

Interpreting segment homologies of the maxilliped of cyclopoid copepods by comparing stage-specific changes during development

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Abstract

Development of the maxilliped of 14 species of cyclopoid copepods from 14 genera in the families Cyclopinidae, Oithonidae and Cyclopidae is described. Segment homologies are inferred from the assumption that homologous setae and arthrodial membranes are added during the same copepodid stage, and from a model of development that patterns the endopod proximally from the proximal of two endopodal segments present at the first copepodid stage. An arthrodial membrane separates the praecoxa and coxa of two Cyclopinidae and two of three Oithonidae. The praecoxa of the Cyclopinidae and the Oithonidae has two groups of setae; the praecoxa of Cyclopidae has no more than one group. The coxa of these copepods has only one group of setae; all Cyclopidae share a coxal lobe with a single seta. The endopod of these three families may include as many as five segments. In general, the distal arthrodial membrane of a segment appears to have been more labile during evolutionary history of the maxilliped than has the ventral seta which inserts on that segment. For purposes of phylogenetic analyses, uncoupling the presence of the distal arthrodial membrane of a segment from the presence of its ventral seta and analyzing each separately may provide a better way of understanding evolutionary transformations of the limb than considering the segment as the basic structural unit of the limb.

Keywords: cyclopoid, copepod, maxilliped, development, segment, homologies

Introduction

The maxilliped of copepods does not bear an exopod and often appears as a series of segments arranged linearly along a proximal-distal axis. For many cyclopoid copepods, segments of the maxilliped usually are counted as a series of arthrodial membranes along the limb. However, the identity of segments for a particular cyclopoid species and homologies of these segments among different species often are difficult to interpret. In providing a general overview of cyclopoids, Huys & Boxshall (1991) describe the maxilliped as having a syncoxa without a praecoxal endite, a basis, and an endopod with at most two segments in all families except the Cyclopinidae, which may have up to five segments, and the subfamily Eurytinae of the Cyclopidae which may have up to three segments. For cladistic analyses of cyclopoid families, Ho (1994) and Ho et al. (1998)

coded without comment an endopod of the maxilliped of the Cyclopinidae and the Oithonidae with five segments, and an endopod of Cyclopidae with three segments. There have been no detailed reviews of the maxilliped of Cyclopinidae, Cyclopidae or Oithonidae, although descriptive works of the latter family mention an endopod with two segments (Ferrari & Orsi, 1984; Nishida, 1985; Ferrari & Boettger, 1986; Ferrari & Ambler, 1992).

To address the general issue of segment homologies of the copepod maxilliped, Ferrari & Dahms (1998) compared patterns of addition of setae during the copepodid phase of development and inferred segment homologies for species with quite disparate maxilliped architecture. For example, the maxilliped of a recently discovered cyclopoid *Troglocyclops janstocki* Rocha & Iliffe, 1994 was interpreted as having a 5-segmented endopod, although the distal arthrodial membrane of two

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of these segments did not form during development of the limb. Here we apply the same method of inference to derive segment homologies for several species of Cyclopinidae, Oithonidae, and Cyclopidae, families usually considered basal among those of the Cyclopoida (Ho, 1994; Ho et al., 1998). First, at different stages of development, we describe the maxilliped as a series of segments; in this descriptive section, each segment is a section of the limb between two arthrodistal membranes. We then reinterpret segmentation of the adult limb using a model of development that patterns the endopod proximally from the proximal of two articulating endopodal segments present on the first copepodid, and assumes that homologous setae are added to homologous segments during the same copepodid stage.

Methods

Specimens were cleared in steps through 50% lactic acid/50% de-ionized freshwater to 100% lactic acid, stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% de-ionized freshwater, and examined with bright-field or with differential interference optics. Drawings were made with a camera lucida. The copepodid phase of development of cyclopoid copepods studied here is composed of six stages, designated CI–CVI. Praecoxa, coxa and basis are protopodal segments; the remaining segments are endopodal. Articulating elements on appendage segments are setae, regardless of their morphology or degree of rigidity. Setules are epicuticular extensions of a seta and denticles are epicuticular extensions of an appendage segment; only the latter are described here. On the maxilliped, most setae originate on the ventral face, often termed medial in descriptive publications; the opposite face is dorsal. We assign setae of the praecoxa, coxa, and basis to groups based on their position relative to one another and based on the copepodid stage at which each seta first appears. In some species, a section of the segment on which the setae of a group insert is attenuated ventrally, forming an enditic lobe, or here simply a lobe. Species examined here are listed in Table 1.

Results

In the following descriptions, articulating segments are identified as bounded by a proximal and distal arthrodistal membrane; they are described in order from proximal to distal.

At CI the maxilliped of *Procylopina feiticiera* is a linear series of five articulating segments with 3, 1, 2, 1, 4 setae, respectively from proximal to distal (Fig. 1A); the 3 setae on the proximal segment are arranged in two groups of 1 proximal and 2 distal setae; a ventral line of denticles begins near the proximal edge of the third segment. There are six articulating segments at CII (Fig.

1B); an unarmed segment has been added between the third and fourth segments of CI; the seta on the fifth segment is posterior, rather than ventral. There are seven articulating segments at CIII (Fig. 1C); a segment with one seta has been added between the fourth and fifth segments, and one seta was added to the second segment. At CIV (Fig. 1D) a second seta has been added to the sixth segment; it is proximal to the posterior seta present at CIII. There is no further change; the maxilliped at CV and CVI has the same segmentation and setation: 3, 2, 2, 0, 1, 2, 4. Lotufo (1995) described the adult maxilliped of *Procylopina feiticiera* as identical to *P. polyarthra* Lotufo, 1995 which is illustrated with the first two segments incompletely separated and armed with 4, 2, 2, 0, 1, 3, 4 setae respectively.

At CI the maxilliped of *Cyclopina caroli* is a linear series of five articulating segments with 3, 1, 2, 1, 4 setae (Fig. 2A); the 3 setae on the proximal segment are arranged in two groups of 1 proximal and 2 distal setae; a ventral line of denticles begins near the proximal edge of the third segment. There are six articulating segments at CII; an unarmed segment has been added between the third and fourth segments of CI; the seta on the fourth segment now is posterior, rather than ventral (Fig. 2B). There are seven articulating segments at CIII (Fig. 2C); an unarmed segment has been added between the fourth and fifth segments of CII, and one seta each is added to the distal group of the first segment, and to the second segment. There is no further change; the maxilliped at CIV, CV and CVI has the same segmentation and setation: 4, 2, 2, 0, 0, 1, 4. Lotufo (1994) illustrated, as incompletely separated, the first two segments of the adult maxilliped of *Cyclopina caroli*, which are described and illustrated here as separated by an arthrodistal membrane.

At CI the maxilliped of *Limnoithana tetraspina* is a linear series of five articulating segments with 3, 1, 2, 1, 3 setae (Fig. 3A); the 3 setae on the proximal segment are arranged in two groups of 1 proximal and 2 distal setae; a ventral line of denticles begins near the proximal edge of the third segment. There is no change at CII. At CIII (Fig. 3B) one seta each has been added to the distal group of the first segment, and to the second segment. There is no further change; the maxilliped at CIV, CV and CVI has the same segmentation and setation: 4, 2, 2, 1, 3. Ferrari & Orsi (1984) incorrectly describe and illustrate the maxilliped of *L. sinensis* (Burckhardt, 1912) with only four articulating segments; the arthrodistal membrane between the first and second segments of *L. tetraspina* is not described or illustrated.

At CI the maxilliped of *Dioithona oculata* is a linear series of five articulating segments with 3, 1, 2, 1, 4 setae (Fig. 4A); the 3 setae on the proximal segment are arranged in two groups of 1 proximal and 2 distal setae; a ventral line of denticles begins near the proximal edge

Table 1. List of species examined in this study and general distribution. Species of Cyclopidae are divided into three groups based on the way swimming legs 1–4 develop.

CYCLOPOIDA	
<i>Cyclopidae</i>	
Delayed Swimming Leg Development	
<i>Acanthocyclops carolinianus</i> (Yeatman, 1944)	<i>Euryte longicauda</i> Philippi 1843
freshwater ponds, North America	bryozoans, White Sea, Arctic Ocean
<i>Acanthocyclops robustus</i> (Sars, 1863)	<i>Halicyclops aberrans</i> Rocha, 1983
freshwater ponds, North America	rivers, South America
<i>Diacyclops dispinosus</i> Ishida, 1994	<i>Macrocyclus albidus</i> (Jurine, 1820)
freshwater ponds, Japan	freshwater ponds, North America
<i>Diacyclops navus</i> (Herrick, 1882)	<i>Neocyclus vicinus</i> (Herbst, 1955)
freshwater lakes, North America	coastal, western South Atlantic Ocean
<i>Diacyclops thomasi</i> (Forbes, 1882)	<i>Paracyclops chiltoni</i> (Thompson, 1883)
freshwater lakes, North America	freshwater ponds, North America
<i>Megacyclops latipes</i> (Lowndes, 1927)	<i>Troglocyclops janstocki</i> Rocha & Iliffe, 1994
freshwater ponds, North America	anchialine caves, Bahamas
<i>Mesocyclops edax</i> (Forbes, 1891)	<i>Tropocyclops jamaicensis</i> Reid & Janetzky, 1996
freshwater lakes, North America	bromeliads, Jamaica
<i>Mesocyclops longisetus</i> (Thiébaud, 1914)	<i>Tropocyclops prasinus</i> (Fischer, 1860)
freshwater lakes, North America	freshwater ponds, North America
<i>Mesocyclops ruttneri</i> Kiefer, 1981	<i>Cyclopinidae</i>
freshwater lakes, South East Asia	<i>Cyclopina caroli</i> Lotufo, 1994
<i>Thermocyclops decipiens</i> (Kiefer, 1929)	intertidal interstitial, South America
freshwater lakes, North America	<i>Procyclopina feiticiera</i> Lotufo, 1995
Truncated Swimming Leg Development	intertidal interstitial, South America
<i>Alloicyclops silvaticus</i> Rocha & Bjornberg, 1988	<i>Oithonidae</i>
temporary ponds, South America	<i>Dioithona oculata</i> (Farran, 1913)
<i>Apocyclops dimorphus</i> (Johnson, 1953)	coast marine, Caribbean Sea
coastal, western North Atlantic	<i>Limnoithona tetraspina</i> Zhang & Li, 1976
<i>Apocyclops panamensis</i> (Marsh, 1913)	Sacramento River, North America
coastal, Caribbean	<i>Oithona similis</i> (Claus, 1866)
<i>Bryocyclops caroli</i> Bjornberg, 1985	oceanic, western South Atlantic Ocean
freshwater, South America	CALANOIDA
<i>Diacyclops eulitoralis</i> Alekseev, 1986	<i>Megacalanidae</i>
interstitial, Lake Baikal	<i>Megacalanus principes</i> Wolfenden, 1904
<i>Graeteriella brehmi</i> (Lescher-Moutoué, 1968)	oceanic, western North Atlantic Ocean
cave freshwater, Europe	<i>Ridgewayiidae</i>
<i>Metacyclops minutus</i> Kiefer 1927	<i>Ridgewayia klausruetzleri</i> Ferrari, 1995
temporary ponds, Europe	coastal, Caribbean Sea
<i>Microcyclus rubellus</i> (Lilljeborg, 1901)	<i>Temoridae</i>
freshwater ponds, North America	<i>Eurytemora velox</i> (Lilljeborg, 1853)
<i>Muscocyclops operculatus</i> (Chappuis, 1923)	rivers, Europe
freshwater ponds, South America	POECILOSTOMATOIDA
<i>Speocyclops racovitzai</i> (Chappuis, 1917)	<i>Clausiiidae</i>
cave freshwater, Europe	<i>Conchylurus quintus</i> Tanaka, 1961
<i>Stolonicyclops heggiensis</i> Reid & Spooner, 1998	marine bivalve molluscs, Asia
freshwater, southeastern North America	<i>Leptinogaster major</i> (Williams, 1907)
Ancestral Swimming Leg Development	marine bivalve molluscs, North America
<i>Cyclops scutifer</i> Sars, 1863	<i>Corycaeidae</i>
freshwater lakes, North America	<i>Corycaeus angelicus</i> Lubbock, 1857
<i>Eucyclops agilis</i> (Koch, 1838)	Baltic Sea, eastern North Atlantic
freshwater ponds, North America	

