelipus Lang, 1936, pp. 451, 457.

Diagnosis.—Adenopleurellidae. Posterolateral corners of genital double somite and free urosomites I and II neither laterally expanded nor with backwardly directed processes. Caudal rami about 3.5 times as long as wide. Rostrum triangular with proximal half tapering abruptly and distal half ending in bifid apex. Antennula armed with smooth setae except for 1 small, pinnate spine on segment II; segment IV slightly longer than segment III; spinous process on segment II moderately developed. Antennal exopod well developed, about 4 times as long as wide, with 2 long setae of about same length; allobasis with long abexopodal seta. Labrum with several patches of minute spinules medially and laterally. Exp–2 P1 with 4 well-developed spines, increasing in length adaxially. Endopod P1 2-segmented, only slightly longer than exp–1; enp–1 twice length of enp–2, asetose; enp–2 with 1 minute seta and 1 strong bipinnate spine. Exp–3 P2–P4 with 3 outer spines. Enp–1 P2–P4 decreasing in size posteriorly, with enp–1,2 P2 of about same length and enp–1 P4 less than half length of enp–2. Enp–2 P3 with 2 inner setae. Female P5 not fused to ventral wall of supporting somite; rami separate; endopodal lobe well developed, subcylindrical, exceeding exopod, with 2 short spines and 1 long seta; exopod well developed, with 4 setae. Female P6 small protuberance with 2 minute spinules and 1 bipinnate seta; anterior pair of secretory tube-pores close to posterior pair. Male P5 fused to wall of supporting somite; exopod defined, with 4 setae; endopodal lobe vestigial, with 2 small setae. Male P3 with modified (external apophysis on enp–2 by far exceeding enp–3), 3-segmented endopod; male P4 with slightly modified endopod (inner seta of enp–2 elongated). Monotypic.

Type Species.—*Sarsocletodes typicus* (Sars, 1920) [by monotypy].

Sarsocletodes typicus (Sars, 1920)

Pseudocletodes typicus, new species, Sars, 1920, pp. 89–91, pl. LXII.
Sarsocletodes typicus Wilson, 1924, p. 22; Smirnov, 1946, pp. 239–240, 259; Lang, 1948, pp. 1429, 1449–1450, 1452, 1495, 1502, 1506, 1510, 1517, 1522–1525, 1529, 1561, Abb. 585; Por, 1964, pp. 237–239, 257, fig. 139; 1965, p. 2; Vervoort, 1964, p. 371; Wells, 1964, p. 6; Drzycimski, 1969, p. 23, tables 2, 4.
Pseudoplatychelipus typicus Lang, 1936, p. 451, Abb. 1; 1948, p. 1429; Vervoort, 1964, p. 371.

Material Examined.—One female from Fanafjorden [station 323/66; 60°14′27″N, 05°17′03″E; see Drzycimski (1969) for location map], western Norway (depth 155 m; silt) collected by Marine Biological Station, Espegrend, on 21 November 1966 (det. Dr. I. Drzy-

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Fig. 3. *Adenopleurella brevipes,* new genus, new species. A, allobasis and exopod of antenna; B, mandible; C, maxillula; D, right paragnath, posterior view; E, rostrum, dorsal view; F, labrum, posterior view; G, maxilla; H, maxilliped.


F
G
E
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20 μ

cimski). Dissected and mounted on 11 slides by present author. Deposited in ZMB under No. 53203. One male from Korsfjorden [station 422–62 (I); see (Por, 1965) for location map)], western Norway (depth 690 m; mud) collected with Petersen grab by Biological Station, Espegrend, on 19 December 1962 (det. Dr. F. D. Por). Dissected and mounted on 7 slides by present author. Deposited in ZMB under No. 53281.

Redescription of Female (Figs. 5A–C, 6A–D, 7A–F, 8A–D, 9A–C, 11D).—Total body length 595 μm from tip of rostrum to posterior margin of caudal rami. Maximum width 165 μm measured at posterior margin of cephalothorax. Rostrum (Fig. 5C) broader than long, slightly deflexed, bilaterally incised about midway, tapering to bifid apex, ornamented with pair of tiny setules laterally and middorsal tube-pore. Body (Fig. 5A, B) covered with minute denticles both laterally and dorsally (Fig. 6D). Epimeral areas of cephalothorax (Fig. 5B) grossly produced ventrally; ventrolateral margins of cephalic shield furnished with 3 clusters of hairs and 2 large globular glands; dorsal surface (Fig. 5A) with 2 similar, but smaller glands near posterior margin and with 2 conspicuous pores on dorsal midline; hind margin not spinulose but with minute protuberances bearing tiny setules. Pleurotergites of thoracic somites bearing P2–P4 narrow; hind margin spinulose and ventrolateral margin furnished with short hairs; small, paired lateral glands present on somites bearing P2 and P3 but absent on following somite. Somite bearing P5 also with small, paired glands laterally; rear margin spinulose dorsally and laterally, but ventral ornamentation absent (Fig. 9A). Last thoracic somite and first abdominal somite completely fused and forming bilaterally constricted genital double somite (Figs. 5A, B, 9A, B); original segmentation also marked by dorsal ornamentation consisting of spinules and setules; thoracic (anterior) half with 2 small, dorsolateral glands, abdominal (posterior) half with 2 large, lateral glands. Ventral surface of genital double somite and all following somites with fine cuticular lamellae arranged in more or less symmetrical pattern, and with small spinules interspersed with long hairs along hind margin (Fig. 9A, C). Lateral glands of antepenultimate and anal somites large, those of penultimate somite small. Anal somite (Figs. 6D, 9A, 11D) with spinulose operculum flanked by 2 tiny sensilla standing on small tubercle; with numerous minute spinules around rear margin. Caudal rami (Figs. 6D, 9A, 11D) long, about 3.6 times as long as maximum width; slightly tapering in middle part; with 7 setae: I and VI minute, VII tri-articulated at base, IV and V longest and pinnate.

Antennula (Figs. 5A, 6A) 4-segmented, backwardly recurved, short. Segment I with several patches of spinules; segment II with moderately developed, spinous, outer process; segment IV slightly longer than segment III. Setal ornamentation: I–1; II–[8 + 1 pinnate spine]; III–[9 + aesthetasc]; IV–[9 + 3].

Antenna (Fig. 7A) with coxa not ornamented; allobasis with minute spinules proximally and plumose abexopodal seta exceeding distal margin; exopod 4 times as long as wide, with 1 pinnate and 1 plumose seta; endopod with 2 pinnate spines and 1 seta laterally, with 2 pinnate spines and 3 geniculate setae distally (outermost geniculate seta fused with short seta).

Labrum (Fig. 7B) simple muscular lobe with median pore and with few armature elements arranged symmetrically.

Mandible (Fig. 7C) with well-developed gnathobase bearing several cuspidate teeth and pinnate recurved spine; palp subcylindrical, basis with numerous spinules and 1 plumose spine, endopod represented by apical process with 3 setae, exopod absent.

Paragnaths (Fig. 6B) well developed and ornamented; with paired, secondary lobes medially.

Maxillula (Fig. 7D) with well-developed arthrite armed with 7 terminal spines, 2 inner setae and 1 outer seta; coxa with spinular row and 2 curved spines on its endite; basis with one endite (=distal one) bearing

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Fig. 4. *Adenopleurella brevipes*, new genus, new species. A, antennula, female; B, left caudal ramus, ventral view; C, left P5, female (exopodal setae missing); D, ventral ornamentation of first postgenital urosomite; E, P3, female, anterior view; F, endopod P2, female, posterior view; G, endopod P4, female, posterior view.

