

DEVELOPMENT OF LEG 5 OF COPEPODS BELONGING TO THE CALANOID SUPERFAMILY CENTROPAGOIDEA (CRUSTACEA)

Frank D. Ferrari and Hiroshi Ueda

(FDF, correspondence) Department of Zoology, MRC-534, National Museum of Natural History, Smithsonian Institution, 4210 Silver Hill Rd., Suitland, Maryland 20746, U.S.A. (ferrari.frank@mse.si.edu); (HU) Center for Marine Environmental Studies, Ehime University, Matsuyama, Ehime 790-8577, Japan (hueda@sei.ehime-u.ac.jp)

ABSTRACT

Leg 5 development is described for 10 species from 10 genera in 6 families of centropagoidean calanoid copepods. Segment homologies are inferred from the order in which arthrodial membranes, setae, and attenuations are added to ramal segments during late copepodid development. Among centropagoidean males, the grasping chela on the side opposite the male genital pore develops in three different ways. The fixed part of the chela may be a ventral attenuation of the basis, or of the proximal exopodal segment, or of the middle exopodal segment, suggesting that a male leg 5 chela is not a synapomorphy of the Centropagoidea because nonhomologous segments make up the convergent morphology. In like manner, a grasping subchela on the side opposite the male genital pore is expressed in three different ways: basis plus proximal, middle and distal exopodal segments; basis plus proximal and distal exopodal segments; or basis plus distal exopodal segment; so nonhomologous segments also result in a convergent subchela morphology. On leg 5 of adult females, a ventral attenuation of the middle exopodal segment, initially formed at copepodid stage V, is present on species of Centropagidae and Diaptomidae. A ventral attenuation of the exopod initially expressed at copepodid stage V on females of Temoridae is considered a homologous structure, although failure to express the proximal arthrodial membrane of the exopod complicates the interpretation of its origin. A ventral attenuation first appears on the exopod of Pontellidae and Acartiidae at copepodid stage V, but its homologies with the above families are more difficult to determine because neither proximal or distal arthrodial membranes nor setae are present on the adult exopod. The species of Tortanidae studied here does not express a ventral attenuation on the exopod at copepodid stage V or at the adult stage, but adults of some other species of *Tortanus* do. The ventral attenuation of the exopod of adult female leg 5, initially present at copepodid stage V, is a more likely synapomorphy for the superfamily although evidence for this homologous structure may be difficult to identify due to the secondary loss of setae and arthrodial membranes on the exopod of some species. Presence at copepodid stage V of the presumptive genital somite complex of the adult female is expressed among all centropagoideans studied here and appears to be an unambiguous synapomorphy for species of the superfamily.

Copepods belonging to the superfamily Centropagoidea are some of the most familiar calanoids. Species are well-represented in fresh waters and estuaries, as well as in habitats of the marine coastal zone and the continental shelf. The superfamily Centropagoidea was established for ten calanoid families by Andronov (1974) based on precise states of antenna 1 and swimming legs, and imprecise attributes of the mouthparts; none of the states are exhaustive of the superfamily and some are represented in other superfamilies. Park (1986) diagnosed Centropagoidea from a cladogram of eleven calanoid superfamilies. Ohtsuka and Huys (2001) used primary and secondary characters of adults to diagnose Centropagoidea from among ten calanoid superfamilies, although many lineages were not diagnosed and character state analyses were not provided for lineages in which more than one state was assigned for the same character. Boxshall and Halsey (2004) diagnosed Diaptomidea, which includes families placed in Centropagoidea, using a set of symplesiomorphies.

Park's diagnosis of the Centropagoidea (1986) invites closer scrutiny because it is the only diagnosis that meets contemporary standards of logic and analysis. Park identified two shared derived character states for the Centropagoidea, "having in the male a strongly geniculated antennule on the right side and an extremely asymmetrical 5th pair of legs with the right leg greatly modified for grasping" (Park, 1986: 193). Previously, Giesbrecht (1892) had suggested that the grasping sections of the chela of the male right leg 5 of

calanoids now included in Centropagoidea are made up of different segments of the limb (compare Giesbrecht, 1892, plate 17, fig. 21 with plate 17, fig. 45, or plate 23, fig. 34). In this paper we show the order in which structures are added to leg 5 of both females and males from copepodid stage III to copepodid stage VI (terminal adult stage) in 10 species from 10 of 98 genera representing six of 10 families of centropagoidean copepods (Table 1). We use this order, or pattern, to infer homologies of limb segments and to discuss possible synapomorphies for the superfamily. We begin by describing at each stage of development the segments of leg 5, with each segment defined as a section of the limb between two arthrodial membranes. We then analyze and interpret ramal segments of the adult limb using a model of development that adds arthrodial membranes and setae from an area toward the proximal edge of the distal ramal segment. We conclude with a discussion of the implications of the analysis for synapomorphies of the superfamily.

METHODS AND TERMINOLOGY

The superfamily name Centropagoidea Andronov (1974) is used here; changes proposed by Andronov (1991), including Diaptomidea for Centropagoidea, are not followed because at the time there was no requirement that a family group name be derived from the oldest included genus name, or by coordination from the oldest included family name (International Code of Zoological Nomenclature 1985, articles 62–64). Table 1 provides sources of the specimens. In the laboratory, copepods were cleared in glycerin and dissected in lactic acid or glycerin following generally accepted protocols. Staining was done in lactic acid by adding

Table 1. Species and families of centropagoidean copepods studied; in order of presentation.

<i>Centropages abdominalis</i> Sato, 1913 (Centropagidae); Auke Bay, Alaska; US; 10-V-1985.
<i>Boeckella poopoenis</i> Marsh, 1906 (Centropagidae); Mar Chiquita, Cordoba, Argentina; 17-V-1986.
<i>Sinocalanus tenellus</i> (Kikuchi, 1928) (Centropagidae); Isahay Bay, Nagasaki, Japan; 28-VIII-1987.
<i>Eodiaptomus japonicus</i> (Burckhardt, 1913) (Diaptomidae); Lake Kiba-gata, Ishikawa; 24-X-1999.
<i>Eurytemora affinis</i> (Poppe, 1885) (Temoridae); Chesapeake Bay, Virginia, US; 02-III-1997.
<i>Temora longicornis</i> Mueller, 1785 (Temoridae); Wadden Sea, Netherlands, in culture, 09/VII/1993.
<i>Pontella chierchia</i> Giesbrecht, 1889 (Pontellidae); Maizura Bay, Kyoto, Japan; 10-IX-1975.
<i>Labidocera pavo</i> Giesbrecht, 1889 (Pontellidae); Ine Harbor, Kyoto, Japan; 12-IX-1978.
<i>Acartia erythraea</i> Giesbrecht, 1889 (Acartiidae); Auke Bay, Alaska; US, 10-V-1985.
<i>Tortanus dextrilobatus</i> Chen and Zhang, 1965 (Tortanidae); San Pablo Bay, California, US; VI-IX-1998.

a solution of chlorazol black E dissolved in 70% ethanol/30% de-ionized freshwater, and specimens were examined with bright-field and with differential interference optics. Initial drawings were made with a camera lucida; final figures were prepared with computer software.

Copepodid stages III to VI are abbreviated CIII–CVI. Leg 5 of calanoid copepods is elongate proximally to distally and flattened anteriorly to posteriorly; structures originating on the surfaces of the third axis of the limb are described here as dorsal and ventral following Cohen (1993), and not the conventional terms 'lateral' and 'medial' of taxonomic literature. Leg 5 begins development as a small, hilde bud ventral on the body at CIII with terminal setae on each lobe. At CIV, the protopod and rami are clearly distinguishable, and the contralateral pair of limbs are united by an intercoxal plate. This limb is called the transformed limb and corresponds to the same step in development as that of swimming legs 1–4 (Ferrari, 2000). A limb segment is the sclerotized portion section of a limb between two arthrodial membranes which bears at most one dorsal and one ventral seta (Ferrari and Benforado, 1998). Failure to form an arthrodial membrane results in a segment complex which may bear more than one dorsal seta and/or more than one ventral seta (Ferrari and Ivanenko, 2001). Segments of the protopod have exact identities, coxa and basis; ramal segments do not. A ramal segment is moved by contraction of two intrinsic muscles proximal to the segment which attach via tendons to the segment's proximal rim (Boxshall, 1982, 1985). Muscles often are not present on leg 5 of immature copepodid stages, apparently because the limb does not function during these stages. The distal segment of exopod or endopod refers to the section of the limb distal to the last arthrodial membrane, although in many cases that section of the limb may be a complex of more than one segment (Ferrari and Benforado, 1998). A seta is an articulating cuticular element connected by an arthrodial membrane to an appendage segment and enclosing the hemocoel; it is not moved by the action of muscles. A segment attenuation is a nonarticulating, cuticular extension of a limb segment; a small, rounded attenuation is a projection. A denticle is an attenuation of the epicuticle of the exoskeleton of the limb. The male genital pore opens on left side of body unless otherwise noted. All figures of limbs are posterior face with distal downward on the page, unless otherwise indicated.

The choice of species from among the 98 genera and 10 families of centropagoidean calanoids is best described as serendipitous because access to conspecific immature copepodid stages restricts the species available for study. As a result, a significant amount of leg 5 architecture of the superfamily is unexamined here. Our intention was to study species whose males had either a chela- or subchela-type leg 5 opposite the side onto which the genital pore opens. Species studied here could not be placed in a phylogenetic context because phylogenetic relationships of species among centropagoidean families or among genera within the individual families remain largely unexplored. Instead, present observations begin with *Centropages abdominalis*, whose adult female leg 5 appears most similar to swimming legs 1–4, and follow what appears to be the simplest order of transformation of that limb through progressively and presumably more

derived states. Reference to swimming legs 1–4 allows comparisons of leg 5 with developmental patterning of the anterior limbs as this is recently understood (Ferrari, 2000; Ferrari and Benforado, 1998).

RESULTS

Centropages abdominalis Sato, 1913.—Left and right leg 5 present at CIII as bilobe bud (Fig. 1A) with 3 setae on the presumptive exopod and 2 on the presumptive endopod.

CIV (Fig. 1B): a transformed limb; coxa without setae, basis with 1 dorsal, posterior seta. Exopod with 3 dorsal, 1 terminal, 3 ventral (7) setae. Endopod with 1 dorsal, 2 terminal, 3 ventral (6) setae.

CV (Fig. 1C): proximal exopodal segment with 1 dorsal seta; distal segment with 3 dorsal, 1 terminal, 4 ventral (8) setae and a ventral attenuation, slightly bent toward the ramus, proximal to the proximal seta. Proximal endopodal segment with 1 ventral seta; distal segment with 2 dorsal, 2 terminal, 3 ventral (7) setae.

CVI female (Fig. 1D): proximal exopodal segment with 1 dorsal seta; middle segment with 1 dorsal seta and a straight, distal, ventral attenuation with denticles on distal face; distal segment with 2 dorsal, 1 terminal, 4 ventral (7) setae. Proximal endopodal segment with 1 ventral seta and denticles; middle segment with 1 ventral seta and denticles; distal with 2 dorsal, 2 terminal, and 2 ventral (6) setae and denticles.

CVI male (Fig. 1E, F): proximal segment of left exopod with one dorsal seta; distal segment with 2 dorsal and 1 terminal (3) setae, and proximal and distal area of denticles ventrally. Proximal endopodal segment with 1 ventral seta and denticles; middle segment with 1 ventral seta; distal segment with 2 dorsal, 2 terminal, and 2 ventral (6) setae. Right proximal exopodal segment with 1 dorsal seta; middle segment with 1 posterior, distal seta and long, ventral attenuation curved toward the ramus; distal segment long and attenuate with simple fluting at tip, 1 small, dorsal seta at mid-length, 1 larger ventral seta with setules at mid-length, and a ventral projection distal to the ventral seta. Proximal endopodal segment with 1 ventral seta, middle segment with 1 ventral seta, distal with 2 dorsal, 2 terminal, and 2 ventral (6) setae.

Boeckella poopoenis Marsh, 1906.—Left and right leg 5 present at CIII as bilobe bud (Fig. 2A) with 3 setae on the presumptive exopod and 2 on the presumptive endopod.

CIV female (Fig. 2B): a transformed limb; coxa without setae, basis with 1 proximal, posterior seta. Exopod with 3 dorsal, 1 terminal, 3 ventral (7) setae. Endopod with 0–2 dorsal [variable within and among specimens; proximal seta most often missing], 2 terminal, 3 ventral (5–7) setae.

