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On the Diphyletic Origin of the Oncaeidae Giesbrecht, 1892 (Copepoda: Poecilostomatoida) with a Phylogenetic Analysis of the Lubbockiidae fam. nov.

RONY HUYS[1] and RUTH BÖTTGER-SCHNACK[2]

[1] Department of Zoology, The Natural History Museum, London, United Kingdom
[2] Christian-Albrechts-Universität, Institut für Meereskunde, Kiel, Germany

Abstract. The monophyly of the Oncaeidae was tested using cladistic methodology. The family (as it is currently recognised) comprises two distinct lineages that do not share a sistergroup relationship and have colonized the open pelagic environment independently. Under the revised family concept the Oncaeidae encompasses only the genera *Conaea* Giesbrecht, *Epicalymma* Heron and the type-genus *Oncaea* Philippi which is regarded as a paraphyletic (or possibly polyphyletic) taxon. A new family Lubbockiidae is proposed to accommodate *Lubbockia* Claus, *Pseudolubbockia* Sars and *Laitmatobius* Humes. The taxonomic position of *Oncaeola* Krämer and *Limnoncaea* Kokubo is briefly discussed. The major morphological trends within the Lubbockiidae are summarized and serve as the basis for a computer-assisted analysis of the phylogenetic relationships between the 13 species. As a result *Lubbockia* is subdivided into five genera and is redefined to include only *L. squillimana* Claus, *L. aculeata* Giesbrecht, *L. wilsonae* Heron & Damkaer and *L. extenuata* Boxshall. The four new genera *Haplopodia*, *Homeognathia*, *Rhamphochela* and *Atrophia* are described largely on the basis of different types of sexual dimorphism, leg 5 morphology and antennulary aesthetasc patterns. The phylogenetic position of both the Oncaeidae and Lubbockiidae in the order Poecilostomatoida is briefly discussed.

Key words. Phylogeny, morphology, cladistics, plankton.

1. INTRODUCTION

Copepods of the family Oncaeidae (Poecilostomatoida) are amongst the most abundant microcrustaceans in the zooplankton (BÖTTGER-SCHNACK 1994, 1996. In the last three decades, considerable interest in the Oncaeidae has been generated by the discovery of their grossly underestimated diversity of species, particularly in deeper waters. This interest has also identified the problem of morphologically similar species having repeatedly been described under the same name (HERON & BRADFORD-GRIEVE 1995). In addition, continued sampling, especially with fine mesh nets (<0.1 mm), has yielded a steady supply of new taxa. Despite this new information, virtually no major reorganisations of genera have been attempted although the heterogeneity of the two speciose genera *Lubbockia* (HERON & DAMKAER 1978) and *Oncaea* (HERON et al. 1984; HERON & BRADFORD-GRIEVE 1995) has been acknowledged. The generic composition of the Oncaeidae has had a varied history and several unusual taxa have been placed in this family. The following list contains the names of all genera that have been included into the Oncaeidae or have been associated with it under a broader concept of the family:

Oncaea Philippi, 1843 (= *Antaria* Dana, 1846)
Lubbockia Claus, 1862
Conaea Giesbrecht, 1891
Oncaeola Krämer, 1895
Pseudolubbockia Sars, 1909
Pachos Stebbing, 1910 (= *Pachysoma* Claus, 1862)
Limnoncaea Kokubo, 1914
Sapphoncaea Olson, [MS], 1949
Epicalymma Heron, 1977
Myspictosum Kazachenko & Avdeev, 1977
Paralubbockia Boxshall, 1977
Laitmatobius Humes, 1987

KRÄMER (1895) assigned *Oncaeola specialis* to the Oncaeidae but his crude description shows the morphology of a typical lichomolgoid-like copepod (HUMES & STOCK 1973; HERON & BRADFORD-GRIEVE 1995). The lichomolgoid complex has recently been revised by HUMES & BOXSHALL (1996) resulting in the recognition of 10 families. Assignment of *Oncaeola* to any of these families is hampered by lack of information on the mandible which is a pivotal appendage in HUMES & BOXSHALL's classification. However, the III,I,5 armature pattern of the 3rd exopod segment of leg 4 excludes the genus from the Octopicolidae, Synapticolidae, Kelleriidae, Sabelliphilidae, Thamnomolgidae and Pseudanthessiidae which all primitively display a II,I,5 formula on this segment. The unmodified antenna of *O. specialis* also prevents it from being a member of the Anchimolgidae, leaving the Lichomolgidae, Rhynchomolgidae and Macrochironidae as the only candidate families to accommodate *Oncaeola*. The form of the antenna, maxilla, female maxilliped, and P4 endopod indicate a relationship with the four macrochironid genera recognized by HUMES & BOXSHALL (1996) and we therefore place *Oncaeola* as *genus incertae sedis* in the Macrochironidae. Many species of this family are associated with scyphozoan hosts or floating algae which is in agreement with KRÄMER (1895) who reported *O. specialis* from the plankton. The position of *Pachos* in the Oncaeidae has been the subject of controversy since it was first proposed as a replacement name for the preoccupied *Pachysoma* (STEBBING 1910). Several authors (e.g. SARS 1918; BOXSHALL 1977) have questioned its oncaeid affinities and HERON & DAMKAER (1978) excluded the genus from the Oncaeidae on the basis of the form of the antennules and mouthparts. The genus *Pachos* should probably be designated the type of a distinct family in order to remove it from its current floating status in the Poecilostomatoida. Descriptions of both *Pachos* species are unfortunately incomplete and more detailed information should therefore be required before this course of action can be taken. KOKUBO (1914) proposed the freshwater genus *Limnoncaea* for three new species *L. genuina*, *L. diuncata* and *L. divergens*. His illustrations leave no doubt that he was dealing with a member of the Ergasilidae and that *Limnoncaea* is either a junior synonym of *Ergasilus* von Nordmann, 1832, or represents an amalgamate of different ergasilid genera. OLSON (1949), in an unpublished thesis, created the genus *Sapphoncaea* for *S. moria* Olson, 1945 which he placed in the Oncaeidae as a transitionary form to the Sapphirinidae. OLSON's manuscript name was inadvertently made available by MINODA (1971) who provided a description of the female. HERON & DAMKAER (1986) removed the genus from the Oncaeidae when they synonymized *S. moria* with *Urocopia singularis* Sars, 1917 (family Urocopiidae). KAZACHENKO & AVDEEV (1977) described *Myspictosum* as a genus of uncertain taxonomic position. The single male of *M. philippinensis* was found on the gills of the deep-sea fish *Myctophum spinosum* collected in the Philippine Trench. MALT (1982) pointed out the undeniable resemblance between *M. philippinensis* and representatives of *Oncaea* and consequently relegated *Myspictosum* (erroneously spelled *Myctospictosum* by MALT) to a junior synonym of the latter. KAZACHENKO & AVDEEV's (1977) record of *O. philippinensis* from 7255 m is the deepest for the genus and like HO's (1984) find of *O. venusta* Philippi, 1843 on hydroid colonies, its association with a fish host has to be regarded as accidental rather than obligatory. BOXSHALL (1977) decribed a new genus *Paralubbockia* from deep-water plankton off the Cape Verde Islands and with some reservations proposed placing it in the Oncaeidae. This temporary assignment required substantial emendation of the family diagnosis which was not followed by HERON et al. (1984) who declined *Paralubbockia* as a valid genus of the Oncaeidae. More recently, BOXSHALL & HUYS (1989) placed the genus in a new family Paralubbockiidae. MALT (1982) subsumed *Conaea* and *Epicalymma* into the genus *Oncaea*. This course of action was not followed by HERON et al. (1984) and HERON & BRADFORD-GRIEVE (1995) who maintained the validity of both genera. We also recognize the distinctness of *Conaea* and *Epicalymma* and reject MALT's suggestion which is based on unsubstantiated evidence. HUMES (1987) recognized the affinities of the hydrothermal vent genus *Laitmatobius* with the family Oncaeidae, particularly with species of *Lubbockia*, yet in the absence of the female the author left its familial position unconfirmed. BOXSHALL & HUYS (1989) decided that the genus should remain *incertae sedis* in the oncaeid-paralubbockiid lineage. The Oncaeidae have been portrayed in past literature as primitive, yet specialised poecilostomatoids which, on account of the dimorphic male antennules and plesiomorphic mandible, occupy a central position in our understanding of the evolutionary history of the order (HUYS & BOXSHALL 1991). This paper challenges the monophyletic status of the Oncaeidae based on a comparative analysis of the genera *Oncaea*, *Lubbockia*, *Conaea*, *Pseudolubbockia*, *Epicalymma* and *Laitmatobius*, with the ultimate goal of revising the family's composition and definition.

2. MATERIAL AND METHODS

The descriptive terminology is adopted from HUYS & BOXSHALL (1991). Abbreviations used in the text are: ae, aesthetasc; P1-P6, first to sixth thoracopod; exp(enp)-1(2, 3) to

denote the proximal (middle, distal) segment of a ramus. Specimens of *Pseudolubbockia dilatata* and various *Lubbockia* species were examined with a Zeiss Axioskop microscope equipped with differential interference contrast. Phylogenetic relationships between taxa were analyzed using the phylogenetic computer package PAUP 3.1 prepared by DAVID L. SWOFFORD of the Laboratory of Molecular Systematics, Smithsonian Institution (SWOFFORD 1993; SWOFFORD & BEGLE 1993). Since evolution within the Copepoda is assumed to proceed typically by oligomerization (HUYS & BOXSHALL 1991), all characters were set irreversible using the CAMIN-SOKAL option. This option suppresses character reversals at the expense of introducing extra convergencies and thereby increasing the tree-length. The options employed in the analysis were BRANCH AND BOUND, which guaranteed to find all most parsimonious trees, and the MINF optimisation, which assigns character states so that the f-value is minimized.