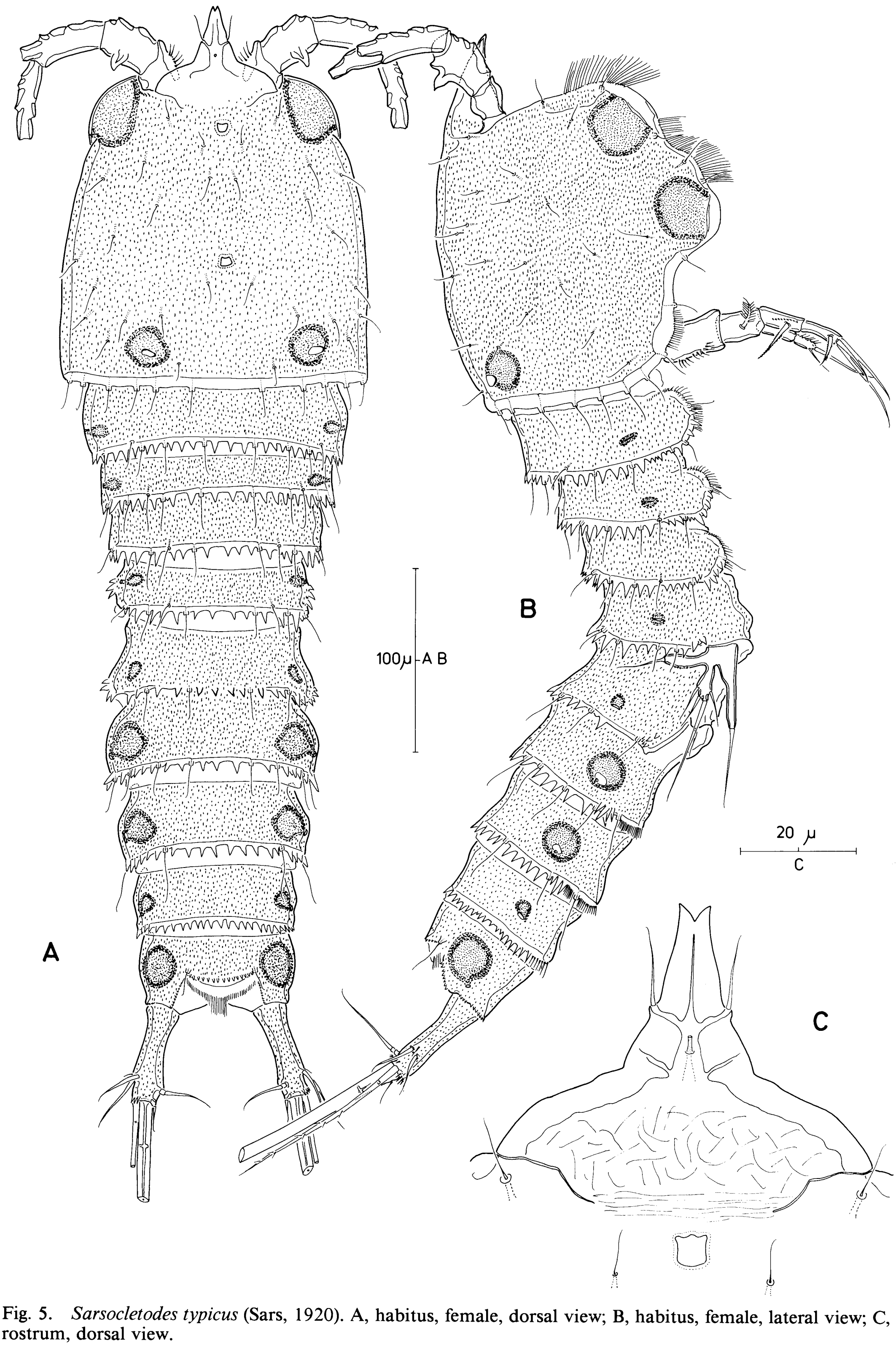

Fig. 5. *Sarsocletodes typicus* (Sars, 1920). A, habitus, female, dorsal view; B, habitus, female, lateral view; C, rostrum, dorsal view.

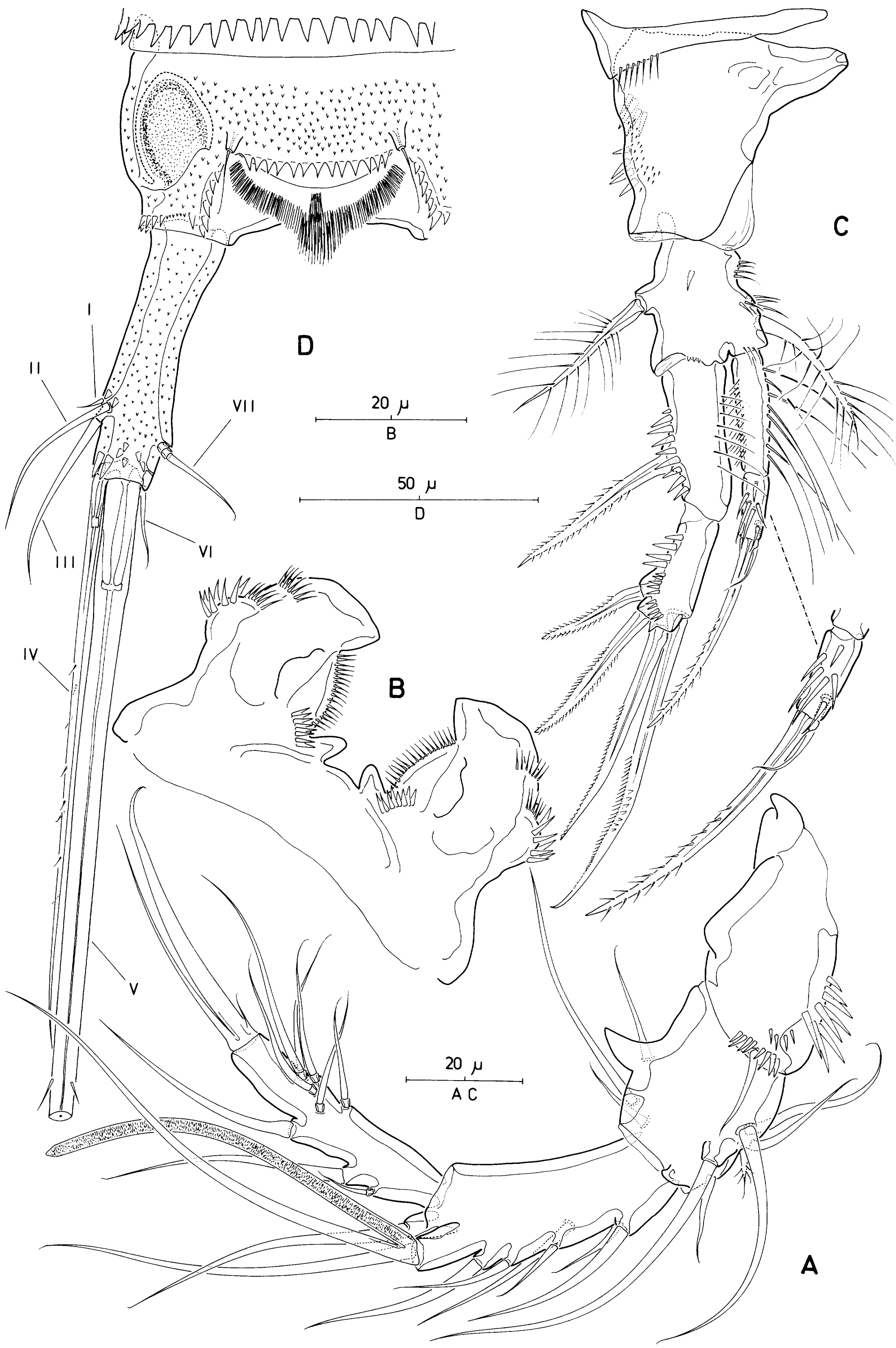

Fig. 6. *Sarsocletodes typicus* (Sars, 1920). A, antennula, female; B, paragnaths, posterior view; C, P1, anterior view; D, anal somite and left caudal ramus, dorsal view.