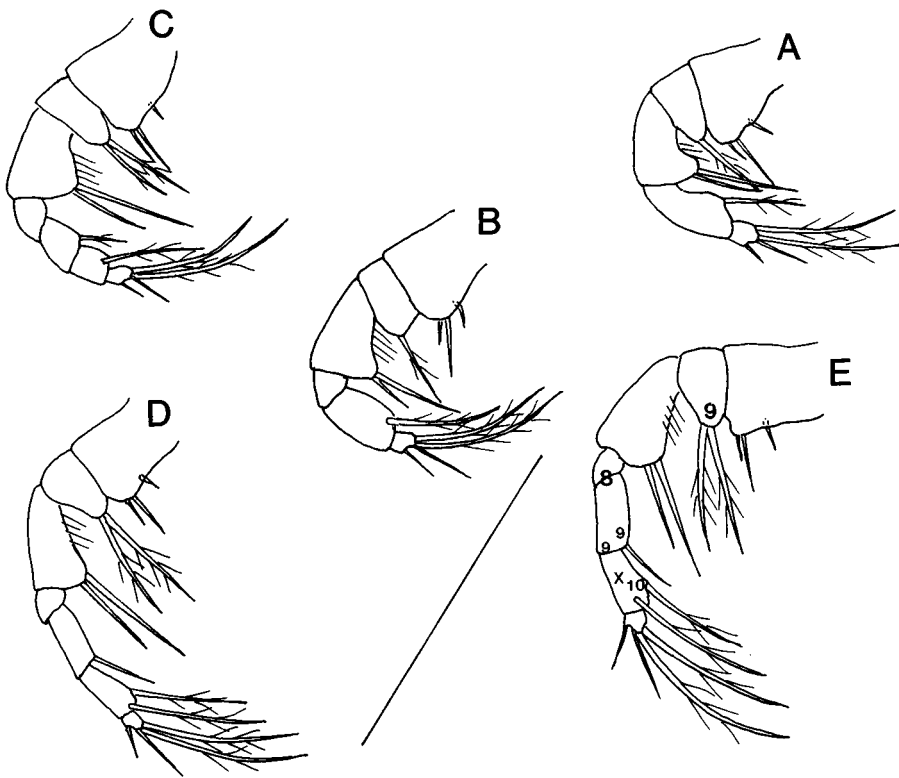


Fig. 1. Maxilliped of *Procylopina feiticera*, posterior. A. CI; B. CII; C. CIII; D. CIV; E. CVI. Number 8, 9, or 10 on an arthrodistal membrane or at base of seta indicates the structure is added at CII, CIII or CIV; 'x' is segment complex of the endopod; scale line is 0.05 mm.

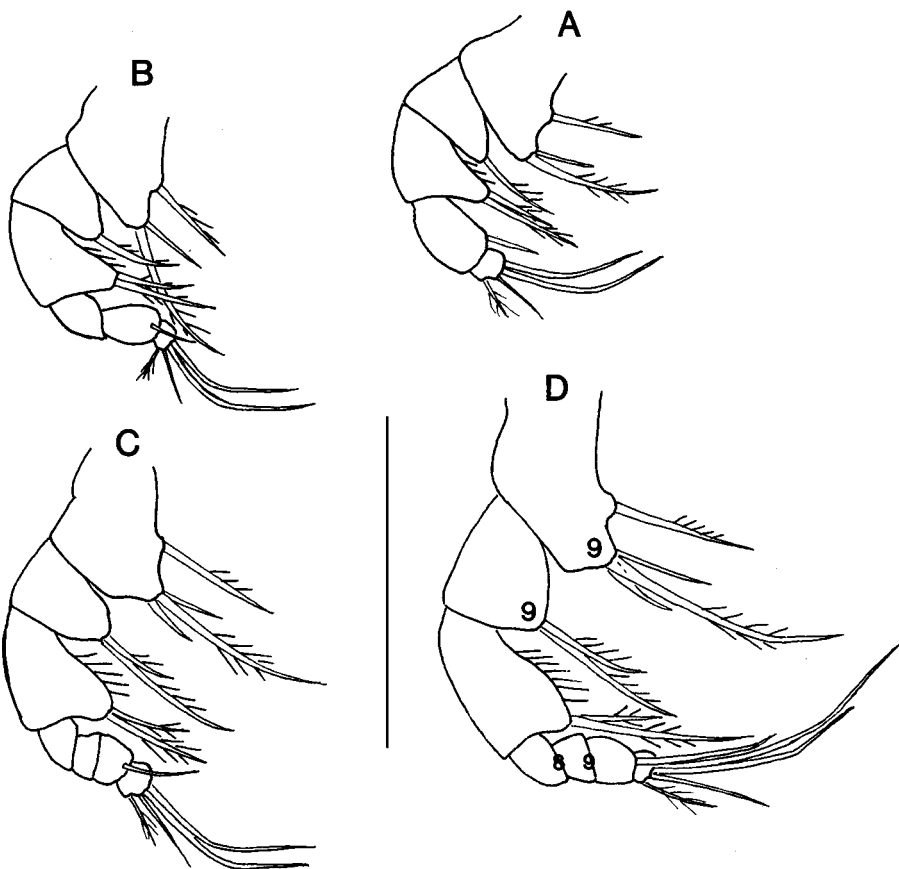


Fig. 2. Maxilliped of *Cyclopina caroli*, posterior. A. CI; B. CII; C. CIII; D. CVI. Number 8, or 9 on an arthrodistal membrane or at base of seta indicates the structure is added at CII or CIII; scale line is 0.05 mm.

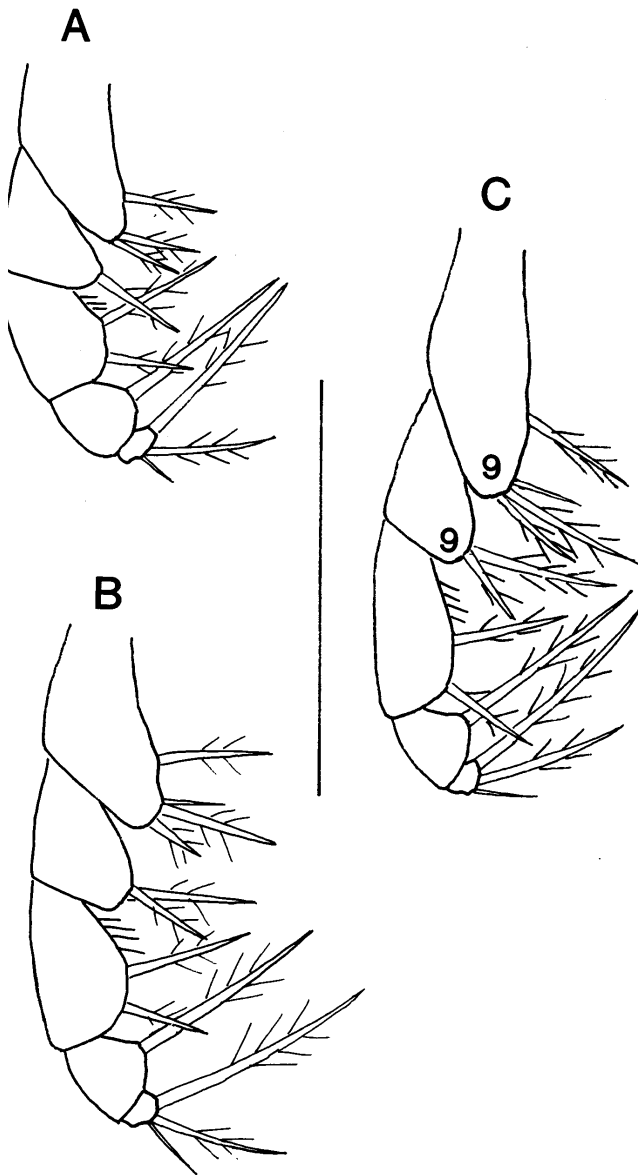


Fig. 3. Maxilliped of *Limnoithona tetraspina*, posterior. A. C1; B. CIII; C. CVI. Number 9 at base of seta indicates the structure is added at CIII; scale line is 0.05 mm.

of the third segment. There is no change at CII. At CIII (Fig. 4B) one seta each has been added to the distal group of the first segment, to the second segment, and to the fourth segment; the seta added to the fourth segment is proximal to and shorter than the seta present at C1. At CIV (Fig. 4C) the arthrodistal membrane between the first and second segments is absent dorsally; a third, short seta has been added to the fourth segment between the two setae present at CIII. There is no further change; the

maxilliped at CV and CVI has the same segmentation and setation: 4, 2, 2, 3, 4. Ferrari & Ambler (1992) describe and illustrate no arthrodistal membrane between the first and second segments at CIV–CVI.

At C1 the maxilliped of *Oithona similis* is a linear series of four articulating segments with 4, 2, 1, 4 setae (Fig. 5A); the 4 setae on the proximal segment are arranged in three groups of 1 proximal, 2 middle and 1 distal setae; a ventral line of denticles begins near the proximal edge of the second segment. There is no change at CII. At CIII (Fig. 5B) two setae have been added to the first segment, one each to the middle and to distal groups of setae, and one seta has been added to the third segment; it is proximal to and shorter than the seta present at C1. At CIV (Fig. 5C) another short seta has been added to the third segment between the two setae present at CIII. There is no further change; the maxilliped at CV and CVI has the same segmentation and setation: 6, 2, 3, 4. Nishida (1985) illustrated the adult maxilliped of *Oithona similis* with five segments similar to *Dioithona oculata* with the proximal segment, presented here, divided into two articulating segments.