3. THE DIPHYLETIC STATUS OF THE ONCAEIDAE

3.1. Problems in the classification of the Oncaeidae

The phylogenetic relationships of the Oncaeidae have always been regarded as enigmatic although the family has occasionally been related to the lichomolgoid group of families. HUMES & STOCK (1973) suggested that the Oncaeidae approached most closely the sabelliphilid and lichomolgid types, particularly in the armature and segmentation of the swimming legs. At the same time they recognized important differences in the "... nonprehensile nature of the second antenna, the form of the mandible, and the presence of a clawed maxilliped in both sexes". HERON & DAMKAER (1978) pointed out that HUMES & STOCK's supposition was based on a comparison with *Oncaea* – not *Lubbockia* – and if the latter genus is taken into account the relationships between the Oncaeidae and Lichomolgoidea are even clearer. A lichomolgoid-oncaeid relationship was not supported by IZAWA's (1987) analysis of the "poecilostome Cyclopoida". IZAWA recognized two phylogenetic "stems" on the basis of naupliar evidence: the antelichomolgus stem including the Lichomolgidae and seven other families, and the antehemicyclops stem, comprising the taeniacanthiform families, being predominantly parasitic on fish hosts, the genus *Hemicyclops* (Clausidiidae) and *Oncaea*. A clausidiid- oncaeid relationship was also favoured by HO (1991) who grouped the two families in a primitive clade which also included the deep-sea Erebonasteridae, the planktonic Paralubbockiidae and the Myicolidae which are associates of bivalve molluscs and brachiopods. This clade was supported by two synapomorphies of doubtful significance, the 7-segmented antennule and the mandible bearing 4 elements. These two conflicting concepts of relationships, depending on which genus is selected as the model oncaeid, assert that the Oncaeidae might well be a diphyletic assemblage. The most recent family diagnosis of HERON & DAMKAER (1978) testifies to this problem since it defines a generalized poecilostomatoid using largely plesiomorphic characters. All defined character states, with their built-in variation, can be found in the majority of unmodified families of the Poecilostomatoida and are therefore phylogenetically uninformative. The major characters that hold the oncaeid genera together are the sexually dimorphic antennules, the medially incised labrum, the primitive mandible with 3-5 elements and the II,I,5 armature formula of P3 exp-3. Sexually dimorphic antennules, with the distal 3 segments fused into a compound terminal segment in the male, are not unique to the Oncaeidae since such a modification is also found in the genus *Rhinomolgus* Sars (Anthessiidae) and is a family diagnostic for the Paralubbockiidae (BOXSHALL & HUYS 1989) and Intramolgidae (MARCHENKOV & BOXSHALL 1995). HUYS & BOXSHALL (1991) interpreted the modification of the distal part of the male antennule as representing a vestige of the ancestral podoplean geniculation mechanism. Evidence in support of this interpretation is provided by the musculature (BOXSHALL & HUYS 1989) suggesting that the absence of geniculate antennules in male Poecilostomatoida is a secondary condition and retention of a sexually dimorphic segmentation pattern in at least four unrelated lineages represents the plesiomorphic state. The medially incised labrum is found in a large number of poecilostomatoids, including the families of the lichomolgoid complex (HUMES & BOXSHALL 1996). Its form and shape is however distinctly different between *Lubbockia-Pseudolubbockia*, which have a deeply cleft labrum resembling the lichomolgoid condition, and *Oncaea-Conaea-Epicalymma* which have a moderately to weakly incised labrum usually provided with strong teeth medially. The major stumbling block to the recognition of oncaeid monophyly is provided by the presence of two fundamentally different mandible types in the family. In *Oncaea*, *Conaea* and *Epicalymma* the mandible has a complex array of five articulated elements around the distal margin. With the exception of the Erebonasteridae which have retained the mandibular palp, this condition represents the most plesiomorphic state to be found in the order, and resembles the type found in other primitive families such as the Clausidiidae where four discrete elements can be identified. The second type is found in *Lubbockia* where the middle element is specialized, forming a curved lash with a typically dentate convex margin. This falcate type of mandible might have been derived from the plesiomorphic *Oncaea*-condition, yet it is extremely unlikely that

this process has happened within the Oncaeidae. The recent discovery of the Intramolgidae (MARCHENKOV & BOXSHALL 1995) revealed a similar type of falcate gnathobase with all five elements arranged and modified in exactly the same way as in *Lubbockia*. The basal position of this family in the Lichomolgoidea gives further support to the hypothesis that the more derived lichomolgoid mandible, retaining the middle element as the main blade (HUMES & BOXSHALL 1996), is derived from the *Lubbockia*-condition by gradual incorporation of the dorsal and ventral elements into the lash (HUYS & BOXSHALL 1991). The presence of only two outer spines on P3 exp-3 is a derived state shared by all oncaeid genera, however, the independent loss of the proximal outer element, either primitively or secondarily, in many other families weakens the phylogenetic significance of this character. Similarly, the reduced fifth legs, represented by an outer basal seta and a bisetose free exopod, is commonly found in other poecilostomatoids such as the families of the Lichomolgoidea. Furthermore, the presence of four setae on the exopod of *Pseudolubbockia* indicates that the bisetose condition evolved within the family. The Oncaeidae is clearly a polyphyletic taxon comprising two major lineages, *Oncaea-Conaea- Epicalymma* and *Lubbockia-Pseudolubbockia*. The most important differences between these lineages are summarized in Table 1. The latter group cannot be placed in any existing poecilostomatoid family and consequently a new family Lubbockiidae is established below to accommodate *Lubbockia*, *Pseudolubbockia* and the problematic genus *Laitmatobius*.

3.2. Revised diagnosis of the Oncaeidae Giesbrecht, 1892

Poecilostomatoida. Body cyclopiform or elongate; not modified. Prosome comprising cephalosome and four distinct pedigerous somites. Urosome 5-segmented in ♀, with genital and first abdominal somite completely fused to form elongate genital double-somite which is usually longer than three free abdominal somites combined. Urosome 6-segmented in ♂; genital somite large, longer than four free abdominal somites combined. P5-bearing somite short in both sexes. Genital apertures paired, located dorsally in ♀, ventrally in ♂; closed off by small operculae derived from vestigial P6 with 1-2 minute elements in ♀, and by well developed symmetrical flaps wit 0-1 elements in ♂. Caudal ramus with 6 or 7 setae, seta I minute or absent, other setae typically pinnate, sometimes bare. Sexual dimorphism in antennule, maxillipeds, P5, P6, and genital segmentation; sometimes in prosome (P2-bearing somite with dorsal projection in ♀), antenna, P1 basis and P1-P4 endopods (enp-3). Antennule distinctly 6-segmented and with very long 3rd segment in ♀; armature formula: 1-[3], 2- [8], 3-[4 + 1 spinule], 4-[3 + ae], 5-[2 + ae], 6-[6 +ae]. Antennule ♂ with segments 4-6 fused forming terminal compound segment; setation and number of aesthetascs as in ♀ except for

Tab. 1. Comparison between two major lineages in the Oncaeidae.

	Lubbockia – Pseudolubbockia	*Oncaea – Conaea – Epicalymma*
Antennule	primitively 7-segmented in ♀ segment 4 with 4 setae in both sexes	6-segmented in ♀ (segments 3-4 fused) segment 4 (as part of compound 3rd segment) with sexually dimorphic seta
Antenna	coxobasis without seta enp-1 with seta enp-2 and -3 primitively free enp-2 with 3 setae	coxobasis with long seta enp-1 without seta enp-2 and -3 always fused enp-2 with maximum of 4 elements
Labrum	deeply incised medially, without teeth/scales	bilobate, with distinct teeth/scales medially
Mandible	with dentate, lash-like median element, 2 dorsal and 1-2 ventral discrete elements	with 5 discrete elements (none lash-like) around distal margin
Maxillule	armature primitively 3 + 3	4 (outer lobe) + 3 (inner lobe)
Maxilla	basis with bifid compound element apically, 1 inner and 2 outer elements	basis drawn out into pinnate claw; with 1 outer and 2 inner elements
Maxilliped	if segmentation sexually dimorphic, endopod with higher number of segments in ♂	endopod with discrete segment and claw in ♀, represented by claw only in ♂
P1-P4	inner coxal seta present	inner coxal seta absent
Genital somite ♂	at most slightly longer than 1st abdominal somite	voluminous, longer than postgenital somites combined

absence of distal seta on 3rd segment. Antenna comprising coxobasis and 2-segmented endopod (enp-2 and – 3 fused); coxobasis with seta, enp-1 without seta, 2nd endopod segment with 3-4 lateral and 6-7 distal elements. Labrum bilobate, medially incised, with distinct teeth or scales medially. Mandible without palp; gnathobase with 4-5 discrete elements around distal margin, typically with 1 ventral seta, 2 medial blades and 2 dorsal setae/spines. Maxillule bilobate with 4 elements on outer and 3 elements on inner lobe. Maxilla 2-segmented; syncoxa without endites; basis drawn out into pinnate claw and with 3 discrete elements: outer margin with 1 seta, inner margin with pinnate spine and naked seta. Maxilliped without seta on syncoxa; basis with 2 setae/spines in both sexes; endopod ♀ 2-segmented with armature 0, 2+claw; endopod ♂ without free segment, with claw. Swimming legs with 3-segmented rami; inner coxal seta absent; armature formula as follows (asterisk indicating variable count):

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	1-1	I-0;I-1;*,I,4	0-1;0-1;I,5
P2	0-0	1-0	I-0;I-1;*,I,5	0-1;0-2;*,I,3
P3	0-0	1-0	I-0;I-1;*,I,5	0-1;0-2;*,I,2
P4	0-0	1-0	I-0;*-1;*,I,5	0-1;0-2;*,I,*

Exp-3 with II-III (P1-P2), I-III (P3) or I-II (P4) outer spines; P2-P4 enp-3 with 0-II outer spines, typically with terminal conical process separating apical and distal outer spines; P4 exp-2 with or without (*Conaea*, *Epicalymma*) outer spine; P4 enp-3 with 1 (*Conaea*, *Epicalymma*) or 2 inner setae. Inner seta of P1 enp-1 possibly absent in *Epicalymma ancora* (Gordejeva, 1973).

Fifth leg with protopod incorporated into somite, represented by dorsal seta on surface of somite but sometimes secondarily lost; exopod 1-segmented with 2 setae or 1 seta and a spinule, or sometimes entirely incorporated into somite. Egg sacs paired, multiseriate. Planktonic, marine; loosely associated with pelagic invertebrate hosts such as appendicularians.

Type genus: *Oncaea* Philippi, 1843

Other genera: *Conaea* Giesbrecht, 1891; *Epicalymma* Heron, 1977.

Oncaea represents a paraphyletic (and possibly polyphyletic) taxon. The genus will be revised in a forthcoming study, resulting in the recognition of several new genera. A key to genera therefore is not provided.

3.3. Lubbockiidae fam. nov.

Poecilostomatoida. Body cyclopiform or elongate(-oval); not modified. Prosome comprising cephalosome and four distinct pedigerous somites. Urosome 5-segmented in ♀, with genital and first abdominal somite completely fused to form genital double-somite; with three free abdominal somites. Urosome 6-segmented in ♂; with four free abdominal somites. Genital apertures paired, located laterally or dorsolaterally in ♀, ventrally in ♂; closed off by operculae derived from vestigial P6 with 0–2 minute elements. Caudal ramus with 6 or 7 setae, seta I minute or absent, other setae typically pinnate, sometimes bare. Sexual dimorphism in antennule, maxilliped (except in *Homeognathia* gen. nov.) and genital segmentation; sometimes in antenna, mouthparts (atrophied in ♂♂), P1 endopod, abdominal somites and caudal ramus.

