THE IDENTITY OF PROTOPODAL SEGMENTS AND THE RAMUS OF MAXILLA 2 OF COPEPODS (COPEPODA)

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ABSTRACT

The protopod of the maxilla 2 of copepods is composed of a proximal syncoxa with a praecoxal endite proximally and a coxal endite distally. The basis bears two endites, and the ramus is an endopod bearing up to five segments. This interpretation is based on protopodal patterning from the point where the limb articulates with the body, and the assumption that this patterning should result in a derivable enditic configuration on the protopod of the serially homologous limbs maxilla 1 anteriorly and maxilliped posteriorly. Processes that affect the morphological diversity of maxilla 2 among copepods include: truncation of protopodal segmentation, suppression of enditic extension, truncation of endopodal segmentation, and segment elongation. Hypotheses about transformations of the basis suggest the following synapomorphies: neither endite of the basis is attenuate on maxilla 2 of Poecilostomatoida; the basis of maxilla 2 of Siphonostomatoida is elongate ventrally.

RÉSUMÉ

Le protopodite de la seconde maxille des copépodes est composé d'un syncoxopodite proximal, avec un endite précoxal proximal et un endite coxal distal. Le basipodite porte deux endites, et la rame est un endopodite portant jusqu'à cinq segments. Cette interprétation est fondée sur le patron protopodal à partir du point où l'appendice s'articule avec le corps, et la supposition que ce modèle aboutirait à une configuration enditique dérivable sur le protopodite des appendices homologues: première maxille antérieurement et maxillipède postérieurement. Les processus qui affectent la diversité morphologique de la deuxième maxille chez les copépodes incluent: la réduction de la segmentation protopodale, la suppression de l'extension enditique, la réduction de la segmentation endopodale et l'allongement des segments. Les hypothèses concernant les transformations du basis suggèrent les synapomorphies suivantes: aucun endite du basis n'est atténué sur la deuxième maxille des Poecilostomatoida; le basis de la deuxième maxille des Siphonostomatoida est allongé ventralement.

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INTRODUCTION

There have been several attempts over the past century to understand the segmental homologies of the maxilla 2 of copepods, but as yet no consensus has emerged. Because maxilla 2 is uniramous on copepods, a basic question concerns which group of segments makes up the protopod and which group makes up the ramus. Several hypotheses, derived from comparative adult morphology, about segmental homologies of this limb, and particularly its protopod, are reviewed here. The order in which elements are added to crustacean limbs during development is used to resolve some of the ambiguities; aligning the protopod of maxilla 2 with the anterior maxilla 1 and the posterior maxilliped also provides valuable insights. Examples of the morphological diversity of this limb are discussed, and several different developmental processes are proposed to explain this diversity.

TERMS

Maxilla 2 is the limb of the last cephalic somite; it has been called the 1st maxilliped by Giesbrecht (1893) or maxilla by Hansen (1925), Gurney (1931), Lang (1948), and Huys & Boxshall (1991). The limb anterior to maxilla 2 is maxilla 1, also known as the maxillule (Hansen, 1925; Gurney, 1931; Huys & Boxshall, 1991) or maxillula (Lang, 1948). The limb posterior to maxilla 2 is the maxilliped, also known as the 2nd maxilliped (Giesbrecht, 1893); it is the limb of the anterior thoracic somite.

The protopod of a copepod limb is composed of at most three segments: the praecoxa is proximal and closest to the body; the coxa is the middle segment; the basis is distal and farthest from the body. An exopod and an endopod, the rami, originate on the basis. An endite is a broad, ventral extension of a protopodal segment; it does not articulate with the segment, and usually bears one or more setae on its ventral face. Endites also have been called lobes (Giesbrecht, 1893; Hansen, 1925; Ferrari, 1995), but here the term "lobe" refers only to a non-articulating, setiferous, ventral extension of an endopodal segment. An endite often is poorly-sclerotized dorsally where it joins the central shaft of the segment. These areas of weak sclerotization presumably facilitate movement of the endite relative to the central shaft of the segment, but these areas may compromise visualization of arthrodial membranes that separate segments. A lobe does not have such poorly-sclerotized areas. Setae may be lost secondarily from both endites and lobes. If an endite or a lobe fails to form secondarily, the setae that originated on either may originate on the ventral face of the segment. Whether each endite of the protopod of a copepod limb is homologous to a segment on the protopod of the ancestral crustacean, as Borradaile (1926) suggested, is not considered here.