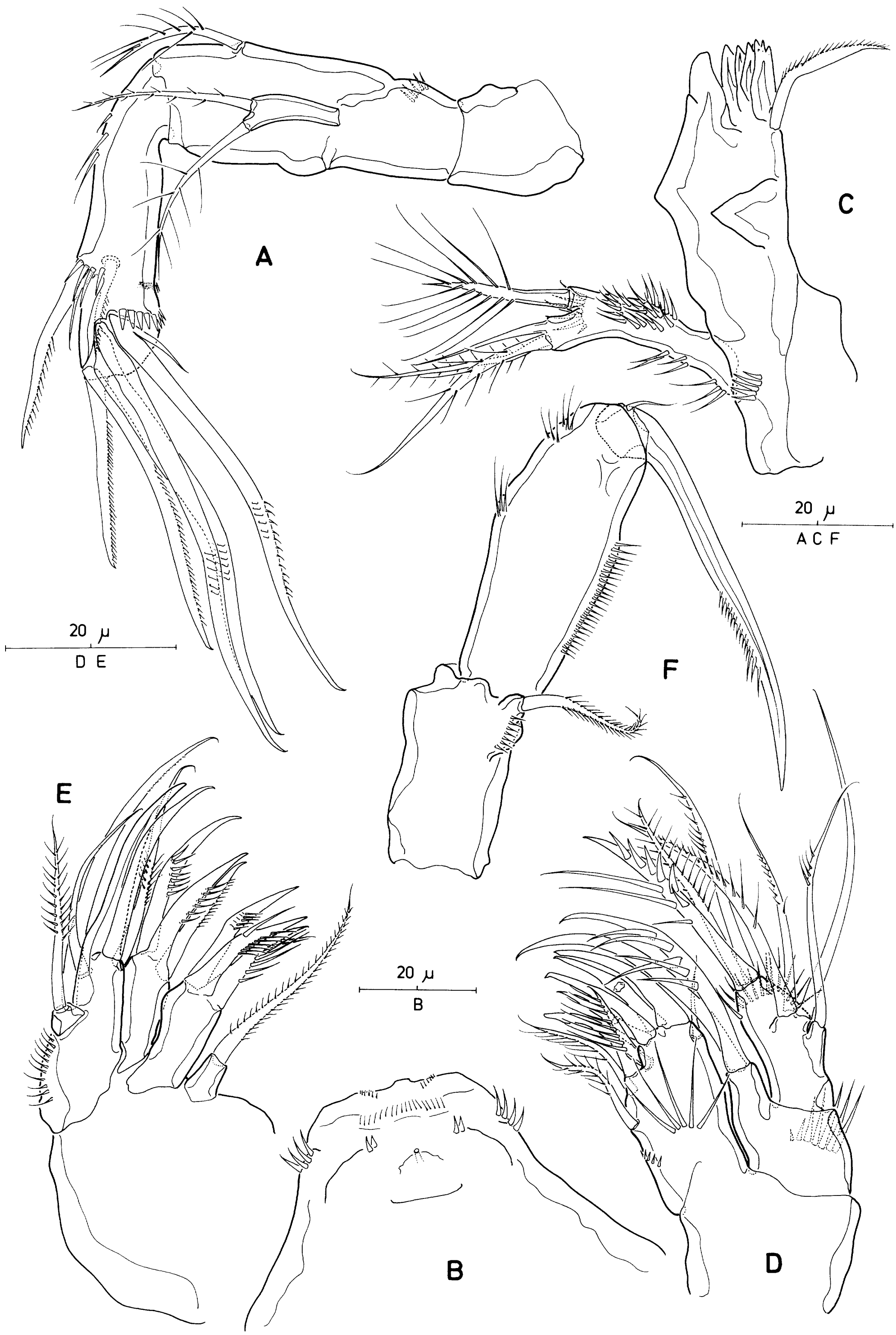

Fig. 7. *Sarsocletodes typicus* (Sars, 1920). A, antenna; B, labrum, posterior view; C, mandible; D, maxillula; E, maxilla; F, maxilliped.

2 setae and 1 claw; rami incorporated into basis: endopod represented by 3 setae, exopod by 1 seta.

Maxilla (Fig. 7E) with 3 endites on syncoxa; proximal (precoxal) endite small, with 1 seta, coxal endites with 3 pinnate spines each; basis produced into clawlike endite with 2 setae and 1 claw; endopod 1-segmented with 1 seta and 1 long spine.

Maxilliped (Fig. 7F) with 1 seta on syncoxa; basis asetose, with inner spinular row and 3 sets of spinules along outer margin; endopod minute segment with 1 setule and 1 long claw serrate along middle third.

Thoracopods with wide intercoxal sclerites and well-developed precoxae. Leg 1 (Fig. 6C) with large coxa, produced adaxially in proximal half and with spinules around outer margin; basis with plumose seta on inner margin and with plumose spine standing on outer process; exp–1 with 1 bipinnate spine, exp–2 with 4 spines increasing in length adaxially (2 bipinnate, 1 unipinnate, 1 geniculate); endopod slightly longer than exp–1, with 1 long, bipinnate spine and 1 setule on enp–2.

P2–P4 (Fig. 8A–C) with spinules around outer margin of precoxa and coxa; basis with tube-pore at anterior surface, with long spinules on inner protuberance, and with outer short, setophore bearing plumose (P2) or smooth (P3 and P4) seta. Length of enp–1 decreasing in length in anteroposterior direction. Spine and seta formulae as follows:

	Exopod	Endopod
P2	0.1.123	0.220
P3	0.1.223	0.221
P4	0.1.223	0.121

Fifth pair of legs (Fig. 8D) laterally displaced (Fig. 9A), not fused to supporting somite, rami separate. Baseoendopod forming inner process with tube-pore, and outer, swollen, setophore with basal seta; endopodal lobe nearly twice length of exopod, with 1 long seta, 1 tube-pore, and 2 tiny setae distally; exopod with 4 setae.

Genital complex (Fig. 9B) with 2 pairs of secretory tube-pores in posterior half; copulatory pore located in median depression with steep anterior face and covered anteriorly by slightly bilobed cuticular eminence; P6 small protuberance with 1 pinnate seta and 2 tiny setules; gonopores fused to median W-shaped slit.

Male (Figs. 9D–F; 10A–C; 11A–C).—Total body length 530 μm from tip of rostrum to posterior margin of caudal rami. Body shape, cuticular ornamentation, and relative size of lateral glands similar to those of female, except for (1) separation of genital and first abdominal somites, (2) ventral ornamentation of postgenital urosomites consisting of slender spinules only, and (3) somite bearing P5 with ventrolateral spinular row (Fig. 10B).

Sexual dimorphism in antennula, endopod P3 and P4, P5, and P6.