CIV male (Fig. 2F): left exopod slightly longer; left and right exopod more rounded terminally.

CV female (Fig. 2C): proximal exopodal segment with 1 dorsal seta; distal segment with 3 dorsal, 1 terminal (4) setae and a straight ventral attenuation. Proximal endopodal segment with 1 ventral seta; distal segment with 0–2 dorsal, 2 terminal, 3 ventral (5–7) setae.

CV male (Fig. 2G): similar to female; distal exopodal segment longer, with ventral projection; right projection with denticles. Proximal endopodal segment without setae, distal with 1 (left) or 2 (right) denticles.

CVI female (Fig. 2D, E): proximal exopodal segment with 1 dorsal seta; middle segment with 1 dorsal seta and

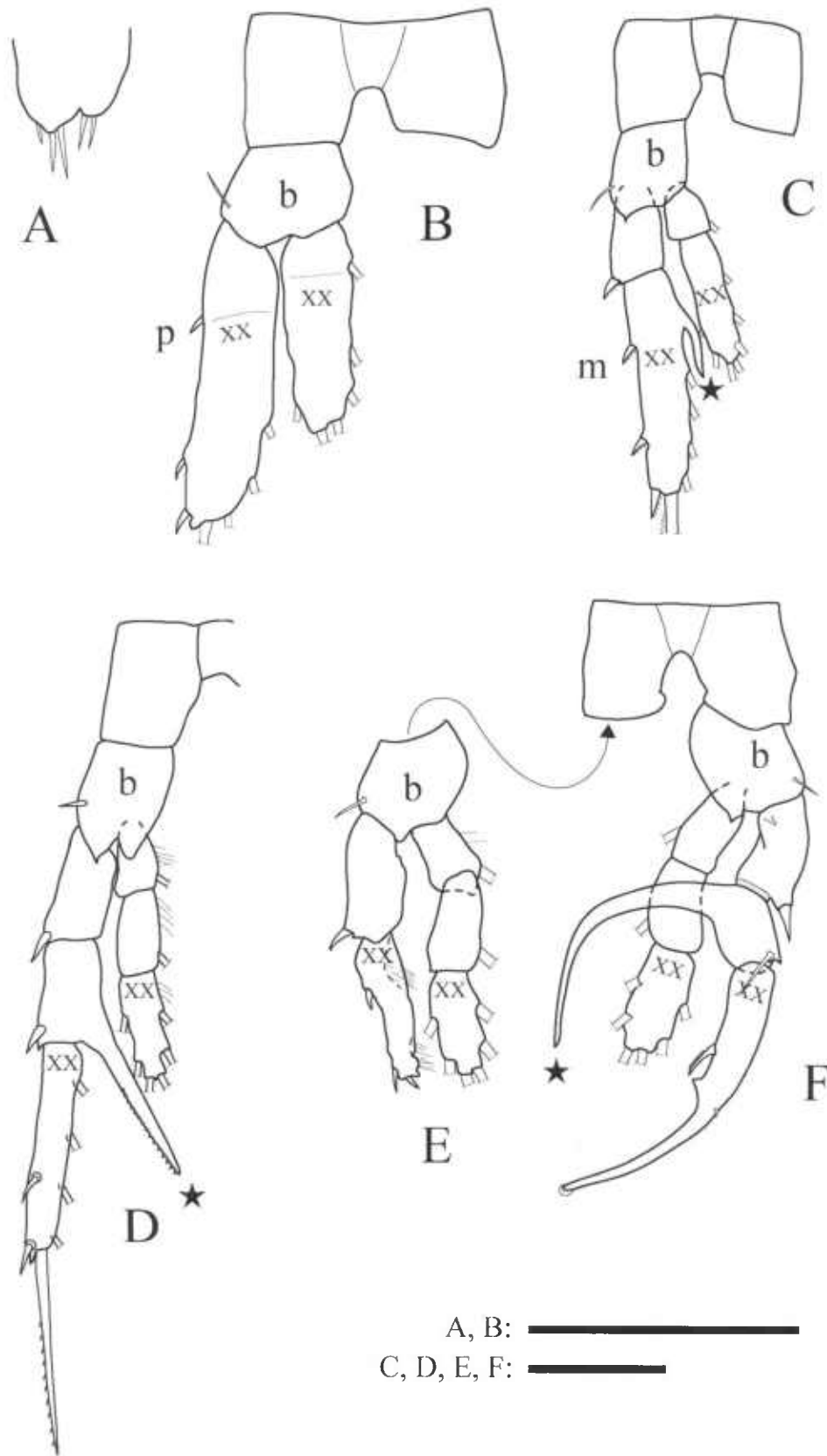


Fig. 1. *Centropages abdominalis*, leg 5. Gender undetermined: A, copepodid III, left basis and rami; B, copepodid IV. C, copepodid V; D, adult female. E, adult male, left coxa, intercoxal plate, right leg. XX is location of patterning area within rami; thin, incomplete line within B indicates position of distal arthrodial membrane of proximal exopodal segment in the following copepodid stage; stippling on F indicates broad arthrodial membrane. b = basis; p = dorsal seta to be allocated to the proximal exopodal segment; m = dorsal seta to be allocated to the middle exopodal segment; star next to ventral attenuation of middle exopodal segment. Scale bars represent 0.1 mm.

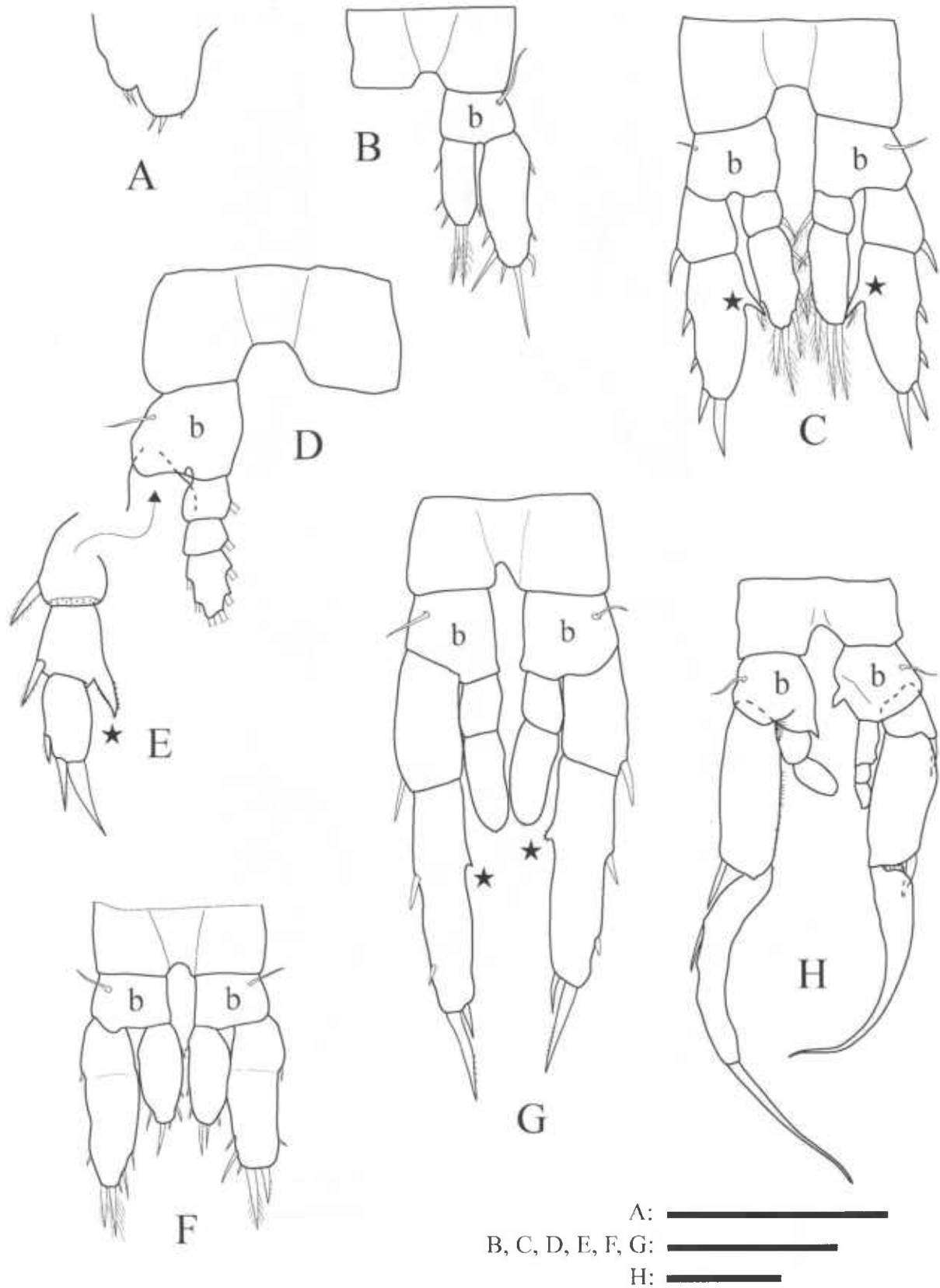


Fig. 2. *Boeckella poopoensis*, leg 5. Gender undetermined: A, copepodid III right limb. Female: B, copepodid IV; C, copepodid V; D, adult, protopod and endopod; E, adult, exopod. Male: F, copepodid IV; G, copepodid V; H, adult. Thin, incomplete line within F indicates position of distal arthrodistal membrane of the proximal exopodal segment in the following copepodid stage; stippling on E and H indicates broad arthrodistal membrane. b = basis; star next to ventral attenuation of middle exopodal segment. Scale bars represent 0.1 mm.

a straight, distal, ventral attenuation with denticles on proximal and distal faces; distal segment with 2 dorsal, 1 terminal (3) setae. Proximal endopodal segment with 1 ventral seta; middle segment with 1 ventral seta; distal with 0–2 dorsal, 2 terminal, and 2 ventral (4–6) setae.

CVI male (Fig. 2H): basis with distal, ventral (left) or mid-ventral (right) attenuation; right basis with proximal/distal ridge posteriorly. Proximal segment of left exopod with one dorsal seta; distal segment with 1 dorsal, proximal, and 1 elongate, terminal (2) setae. Proximal and distal endopodal segments without setae. Right proximal exopodal segment with 1 dorsal, distal seta; middle segment with 1 dorsal, distal seta; distal segment elongate, attenuate and without setae. Proximal, middle and distal endopodal segments without setae.

Sinocalanus tenellus (Kikuchi, 1928).—Left and right leg 5 present at CIII as bilobe bud (Fig. 3A) with 3 setae on the presumptive exopod and 2 on the presumptive endopod.

CIV female (Fig. 3B): a transformed limb; coxa without setae, basis with 1 dorsal, distal seta. Exopod with 1 dorsal, 1 terminal, 3 ventral (5) setae. Endopod with 1 dorsal, 2 terminal, 2 ventral (5) setae.

CIV male (Fig. 3G): exopod with 1 (left) or 3 (right) dorsal setae.

CV female (Fig. 3C, D): proximal exopodal segment without setae; distal segment with 1 dorsal, 1 terminal, 4 ventral (6) setae and a ventral attenuation, slightly bent toward the ramus, proximal to the proximal seta. Proximal endopodal segment without setae; distal segment with 2 dorsal, 2 terminal, 3 ventral (7) setae.

CV male (Fig. 3H): proximal exopodal segment without setae (left) or with 1 dorsal seta (right). Distal exopodal segment with 1 (left) or 3 (right) dorsal setae, 1 terminal seta, and 4 (left) or 3 (right) ventral setae; ventral seta small on left exopod.

CVI female (Fig. 3E, F): proximal exopodal segment without setae; middle segment with 1 slightly curved, ventral attenuation with denticles on proximal face; distal segment with 1 dorsal, 1 terminal, 4 ventral (6) setae. Proximal endopodal segment without setae, with ventral denticles; middle segment with 1 ventral seta and denticles; distal with 2 dorsal, 2 terminal, and 2 ventral (6) setae and dorsal denticles.