ANALYSIS

The problem

Thorell (1859: 84) considered some copepod limbs to be composed of basis, medial and ultima parts, the latter including the rami; however, he did not apply these terms uniformly or consistently. For Giesbrecht (1893, pl. 7 fig. 17) maxilla 2 (1st maxilliped) of the calanoid copepod *Calanus gracilis* Dana, 1852 [now *Neocalanus gracilis*] is made up of a protopod of two segments (termed basipod 1 and basipod 2). The proximal protopodal segment (basipod 1) has four lobes (endites) and the distal segment (basipod 2) has one lobe. The ramus is an endopod of three segments. Although Giesbrecht considered the protopod as 2-segmented, from the dorsal face of his illustration it appears to be 3-segmented. Giesbrecht (1893, pl. 27 fig. 13) illustrated the protopod of calanoid copepods like *Hemicalanus mucronatus* Claus, 1863 [now *Haloptilus mucronatus*] with a 6th endite distally on its own articulating segment so that the protopod appears to be 4-segmented. The remaining three segments are endopodal.

In documenting a hypothesis of three segments for the crustacean protopod, Hansen (1925, pl. 2 fig. 5a) shows the dorsal face of the protopod of maxilla 2 (maxilla) of *Megacalanus princeps* Wolfenden, 1904 with three segments. The number of endites associated with the praecoxa is not shown in the figure, although Hansen writes that two endites are associated with the coxa, and two endites associated with the basis (Hansen, 1925: 40). The ramus of maxilla 2 is an endopod of five segments; the proximal endopodal segment is long and bears a lobe (Hansen, 1925: 39-40). A general sense of Hansen's configuration can be found in fig. 1B. Gurney (1931: 59, figs. 55-64) generally agrees with Hansen's interpretation. In contrast, maxilla 2 (maxilla) of Lang (1948: 56, fig. 25) is composed of a praecoxa with two endites, a coxa with two endites, a basis with one endite, and an endopod of up to five segments (fig. 1B). The hypothesized ancestral copepod of Huys & Boxshall (1991, fig. 1.1.5) follows Lang's (1948) interpretation although the proximal segment of the endopod may be fused to the basis to form an allobasis.

