

A redescription of the presumed associated *Caligopsyllus primus* Kunz, 1975 (Harpacticoida, Paramesochridae) with emphasis on its phylogenetic affinity with *Apodopsyllus* Kunz, 1962

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Abstract

Caligopsyllus primus Kunz, 1975, reported from tidal pools near East London (South Africa), is redescribed and figured on the basis of type material. An amended diagnosis of the genus *Caligopsyllus* Kunz, 1975 is presented. Cladistic analysis falsified the hypothesis of a close relationship between *Caligopsyllus* and *Kliopsyllus* Kunz, 1962, favouring instead a link with *Apodopsyllus* Kunz, 1962. The morphological modifications are discussed within the context of a possible ecto-associated life-style. Finally, a standard format of abbreviations and terminology is proposed for the paramesochrid caudal ramus.

Introduction

Whilst muds and very fine sands are regularly nematode dominated, a special fauna is found in the interstices between the sand grains of capillary sediments; this fauna was termed the 'interstitial fauna' by Nicholls (1935) while Remane (1940) coined the word 'mesopsammon'. Adaptation to life in the interstices of the sand has resulted in the independent evolution of a number of morphological features within many taxa. One of these is small size.

Paramesochrids are among the smallest harpacticoid copepods known from the interstitial environment. They are cylindrical, elongate animals that occupy the labyrinth of interstices by wriggling around and between the particles. Some of them have attained a vermiform shape (e.g. *Apodopsyllus*) usually accompanied by a reduction of the swimming legs and by a gliding movement.

Until Kunz (1975) described a new genus from tid-

al pools of a reef situated near East London (South Africa), the family Paramesochridae Lang, 1948 consisted exclusively of free-living representatives. The author named the genus *Caligopsyllus* because the general habitus and the structure of the fourth leg resembled that of the parasitic copepod *Caligus* Müller, 1785 (Siphonostomatoida, Caligidae).

Opinions have varied as to the affinities of *Caligopsyllus* within the Paramesochridae. Kunz (1975) related *Caligopsyllus* to *Apodopsyllus* Kunz, 1962 on the basis of the endopodital loss in legs 2–4. When revising the Paramesochridae, Kunz (1981) further explored the relationships of this monotypic genus and concluded that the similarity with *Apodopsyllus* is superficial, favouring instead a link with *Kliopsyllus* Kunz, 1962 and placing special emphasis on the occurrence of three setae on the distal exopodite segment of P2–P3. In this paper Kunz (1981) drew attention to the morphological adaptations for an ectoparasitic life-style.

Most recently, Huys (1987) indicated that *Caligopsyllus* was the weakest component in Kunz' (1981) cladogram and falsified the hypothesis of a close relationship between *Kliopsyllus* and *Caligopsyllus* on the basis of a cladistic analysis, excluding consequently the latter genus from the *Kliopsyllus*-group. Despite the profound modifications upon the basic morphological plan, Huys (1987) argued strongly for the incorporation of *Caligopsyllus* into the *Scottopsyllus*-group of the subfamily Paramesochrinae Lang, 1948, suggesting that its affinity may lie with *Apodopsyllus*.

In the present paper a complete redescription of *Caligopsyllus primus* Kunz, 1975 is presented in order to support the reassessment of its phylogenetic relationships.

Material and methods

Material examined: 1 ♀ (holotype) and 1 ♂ (allotypic paratype), spirit preserved and deposited in the Zoologisches Museum, Hamburg under no. K 30370.

Before dissection the habitus was drawn in lactophenol and body length measurements were made. The male was dissected in lactic acid and the dissected parts were placed in polyvinyl lactophenol mounting medium, between two coverslips, and individually positioned on 7 Cobb aluminium slide frames. This mounting procedure allows the slide to be placed on either of its surfaces so that both anterior and posterior aspects of the appendages can be observed. Of the holotype female only the left antennula was mounted on a slide.

Apodopsyllus spec. was examined by scanning electron microscopy (SEM) with a JEOL JSM-840 microscope. Specimens of both sexes were prepared by dehydration through graded ethanol, critical point dried, mounted on stubs and sputter coated with gold.

All figures have been prepared using a camera lucida. Abbreviations used throughout the text and figures are: A1 = antennula, A2 = antenna, P1–P6 = first to sixth leg, exp = exopodite, enp = endopodite, benp = baseoendopodite. The terminology and presentation of the setal formulae are adopted

from Lang (1948, 1965). The terms *pars incisiva*, *lacinia mobilis* and *pars molaris* are omitted in the description of the mandibular gnathobasis (Mielke, 1984a). Concerning the segmental composition of the maxilliped and the mandible, the interpretation of Boxshall (1985) is followed.

Systematics

Family Paramesochridae Lang, 1948

Subfamily Paramesochrinae Lang, 1948

Genus *Caligopsyllus* Kunz, 1975

Amended diagnosis

Body depressed, ventral side of metasoma flattened without any trace of demarcation between somites. Cephalosoma large, with epimera deflexed and deep, including between them the oral parts and forming a rounded extension at each posterolateral corner. Except for P5-bearing somite, free pedigerous somites laterally produced. Urosoma narrow and extremely short. Pseudopericulum rounded. Caudal rami longer than wide; all setae well developed.

Sexual dimorphism in antennula, fifth and sixth legs and in genital segmentation.

Rostrum prominent, defined at base. Antennula seven-segmented in female, first segment much broader than long, furnished with aesthetasc on fourth and seventh segments; five-segmented and chirocer in male, furnished with aesthetasc on fourth segment. Antenna with basis, unisegmented exopodite with hollow, funnel-shaped setae. Mandible with long and narrow coxa, 3-segmented endopodite and 1-segmented exopodite. Maxillula with well developed praecoxal arthrite, endopodite 1-segmented, exopodite represented by one seta. Maxilla with 3 endites, endopodite 1-segmented. Maxilliped robust with 2-segmented endopodite. Exopodite of P1 1-segmented, furnished with 5 setae; endopodite 2-segmented, proximal segment long and devoid of inner seta, distal segment minute and with 2 terminal abruptly curved claws. P2–P4 with coxa and basis prolonged along dorso-ventral axis, exopodites laterally directed, endopodites completely absent.

Exopodite P2–P3 3-segmented; appendicular hyaline frill strongly developed; proximal and middle segment with outer seta, distal segment with 2 setae. Exopodite P4 1-segmented with 1 lateral and 2 distal setae. Genital double-somite without any trace of subdivision, genital complex denticulated. Both P5 forming a transverse plate in female, with 5 setae on both sides. Baseoendopodite and exopodite P5 in male forming a common plate with 4 setae; P6 forming a plate with 3 setae which is fused at basis with last thoracic somite.

Type species: *Caligopsyllus primus* Kunz, 1975

Type locality: shell gravel from tidal pools of a reef situated in the mouth of the Gonubie River east of East London, South Africa.

Redescription

The descriptions of the mouth parts (except for female antennula) and of the natatorial legs P1–P4 are based on the paratype male.

Female (holotype)

Body length: 353 μm rostrum and caudal rami excluded; 385 μm rostrum and caudal rami included. Maximum width (178 μm) measured at posterior margin of cephalic shield.

Body (Fig. 1-A) depressed dorsoventrally, distinctly tapering posteriorly, almost colourless and not transparent. Nauplius eye absent. Integument smooth (except for cephalic shield).

Rostrum (Fig. 4-A) prominent, about 1.6 times as long as basal width; slightly tapering distally; not fused with cephalosoma, defined at base; furnished with a pair of delicate sensillae at 1/6 distance from the tip which is pointing downwards; longer than first antennular segment.

Cephalosoma large, broader than long, narrowing anteriorly; occupying about 1/3 of the total body length; furnished with seven sets of delicate sensillae. Cephalic epimera deflexed and deep, including between them the oral parts; each posterolateral corner forming a prominent rounded extension. Dorsal surface of cephalic shield provided with a series of

cuticular ridges arranged in a circular pattern and extending from base of rostral projection to almost posterior margin; lateral and posterolateral margin forming a hyaline membrane. Pleurotergite of first pedigerous somite not covered with cephalic integument.

