



New Family of Deep-Sea Planktonic Copepods, the Paralubbockiidae (*Copepoda: Poecilostomatoida*)

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Abstract *The deep-sea planktonic copepod Paralubbockia longipedia is redescribed from the type specimens, and a new family of Poecilostomatoida is proposed to accommodate it. The Paralubbockiidae fam. nov. is characterized by two unique plesiomorphies, the ventrally located fifth legs and the retention of a separate maxillulular palp, and by the apomorphic states of the endopods of the swimming legs and of the antenna. The sister group of the Paralubbockiidae is identified as the family Oncaeiidae. These are the only two poecilostomatoid families that have retained a vestige of the geniculation mechanism in the antennules of the male. The genus Laitmatobius Humes is here regarded as incertae sedis within the lineage comprising the Oncaeiidae and the Paralubbockiidae.*

Keywords Planktonic copepods, deep-sea, Paralubbockiidae fam. nov., Oncaeiidae.

Introduction

Boxshall (1977) has described *Paralubbockia*, a genus of poecilostomatoid from the deep-water plankton in the North Atlantic off the Cape Verde Islands. He recognized problems with the familial affinities of the genus but proposed placing it in an emended Oncaeiidae, with some reservations because of differences in the structure of the anten-

Contribution No. 458 of the Delta Institute for Hydrobiological Research, Yerseke, The Netherlands.

nae and swimming legs. Subsequent workers, notably Heron et al. (1984), declined to accept *Paralubbockia* as a valid member of the Oncaeidae.

As part of a revision of the ordinal phylogeny of the Copepoda, *P. longipedia* was re-examined because it exhibits several plesiomorphic character states, at least one of which is unique within the Poecilostomatoida. As a result of this study, a new family to accommodate this genus is proposed.

Material and Methods

Type series: Holotype ♀, 5♀♀, and 1♂ paratypes. BM(NH) reg. nos. 1976.8 (holotype), 1976.9 (male paratype) and 1976.10–13 (female paratypes). All specimens from RRS *Discovery* Station 7089 off the Cape Verde Islands at about 18°N 25°W, at depths from 410 to 1250 m (see Boxshall, 1977).

Specimens were examined as permanent slide preparations in polyvinyl lactophenol or as semipermanent preparations mounted in lactophenol sealed with glycel. All figures were prepared using a camera lucida on a Leitz Dialux 20 interference microscope. The terminology of the caudal ramus armature follows Huys (1988).

Paralubbockia longipedia

Adult female slender cyclopiform; comprising 5-segmented prosome and 5-segmented urosome (Fig. 1a, b). Prosome widest at level of first pedigerous somite. Cephalosome with numerous pores distributed over dorsal shield, plus 2 pairs of sensilla posteriorly, either side of dorsal midline. Articulation between first pedigerous somite and cephalosome nonfunctional, but marked by an entire suture line. First pedigerous somite bearing several pairs of pores but no sensilla. Second to fourth pedigerous somites free, each bearing 2 pairs of sensilla and several pairs of pores.

Urosome (Fig. 2a) comprising fifth pedigerous somite, genital double somite, and three free abdominal somites. Fifth pedigerous somite bearing leg 5 ventrally near posterior margin (Fig. 2a); ornamented with a middorsal and pair of lateral pores. Genital double somite comprising completely fused genital and first abdominal somites, each ornamented with a middorsal and pair of lateral pores (Fig. 2e). Genital apertures located in anterior third, at widest point of double somite; dorsolateral in position and each closed off by operculum armed with 2 small spines representing sixth leg (Fig. 2f). Posterior margin ornamented with irregularly serrated membrane. First and second free abdominal somites ornamented with a middorsal and pair of lateral pores, and serrated membrane along posterior margin. Anal somite with a middorsal and 2 pairs of lateral pores, and with a row of minute denticles laterally and ventrally on posterior margin (Fig. 2c–d).