CVI male (Fig. 3I, J): basis with distal, ventral (left) or proximal, ventral (right) attenuation; proximal segment of left exopod without setae, with a small, distal attenuation. Distal segment with 1 dorsal and 1 terminal (2) setae; ventral surface with 2 projections, each with denticles. Proximal endopodal segment without setae, with distal, ventral thumb-like attenuation; middle segment with 1 ventral seta and two areas of denticles; distal with 2 dorsal, 2 terminal, and 2 ventral (6) setae. Right proximal exopodal segment with 1 dorsal seta; distal segment attenuate distally and curved ventrally with 1 ventral seta, ventral projections proximally and ventral denticles distally. Proximal endopodal segment without setae, middle segment with 1 ventral seta, distal with 2 dorsal, 2 terminal, and 2 ventral (6) setae.

Eodiaptomus japonicus (Burekhardt, 1913).—Left and right leg 5 present at CIII as bilobe bud (Fig. 4A) with 1 seta on the presumptive exopod and presumptive endopod without setae.

CIV female (Fig. 4B): a transformed limb; coxa without setae, basis with 1 dorsal, distal seta. Exopod with 1 dorsal, 1 terminal (2) setae. Endopod without setae.

CIV male (Fig. 4E): exopod with 1 terminal seta, right longer than left.

CV female (Fig. 4C): coxa fused to intercoxal plate; proximal exopodal segment without setae; distal segment with 1 dorsal, 1 terminal (2) setae, with a projection between the setae and a large distal, ventral attenuation. Endopod without setae, with terminal denticles.

CV male (Fig. 4F): left exopod with 1 dorsal, 1 terminal setae; endopod with 1 ventral seta and terminal denticles. Right exopod and setae larger than left; endopod larger, with terminal denticles.

CVI female (Fig. 4D): coxa with dorsal and ventral distal attenuation; intercoxal plate distinct; basis triangular with distal, posterior projection near endopod. Proximal exopodal segment without setae; middle segment with 1 dorsal seta and distal, ventral attenuation with 2 areas of denticles; distal segment small with 1 terminal seta. Endopod 2-segmented, without setae; distal segment with ventral denticles.

CVI male (Fig. 4G, H): left coxa with wide rounded distal attenuation, terminally acute; right coxa with mid-ventral and distal attenuations, distal attenuation terminally acute; right basis with broad ventral lobe and posterior projection. Proximal segment of left exopod without setae, with ventral denticles; middle segment with 1 seta near distal segment and 1 attenuation; distal segment small with 1 terminal seta. Proximal endopodal segment small without seta; distal segment weakly articulating with proximal segment, acute and curved distally with 1 seta plus denticles. Right proximal exopodal segment without setae; middle segment with 1 dorsal, distal seta curved toward tip; distal segment small with long curved weakly articulating terminal seta. Endopod with 2 small ventral and 1 distal attenuations, plus terminal denticles.

Eurytemora affinis (Poppe, 1885).—Left and right leg 5 present at CIII as unilobe bud (Fig. 5A) with 2 setae on the presumptive exopod.

CIV female (Fig. 5B): a transformed limb; coxa fused to intercoxal plate; basis with 1 dorsal seta. Exopod with 2 dorsal, 1 terminal (3) setae. Endopod absent.

CIV male (Fig. 5E): right basis with distal, ventral projection. Exopod with 3 dorsal, 1 terminal (4) setae. Endopod absent.

CV female (Fig. 5C): coxa articulates with intercoxal plate; exopodal segment with 1 pointed ventral attenuation and 3 dorsal, 1 terminal (4) setae plus 1 posterior and 1 proximal dorsal denticles.

CV male (Fig. 5F): left basis with 1 dorsal seta and 1 posterior denticle; right basis with 1 dorsal seta, 1 posterior denticle, plus distal, ventral projection. Proximal exopodal segment with 1 dorsal seta plus 1 posterior denticle; distal segment with 3 dorsal, 1 terminal (4) setae and proximal posterior denticle; right exopod narrower than left.

CVI female (Fig. 5D): coxa articulates with intercoxal plate; proximal exopodal segment with 2 dorsal setae and pointed distal, ventral attenuation; distal segment with 1 dorsal, 1 terminal (2) setae, and 3 ventral denticles.

CVI male (Fig. 5G, H): genital pore ventral (not illustrated); intercoxal plate small, triangular with base

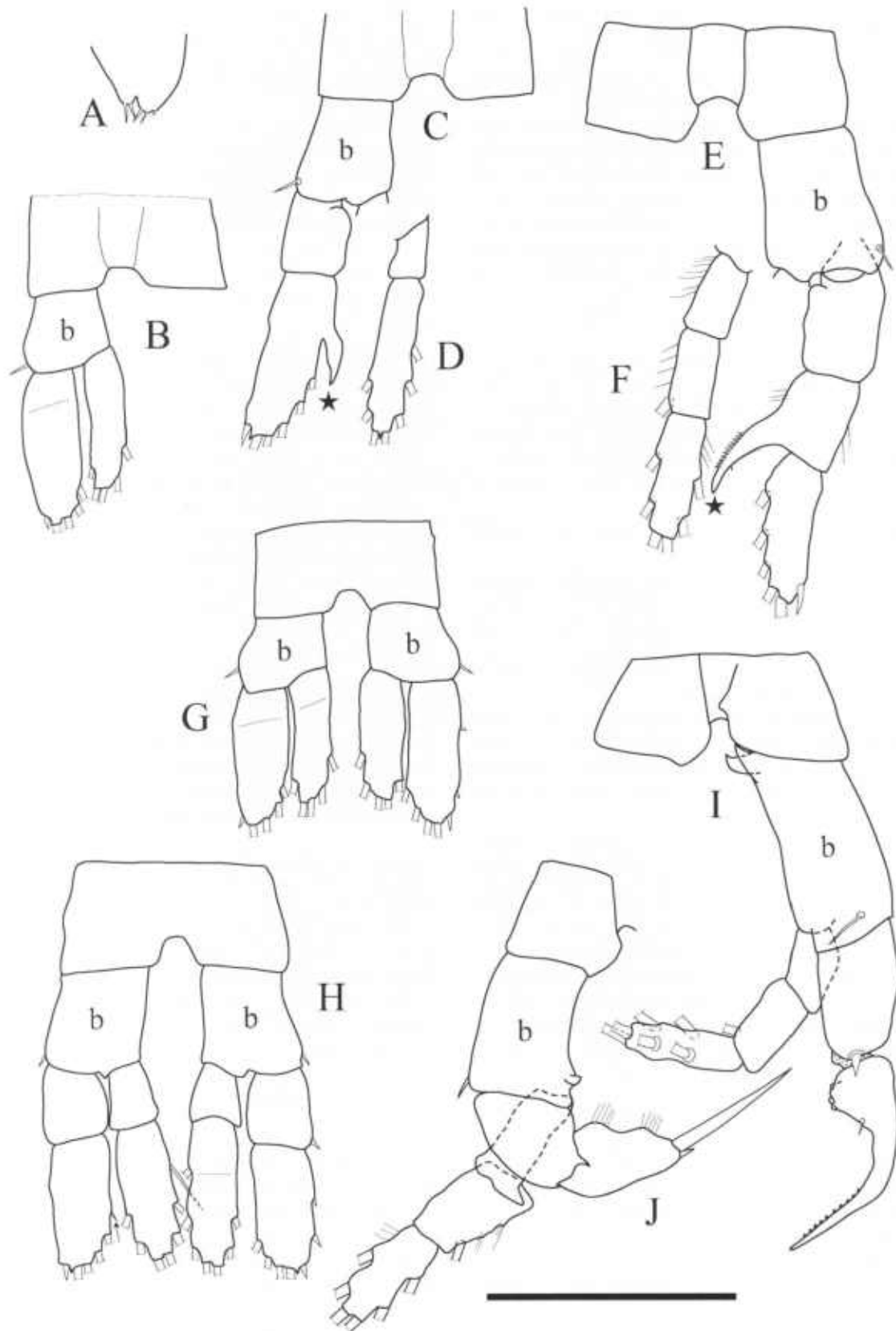


Fig. 3. *Sinocalanus affinis*, leg 5. Gender undetermined: A, copepodid III, right limb. Female: B, copepodid IV; C, copepodid V, protopod and exopod; D, copepodid V, endopod; E, adult, protopod and exopod; F, adult, endopod. Male: G, copepodid IV; H, copepodid V; I, adult, left coxa, intercoxal plate and right leg; J, adult, left basis and rami. Thin, incomplete line within B and G indicates position of distal arthrodial membrane of proximal exopodal and/or endopodal segment in following copepodid stage; within H, it indicates position of distal arthrodial membrane of middle segment of following stage; stippling on I indicates broad arthrodial membrane. b = basis; star next to ventral attenuation of middle exopodal segment; arrow to small seta on left exopod. Scale bar represents 0.1 mm.

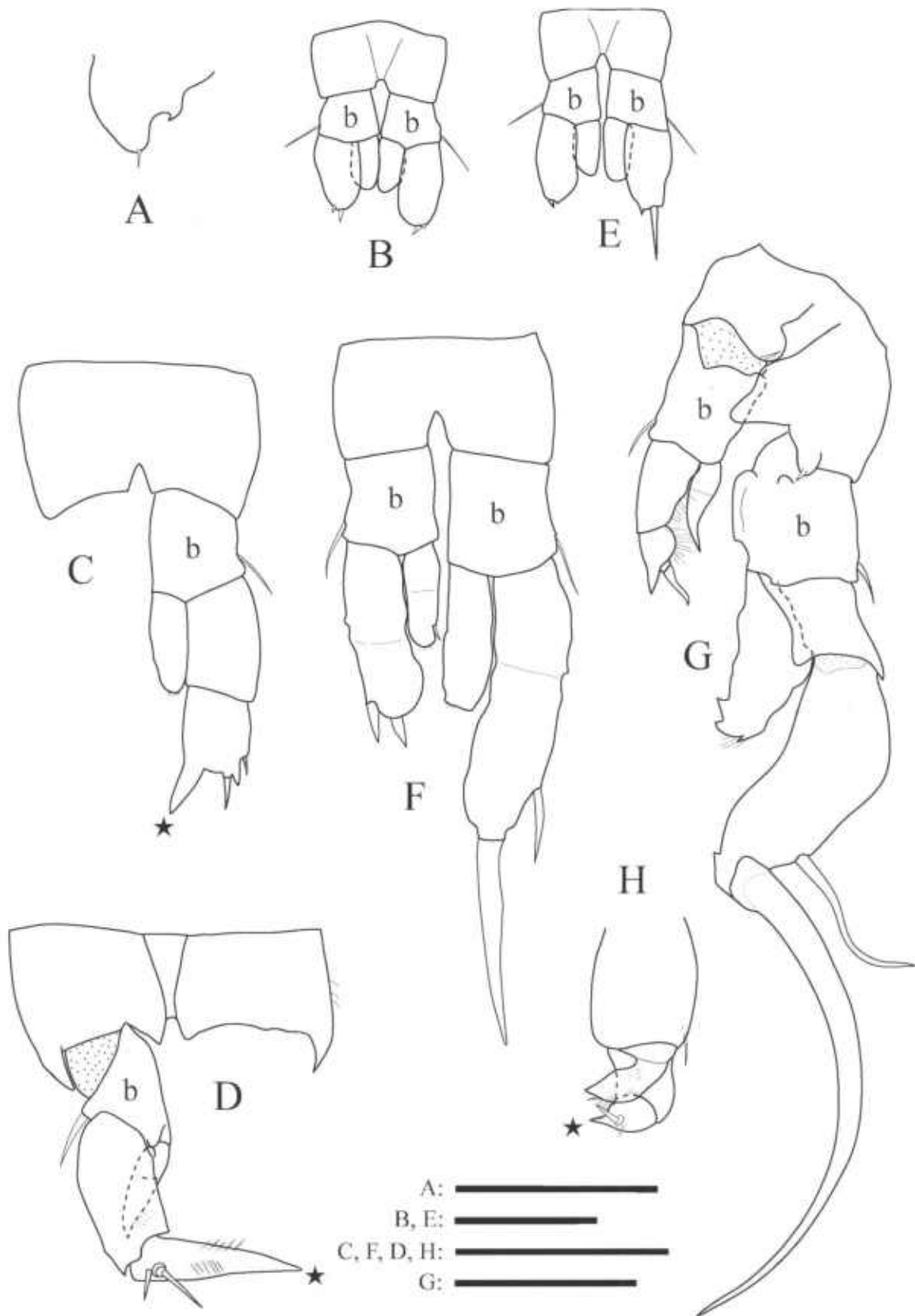


Fig. 4. *Eodiaptomus japonicus*, leg 5. Gender undetermined: A, copepod III, left limb. Female: B, copepod IV; C, copepod V; D, adult (large arthrodistal membrane stippled). Male: E, copepod IV; F, copepod V; G, adult (large arthrodistal membrane stippled; dotted line weakly contrasted arthrodistal membrane); H, adult, left leg, medial view. Thin, incomplete line within F indicates position of distal arthrodistal membrane of proximal exopodal and endopodal segment in the following copepodid stage; stippling on D and G indicates broad arthrodistal membrane. b = basis; star next to ventral attenuation of middle exopodal segment. Scale bars represent 0.05 mm for A and 0.1 mm for others.