Antennule primitively 7-segmented in ♀ with segment boundaries sometimes weakly defined or lost between segments 2-3, 3-4 and 5-6; armature formula: 1-[4], 2-[6-13 + 0-1 ae], 3-[2-4], 4-[4], 5-[3-4 + ae], 6-[2 +ae], 7-[7 + ae or 6 + 2ae]. Antennule ♂ with segments 5-7 fused forming terminal compound segment; setation as in ♂ but additional aesthetascs sometimes present on segments 2 and 4. Antenna comprising coxobasis and 2- (enp-2 and -3 fused) or 3-segmented (*Laitmatobius*) endopod; coxobasis without seta, enp-1 with 1 seta, enp-2 with 2-3 setae, enp-3 with 2 subapical setae and 4-5 apical claws. Labrum deeply incised, without distinct teeth or scales. Mandible without palp; gnathobase falcate, with median dentate lash, 2 dorsal and 1-2 ventral elements. Maxillule bilobate with 2-3 elements on each lobe. Maxilla 2-segmented; syncoxa without endites; basis with total of 5 elements: outer margin with 1 minute and 1 bipinnate seta, apex with 2 basally fused spines forming bifid element, inner margin with multipinnate spine. Maxilliped without seta on syncoxa; basis with 0-1 seta in ♀ and 0 or 2 setae in ♂; endopod indistinctly 3-segmented or 2-segmented or without free segment in ♀, 2- or 3-segmented in ♂ with maximum armature 0, 2, 1+claw. Swimming legs with 3-segmented rami; inner coxal seta present; armature formula as follows (asterisk indicating variable count):

Leg	Coxa	Basis	Exopod	Endopod
P1	0-1	1-*	I-0;I-1;*,I,4	0-1;0-1;I,5
P2	0-1	1-0	I-0;I-1;*,I,5	0-1;0-2;I,II,3
P3	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,*
P4	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,*

P1 inner basal spine present or absent. P1-P2 exp-3 with II-III outer spines; P3 enp-3 with 2-3 setae or 2+I elements; P4 enp-3 with 1-2 setae or 1+I elements.

Fifth leg with protopod incorporated into somite, represented by dorsal seta on surface of somite but sometimes secondarily lost; exopod 1-segmented with 2 or 4

(*Pseudolubbockia*) setae/spines, or entirely lost (*Haplopodia* gen. nov.). Egg sacs paired, multiseriate.
Planktonic, marine; probably loosely associated with pelagic invertebrate hosts.
Type genus: *Lubbockia* Claus, 1862.
Other genera: *Pseudolubbockia* Sars, 1909; *Laitmatobius* Humes, 1987; *Atrophia* gen. nov.; *Haplopodia* gen. nov.; *Homeognathia* gen. nov.; *Rhamphochela* gen. nov.

4. PHYLOGENETIC ANALYSIS OF THE LUBBOCKIIDAE FAM. NOV.

4.1. Morphological transformations

General body morphology. Lubbockiid females are characterized by the presence of a cephalosome, five free pedigerous somites, a genital double-somite and three abdominal somites. The first pedigerous somite is entirely individualized in *Pseudolubbockia* and *Laitmatobius*, but seems to be functionally fused to the cephalosome in the other members of the family. By changes in the proportions of the cephalosome and various free somites, the general form of the lubbockiid body changes significantly. In *Pseudolubbockia* and *Laitmatobius* the body is typically cyclopiform with the prosome elongate-oval in shape and robust in lateral and dorsal aspect. In the species-complex *Lubbockia* there is a clear trend towards an elongate prosome and progressive elongation of the postgenital somites (e.g. *L. squillimana*, *L. wilsonae*). Although body shape has not been used in our analysis, this sequence is a depiction of the evolutionary history within the Lubbockiidae (Fig. 5). In two species of *Lubbockia*, *L. glacialis* and *L. minuta* there is a form of sexual dimorphism in the abdomen with the penultimate somite being distinctly longer in the male.
Antennule segmentation. The lubbockiid antennule is primitively 7-segmented in the female and all segments are expressed in *Pseudolubbockia* (Fig. 1). Most females, however, have been described as having 4, 5 or 6 segments since segment boundaries in the middle part of the antennule are typically incomplete ventrally and along the anterior margin and only clearly expressed dorsally and posteriorly. Faint suture lines indicating original segmentation patterns are usually present between segments 3 and 4 and between 5 and 6, such as in *L. minuta* and *L. flemingi*. In the majority of species the antennule is distinctly segmented only between segments 1 and 2, 4 and 5, and 6 and 7. In *L. petersoni* all segment boundaries are incomplete, except for 4-5, resulting in an essentially 2- segmented appendage. The segmental homologies of the lubbockiid 7-segmented female antennule can be identified as I-V, VI-XIV, XV-XVII, XVIII-XX, XXI-XXIV, XXV, XXVI-XXVIII by reference to the ancestral poecilostomatoid pattern as proposed by HUYS & BOXSHALL (1991) and modified by MARCHENKOV & BOXSHALL (1995).

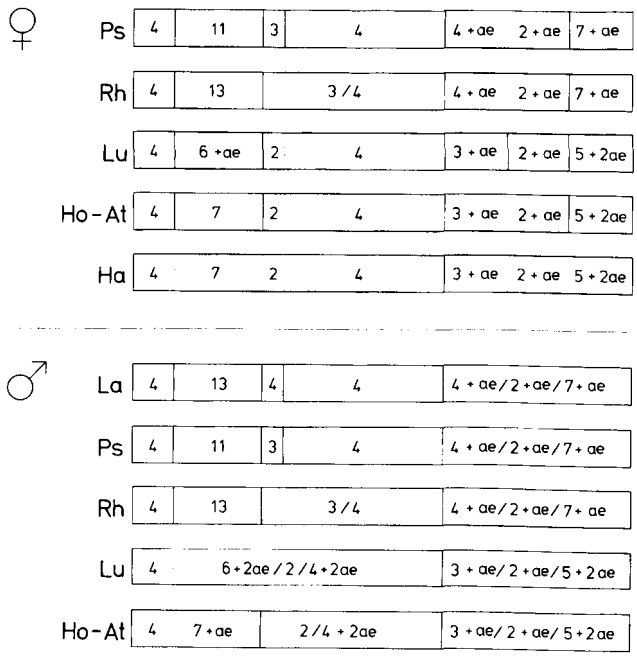


Fig. 1. Schematic comparison of segmental homologies and armature patterns in female and male antennules of various lubbockiid genera [Ps = *Pseudolubbockia*; Rh = *Rhamphochela*; Lu = *Lubbockia*; Ho = *Homeognathia*; At = *Atrophia*; Ha = *Haplopodia*; La = *Laitmatobius*; ae = aesthetasc].

In all species the antennules are sexually dimorphic with the distal segments 5-7 fused into a compound terminal segment in the male. The 5-segmented condition with all other segments expressed represents the plesiomorphic state in the family and is found in the males of *Pseudolubbockia* and *Laitmatobius*. Additional fusions in the proximal part of the antennule are common in other male lubbockiids, and in all of them the tiny segment 3 is incorporated in segment 4, resulting in indistinctly 4-segmented (e.g. *L. carinata*, *L. forcipula*) or, by further fusion of segment 2, 3-segmented (e.g. *L. wilsonae*, *L. extenuata*) appendages. In many species only one clearly defined segment boundary is discernible, corresponding with the suture between segments 2 and 3 of the female.
Antennule armature. The most plesiomorphic armature pattern present on the female antennule (Fig. 1) is found in *L. carinata* and *L. forcipula* which both have 13 setae on segment 2, 3 elements on segment 3 (which is fused to segment 4), 4 setae plus an aesthetasc on

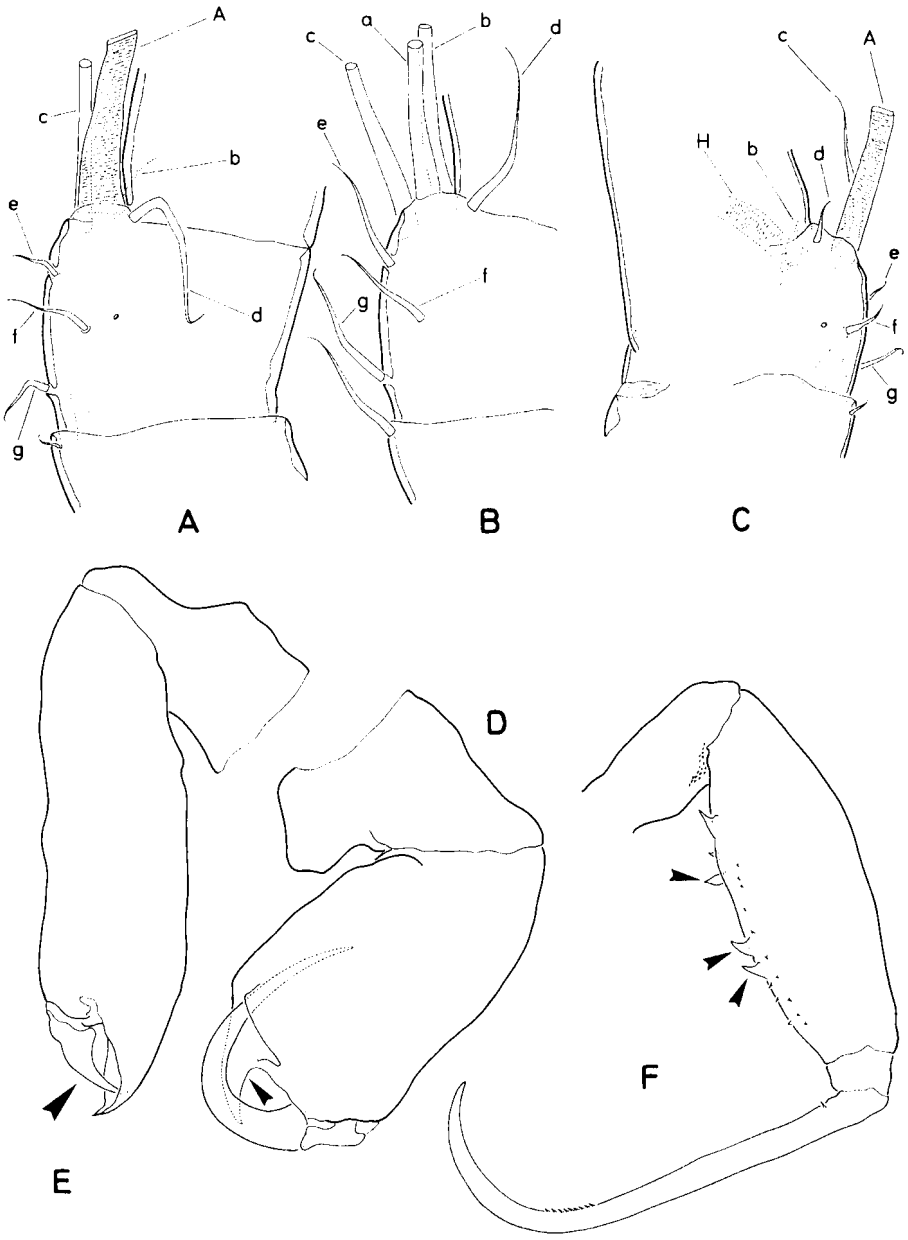
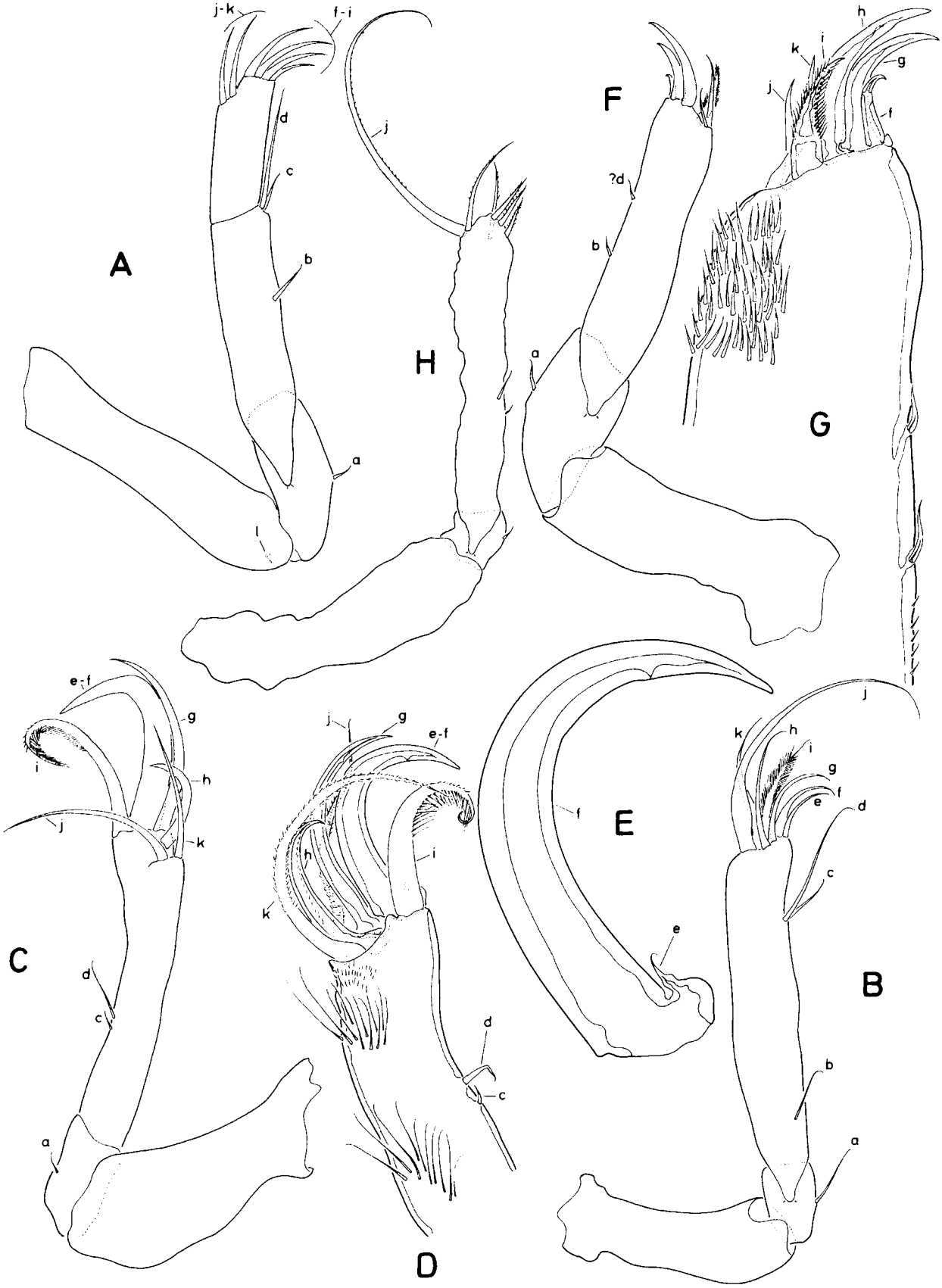