At C1 the maxilliped of *Paracyclops chiltoni* is a linear series of four articulating segments with 2, 2, 1, 3 setae (Fig. 6A); the 2 setae on the proximal segment arranged are in two groups of one proximal and one distal seta; there are denticles near the insertion of the proximal seta of the first segment and along the dorsal face of second segment. There is no change at CII. At CIII (Fig. 6B), one seta has been added to the proximal group of the first segment. There is no further change; the maxilliped at CIV, CV and CVI has the same segmentation and setation: 3, 2, 1, 3.

At C1 the maxilliped of *Macrocyclus albidus* and *Megacyclus latipes* is a linear series of four articulating segments with 2, 2, 1, 3 setae (Figs. 7A, 8A); the 2 setae on the proximal segment are arranged in two groups of one proximal seta and one distal seta; a ventral line of denticles begins near the proximal edge of the second segment, and scattered denticles are found dorsally and posteriorly. There is no change at CII. At CIII (Figs. 7B, 8B) one seta has been added to the proximal group of first segment. There is no further change; the maxilliped at CIV, CV and CVI has the same segmentation and setation: 3, 2, 1, 3.

At C1 the maxilliped of *Halicyclops aberrans* is a linear series of three articulating segments with 2, 3, 2 setae (Fig. 9A); two setae on the proximal segment are arranged in two different groups of one seta each, and three setae of the middle segment are in two different groups of two proximal setae and of one seta. There is no change at CII. At CIII (Fig. 9B) one distal seta has been added to the proximal group of the first segment. There is no further change; the maxilliped at CIV, CV and CVI has the same segmentation and setation: 3, 3, 2.

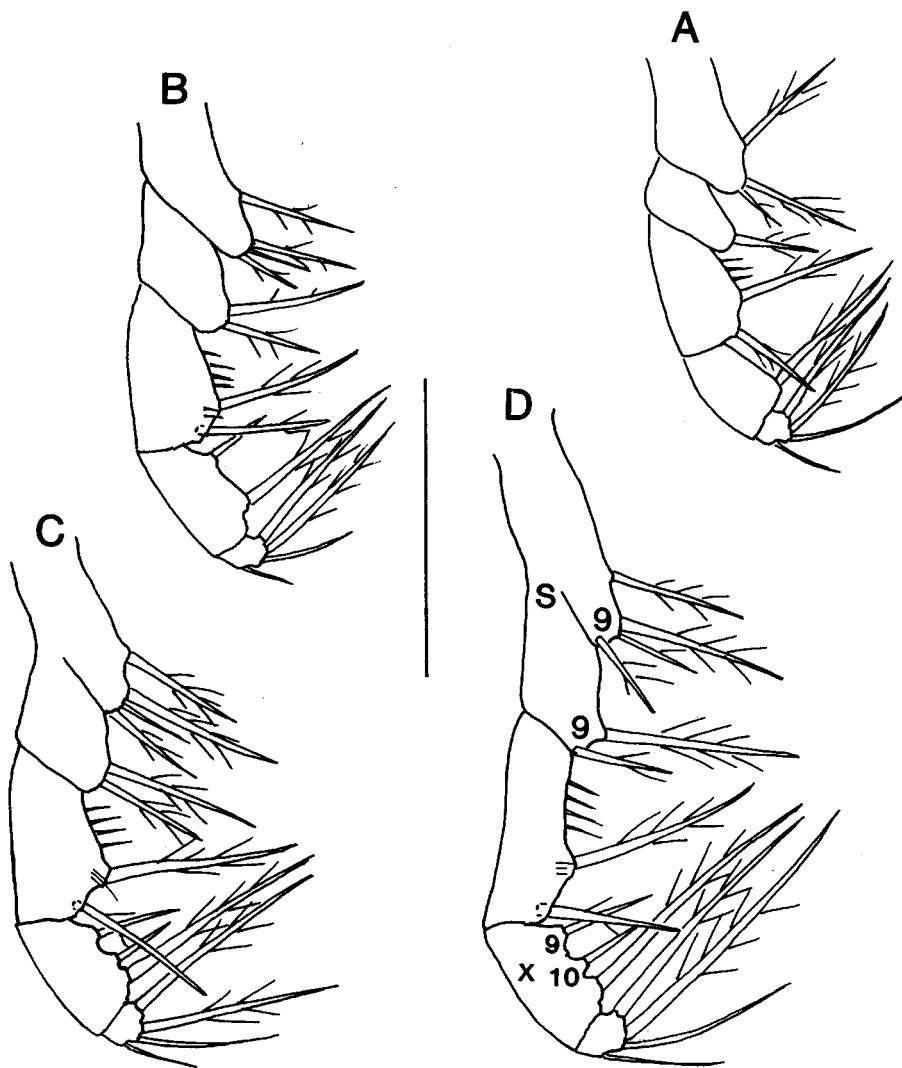


Fig. 4. Maxilliped of *Dioithona oculata*, posterior. A. CI; B. CIII; C. CIV; D. CVI. Number 9 or 10 at base of seta indicates the structure is added at CII, CIII or CIV; s is a syncoxa; 'x' is segment complex of the endopod; scale line is 0.05 mm.

At CI the maxilliped of *Stolonicyclops heggiensis* is a linear series of four articulating segments with 1, 2, 1, 2 setae (Fig. 10A); a ventral line of denticles begins near the proximal edge of the second segment. There is no change at CII. At CIII (Fig. 10B) one seta is added to the first segment, proximal to the seta present at CI. There is no further change; the maxilliped at CIV, CV and CVI has the same segmentation and setation: 2, 2, 1, 2. Reid & Spooner (1998) describe the setation of *S. heggiensis* as 2, 1, 1, 3.

At CI the maxilliped of *Speocyclops racovitzai* is a linear series of four articulating segments with 1, 2, 1, 2 setae (Fig. 11A); a ventral line of denticles begins near the proximal edge of the second segment. There are denticles dorsally on the first and second segments, and distal-ventrally on the third segment. There is no change in segmentation or setation during the copepodid phase of development.

At CI the maxilliped of *Neocyclops vicinus* is a linear series of four articulating segments with 2, 2, 1, 3 setae (Fig. 12A); the two setae on the proximal segment are arranged in two different groups of one proximal seta and one distal seta; a ventral line of denticles begins near the proximal edge of the second segment, and there are denticles scattered dorsally. There is no change at CII. At CIII (Fig. 12B) one seta has been added to the proximal group of the first segment. At CIV (Fig. 12C) one seta is added to the third segment, it is proximal to and shorter than the seta present at CI. There is no further change; the maxilliped at CV and CVI has the same segmentation and setation: 3, 2, 2, 3.

At CI the maxilliped of *Euryte longicauda* is as a linear series of four articulating segments with 1, 1, 1, 3 setae; the seta on the second segment is located distally on a prominent, ventral lobe and the seta on the third segment is posterior; there are denticles proximally and

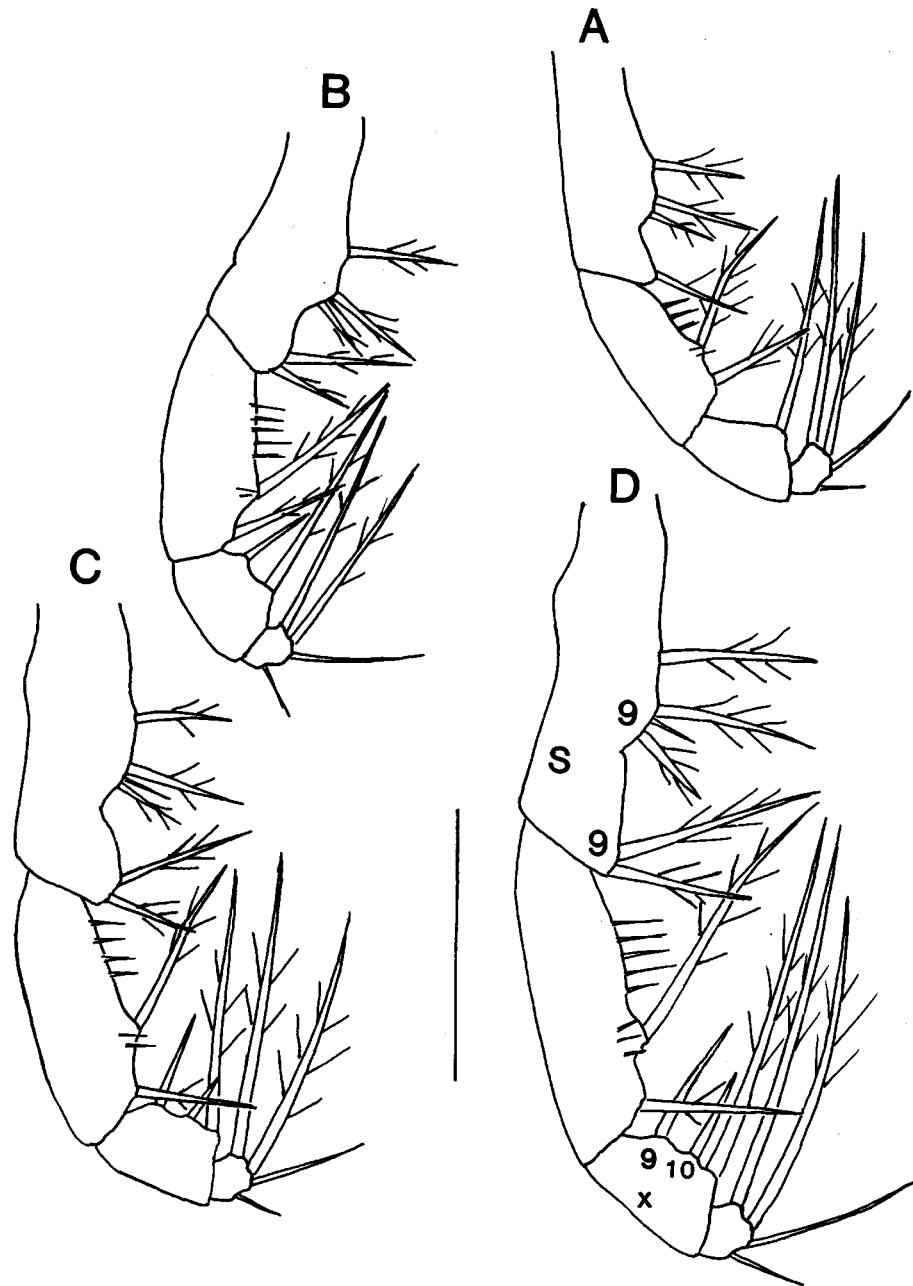


Fig. 5. Maxilliped of *Oithona similis*, posterior. A. CI; B. CIII; C. CIV; D. CVI. Number 9 or 10 at base of seta indicates the structure is added at CII, CIII or CIV; 's' is a syncoxa; 'x' is segment complex of the endopod; scale line is 0.05 mm.

ventrally on the second segment, and dorsally and ventrally on the third (Fig. 13A). At CII an unarmed segment, with denticles dorsally, has been added between the second and third segments of CI; the seta on the third segment is now dorsal rather than posterior (Fig. 13B). At CIII (Fig. 13C) a second seta has been added to the first segment, proximal to the seta of CI and another to the fourth segment, posteriorly; the latter seta is distal to a well-sclerotized knob and proximal to the seta present at CI, which is now thicker and curved. At CIV (Fig. 13D) a third seta has been added posteriorly on the

fourth segment; it is between the posterior seta and the dorsal seta present at CIII. CV is not known, but there is no further change at CVI (6E) which has the same segmentation and setation as CIV: 2, 1, 0, 3, 3.

