

## SEGMENTAL HOMOLOGIES OF THE MAXILLIPED OF SOME COPEPODS AS INFERRED BY COMPARING SETAL NUMBERS DURING COPEPODID DEVELOPMENT

Frank D. Ferrari and Hans-Uwe Dahms

### ABSTRACT

Segmental homologies of the maxillipeds of *Longipedia americana*, *Coullana canadensis*, *Macrosetella gracilis*, *Hemicyclops adherens*, and *Troglocyclops janstocki* are inferred by comparing segmental and setal numbers at CI, and changes in setal numbers during the copepodid phase of development, with published accounts of the calanoids *Ridgewayia klausruetzleri* and *Pleuromamma xiphias*. The unsegmented endopod of *L. americana* is a complex of 4 presumptive segments and the unsegmented endopod of *C. canadensis* is a complex of 3 presumptive segments. The endopod of *T. janstocki* appears to be 3-segmented, but the middle segment is a complex of 3 presumptive segments. *Macrosetella gracilis* has an unsegmented endopod of 2 presumptive segments; the distal segment is attenuate, forming a clawlike structure. *Hemicyclops adherens* has a 2-segmented endopod; the prominent, clawlike terminal structure on the maxilliped of the adult male is an attenuation of the distal endopodal segment. A homologous but more complex attenuation of that segment is present on the maxilliped of all of its copepodid stages including the adult female.

Copepods exhibit a significant diversity in the morphology of their maxilliped, particularly in the number of segments and segmental armature of the endopod. We examine the development of several kinds of maxillipeds whose endopod is so poorly sclerotized that it appears as an unsegmented ramus, e.g., the harpacticoids *Longipedia americana* Wells, 1980, and *Coullana canadensis* (Willey, 1923), or those in which the endopod is segmented, but some of whose segments may be complexes of more than one segment, e.g., *Macrosetella gracilis* (Dana, 1847), a harpacticoid, and *Troglocyclops janstocki* Rocha and Iliffe, 1994, a cyclopoid. We also describe the morphology of the clawlike appendage of *M. gracilis* and of *Hemicyclops adherens* (Williams, 1907), a poecilostomatoid. We derive endopodal segmental homologies for the maxillipeds of these copepods by comparing segmental and setal numbers at copepodid I (CI), and changes in setation during the copepodid phase development with published accounts of the calanoids *Ridgewayia klausruetzleri* Ferrari, 1995, and *Pleuromamma xiphias* (Giesbrecht, 1889).

### METHODS

In the following analysis, endopodal segments and their setae which form during the same copepodid stage in the development of different copepods are assumed to be homologous. In order to facilitate comparisons of homologous segments, endopodal segments are numbered in the order in which each is formed during copepodid development. Calanoids like *R. klausruetzleri* and *P.*

*xiphias* were chosen for comparative purposes, because, with 19 or 18 setae, respectively, on 5 endopodal segments of the maxilliped, they have as many segments and more setae than any other copepod species whose development is known. The maxilliped of adult *R. klausruetzleri* consists of a syncoxa of 4 medial lobes, 3 praecoxal and 1 coxal, bearing 1, 2, 4, and 3 setae, respectively, and a basis with an undifferentiated medial lobe with 3 setae and a distomedial lobe with 2 setae; the endopod is 5-segmented. Its distal segment and the penultimate segment, which are present at CI, by convention are segment 1 and segment 2, respectively; the proximal segment, adjacent to the basis, forms at CII and is segment 3. Segment 4 is distal to segment 3 and forms at CIII; the middle segment forms at CIV and is segment 5. The 5 endopodal segments have 4, 4, 4, 4, and 3 setae (Table 1). Three of the 4 syncoxal lobes of the maxilliped bear setae at CI, and the endopod is 2-segmented. The penultimate (second) segment of the endopod at this stage has 1 seta and the distal (first) segment has 4 setae; the number of setae on the first segment does not change during the remainder of development. During the molt to CII, setae are added to all lobes of the syncoxa, and on the basis a third seta is added medially to the undifferentiated lobe and a second seta is added to the distomedial lobe. Setation of the syncoxa and basis is complete at CII. One new endopodal segment each is added at CII-CIV (segments 3-5, respectively). The position of each new segment is proximal to the penultimate (second) segment of the endopod, and each new segment bears a single, medial seta (defined here as its formation seta). A lateral, postformation seta is added to segment 2 at CIII. A medial, postformation seta is added to segments 3 and 4 simultaneously at CIV. A second and third set of 1 medial, postformation seta each are added simultaneously to segments 2-5 at CV and CVI, respectively (Ferrari, 1995). *Pleuromamma xiphias* begins with 1 seta more on the fourth syncoxal lobe (Table 1). Setation of the syncoxa and basis is complete at CIII. No lateral postformation seta is added to the penultimate (second) segment at CIII (Ferrari, 1985, and unpublished data for CI). In

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Table 1. Setation of the maxilliped of *Ridgewayia klausruetzleri* and *Pleuromamma xiphias*. Lobes of the syncoxa (s1-s4), the basis (b), and its distomedial lobe (l), and the endopodal segments (n1-n5 numbered in order of appearance during development) are arranged from proximal (left) to distal (right). a = endopodal segment not formed.