Fig. 2. Second antennulary segment of **A,** *Lubbockia extenuata* (♀); **B,** *Homeognathia brevis* (♀); **C,** *L. extenuata* (♂). Maxilliped of **D,** *Rhamphochela carinata* (♀); **E,** *R. forcipula* (♀); **F,** *Lubbockia wilsonae* (♀). [A-C: originals; D-E after HERON & DAMKAER (1978), F after HERON & DAMKAER (1969)].

segment 4 and 7 setae plus an aesthetasc on segment 7. Female *Pseudolubbockia* also have retained the ancestral armature complement except for segment 2 which carries only 11 setae. It is conceivable, however, that the unknown female of *Laitmatobius crinitus* displays the maximum setation found in the family since the third segment of the male has 4 setae on segment 3, the largest number known for any lubbockiid (Fig. 1). Species currently allocated to *Lubbockia* (except *L. forcipula* and *L. carinata*) have a reduced armature formula with setal reductions occurring on segments 2, 3 (2 minute setae) and 7 (5 setae). Two patterns can be identified with regard to the armature of segment 2. In *L. minuta*, *L. glacialis*, *L. brevis*, *L. petersoni* and *L. flemingi* the second segment or its equivalent within a compound segment carries 7 setae (labelled a-g in Fig. 2B). In the other species *L. aculeata*, *L. squillimana*, *L. extenuata* and *L. wilsonae* only 6 setae and a spinule can be discerned but a large aesthetasc (labelled A in Fig. 2A) is present on the anterior margin. The presence of an aesthetasc on this segment of the female antennule is a unique feature in the Lubbockiidae (Fig. 1) and its precise position indicates unequivocally that it is derived from the missing seventh seta (labelled a in Fig. 2B) present in other *Lubbockia* species (Figs 1, 2B). In both sexes of *Laitmatobius*, *Pseudolubbockia*,


A
H
F
G
C
D
E
B
j-k
f-i
d
c
b
a
l
?d
h
k
i
g
j
f
e-f
e

L. carinata and the female of *L. forcipula* (the male is unknown) the apical segment or part corresponding to segment 7 carries 7 setae and an aesthetasc (Fig. 1). In males and females of all other lubbockiids one of the distal elements is replaced by an aesthetasc and a second seta is lost, resulting in a [5 + 2ae] formula (Fig. 1). Males of this species group can also be distinguished from the primitive members of the family by the addition of 1 aesthetasc on ancestral segment 2 (resulting in a 6 + 2ae formula in *L. aculeata* and related species: sexually dimorphic aesthetasc labelled H in Fig. 2C) and 2 aesthetascs on ancestral segment 4. Within this group the sexually dimorphic aesthetascs and those on ancestral segments 6 and 7 (only the terminal one) are slender and not modified in the males of *L. brevis* and *L. flemingi* but in all other species these elements are very long and equipped with a seta-like supporting rib.

Antenna. The antenna is 4-segmented in *Laitmatobius*, comprising a coxobasis and a 3-segmented endopod which is directed at a right angle (Fig. 3A). In all other species the middle and distal endopod segments are fused forming a 2-segmented ramus (Fig. 3B,C,F,H). The coxobasis bears a vestigial seta in *Laitmatobius* (labelled l in Fig. 3A) but in all other Lubbockiidae this compound segment is bare although re-examination of some *Lubbockia* species revealed a small pore or scar in this position. The ancestral setation formula for the endopod is [1,3,7] and is retained as [1,3+7] in most *Lubbockia* species (Fig. 3B) with the exception of the species related to *L. squillimana* (Fig. 3C-E). The lateral elements on enp-2 show a typical pattern with 1 seta (b) inserted proximally and 2 distally (c-d), usually unequal in length and located at a point marking the original fusion plane between enp-2 and enp-3. This distribution is a useful reference for homologizing individual setae in species where only two elements are retained. In *Pseudolubbockia* it is one of the distal elements that has been lost (likely the shorter seta c; Fig. 3F-G)) whereas in *L. squillimana*, *L. extenuata*, *L. aculeata* and *L. wilsonae* both distal elements are retained and the proximal one (b) is lost (Fig. 3C). The apical armature derived from enp-3 typically comprises 2 subapical (j-k) and 5 apical (e-i) elements. Seta (i) can be identified in most species as a pinnate or densely plumose element (Fig. 3B-D,F,G). In both *Laitmatobius* and *Pseudolubbockia* one of the apical elements is lost, leaving one pinnate spine (located slightly anteriorly; labelled i in Fig. 3G) and 3 claws (f-h) decreasing in size towards the inner margin (Fig. 3F-G). The subapical elements are setiform and short in both genera (Fig. 3A, F-G). A total of 6 terminal elements is also retained in *L. squillimana* and related species (Fig. 3C-E). In the females 3 apical claws [(e-f), g, h] are present which are stouter and increasing in size towards the inner margin, and the anterior pinnate spine (i) is shifted to the inner subdistal corner. The detailed morphology of the largest claw (labelled f in Fig. 3E) reveals that the missing fourth claw (e) is vestigial and incorporated into this element. In *Pseudolubbockia*, *Laitmatobius*, *L. carinata* and *L. forcipula* the subapical setae are typically short whereas in the other lubbockiids the outermost one of these elements is modified into a lash-like structure, at least in the male (Fig. 3B, H). The antennae are sexually dimorphic in a number of *Lubbockia* species. The male second (compound) endopod segment is more slender and less chitinized, and bears slender setiform elements replacing the 4 apical claws of the female (compare Fig. 3C and H). Antennary sexual dimorphism is a common phenomenon in planktonic Poecilostomatoida as it has been recorded for the Paralubbockiidae (BOXSHALL & HUYS 1989), Corycaeidae and Sapphirinidae (GIESBRECHT 1892), Urocopiidae (HERON & DAMKAER 1986) and the genera *Pachos* (BOXSHALL 1977) and *Oncaea* (HERON & BRADFORD-GRIEVE 1995).

Mouthparts. The mandible is relatively conservative in the family and is very similar in structure to that of the Intramolgidae (MARCHENKOV & BOXSHALL 1995). It is typically drawn out into a tapering median lash which is conspicuously dentate along the ventral edge. Two discrete blades are located ventral to the lash in all species. Two additional elements are located dorsal to the lash along the concave margin, the proximal one being a pinnate or hirsute seta, the distal one being a short multipinnate element. The distal dorsal element is well developed in e.g. *L. extenuata* (cf. HUYS & BOXSHALL 1991: Fig. 2.10.10B) but there is a trend toward the gradual incorporation of the element into the dorsal margin where it persists as a hirsute patch (e.g. *Laitmatobius*) or as a close-set row of dentiform spinules (*Pseudolubbockia*).

The maxillule is a flat, bilobate appendage with 3 setae on the outer lobe (representing the palp) and a maximum of 3 elements on the inner lobe. The innermost element of the latter is typically minute and can be absent in some species (*L. forcipula*, *L. carinata*). In *Pseudolubbockia* both lobes are reduced and bear 2 elements each.

Fig. 3. Antenna of **A,** *Laitmatobius crinitus* (♂); **B,** *Atrophia glacialis* (♀); **C,** *Lubbockia aculeata* (♀); **F,** *Pseudolubbockia dilatata* (♀); **H,** *Lubbockia wilsonae* (♂). Distal portion of second antennary endopod segment in **D,** *Lubbockia extenuata* (♀); **G,** *P. dilatata* (♀). **E,** Close-up of large antennary claw in *L. extenuata*. [D-E, G: originals; A after HUMES (1987), B after HERON et al. (1984), C and H after HERON & DAMKAER (1978), F after HERON & DAMKAER (1969)].

The maxilla varies only slightly among the various lubbockiid species. It consists of a robust, unarmed syncoxa which lacks any trace of endites. The distal segment or basis is drawn out into a bifurcate apical element which is largely defined at the base and consists of a naked, spiniform inner branch and a pinnate, setiform outer branch. The distal parts of the branches are usually twisted and superimposed on each other. The inner margin has one densely pinnate seta, the outer margin has a well developed seta distally and a hyaline papilla or setule proximally.