At CI the maxilliped of *Troglocyclops janstocki* is a linear series of four articulating segments with 2, 2, 1, 3 setae (Fig. 14A); the two setae on the proximal segment are in two different groups of one proximal seta and one distal seta. At CII an unarmed segment has been added between the second and third segments of CI (Fig. 14B). At CIII (Fig. 14C) a ventral seta has been added to the

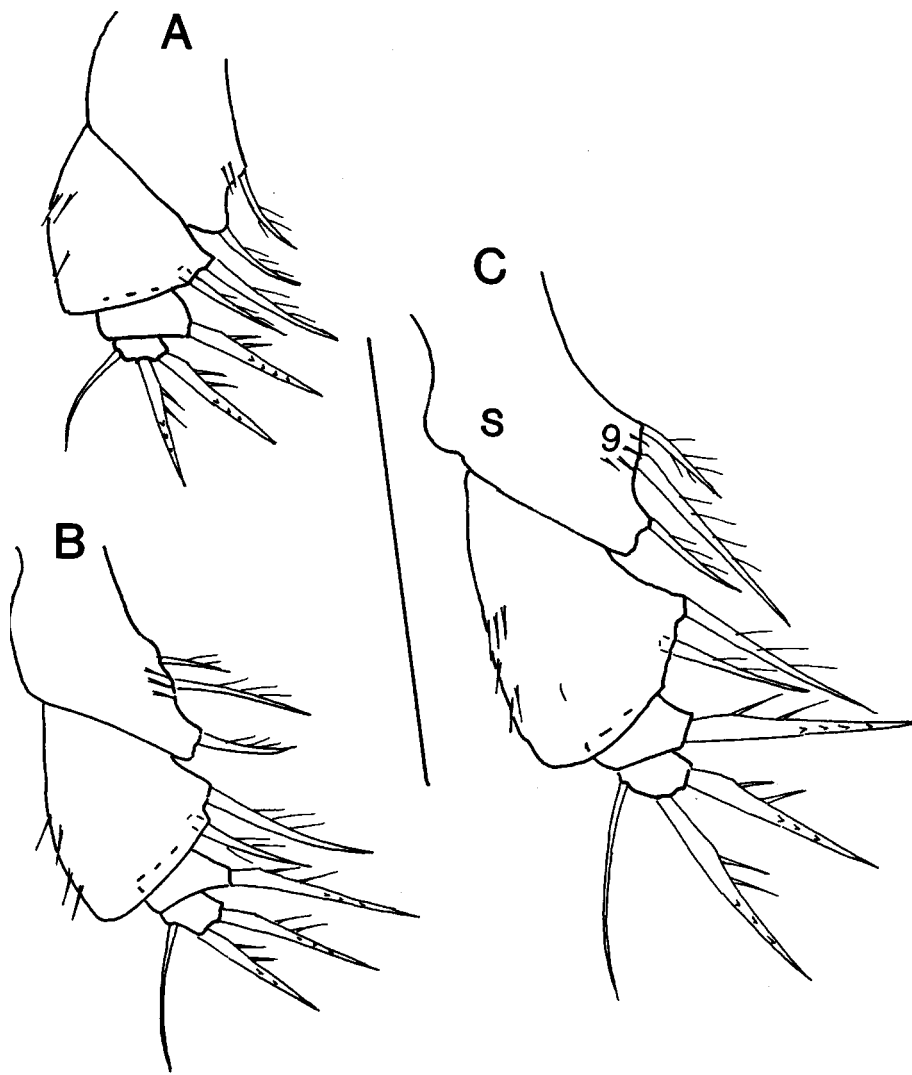


Fig. 6. Maxilliped of *Paracyclops chiltoni*, posterior. A. CI; B. CIII; C. CVI. Number 9 at base of seta indicates the structure is added at CIII; 's' is a syncoxa; scale line is 0.05 mm.

proximal group of the first segment and a second seta is added ventrally and proximally to the fourth segment; the seta added to the fourth segment is proximal to the seta present at CI. At CIV (Fig. 14D) a third seta has been added to the fourth segment between the two setae already present. CV is not known, but there is no further change at CVI, which has the same segmentation and setation as CIV: 3, 2, 0, 3, and 3.

Interpretation

The following descriptive model is derived from the development of the maxilliped of *Ridgewayia klausruetzleri*, a calanoid copepod (Ferrari, 1995). The syncoxa of the calanoid maxilliped consists of four ventral groups of setae, and no arthrodial membrane separates praecoxa and coxa during development. Setation of the pro-

topod is complete by CII. The endopod has two articulating segments at CI, a distal segment 1 bearing four setae and a proximal segment 2 bearing one seta. Segment 1 appears to be a segment complex (Fig. 15B) of a terminal part bearing two apical setae homologous to those on the appendage bud at N6 of other calanoids (Fig. 15A), and an adjacent part with a dorsal and a ventral seta (Fig. 15B). This morphology suggests some distal patterning during limb transformation. The setation of segment 1 does not change during copepodid development. The rest of the ramus is patterned proximally from within segment 2 during copepodid development. The setation of segment 2 does not change during copepodid development. The rest of the ramus is patterned proximally from within segment 2 during copepodid development. The setation of segment 2 does not change during copepodid development. The rest of the ramus is patterned proximally from within segment 2 during copepodid development. The setation of segment 2 does not change during copepodid development. The rest of the ramus is patterned proximally from within segment 2 during copepodid development.

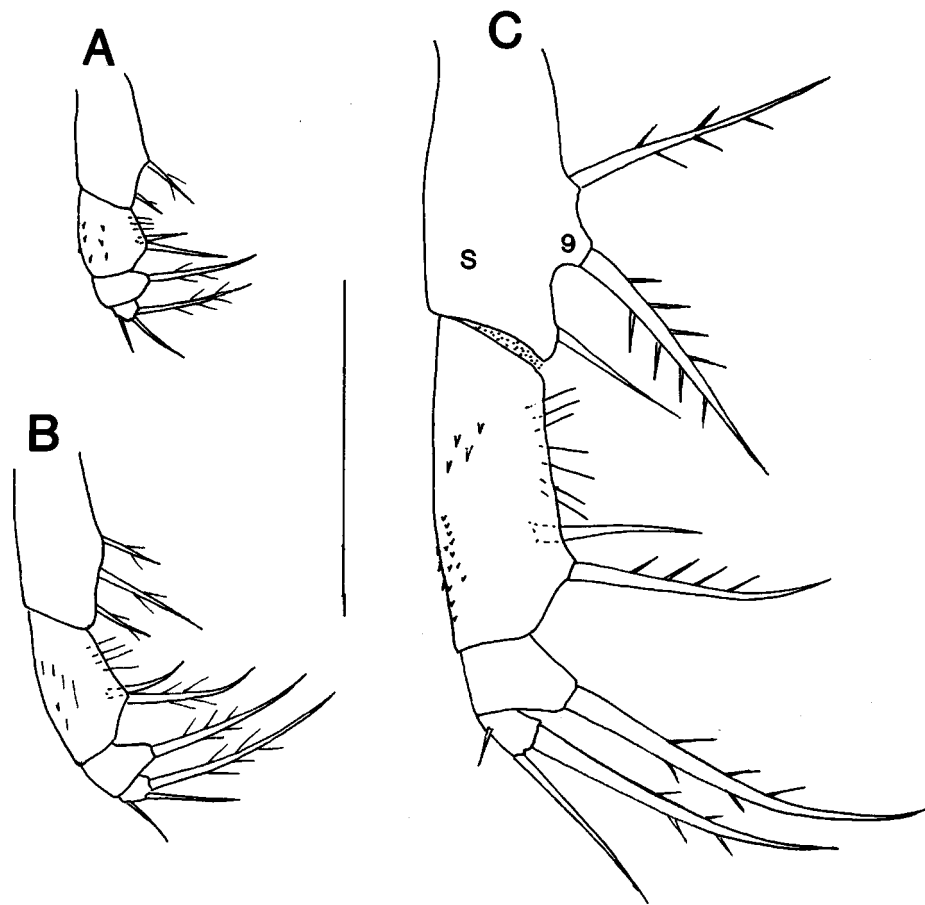


Fig. 7. Maxilliped of *Macrocyclus albidus*, posterior. A. CI; B. CIII; C. CVI. Number 9 at base of seta indicates the structure is added at CIII; 's' is a syncoxa; scale line is 0.1 mm.

mation setae may be added to the endopodal segments 2-5 at CIV-CVI.

The maxilliped of cyclopoids initially appears as a transformed limb at CI; no limb bud is present at N6 (Ferrari & Ambler, 1992). We assume that setae and arthrodistal membranes of segments of cyclopoids are added during the same stage of copepodid development as their calanoid homologues, and we interpret endopod development in the same way (Ferrari & Dahms, 1998). Fig. 15D is a stylized drawing of the ground pattern of the cyclopoid maxilliped indicating when homologous setae and arthrodistal membranes are added during development. We also define four variations of an endopodal segment in order to explain the architecture found in different cyclopoids. An endopodal segment has a distal arthrodistal membrane and a formation seta. An unarmed endopodal segment lacks a formation seta but retains its distal arthrodistal membrane. A presumptive endopodal segment lacks its distal arthrodistal membrane but retains a formation seta. A blank endopodal segment lacks both its distal arthrodistal membrane and its formation seta; its presence is inferred indirectly, by the addition of setae or arthrodistal membranes later in development. The last

two types of segments, presumptive and blank, form segment complexes with endopodal segments distal to them because each kind of segment lacks a distal arthrodistal membrane.

The maxilliped of the adult female of *Procyclus feiticeira* (Fig. 1E) consists of a praecoxa with a middle group of one seta and a distal lobe bearing two setae; a coxa of one lobe bears two setae, one of which is added at CIII; a basis has two setae on a lobe. A proximal, unarmed third endopodal segment is added at CII; a fourth endopodal segment added at CIII bears its formation seta; a fifth presumptive endopodal segment added at CIV bears its formation seta but lacks a distal arthrodistal membrane and is fused to a second endopodal segment bearing one seta; the distal endopodal segment bears four setae. The endopod has one segment complex of the fifth and second segments, inferred from the age of its proximal seta added at CIV, which corresponds to the stage that a fifth articulating segment with its ventral formation seta is added to the maxilliped of the calanoid.