Antennula (Fig. 9D–F) 7-segmented, modified, geniculation between segments IV and V; segment I with 2 spinular rows; segment II with moderately developed, outer, spinous process; segment IV swollen with complex ornamentation; setal ornamentation: I–1; II–[8 + 1 pinnate spine]; III–9; IV–[16 + aesthetasc]; V–4; VI–1; VII–[8 + 3].

Endopod of P3 (Fig. 11B) 3-segmented; enp–2 with strong apophysis homologous with outer seta of enp–2 of female; apophysis exceeding distal margin of enp–3; enp–3 short, with 4 setae.

Endopod of P4 (Fig. 11C) with enp–1 shorter but wider than in female; enp–2 only 3 times as long as wide (instead of 7 times in female), inner and particularly inner apical seta elongated.

P5 (Figs. 10B, C, 11A) fused to supporting somite, laterally displaced; baseoendopod represented by swollen setophore bearing outer basal seta, vestigial endopodal lobe with 2 small setae, and tube-pore near ventral midline; exopod defined at base, with 4 setae.

Sixth pair of legs (Figs. 10B, C, 11A) fused to supporting somite, slightly asymmetrical; represented on both sides by bilobed process bearing small outer seta and long, pinnate, inner seta. Only one gonopore functional (right one in Figs. 10C, 11A).

One small, ovoid spermatophore with short neck.

Remarks.—The only information on the male of *S. typicus* was provided by Lang (1936), who considered the sexual dimorphism on the endopod of P3 as sufficient evidence to include the genus *Sarsocletodes*

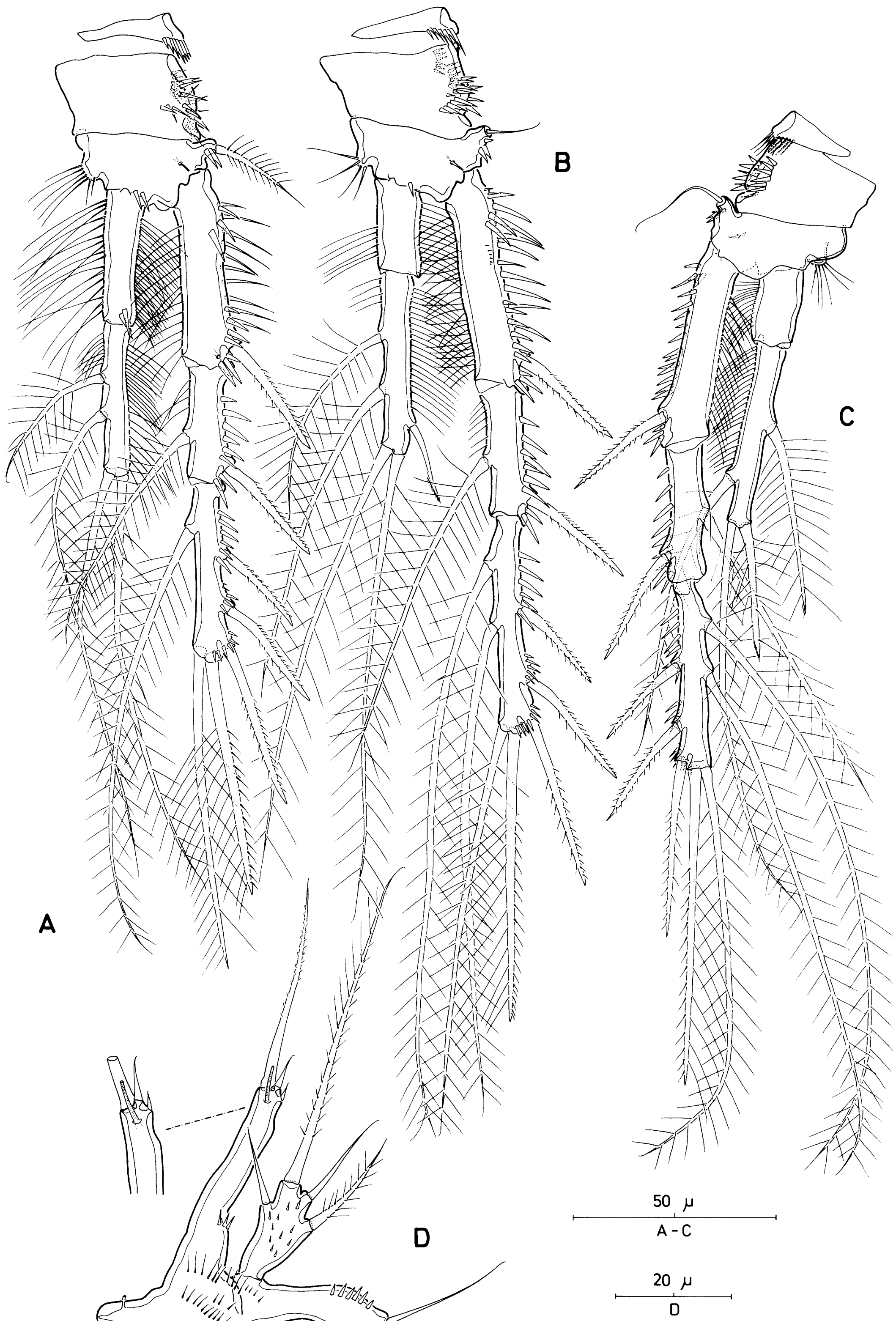

Fig. 8. *Sarsocletodes typicus* (Sars, 1920). A, P2, female, anterior view; B, P3, female, anterior view; C, P4, female, posterior view; D, right P5, female (distal part of endopodal lobe enlarged separately).

in the Laophontidae. A phylogenetic analysis of other families related to the Laophontidae (Huys, in press a), however, proved this character to be one of the synapomorphies for the Laophontoidea as a whole, and questioned its diagnostic significance at the family level. The slight sexual dimorphism on the endopod of leg 4 might be unique to *Sarsocletodes* and should therefore be used only as a potential family trait. The genus, as defined herein, encompasses exclusively the type species *S. typicus*; the second species is assigned to a separate genus defined below, because of the discrepancies noticed in the morphology of P1, P5 of both sexes, rostrum, and the endopods of P2–P4.

Proceropes, new genus

Sarsocletodes Wilson, 1924 (part.)

Diagnosis.—Adenopleurellidae. Posterolateral corners of genital double somite and free urosomites I and II neither laterally expanded nor with backwardly directed processes. Caudal rami 1.5–2 times as long as wide. Rostrum triangular, broad at apex. Antennula probably armed with bare setae and spines; segment IV slightly shorter than segment III; spinous process on segment II strongly developed. Antennal exopod well developed, about 4 times as long as wide, with 2 long setae; allobasis with long abexopodal seta. Labrum unconfirmed. Exp–2 P1 with 4 well-developed spines, increasing in length adaxially. Endopod P1 2-segmented, long, 1.7 times as long as exopod; armed with 1 strong bipinnate spine [and 1 minute seta?]. Exp–3 P2–P4 with 3 outer spines. Enp–1 P2–P4 small, square segment. Enp–2 P3 with 2 inner setae. Female P5 not fused to ventral wall of supporting somite; rami separate; endopodal lobe well developed, not exceeding exopod, triangular, with 2 long setae; exopod well developed, with 4 setae. Female genital complex unknown. Male P5 fused to wall of supporting somite; exopod defined, with 4 setae; endopodal lobe represented by 1 long seta (and 1 short seta?). Male P3 with modified (external apophysis on enp–2 extending to distal margin of enp–3), 3-segmented endopod; sexual dimorphism of enp–P4 not confirmed. Monotypic.