<i>Ridgewayia klausruetzleri</i>											
	s1	s2	s3	s4	b	l	n3	n4	n5	n2	n1
CI	0	1	2	2	2	1	a	a	a	1	4
CII	1	2	4	3	3	2	1	a	a	1	4
CIII	1	2	4	3	3	2	1	1	a	2	4
CIV	1	2	4	3	3	2	2	2	1	2	4
CV	1	2	4	3	3	2	3	3	2	3	4
CVI	1	2	4	3	3	2	4	4	3	4	4

<i>Pleuromamma xiphias</i>											
	s1	s2	s3	s4	b	l	n3	n4	n5	n2	n1
CI	0	1	2	3	2	1	a	a	a	1	4
CII	1	2	3	3	2	2	1	a	a	1	4
CIII	1	2	4	4	3	2	1	1	a	1	4
CIV	1	2	4	4	3	2	2	2	1	1	4
CV	1	2	4	4	3	2	3	3	2	2	4
CVI	1	2	4	4	3	2	4	4	3	3	4

all other respects, development is identical to *R. klausruetzleri*.

For *L. americana*, *C. canadensis*, *M. gracilis*, *H. adherens*, and *T. janstocki*, the setal number at CI and the following patterns of setal addition found for the 2 calanoids were assessed during maxilliped development: (1) the stage at which setation of the proximal and middle regions of the appendage [syncoxa and basis] is complete; (2) a sequential addition to the distal region of a medial seta at CII-CIV [representing the medial, formation seta of new endopodal segments 3-5]; (3) the addition to the distal region of a lateral seta distally at CIII [i.e., to endopodal segment 2]; (4) at CIV, additions to the distal region of a medial seta adjacent to an existing seta [representing 1 medial, postformation seta added to endopodal segments 3 and 4]; (5) at CV and CVI, additions to the distal region of 2 sets, respectively, of medial setae to the adjacent area of existing setae [representing 1 medial, postformation seta each to endopodal segments 2-5].

## RESULTS

Throughout the copepodid phase of development, the maxilliped of *L. americana* (Fig. 1) is to be divided into proximal, middle, and distal regions. Setation of the proximal region is complete at CIV; there is no change in setation of the middle region, and setation of the distal region is complete at CV. Distinctive characteristics of the distal region include: (1) a crossed-pair of setae at the distolateral corner of the distal region in all stages; (2) a lateral seta first present at CIII; and (3) late in development, three medial pairs of setae comprising a proximal, long, thick seta and a distal, short, thin seta along the medial margin of the distal region. The proximal, long, thick seta of the three pairs is present at CI, or added at CII or CIII, re-

spectively. The distal, short, thin seta of the proximal two pairs is added simultaneously at CIV, and the distal seta of the distal pair is added at CV.

During the copepodid phase of development, the maxilliped of *C. canadensis* (Fig. 2) also can be divided into proximal, middle, and distal regions. Beginning at CII, this species is dimorphic and based on setal number of the proximal region at CVI, when the sexual dimorphism of antenna 1 and leg 6 are also apparent, we believe that the dimorphism is a sexual dimorphism. Setation of the proximal and distal regions of the male is complete at CIII, but, for the female, setation of these regions is complete at CV. There is no change in either sex in setation of the middle region. Distinctive characteristics of the distal region include: (1) a crossed-pair of setae at the distolateral corner of the distal region in all stages; (2) a lateral seta first present at CIII; and (3) late in development, two pairs of setae comprising a proximal, short, thin seta and a distal, long, thick seta along the medial margin of the distal region; the thicker, distal seta of the two pairs is present at CI or added at CII, while the thinner proximal seta is added at CV of females.

The maxilliped of *M. gracilis* (Fig. 3) can be divided into proximal, middle, and distal regions; a claw is associated with the distal region. At CI, the proximal region does not bear setae; the elongate middle region has two setae. The claw of the distal region articulates with the middle region, and there are two se-