The maxilliped of the adult female *Cyclopina caroli* (Fig. 2D) consists of a praecoxa with a middle lobe

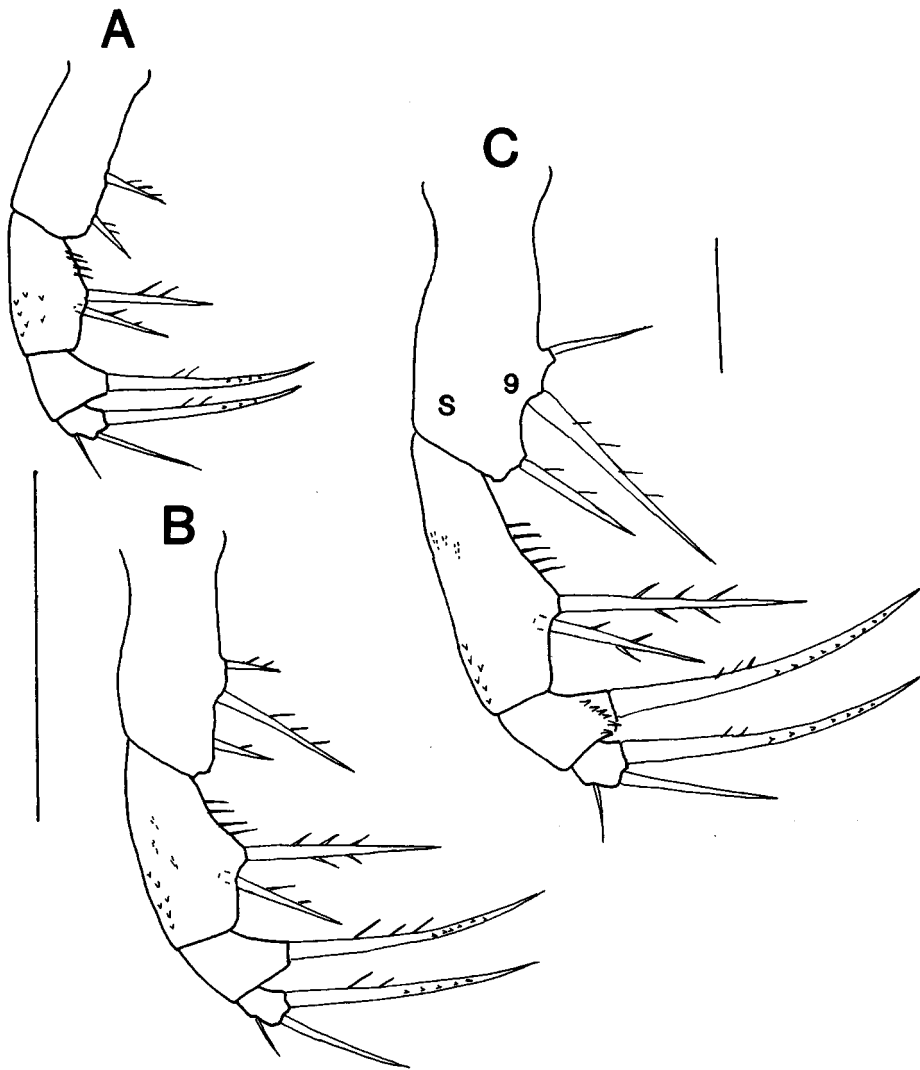


Fig. 8. Maxilliped of *Megacyclops latipes*, posterior. A. CI; B. CIII; C. CVI. Number 9 at base of seta indicates the structure is added at CIII; 's' is a syncoxa; scale lines are 0.1 mm.

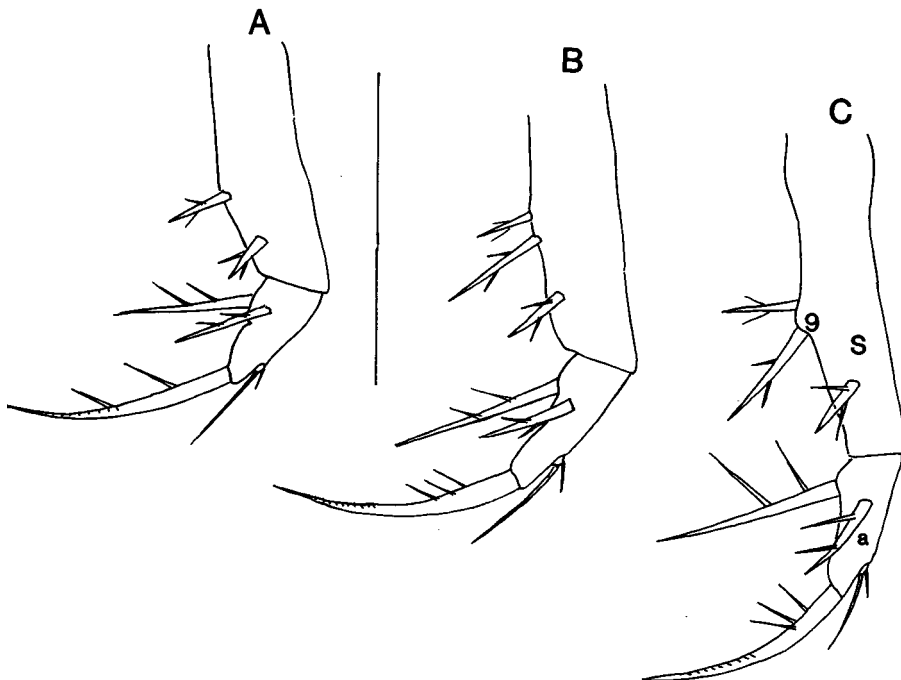


Fig. 9. Maxilliped of *Halicyclops aberrans*, anterior. A. CI; B. CIII; C. CVI. Number 9 at base of seta indicates the structure is added at CIII; 's' is a syncoxa; 'a' is an allobasis; scale line is 0.05 mm.

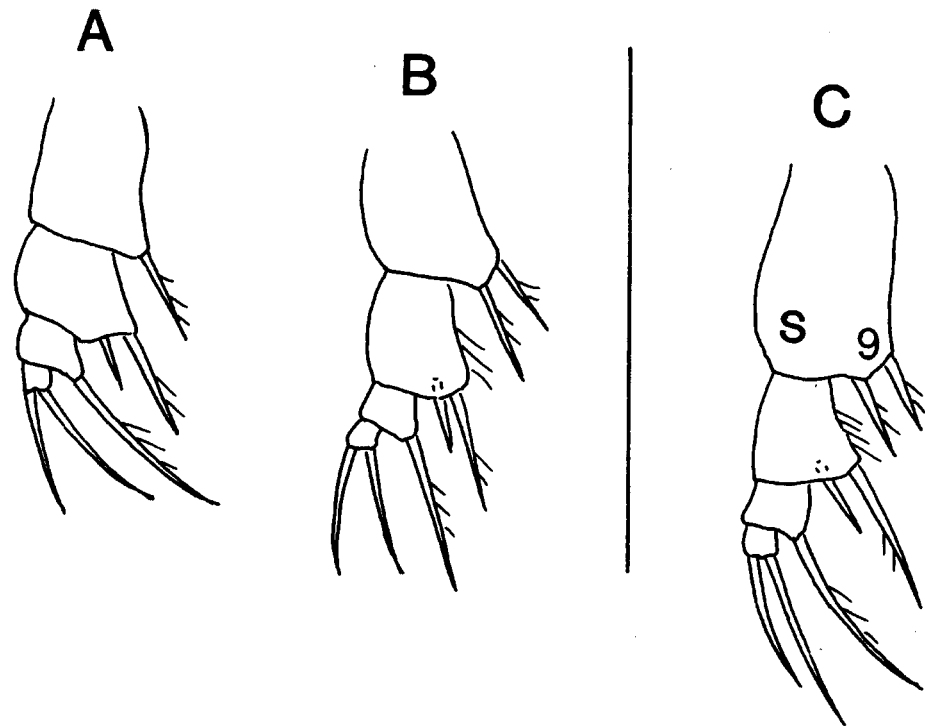


Fig. 10. Maxilliped of *Stolonicyclops heggiensis*, posterior. A. C1; B. CIII; C. CVI. Number 9 at base of seta indicates the structure is added at CIII; 's' is a syncoxa; scale line is 0.05 mm.

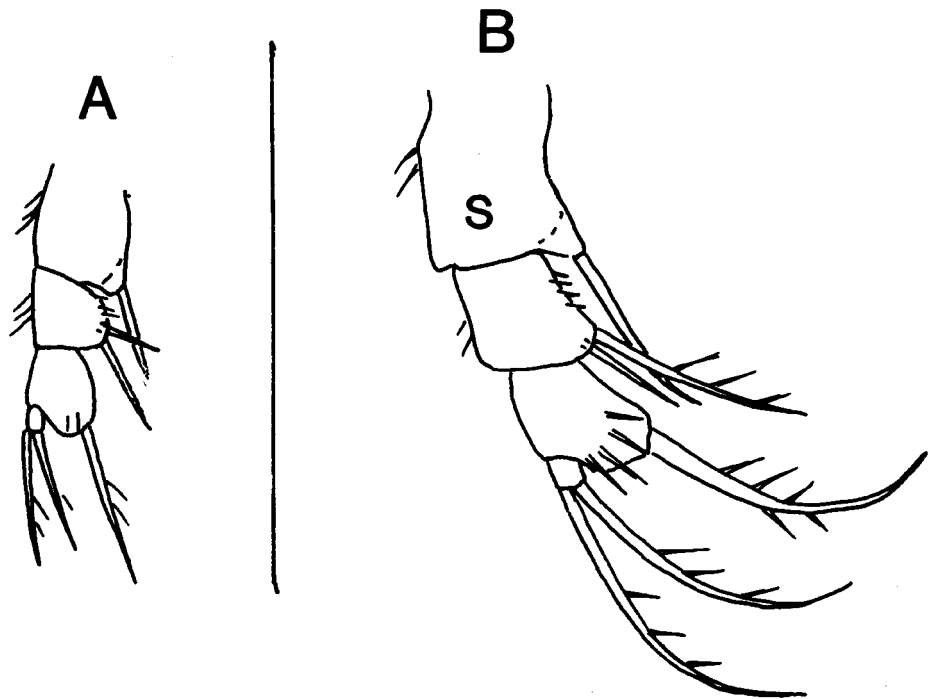


Fig. 11. Maxilliped of *Speocyclops racovitzai*, posterior. A. C1; B. CVI; 's' is a syncoxa; scale line is 0.05 mm.

bearing one seta and a distal lobe bearing three setae, one of which is added at CIII; a coxa of one lobe has two setae, one of which is added at CIII; a basis bears two setae on a lobe. A proximal, unarmed third endopodal segment is added at CII; an unarmed fourth endopodal

segment is added at CIII; a second endopodal segment bears its formation seta; the distal endopodal segment bears four setae.