The mandible, maxillule and maxilla are atrophied in the males of a number of *Lubbockia* species. According to HERON & DAMKAER (1977) the degree of degeneration varies between specimens and between left and right sides. Males with atrophied mouthparts have been reported in a number of planktonic families such as the Aegisthidae in the Harpacticoida (HUYS 1988), the Mormonillidae in the Mormonilloida (HUYS et al. 1992), the Pontoeciellidae in the Siphonostomatoida (FARRAN 1936; BOXSHALL 1977) and in several representatives of the calanoid families Euchaetidae, Aetideidae, Clausocalanidae, Eucalanidae and Paracalanidae. In the planktonic Poecilostomatoida only the genus *Copilia* Dana in the Sapphirinidae (GIESBRECHT 1892) and the monotypic Paralubbockiidae (BOXSHALL & HUYS 1989) possess non-feeding males with atrophied mouthparts.

Maxilliped. The maxillipeds are sexually dimorphic in lubbockiids, representing the ancestral state in the order Poecilostomatoida which is clearly related to the mating behaviour. The absence of sexual dimorphism in two species of *Lubbockia*, *L. brevis* and *L. flemingi*, is regarded as secondary. The maxilliped is primitively 5-segmented in both sexes, comprising a syncoxa, basis and 3-segmented endopod. At least in some species the endopodal claw carries 1 or 2 elements at its base and is therefore regarded as representing the third endopod segment. The syncoxa is unarmed in all lubbockiids. The basis also typically lacks armature with the exception of the males of *Pseudolubbockia* and *Laitmatobius* which have 2 unequal setae on the palmar margin and the female of the former which has retained 1 minute element. In a number of species the palmar margin of the basis is modified forming distinct spinous processes in the female (e.g. *L. squillimana* and *L. wilsonae*; Fig. 2F). In *L. carinata* (Fig. 2D) and particularly *L. forcipula* (Fig. 2E) the female maxilliped is strongly modified forming an anterior keel-like process on the basis which is associated with a cuticular pocket in which the endopodal claw can be withdrawn. In *L. forcipula* the claw is strongly reduced so that it becomes shorter than the anterior process, giving the maxilliped a chelate rather than a subchelate appearance (Fig. 2E).

The endopod is 3-segmented in the males of *Pseudolubbockia*, *Laitmatobius* and *L. carinata*, and indistinctly so in the female of *P. dilatata* (the ♀ of *Laitmatobius crinitus* is unknown). In other lubbockiids the endopod is typically 2-segmented in both sexes (1 segment + claw), except for the species that lack sexual dimorphism where the endopod is more condensed and represented by the claw only.

Swimming legs 1-4. Although swimming leg armature patterns are useful in constructing keys (HERON & DAMKAER 1978), phylogenetic importance to these patterns should be attributed with considerable caution. Convergent reductions in setal counts are commonplace in most copepod families and should consequently not be used as the sole basis to infer phylogenetic relationships. Important transformations within the Lubbockiidae include the loss of the inner basal spine of P1 and the reduction from 3 to 2 outer spines in P1-P2 exp-3. The [I,II,I+2] formula of P3 enp-3 is regarded as the ancestral state by inference from the condition in closely related families such as the Intramolgidae. This condition is retained in *Pseudolubbockia*, *Laitmatobius*, *L. forcipula*, *L. carinata* and *L. petersoni*. Only two other species (*L. brevis*, *L. flemingi*) have 3 elements on the inner margin, all of which are setiform. The transformation of the distal inner spine into a seta is regarded as apomorphic, however the state of this character could not be scored in the species possessing only 2 inner elements since it is unknown whether the spine was already transformed before being lost. A similar interpretation applies to the P4 endopod.

HERON & DAMKAER (1978) pointed out the presence of a hyaline papilla partially covering a vent on the outer margin of the P1 coxa in the majority of *Lubbockia* species. This raised structure might well be homologous to the large spiniform process found in a similar position in *Chauliolobion* Humes (Synapticolidae).

Leg 5. The ancestral state of the P5 is 2-segmented, with an undivided protopod bearing the outer basal seta and being largely incorporated into the somite, and a 1-segmented exopod bearing 4 elements. This condition has persisted only in both sexes of *Pseudolubbockia*. The most common modification is the reduction in exopodal setation to 2 distal setae. These elements can be secondarily enlarged and provided with strongly developed serrate flanges, such as in *L. extenuata*. The outer basal seta is lost in the majority of lubbockiids but is retained as the only vestige of leg 5 in *L. petersoni* which lacks the exopod.

Leg 6. Leg 6 is highly reduced and represented by 1-2 minute setae in both sexes. In some species it is further reduced forming a small spinous process. In general it appears of little use as a generic character, since the number of elements can differ between species as in *Lubbockia*.

Caudal ramus. The caudal ramus in the great majority of the lubbockiids has been illustrated as bearing 6

setae. The minute seta I is usually overlooked although its position has been indicated by a pore in more recent descriptions (HERON et al. 1984). In the primitive genera *Pseudolubbockia* and *Laitmatobius* setae IV-VII are typically resilient and about equal in length. This condition is also found in *L. carinata* and *L. forcipula* but in all other species setae IV and VI are reduced and seta IV is distinctly shorter than seta VII. In *L. glacialis* and *L. minuta* the caudal ramus shows slight sexual dimorphism in that seta IV is much longer in the male.

4.2. Data matrix

HERON & DAMKAER (1978) alluded to the complexity of the genus *Lubbockia* by stating that it is "...far more variable than many other polytypic poecilostome genera". In order to resolve the relationships within the genus *Lubbockia* the analysis was executed at the species level. The characters used in the analysis of phylogenetic relationships between *Laitmatobius crinitus*, *Pseudolubbockia dilatata* and the 11 species of *Lubbockia* are listed in Table I. The character states are explained inside square brackets using the multistate system: 0 = the ancestral state, 1 = the derived state, 2 = a further derived state. The scores for each character and taxon are compiled in matrix format in Table 2. A question mark indicates missing data, either because the appendage or structure is absent (e.g. P5 exopod in *L. petersoni*) or unknown in that genus (certain sexually dimorphic characters could not be scored

Tab. 2. Characters used in the phylogenetic analysis. Apomorphic character states are referred to in square brackets. Characters 3, 5 and 24 are multistate characters. Antennulary segment numbers (characters 3-10) refer to segments/portions homologous to the segments identified in the generalized 7-segmented ♀ antennule [see text].

1	Penultimate abdominal somite of equal length in both sexes [elongate in ♂]
2	Antennule ♂ 5-segmented with segment 3 discrete [at most 4-segmented with segment 3 incorporated in segment 4]
3	Antennulary segment 2 (♀) with 13 setae and 1 spinule [state 1: with 11 setae; state 2: with 7 elements and 1 spinule]
4	Antennulary segment 2 (♀) without aesthetasc [1 seta modified into aesthetasc]
5	Antennulary segment 3 (♀) with 4 setae [state 1: with 3 setae; state 2: with 2 setae]
6	Antennulary segment 5 (both sexes) with 4 setae + aesthetasc [3 + aesthetasc]
7	Antennulary segment 7 (both sexes) with 7 setae + aesthetasc [6 + 2 aesthetascs]
8	Antennulary segment 2 (♂) without sexually dimorphic aesthetascs [addition of 1 aesthetasc]
9	Antennulary segment 4 (♂) without sexually dimorphic aesthetascs [addition of 2 aesthetascs]
10	Aesthetasc of segment 6, terminal aesthetasc of segment 7 and sexually dimorphic aesthetascs (segments 2 and 4) not modified [very long and with seta-like supporting rib]
11	Antenna not sexually dimorphic [sexually dimorphic]
12	Antennary endopod 3-segmented [2-segmented by fusion of enp-2 and -3]
13	Antennary endopod subapical setae (derived from enp-3) short and about equal [1 seta long and lash-like, at least in ♂]
14	Antennary endopod with 5 apical claws [1 claw lost]
15	Antennary endopod with 5 (or 4) short apical claws [4 claws enlarged, innermost one diminutive and absorbed in largest one]
16	Antennary endopod with 1 proximal and 2 distal lateral setae [proximal lateral seta lost]
17	Mandible, maxillule and maxilla not sexually dimorphic [mouthparts atrophied in ♂]
18	Maxilliped sexually dimorphic [not sexually dimorphic]
19	Maxilliped without spinous processes on palmar margin of basis [with]
20	Maxillipedal basis (♀) with 1 seta [without setae]
21	Maxillipedal basis (♂) with 2 unequal setae [without setae]
22	Maxillipedal basis without anterior keel-like process [process present]
23	Maxillipedal endopod (♀) indistinctly 3-segmented [2-segmented or reduced to claw only]
24	Maxillipedal endopod (♂) 3-segmented [state 1: 2-segmented; state 2: represented by claw only]
25	P1 inner basal spine present [absent]
26	P1 exp-3 with 3 outer spines [2 outer spines]
27	P2 exp-3 with 3 outer spines [2 outer spines]
28	P3 enp-3 with 2 setae and 1 spine or total of 3 setae on inner margin [with 2 setae]
29	P4 enp-3 with 1 seta and 1 spine or total of 2 setae on inner margin [with 1 seta]
30	P3 enp-3 with distalmost (i.e. 3rd) element of inner margin spiniform [setiform]
31	P4 enp-3 with distalmost (i.e. 2nd) element of inner margin spiniform [setiform]
32	P5 (both sexes) with outer basal seta [lost]
33	P5 (both sexes) with normal-sized spines/setae [enlarged with strongly developed serrate flanges]
34	Caudal ramus with (about equally) long, resilient setae IV-VII [setae IV and VI reduced with seta IV markedly shorter than seta VII]
35	Caudal ramus seta IV of equal length in both sexes [sexually dimorphic, much longer in ♂]

Tab. 3. Character states of 35 characters listed in Tab. 2 for *Laitmatobius*, *Paralubbockia* and 11 species of *Lubbockia*.

Character	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35
LAITMATOBIUS	0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 ? 0 ? 0 0 ? 0 1 1 1 0 0 0 0 0 0 0 0
PARALUBBOCKIA	0 0 1 0 1 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0
squillimana	0 1 2 1 2 1 1 1 1 1 1 1 1 0 1 1 1 0 1 1 1 0 1 1 0 1 1 1 1 ? ? 1 1 1 0
aculeata	0 1 2 1 2 1 1 1 1 1 1 1 1 0 1 1 1 0 1 1 1 0 1 1 0 1 1 1 1 ? ? 1 1 1 0
glacialis	1 1 2 0 2 1 1 1 1 1 1 1 1 0 0 0 1 0 0 1 1 0 1 1 1 0 0 1 1 ? ? 1 0 1 1
minuta	1 1 2 0 2 1 1 1 1 1 1 1 1 0 0 0 1 0 0 1 1 0 1 1 1 0 0 1 1 ? ? 1 0 1 1
brevis	0 1 2 0 2 1 1 1 1 0 0 1 1 0 0 0 0 1 0 1 1 0 1 2 0 0 0 0 0 1 1 1 0 1 0
extenuata	0 1 2 1 2 1 1 1 1 1 1 1 1 0 1 1 1 0 0 1 1 0 1 1 0 1 1 1 1 ? ? 1 1 1 0
carinata	0 1 0 0 1 0 0 0 0 1 0 0 0 0 0 0 1 1 1 1 0 1 1 1 0 0 0 0 0 0 0 0 0 0
flemingi	0 1 2 0 2 1 1 1 1 0 0 1 1 0 0 0 0 0 1 0 1 1 0 1 2 0 0 0 0 0 1 1 1 0 1 0
forcipula	? ? 0 0 1 0 0 ? ? ? 1 0 0 0 0 0 ? ? 0 1 ? 1 1 ? 0 1 1 0 0 0 0 0 0 0 0 0
petersoni	0 1 2 0 2 1 1 1 1 0 0 1 1 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 0 ? 1 0
wilsonae	0 1 2 1 2 1 1 1 1 1 1 1 1 0 1 1 1 0 1 1 1 0 1 1 0 1 1 1 1 ? ? 1 1 1 0

because only one sex is known, e.g. *L. forcipula*, *L. crinitus*) or because it was impossible to score the character accurately using the rigorous definition of homology (e.g. transformation of distal inner spine: characters 30-31).