Free thoracic somites (P2–P4) laterally produced; each furnished with 6 delicate sensillae. Ventral side of metasoma flattened without any trace of demarcation between somites. P5-bearing somite short and much narrower than preceding ones; posteroventral free edge forming 2 rounded lappets which partially cover P5.

Genital double-somite without any trace of subdivision; markedly protruded ventrally over first abdominal segment; slightly tapering posteriorly; furnished with 8 sensillae.

Abdomen strongly reduced in size (40 μm , = less than 1/8 of total body length). First abdominal somite provided with 6 sensillae; posterior edge forming a mid-ventral outgrowth which extends almost to hind edge of penultimate somite. The latter somite is devoid of sensillae; dorsal posterior margin forming a rounded pseudoperculum. Anal somite furnished with 2 dorsolateral sensillae.

Caudal rami (Fig. 1-A; 5-A, B) parallel, about 1.5 times as long as greatest width; tapering posteriorly; furnished in proximal half with two lateral bare setae of which dorsalmost shorter. Subapical outer seta strong and two-sided spinulose. So-called principal terminal seta well-developed, fused at basis with long spinulose outer seta and accompanied with a short seta (proximal part swollen) on inner side. Dorsal seta bare and bi-articulated at base.

Antennula. (Fig. 1-B) Seven-segmented. First segment broader than long; inner margin furnished with long spinules. Second segment provided with nine slender setae, of which one bi-articulated at base; the others situated along inner side. Third segment furnished with eight bare setae along inner margin of which one sub-proximally geniculate and two biarticulated at base. Inner distal corner of fourth segment forming a sub-cylindrical processus provided with a slender aesthetasc (L: 55 μm) which is confluent at base with a long bare seta; one bare seta arises from inner side of processus just men-

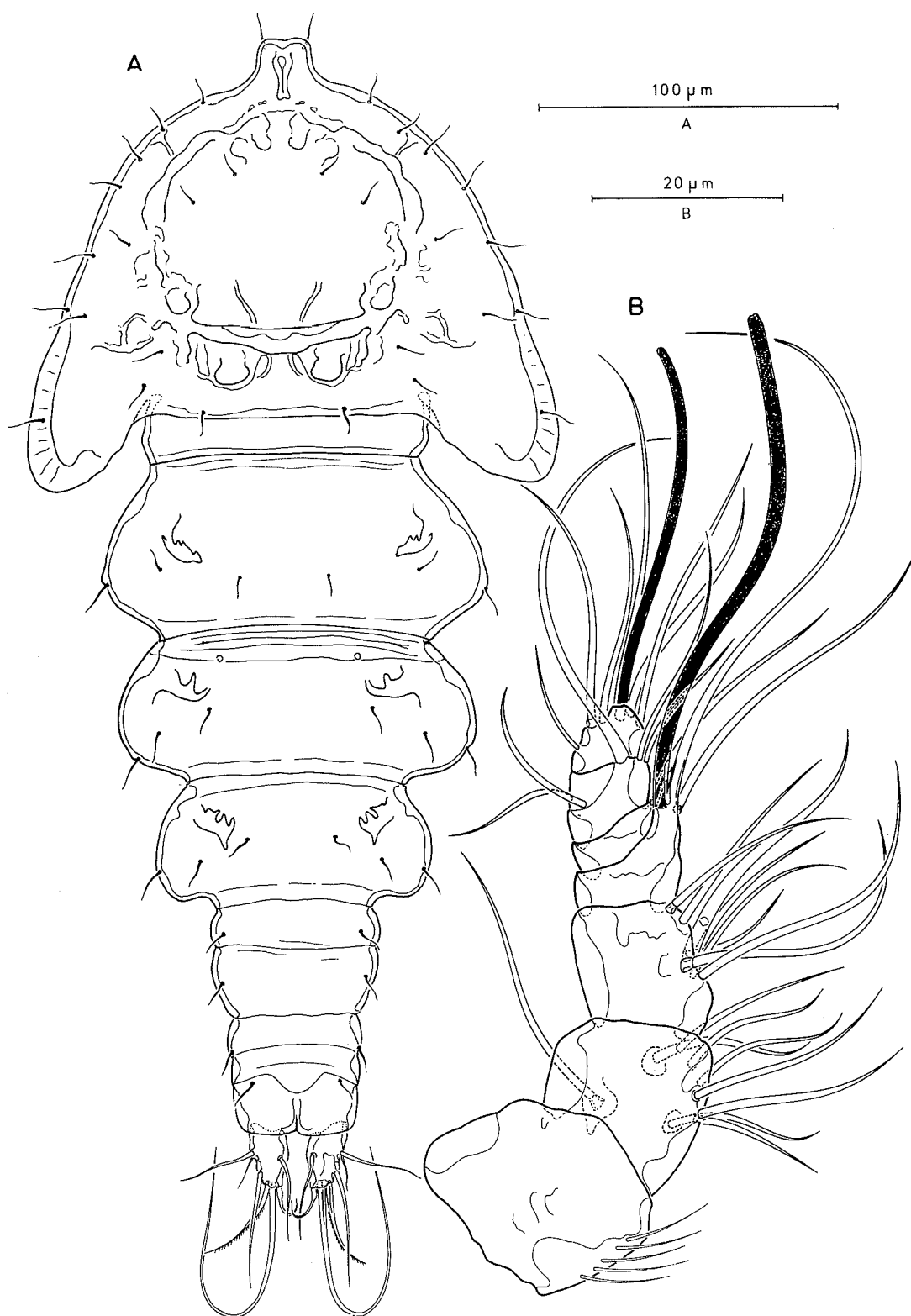


Fig. 1. *Caligopsyllus primus* Kunz, 1975 (♀). — A. Habitus, dorsal. — B. Antennula.

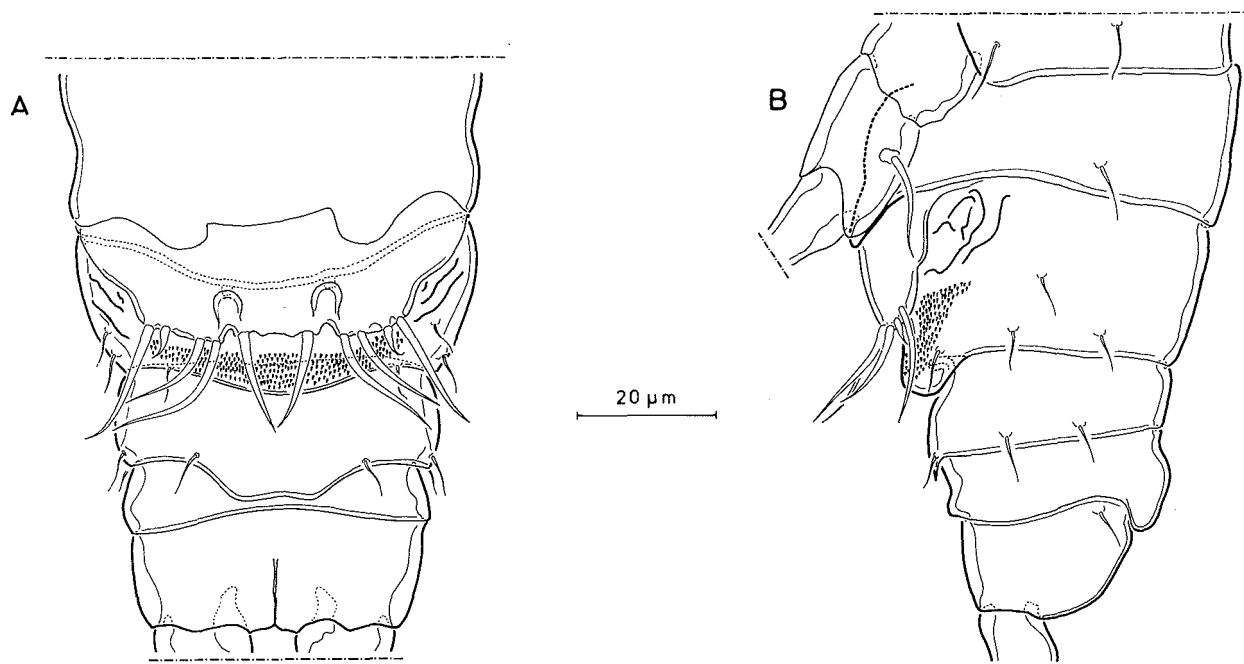


Fig. 2. *Caligopsyllus primus* Kunz, 1975 (♀). — A. Urosoma ventral. — B. Urosoma, lateral.

tioned. Inner subdistal corner of fifth segment provided with a slender seta. Penultimate segment undistinctly subdivided; armed with two lateral outer setae and three setae at distal end. Last segment narrowing distally, furnished with six bare setae and one apical slender aesthetasc (L: 40 μ m).