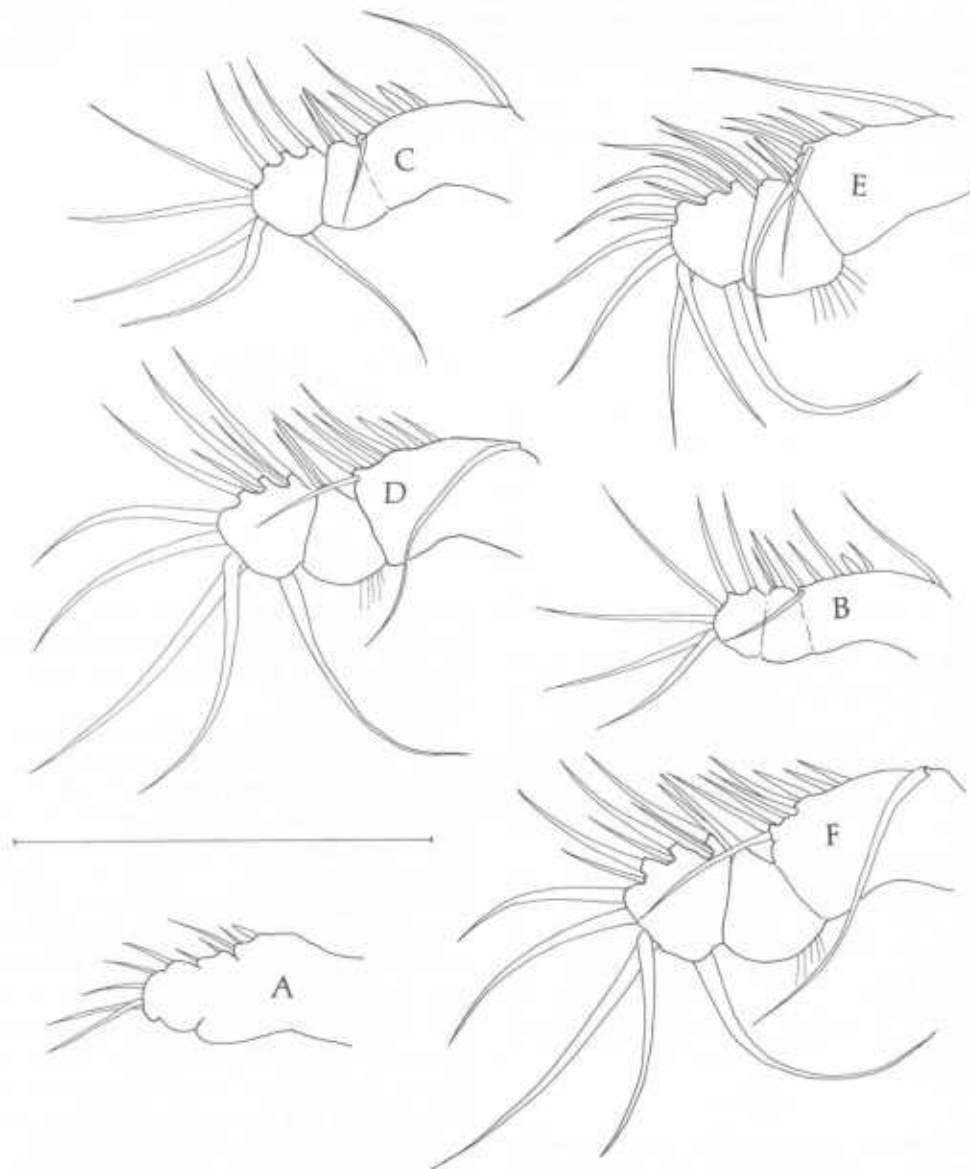


Fig. 1. Maxilliped of *Longipedia americana*. A, CI; B, CII; C, CIII; D, CIV; E, CV; F, CVI, female. Proximal is right, medial is up. Scale = 0.01 mm. Setules on all setae are omitted.

tae, one adjacent to the claw and one proximal to the claw. A seta is added to the proximal region at CII. There is no change in setation during later copepodid development.

The maxilliped of *H. adherens* (Fig. 4) can also be divided into proximal, middle, and distal regions. At CI, the proximal region bears two setae, the middle region two setae, while the distal region is 2-segmented with a seta on the proximal segment and two setae, medial and lateral, on the distal segment. On the distal segment, a complex attenuation is

homologous to the large, subchaelate, claw of the adult male. This attenuation is present on the distal segment at all subsequent copepodid stages. At CII, the seta of the proximal segment of the distal region is absent. An attenuate point is added medially to the distal segment at CIII and a second attenuate point is added laterally to the distal segment at CIV.

At CI, the maxilliped of *T. janstocki* is a linear series of four distinct segments with 2, 2, 1, and 3 setae, respectively, from proximal to distal (Fig. 5). An unarmed segment