Caudal ramus (Fig. 2c) widest and deepest distally, about 2 times longer than wide; armed with a midmargin lateral seta (II), short inner (VI) and outer (III) apical setae, 2 long terminal setae (IV, V), and a long dorsal seta (VII); seta I is absent; ornamented with a row of minute denticles ventrally and 2 pairs of pores (Fig. 2d).

Antennule 7 segmented (see Fig. 5a); lengths of segments measured along posterior, nonsetiferous margin 3; 18; 5; 106; 23; 8; 15 µm (based on figured paratype). Segments armed as follows I–1, II–3, III–1 + tube pore, IV–3, V–2, VI–2, VII–5 + 1 aesthetasc. Two apical setae fused at base; long setae on segments IV to VII sparsely plumose, short setae all naked.

Antenna (Fig. 3a) 2 segmented; first segment representing fused coxa, basis and first

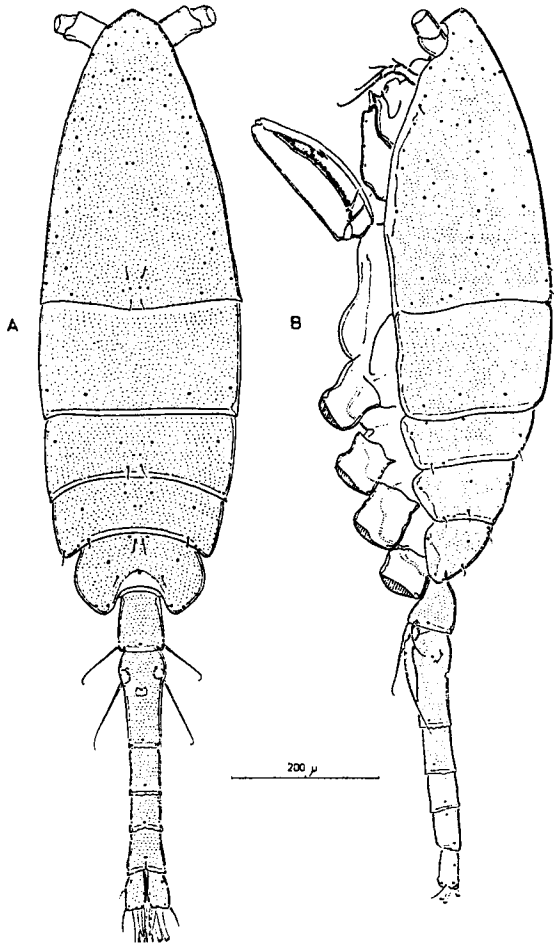


Figure 1. *Paralubbockia longipedia* female. (a) Dorsal; (b) lateral, with antennules and swimming legs removed.

endopodal segment, armed with a spinulate seta; second segment representing fused second and third endopodal segments, armed with a long apical and 2 shorter subapical setae, ornamented with 2 patches of fine setules.

Labrum (Fig. 4b) a small flattened plate, unarmed but with a large apical pore.

Mandible (Fig. 3b; see also Fig. 6c) 1 segmented, armed with 3 blades; outer blade smooth, terminal and inner blades with stout spinules; inner distal margin bearing row of long spinules. Some individual variation noted in precise spinulation pattern on segment margin.

Maxillule (Figs. 3c, 5b) comprising a proximal segment bearing a gnathobase, the praecoxal endite, and a discrete distal palp. Gnathobase produced medially into a serrated process armed with an inner serrated spine and a short, naked, nonarticulating spine. Palp armed with 4 spinulate setae along inner and distal margins.