Type Species.—*Proceropes secunda* (Smirnov, 1946), new combination.

Sarsocletodes secundus Smirnov, 1946, pp. 239–240, 259, fig. 9 (1–9); Vervoort, 1964, p. 371.

Etymology.—The generic name is derived from the Latin *procerus,* meaning slender, and *pes,* meaning leg, and refers to the long, slender endopod of P1.

Gender.—Feminine.

Remarks.—*Proceropes* is the most primitive genus known within the Adenopleurellidae and shows plesiomorphic character states for the endopod of P1 [elongated, enp–1 exceeding exp.], P5 of female [endopodal lobe well developed, with 2 long setae] and male [endopodal lobe with 1 long seta (and 1 short seta?)], and the spinous antennular process [strongly developed] which are not found in other adenopleurellid genera. A diagnostic apomorphy is noticed in the reduced, square enp–1 of P2–P4. The paired pleural glands, characteristic of the family, were neither drawn nor mentioned in the original description of *S. secundus,* but it is likely that they were overlooked by Smirnov (1946) who did not go into details.

Genus *Miroslavia* Apostolov, 1980

Diagnosis.—Adenopleurellidae. Posterolateral corners of genital double somite and free urosomites I and II neither laterally expanded nor with backwardly directed processes. Caudal rami about 5 times as long as wide. Rostrum and labrum unconfirmed. Setae of antennula probably smooth; segments III and IV of about same length; spinous process on segment II moderately developed. Antennal exopod small, with 1 long and 1 short seta; allobasis with short abexopodal seta. Exp–2 P1 with 4 short spines. Endopod P1 1-segmented, short, slightly longer than exp–1; armed with 1 strong pinnate spine [and 1 minute seta?]. Exp–3 P2–P4 with 2 outer spines. Enp–1 P2–P4 decreasing in size posteriorly, with enp–1,2 P2 of the same length and enp–1 P4 nearly square. Enp–2 P3 with 1 inner seta. Female P5 not fused to ventral wall of supporting somite; rami fused; endopodal lobe well developed, exceeding exopod, triangular with 1 short and 1 long seta; exopodal lobe oval, with 4 setae. Genital complex unknown. Male unknown. Monotypic.

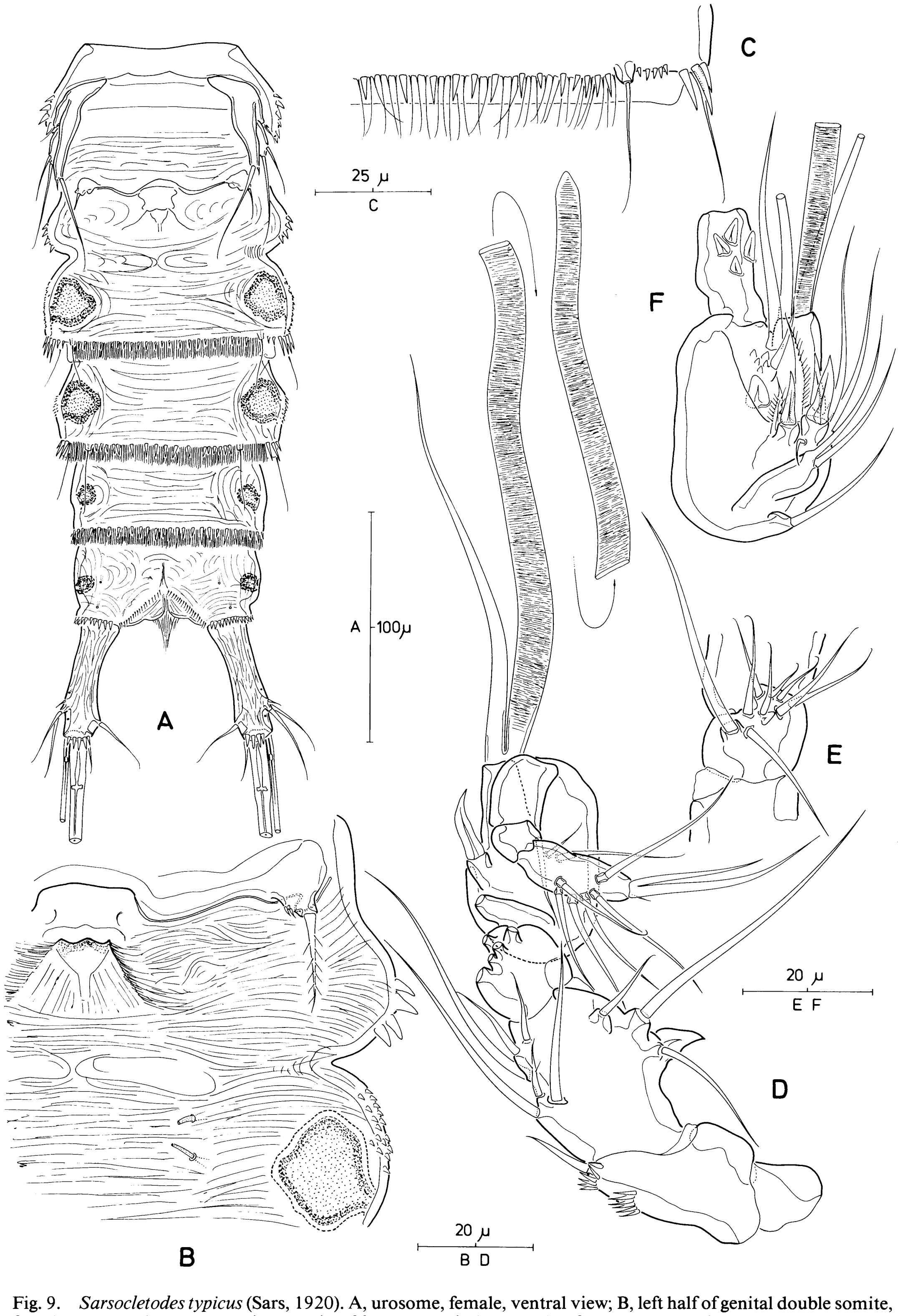

Fig. 9. *Sarsocletodes typicus* (Sars, 1920). A, urosome, female, ventral view; B, left half of genital double somite, female, ventral view; C, posterior margin of first postgenital urosomite, female, ventral view; D, antennula, male