Segmentation of maxilla 2 does not change during development so that limb patterning cannot be used to resolve the above inconsistencies in endite number. However, Ferrari (1995) found that setation of maxilla 2 is completed early in copepodid development, much like setation of the exopod of the cephalic limbs antenna 2, mandible, and maxilla 1, and unlike setation of the endopod of the cephalic limbs and maxilliped that often continues throughout the copepodid phase. Using the protopodal segmentation of Huys & Boxshall (1991), Ferrari (1995) proposed that the ramus of maxilla 2 is an exopod. This hypothesis is based on differences in timing of the addition of setae, although homologies of the added setae were not determined.
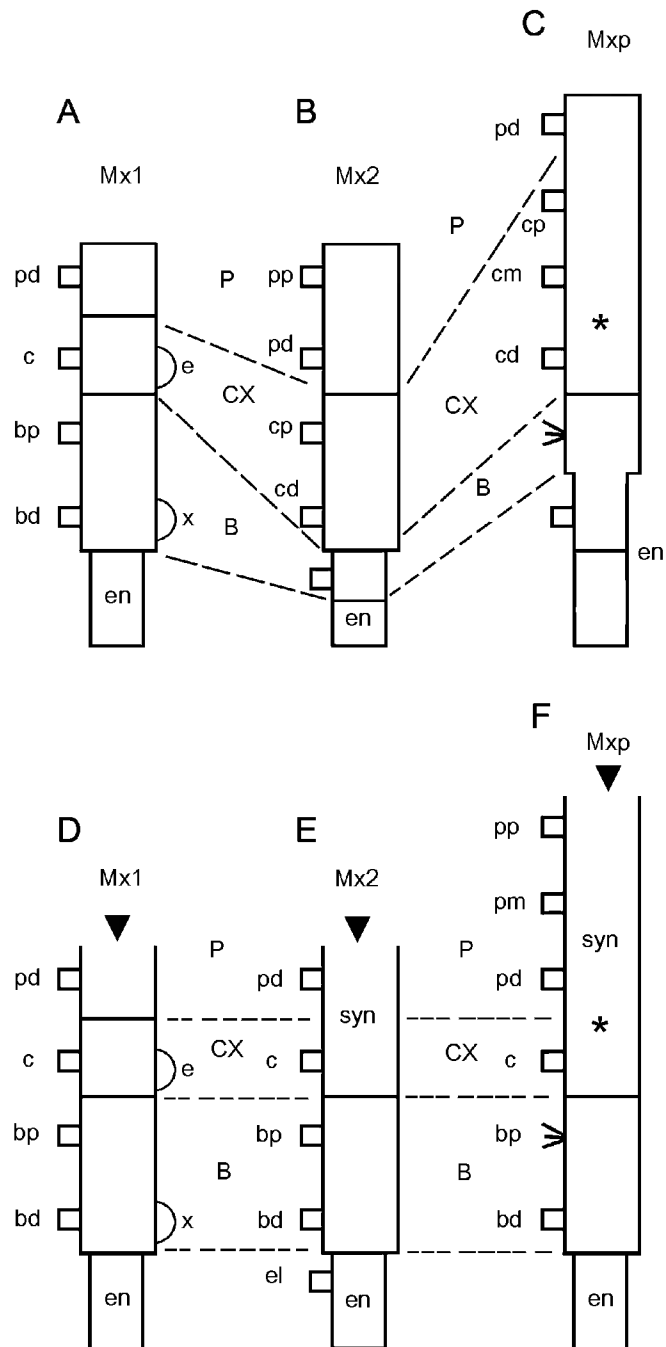
Adjacent serial homologs

Problems with the resolution of segmental homologies of maxilla 2 become more apparent when the configuration of the protopod of the adjacent serial homologs maxilla 1 (anterior) and maxilliped (posterior) are compared to maxilla 2 (fig. 1A-C). For Giesbrecht (1893), the proximal protopodal segment (basipod 1) of the calanoid maxilla 1 includes all endites and exites associated with what were later considered the praecoxa and coxa, plus the proximal lobe of what was later considered the basis. The distal protopodal segment (basipod 2) of calanoids includes only the distal lobe of what was later considered the basis. Giesbrecht's proximal protopodal segment of the calanoid maxilliped (2nd maxilliped), now considered a syncoxa, has four endites and the distal segment, now considered the basis, has a distoventral endite.

Hansen (1925) found maxilla 1 (maxillule) with a praecoxa with two endites, a coxa with one endite, and a basis without an endite but with several setae on the distoventral face; an endopod is composed of up to three segments (fig. 1A). Maxilla 1 (maxillule) of Gurney (1931: 49, figs. 34-38) has a protopod of up to four endites; the proximal endite of the basis originates on its own segment or is fused with the coxa and its endite. Maxilla 1 (maxillula) of Lang (1948: 54, fig. 24) has a praecoxa with one endite, a coxa with one endite, a basis with two endites (respectively, the distal coxal endite and distoventral setae of Hansen, 1925), and an endopod of up to three segments. Huys & Boxshall's (1991) interpretation of maxilla 1 (maxillule) follows Lang (1948).