Leg 5. (Fig. 2-A, B) Fifth pair of legs confluent, forming a distinct transverse plate, covering anterior half of genital double-somite; exopodite and baseoendopodite confluent; furnished with 5 bare setae on each side, the outer one long and almost straight, the following one spiniform and short, the three inner ones long and curved.

Genital complex. (Fig. 2-A, B) Provided with minute denticles in posterior half; devoid of setae (cfr. P6).

Male (allotypic paratype)

Body length: 306 μ m rostrum and caudal rami excluded; 338 μ m rostrum and caudal rami included. Maximum width (157 μ m) at posterior edge of cephalic shield.

General body shape (Fig. 3-A, B), colour, ornamentation and sensillar pattern as in female. Sex-

ual dimorphism in antennula (Fig. 4-B), fifth and sixth legs (Fig. 5-A, B, B'); genital segmentation. Distinct separation between prosoma and urosoma. P6-bearing somite with two dorsolateral sensillae; ventral side swollen and fused on both sides with sixth pair of legs. (Fig. 5-B, B'). First abdominal somite small, furnished with two lateral and two ventrolateral sensillae; no denticles observed in genital area. Spermatophore kidney-shaped, occupying third and fourth thoracic somites (L: 60 μ m).

Antennula. (Fig. 4-B) Five-segmented, short, robust; chirocer. First segment much broader than long, furnished with a minute spiniform seta in inner subdistal sector. Second segment forming a distinct medial processus at distal end; provided with nine slender setae of which two biarticulated at base. Distal inner margin of third segment furnished with four setae; anterior margin provided with one long and one short seta which are biarticulated at base. Fourth segment swollen, largest; subcircular with a concave depression at anterior margin; an irregularly shaped aesthetasc (L: 35 μ m) arises from the central dorsal surface and is confluent at base with a bare seta; a complex arrangement composed of 16

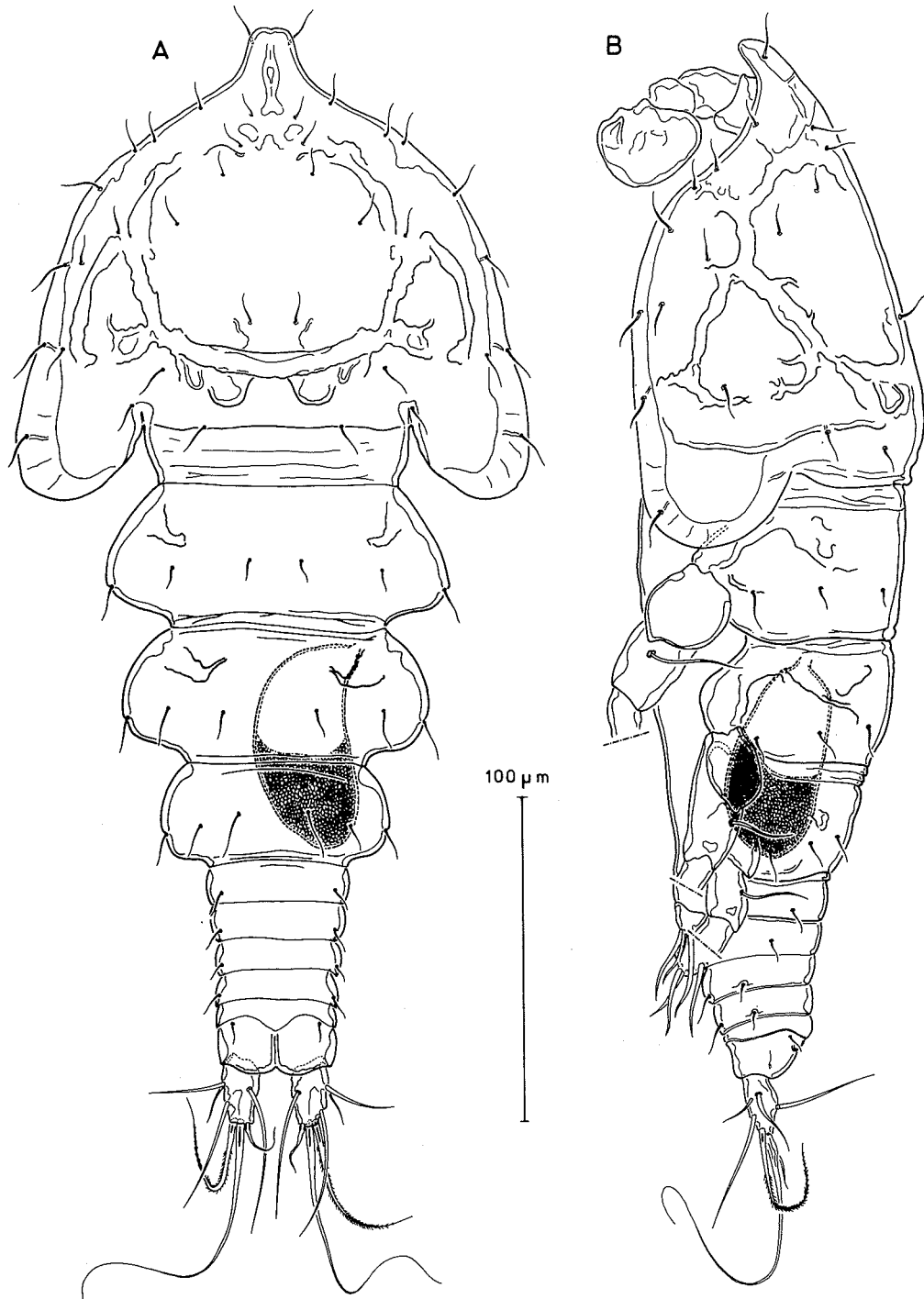


Fig. 3. *Caligopsyllus primus* Kunz, 1975 (♂). — A. Habitus, dorsal. — B. Habitus, lateral.