The maxilliped of the adult female of *Limnoithana tetraspina* (Fig. 3C) consists of a praecoxa with a mid-

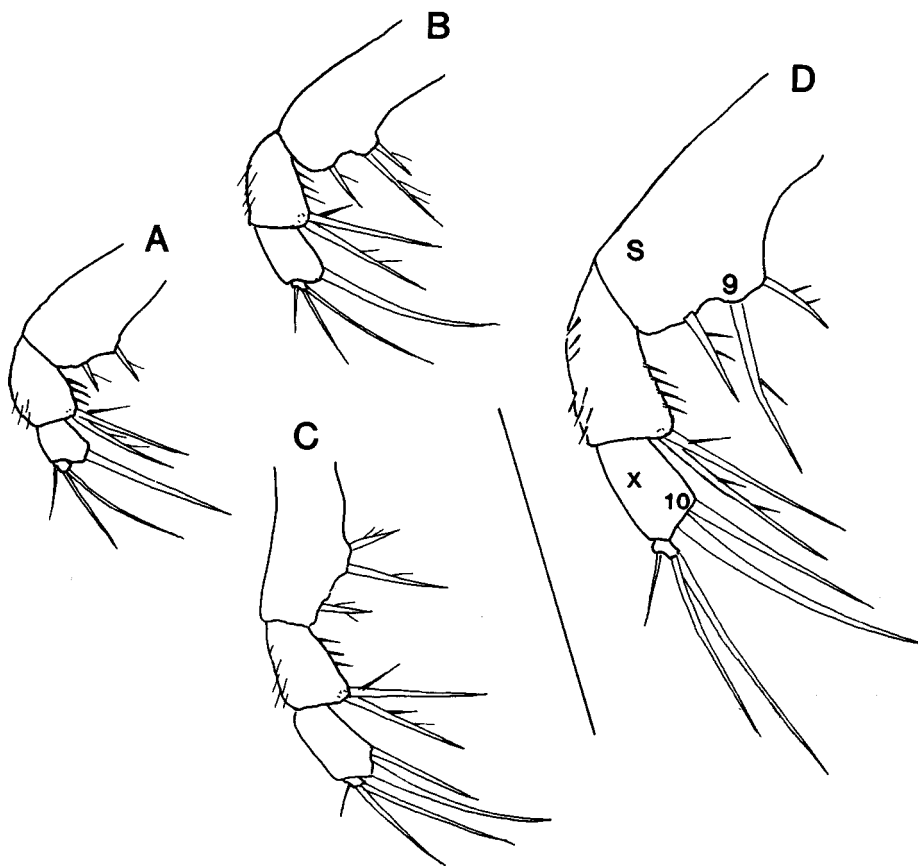


Fig. 12. Maxilliped of *Neocyclops vicinus*, posterior. A. CI; B. CII; C. CIII; D. CVI. Number 9 or 10 at base of seta indicates the structure is added at CIII or CIV; 's' is a syncoxa; 'x' is segment complex of the endopod; scale line is 0.05 mm.

dle group of one seta and a distal lobe bearing three setae, one of which is added at CIII; a coxa of one lobe bears two setae, one of which is added at CIII; a basis has two setae. A proximal second endopodal segment bears its formation seta; the distal endopodal segment bears three setae.

The maxilliped of the adult female of *Dioithona oculata* (Fig. 4D) consists of a praecoxa with a middle group of one seta and a distal group bearing three setae, one of which is added at CIII, fused dorsally to a coxa of one lobe bearing two setae, one of which is added at CIII; a basis has two setae. A proximal, blank, third endopodal segment added at CII without a formation seta or a distal arthrodistal membrane is fused to a presumptive, fourth endopodal segment added at CIII bearing its formation seta but without a distal arthrodistal membrane; these are fused to a presumptive, fifth endopodal segment added at CIV bearing its formation seta but without a distal arthrodistal membrane, and to a second endopodal segment bearing its formation seta. The distal endopodal segment bears four setae. The proximal endopodal complex, made up of segments 3, 4, 5, and 2, is inferred from the age of the proximal and middle setae added at CIII and CIV respectively.

The maxilliped of the adult female of *Oithona similis* (Fig. 5D) consists of a praecoxa with a middle group of one seta and a distal group bearing three setae, one of which is added at CIII, fused to a coxa of one lobe bearing two setae, one of which is added at CIII; a basis has two setae. A proximal, blank third endopodal segment added at CII without a formation seta or a distal arthrodistal membrane is fused to a presumptive, fourth endopodal segment added at CIII bearing its formation seta but without a distal arthrodistal membrane, and to a second endopodal segment bearing its formation seta. The distal endopodal segment has four setae. The syncoxa of a praecoxa and a coxa is inferred from a single segment complex proximal to the basis, and the age of the setae, added at CIII to its middle and distal lobes. The proximal endopodal complex, made up of segments 3, 4, 5, and 2, is inferred from the age of its proximal and middle setae added, at CIII and CIV respectively.

The maxilliped of the adult female of *Paracyclops chiltoni* (Fig. 6C) consists of a praecoxa with a distal lobe bearing two setae, one of which is added at CIII,

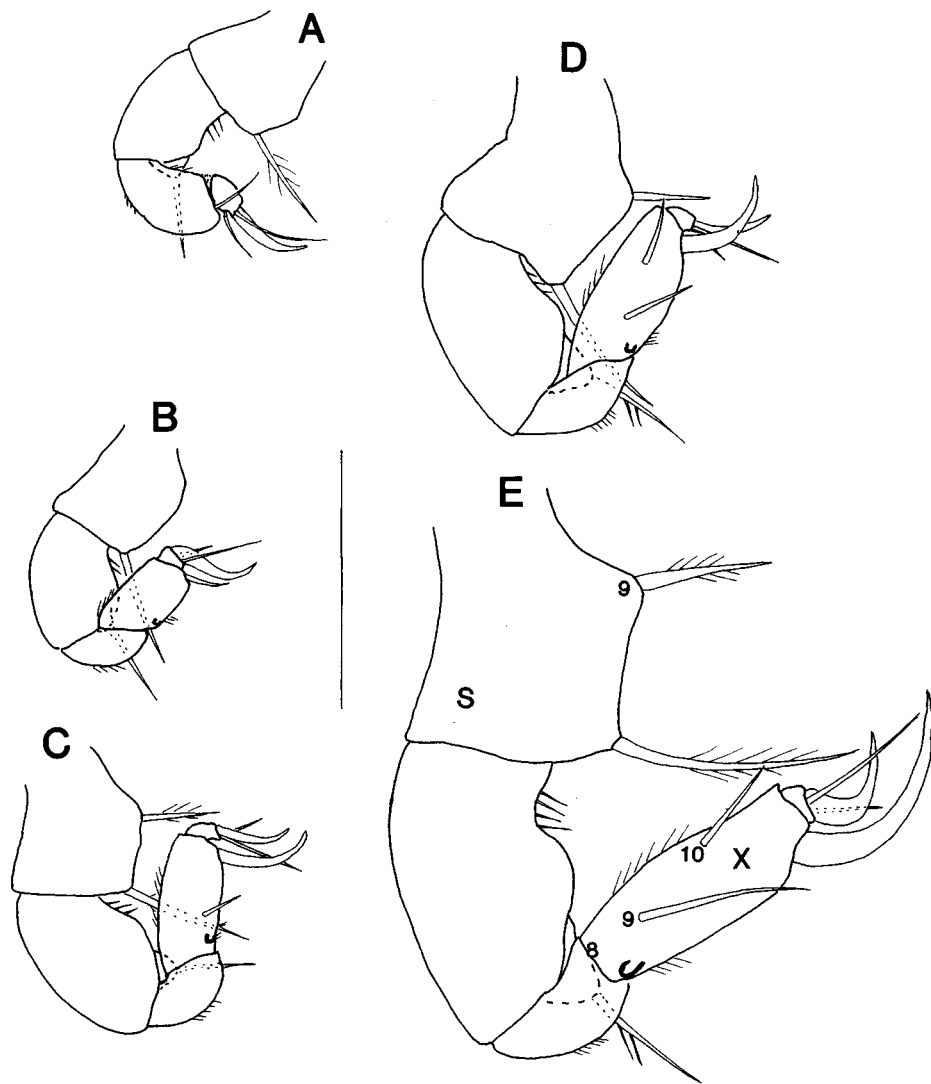


Fig. 13. Maxilliped of *Euryte longicauda*, posterior. A. CI; B. CII; C. CIII; D. CVI. Number 8, 9 or 10 an arthrodial membrane or at base of seta indicates the structure is added at CII, CIII or CIV; 's' is a syncoxa; 'x' is segment complex of the endopod; scale line is 0.05 mm.

fused to a coxa of one lobe bearing one seta; a basis bears two setae. A proximal, second endopodal segment bears its formation seta; the distal endopodal segment has three setae. A syncoxa of a praecoxa and a coxa is inferred from the addition of a ventral seta to the proximal lobe at CIII.

The maxilliped of the adult female of *Macrocyclops albidus* (Fig. 7C) and that of *Megacyclops latipes* (Fig. 8C) consists of a praecoxa with a broad, distal lobe bearing two setae, one of which is added at CIII, fused to a coxa of one lobe bearing one seta; a basis has two setae. A proximal, second endopodal segment bears its formation seta; the distal endopodal segment has three setae. A syncoxa of a praecoxa and a coxa is inferred from the addition of a ventral seta to the proximal lobe at CIII.

The maxilliped of the adult female of *Halicyclops aberrans* (Fig. 9C) consists of a praecoxa with a distal

lobe bearing two setae, one of which is added at CIII, fused to a coxa of one seta. A basis with two setae is fused to a second endopodal segment bearing one seta; the distal endopodal segment bears two setae. A syncoxa of a praecoxa and a coxa is inferred from the addition of a ventral seta to the proximal lobe at CIII. An allobasis is inferred from the proximal position of two setae, corresponding to those on the basis, and distal position of one seta, corresponding to the formation seta of the proximal endopodal segment at CI.

The maxilliped of the adult female of *Stolonicyclops heggiensis* (Fig. 10C) consists of a praecoxa bearing one seta, which is added at CIII, fused to a coxa bearing one seta; a basis has two setae. A proximal, second endopodal segment has one seta; the distal endopodal segment has two setae. A syncoxa of a praecoxa and a coxa is inferred from the addition of a ventral seta to the proximal lobe at CIII.