The maxilliped of Hansen (1925) has a praecoxa with one endite and a coxa with three endites, and a basis without an endite but with midventral setae and a distoventral seta (fig. 1C). The endopod is 5-segmented. The protopod of the maxilliped of Gurney (1931) agrees with that of Hansen (1925) except that the

Fig. 1. A-C, schematic of limb segmentation: A, maxilla 1 (interpreted from Lang, 1948); B, maxilla 2 (interpreted from Lang, 1948); C, maxilliped (interpreted from Hansen, 1925). Basal endite number decreases from 2 (maxilla 1) to 1 (maxilla 2) to 0 (maxilliped); coxal endite number increases from 1 (maxilla 1) to 2 (maxilla 2) to 3 (maxilliped); praecoxal endite number increases from 1 (maxilla 1) to 2 (maxilla 2), then decreases to 1 (maxilliped). D-F, schematic of limb segmentation as interpreted in the present analysis: D, maxilla 1; E, maxilla 2; F, maxilliped. Basal endite number remains the same although the proximal basal endite of the maxilliped does not attenuate and only its setae are present; coxal endite number remains the same; praecoxal endite number increases from 1 (maxilla 1 and maxilla 2) to 3 (maxilliped). Protopod is patterned where the limb joins the body (arrowhead). Proximal up, ventral left. b, basis; cx, coxa; p, praecoxa; syn, coxa and praecoxa not separated by arthrodial membrane; en, endopod; x, exopod of maxilla 1; pd, distal endite of praecoxa; pm, middle endite of praecoxa; pp, proximal endite of praecoxa; c, endite of coxa; cd, distal endite of coxa; cm, middle endite of coxa; cp, proximal endite of coxa; bd, distal endite of basis; bp, proximal endite of basis; e, coxal exite of maxilla 1; el, enditic-like lobe of proximal endopodal segment of maxilla 2; *, star locates arthrodial membrane on maxilliped of basal cyclopoids.

distoventral setae of the basis originate on a lobe considered the proximal of six endopodal segments. Lang (1948: 58, figs. 26, 27-31) does not provide a consistent interpretation of the protopod of the maxilliped. The protopod of the maxilliped of Huys & Boxshall (1991) is similar to that of Hansen (1925), and their endopod is 6-segmented like that of Gurney's (1931) with the proximal endopodal segment fused to the basis. Ferrari (1995) found that the two setae on this presumed endopodal segment are added during development in a pattern similar to setal additions to other protopodal endites and out of register with the setation of the distal endopodal segments. He proposed that this structure is a distal endite of the basis; the proximal endite of the basis does not form in calanoids but up to three of its setae are present on the proximoventral face of the basis (Ferrari & Dahms, 1998).

A quite different interpretation of the protopod of the maxilliped of copepods is available from Monchenko (1977, 1979), who illustrated but did not interpret a coxa with one endite for several basal cyclopoids; the praecoxa of these copepods has two endites. Later Ferrari & Ivanenko (2001) confirmed Monchenko's observations and reinterpreted the syncoxa of the maxilliped of calanoids as a coxa with one endite, distally, and a proximal praecoxa with three endites. This interpretation (fig. 1F) brings the configuration of the protopod of the maxilliped in line with that of maxilla 1, because both have one coxal endite and two basal endites.

Generalizing from the above earlier interpretations, maxilla 1, maxilla 2, and maxilliped bear respectively: one, two, or three endites on the coxa; two, one, or no endites on the basis; and one, two, or one endite on the praecoxa (fig. 1A-C). This set of configurations is not intuitive for a set of adjacent serially homologous limbs. Variation in the number of coxal endites would imply that protopodal patterning occurs in the middle of the protopod, but variations in the number of endites of the praecoxa and basis does not support this implied patterning process.

Resolution

Ferrari & Grygier (2003) proposed from direct observations that the protopod of a branchiopod limb is patterned from the point where the limb articulates with the body. This interpretation is supported by inferences about the progressive decrease in the number of praecoxal endites present on the maxilliped of several cyclopoid copepods. That number decreases from two praecoxal endites for basal cyclopoids, through one praecoxal endite for some derived cyclopoids, to a maxilliped without a praecoxal endite for the more derived cyclopoids studied by Ferrari & Ivanenko (2001). This interpretation also is reflected in a general way in the numerical symbols assigned by Lang (1948: 58, fig. 26) to the segments of some limbs. One result of the way that the protopod is patterned during development is that a praecoxa or a coxa may not be present on every limb, but the coxa must be present if the praecoxa is present (see Ferrari & Dahms, 2007, Rule of Serial Homologs).