4.3. Analysis

A single optimal tree was obtained with tree-length 47 and consistency index 0.809 (Fig. 4). Five major results can be inferred from the cladogram:

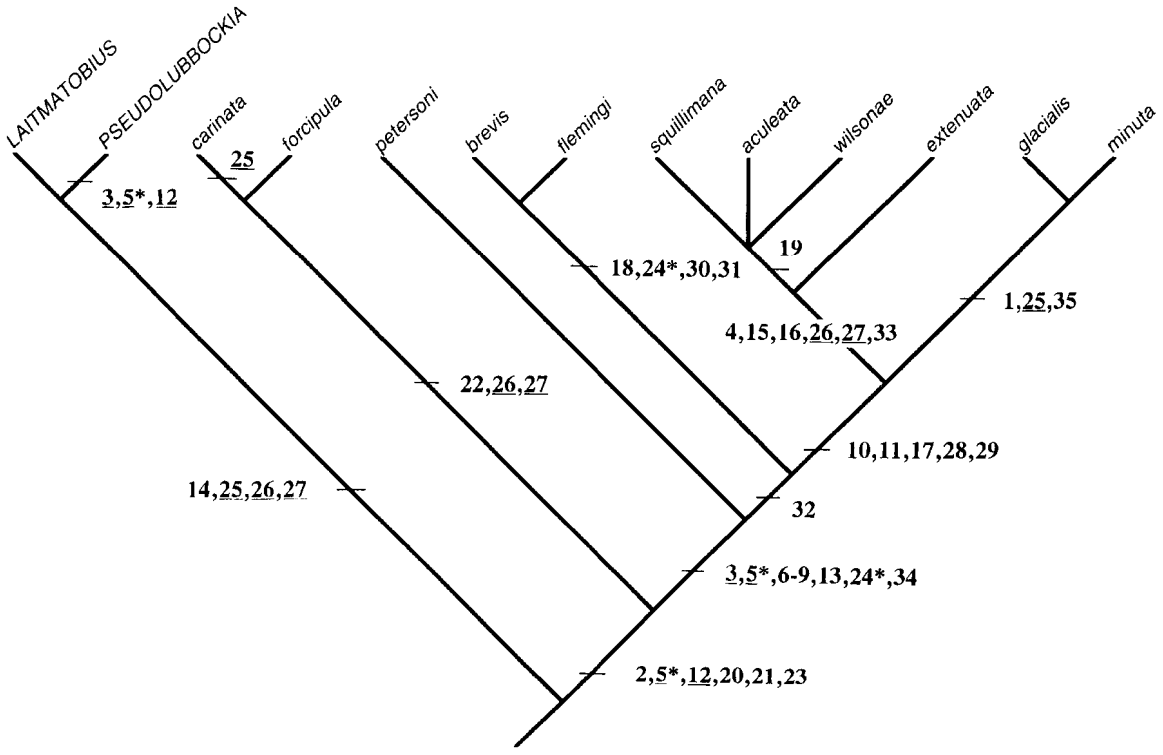


Fig. 4. Cladogram depicting relationships between *Laitmatobius*, *Pseudolubbockia* and 11 species of *Lubbockia*. Numbers refer to apomorphic states of characters listed in Tab. 2 [underlined numbers refer to convergences, * indicate multistate characters].

(a) *Laitmatobius* and *Pseudolubbockia* are the most primitive genera of the family and their sistergroup relationship is supported by the presence of 6 apical elements on the distal endopod segment of the antenna, the absence of the inner basal spine of leg 1 and the presence of only 2 outer spines on the distal exopod segment of P1-P2. (b) All *Lubbockia* species are grouped in a monophyletic lineage which represents the sistergroup to the *Laitmatobius-Pseudolubbockia* clade. This is a strongly supported group characterized by the fusion of segments 3 and 4 in the male antennule, the presence of only 2 or 3 setae on the 3rd antennulary segment in the female, the 2-segmented antennary endopod, the unarmed maxillipedal basis in both sexes and segmental reduction in the maxillipedal endopod of the female. (c) *L. carinata* and *L. forcipula* are the most primitive *Lubbockia* species which split off together from the main lineage on account of the modified maxillipeds. The primitive position of these species was alluded to by HERON & DAMKAER (1978) who recognized the close affinity between *Lubbockia* and *Pseudolubbockia* provided the comparison be based on these two species and *L. petersoni*. The latter species occupies an intermediate and isolated position between the *carinata-forcipula* branch and the other *Lubbockia* species. It belongs to a clade that is characterized by setal reductions in the antennules, the transformation of setae into aesthetascs on antennulary segment 7, the presence of sexually dimorphic aesthetascs in the male, the modification of a subapical antennary seta into a lash- like element, and reductions in the male maxillipedal endopod and setae IV and VI of the caudal rami. (d) The remaining *Lubbockia* species cluster in three sharply delineated groups. The *brevis-flemingi* clade is defined by the loss of sexual dimorphism in the maxillipeds, the reduction of the endopod

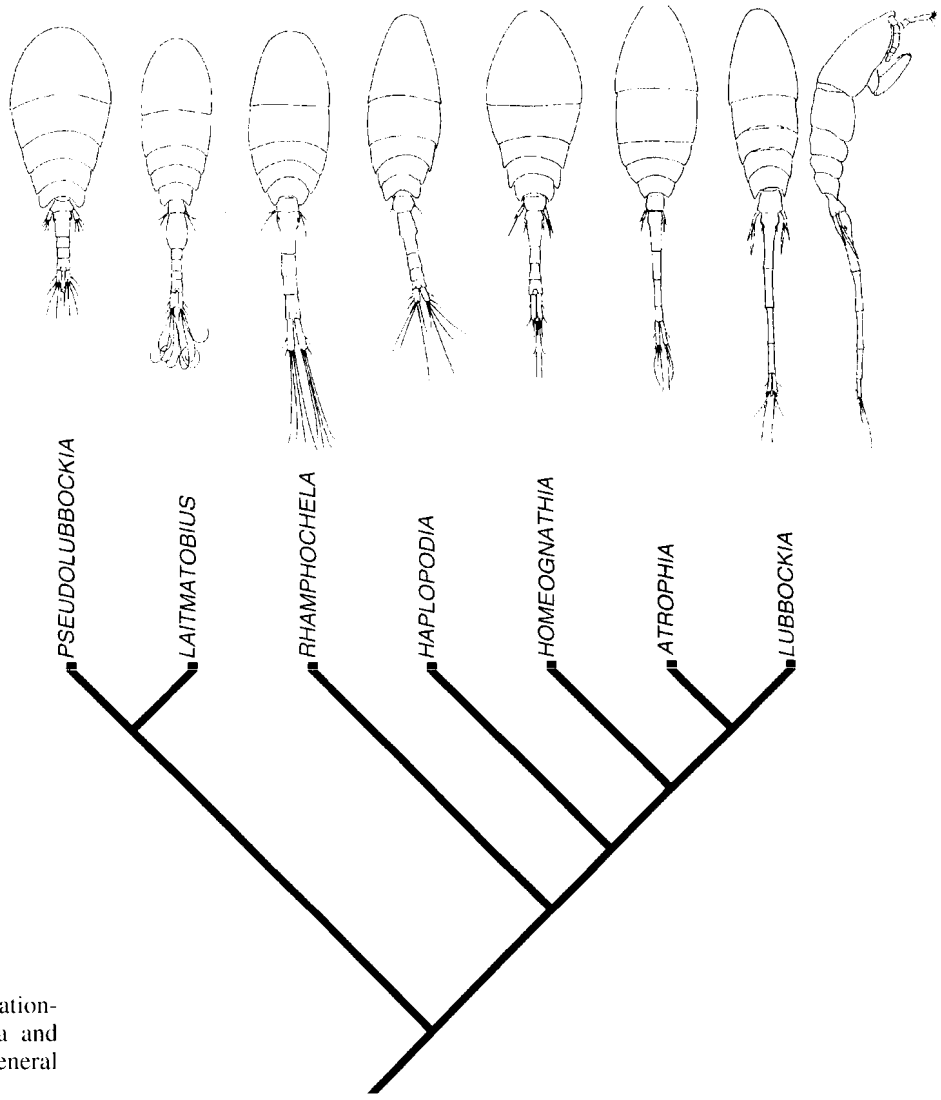


Fig. 5. Cladogram depicting relationships between lubbockiid genera and showing evolutionary trend in general body shape.

in the maxillipeds of both sexes and the secondary transformation of the distal inner spine of P3-P4 enp- 3 into a setiform element. The *glacialis-minuta* lineage displays sexual dimorphism in the penultimate abdominal somite and the length of seta IV on the caudal ramus, and has lost the inner basal spine of leg 1. The *squillimana* group combines species that have lost the proximal lateral seta on the antennary endopod, possess a modified antenna and an aesthetasc on antennulary segment 2 in the female, have only 2 outer spines on P1-P2 exp-3 and enlarged spines on leg 5. The latter two lineages are sistergroups on the basis of the presence of atrophied mouthparts and modified antennulary aesthetascs in the males, the sexually dimorphic antennae and setal reductions on the P3-P4 endopods. (e) The present analysis corroborates HERON & DAMKAER's (1978) supposition that variable armature characteristics on the swimming legs do not appear to reflect natural groupings as is the case in the *Oncaea-Conaea-Epicalymma* complex. This is particularly illustrated by the fact that the loss of the inner basal spine of leg 1 and the proximal outer spine of P1-P2 exp-3 (characters 25-27) show up as convergences in the cladogram (Fig. 4).

The genus *Lubbockia*, as it is currently diagnosed, clearly contains several lineages characterized by major differences in sexual dimorphism in the antenna, mouthparts, urosome and caudal rami, warranting the creation of distinct genera. On the basis of these differences supplemented by additional discrepancies in aesthetasc patterns and swimming legs armature it is proposed here to split up *Lubbockia* in five genera (Fig. 5) according to the topology depicted in Fig. 4.