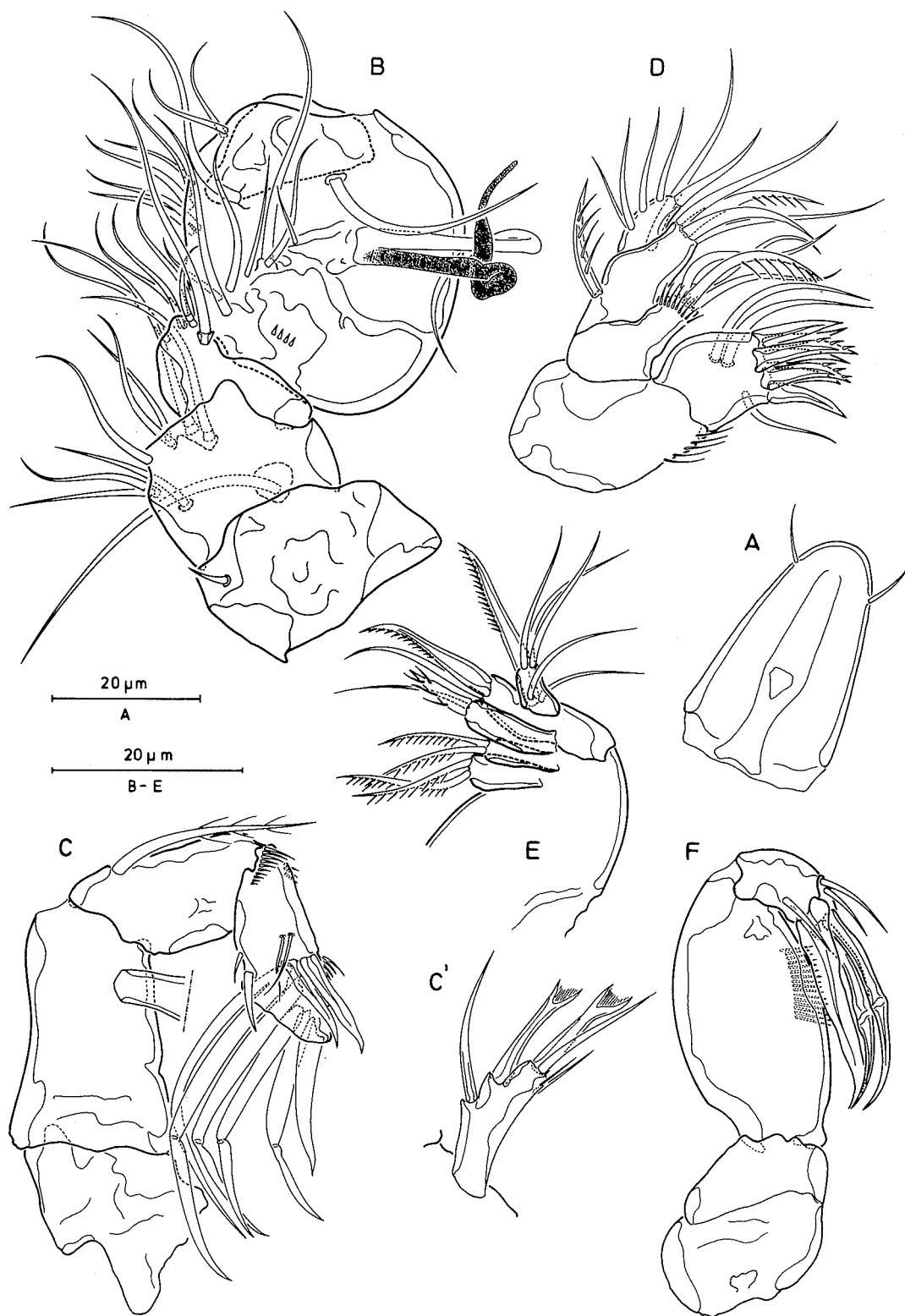


Fig. 4. *Caligopsyllus primus* Kunz, 1975 (♂). — A. Rostrum. — B. Antennula. — C. Antenna. — C'. Antennal exopodite. — D. Maxillula. — E. Maxilla. — F. Maxilliped.

bare setae is situated in inner half; a few minute spinules are observed near posterior margin. The small subtriangular terminal segment is devoid of setae or other armature and lies in close contact with the penultimate segment.

Antenna. (Fig. 4-C, C') Coxa well defined, forming a distinct proximal processus. Basis slightly narrowing distally, approximately 1.4 times as long as maximum width, without any spinules or setae. Exopodite unisegmented, slightly bending outwards, about 3.6 times as long as wide; inner side furnished with two setae, the distal one funnel-shaped at tip; apex provided with a funnel-shaped seta, accompanied by a bare seta and two subapical minute spinules. First endopodite-segment furnished with a two-sided spinulose seta at about a third the length of inner margin. Anterior margin of second endopodite-

segment furnished with two slender setae and two strong claw-like setae in distal half, and with some diminutive spinules subproximally; posterior margin with a spiniform seta and a small spinule; distal edge furnished with one spiniform and four geniculate setae, the posterior one longest and confluent at base with a slender bare seta.

Mandible. (Fig. 5-C, C') Coxa (corpus mandibulae) long and narrow. Cutting-edge with six (bidentate) spines and one slender bare seta on the dorsal side. Palp well developed. Basis rectangular, inner margin furnished with fine spinules and two bilaterally spinulose setae. Exopodite unisegmented, with four bare setae (two distally, two laterally). Endopodite long, three-segmented; first segment about 2.7 times as long as greatest width, furnished with two bare setae at inner subdistal corner; second segment slightly

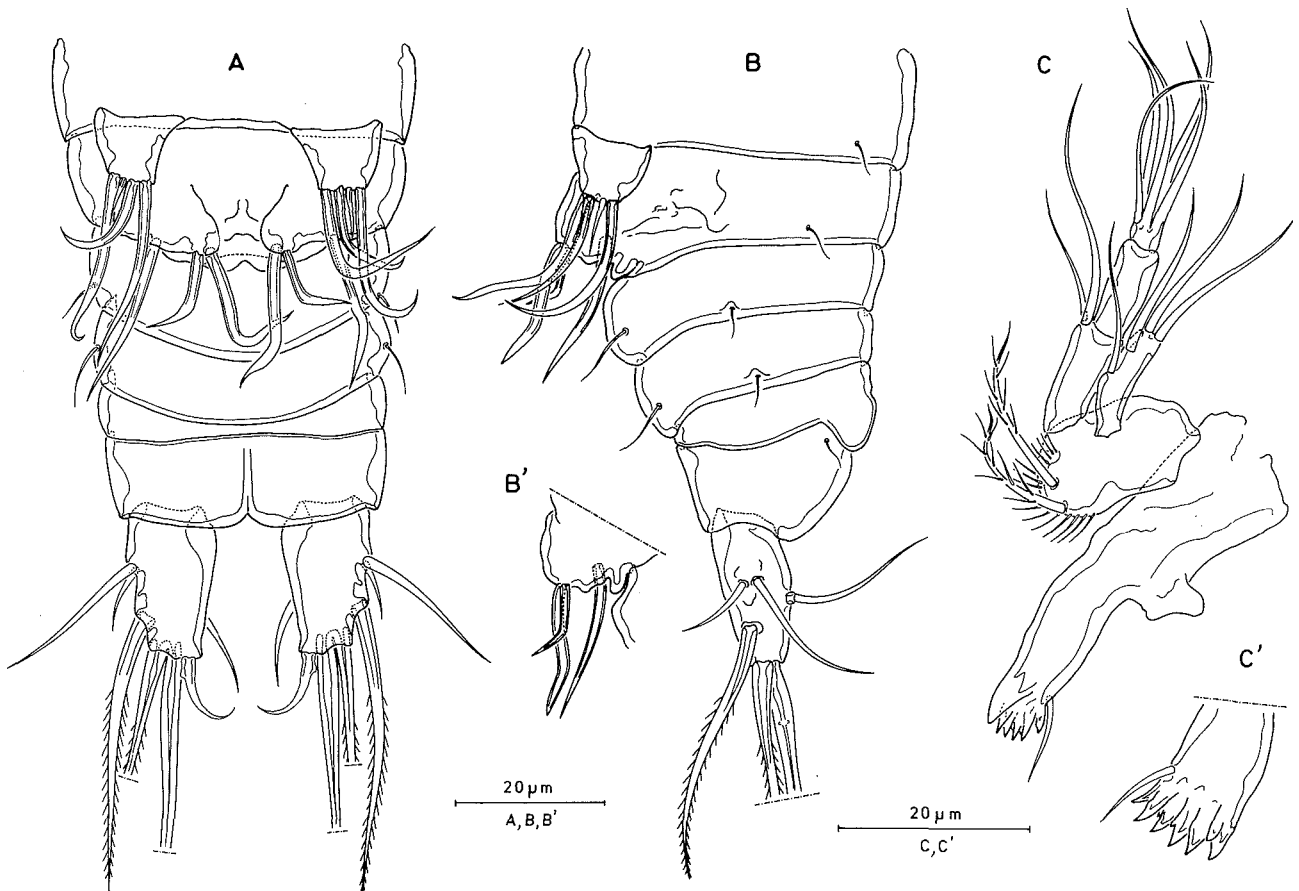


Fig. 5. *Caligopsyllus primus* Kunz, 1975 (♂). — A. Urosoma, ventral. — B. Urosoma, lateral. — B'. P6, lateral. — C. Mandible. — C'. Mandible, cutting edge of praecoxa.

shorter than preceding one, without any ornamentation; distal segment small, with five slender apical setae of which at least three confluent at base.