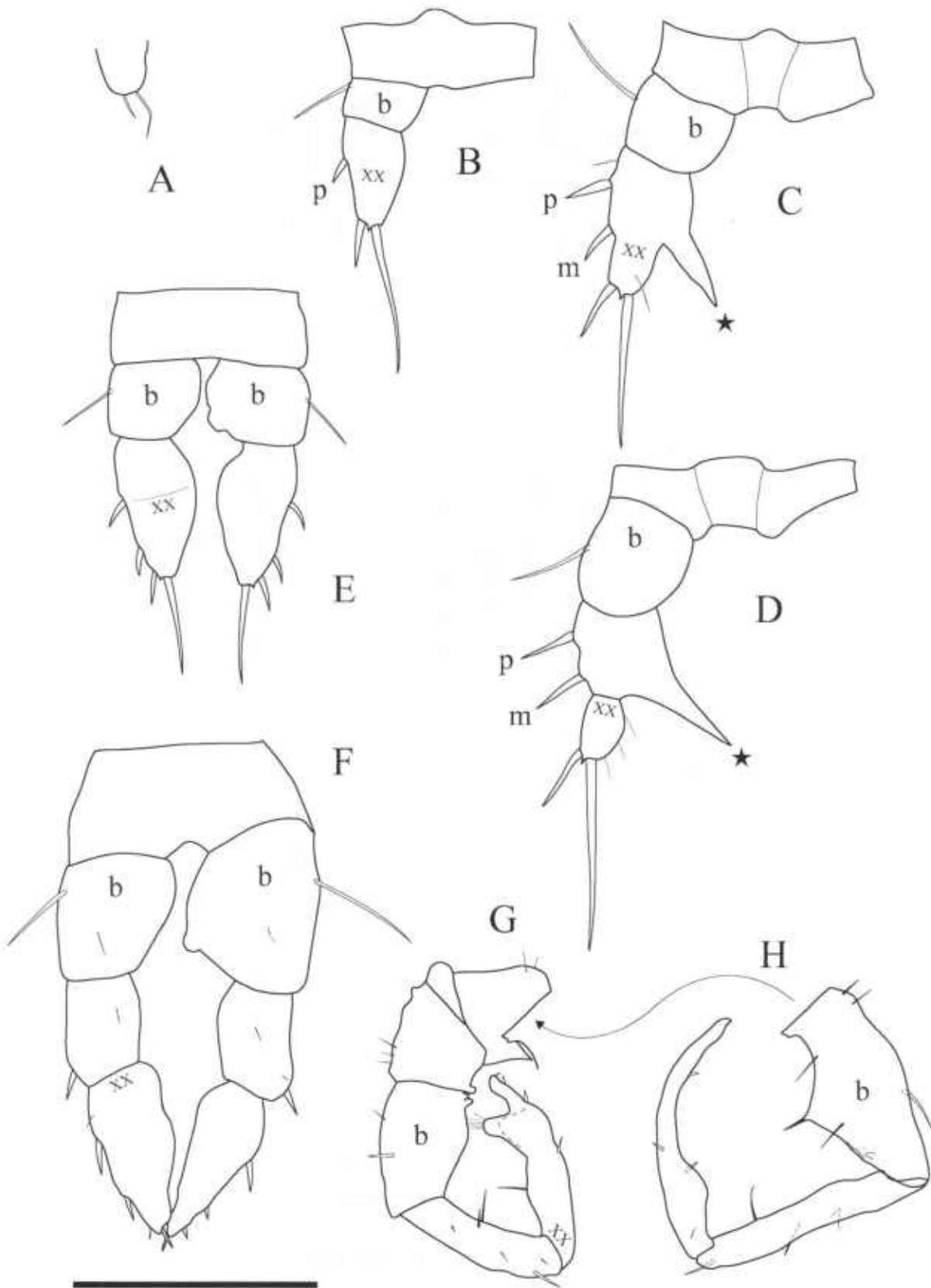


Fig. 5. *Eurytemora affinis*, leg 5. Gender undetermined: A, copepodid III. Female: B, copepodid IV; C, copepodid V; D, adult. Male: E, copepodid IV; F, copepodid V; G, adult, protopodite and left leg; H, adult, right leg. XX is location of patterning area within rami; thin, incomplete line within E indicates position of distal arthrodial membrane of proximal exopodal segment in the following copepodid stage. b = basis; p = dorsal seta to be allocated to the proximal exopodal segment; m = dorsal seta to be allocated to the middle exopodal segment; star next to ventral attenuation of presumptive middle exopodal segment. Scale bar represents 0.1 mm.

proximal. Left coxa with distal, ventral attenuation and 3 dorsal denticles; basis with 1 posterior seta and 1 proximal denticle. Proximal segment of left exopod with 1 dorsal, distal seta and 3 posterior plus 2 ventral denticles; distal segment with 3 dorsal, 1 terminal (4) setae plus 1 proximal, ventral denticle and area of denticles on a distal lobe of segment. Right coxa with distal ventral attenuation and 2 dorsal denticles; basis with ventral projection, 1 posterior seta and 3 ventral plus 2 proximal dorsal denticles. Proximal exopodal segment with 1 dorsal distal seta and 2 anterior plus 1 ventral denticles; distal segment with 1 dorsal, 2 posterior (3) setae and 1 proximal denticle.

Temora longicornis (Mueller, 1785).—Left and right leg 5 present at CIII as unilobe bud (Fig. 6A) with 2 setae on the presumptive exopod.

CIV female (Fig. 6B): a transformed limb; coxa articulating with intercoxal plate; basis with 1 posterior, dorsal seta. Exopod with 2 dorsal, 1 terminal (3) setae. Endopod absent.

CIV male (Fig. 6E): left basis with small distal attenuation; right basis quadrate ventrally. Left exopod with 3 dorsal, 1 terminal (4) setae, and pointed terminal attenuation. Right exopod smaller, with rounded terminal attenuation.

CV female (Fig. 6C): exopod with 1 dorsal seta, and 1 pointed mid-ventral plus 2 pointed terminal attenuations.

CV male (Fig. 6F): coxa with posterior denticles; left basis with broad distal attenuation; right basis with distal projection. Exopod with 3 dorsal, 1 terminal (4) setae and 1 terminal, digitiform attenuation; right exopod smaller than left with terminal attenuation more rounded.

CVI female (Fig. 6D): exopod with 1 dorsal seta, plus 1 ventral attenuation and 2 terminal attenuations.

CVI male (Fig. 6G): genital pore opens on right side (not illustrated); coxa with posterior denticles. Left basis with elongate, curved distal attenuation; right basis with 1 posterior seta plus 1 distal ventral and 1 distal projection. Proximal segment of left exopod with 1 dorsal seta; distal with 3 posterior, 1 terminal (4) setae plus 1 terminal attenuation. Distal segment of right exopod with thicker, terminal attenuation plus 2 ventral and 1 dorsal (3) setae.

Pontella chierchia Giesbrecht, 1889.—Left and right leg 5 present at CIII as bilobe bud (Fig. 7A) with 2 setae on the presumptive exopod and 1 seta on the presumptive endopod.

CIV female (Fig. 7B): a transformed limb; coxa without setae, fused to intercoxal plate; basis with 1 distal, posterior seta with small attenuation adjacent to seta. Exopod with 2 small dorsal, 1 small terminal (3) setae plus 1 small terminal attenuation. Endopod rounded distally without setae.

CIV male (Fig. 7E): left basis with distal, ventral projection. Left exopod with 2 small dorsal, 1 terminal, 1 ventral attenuations; right exopod slightly longer.

CV female (Fig. 7C): exopod with 3 dorsal, 2 terminal, plus 2 ventral attenuations. Endopod rounded proximally, acute distally, without setae.

CV male (Fig. 7F): left basis with ventral projection. Left exopod with 3 dorsal, 2 terminal attenuations; right exopod longer.

CVI female (Fig. 7D): exopod with 3 dorsal, 2 terminal, 2 distal ventral attenuations. Endopod bifurcate distally as 2 terminal attenuations.

CVI male (Fig. 7G): intercoxal plate small, triangular. Left coxa with small ventral depression; right coxa with broad, proximal ventral attenuation. Left basis smaller than right. Proximal segment of left exopod with 1 posterior seta plus 1 dorsal attenuation. Distal segment proximal/distal anterior ridge with 2 simple posterior and 1 modified terminal (3) setae, 2 dorsal distal attenuations plus 1 terminal attenuation with denticles; proximal and distal ventral area of denticles. Proximal segment of right exopod with 1 dorsal, 1 mid-ventral (2) setae plus 1 long, proximal ventral attenuation, 1 proximal recurved attenuation, 1 round, mid-ventral projection [with a seta], and 1 round distal projection. Distal segment curved with 1 proximal posterior, 1 proximal ventral, 1 distal anterior, 1 terminal (4) setae plus 1 proximal ventral attenuation [with a seta].

Labidocera pavo Giesbrecht, 1889.—Left and right leg 5 present at CIII as bilobe bud (Fig. 8A) with 1 terminal attenuation on the presumptive exopod; presumptive endopod round.

CIV female (Fig. 8B): a transformed limb; coxa without setae; basis with 1 proximal, posterior seta. Exopod with 2 small dorsal, 2 small terminal attenuations. Endopod rounded distally without setae.

CIV male (Fig. 8E): Basis with distal attenuation; exopod with 2 small dorsal, 2 small terminal attenuations.

CV female (Fig. 8C): coxa fused to intercoxal plate. Exopod with 3 dorsal, 1 terminal, 1 distal ventral attenuations. Endopod rounded distally, without setae.

CV male (Fig. 8F): left basis with distal attenuation; right basis with distal projection. Left exopod with 3 dorsal, 2 terminal attenuations. Right exopod longer than left with 1 terminal attenuation. Endopod absent.

CVI female (Fig. 8D): exopod with 3 dorsal, 1 terminal, 1 distal ventral attenuations. Endopod acute distally, without setae.

CVI male (Fig. 8G): intercoxal plate small, quadrate; left coxa with small ventral attenuation; right coxa with broad, proximal ventral projection; left basis smaller than right. Proximal segment of left exopod with 1 dorsal attenuation; distal segment with 2 dorsal plus 2 terminal attenuations and ventral denticles. Proximal segment of right exopod with 1 mid-ventral, 1 distal ventral (2) setae, plus 1 small proximal ventral projection, 1 long, proximal, posterior attenuation, 1 short proximal anterior projection, plus 1 short, mid-ventral attenuation. Distal segment with 1 mid-ventral, 1 posterior, 1 anterior, 1 terminal (4) setae plus 1 terminal attenuation and a proximal/distal ridge in proximal section.

Acartia erythraea Giesbrecht, 1889.—Leg 5 not discernable at CIII.

CIV female (Fig. 9A): a transformed limb; coxa without setae, fused to intercoxal plate; basis fused to coxa, with 1 distal dorsal seta. Exopod rounded without setae.

CIV male (Fig. 9D): basis, coxa, intercoxal plate fused. Left exopod with 1 dorsal, 1 terminal, 1 ventral (3) setae. Right exopod with 1 dorsal, 1 terminal (2) setae.

CV female (Fig. 9B): basis articulates with coxa. Rounded section of exopod proximal; attenuated section distally, without setae.