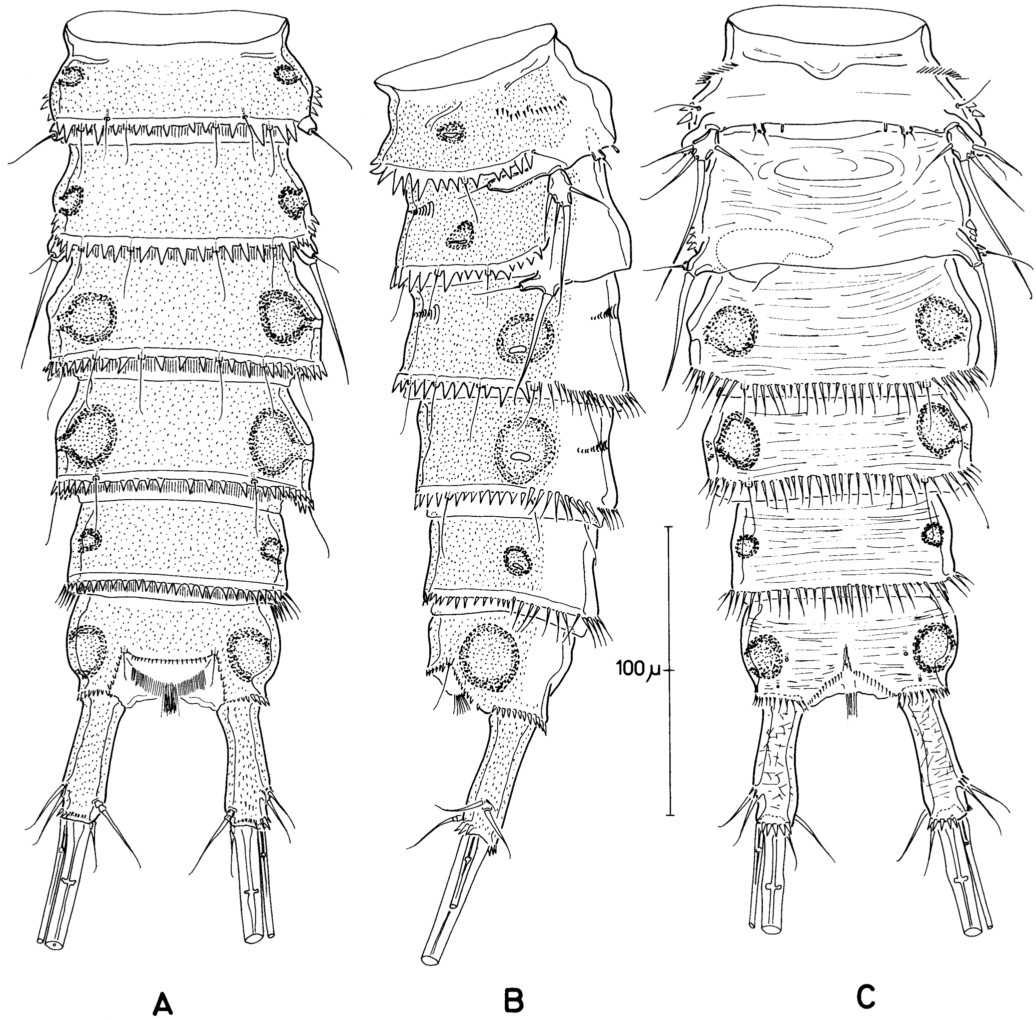

Fig. 10. *Sarsocletodes typicus* (Sars, 1920). A, urosome, male, dorsal view; B, urosome, male, lateral view; C, urosome, male, ventral view.

Type species.—*Miroslavia longicaudata* Apostolov, 1980 [by monotypy].

Miroslavia longicaudata, new species, Apostolov, 1980, pp. 171–174, fig. II (1–9); Apostolov and Marinov, 1988, pp. 319–320, fig. 125 (1a–e).

Remarks.—Despite being inadequately described, there can be no doubt that *M. longicaudata* belongs to the Adenopleurellidae. The morphology of P1, the reduced antennal exopod, and the setation of P2–P4 link the genus closely to *Adenopleurella*. Apostolov (1980) showed large pleural glands in the genital double somite and the antepenultimate somite only, indicating that they might be at least reduced (if not absent) in the remaining two abdominal somites. The glands in the anal somite of *Adenopleurella* were small-sized as well, which reinforces the close relationship between the two genera. The outer terminal seta (IV) on the caudal ramus was not drawn in the original

←

(setation of segments III–V omitted); E, antennula, male, inner side view of segment III; F, antennula, male, inner side view of segments IV and V.

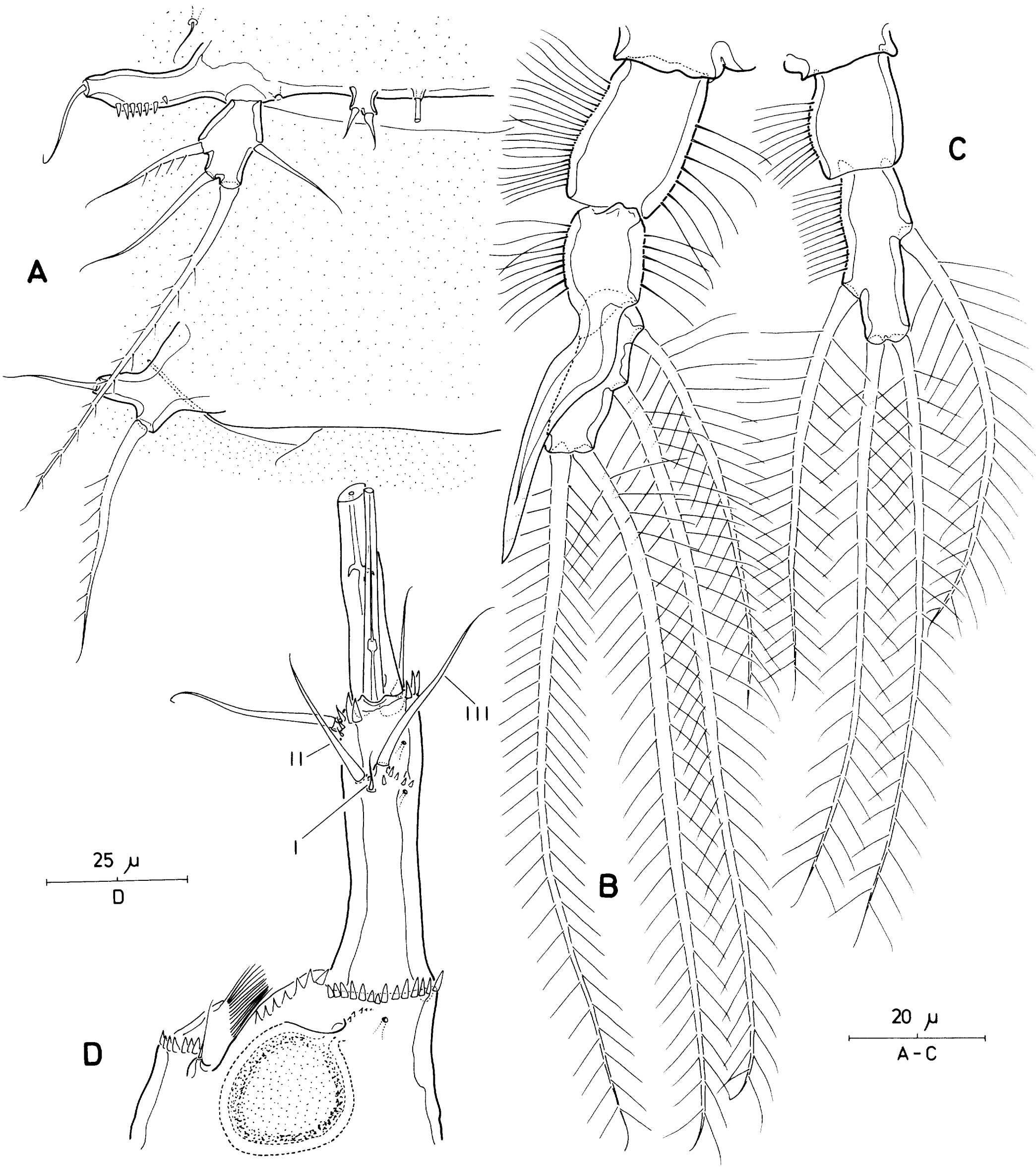

Fig. 11. *Sarsocletodes typicus* (Sars, 1920). A, right P5 and P6, male; B, endopod P3, male; C, endopod P4, male; D, anal somite and left caudal ramus, lateral view.

description; this might indicate that it is reduced in *Miroslavia,* whereas it is well developed in all other Adenopleurellidae. Very striking is the presence of two inner setae on exp–2 P2, a character not found in any of the extant copepods. It leaves no doubt that this extraordinary setal number resulted from a teratological origin; it was nevertheless used in the armature formula presented by Apostolov (1980) and Apostolov and Marinov (1988).