4.4. Diagnoses of genera

• *Lubbockia* Claus, 1862

Lubbockiidae. Body slender, with elongate prosome; postgenital somites moderately to distinctly elongate. Antennule ♀ indistinctly 7-segmented with segments 3-4 partially or completely fused; armature formula: 1-[4], 2-[6 + ae + 1 spinule], 3-[2], 4-[4], 5-[3 + ae], 6-[2 + ae], 7-[5 + 2 ae]. Antennule ♂ indistinctly 3-segmented with segments 1-2 partially fused; segments 2 and 3 homologous to fused segments 2-4 and 5-7 of ♀, respectively; armature formula: 1-[4], 2-[(6 + 2 ae + 1 spinule),(2),(4 + 2 ae)], 3-[(3 + ae),(2 + ae),(5 + 2 ae)]; 6 aesthetascs very long and with seta-like supporting rib. Antenna sexually dimorphic (enp-2); coxobasis without seta; endopod 2-segmented (enp-2 and -3 fused); enp-1 small, with 1 seta; lateral armature (derived from enp-2) of distal endopod segment comprising 1 short and 1 long seta (proximal seta lost); ♀ apical armature (derived from enp-3) consisting of 2 subdistal pinnate setae and 4 distal claws, innermost strongly developed and with enlarged base incorporating vestigial 7th element, anteriormost setulose and with flexible apex; distal endopod segment more slender in ♂, with naked distal claws replaced by setae and 1 subdistal seta elongate and lash-like. Mandible with toothed median lash, and 2 ventral plus 1-2 dorsal discrete elements. Maxillule bilobate, armature 3 + 3. Mandible, maxillule and maxilla atrophied in ♂. Maxilliped sexually dimorphic, subchelate; basis without armature, palmar margin with spinous processes in ♀ (except *L. extenuata*), with multiple spinule rows in ♂; endopod ♀ 2-segmented, with strong recurved claw bearing 1 minute accessory seta basally; endopod ♂ 2-segmented, distal claw slender and undulant (*extenuata*, *wilsonae*) or robust and strongly recurved (*squillimana*, *aculeata*), with minute accessory seta basally. Outer spine of P1 enp-3 not sexually dimorphic. Inner basal spine of P1 short and thorn-like. Swimming leg armature formula as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-1	1-I	I-0;I-1;II,I,4	0-1;0-1;I,5
P2	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,3
P3	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,2
P4	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,1

P5 of both sexes represented by free cylindrical exopod segment with 2 spines; outer basal seta absent; exopodal spines very large and with strongly developed serrate flanges. Caudal rami not sexually dimorphic; setae IV and VI reduced with seta IV markedly shorter than seta VII.

Type species. *Lubbockia squillimana* Claus, 1863 [by monotypy]

Other species. *L. aculeata* Giesbrecht, 1891; *L. wilsonae* Heron & Damkaer, 1969; *L. extenuata* Boxshall, 1977.

L. extenuata occupies an isolated position in the genus because of the lack of spinous processes on the palmar margin of the maxilliped. Since it forms part of a strongly supported clade diagnosed by 6 synapomorphies its allocation to *Lubbockia* is preferred over the erection of a monotypic genus.

Key to species.

1. P6 with 2 elements in both sexes ..... *L. wilsonae*.
   P6 with 1 element in both sexes ..... 2.
2. Maxilliped ♀ without spinous processes on palmar margin of basis; P5 ♂ almost as long as genital somite ..... *L. extenuata*.
   Maxilliped ♀ with spinous processes on palmar margin of basis; P5 ♂ about half as long as genital somite ..... 3.

3. Maxilliped ♀ with spinous process on syncoxa; epimeral plates of P4-bearing somite with posterolateral angles produced; ♂ anal somite not constricted ..... *L. aculeata.*
Maxilliped ♀ without spinous process on syncoxa; epimeral plates of P4-bearing somite with posterolateral angles not produced; ♂ anal somite with conspicuous constriction in middle of somite ..... *L. squillimana.*

• *Pseudolubbockia* Sars, 1909

The following diagnosis is based on HERON & DAMKAER's (1969) excellent redescription of *P. dilatata* supplemented by subsequent reinterpretations of the female antennule (HERON & DAMKAER 1978) and male maxilliped (HUYS & BOXSHALL 1991). Re-examination of the type slide of *P. dilatata* held in the Zoologisk Museum, Oslo (reg. no. F5474) revealed the female maxilliped to be indistinctly 3-segmented.

Lubbockiidae. Body cyclopiform; prosome elongate-oval and robust in dorsal and lateral aspect; postgenital somites short. Antennule ♀ indistinctly 7-segmented with segments 5-6 incompletely fused; armature formula: 1-[4], 2-[11], 3-[3], 4-[4], 5-[4 + ae], 6-[2 + ae], 7-[7 + ae]. Antennule ♂ 5-segmented; segment 5 homologous to fused segments 5-7 of ♀, original segmentation marked by faint suture lines; armature formula: 1-[4], 2-[11], 3-[3], 4-[4], 5-[(4 + ae),(2 + ae),(7 + ae)]; aesthetascs short and typically associated with seta. Antenna not sexually dimorphic; coxobasis without seta; endopod 2-segmented (enp-2 and -3 fused); enp-1 with 1 seta; lateral armature (derived from enp-2) of distal endopod segment comprising 2 short setae (1 distal seta lost); apical armature (derived from enp-3) of distal endopod segment consisting of 2 short naked setae subdistally and 4 small claws distally, innermost shortest, anteriormost bipinnate. Mandible with toothed median lash, and 1 dorsal plus 2 ventral discrete elements; concave margin with scale-like denticles. Maxillule bilobate, armature 2 + 2. Mouthparts not atrophied in ♂. Maxilliped sexually dimorphic, subchelate; palmar margin of basis with 1 minute seta in ♀ and 2 small unequal setae in ♂; endopod indistinctly (♀) or distinctly (♂) 3-segmented, armature formula [0,0,claw + 1 minute accessory seta] in ♀ and [0,2,claw + 1 minute accessory seta] in ♂; distal claw robust and recurved in both sexes. Outer spine of P1 enp-3 sexually dimorphic. Inner basal spine of P1 absent. Swimming leg armature formula as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-1	1-0	I-0;I-1;II,I,4	0-1;0-1;I,5
P2	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,3
P3	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,2+I
P4	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,1+I

P5 of both sexes represented by free flat exopod segment with 4 spines; outer basal seta present; exopodal spines slender and with finely serrated flanges. Caudal rami not sexually dimorphic; setae IV-VII resilient and about equally long.

Type and only species. *Pseudolubbockia dilatata* Sars, 1909 [by monotypy]

The genus is characterised by the following apomorphies: (a) presence of only 11 and 3 setae on the 2nd and 4th antennulary segments, respectively; (b) 2-segmented antennary endopod; (c) loss of distal lateral element on enp-2 of antenna; (d) reduction of the maxillule bearing 2 setae on each lobe.

• *Laitmatobius* Humes, 1987

The diagnosis below is based on the male only.

Lubbockiidae. Body cyclopiform; prosome elongate-oval and robust in dorsal and lateral aspect; postgenital somites short. Antennule ♂ distinctly 5-segmented; segment 5 homologous to fused segments 5-7 of other lubbockiid ♀♀, original segmentation marked by faint suture line; armature formula: 1-[4], 2-[13], 3-[4], 4-[4], 5-[(4 + ae),(2 + ae), (7 + ae)]; aesthetasc derived from portion homologous to segment 5 in ♀. Antenna probably not sexually dimorphic; coxobasis with vestigial setule; endopod 3-segmented; enp-1 with 1 seta; enp-2 with 1 proximal and 2 distal setae; enp-3 with apical armature consisting of 2 short naked setae subdistally and 4 small claws distally, innermost shortest. Mouthparts not atrophied in ♂. Mandible with toothed median lash, and 1 dorsal plus 2 ventral discrete elements; concave margin pinnate. Maxillule bilobate, armature 3 + 2. Maxilliped sexually dimorphic, subchelate; palmar margin of basis with 2 small unequal setae in ♂; endopod indistinctly 3-segmented in ♂, armature formula [0,0,claw + 1 minute accessory seta]; distal claw robust and recurved.

Outer spine of P1 enp-3 not sexually dimorphic. Inner basal spine of P1 absent. Swimming leg armature formula as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-1	1-0	I-0;I-1;II,I,4	0-1;0-1;I,5
P2	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,3
P3	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,2+I
P4	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,1+I

P5 ♂ represented by free cylindrical exopod segment with 2 setae; outer basal seta present; exopodal setae unequal, longest with slightly developed serrate flanges. Caudal rami with about equally long, resilient setae IV-VII; sexual dimorphism unconfirmed.

Type and only species. *Laitmatobius crinitus* Humes, 1987 [by monotypy]
Laitmatobius differs from *Pseudolubbockia* in the segmentation of the antennary endopod, the setation and shape of leg 5, and the absence of armature on the male P6.

• *Rhamphochela* gen. nov.

Lubbockiidae. Body slender, with elongate prosome; postgenital somites relatively short. Antennule ♀ indistinctly 6-segmented with ancestral segments 3-4 completely and segments 5-6 partially fused; armature formula: 1-[4], 2-[13 + 1 spinule], 3-[(3),(4)], 4-[4 + ae], 5-[2 + ae], 6-[7 + ae]. Antennule ♂ 4-segmented; segments 3 and 4 homologous to fused ancestral segments 3-4 and 5-7 of ♀, respectively; armature formula as in ♀; aesthetascs short. Antenna not sexually dimorphic; coxobasis without seta; endopod 2-segmented (enp-2 and -3 fused); enp-1 small, with 1 seta; lateral armature (derived from enp-2) of distal endopod segment consisting of 1 proximal and 2 distal setae; apical armature elements (derived from enp-3) short, comprising 2 subdistal setae and 5 distal naked claws, the latter decreasing in size medially. Mandible with toothed median lash, and 2 ventral plus 2 dorsal discrete elements. Maxillule bilobate, armature 3 + 2. Mandible, maxillule and maxilla not atrophied in ♂. Maxilliped sexually dimorphic; basis without armature, in ♀ with anterior keel-like process and palmar margin forming sheath for endopodal claw (subchelate in *R. carinata*, chelate in *R. forcipula*), in ♂ not modified and palmar margin with spinular patch; endopod ♀ 2-segmented, with moderately short to very short claw, no accessory setae; endopod ♂ 3-segmented, armature formula [0,0,claw + 1 minute accessory seta] with distal claw robust, long and recurved. Outer spine of P1 enp-3 not sexually dimorphic. Inner basal spine of P1 absent (*R. carinata*) or present (*R. forcipula*). Swimming leg armature formula as follows (asterisk indicating variable count):

Leg	Coxa	Basis	Exopod	Endopod
P1	0-1	1-*	I-0;I-1;II,I,4	0-1;0-1;I,5
P2	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,3
P3	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,2+I
P4	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,1+I

P5 of both sexes represented by free cylindrical exopod segment with 2 setae; outer basal seta present; exopodal setae slender, with reduced serrate flanges. Caudal rami not sexually dimorphic; setae IV-VI about equally long and resilient.