Maxilla (Fig. 3d) comprising large, robust proximal segment and short distal segment. Proximal segment, representing the syncoxa, ornamented with 3 large pores. Distal segment, representing the basis, tapering to a spinous process bearing on outer

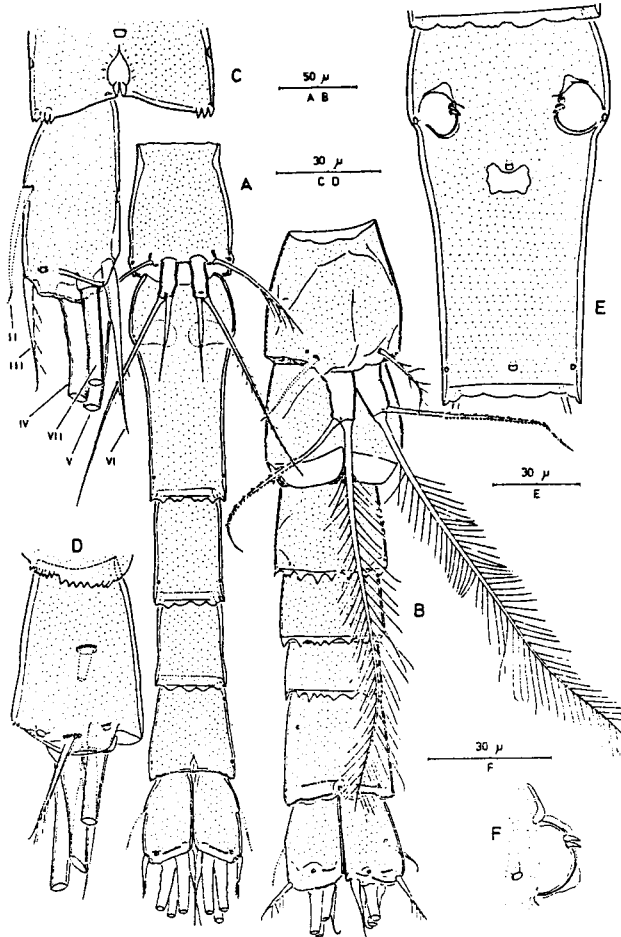


Figure 2. *P. longipedia*. (a) Female urosome, ventral; (b) male urosome, ventral; (c) anal somite and caudal ramus, dorsal; (d) caudal ramus, lateral; (e) female genital double somite, dorsal; (f) female sixth leg, lateral.

side a pore and a curved spine armed with 3 denticles on concave margin, and on inner side a row of slender spinules. Basis armed with 2 proximal elements, a long inner seta, and a short spinulate seta on posterior surface.

Maxilliped (Fig. 3e) indistinctly 4 segmented; comprising unarmed syncoxa, long muscular basis, free endopodal segment, and long slender claw. Basis ornamented with a strip of strongly denticulate membrane along medial margin, plus 2 isolated spinules; armed with 2 medial setae, one with articulated base and located proximally, the other fused to segment and located distally. First endopodal segment small, unarmed. Claw apparently representing fused second endopodal segment plus terminal claw, with trace of suture separating them. Concave margin of second endopodal segment armed with 3 rows of spinules, increasing in size distally and overlapping each other. Claw with slightly spatulate tip.

Swimming legs 1 to 4 biramous, with 3-segmented exopods and 2-segmented endopods; original second and third endopodal segments fused. Armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0-0	1-0	0-1;6	0-0;0-1;I,I,4
leg 2	0-0	1-0	0-1;II,5	I-0;0-1;I,I,5
leg 3	0-0	1-0	0-1;II,4	I-0;0-1;I,I,5
leg 4	0-0	1-0	0-1;II,2	I-0;I-1;I,I,5

All legs (Figs. 4c, 5c, 6a-b) with pinnule rows along outer margins of endopodal segments and inner margins of first exopodal segments. Outer margins of third exopod segments (Fig. 4d) dentate. Terminal elements on endopods of legs 2 to 4 both bilaterally serrate (Fig. 5d). Terminal elements on exopods of legs 1 to 4 longer than ramus, serrate laterally and pinnate medially (Fig. 4d). Leg 4 (Fig. 6b) armed with few long spinules on inner distal margin of basis. All intercoxal plates unarmed but medially incised.