Discussion

Members of the family Adenopleurellidae can be readily recognized on the basis of distinct, paired lateral glands found on the cephalothorax and on all but one (P4) of the body somites. Sars (1920) illustrated these structures for *S. typicus,* but did not mention them in the description. Por (1964) was the first to formally recognize their glandular character and described their detailed distribution pattern. The consistency in size of the various glands between Por's fig. 139 and the present redescription suggests that glandular size might be a useful diagnostic character at the generic level; e.g., the glands of the anal somite in *Adenopleurella* and *Miroslavia* are strongly reduced and in the latter genus those of the penultimate somite are also weakly developed. The globular glands of the Adenopleurellidae are derivations of pleural, secretory pores found in the same position in many other families, and are not homologous with the lateral accessory nuchal organs found on the thoracic pleurotergites of Tachidiidae (Huys, in press b). The latter probably play a rôle in osmoregulation and SEM revealed that they are not associated with integumental pores. Within the superfamily Laophontoidea distinct glandular modifications are also found in the genus *Esola* Edwards. Mielke's (1981) excellent figures of *E. longicauda galapagoensis* show peculiar, sclerotized invaginations at the inner margin of the caudal rami (and probably also on the anterior half of the genital double somite). These structures were also reported by other authors (e.g., Hamond, 1969, and Noodt, 1955), but only Vervoort (1964) mentioned two cup-shaped depressions anteriorly on the cephalic shield of *E. longicauda*. Although these modifications might be derived from enlarged secretory pores as well, they cannot be applied to link the Adenopleurellidae with the Laophontidae because they are not serially homologous and must therefore be a product of parallel evolution.

During its taxonomic history, *Sarsocletodes* has been invariably linked to the genus *Platychelipus*. Lang (1936), inspired by the short endopod of leg 1 in both genera, created the replacement name *Pseudoplatychelipus* for Sar's species, and later (1948: 1450) put *Sarsocletodes* closest to *Platychelipus* in his phylogenetic scheme of the Laophontidae. Nicholls (1941) also reckoned that both genera deviated from typical laophontids and even suggested placing them in a separate family intermediate between the Laophontidae and the Cletodidae. All these presumed affiliations are based primarily on the morphology of P1, and it is, therefore, a crucial step to assess its homology. A comparison is made between *Platychelipus littoralis* Brady (material from the Eastern Scheldt, The Netherlands) and the type species of the family, *Laophonte cornuta* (material from Corsica, Mediterranean) (Figs. 12A, B). In relation to the first thoracopod, Laophontidae have three important characters in common, which can be regarded as synapomorphic of the family: (a) the inner part of the distal margin of the basis has developed a well-defined, broad pedestal which acts as a major articulation point for the enlarged, prehensile endopod; because of the size of this protuberance the insertion plane of the endopod is positioned relatively much more distally than the plane of the basis–[exp–1] joint; the pedestal is often surrounded on the outer margin with areas of flexible membrane; (b) the inner spine of the basis is displaced from the ancestral position at the inner margin and has migrated to the anterior surface and very often near the middle of the basis; this is the obvious reason why it has been omitted in earlier descriptions; (c) the major armature element of the distal endopod segment is a curved claw, variable in size and shape, with ornamentation along the outer margin only; an accessory, small seta is found at the basis of the claw. All three characters were found to be present in *Platychelipus* but not in any of the Adenopleurellidae, which justifies the current taxonomic position of the former. In the latter, there is no difference in the plane of articulation with the basis between the exopod and the endopod, the inner basal spine (or seta) is located at the inner margin, and the major armature element on enp–2 is a bipinnate spine. In addition, the coxa of the Adenopleurellidae is typically adaxially produced (Figs. 1C, 6C), which is never so in the Laophontidae. The short and reduced nature gives the adenopleurellid P1 a juvenile appearance, raising the possibility of a heterochronic (i.e., neotenic) origin. This eventually would relegate the Adenopleurellidae merely as advanced Laophontidae. Conclusive evidence to solve this dilemma can be found in the literature on postembryonic development of Laophontidae, which is unfortunately scarce (Raibaut, 1963; Barnett, 1966; Goswami, 1977). There is no doubt that Goswami's cultures were not *Laophonte setosa* but belonged to a different family; moreover, his poor drawings indicate that he was dealing with two different species. Raibaut's (1963)