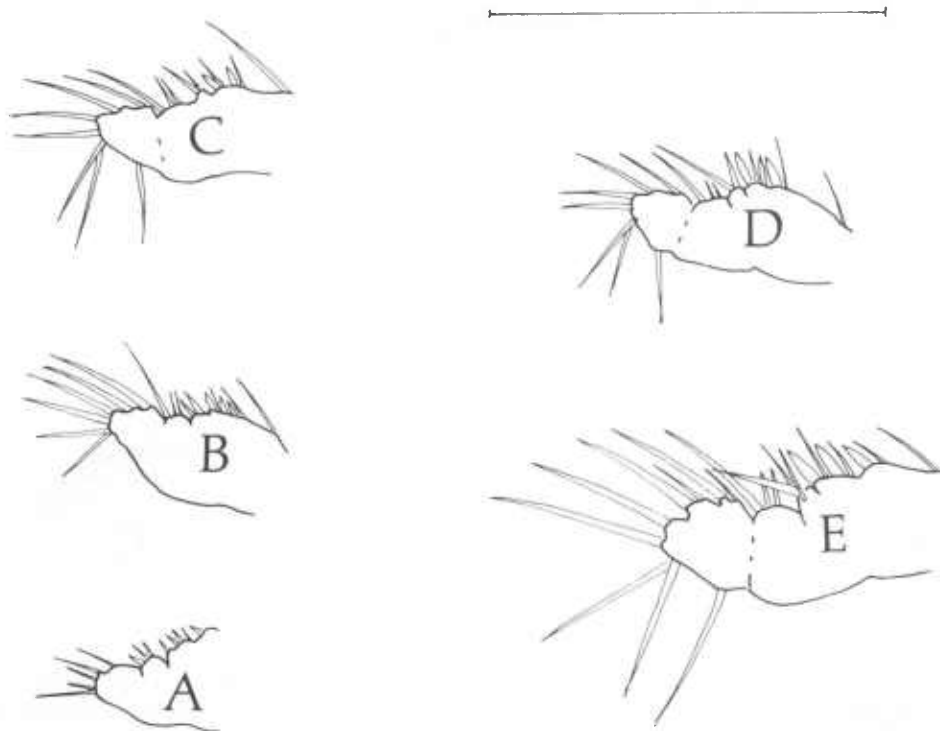


Fig. 2. Maxilliped of *Coullana canadensis*. A, CI; B, CII, female; C, CIII, male; D, CIV, female; E, CVI, female. Proximal is right, medial is up. Scale = 0.01 mm.

is added between the second and third segments at CII. At CIII, a medial seta is added to the proximal segment and a second seta is added medially and proximally to the penultimate segment. A medial seta is added to the penultimate segment at CIV; it is adjacent and proximal to the distomedial seta. CV of *T. janstocki* is unknown, but at CVI segmentation and setation of the maxilliped is identical to CIV (Rocha and Iliffe, 1994).

#### INTERPRETATION

The three regions of the maxilliped of *L. americana* correspond to the syncoxa, basis, and endopod of the maxilliped of the two calanoids. There are four setiferous lobes on the proximal region (Table 2, Fig. 6). Setation of these syncoxal lobes is complete at CIV, and not at CII or CIII, as in the case of the calanoids. The middle region of this maxilliped is the basis and the two setae which are present at CI are homologous to the two setae on the undifferentiated medial lobe present at CI of the basis of the two calanoids. Unlike the two calanoids, the maxilliped of *L. americana* does not add a third seta to its

undifferentiated medial lobe and there is no distomedial lobe.

The distal region begins with five setae which correspond to the terminal set of four setae (including the crossed-pair) on the distal (first) segment and one seta on the penultimate (second) segment of the two calanoids. There is a sequential addition of a large, thick, medial seta each at CII and CIII (homologous to the medial formation seta of new endopodal segments 3 and 4 of the two calanoids). There is an addition of a lateral seta distally at CIII (homologous to that seta on endopodal segment 2 of the calanoids), and there is an addition medially of a short, thin seta adjacent to the proximal two, long, thick setae at CIV (homologous to the first set of a medial, postformation seta added simultaneously to endopodal segments 3 and 4 of the two calanoids). These data are congruent with a presumptive 4-segmented endopod for the maxilliped of *L. americana*. Because no large, medial seta is added at CIV, the stage at which the fifth segment and its formation seta are added to the calanoids, we believe the maxilliped of *L. americana* has no fifth pre-

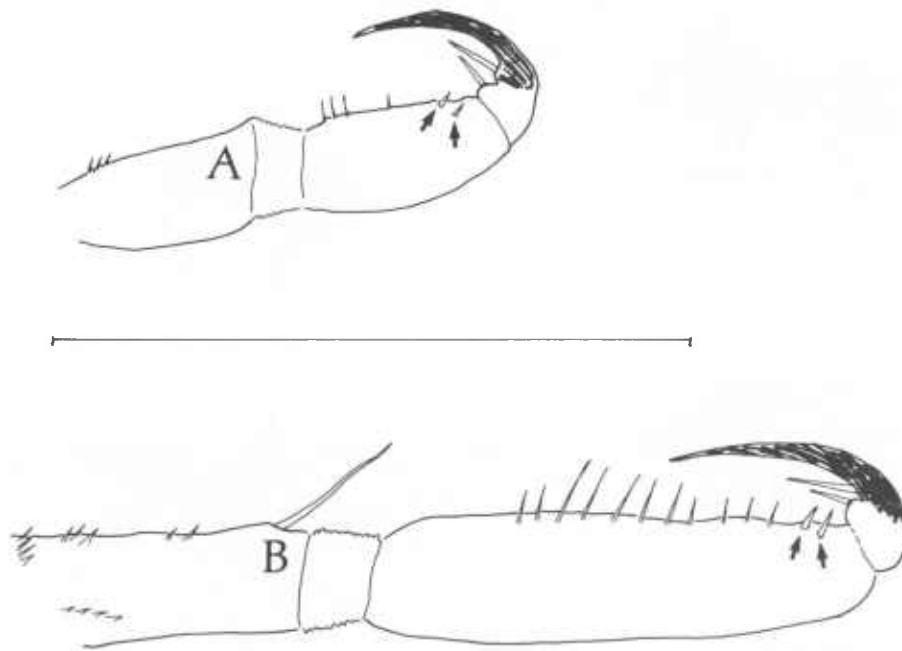


Fig. 3. Maxilliped of *Macrosetella gracilis*. A, CI; B, CVI, female. Proximal is left, medial is up. Scale = 0.01 mm. Arrows point to setae of basis (middle region). Wavy lines indicate poorly sclerotized region between syncoxa and basis. The area comprising the presumptive distal segment is darkened.

sumptive segment. We also note that no simultaneous additions occur which correspond to the two sets of medial setae added at CV and CVI, respectively, of the two calanoids (homologous to the medial, postformation seta to each of endopodal segments 2–5). Instead, there is the addition medially of a short, thin seta to its proximal, long, thick pair member at CV (homologous to the second medial, postformation seta added to presumptive segment 2 of the calanoids).