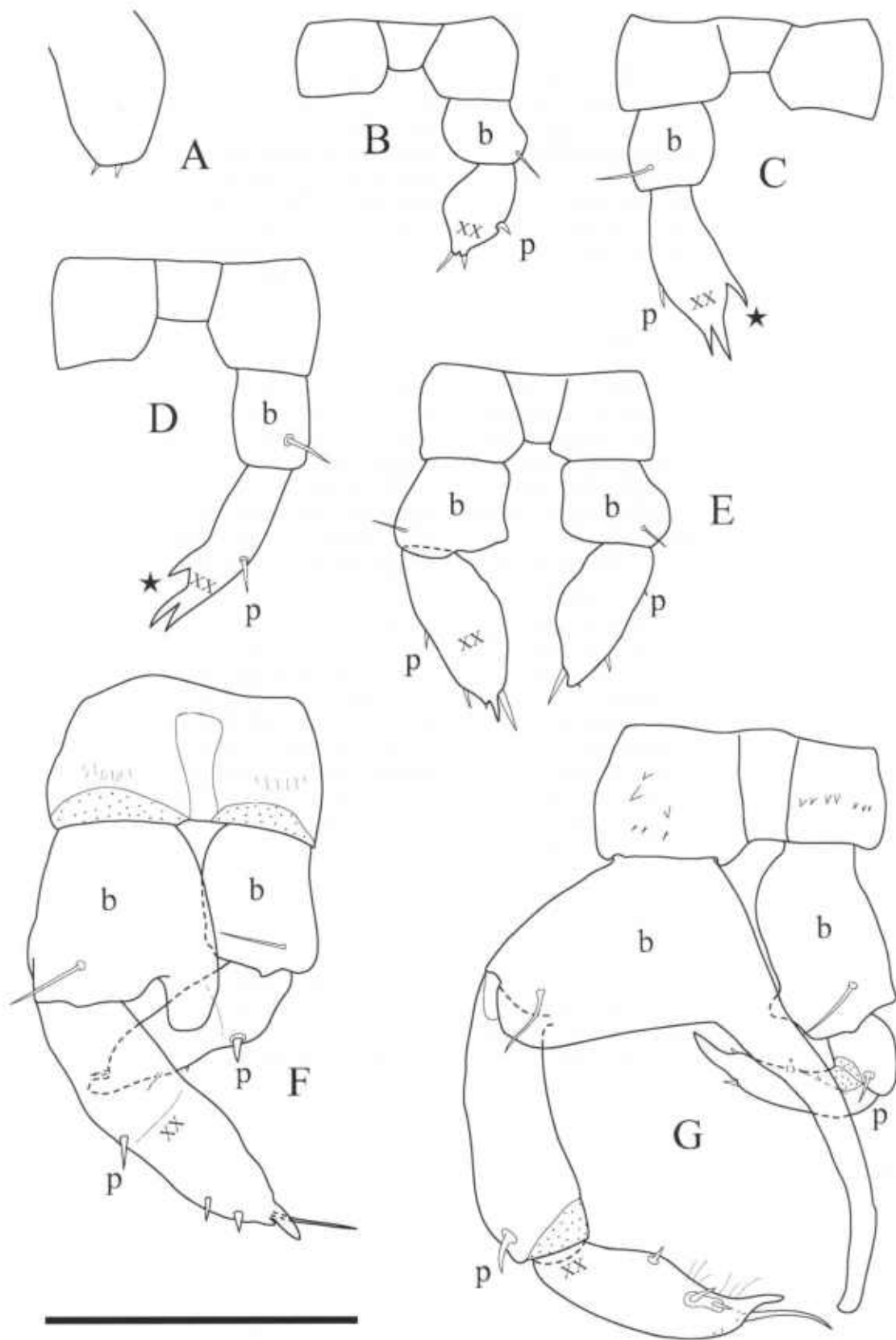


Fig. 6. *Temora longicornis*, leg 5. Gender undetermined: A, copepodid III. Female; B, copepodid IV; C, copepodid V; D, adult. Male; E, copepodid IV; F, copepodid V; G, adult. XX is location of patterning area within rami; thin, incomplete line within F indicates position of distal arthrodial membrane of the proximal exopodal segment in following copepodid stage; stippling on F and G indicates broad arthrodial membrane. b = basis; star next to ventral attenuation of presumptive middle exopodal segment; p = dorsal seta of presumptive proximal exopodal segment. Scale bar represents 0.1 mm.

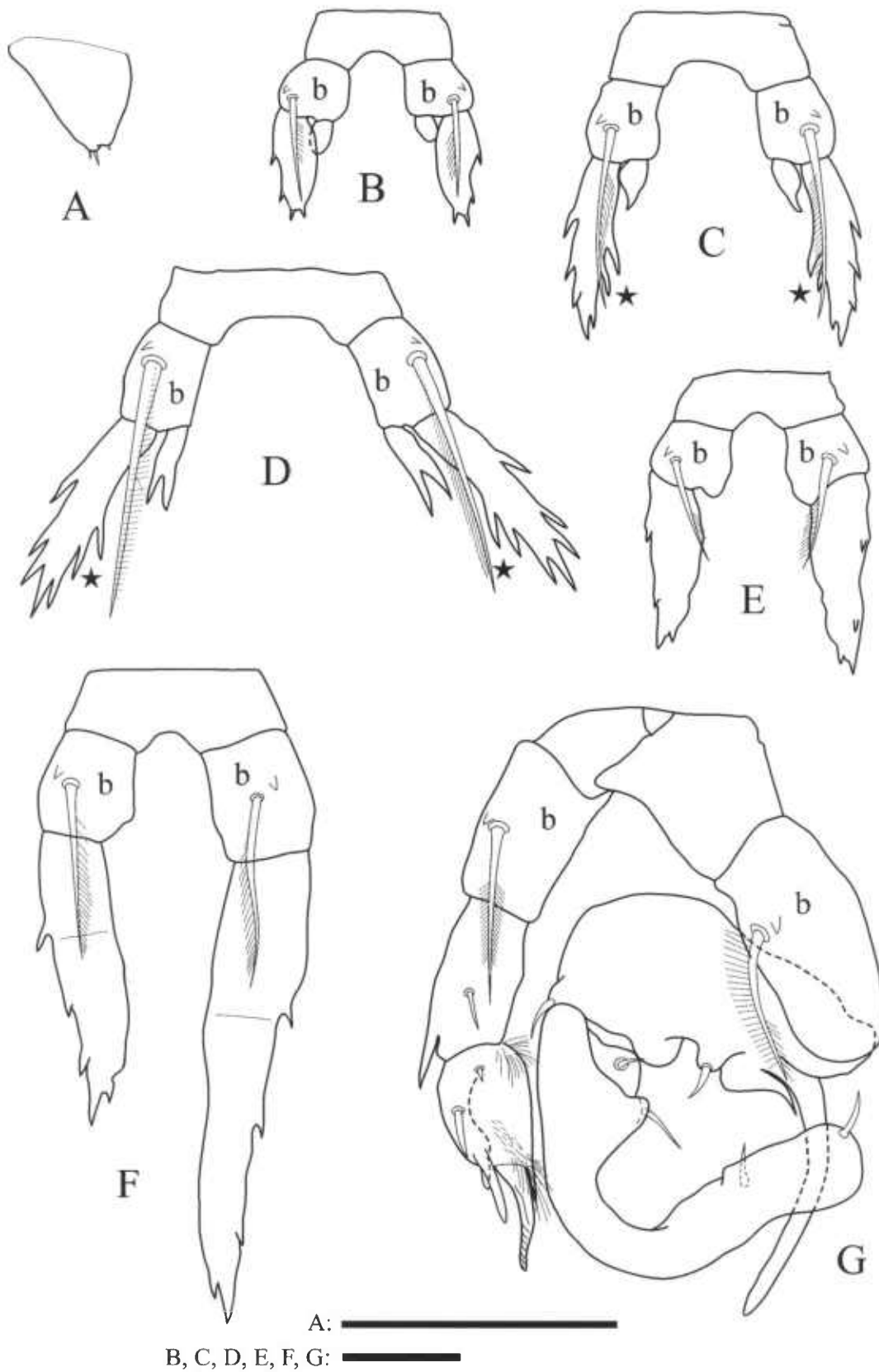


Fig. 7. *Pontella chierchiai*, leg 5. Gender undetermined: A, copepodid III. Female: B, copepodid IV; C, copepodid V; D, adult. Male: E, copepodid IV; F, copepodid V; G, adult. Thin, incomplete line within F indicates position of distal arthroal membrane of the proximal exopodal segment in following copepodid stage. b = basis; star next to ventral attenuation of presumptive middle exopodal segment. Scale bars represent 0.1 mm.

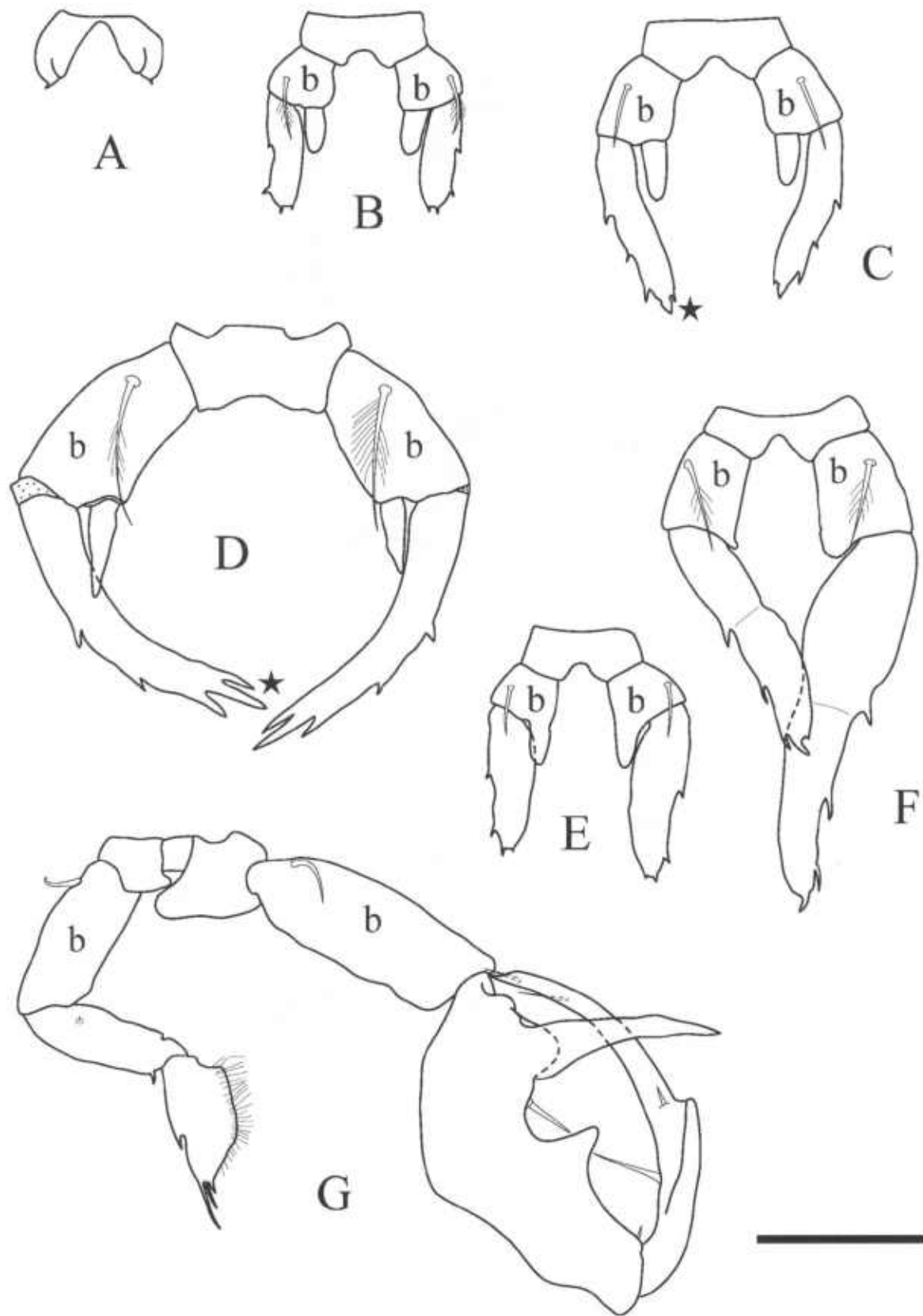


Fig. 8. *Labidocera pavo*, leg 5. Gender undetermined: A, copepodid III. Female; B, copepodid IV; C, copepodid V; D, adult. Male: E, copepodid IV; F, copepodid V; G, adult. Thin, incomplete line within F indicates position of distal arthrodistal membrane of the proximal exopodal segment in following copepodid stage; stippling on D indicates broad arthrodistal membrane. b = basis; star next to ventral attenuation of presumptive middle exopodal segment. Scale bar represents 0.1 mm.