Maxillula. (Fig. 4-D) Praecoxa squarish, inner edge with a few long fine spinules subdistally. Arthrite of praecoxa armed with seven curved spines on apical edge, one slender seta on dorsal edge and two juxtaposed slender setae on anterior surface near the convex ventral edge. Coxal inner processus cylindrical, furnished with three closely set setae and one spinulose claw apically, which are accompanied at base with some fine spinules. Inner processus of basis extending beyond coxal inner processus, armed with four closely set setae apically (of which one spinulose and claw-like) and one long, slender subdistal seta on ventral edge. Endopodite unisegmented, tapering distally; furnished with five bare setae. Exopodite represented by a stout curved spine which is spinulose along inner edge.

Maxilla. (Fig. 4-E) Syncoxa furnished with three closely set, subcylindrical endites. Proximal and middle endites armed apically with two unilaterally spinulose setae. Distal endite longest, furnished with one stout spinulose spine accompanied with a slender seta. Basis armed apically with one slender seta and one strong claw which is spinulose along subdistal inner edge. Endopodite well defined, furnished with five slender setae and one strong claw.

Maxilliped. (Fig. 4-F) Robust. Syncoxa showing trace of partial subdivision, approximately 1.4 times as long as wide, unornamented. Basis about 2 times as long as maximum width, furnished with fine spinules along middle inner margin. Endopodite two-segmented; first segment with a short spiniform seta and a strong claw which is acutely bending at tip; second segment minute, with two medially geniculate claws distally and two spiniform setae near junction with preceding segment.

Natatorial legs. (Fig. 6) P1 prehensile, biramous; P2–P4 uniramous (endopodite absent), laterally directed.

P1. (Fig. 6-A) Coxa well developed, furnished with

a spinular row in proximal half of anterior surface near outer edge. Basis prolonged transversely; outer part furnished with long marginal spinules and two oblique spinular rows; inner side provided with a stout bilaterally spinulose seta. Exopodite unisegmented; approximately 2.5 times as long as maximum width; much shorter than endopodite; fringed with spinules along outer edge and provided with one subapical outer seta and four plumose setae of different lengths at distal end. Endopodite two-segmented, directed inwards; first segment strongly developed and exceeding exopodite, devoid of setae, about 3 times as long as wide, slightly tapering distally, inner margin spinulose in distal half, subdistal inner part fringed with a transverse spinular row; second segment minute, triangular, armed with two (1 lateral, 1 subterminal) strong, short claws which are abruptly curved.

P2. (Fig. 6-B) Coxa well developed, not ornamented, markedly protruding outwards over basis. Basis prolonged along dorso-ventral axis, except for a bare seta near subproximal outer corner without any ornamentation. Exopodite three-segmented, laterally directed; proximal segment furnished with long spinules along outer margin and a unilaterally spinulose seta near subdistal outer corner; demarcation with middle segment at an oblique angle; middle segment with strongly developed inner hyaline frill which covers proximal part of distal segment, furnished with minute spinules and a basally swollen seta at outer margin; distal segment tapering proximally, inner hyaline frill well developed, furnished with diminutive spinules and two stout setae (spinulose along subdistal margin) at distal edge, the inner being the longer. Endopodite completely absent.

P3. (Fig. 6-C) General form and setation as in preceding leg.

P4. (Fig. 6-D) Small, uniramous. Coxa small, slightly protruding outwards over basis. Basis prolonged, furnished with a bare seta at outer margin. Exopodite unisegmented, showing trace of subdivision in middle part which is slightly constricted; furnished in proximal half with a row of long spinules along outer edge and a spinulose seta which is arising from

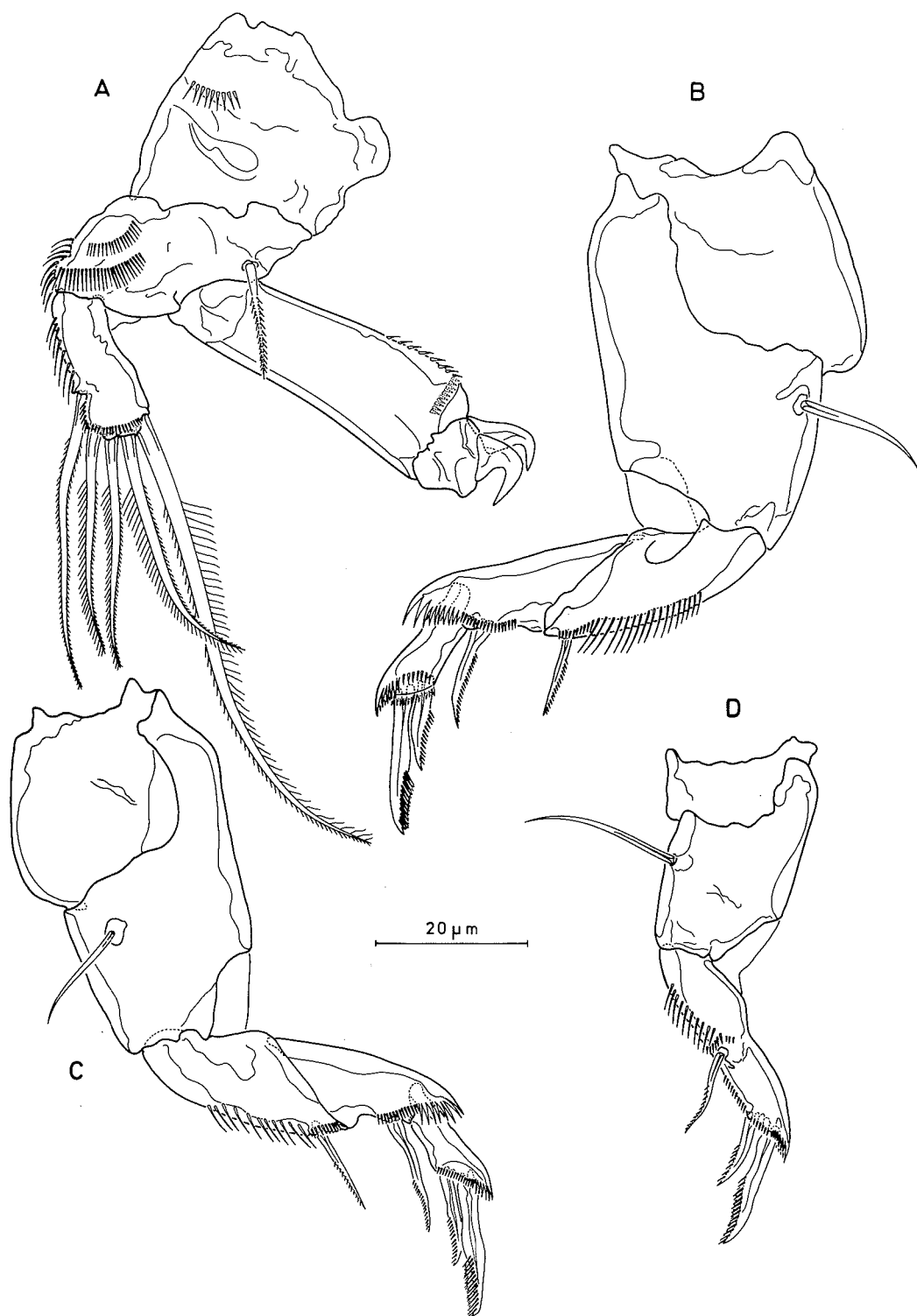


Fig. 6. *Caligopsyllus primus* Kunz, 1975 (♂). A. P1. B. P2. C. P3. D. P4.

about middle outer margin and which is accompanied at base by some minute spinules; distal half armed with two setae which are spinulose along sub-distal end and with a well developed hyaline frill at inner side. Endopodite completely absent.