The three regions of the maxilliped of *C. canadensis* also correspond to the syncoxa, basis, and endopod of the maxilliped of the calanoids. There are four setiferous lobes on the proximal region of the maxilliped. Seta-tion of these syncoxal lobes is complete at CV for females and CII for males (Table 3, Fig. 6). The middle region of the maxilliped of *C. canadensis* is the basis and the three setae which are present at CI are homologues of the two setae on the undifferentiated medial lobe plus the single seta on the distomedial lobe of the basis of the calanoid maxilliped at CI. Unlike the two calanoids, the maxilliped of *C. canadensis* does not add a third seta to the undifferentiated medial lobe or a second seta to the distomedial lobe.

The distal region of *C. canadensis* begins with five setae which correspond to the terminal set of four setae (including the crossed-pair) on the distal (first) segment and one seta on the penultimate (second) segment of the calanoids. The medial seta added at CII is homologous to the medial, formation seta of presumptive endopodal segment 3. The addition of a lateral seta distally at CIII occurs on presumptive endopodal segment 2. There is an addition medially of one short, thin seta to its distal, long, thick pair member at CV (homologous to the second medial, postformation seta added simultaneously to each of endopodal segments 2 and 3 of the two calanoids). These data are congruent with a presumptive 3-segmented endopod for the maxilliped of *C. canadensis*. Because no thick, medial seta is added at CIII or CIV, the stages at which the fourth and fifth segment plus the formation seta of each are added to the calanoids, the maxilliped of this harpacticoid has no fourth or fifth presumptive segments.

The medial pairs of a short, thin, plus long, thick setae representing presumptive endopodal segments 2–4 of *L. americana* and presumptive endopodal segments 2 and 3 of *C. canadensis* appear similar; however, the