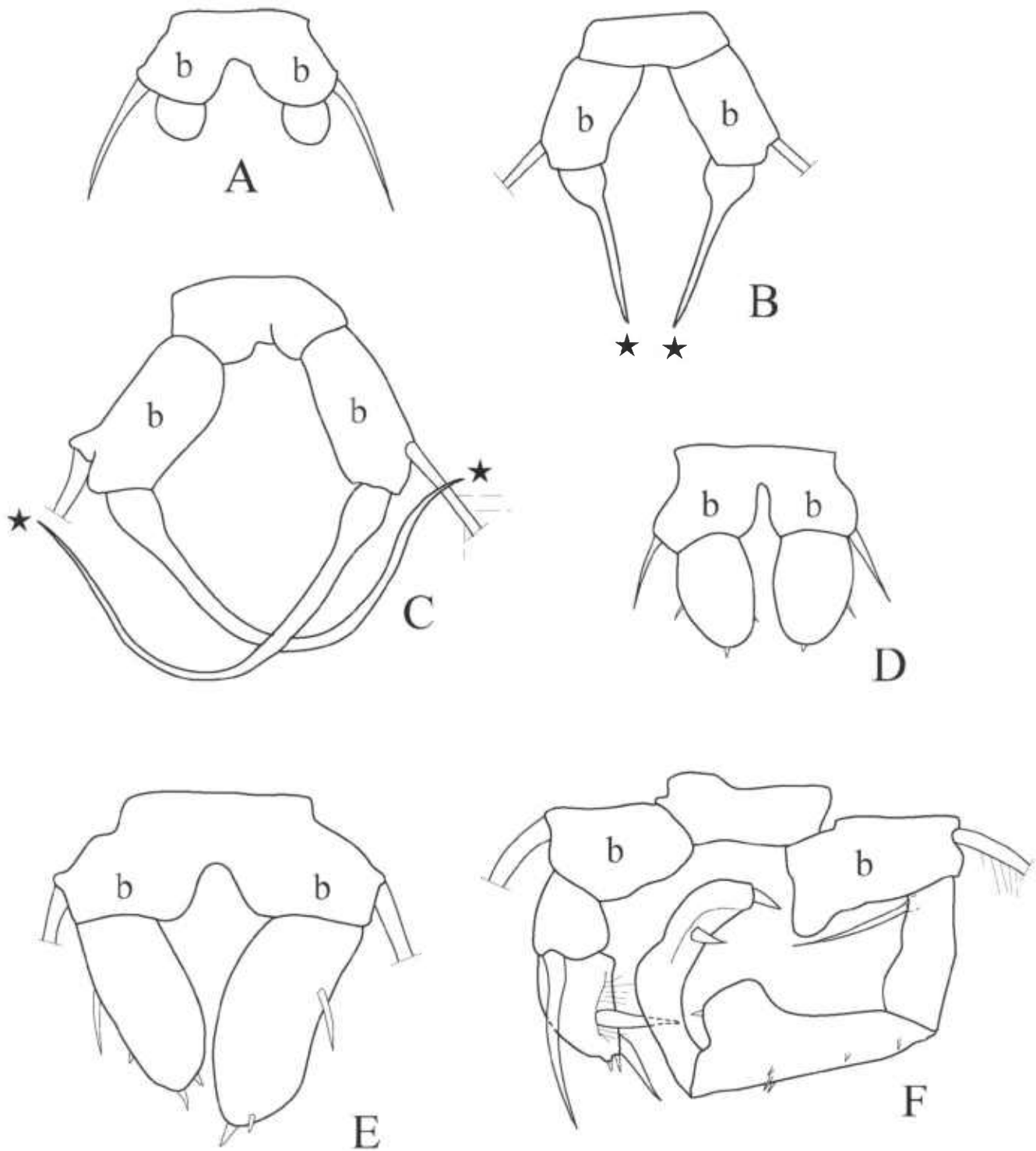


Fig. 9. *Acartia erythraea*, leg 5. Female: A, copepodid IV; B, copepodid V; C, adult. Male: D, copepodid IV; E, copepodid V; F, adult. b = basis; star next to ventral attenuation of presumptive middle exopodal segment. Scale bar represents 0.1 mm.

CV male (Fig. 9E): exopod with 2 dorsal, 1 terminal, 0–1 ventral (3–4) setae. Right exopod longer than left.

CVI female (Fig. 9C): attenuated section of exopod longer, poorly distinguished from rounded section.

CVI male (Fig. 9F): coxa and intercoxal plate fused; right basis with rounded distal attenuation. Proximal segment of left exopod with 1 posterior distal seta; distal segment with 3 terminal, 1 ventral (4) setae and ventral denticles; 1

terminal seta on a projection. Proximal segment of right exopod with 1 ventral seta on a projection; middle segment with 1 ventral seta on a broad rounded projection, denticles dorsally; distal segment slightly curved with 1 posterior, 1 terminal (2) setae.

Tortanus dextrilobatus Chen and Zhang, 1965.—Left and right leg 5 present at CIII as unilobe bud (Fig. 10A) with an attenuation on the presumptive exopod.

CIV female (Fig. 10B): a transformed limb; coxa without setae, fused to intercoxal plate; basis with 1 distal dorsal seta. Exopod elongate, distinctly narrow distally with somewhat irregular ventral edge, without setae.

CIV male (Fig. 10E): coxa fused to intercoxal plate; right basis with distal ventral projection. Exopod with 2 dorsal, 2 terminal (4) setae.

CV female (Fig. 10C): distal section of exopod not as abruptly narrow; left exopod with scattered ventral denticles.

CV male (Fig. 10F): distal ventral attenuation of right basis with denticles. Proximal segment of left exopod with 1 dorsal seta; distal segment with 2 dorsal, 1 terminal, 1 ventral (4) setae and distal ventral denticles. Right exopod longer than left; proximal segment of right exopod with 1 dorsal seta; distal segment with 2 dorsal, 1 terminal (3) setae.

CVI female (Fig. 10D): exopod with ventral denticles, more on left exopod than on right.

CVI male (Fig. 10G): left and right coxa fused to intercoxal plate; right coxa with rounded posterior projection near articulation with basis. Right basis with a distal ventral series of broad low epicuticular extensions plus proximal ventral and mid-ventral attenuations; proximal attenuation with series of broad low epicuticular extensions. Proximal segment of left exopod with 1 dorsal seta; distal segment with a series of broad low epicuticular extensions dorsally and 1 anterior, 1 dorsal, 1 terminal, 2 ventral (5) setae, plus 3 mid-ventral areas of denticles. Right exopod with 6 ventral setae and series of broad low epicuticular extensions along ventral face.

Analysis and Interpretation

Leg 5 of calanoids usually develops over a series of steps, from CIII to CVI, and that development is similar to development of swimming legs 1–4 of many copepods (Ferrari and Ambler, 1992; Ferrari and Benforado, 1998; Ferrari, 2000). As an example, leg 5 of *Centropages abdominalis* begins as a small, bilobe, limb bud; both lobes are armed terminally with setae (Fig. 1A). The step immediately following the limb bud is a transformed limb at CIV (Fig. 1B). The protopod of the transformed limb is well-differentiated from the rami and the basis bears 1 seta distally and dorsally; addition of arthrodistal membranes and setae to the protopod is complete. In the following two stages, each ramus is patterned from an area toward the proximal edge of the distal ramal segment (e.g., Figs. 1B–F, 5B–G, 6B–G) in the following way. The arthrodistal membrane which separates the proximal segment of the ramus is added during the molt to CV (Fig. 1C); the arthrodistal membrane which separates the middle segment is added during the molt to CVI (Fig. 1D). Formation of a dorsal seta and/or a ventral seta, eventually located on the

proximal and middle segments, precedes the formation of the associated arthrodistal membrane by one stage so that a dorsal seta and/or a ventral seta of the presumptive proximal segment initially forms on the distal segment (Fig. 1B) during the molt to CIV. The same situation is true for the dorsal seta and the ventral seta of the middle segment; initially each forms during the molt to CV but on the distal segment (Fig. 1C). In general, then, a new dorsal or ventral seta usually is located on the distal segment, proximal to older setae on that segment (Fig. 1B, C). The delay between formation of a segmental seta and its arthrodistal membrane is called setal precedence.

Leg 5 development exhibits two examples of setal precedence for both exopod and endopod. At CIV, the exopod of the transformed limb of leg 5 appears to be a 1-segmented complex. The proximal dorsal seta belongs to the presumptive proximal segment (Fig. 1B) and will be allocated to that segment when the arthrodistal membrane separating the proximal segment from the distal segment is formed at CV (Fig. 1C). At CV the proximal dorsal seta of the distal segment is new (Fig. 1C); it belongs to the presumptive middle segment and will be allocated to that segment when the arthrodistal membrane separating the middle segment is formed at CVI (Fig. 1D). The same mechanism explains patterning of two new setae to the endopod. At CIV, the proximal ventral seta belongs to the presumptive proximal segment (Fig. 1B) and will be allocated to that segment when the arthrodistal membrane separating the proximal segment from the distal segment is formed at CV (Fig. 1C). At CV the proximal dorsal seta and the proximal ventral seta are new (Fig. 1C). The proximal ventral seta belongs to the presumptive middle segment and will be allocated to that segment when the arthrodistal membrane is added at CVI (Fig. 1D). The proximal dorsal seta is allocated to a new segment of the distal complex; the arthrodistal membrane which would have separated that segment from the distal segment complex never develops. In the following analysis of leg 5, identification of the ramal segments utilizes arthrodistal membrane formation, when present, of the rami. However, the stage of formation, location of dorsal setae, and location of ventral segmental attenuations are used to clarify homologous segments of an exopod for which arthrodistal membranes secondarily fail to form.

Centropages abdominalis.—A ventral attenuation on the female exopod is present proximally on the distal segment complex at CV (Fig. 1C); the homologous ventral attenuation is present distally on the middle segment at CVI (Fig. 1D). The distal arthrodistal membrane separating the proximal exopodal and endopodal segment is present initially at CV, although the eventual location of this arthrodistal membrane can be observed through the cuticle of CIV (Fig. 1B). The arthrodistal membrane separating the middle exopodal and endopodal segment is present initially at CVI.

Patterning of the male endopod, as well as the proximal segment of its left exopod, and the proximal and middle segment of its right exopod follows that of the female. Development of the right exopod results in a chela whose fixed part is the attenuation of the middle exopodal segment (Fig. 1F) which is homologous to the ventral attenuation of