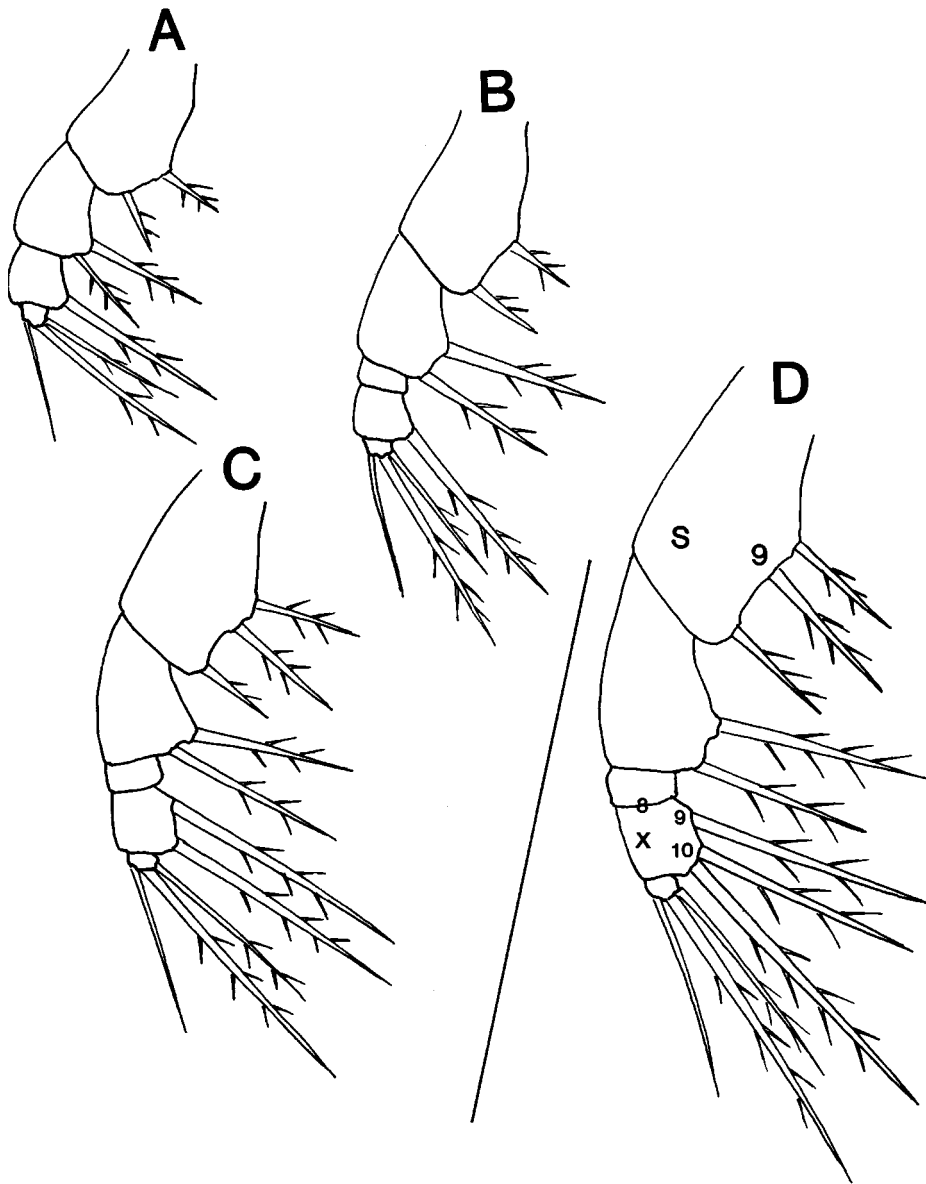


Fig. 14. Maxilliped of *Troglodyclops janstocki*, posterior (revised from Ferrari & Dahms 1998). A. C1; B. C2; C. C3; D. C6. Number 8, 9 or 10 on an arthrodistal membrane or at base of seta indicates the structure is added at C2, C3 or C4; 's' is a syncoxa; 'x' is segment complex of the endopod; scale line is 0.05 mm.

The maxilliped of the adult female of *Speocyclops racovitzai* (Fig. 11B) consists of a praecoxa without setae, fused to a coxa bearing one seta; a basis has two setae. A proximal, second endopodal segment bears its formation seta; the distal endopodal segment has two setae. A syncoxa of a praecoxa and a coxa is inferred from the distal position of its ventral seta, corresponding to the position of the coxal lobe.

The maxilliped of the adult female of *Neocyclops vicinus* (Fig. 12D) consists of a praecoxa with a broad, distal lobe bearing two setae, one of which is added at C3, fused to a coxa bearing one seta; a basis has two setae on a lobe. A proximal, blank third endopodal seg-

ment added at C2, without a formation seta or a distal arthrodistal membrane, is fused to a blank, fourth endopodal segment added at C3, without its formation seta or distal arthrodistal membrane; these are fused to a presumptive, fifth endopodal segment added at C4 bearing its formation seta but without a distal arthrodistal membrane and to a second endopodal segment bearing its formation seta. The distal endopodal segment has three setae. A syncoxa of a praecoxa and a coxa is inferred from the addition of a ventral seta to the proximal lobe, corresponding to the distal praecoxal lobe, at C3. A proximal endopodal complex, made up of segments 3, 4, 5, and 2, is inferred from the addition of a seta imme-

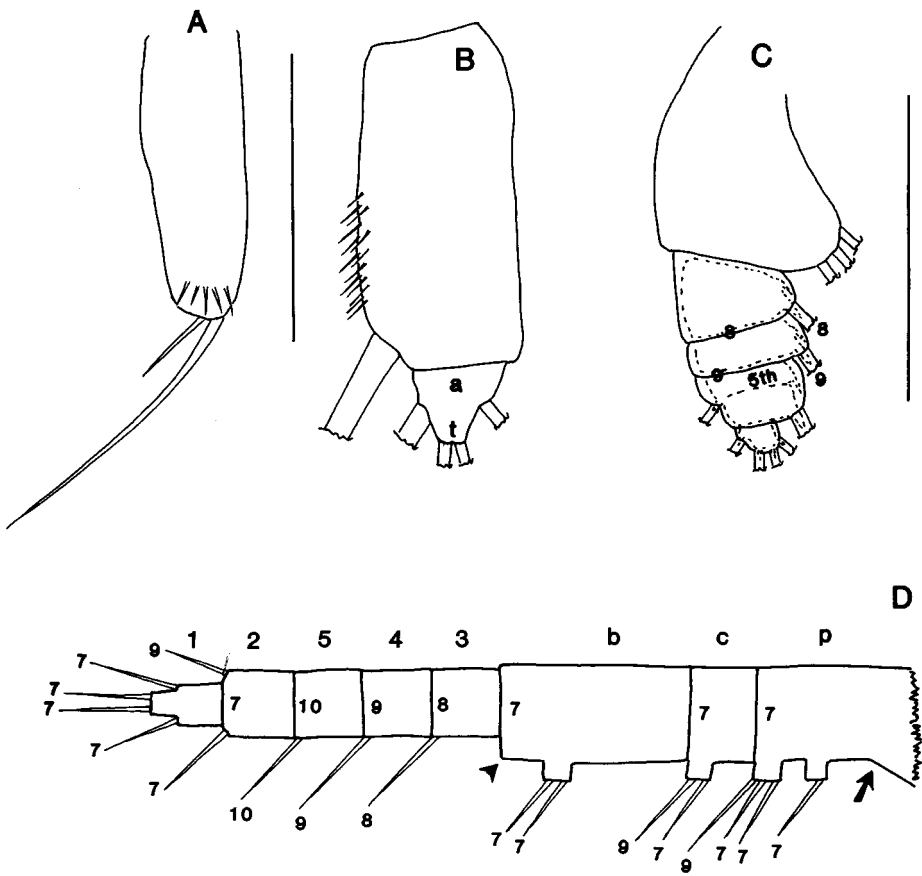


Fig. 15. A. Bud of maxilliped of *Temora longicornis* (Mueller, 1792) N6, anterior; B. Endopod of maxilliped of *Pleuromamma xiphias* (Giesbrecht, 1889) CI, posterior, t=terminal part, a=adjacent part of presumed distal complex; C. Basis and endopod of maxilliped of *Eurytemora velox* CIII, posterior (distal ventral lobe of basis not visible from this view), showing outline (broken lines) of developing endopod of CIV; 5th is fifth segment with its formation seta within the second (at CI the proximal) endopodal segment; second and third segments of CIV with a post-formation seta proximal to formation seta. Number 8, or 9 on an arthrodial membrane or at tip of cut-off seta indicates the structure is added at CII or CIII; scale line for A, B is 0.05mm, scale line for C is 0.05mm; D. Ground pattern of the cyclopoid maxilliped. Proximal is to the right, dorsal is up. Above the limb p = praecoixa, c = coxa, b = basis; Arabic numerals identify the ramal segments by developmental age. Number 8, 9, or 10 to right of arthrodial membrane or at the tip of seta indicates the structure is added at CII, CIII or CIV. Arrow indicates location of the proximal praecoaxal lobe of calanoids; arrowhead indicates location of the distal basal lobe of calanoids. Maximum number of setae on praecoaxal, coxal, and basal lobes is assumed ancestral, as is the number of ramal segments; new seta added to distal praecoaxal and coxal lobes are shown as to be distal to pre-existing setae; setae of basis are assumed to have been on a lobe. Dorsal seta on ramal segment 2 is assumed to be added at CIII, the same stage as calanoids and polyarthran harpacticoids. More than one seta on endopodal segments of cyclopoids *Smirnovipina barentsiana* (Smirnov, 1931) see Martínez Arbizu (1997) or *Cyclopina longifurcata* Scott, 1901 see Huys & Boxshall (1990) is assumed to be derived, a transformation similar to those of calanoids and polyarthran harpacticoids.

diately proximal to the distal, formation seta of the complex at CIV, which corresponds to the stage that a fifth articulating segment with its ventral formation seta is added.

The maxilliped of the adult female of *Euryte longicauda* (Fig. 13D) consists of a praecoixa with a distal seta added at CIII, fused to a coxa of one lobe bearing one seta; both setae are on a broad lobe. A basis also bears one seta. A proximal, unarmed third endopodal segment is added at CII; a presumptive fourth endopod-

dal segment added at CIII and bearing its formation seta, but without a distal arthrodial membrane, is fused to a presumptive fifth endopodal segment added at CIV bearing its formation seta but without a distal arthrodial membrane, and to a second endopodal segment bearing its dorsal, curved formation seta. The distal endopodal segment bears three setae. A syncoxa of a praecoixa and a coxa is inferred from the distal position of the seta present at CI and the proximal position of the seta added at CIII. A middle endopodal segment complex, made up of

segments 4, 5, and 2, is inferred from the age of its proximal and middle setae, added at CIII and CIV respectively.