Leg 5 (Fig. 2a) located ventrally on somite; comprising free distal segment and proximal protopodal segment incorporated into somite. Seta on surface of somite repre-

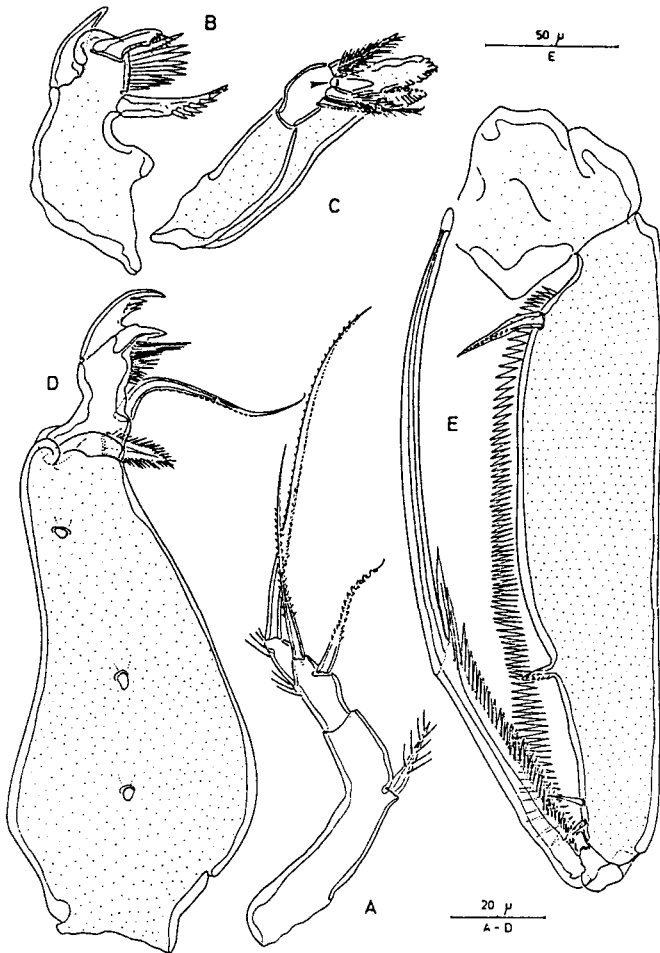


Figure 3. *P. longipedia* female. (a) Antenna, posterior; (b) mandible, anterior; (c) maxillule, ventral, with scar left by missing element indicated by arrow; (d) maxilla, posterior; (e) maxilliped, lateral.

senting outer seta of basis. Free segment (exopod) about twice as long as wide, armed with a pore, a short inner and long outer seta on distal margin. Outer seta sparsely plumose.

Adult male (paratype 1976.9) similar to female except urosome 6 segmented, comprising fifth pedigerous somite, genital somite, and 4 free abdominal somites. Fifth pedigerous somite bearing leg 5 ventally at posterior border (Fig. 2*b*); ornamented with pair of lateroventral pores. Genital somite with large, unarmed genital lappets, representing sixth legs, closing off paired ventral genital apertures. First to third abdominal somites each ornamented with irregularly serrate membrane along posterior margin. First only with pair of lateral pores. Anal somite ornamented with 2 pairs of lateral pores and 2 rows of tiny denticles on ventral surface near posterior margin.

Caudal rami apparently slightly broader than in female ($57 \times 37 \mu\text{m}$) but possibly because of squashing on slide; armature as in female; ornamented with 2 rows of tiny denticles ventrally near posterior margin (Fig. 2*b*).