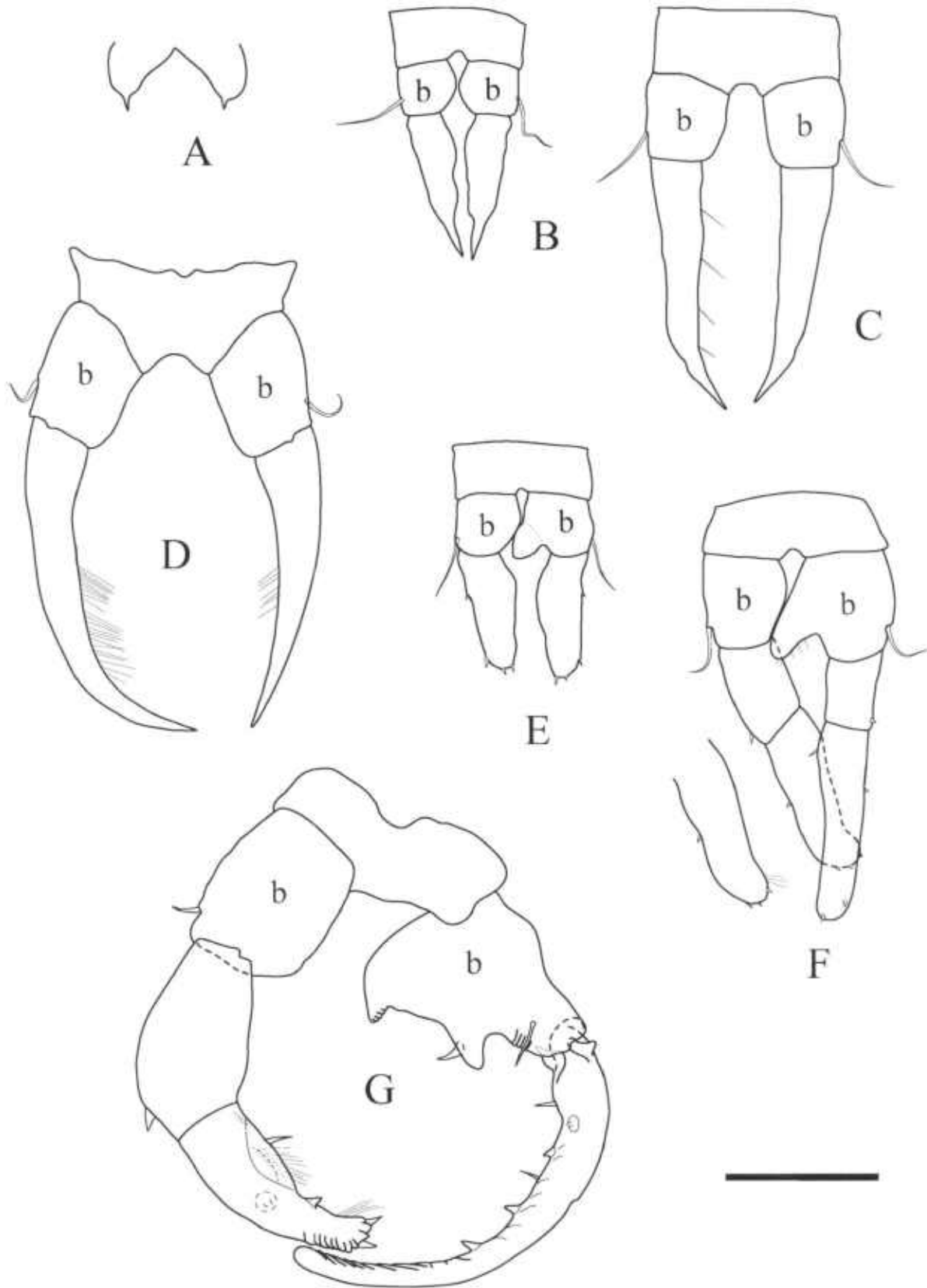


Fig. 10. *Tortanus dextrilobatus*, leg 5. Gender undetermined: A, copepodid III. Female: B, copepodid IV; C, copepodid V; D, adult. Male: E, copepodid IV; F, copepodid V; G, adult. Thin dotted line in E is a weakly contrasted arthrodial membrane. b = basis. Scale bar represents 0.1 mm.

the female. An arthrodistal membrane fails to form and separate the left middle exopodal segment from the left distal segment (Fig. 1E) so that the exopod appears to be 2-segmented. However, the proximal dorsal seta of the distal segment, added at CV, belongs to the presumptive middle segment of that exopod.

Boeckella poopoensis.—Development of the female is similar to the female of *Centropages abdominalis* except that at CIV the proximal ventral seta on the exopod, which would be allocated to the proximal segment, fails to form. The male has ventral attenuations on left and right basis which initially appear at CVI. A small ventral attenuation on the left and right exopod at CV (Fig. 2G) corresponds to that on the female exopod of *Centropages abdominalis*; it fails to form at CVI. An arthrodistal membrane fails to form and separate a left middle exopodal segment from the distal segment. The terminal element is a seta because there are no muscles that attach to its proximal rim within the adjacent segment. The right exopod is a subchela; its terminal element is a segment because there are muscles that attach to its proximal rim within the adjacent segment.

Sinocalanus tenellus.—Development of the female is similar to the female of *Centropages abdominalis* except that the dorsal seta of the proximal and middle exopodal segments and the ventral seta of the proximal and middle endopodal segments do not form (Fig. 3B–J). The male has ventral attenuations on left basis and right coxa and basis at CVI, but lacks the ventral attenuation of exopod at CV or CVI; no chela forms (Fig. 3J). Arthrodistal membranes fail to form and separate a middle segment from the distal segment on both left and right exopod. The right exopod is a subchela.

Eodiaptomus japonicus.—The third exopodal segment of the adult female is very small and bears only a terminal seta so that the terminal part of the ramus is dominated by the middle segment and its attenuation. The male right and left coxa, and left basis have ventral attenuations formed at CVI. An arthrodistal membrane fails to form and separate a left middle endopodal segment from the distal segment and right proximal and middle endopodal segments from the distal segment. The left basis and rami are similar to the female. The terminal element of the right exopod is a small distal segment poorly articulated with a long terminal seta. Muscle masses in middle segment with tendons to proximal rim of the distal complex identify the base of this structure as an exopodal segment. The right exopod is a subchela.

Eurytemora affinis.—An arthrodistal membrane fails to form and separate a proximal and a middle exopodal segment of the female at CV (Fig. 5C). An arthrodistal membrane does form at CVI and separates the middle from distal exopodal segment so that the ventral attenuation of the middle segment is present on the proximal segmental complex (Fig. 5D). This ramal architecture is unusual for copepods, but can be observed in the swimming legs 2–4 of centropagoidcans belonging to Acartiidae, Candaciidae, Parapontellidae, Pontellidae, Temoridae, and Tortanidae (Giesbrecht, 1892: 334, pl. 17 fig. 13; Ferrari and Benforado, 1998: figs. 4–6).

Setae on the adult male leg 5 are small and often difficult to distinguish from denticles. We assume here that no new

setae have been added between CV and CVI males and that setae of CV have not changed relative positions. Attenuations of the left and right coxa of the male initially are present at CVI. A distal ventral attenuation of right basis initially is present at CIV, with a denticle added at CVI. An arthrodistal membrane fails to separate a middle segment from the distal segment of the left and right exopod. Both left and right exopods are a subchela.

Temora longicornis.—The dorsal seta of the female exopod belongs to a presumptive proximal segment of exopod because it initially is present at CIV (Fig. 6B). One ventral and 2 terminal attenuations are added to the female at CV (Fig. 6C), although the two terminal attenuations may be interpreted as a bifurcate single attenuation. The ventral attenuation is distal to the dorsal seta and is assumed to be homologous to the ventral attenuation of the middle segment of *Centropages abdominalis*. Arthrodistal membranes fail to separate proximal or middle exopodal segment from the distal segment at CV or CVI respectively.

A distal ventral attenuation on the left basis of the male initially is present at CIV (Fig. 6E), becoming more distinct and distal in position at CV (Fig. 6F) and elongate at CVI (Fig. 6G). It comprises the fixed part of the chela. An arthrodistal membrane separating the proximal segment from distal segment of the left and right exopod is delayed until CVI. The single dorsal seta on the proximal exopodal segment at CIV (Fig. 6E) remains at CVI, indicating that the proximal segment of the adult male is not a complex of the proximal and middle segments.

Pontella chierchia.—Dorsal setae are present at CIV of the female (Fig. 7B) but are replaced by dorsal attenuations at CV when two ventral attenuations are added to the 1-segmented exopod (Fig. 7C). The dorsal attenuations are not assumed to be positional homologous of the setae (see interpretation of the male, below). Both ventral attenuations are distal to the proximal dorsal attenuation and toward the terminal part of the ramus. The distal, ventral attenuation is assumed to be homologous to the ventral attenuation of the middle segment of *Centropages abdominalis*, although the two ventral attenuations may be interpreted as a bifurcate single attenuation. Arthrodistal membranes fail to separate a proximal or a middle exopodal segment from the distal segment at CV or CVI respectively (Fig. 7D).

A small distal attenuation on the left basis is present on the male at CIV (Fig. 7E) and CV (Fig. 7F), but is absent at CVI (Fig. 7G). A coxal attenuation initially is present at CVI. An arthrodistal membrane separating the proximal segment from the distal segment of left and right exopod is delayed until CVI when it is expressed along with the arthrodistal membrane separating the middle and distal segments. The exopod then appears to be segmented only in adult males. The exopodal segment of both rami has four attenuations at CV. At CVI, three dorsal attenuations can be located: one on the proximal segment and two on the distal segment. The fourth attenuation is terminal on the distal segment and bears numerous denticles. Four setae have been added at CVI; one posterior on the segment, and two posterior and one terminal on the distal segment. The presence of setae and attenuations suggests that the dorsal attenuations are not replacements

for or positional homologues of dorsal setae. On the right leg, the long attenuation of the proximal exopodal segment forms the fixed part of a chela.

Labidocera pavo.—A distal ventral attenuation is added to the 1-segmented exopod at CV (Fig. 8C) and is assumed to be homologous to the ventral attenuation of the middle segment of other centropagoideans. The architecture of this ramus is assumed to be similar to *Eodiaptomus japonicus*, with the distal section of the ramus dominated by the middle segment. Arthrodiol membranes fail to separate a proximal or a middle exopodal segment from the distal segment at CV or CVI respectively (Fig. 8D).

Ventral distal attenuations on the left and right basis of the male, which are present at CIV (Fig. 8E), are retained at CV but are absent at CVI (Fig. 8F, G). A coxal attenuation is present at CVI. Arthrodiol membranes separating the proximal segment of left and right exopod from the distal segment are delayed until CVI. An arthrodiol membrane separating a middle segment of left and right exopod from the distal segment fails to form at CVI. The proximal exopodal segment of right leg has four attenuations; the long proximal attenuation forms the fixed part of a chela. Setae are added to the right exopodal segment at CVI, like *Pontella chierchia*. These setae are not present on the left exopod.

Acartia erythraea.—A limb bud is not present at CIII (as is the case for CIII for *Candacia* sp., unpublished observations); an attenuation of the female exopod initially is present at CV (Fig. 9B) and becomes more pronounced at CVI (Fig. 9C). Arthrodiol membranes fail to separate a proximal and a middle exopodal segment from the distal segment at CV or CVI respectively (Fig. 9B, C).

Ventral projections of the right basis and the right middle segment are present on the male at CVI. Arthrodiol membranes separating the proximal segment of left and right exopod from the distal segment are delayed until CVI; arthrodiol membranes separating a middle segment from distal segment of left exopod fail to form at CVI. The right leg 5 apparently is a subchela.

Tortanus dextrilobatus.—The female leg 5 lacks attenuations and setae; arthrodiol membranes fail to separate a proximal and a middle exopodal segment at CV or CVI respectively (Fig. 10B, C).

A distal ventral attenuation of right basis of male initially forms at CIV (Fig. 10E) and is present at CV (Fig. 10F). It is interpreted as homologous to the distal attenuation of the right basis at CVI (Fig. 10G). A proximal ventral attenuation on the right basis and the two on the left and right proximal exopodal segments are present at CVI. An arthrodiol membrane separating the proximal segment of the right exopod from the distal segment forms at CV, but fails to reform CVI. An arthrodiol membrane separating a middle segment from distal segment of the left and right exopod fails to form CVI. The right leg is a subchela. Loss of the arthrodiol membrane separating the proximal segment of the right exopod from distal segment is unusual among copepods, but has been reported previously for *Tortanus gracilis* (Brady, 1883) by Ohtsuka and Reid (1998) and for *T. derjugini* Smirnov, 1935, by Soh *et al.* (2001).

DISCUSSION

The preceding descriptions suggest a series of derived states shared among some species of centropagoideans which should provide valuable data about relationships within the superfamily: delay or suspension of arthrodiol membrane formation; delay or suspension of formation of setae; suppression of the leg bud; presence of a non-articulating distal attenuation or projection on the basis of males in the location of the endopod which is absent. However, the following discussion considers the male chela and subchela and the ventral attenuation of the female exopod as possible synapomorphies for the superfamily.

The function of the male leg 5 chela on the side opposite the genital opening during copulation of *Diaptomus gracilis* Sars, 1863, has been understood in a general way for a century (Wolf, 1905). The chela of the right leg is used to grasp the female's urosome in order to position the male prior to spermatophore transfer with the left leg 5 (Blades and Youngbluth, 1980). Observations by Blades (1977) of copulation of *Centropages typicus* Kroyer, 1849, and Blades and Youngbluth (1979) of copulation of *Labidocera aestiva* Wheeler, 1901, confirmed the basic function of the right leg 5 and expanded the number of locations grasped by the chela. Gauld (1957) was not specific about the function of the chela of the male left leg 5 of *Temora longicornis*, although the general architecture of both left and right male leg 5 and the right ventral, lateral position of the genital pore suggest a function for the chela similar to the diaptomid, centrogid, and pontellid through a simple reversal of asymmetry. In passing, it should be noted that the chela-like leg 5 of an augaptiloidcan male, *Pleuromamma gracilis* forma *piseki* Farran, 1929, [now *Pleuromamma piseki*], may function in spermatophore transfer (Steuer, 1932: 37, text fig. 140), rather than grasping the female's urosome. Functions of the left and right centropagoidean male leg 5 in species for which one side of the leg appears to be subchela have not been determined. Katona (1975) was unable to provide detailed observations of *Eurytemora affinis*, although he noted that the left leg 5 was used to hold the spermatophore. In this species both legs appear to be a subchela, and the genital pore is ventral. In males of *Pseudodiaptomus*, the subchela right leg 5 (Walter *et al.*, 2002), opposite the genital pore, is used to grasp the female urosome during copulation by three species (Jacoby and Youngbluth, 1983). In summary, it appears that for male centropagoideans, leg 5 on the side opposite the genital pore functions to grasp the female urosome during copulation regardless of whether that leg is a subchela or a chela. Among different species, both chela and subchela may be composed of segments that are not homologues.