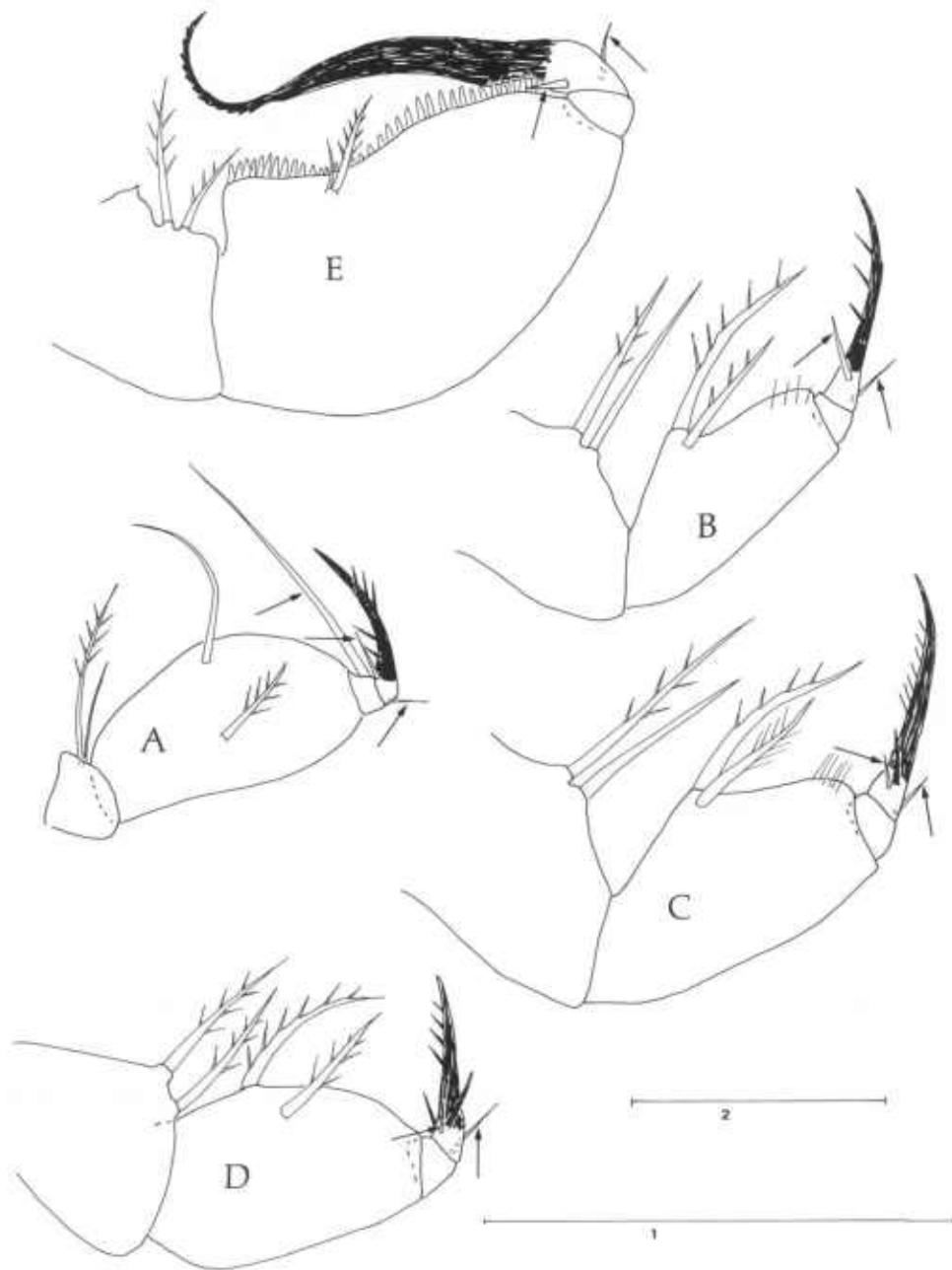


Fig. 4. Maxilliped of *Hemicyclops adherens*. A, C1; B, C11; C, C111; D, CV, female; E, CVI, male. Proximal is left, medial is up. Scale 1 = 0.01 mm for A-C and scale 2 = 0.01 mm for D-E. The area comprising the attenuate portion of the distal segment is darkened. Arrows point to endopodal setae.

short, thin setae are not homologous. In *L. americana* they are a first set of postformation setae added to segments 3 and 4 at CIV plus a second postformation seta added to segment 2 at CV. In the female of *C. canadensis* the setae are a second postfor-

mation seta added to each of segments 2 and 3 at CV.

The three regions of the maxilliped of *M. gracilis* (Table 2) are the syncoxa, with a coxal seta added at CII, the basis, and an endopod. This interpretation assumes that the

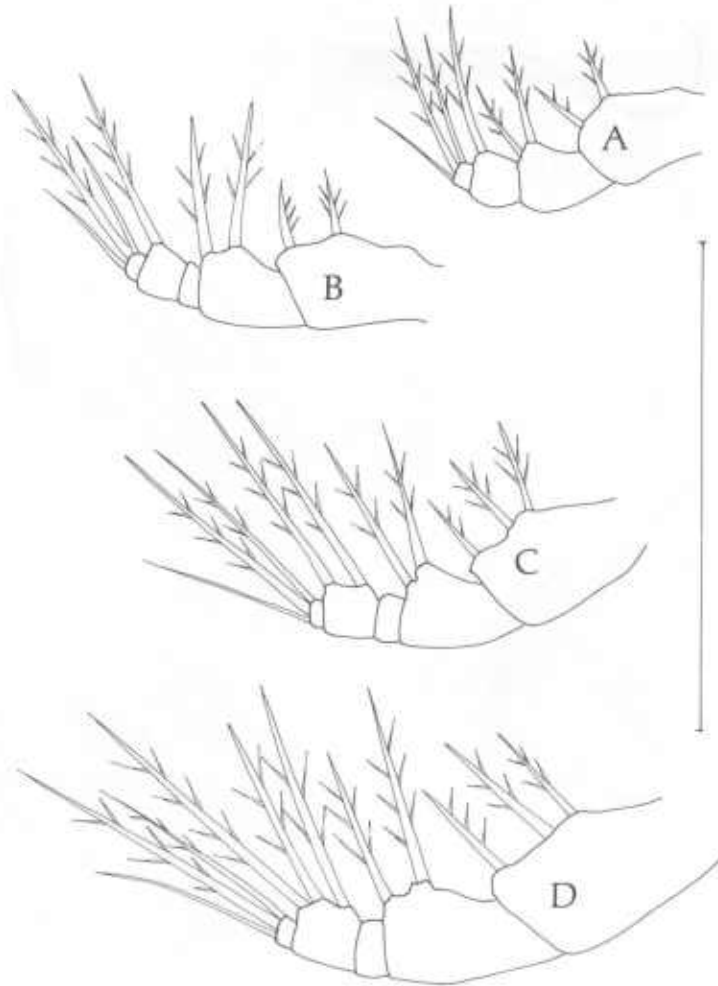


Fig. 5. Maxilliped of *Troglodyclops janstocki*. A, CI; B, CII; C, CIII; D, CIV. Proximal is right, medial is up. Scale = 0.01 mm.

Table 2. Setation of the maxilliped of *Longipedia americana* and *Macrosetella gracilis*. Explanations as in Table 1.

<i>Longipedia americana</i>											
	s1	s2	s3	s4	b	l	n3	n4	n5	n2	n1
CI	0	0	1	2	2	0	a	a	a	1	4
CII	1	2	2	2	2	0	1	a	a	1	4
CIII	1	2	2	2	2	0	1	1	a	2	4
CIV	1	2	3	3	2	0	2	2	a	2	4
CV	1	2	3	3	2	0	2	2	a	3	4
CVI	1	2	3	3	2	0	2	2	a	3	4
<i>Macrosetella gracilis</i>											
	s1	s2	s3	s4	b	l	n3	n4	n5	n2	n1
CI	0	0	0	0	2	0	a	a	a	1	1
CII	0	0	0	1	2	0	a	a	a	1	1
CIII	0	0	0	1	2	0	a	a	a	1	1
CIV	0	0	0	1	2	0	a	a	a	1	1
CV	0	0	0	1	2	0	a	a	a	1	1
CVI	0	0	0	1	2	0	a	a	a	1	1