P5. (Fig. 5-A, B) Fifth pair of legs not medially fused. Exopodite and baseoendopodite fused, forming a square plate which narrows distally; furnished with four setae, three of which are strongly developed and curved.

P6. (Fig. 5-A, B) Sixth pair of legs not medially fused. Exopodite and baseoendopodite forming a thick protruding plate which is fused with the somitic wall; furnished with two stout, curved setae near inner corner and a long bare seta at about middle distal margin.

Discussion

1. Morphological considerations

Kunz' (1975) figures can be completed with the present redescription. Some important amendments have to be mentioned:

- apparently the rostrum has been figured in a wrong position; it is much longer than wide instead of the reverse;
- the minute inner seta on the distal segment of exopodite P2–P4 and the inner seta of the middle exopodite-segment P2–P3 are misinterpretations of the strongly developed appendicular hyaline frill;
- the P5 and P6 of the male are furnished with 4 and 3 setae, instead of 3 and 2 setae, respectively;
- the male antennula is chirocer;
- the unisegmented antennal exopodite has bifid setae.

There is a certain resemblance in general habitus between the males of some Caligidae (e.g. *Caligus minimus* Otto, 1921; *Lepeophtheirus nordmanni* (Edwards, 1840)) and *Caligopsyllus*: even more striking is the similarity in the fourth leg, the cephalothoracic sutures in H-shaped pattern, the posterolaterally produced cephalic shield with its

peripheral hyaline membrane, the reduced urosoma and the short antennulae which are closely set to the cephalon.

Though the type specimens were found in sediment samples, Kunz (1981) was the first to postulate an ectoparasitic existence for *Caligopsyllus*. Various aspects of its morphology can be interpreted as adaptations to a parasitic life on invertebrate hosts, or at least to a life in intimate association with other organisms. If this interpretation is correct, *Caligopsyllus* has no 'need' for a streamlined, well-articulated body or for adaptations which augment its locomotory ability. Hence, its body is dorsoventrally flattened and displays a weakening of the somitic boundaries. In addition, a most striking feature is the similarity in general appearance between *Caligopsyllus* and some recently described cephalopod associated *Cholidiella* species (Tisbidae, Cholidiinae) (Avdeev, 1982, 1986). Of course, *Caligopsyllus*' morphology is not profoundly changed as in many truly ectoparasitic species with a bizarre appearance, yet a copepod can become dependent on another living organism without making gross morphological changes (Kabata, 1979). The absence of such gross modifications is probably due to its type of life-style, phylogenetically probably rather recent and requiring only a fairly loose association with the host.

Morphologically, the adoption of an ectoparasitic or -associated life-style is linked to the evolution of attachment organs, i.e. the adaptation of existing appendages to a new role. The holdfast apparatus in *Caligopsyllus* consists mainly of the modified endopodite of the first leg, which seems to have lost its prehensile character as found in other Paramesochridae. The strong, curved claws serve as anchors ensuring attachment to a presumed host. The other legs have undergone little or no change and are in fact preadapted to an ecto-associated existence. The second through fourth leg are laterally directed in both *Caligopsyllus* and *Apodopsyllus* (synapomorphy, see below). Whilst the position of the 'swimming legs' may have evolved initially to enhance wriggling ability in the interstitial habitat (*Apodopsyllus*), it secondarily ensured optimal contact in the associate-host relation (*Caligopsyllus*).

Though the maxillipeds do not differ fundamen-

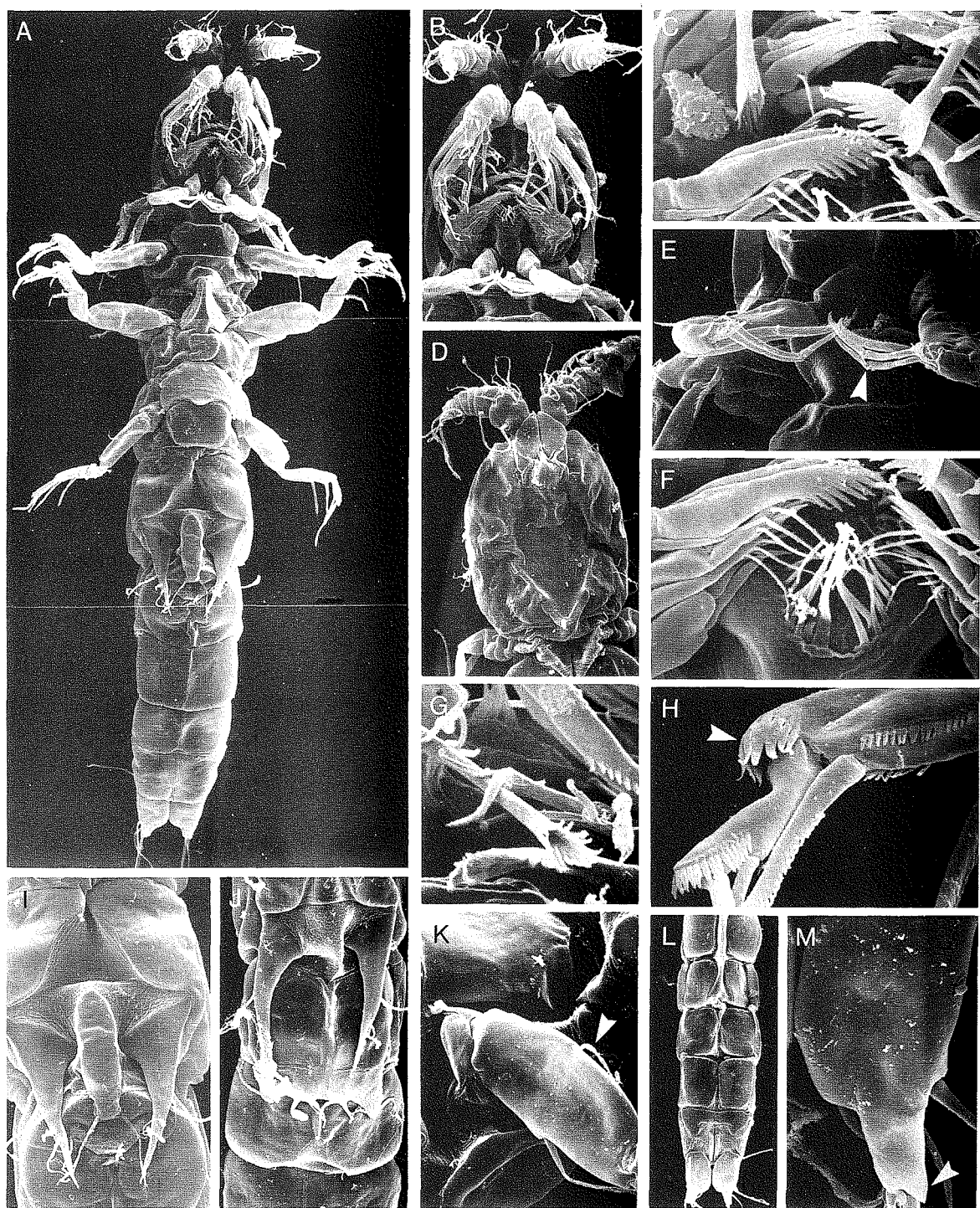


Fig. 7. *Apodopsyllus* spec. (SEM-photography). – A. Habitus, ventral (♀). – B. Cephalosoma, ventral (♀). – C. Funnel-shaped seta of A2. – D. Cephalosoma, dorsal (♀). – E. Maxilliped. – F. Ornamentation of labium and detail of maxillae. – G. Detail of funnel-shaped seta of A2. – H. Appendicular hyaline frill of distal podomeres P3. – I. P5 and genital complex (♀). – J. P5 and P6 (♂). – K. P4, showing minute endopodite. – L. Urosoma, dorsal. – M. Caudal ramus, ventral.

tally from those of other Paramesochridae, it is possible that the functions served by these appendages (manipulation of food, see e.g. Marcotte, 1984) in free-living copepods are no longer performed; for example, a robust maxilliped with strong distal claws (as in *Caligopsyllus*) might be used by an associate to hold on to its host.