With this interpretation of protopodal patterning, hypotheses that maxilla 1, maxilla 2, and maxilliped bear one, two, and three coxal lobes, respectively, become less satisfying. If a praecoxa has a distal endite, then all serially homologous structures of the protopod, e.g., the coxa, that form earlier during development and distal to the praecoxa should be present (Ferrari & Dahms, 2007). Because a praecoxa is presumed to be present on maxilla 1, maxilla 2, and the maxilliped, the complete enditic configuration of the coxa also should be present on these limbs. Maxilla 1 with one coxal endite, maxilla 2 with two coxal endites, and a maxilliped with three coxal endites (fig. 1A-C) is inconsistent with this analysis.

Application

The resolution of these inconsistencies may lie in the correct alignment of the protopod of the three limbs. The configuration of the protopod of maxilla 2 of a copepod like *Oithona frigida* Giesbrecht, 1902 (fig. 2A) can be brought into line with maxilla 1 anterior to it and the maxilliped posterior to it if the proximal 'segment' of maxilla 2 is not a praecoxa but rather a complex of the praecoxa and coxa, i.e., a syncoxa. Then the distal endite on this syncoxa is the coxal endite. The proximal endite is a praecoxal endite, and it is homologous to the praecoxal endite of maxilla 1 and the distal praecoxal endite of the maxilliped. The following segment of maxilla 2 is the basis with a proximal and a distal endite, and this configuration conforms to that of maxilla 1, as proposed by Huys & Boxshall (1991). It also conforms to the basis of the maxilliped of calanoid copepods (Ferrari & Dahms, 1998).

The remaining segments of maxilla 2 of *O. frigida* belong to the ramus (fig. 2A). In most calanoids, maxilla 2 is foreshortened along the proximal/distal axis; maxilla 2 of *Spinocalanus abyssalis* Giesbrecht, 1888 (fig. 2B) is more elongate allowing better visualization of the segmentation. The proximal ramal segment often bears an enditic-like, distoventral lobe that is large on cyclopoids and on calanoids like *Spinocalanus abyssalis*. This segment does not bear a dorsal seta and has more than one ventral seta, so its identity is that of an endopodal segment (Huys & Boxshall, 1991; Ferrari & Dahms, 2007) with a ventral extension. The 6th lobe of calanoids like *Haloptilus mucronatus* also bears more than one ventral seta; its identity is that of the ventral extension of the endopodal segment adjacent to the proximal segment of *O. frigida*, which segment also has a ventral extension. The ramus of maxilla 2 then is an endopod, and not an exopod as proposed by Ferrari (1995). The endopod of the cyclopoid (fig. 2A) is composed of four segments; that of the calanoid (fig. 2B) of four or five segments, depending upon the association of setae and arthrodial membranes (see below). At present, it is not possible to determine which segment of a 5-segmented endopod may be missing
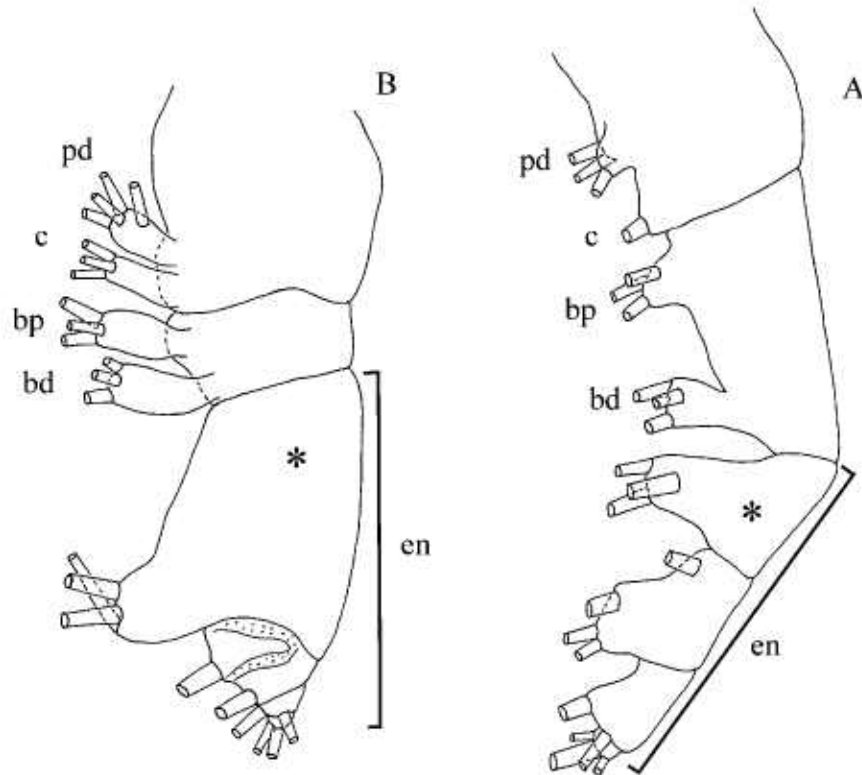
Fig. 2. A, maxilla 2 of *Oithona frigida* Giesbrecht, 1902 adult male, posterior; B, maxilla 2 of *Spinocalanus abyssalis* Giesbrecht, 1888 adult male, posterior. Proximal up, ventral left; pd, praecoxal endite; c, coxal endite; bp, proximal basal endite; bd, distal basal endite.