Antennules indistinctly 5 segmented (Fig. 4*a*), with distal segment representing 3 fused segments of female; lengths of segments measured along posterior nonsetiferous

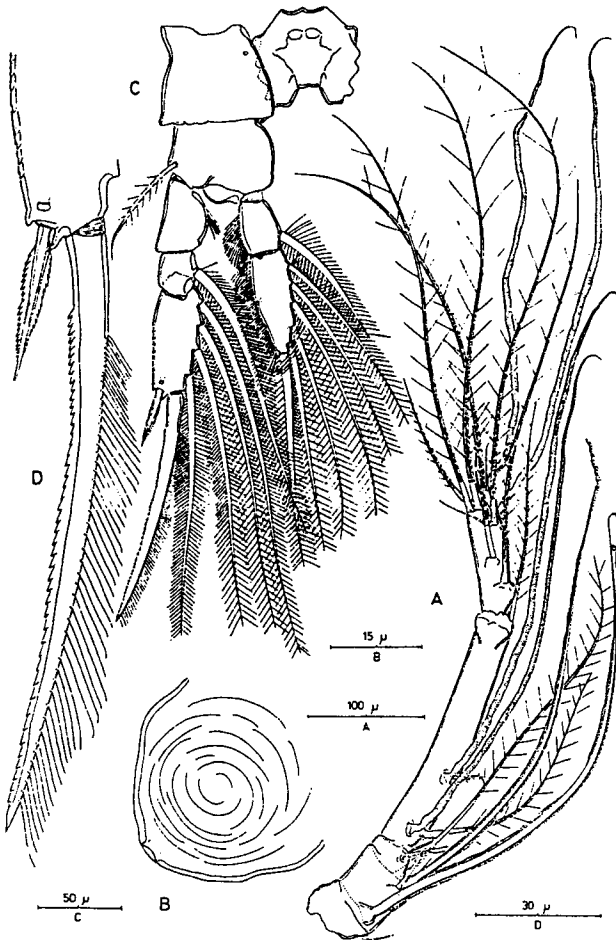


Figure 4. *P. longipedia*. (a) Male antennule, ventral; (b) labrum, ventral; (c) first leg, anterior; (d) same, showing detail of distal part of exopod segment 3.

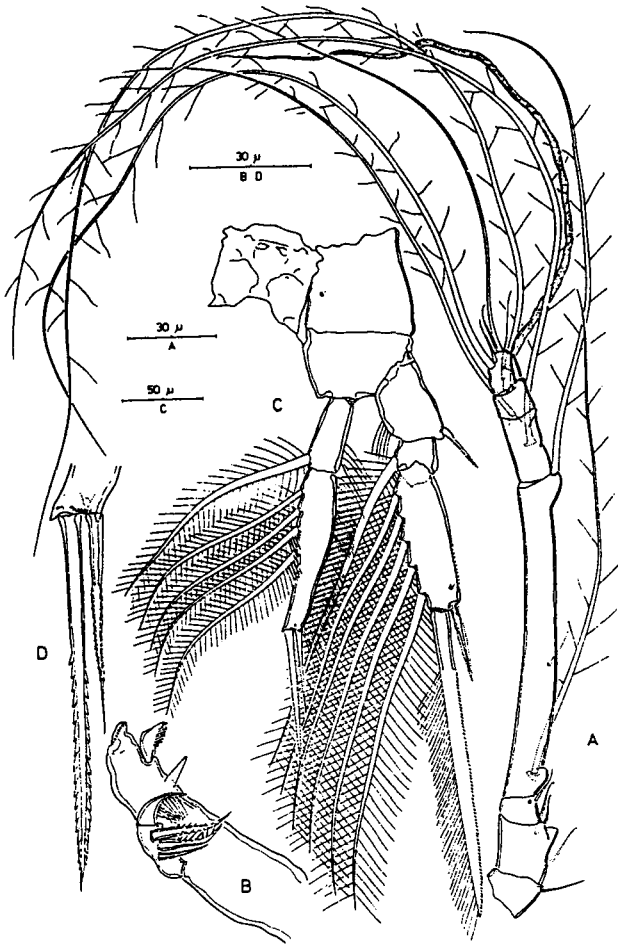


Figure 5. *P. longipedia*. (a) Female antennule, dorsal; (b) maxillule, ventral; (c) third leg, anterior (outer basal seta missing); (d), same, showing detail of tip of endopod.

margin 36; 39; 9; 212; 103 μm . Segments armed as follows I-1, II-3 + 2 aesthetascs, III-1 + tube pore, IV-3 + 2 aesthetascs, V-9 + 2 aesthetascs. Aesthetascs on segment II setiform. Long setae on segments II, IV, and V sparsely plumose.