In addition, the low-profile body shape will help the copepod to maintain its position on the host, especially when water currents are sweeping the host's surface. As in the Caligidae, the cephalosoma is provided with a marginal membrane which helps to seal off the concavity beneath the cephalic shield and facilitates its adhesive function.

Despite the fact that *Caligopsyllus* is relatively little modified, the fact of being an associate might have an important impact on the reproduction. Fertilization of the female requires efficient locomotory ability of the male, at least until the sex partner is localized. The female genital aperture surrounded by spinules (cfr. *Caligus curtus* Müller, 1785) and the strong curved setae of the fifth and sixth legs in the male are probably evolved to augment indirectly the chance of successful reproduction, i.e. to facilitate manipulation and attachment of the spermatophore.

In conclusion, one can imagine that *Caligopsyllus* is an ecto-associate clinging to its hosts' surfaces with the aid of prehensile appendages (P1, maxilliped, ?A2), but remains capable of free movement over these surfaces. However, until the discovery of the presumed host, one cannot preclude the possibility that the morphological adaptations of *Caligopsyllus* might serve as well for clinging to e.g. flat pebbles, algae,... since many harpacticoids known – with certainty – to live as associates of invertebrates have quite different adaptations.

2. Phylogenetic implications

On the basis of the absence of endopodites in P2–P4, Kunz (1975) originally related *Caligopsyllus* to *Apodopsyllus*. Later, Kunz (1981) questioned whether the endopodital loss might not be convergence and favoured instead a link with *Kliopsyllus*. Recently, Huys (1987) showed that *Caligopsyllus* in

Kunz' (1981) cladogram could not be the sister group of the *Kliopsyllus*-*Kunzia* complex since synapomorphies which can substantiate the monophyletic status of the latter do not exist. Since Kunz (1975, 1981) misinterpreted the appendicular hyaline frill as a supplementary seta, the distal exopodital segment of P2–P4 is furnished with only two setae. Based on this apomorphy *Caligopsyllus* must consequently be assigned to the *Scottopsyllus*-group (Huys, 1987).

Despite some fundamental differences, *Caligopsyllus* seems to be the closest relative of the interstitial genus *Apodopsyllus*. Moreover, these two genera constitute a monophyletic taxon characterized by at least five synapomorphies (*Apodopsyllus aberrans* Mielke, 1984, with its modified caudal rami, reduced mouthparts and an obsolete P5 should undoubtedly be assigned to a new genus (Huys, in prep.) and is purposely omitted from the following discussion):

1. P2–P4: coxa and basis prolonged along dorso-ventral axis, exopodites laterally directed (Fig. 7-A). In the species assigned to the genus *Leptopsyllus* T. Scott, 1894 the coxa and the basis show the same outline, yet the exopodites are directed inwards.
 2. Antenna: exopodite furnished with hollow, funnel-shaped setae which are fringed at tip (these setae are known from the literature as bifid setae, e.g. Lang, 1965; Coull & Hogue, 1978; Mielke, 1975, 1984b) (Fig. 7-C, G). It must be emphasized that, despite the superficial similarity, the structure of these setae is fundamentally different from those found in e.g. *Paramesochra* T. Scott, 1892, *Kliopsyllus* Kunz, 1962 and some species of *Scottopsyllus* Kunz, 1962 *sensu lato*, which are obliquely truncate and fringed at tip. In their description of *A. unguiformis* Coull and Hogue (1978) figured only slender setae; re-examination of the antennal exopodite revealed three funnel-shaped setae.
 3. Endopodite P4 strongly reduced (Fig. 7-K).
 4. Baseoendopodite and exopodite of fifth leg fused in both sexes (Fig. 7-A, I, J). This character is further only found in *Leptopsyllus reductus* Lang, 1948 and *L. elongatus* Drzycimski, 1967.
 5. Appendicular hyaline frill of podomeres II and III in P2–P3 strongly developed (Fig. 7-H).
- Though both genera show a series of derived charac-

ters (autapomorphies), I prefer to treat *Caligopsyllus* as the apomorphic branch of the monophylum because of its secondarily evolved modifications. The genus *Apodopsyllus* (excluding *A. aberrans*) then constitutes the plesiomorphous lineage which is defined by the following autapomorphies:

1. Coxa and basis of P4 fused (Fig. 7-K).
2. Rostrum diminutive, not defined at base (Fig. 7-D).
3. Endopodite P4 represented as a minute hyaline structure (Fig. 7-K).
4. Caudal rami: outer terminal seta (IV) (see remark below) reduced; posterior margin forming a ventral triangular lappet which is covering the basis of the inner terminal seta (V) (Fig. 7-M).
5. Reduction of the integument and partial fusion of body somites allowing a maximum wriggling ability in the interstitial habitat (Fig. 7-L).

At least eight autapomorphies characterize the monotypic genus *Caligopsyllus*:

1. General body shape: cephalosoma and free thoracic somites (except P5-bearing segment) laterally produced; abdomen strongly diminished in size.
2. Antennula: first segment broader than long; chirocer in male.
3. Exopodite P1 short, 1-segmented.
4. Endopodite P1 modified with two terminal strong claws.
5. Exopodite P4 short, 1-segmented.
6. Endopodite P4 completely absent.
7. Genital area provided with numerous denticles.
8. Male P6 fused with thoracic somite.

As a result of these considerations, a cladogram (Fig. 8) can be drawn.

Remarks

It is clear that the crucial step in a phylogenetic study of any group of animals is knowledge of its morphology and systematics. At present the detailed morphology of paramesochrid harpacticoids is only poorly known, except for the excellent studies of Mielke (1975, 1984b, c, 1985a, b). One of the reasons for this state is the small size of these animals. Morphological minutiae of small species are often ig-

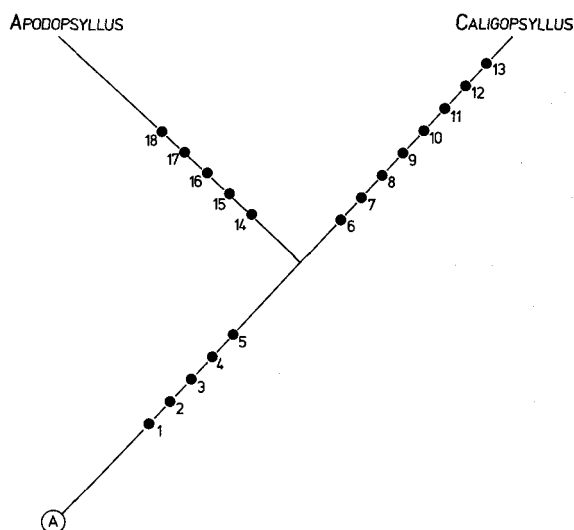


Fig. 8. Cladogram depicting the relationships between *Apodopsyllus* Kunz, 1962 and *Caligopsyllus* Kunz, 1975. Derived characters are: 1 = coxa and basis P2–P4 prolonged, exp laterally directed; 2 = exp A2 with funnel-shaped setae; 3 = enp P4 strongly reduced; 4 = benp and exp P5 fused in both sexes; 5 = exp P2–P3 with strongly developed appendicular hyaline frill; 6 = general body shape: cephalosoma and free thoracic somites laterally produced, abdomen strongly diminished in size; 7 = first segment A1 broader than long, chirocer in male; 8 = exp P1 1-segmented; 9 = enp P1 modified with 2 strong claws; 10 = exp P4 1-segmented; 11 = enp P4 completely absent; 12 = genital aperture surrounded by denticles; 13 = male P6 fused with thoracic somite; 14 = coxa and basis P4 fused; 15 = rostrum minute, not defined at base; 16 = enp P4 represented as a minute hyaline structure; 17 = caudal rami: seta IV reduced, posterior margin forming a ventral triangular lappet; 18 = reduction of integument, partial fusion of body somites. A = ancestor.

nored by observers just because they are small. Most of the time illustrations of the mouth parts and the caudal rami are so inadequate that they are valueless for identification purposes. Hence, it is a difficult task to define true apomorphies and to look how they are distributed throughout the family. Consequently, it is not surprising that taxonomy in this group rarely went beyond the descriptive level.