from an endopod with four or fewer segments because no model for patterning this ramus has been proposed. Other rami of copepod limbs, however, usually are patterned from a source segment often in the middle of the ramus. During development new segmental elements may be added to a ramus either proximally or distally from the source segment (Ferrari & Dahms, 2007). As a result, there is no direct correlation between the developmental age of a ramal segment and its distance from the basis of the protopod or from the tip of the ramus. Nor can a determination of homologous segments of a ramus be made by a simple counting exercise; the application of numerical symbols in a simple, proximodistal progression is a misleading exercise (see Ferrari & Dahms, 2007).

The above interpretation of the configuration of the protopod of maxilla 1, maxilla 2, and the maxilliped requires two endites on the basis and one endite on the coxa (fig. 1D-F) of copepods with a protopod that has not been transformed. During the course of evolution, endite extension may fail secondarily, e.g., the proximal basal endite of the maxilliped of calanoids, or the proximal and distal

basal endites of the maxilliped of many other copepods. This interpretation is permissive for the number of praecoxal endites, which may vary due to the truncation of protopodal patterning from the point where the limb attaches to the body. For example, a praecoxa may bear a proximal, a middle, and a distal endite (the maxilliped of most calanoids), only the middle and distal endites (the maxilliped of basal cyclopoids), or only a distal endite (maxilla 1 and maxilla 2 of many copepods).

Among copepods, maxilla 2 is morphologically quite diverse. Some of this diversity results from the action of different processes on different parts of the limb. As explained above, the protopod of a calanoid like *Spinocalanus abyssalis* (fig. 2B) is similar to that of a cyclopoid like *Oithona frigida* (fig. 2A). The endopod of *S. abyssalis* is 5-segmented if the articulating part of the endopod distal to the long proximal segment is a segment complex with its two ventral setae originating on separate but fused segments. An alternate hypothesis is that the seta distal to the proximal segment is homologous to the proximal seta of the antepenultimate segment of *O. frigida*, and thus the calanoid *S. abyssalis* has a 4-segmented endopod, like *O. frigida*. The proximal segment of the endopod of both species has a lobe, which suggests that these are homologous segments; the distal segments with terminal, or crown, setae also probably are homologous.