The maxilliped of the adult female of *Troglocyclops janstocki* (Fig. 14D) consists of a praecoxa with a distal lobe bearing two setae, one of which is added at CIII, fused to a coxa of one lobe bearing one seta; a basis has two setae. A proximal, unarmed third endopodal segment is added at CII; a presumptive fourth endopodal segment added at CIII, bearing its formation seta but without a distal arthrodistal membrane, is fused to a presumptive fifth endopodal segment added at CIV bearing its formation seta but without a distal arthrodistal membrane, and to a second endopodal segment bearing its formation seta. The distal endopodal segment has three setae. A syncoxa of a praecoxa and a coxa are inferred from the addition of a ventral seta to the proximal lobe at CIII. The middle endopodal segment complex, made up of segments 4, 5, and 2, is inferred from the age of its proximal and middle setae, added at CIII and CIV respectively.

Discussion

The choice of the calanoid morphology for comparison is based on our belief that analyses of homology should account for the largest number of serial elements present among the group of species being analyzed. This does not imply that we believe the calanoid maxilliped is necessarily more similar to the state of the copepod ancestor than the maxilliped of the ancestral cyclopoid.

A coxa with a single group of two setae and separated by an arthrodistal membrane from a proximal praecoxa with one or two groups of setae has been illustrated for adult cyclopoid copepods by Monchenko (1977, 1979), Nishida (1985) and Rocha & Iliffe (1991, 1993), and illustrated and described by Ferrari & Ambler (1992), Martínez Arbizu (1997, 2000b) and Elwers, Martínez Arbizu & Fiers (2000). This morphology does not provide an unequivocal determination of which of the three praecoxal groups of setae of calanoids is missing on cyclopoids. We assume the proximal of the three praecoxal lobes and the distal lobe of the basis of calanoids fail to develop or bear setae on cyclopoids.

An alternate hypothesis for homologies of protopodal segments of the copepod maxilliped is that of Hansen (1925) and Huys & Boxshall (1991). The adult maxilliped of *Megacalanus princeps* was described and illustrated with an unarmed praecoxa articulating with a coxa bearing three groups of setae (Hansen, 1925:40, pl. II, Fig. 5b). The adult maxilliped of *Archimiosphria discoveryi* Boxshall, 1983 was described and illustrated with a praecoxa of a single seta articulating with a coxa bearing three groups of setae (Huys & Boxshall,

1991:90, Fig. 2.3.7C). A re-examination of *Megacalanus princeps* shows a single seta on a distinct, proximal enditic lobe which is somewhat offset posteriorly from a ventral position on the syncoxa and which is followed by three groups of 2, 4 and 4 setae. The areas proximal and distal to the base of this proximal endite are poorly sclerotized, as they are near the endites. Dorsally, anteriorly or ventrally, however, the cuticle is well-sclerotized. There is no indication of an arthrodistal membrane. The proximal segment of the maxilliped of *Megacalanus princeps* is a syncoxa with four setiferous lobes, the condition found in all calanoid copepods described to date. A re-examination of *Archimiosphria discoveryi* suggests that its support for the alternate hypothesis resulted from an artifact of slide preparation; the segmentation of the protopod is the same as that of the cyclopoids (Martínez Arbizu, e-mail), a coxa with one group of setae separated by an arthrodistal membrane from a praecoxa.

It is reasonable to ask whether blank segments are a construct without biological meaning, used here simply to maintain in assumed register the formation of structures whose presentation during development actually has been delayed one or two successive stages. If this alternate interpretation is correct then the seta added to the proximal articulating endopodal segment of *Dioithona oculata* and *Oithona similis* at CIII (Figs. 4B, 5B), which is the first seta added after limb presentation, should be homologous to the seta added to the proximal articulating endopodal segment of *Neocyclops vicinus* at CIV (Fig. 12D), which is the first seta added after its limb presentation. However, the seta added to the proximal endopodal segment of *Dioithona oculata* and *Oithona similis* at CIII is proximal to and well separated from the formation seta of the second segment present at CI. The seta added to the proximal endopodal segment of *Neocyclops vicinus* at CIV is proximal but immediately adjacent to the formation seta of the second segment. Furthermore, *Dioithona oculata* and *Oithona similis* add a third seta at CIV between the two setae which are present at CIII (Figs. 4C, 5C). This third seta is proximal, but immediately adjacent, to the formation seta of the second segment; it is comparable in position to the seta added at that same copepodid stage by *Neocyclops vicinus*. We believe that the relative location and exact copepodid stage of formation of a seta are more reliable indicators of setal and segment homology than are setal morphology and relative copepodid stage of formation. Our interpretation is that setation of the endopod of *Dioithona oculata* and *Oithona similis* (Figs. 4D, 5D) corresponds more closely to that of *Euryte longicauda* or *Troglocyclops janstocki* (Figs. 13D, 14D). The only architectural difference among the endopods of these species, aside from three setae on the distal segment of the first two species and the four setae

on the latter two species, is the distal arthrodistal membrane of the proximal articulating endopodal segment of *Euryte longicauda* and *Troglocyclops janstocki* which fails to form in *Dioithona oculata* and *Oithona similis*. Similarly, setation of the endopod of *Neocyclops vicinus* (Fig. 12D) is like that of *Procylopina feiticera* (Fig. 1E). Aside from four setae on the distal segment of the first species and the three setae on the latter species, differences between the two species are the distal arthrodistal membrane of the third segment and of the fourth segment with its formation seta of *Procylopina feiticera*, which fail to form in *Neocyclops vicinus*.

The endopod of the adult female *Cyclopina caroli* is 4-segmented with two unarmed segments and differs from *Procylopina feiticera* which adds a presumptive fifth segment and has only one unarmed segment. However, the maxilliped of adult cyclopinids is much more variable than suggested by these two species, although some of these species may not belong to the Cyclopinidae. For example, species with an adult maxilliped with apparently truncated architecture have been removed to a new family (Martínez Arbizu, 2000a).

In contrast, architecture of the maxilliped of oithonids is not as variable. The only difference between *Dioithona oculata* and *Oithona similis* is the degree to which an arthrodistal membrane forms between the praecoxa and the coxa. The adult morphology of *Paroithona pacifica* Nishida, 1985 described by Ferrari & Boettger (1986) suggests a development similar to *Oithona similis*. Our analysis implies that the endopod of most oithonids includes five segments, and supports the coding of Ho (1994) and Ho et al. (1998), in contrast to the descriptions of Ferrari & Orsi (1984), Nishida, (1985), Ferrari & Boettger (1986), Ferrari & Ambler (1992). The two species of *Limnoithona* Burckhardt, 1913 are the only oithonids whose endopod is not patterned during development.

Eighteen species of Cyclopidae were placed in two monophyletic groups whose swimming leg development was either delayed or truncated; nine species remained in an apparently polyphyletic group whose swimming leg development retains the ancestral pattern (Ferrari, 1998). The maxilliped of these cyclopid species, along with the recently analysed *Cyclops scutifer*, *Diacyclops eulitoralis*, *Euryte longicauda*, *Metacyclops minutus*, and *Stolonicyclops heggiensis*, shares a syncoxa whose coxal lobe bears only one seta, present at CI; a second seta is not added at CIII, unlike the situation for the Cyclopinidae and Oithonidae. Within each group of cyclopid species, species may differ in patterning of the endopod or in setal number on the distal lobe of the praecoxa.

Maxilliped development of all species with delayed swimming leg development (see Table 1) is identical to *Megacyclops latipes* (Fig. 8A-C). Cyclopid species with

truncated swimming leg development express a more diverse maxilliped architecture. Four species are identical to *Megacyclops latipes*. *Allocyclops silvaticus* differs in having no praecoxal seta at CI, although a praecoxal seta is added at CIII. *Diacyclops eulitoralis* and *Stolonicyclops heggiensis* (Fig. 10A-C) also lack a praecoxal seta at CI, but have two only setae on the distal endopodal segment. *Bryocyclops caroli*, *Graeteriella brehmi*, *Muscocyclops operculatus*, and *Speocyclops racovitzai* (Fig. 11A, B) lack both praecoxal setae and have only two setae on the distal endopodal segment.

Diversity in cyclopid maxilliped architecture and development is greatest among species that have retained the ancestral swimming leg development. The endopod of the maxilliped of *Troglocyclops janstocki*, *Euryte longicauda*, and *Neocyclops vicinus* is patterned during the copepodid phase of development. The third and fourth endopodal segment of *Neocyclops vicinus* (Fig. 12D) are blank segments fused to segments 5 and 2, both of which have one seta. The third endopodal segment of both *Euryte longicauda* (Fig. 13D) and *Troglocyclops janstocki* (Fig. 14D) is unarmed, and segments 4 and 5, with one seta each, are fused to segment 2. However, *Euryte longicauda* differs from all other cyclopid species of the three families studied because the basis bears only one seta. The endopod of seven remaining species is not patterned during copepodid development; six of them are identical to *Megacyclops latipes*. *Hali-cyclops aberrans* (Fig. 9C) differs because its proximal endopodal segment is fused with the basis to form an allobasis, and its distal endopodal segment has only two setae.

Among other adult Cyclopoida, the endopod of the adult maxilliped of *Speleoithona* (see Rocha & Iliffe, 1991; 1993) has an unarmed proximal segment like *Cyclopina caroli*, *Procylopina feiticera*, *Euryte longicauda* and *Troglocyclops janstocki*. This third segment is not homologous to the unarmed proximal second segment of adult poecilostomes which initially bears a formation seta at CI that fails to develop at CII and later copepodid stages. Loss of this formation seta of the second segment after CI, and the sexual dimorphism of the distal segment of the adult maxilliped appear to be apomorphies for the poecilostomes *Hemicyclops adherens* (Williams, 1907) (see Ferrari & Dahms, 1998), as well as *Conchylurus quintus*, *Leptinogaster major* and *Corycaeus angelicus* (unpublished observations).

In this study, segment complexes including the syncoxa and allobasis are more common than unarmed segments, despite the presence of unarmed segments on the maxilliped of *Procylopina feiticera*, *Cyclopina caroli*, *Euryte longicauda* and *Troglocyclops janstocki*. An arthrodistal membrane fails to form between the praecoxa and coxa of nine species, in which the praecoxa and the coxa retain at least one seta. Six species have an endo-

pod segmental complex in which the formation seta of at least two segments inserts on the complex. An arthro-dial membrane of one species fails to form between the basis and proximal endopodal segment, both of which bear setae. These data suggest that the distal arthro-dial membrane of a segment has been more labile during the evolutionary history of the maxilliped than have the setae which insert on a protopodal segment or has the seta which inserts on the ramal segment. For purposes of phylogenetic analyses, we suggest from this inference that the presence of the arthro-dial membrane of a segment should be uncoupled from the presence of the ventral seta of the segment, and each analyzed as separate character. Analyzing the transformation of an arthro-dial membrane independently of the ventral seta of a segment may provide a better way of understanding thoracopod history (Ferrari & Benforado, 1998) than considering the segment, seta plus distal arthro-dial membrane, as the basic structural unit of the limb.

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