Comparing the different paramesochrid genera it is apparent that the morphology of the caudal rami may be a character of central importance in understanding the phylogeny of the Paramesochridae in general, and that of the *Scottopsyllus*-group in particular. Paramesochridae have a variety of caudal rami types which can be derived from one ancestral

type. The generalized caudal ramus is characterized by a rectangular shape, a complete lack of sexual dimorphism and a distinct pattern of 7 setae, i.e. 3 lateral, 1 dorsal and 3 terminal ones, two of which are strongly developed.

Although seven well developed setae are common among the Paramesochridae (*Diartrodella*, *Rosopsyllus*, *Paramesochra*, *Kliopsyllus*), these setae may reduce in size and number. The two main terminal setae are usually well developed. Exceptions are found in some species assigned to the subgenus *Scotopsyllus* (*Scotopsyllus*) where the caudal ramus is elongate oval in shape and the terminal setae are reduced to small spiniform appendages (*S. robertsoni* (T. & A. Scott, 1895); *S. pararobertsoni* Lang, 1965; *S. langi* Mielke, 1984). In the genus *Apodopsyllus* and in some *Leptopsyllus* species only one of the terminal setae (the inner one) is normally developed. Occasionally both setae may be vestigial in correlation with a very specialized and exaggerated development of the posterolateral and lateral accessory setae (*A. aberrans*, *L. platyspinosus* Mielke, 1984). In the *Scotopsyllus*-group caudal rami frequently display sexual dimorphism in the shape of the ramus and/or the setae (e.g. *S. minor* (T. & A. Scott, 1895); *Intermedopsyllus intermedius* (T. & A. Scott, 1895); *S. langi*).

Characters of the caudal rami may help to reveal phylogenetic relationships between the paramesochrid genera, if one assumes that the rectangular and heptasetose condition as commonly found in members of the Diartrodellinae is primitive. Such an assumption fits well with the analysis of other characters in these genera (Huys, 1987). The fact that the caudal ramus structure in any one species appears to be constant (except for small variations in the length: width ratio) and may vary between so-called closely related genera, indicates not only its potential as a taxonomic character, yet underlines also its phylogenetic significance. Furthermore, it is one of the relatively few characters which can be observed optimally without the need of dissection.

As previously stated, substantial modifications in the structure and the shape may be found among the various major taxa, however, the occurrence of different caudal ramus types within one genus (e.g.

Scotopsyllus, *Leptopsyllus*) raises some doubt as to the validity of these taxa. It could be assumed that the paramesochrid caudal ramus has evolved along different pathways during which the various setae have undergone profound modifications leading to different types. To reflect the homologies in the basic arrangement of the ramal setae a standard format of abbreviations and terminology is proposed for the Paramesochridae (Fig. 9). This format is pertinent to other harpacticoid families too since Lang's (1948, p. 28) claim that a few Canuellidae such as *Canuella perplexa* T. & A. Scott, 1893 (see Mielke, 1975) and *Sunaristes* Hesse, 1867 (see e.g. Humes & Ho, 1969; Humes, 1971; Hamond, 1973) possess 8 setae on the caudal ramus, cannot be supported.

Most recently, however, Boxshall (1979) described some new mesopelagic tishid genera (*Volkmannia* Boxshall, 1979; *Neotishella* Boxshall, 1979) from the northeastern Atlantic which possess an elongate caudal ramus with 9 armature elements, a character also shared by *Bathyidia* Farran, 1926. Boxshall (1979) considered these genera a distinct lineage which evolved from the ancestral stock of the *Tisbe*-group by adoption of a planktonic habit. This change to a pelagic life-style seemed to be associated with the acquisition of a long modified caudal ramus with a supernumerary arrangement of 9 setae. The two extra elements, however, are thin-walled, flaccid and not like normal setae (tubular pores?) at all (Boxshall, pers. comm.). This deviation from the basic pattern can be considered as a synapomorphy of the *Volkmannia-Bathyidia* lineage.

The following terminology is proposed:

- I. anterolateral accessory seta (often reduced or absent)
- II. anterolateral seta
- III. posterolateral seta
- IV. outer terminal seta
- V. inner terminal seta (often called principal terminal seta)
- VI. terminal accessory seta
- VII. dorsal seta

A comparison of the caudal rami of *Apodopsyllus* and *Caligopsyllus* with the basic pattern is presented in Fig. 9.

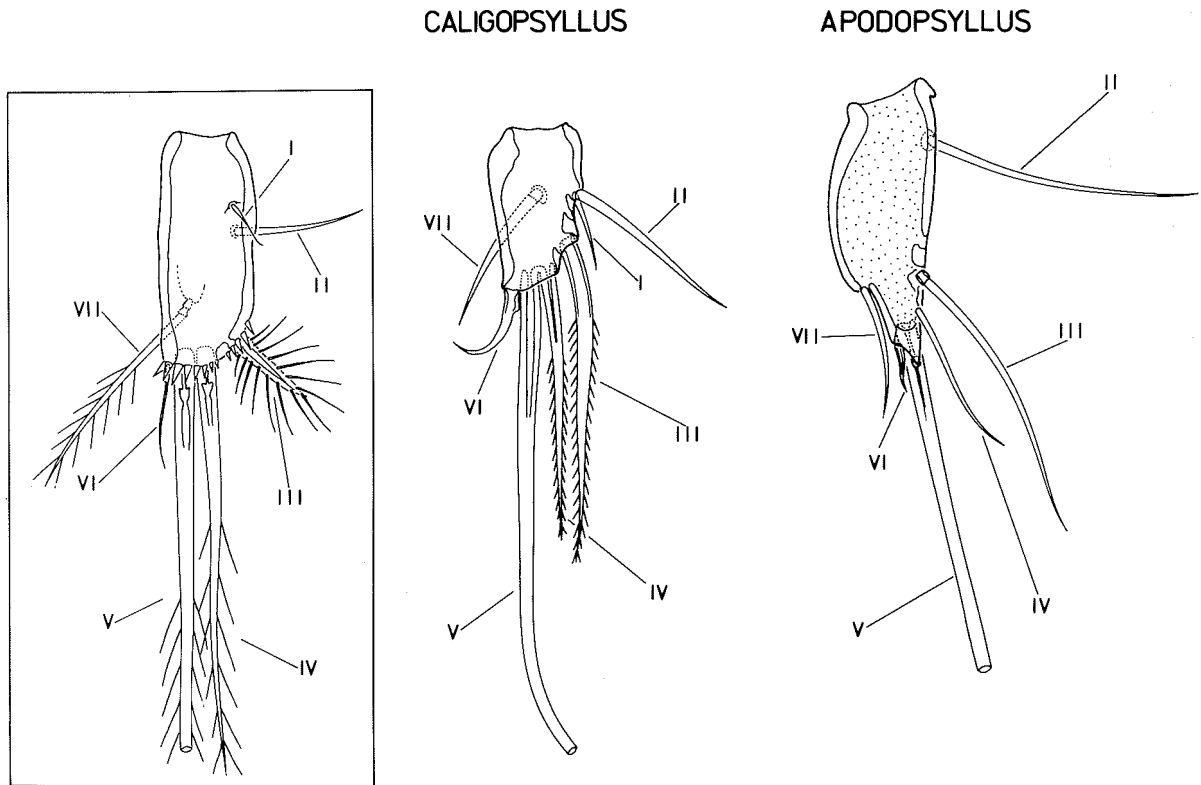


Fig. 9. Proposed standard format for paramesochrid caudal ramus terminology and abbreviations (left), and a comparison with the genera *Apodopsyllus* and *Caligopsyllus*: I = anterolateral accessory seta, II = anterolateral seta, III = posterolateral seta, IV = outer terminal seta, V = inner terminal seta, VI = terminal accessory seta, VII = dorsal seta.

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