Maxilla 2 of the cyclopoid *Euryte longicauda* Philippi, 1843 (fig. 3A) has a syncoxa without endites. Both endites of the basis bear one seta each and the distal basal endite is attenuate proximally. A well-developed, 3-segmented ramus is present. Its proximal segment appears lobe-like, suggesting that it is homologous to the proximal endopodal segment of *O. frigida* and *S. abyssalis*, and its distal segment with crown setae is probably homologous to the distal segment of the calanoid and the cyclopoid. Maxilla 2 of the harpacticoid *Tegastes falcatus* (Norman, 1868) (fig. 3B) has a syncoxa with a praecoxal endite bearing three setae, and a coxal endite with two setae. Both basal endites have three setae each. The endopod appears to be represented by three setae, perhaps including two crown setae, on the distal edge of the basis. However, the identity of these setae as endopodal is difficult to differentiate from those ventral setae on the distal basal endite.

The syncoxa of maxilla 2 of the poecilostomatoid *Hemicyclops adherens* (Williams, 1907) (fig. 3C) bears a proximal, praecoxal endite with two setae juxtaposed to the distal coxal endite, which bears one seta. However, the endites of the basis are not extended. Setae of those endites appear ventrally on the basis; two sets each of one ventral seta and one posterior seta are hypothesized to represent the proximal and distal endites of the basis. An endopod is not present. Maxilla 2 of the siphonostomatoid *Stygiopontius lomonosovi* Ivanenko & Martínez-Arbizu, 2006 (fig. 3D) has a syncoxa with only a coxal endite distally; the coxal endite
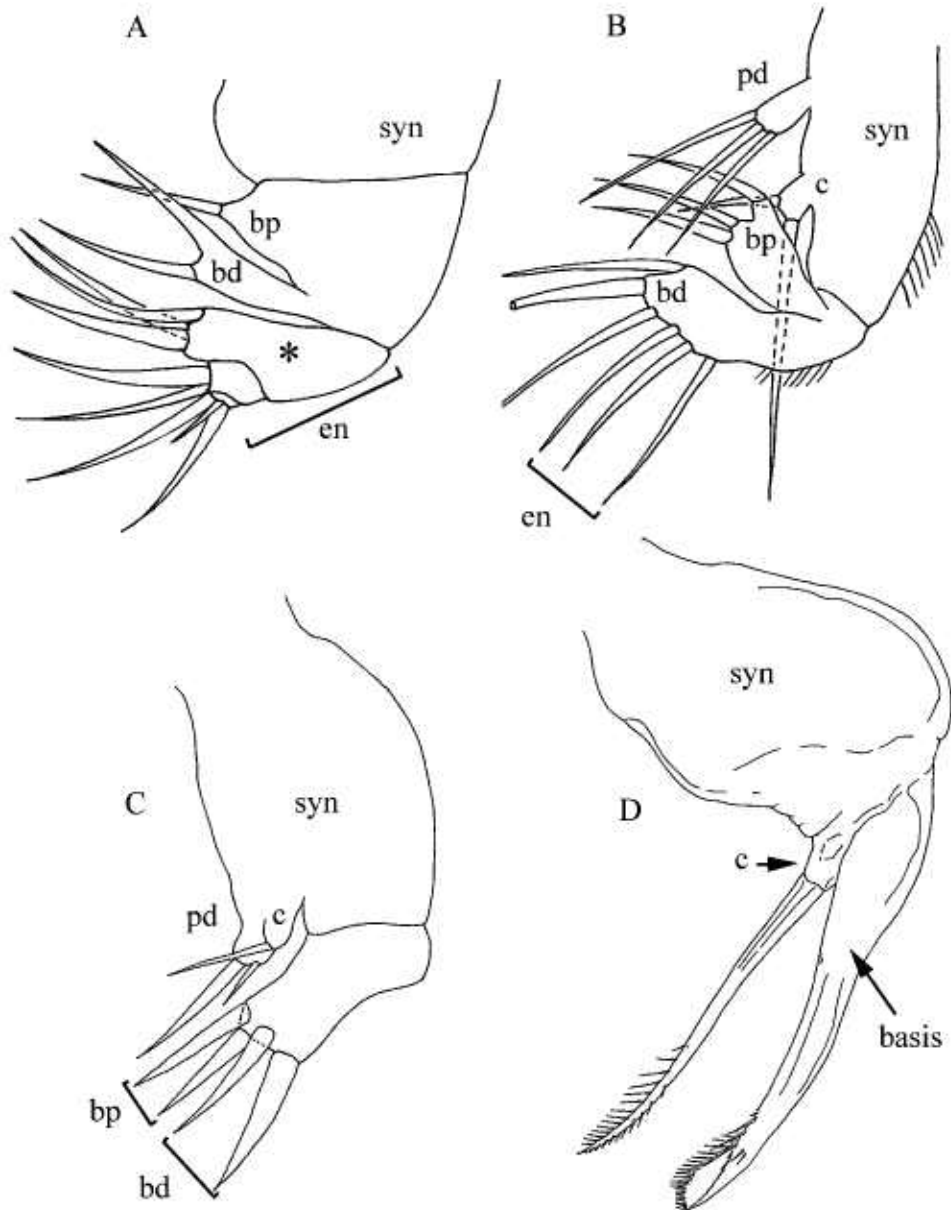
Fig. 3. A, maxilla 2 of *Euryte longicauda* Philippi, 1843 adult female, posterior (from Ferrari & Ivanenko, 2005); B, maxilla 2 of *Tegastes falcatus* (Norman, 1868) adult female, posterior; C, maxilla 2 of *Hemicyclops adherens* (Williams, 1907) adult male, posterior; D, maxilla 2 of *Stygiopontius lomonosovi* Ivanenko & Martínez-Arbizu, 2006 adult female (from Ivanenko et al., 2006), posterior. Proximal up, ventral left; syn, coxa and praecoxa not separated by arthrodial membrane; pd, praecoxal endite; c, coxal endite; bp, proximal basal endite; bd, distal basal endite.