Antenna (Fig. 7a) as in female; armed with relatively longer setae and setules. Mandible (Fig. 7b) reduced, comprising single lobe with wrinkled surface, armed with 3 simple blades and a few setules. Maxillule as in female (Fig. 7c) except gnathobase weakly developed, armed with 3 slender elements; palp discrete as in female but 4 distal setae relatively longer. Maxilla (Fig. 7d) possibly incomplete in available material; large proximal segment bearing a seta basally and 2 conspicuous pores.

Maxilliped (Fig. 7e) comprising unarmed syncoxa, long muscular basis, and slender distal claw. Basis ornamented with several rows of tiny spinules extending along part or all of medial surface; single medial seta present about at midlevel of segment. Claw apparently representing an endopodal segment plus terminal claw, with trace of suture between them. Claw with slightly reflexed tip. Inner margin of incorporated endopodal segment bearing a row of spinules and an apical seta.

Swimming legs 1 to 4 as in female. Fifth leg (Fig. 2b) inserted midventrally at posterior margin of fifth pedigerous somite, as in female; outer seta of basis located on somite surface. Free exopodal segment bearing a plumose inner seta extending beyond posterior border of anal somite, and an outer seta about half as long as inner and armed with short spinules.

Sixth leg represented by unarmed genital lappets closing off genital apertures.

Discussion

As its name indicates, *Paralubbockia* closely resembles the oncaeid genera *Lubbockia* Claus, 1863 and *Pseudolubbockia* Sars, 1909 in general facies. There are other similarities between *Paralubbockia* and members of the family Oncaeidae as defined by Heron and Damkaer (1978). The most important similarity is the sexual dimorphism in antennular segmentation. These are the only poecilostomatoids that exhibit this dimorphism, in which the male has fewer antennule segments than the female because of fusion of the three distal segments. This can be interpreted as representing a vestige of the ancestral dimorphism in which the males have geniculate antennules showing some fusion of segments at or around the geniculation. The arrangement of the antennularly musculature in male *Oncaea* Philippi, 1843 indicates that the fused distal segment represents the entire part of the limb distal to the geniculation. As such, this is a plesiomorphic character state retained in both *Paralubbockia* and the Oncaeidae and is not indicative of a close phylogenetic relationship.

The mandible of the male is described here for the first time. Boxshall (1977) had

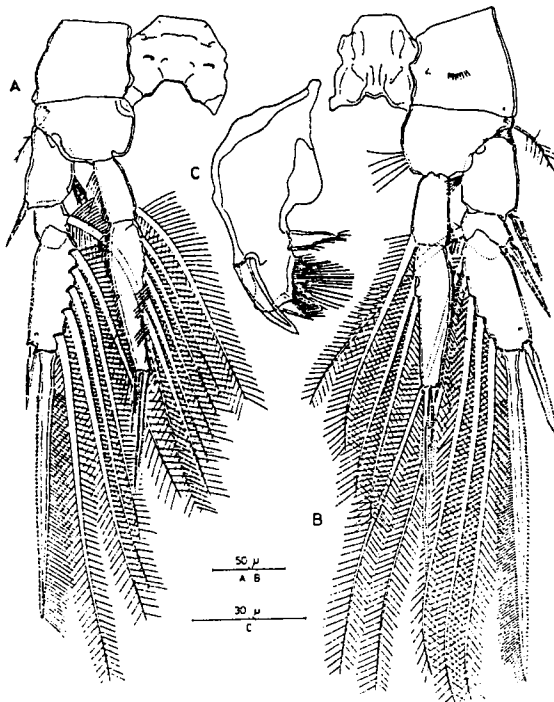


Figure 6. *P. longipedia*. (a) Second leg, anterior; (b) fourth leg, anterior; (c) mandible of second female paratype showing variation in spinulation pattern.