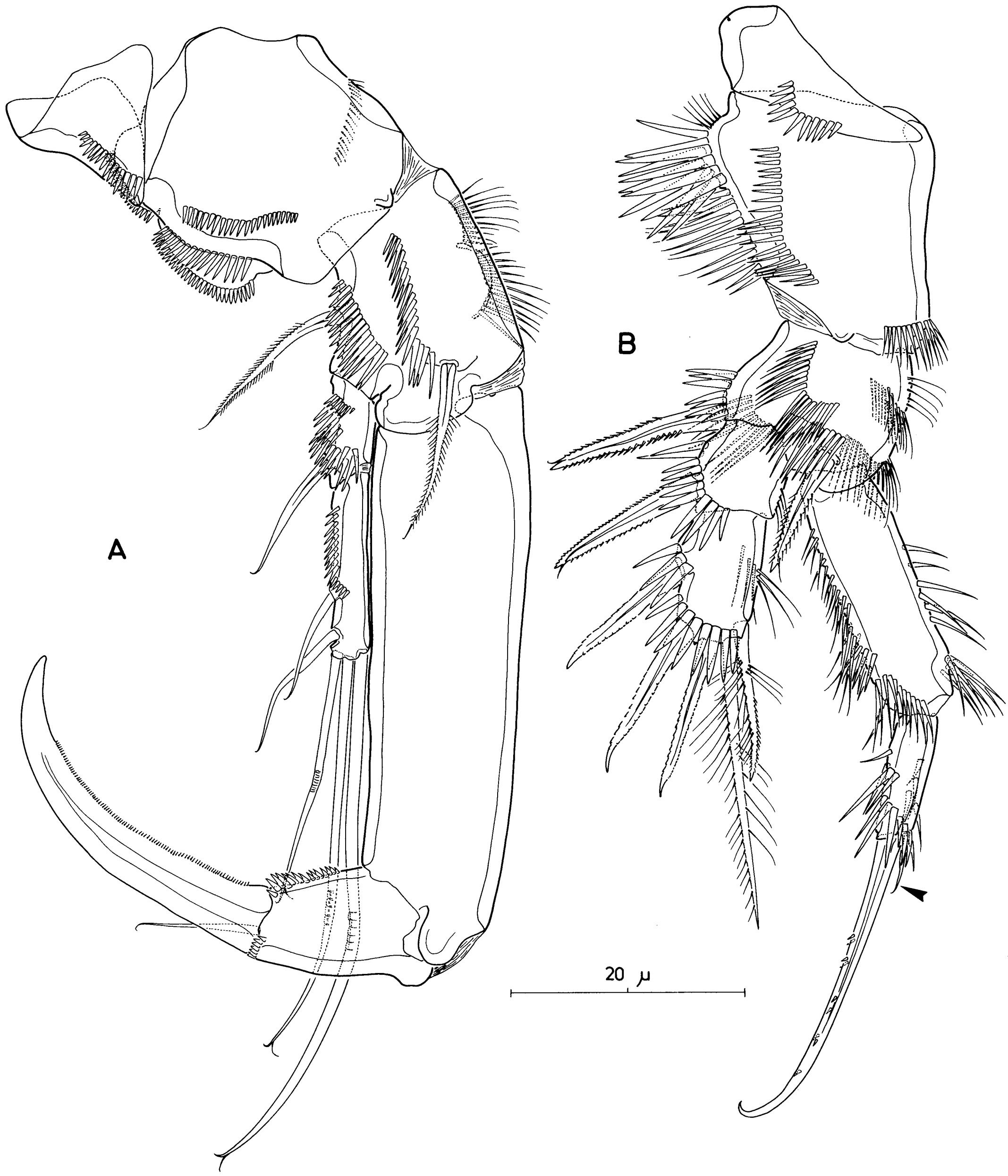

Fig. 12. A, *Laophonte cornuta* Philippi, 1840: P1, anterior view; B, *Platychelipus littoralis* Brady, 1880: P1, male, anterior view (arrow indicating small setule on enp–2).

study on *L. commensalis* is more useful as it provides data on P1 in the first copepodid stage. Two important points emerge from his drawings and from personal observations on *Paronychocamptus nanus* (material from Dievengat, Belgium): (a) the claw on enp–2 is present from copepodid I onwards and does not change profoundly during the successive molts; (b) the inner basal spine is located on the anterior surface and not at the inner margin from the very first appearance (copepodid I in *L. commensalis*, see Raibaut, 1963, figs. 2, 3; copepodid II in *P. nanus*). Barnett's drawings of *Platychelipus littoralis* and *P. laophontoides*, despite being poor, clearly show that the slen-

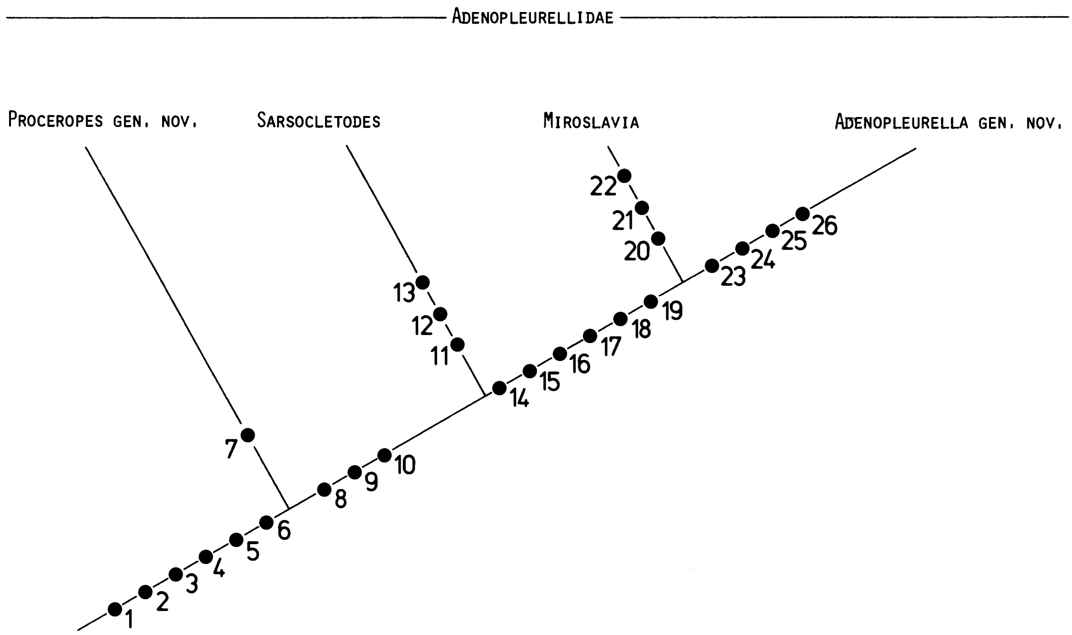

Fig. 13. Cladogram depicting the phylogenetic relationships within the Adenopleurellidae. Monophyly of various clades supported by the following (syn)apomorphies: (1) pleural glands; (2) rostrum fused medially to cephalic shield; (3) exp. A2 bisetose, (4) exp. P1 2-segmented, exp–2 with 4 spines; (5) benp. female P5 with 2 setae; (6) P6 male only slightly asymmetrical, fused to supporting somite; (7) enp–1 P2–P4 reduced, square; (8) enp. P1 slightly longer than exp–1; (9) spinous process on segment II of A1 moderately developed; (10) endopodal lobe female P5 with 1 short and 1 long seta; (11) cephalic shield with 2 large middorsal pores; (12) bifid rostrum; (13) loss of ornamentation on setae of A1; (14) reduction exp. A2; (15) reduction of glands on anal somite; (16) exp–1 P1 with short spines; (17) enp. P1 1-segmented; (18) exp–3 P2–P4 with 2 outer setae; (19) rami of female P5 fused; (20) reduction of glands on penultimate somite; (21) enp–3 P3 with 1 inner seta; (22) seta IV on caudal rami reduced; (23) enp. P1 shorter than exp–1; (24) pleurotergites of abdominal somites laterally expanded and backwardly directed; (25) loss of endopodal lobe of P5, reduction of exp.; (26) female P5 fused to supporting somite.

der terminal claw of enp–2 already appears in the first copepodid stage; the inner spine is located at the inner distal corner (not on the surface as in the adults, but this might be due to distortion during mounting) and not midway on the inner margin as in the Adenopleurellidae. These observations make the possibility of a neotenic origin of the adenopleurellid P1 rather unlikely and favor instead the hypothesis that at least some of the characters (position of inner spine; unmodified spine or seta on enp–2) of the Adenopleurellidae were already present in the ancestral stock of the superfamily Laophontoidea. Other characters excluding the Adenopleurellidae from the laophontids are the antennula with pinnate setae found at least in *Adenopleurella* [except for 1 or 2 possible pinnate spines on segment II (see, e.g., Mielke, 1981), all others are bare in Laophontidae] and the male P6 which is fused to the supporting somite on both sides [one member free in Laophontidae]. A detailed analysis of the phylogenetic relationships at the family level within the Laophontoidea is given in a separate paper (Huys, in press a). A scheme of the possible relationships within the Adenopleurellidae is presented in Fig. 13. The phylogenetic scheme was generated by hand; it illustrates that the evolution within the family went primarily along reductions in the P1, P5, and the pleural glands.

Adenopleurellidae are predominantly inhabitants of deep muddy sediments or sands containing a high amount of silt. Only *Adenopleurella* was found in coarse coralligenous sand. The egg sac of *S. typicus* contains about 25 eggs. The precopulatory clasping mode is unknown.

Key to the Genera of the Adenopleurellidae

1. Enp. P1 2-segmented; exp-3 P2–P4 with 3 outer spines 2
- Enp. P1 1-segmented; exp-3 P2–P4 with 2 outer spines 3
2. Rostrum bifid at tip; enp. P1 shorter than exp .... *Sarsocletodes* Wilson
- Rostrum not bifid at tip; enp. P1 longer than exp .... *Proceropes,* new genus
3. Pleural areas of abdominal somites laterally expanded; P5 female without endopodal lobe .... *Adenopleurella,* new genus
- Pleural areas of abdominal somites not laterally expanded; P5 female with long endopodal lobe .... *Miroslavia* Apostolov

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