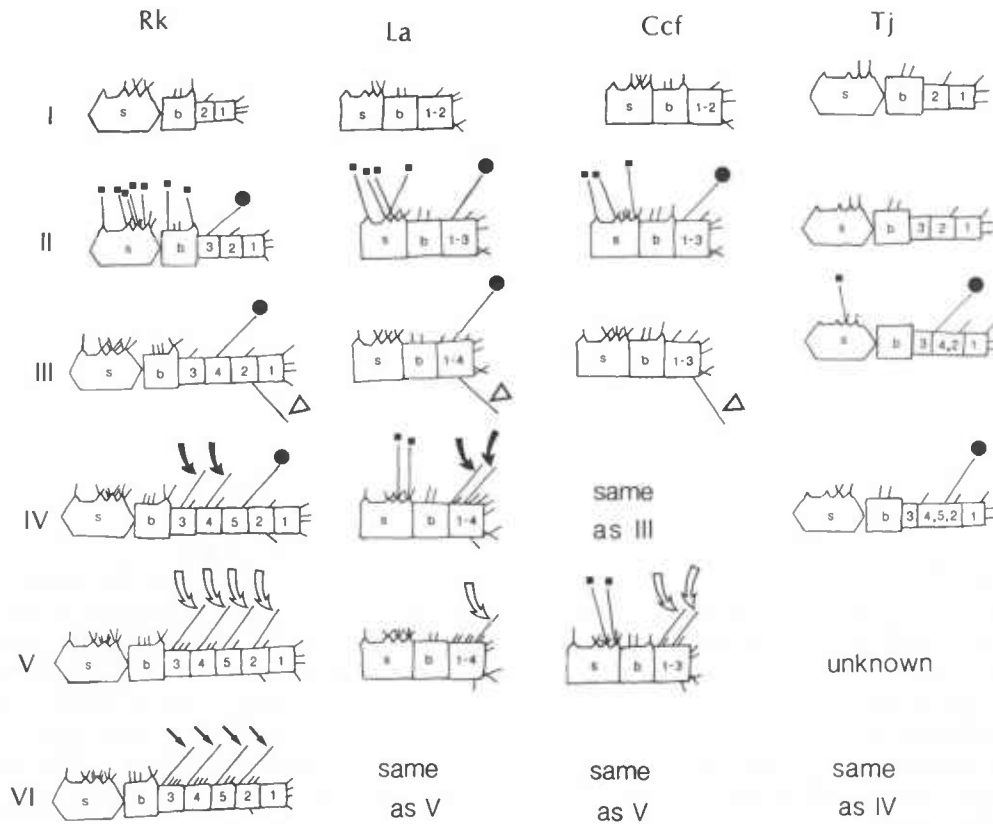


Fig. 6. Stylized representation of the addition of setae during copepodid development to syncoxa (s), basis (b), and endopodal segments of the maxilliped of *Ridgewayia klausruetzleri* (Rk), *Longipedia americana* (La), *Coullana canadensis* female (Ccf), and *Troglocyclops janstocki* (Tj). Proximal is left and medial is up. Lobes of the syncoxa and basis are pointed. Free endopodal segments are numbered by their order of appearance during development with the distal segment as the first; fused endopodal segments are noted by their inclusive numbers; new setae added at any stage are long; position of new setae on a segment or a lobe bearing more than one seta is arbitrarily indicated as proximal, except for the third endopodal segment of *Troglocyclops janstocki* for which the position of new setae at CIII and CIV has been established. Squares indicate seta added to lobe of syncoxa or basis; circles indicate the medial formation seta added to new endopodal segments 3-5 at CII-CIV, respectively; open triangles indicate lateral, postformation seta added to endopodal segment 2 at CIII; closed, curved arrows indicate first set of one medial, postformation seta each added simultaneously to endopodal segments 3 and 4 at CIV; open, curved arrows indicate second set of one medial, postformation seta added simultaneously to each of endopodal segments 2-5 at CV; closed, straight arrows indicate third set of one medial, postformation seta added simultaneously to each of endopodal segments 2-5 at CVI.

elongate middle region is a basis with two inner setae, and agrees with Huys and Boettger-Schnack (1994). Patterns of setal additions of calanoids fail to resolve the segmentation of the endopod, which can be interpreted in one of two ways. The endopod is a complex of the two segments present at C1. The claw is an attenuation of the distal endopodal segment which also bears a lateral seta; a second seta is associated with the presumptive second, penultimate segment. The two endopodal segments are not separated by an

arthrodial membrane during development. Alternately, the endopod may be composed of a single segment, including a heavily sclerotized claw with two setae. We prefer the first hypothesis.

The three regions of the maxilliped of *H. adherens* are the syncoxa, with one seta each on the third praecoxal lobe and the coxal lobe, a basis, and an endopod. Patterns of setal addition of the two calanoids fail to predict the loss of a seta to the proximal segment of the endopod (Table 4). An attenuate, distal seg-

Table 3. Setation of the maxilliped of *Coullana canadensis* female and male. Explanations as in Table 1.