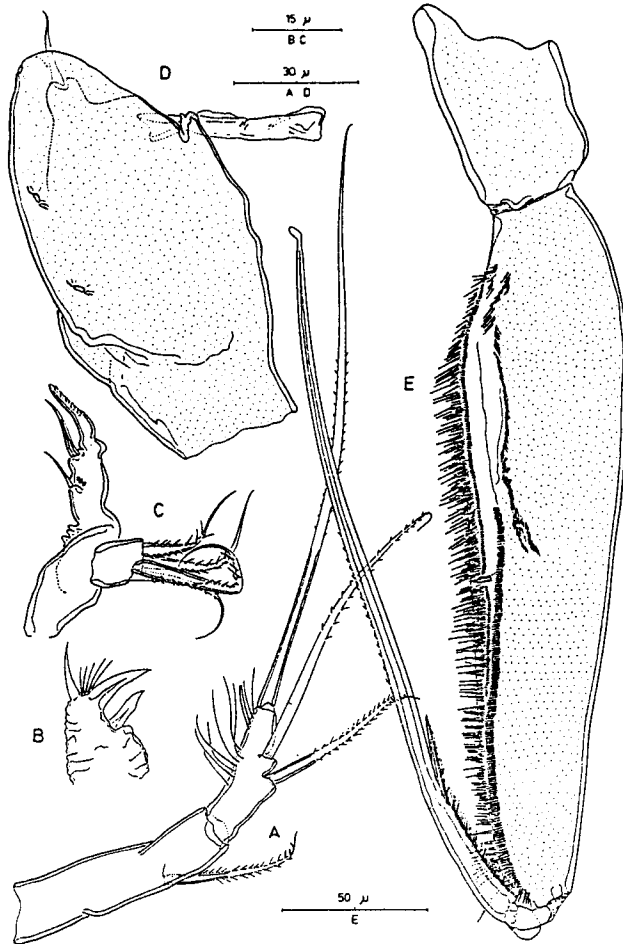


Figure 7. *P. longipedia* male. (a) Antenna, lateral; (b) mandible, anterior; (c) maxillule, ventral; (d) maxilla, possibly incomplete; (e) maxilliped, lateral.

been unable to find it. The reduction in the mandible and in the praecoxal endite of the maxillule suggests that the adult male is nonfeeding. This is quite a common strategy among planktonic poecilostomatoids, also found in males of the sapphirinid genus *Copilia* Dana, 1852, for example. In both sexes the palp of the maxillule is separated from the proximal segment by a complete suture. This is another unique plesiomorphy within the Poecilostomatoida, since the maxillule is typically reduced to a bilobed process in poecilostomatoids.

Paralubbockia is the only poecilostomatoid with ventral fifth legs in either sex. In all others the fifth legs are located laterally on the somite. We regard the ventral position as ancestral for the Copepoda, and its migration to a lateral position, at least in the females, is typically associated with the dorsolateral migration of the genital apertures. Female *Paralubbockia* have dorsolateral genital apertures but ventral fifth legs. This unique plesiomorphy within the Poecilostomatoida indicates that the migrations of the genital apertures and of the fifth legs are independent and that the later migration has occurred at least twice within the order.