Type species. *Lubbockia carinata* Heron & Damkaer, 1978 = *Rhamphochela carinata* (Heron & Damkaer, 1978) comb. nov.
Other species. *Lubbockia forcipula* Heron & Damkaer, 1978 = *Rhamphochela forcipula* (Heron & Damkaer, 1978) comb. nov.
Etymology. The generic name is derived from the Greek *rhamphos*, meaning beak, and *chele*, meaning claw, and alludes to the modified female maxillipeds. Gender: feminine.
R. carinata and *R. forcipula* differ in the detailed morphology of the maxilliped and the presence or absence of the inner basal spine on leg 1. A re-run of the phylogenetic analysis with all characters unpolarized, i.e. allowed to change in any direction, resulted in a shorter tree (tree-length 43) which differed only in the topology of both *Rhamphochela* species and did not support their sistergroup relationship (i.e. *R. carinata* and *R. forcipula* successively diverging as monotypic branches). Examination of the character change list revealed that the reason for the branch rearrangement lies in the sexually dimorphic features for which ambiguous states were assigned despite the male of *R. forcipula* being unknown.

• *Haplopodia* gen. nov.

Lubbockiidae. Body slender, with elongate prosome; postgenital somites short. Antennule ♀ indistinctly 7-segmented with all segment boundaries incompletely defined except for plane between segments 4-5; armature formula: 1-[4], 2-[7 + 1 spinule], 3-[2], 4-[4], 5-[3 + ae], 6-[2 + ae], 7-[5 + 2 ae]. Antennule ♂ with segmentation as in ♀ except for segments 5-7 forming compound segment with original segmentation marked by faint suture lines; armature formula: 1-[4], 2-[7 + ae + 1 spinule], 3-[2], 4-[4 + 2 ae], 5-[(3 + ae),(2 + ae),(5 + 2 ae)]; aesthetascs very long. Antenna not sexually dimorphic; coxobasis without seta; endopod 2-segmented (enp-2 and -3 fused); enp-1 small, with 1 seta; lateral armature (derived from enp-2) of distal endopod segment comprising 1 proximal and 2 distal setae; apical armature (derived from enp-3) consisting of 1 very long and 1 short seta subdistally and 5 slender distal claws decreasing in size medially. Mandible with toothed median lash, and 1 dorsal and 2 ventral discrete elements; concave margin with long setules representing incorporated element. Maxillule bilobate, armature 3 + 3. Mandible, maxillule and maxilla not atrophied in ♂. Maxilliped sexually dimorphic, subchelate; basis without armature, palmar margin naked in ♀, with spinule row in ♂; endopod 2-segmented, with relatively short claw in ♀ and long, elongate claw plus minute accessory seta in ♂. Outer spine of P1 enp-3 not sexually dimorphic. Inner basal spine of P1 slender.

Proximal outer spine P1-P2 exp-3 minute. Swimming leg armature formula as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-1	1-1	I-0;I-1;III,I,4	0-1;0-1;I,5
P2	0-1	1-0	I-0;I-1;III,I,5	0-1;0-2;I,II,3
P3	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,2+I
P4	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,1+I

P5 of both sexes strongly reduced; represented by outer basal seta only. Caudal rami not sexually dimorphic; setae IV-VII long.

Type and only species. *Lubbockia petersoni* Heron & Damkaer, 1978 = *Haplopodia petersoni* (Heron & Damkaer, 1978) comb. nov.

Etymology. The generic name is derived from the Greek *haploos*, meaning simple, and *pous*, meaning foot, and alludes to the reduced fifth leg represented by the outer basal seta only. Gender: feminine.

• *Atrophia* gen. nov.

Lubbockiidae. Body slender, with elongate prosome; postgenital somites distinctly elongate; anal somite much shorter than preceding somite. Antennule indistinctly 7-segmented with segments 3-4 and 5-6 partially fused; armature formula: 1-[4], 2-[7 + 1 spinule], 3-[2], 4-[4], 5-[3 + ae], 6-[2 + ae], 7-[5 + 2 ae]. Antennule ♀ indistinctly 3- or 4-segmented with clear segment boundary only between segments homologous to 2-3 of ♀; incomplete suture lines present between segments homologous with 1-2 and 4-5 of ♀; armature formula: 1-[4], 2-[7 + ae + 1 spinule], 3-[(2),(4 + 2 ae)], 4-[(3 + ae),(2 + ae),(5 + 2 ae)]; aesthetasc of segment 6 and sexually dimorphic ones very long and with seta-like supporting rib; terminal aesthetasc transformed into remarkably long element reaching 2nd abdominal somite. Antenna sexually dimorphic (enp-2); coxobasis without seta; endopod 2-segmented (enp-2 and -3 fused); enp-1 small, with 1 seta; lateral armature (derived from enp-2) of distal endopod segment comprising 1 proximal and 2 distal setae; ♀ apical armature (derived from enp-3) consisting of 4 short claws and 3 setae, 1 naked, 1 setulose and 1 long and lash-like; distal endopod segment more slender in ♂, with naked distal claws replaced by slender setae. Mandible with toothed median lash, and 1 dorsal plus 2 ventral discrete elements; concave margin with long setules representing incorporated element. Maxillule bilobate, armature 3 + 3. Mandible, maxillule and maxilla atrophied in ♂. Maxilliped sexually dimorphic, subchelate; basis without armature, palmar margin with short (♀) or long (♂) spinules, outer margin rugose in ♂; endopod ♀ 2-segmented, with slender recurved claw, accessory setae absent; endopod ♂ not defined, represented by claw only. Outer spine of P1 enp-3 not sexually dimorphic. Inner basal spine of P1 absent. P1-P2 exp-3 proximal outer spine well developed. Swimming leg armature formula as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-1	1-0	I-0;I-1;III,I,4	0-1;0-1;I,5
P2	0-1	1-0	I-0;I-1;III,I,5	0-1;0-2;I,II,3
P3	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,2
P4	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,1

P5 of both sexes represented by free cylindrical exopod segment with 2 spines; outer basal seta absent; exopodal spines slender and with moderately developed serrate flanges.

Caudal rami sexually dimorphic with seta IV distinctly longer in ♂; setae IV (in ♀) and VI (both sexes) reduced with seta IV (in ♀) markedly shorter than seta VII.

Type species. *Lubbockia minuta* Wolfenden, 1905 = *Atrophia minuta* (Wolfenden, 1905) comb. nov.

Other species. *Lubbockia glacialis* Sars, 1900 = *Atrophia glacialis* (Sars, 1900) comb. nov.

Etymology. The generic name is derived from the Greek *a*, meaning without, and *trophe*, meaning nourishment, and alludes to the atrophied mouthparts in the males, a character shared with *Lubbockia*. Gender: feminine.

• *Homeognathia* gen. nov.

Lubbockiidae. Body slender, with elongate-oval prosome; postgenital somites short. Antennule ♀ indistinctly 7-segmented with segments 3-4 and 5-6 partially fused; armature formula: 1-[4], 2-[7 + + 1 spinule], 3-[2], 4-[4], 5-[3 + ae], 6-[2 + ae], 7-[5 + 2 ae]. Antennule ♂ indistinctly 4-segmented with apical compound segment representing fused segments 5-7 of ♀; armature formula: 1-[4], 2-[(7 + ae + 1 spinule)], 3-[(2),(4 + 2 ae)], 4-[(3 + ae),(2 + ae),(5 + 2 ae)]; aesthetasc of ancestral segment 6 and sexually dimorphic ones slightly longer than in ♀. Antenna not sexually dimorphic, abbreviated; coxobasis without seta; endopod 2-segmented (enp-2 and -3 fused); enp-1 very small, with 1 seta; lateral armature (derived from enp-2) of distal endopod segment comprising 1 short proximal and 2 distal setae; apical armature (derived from enp-3) consisting of 2 subdistal setae and 4 claws (descreasing in size medially) plus 1 setulose spine distally. Mandible with toothed median lash, and 1 dorsal plus 2 ventral discrete elements; concave margin with long setules representing incorporated element. Maxillule bilobate, armature 3 + 3. Mandible, maxillule and

maxilla not atrophied in ♂. Maxilliped not sexually dimorphic, subchelate; basis without armature, palmar margin with multiple spinule rows; endopod 2-segmented, with strong recurved claw, accessory setae absent. Outer spine of P1 enp-3 not sexually dimorphic. Inner basal spine of P1 long and with serrate flanges. P1-P2 exp-3 proximal outer spine well developed. Swimming leg armature formula as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-1	1-I	I-0;I-1;III,I,4	0-1;0-1;I,5
P2	0-1	1-0	I-0;I-1;III,I,5	0-1;0-2;I,II,3
P3	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,3
P4	0-1	1-0	I-0;I-1;II,I,5	0-1;0-2;I,II,2

P5 of both sexes represented by free cylindrical exopod segment with 2 spines; outer basal seta absent; exopodal spines slender and with moderately developed serrate flanges. Caudal rami not sexually dimorphic; setae IV and VI reduced with seta IV markedly shorter than seta VII.

Type species. *Lubbockia flemingi* Heron & Damkaer, 1978 = *Homeognathia flemingi* (Heron & Damkaer, 1978) comb. nov.

Other species. *Lubbockia brevis* Farran, 1908 = *Homeognathia brevis* (Farran, 1908) comb. nov.

Etymology. The generic name is derived from the Greek *homoios*, meaning alike, and *gnathos*, meaning jaw, and alludes to the lack of sexual dimorphism in the maxillipeds. Gender: feminine.

4.5. Key to genera

1. P1-P2 exp-3 with 2 outer spines ..... 2.
   P1-P2 exp-3 with 3 outer spines ..... 5.
2. Antennary endopod 3-segmented .... *Laitmatobius* Humes, 1987.
   Antennary endopod 2-segmented ..... 3.
3. P5 exopod of both sexes represented by flat segment with 4 serrate spines .... *Pseudolubbockia* Sars, 1909.
   P5 exopod of both sexes represented by cylindrical segment with 2 setae/spines ..... 4.
4. P3 enp-3 and P4 enp-3 with armature formula I,II,2+I and I,II,1+I, respectively; maxillipedal basis with anterior keel-like process in ♀; ♂ mouthparts not atrophied ..... *Rhamphochela* gen. nov.
   P3 enp-3 and P4 enp-3 with armature formula I,II,2 and I,II,1, respectively; maxillipedal basis without anterior keel-like process in ♀; ♂ mouthparts atrophied ..... *Lubbockia* Claus, 1862.
5. Inner margin of P3 enp-3 and P4 enp-3 with 2 and 1 setae/spines, respectively; antennae sexually dimorphic; ♂ mouthparts atrophied ... *Atrophia* gen. nov.
   Inner margin of P3 enp-3 and P4 enp-3 with 3 and 2 setae/spines, respectively; antennae not sexually dimorphic; ♂ mouthparts not atrophied ..... 6.
6. Maxillipeds sexually dimorphic; P3 enp-3 and P4 enp-3 with armature formula I,II,2+I and I,II,1+I, respectively; P5 of both sexes represented by outer basal seta only (exopod lost) .... *Haplopodia* gen. nov.
   Maxillipeds not sexually dimorphic; P3 enp-3 and P4 enp-3 with armature formula I,II,3 and I,II,2, respectively; P5 of both sexes represented by cylindrical exopod with 2 elements (outer basal seta lost) ..... *Homeognathia* gen. nov.

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Authors' addresses: Rony HUYS, Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom; Ruth BÖTTGER-SCHNACK, Christian-Albrechts-Universität, Institut für Meereskunde, Düsternbrooker Weg 20, D-24105 Kiel, Germany.

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Corresponding Editor: G. A. BOXSHALL