<i>Coullana canadensis</i> female											
	s1	s2	s3	s4	b	l	n3	n4	n5	n2	n1
CI	0	1	3	1	2	1	a	a	a	1	4
CII	1	2	3	2	2	1	l	a	a	1	4
CIII	1	2	3	2	2	1	l	a	a	2	4
CIV	1	2	3	2	2	1	l	a	a	2	4
CV	1	2	4	3	2	1	2	a	a	3	4
CVI	1	2	4	3	2	1	2	a	a	3	4

<i>Coullana canadensis</i> male											
	s1	s2	s3	s4	b	l	n3	n4	n5	n2	n1
CI	0	1	2	1	2	1	a	a	a	1	4
CII	1	2	2	2	2	1	l	a	a	1	4
CIII	1	2	2	2	2	1	l	a	a	2	4
CIV	1	2	2	2	2	1	l	a	a	2	4
CV	1	2	2	2	2	1	l	a	a	2	4
CVI	1	2	2	2	2	1	l	a	a	2	4

ment is present throughout copepodid development. The attenuate region is long and thick in the adult male; in adult females (Huys and Boxshall, 1991) and immature copepodids it is shorter and thinner but more complex, having many secondary attenuate points. The addition of attenuate points on the proximal section of the distal segment is also unique. Our interpretation of segmental armament during development does not agree with previous analysis of two different species of the genus (Kim and Ho, 1992; Itoh and Nishida, 1995).

The maxilliped of *T. janstocki* at CI is composed of a syncoxa with one seta each on the third praecoxal lobe and the coxal lobe and

a basis with two setae; the endopod is two-segmented with one seta on the proximal segment and three setae on the distal segment (Table 4, Fig. 6). At CII an unarmed, antepenultimate, third segment is added to the endopod. At CIII a medial seta is added to the third praecoxal lobe, and a second seta, medial and proximal, is added to the middle segment of the endopod. This endopodal seta is homologous to the formation seta of the fourth endopodal segment of the two calanoids, because that seta is the only one added medially during the molt to CIII. During the molt to CIV, a medial seta, immediately proximal to the distomedial seta, is added to the middle segment of the endopod.

Table 4. Setation of the maxilliped of *Hemicyclops adherens* for stages CI–CVI, and *Troglocyclops janstocki* for stages CI–CIV. Explanations as in Table 1.

<i>Hemicyclops adherens</i>											
	s1	s2	s3	s4	b	l	n3	n4	n5	n2	n1
CI	0	0	1	1	2	0	a	a	a	1	2
CII	0	0	1	1	2	0	a	a	a	0	2
CIII	0	0	1	1	2	0	a	a	a	0	2
CIV	0	0	1	1	2	0	a	a	a	0	2
CV	0	0	1	1	2	0	a	a	a	0	2
CVI	0	0	1	1	2	0	a	a	a	0	2

<i>Troglocyclops janstocki</i>											
	s1	s2	s3	s4	b	l	n3	n4	n5	n2	n1
CI	0	0	1	1	2	0	a	a	a	1	3
CII	0	0	1	1	2	0	0	a	a	1	3
CIII	0	0	1	1	2	0	0	l	a	1	3
CIV	0	0	1	1	2	0	0	l	l	1	3
CV	unknown										
CVI	0	0	1	1	2	0	0	l	l	1	3

This seta is homologous to the formation seta of the fifth endopodal segment of the calanoids, because its position is proximal and adjacent to the distomedial seta of the middle segment. This seta is not homologous to a medial, postformation seta added to endopodal segment 4 of calanoids at this molt, because a position adjacent to the proximomedial seta of the segment would be expected.

The analysis of comparative setal additions used here is based on three assumptions: (1) at CI of these copepods, the maxilliped, which may have been transformed from an appendage bud in the last naupliar stage, has an endopod composed of two segments, which may be fused; the proximal segment always bears a medial seta and the distal segment may bear up to four setae whose number does not change during subsequent development; (2) endopodal segments and their setae which form during the same copepodid stage of different copepods are homologous; (3) the addition of setae to endopodal segments follows an orderly sequence which can best be understood by comparing setal additions to the calanoids *R. klausruetzleri* and *P. xiphias*. The second assumption does not hold for setation of the praecoxa, coxa, and basis. Choice of the calanoid morphology for the comparisons is based on our belief that analyses of homology must 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 any of the other maxillipeds analyzed here. Our use of comparative setal additions during development provides more reliable hypotheses about homologies when more setae are present to be compared, e.g., *L. americana* and *C. canadensis*. The interpretation of maxillipeds with comparatively fewer setae are more problematical, e.g., *T. janstocki*. For species in which there are no additions of setae after CI, e.g., *M. gracilis* and *H. adherens*, inferences are weakest.

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Addresses: (FDF) Invertebrate Zoology/MS (MRC 534), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A. (e-mail: ferrarif@simsc.si.edu) (H-UD), Universitaet Oldenburg, Arbeitsgruppe Zoomorphologie, Fachbereich 7, D-26111 Oldenburg, Germany. (e-mail: hudahms@hrz1.uni-oldenburg.de)