bears one seta. The ventral face of the basis is attenuate as a single lobe; its endites are not present, and there are no setae. An endopod is not present.

Evidence for truncation of endopodal patterning can be observed by the lesser number of endopodal segments on maxilla 2 of *E. longicauda* and *T. falcatus*, and the absence of an endopod on maxilla 2 of *H. adherens* and *S. lomonosovi*. Maxilla 2 of *S. lomonosovi* and *E. longicauda* also exhibit evidence for the truncation of protopodal patterning by the absence of a praecoxal endite, or a praecoxal and a coxal endite, respectively. Extension of the proximal and distal lobes of the basis of *H. adherens* has been suppressed. One interpretation of the basis of *S. lomonosovi* is that the central area of the segment is elongate ventrally. This elongation is better visualized on maxilla 2 of the copepodid stage of caligid-like siphonostomatoids; this stage retains enditic setae on species like *Alebion lobatus* Cressey, 1970 (see Benz, 1989, fig. 3B) and *Caligus elongatus* Nordmann, 1832 (see Piasecki, 1996, fig. 17). Diversity in the configuration of maxilla 2 of copepods then can be explained, in part, by truncation of ramal segmentation, truncation of protopodal segmentation, suppression of segmental extension, and secondary segmental elongation.

CONCLUSIONS

The above character state analysis suggests the following assumptions about phylogenetic transformations. Suppression of the formation of both endites of the basis of maxilla 2 may be an apomorphy of the Poecilostomatoida, although the ventral face may have a secondarily derived attenuation which does not bear setae, e.g., *Ambilimbus tuerkayi* (Martínez Arbizu, 1999) [see fig. 5E of *Amphicrossus tuerkayi*], *Fratia gaditana* Ho, Conradi & López-González, 1998 [see fig. 2f] or *Clausidium vancouverense* (Haddon, 1912) [see Huys & Boxshall, 1991, fig. 2.10.13D]. A ventral elongation of the basis may be an apomorphy of the Siphonostomatoida.

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