Detailed examination of the setation of the swimming legs provides valuable infor-

mation on the pattern of seta loss from anterior to posterior through the leg series. The distal endopod segment of the first leg has 5 setae on its inner margin; the 3 distal setae are bilaterally plumose and have an additional lateral comb of spinules basally (Fig. 4c). The 2 proximal setae on the same segment lack this comb. The second leg has the same pattern of setae (Fig. 6a). The third leg has only 4 setae on the inner margin of the same segment (Fig. 5c), and it is the distalmost of the comb-bearing setae that has been lost. The fourth leg (Fig. 6b) has only 2 setae on that margin, and neither bears a comb. The 2 distal comb-bearing setae are missing. It is interesting to note that even such fine details of setal ornamentation can provide valuable data on the homology of particular setation elements. A similar comb of spinules is present on some setae on the inner margin of the third endopodal segment of *Laitmatobius* (Humes, 1987), a genus of uncertain familial affinity.

Boxshall (1977) tentatively placed *Paralubbockia* in the family Oncaeidae. The present reexamination, in combination with our wider review of evolution within the Copepoda, has provided a new perspective on the affinities of this genus. The ventral position of the fifth legs is a unique plesiomorphy for the Poecilostomatoida and indicates an early divergence from the rest of the poecilostomatoids, as does the presence of a discrete palp on the maxillule. The retention of traces of the geniculation in the male antennule also reinforces this early separation, although this plesiomorphy is shared with the Oncaeidae. The apomorphic states of the swimming legs (with 2-segmented endopods) and of the antenna in *Paralubbockia* distinguish it from the Oncaeidae. We propose to establish a new family, the Paralubbockiidae, to accommodate this genus.

Paralubbockiidae nov.fam.

Diagnosis

Poecilostomatoida. Body cycloform; prosome 5 segmented, with first pedigerous somite partly fused to cephalosome; urosome 5 segmented in female with genital and first abdominal somites completely fused to form genital double somite, 6 segmented in male. Female genital apertures dorsolateral on double somite. Antennules sexually dimorphic; 7 segmented in female, 5 segmented in male. Antennae 2 segmented in both sexes, first segment bearing 1 seta, second bearing 3 setae. All postantennary cephalic appendages sexually dimorphic, reduced in males. Mandible with 3 stout distal blades in female. Female maxillule bilobed; inner lobe representing praecoxal endite, armed with 3 elements, outer lobe representing palp, separated by basal suture and carrying 4 elements. Male maxillule similar in structure but with poorly developed endite. Female maxilla 2-segmented, second segment armed with 4 elements. Male maxilla reduced. Female maxilliped comprising syncoxa, basis, and a small free endopodal segment bearing the claw; male maxilliped similar but lacking free endopodal segment. Swimming legs 1 to 4 biramous with 3-segmented exopods and 2-segmented endopods. Fifth legs in both sexes located midventrally, either side of midline; comprising protopodal segment incorporated into somite and single free exopod segment bearing 2 setae. Type and only genus: *Paralubbockia* (Boxshall, 1977).

The new family shares a sister group relationship with the family Oncaeidae, as indicated by setation of the exopods of the swimming legs. For example, all oncaeid genera (Heron and Damkaer, 1969, 1978; Heron et al., 1984) and *Paralubbockia* lack an inner seta on the first exopodal segment of all four swimming legs. This oncaeid-

paralubbockiid lineage is also characterized by the retention of a vestige of the geniculation of the male antennule, a feature lost in all other poecilostomatoids. Humes (1987) recognized the affinities of the genus *Laitmatobius* with the family Oncaeidae. However, *Laitmatobius* is known only from the male, and until the female is discovered we consider that it should remain *incertae sedis* within the oncaeid-paralubbockiid lineage. The presence of the comb on some of the endopodal setae may be a synapomorphy of the Oncaeidae and Paralubbockiidae.

Acknowledgments

Part of this research was carried out under Research Grant No. 2.0009.81 of the Belgian Fund for Collective Fundamental Research and CEC contract ST2 *0443. The original donation of material from the *Discovery* collections of the Institute of Oceanographic Sciences, NERC, was arranged by Howard Roe.

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