Based on segmental homologies, three kinds of chela are observed on the leg 5 of centropagoidean males in this study: the fixed part is an attenuation of the middle exopodal segment, and the moveable part is the distal exopodal segment [right leg of *Centropages abdominalis*]; the fixed part is an attenuation of the proximal exopodal segment, and the moveable part is the middle plus distal exopodal segments which fail to articulate [right leg *Pontella chierchia* and of *Labidocera pavo*]; the fixed part is an attenuation of the basis, and the moveable part is the

proximal and distal exopodal segment [left leg of *Temora longicornis*] or the moveable part is a 1-segmented exopod [right leg of *Tortanus dextrilobatus*]. The left leg 5 of *Temora longicornis* appears to function similarly to the right leg of *Centropages abdominalis*, *Labidocera pavo*, and *Pontella chierchia* as suggested by the fact that the genital pore always opens on the side opposite the chela leg [right for *Temora longicornis* but left for *Centropages abdominalis*, *Labidocera pavo*, and *Pontella chierchia*]. The same inference cannot be drawn for *Tortanus longipes* whose chela is found on the same side as the genital pore. Because of these convergences from nonhomologous segments, the chela of the male leg 5 of centropagoideans cannot be considered a synapomorphy of the superfamily. Neither is the subchela of the male leg 5, which can be made up of the basis plus proximal, middle, and distal exopodal segments [*Boeckella poopoenis*, *Eodiaptomus japonicus*, and *Acartia erythraea*], on the basis plus proximal and distal exopodal segments [*Siuocalanus tenellus*, *Eurytemora affinis*, and *Tortanus dextrilobatus*]. However, both chela and subchela should provide useful phylogenetic information for analyzing relationships within the superfamily.

A ventral attenuation on the middle exopodal segment of leg 5 of females is diagnostic for the family Centropagidae (Bayly, 1992). An attenuation corresponding to it initially appears on the distal segment of leg 5 of females of *Centropages abdominalis*, *Siuocalanus tenellus*, and *Boeckella poopoenis* at CV (Figs. 1C, 2C, 3C), but is allocated to the middle segment when the arthrodistal membrane separating the middle from the distal segment forms during the molt to CVI. A similar attenuation initially is formed on the distal segment of leg 5 at CV of females of *Eodiaptomus japonicus* (Fig. 4C), and also is allocated to the middle segment during the molt to CVI. It is known as the end claw of adult female diaptomids (Ranga Reddy, 1994), although it is an attenuation of the middle exopodal segment; the distal exopodal segment is reduced in size and bears only one or two setae. A ventral attenuation formed during the molt to CV (Fig. 5C) appears to be located on the proximal segment of the 2-segmented exopod of the adult female leg 5 of *Eurytemora affinis* (Fig. 5D). However, the presence of two dorsal setae on the proximal segment suggests that this segment is a complex made up of the proximal and middle segments. The complex results from the failure to form an arthrodistal membrane separating the proximal and middle segments. The ventral attenuation then is homologous to those found on the middle segment of the exopod of the centropagids and diaptomids.

The exopod of leg 5 of females of *Temora longicornis*, *Pontella chierchia*, *Labidocera pavo*, and *Acartia erythraea* appears to be 1-segmented, but the presence of a ventral attenuation initially at CV suggests the exopod is a complex of proximal, middle and distal segments. The ventral attenuation at CV of *T. longicornis* is found distad relative to the dorsal seta of the presumptive proximal segment, and this location assists in establishing its homology (Fig. 6C). Two attenuations are found at CV of *P. chierchia* (Fig. 7C), although these might be considered a single attenuation with a bifurcate tip; alternately the second attenuation may be a synapomorphy for species of the genus. The ventral

attenuation at CV of *L. pavo* (Fig. 8C) and *A. erythraea* (Fig. 9C) is located more distally, and there are no setae or other attenuations to aid in establishing segmental homologies. However, during leg 5 development of females of the acartiid *Paralabidocera antarctica* (Thompson, 1898), a seta is found on a 1-segmented exopod at CIV; the addition of a ventral attenuation follows at CV, and there is no change at CVI (Tanimura, 1992: figs. 9K, 9M, 11B). Development of this adult architecture provides support that the ventral attenuation of the above four species is homologous to that of the first five species in this study.

Although, females of *T. dextrilobatus* do not express a ventral attenuation during development, this structure has been observed on some derived adult females of the genus, e.g., *Tortanus (Atortus) erabuenensis* Ohtsuka, Fukuura, and Go, 1987, or *Tortanus (Acutanus) ecornatus* Ohtsuka and Reid, 1998. It is interesting to note that adult female leg 5 of the acartiid *Paracartia grani* (Sars, 1904) is quite similar in architecture to the adult female of *T. dextrilobatus*. The exopod is elongate, acute, and curved ventrally. However, leg 5 development of *P. grani* is similar to *A. erythraea*; a distinctive attenuation is added at CV which apparently becomes the terminal part of the elongate exopod at CVI (Vilela, 1972: pl. V fig. 3, pl. VI fig. 6, pl. VIII fig. 3). No ventral attenuation is added to leg 5 of *T. dextrilobatus* so the elongation of the exopod of this species appears not to be homologous to that of *P. grani*.

The ventral attenuation present on the middle exopodal segment of leg 5 of the ancestral female centropagoidean may have been lost secondarily on *T. dextrilobatus*. Further evidence to support this hypothesis may be provided in either of two ways. A new derived state may be discovered that is present in *T. dextrilobatus* and in some other centropagoideans that possess a ventral attenuation on leg 5. This new derived state then would successfully link species with and without a ventral attenuation. An alternate solution is to find a derived state that is exclusive to and exhaustive of the centropagoideans, and one was found during the present study. The urosome of CV centropagoidean females has no more than three apparent somites at CV, and the anterior somite is longer and larger than the remaining somites. To our knowledge, the urosome of females of all other calanoids is comprised of four somites at CV. The centropagoidean morphology suggests that the anterior somite and the somite posterior to it (the posterior thoracic somite and the anterior abdominal somite) fuse during the molt to CV to form the presumptive genital complex present in the adult. Our unpublished observations include CIV–VI females of Candaciidae [*Candacia pachydactyla* (Dana, 1849)], Parapontellidae [*Neopontella typica* Scott, 1909] and Pseudodiaptomidae [*Pseudodiaptomus forbesi* (Poppe and Richard, 1890)]; the anterior somite and the somite posterior to it also fuse at CV. In *Acartia erythraea*, the anterior somite and the somite posterior to it fuse during the molt to CIV, and remain fused through CV and CVI; this is a secondarily derived state within the centropagoidea. If a genital complex forms in noncentropagoidean calanoids with four urosome somites at CV, fusion of the anterior somite and the somite posterior to it takes place during the molt to CVI. A female with a urosome of fewer than four somites at CV, including an

anterior complex of two somites, appears to be a synapomorphy of all centropagoideans and suggests that the ventral attenuation on leg 5 initially present at CV has been secondarily lost in *T. dextrilobatus*.

Presence of a ventral attenuation on the middle exopodal segment of leg 5 females, to our knowledge, is confined to species of Centropagoidea. Females of some augaptiloidean families (e.g., Heterorhabdidae, Lueieutiidae, or Augaptilidae) have a modified ventral seta on the middle segment of a 3-segmented exopod, but this seta is not homologous to the attenuation of centropagoideans. A modified ventral seta on an apparently 1-segmented exopod is known for females of the enigmatic *Fosshageni ferrarii* Suarez Morales and Iliffe, 1996, but there are no ventral attenuations on this ramus and the ventral seta is not homologous to the ventral attenuation of female centropagoideans. In addition, the urosome of CV females of *F. ferrarii* is 4-segmented (Fosshagen, e-mail of 07 Oct 2004 to FDF). *Fosshagenia ferrarii* is not a member of the Centropagoidea and should be retained in the Fosshagenoidea.

ACKNOWLEDGEMENTS

We thank Drs. Juan Cesar Paggi, John Fornshell, Wim Klein Bretler, and Wim Kimmerer for specimens of *Boeckella poopoensis*, *Eurytemora affinis*, *Temora longicornis*, and *Tortanus dextrilobatus*, respectively. HU was supported by funds from the Rathhun Endowment of the National Museum of Natural History, Smithsonian Institution.

LITERATURE CITED

- Andronov, V. N. 1974. Filogeneticheskie otnosheniya krupnykh taksonov podotryada Calanoida (Crustacea, Copepoda) [Phylogenetic relations of large taxa within the suborder Calanoida (Crustacea, Copepoda)].—*Zoologicheskii Zhurnal* 53: 1002–1012. [Translated from Russian for the U.S. Department of Commerce and the National Science Foundation, Washington, D.C. (1980).]
- . 1991. On renaming of some taxa in Calanoida (Crustacea).—*Zoologicheskii Zhurnal* 70: 133–134. [In Russian. English summary.]
- Bayly, I. A. E. 1992. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World. 2. The Non-marine Centropagidae (Copepoda: Calanoida) of the World. SPB Academic Publishing bv, The Hague. II + 30 pp.
- Blades, P. I. 1977. Mating behavior of *Centropages typicus* (Copepoda: Calanoida).—*Marine Biology* 40: 57–64.
- , and M. J. Youngbluth. 1979. Mating behavior of *Labidocera aestiva* (Copepoda: Calanoida).—*Marine Biology* 51: 339–355.
- , and —. 1980. Morphological, physiological, and behavioral aspects of mating in calanoid copepods. Pp. 39–51 in W. C. Kerfoot, ed. *Evolution and Ecology of Zooplankton Communities*. Special Symposium no. 3, American Society of Limnology and Oceanography, Hanover, New Hampshire. 793 pp.
- Boxshall, G. A. 1982. On the anatomy of the misophrioid copepods, with special reference to *Benthomispohria palliata* Sars.—*Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 297: 125–181.
- . 1985. The comparative anatomy of two copepods, a predatory calanoid and a particle-feeding mormonilloid.—*Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 311: 303–377.
- , and S. H. Halsey. 2004. An Introduction to Copepod Diversity. Part I. The Ray Society, London. 421 pp.
- Brady, G. S. 1883. Report on the Copepoda collected by H.M.S. *Challenger* during the years 1873–76.—*Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76.*—*Zoology* 8(23): 1–142 figs. 1–4, pls. 1–55.
- Burekhardt, G. 1913. Wissenschaftliche Ergebnisse einer Reise um die Erde von M. Pernod und C. Schroter. III. Zooplankton aus ost- und sudasiatischen Binnengewässern.—*Zoologische Jahrbucher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 34: 341–472, pls. 9–17.
- Chen, Q. C., and S. Z. Zhang. 1965. The planktonic copepods of the Yellow Sea and the East China Sea. I. Calanoida.—*Hai Yang K'o Hsueh Chi K'an* [Studia Marina Sinica] 7: 20–131, pls. 1–53. [In Chinese, English summary.]
- Cohen, S. M. 1993. Imaginal disc development. In A. Martínez-Arias and M. Bate, eds. *Drosophila Development*, 2nd ed. Cold Spring Harbor Press, Cold Spring Harbor, New York.
- Dana, J. D. 1849. *Conspectus Crustaceorum quae in Orbis Terrarum Circumnavigatione, Carolo Wilkes a Classes Reipublicae Foederatae Duce, lexit et descripsit Jacobus D. Dana. Pars II.*—*Proceedings of the American Academy of Arts and Sciences* 2: 9–61.
- Farran, G. P. 1929. Crustacea. Part X.—Copepoda.—*Natural History Reports of the British Museum, British Antarctic ('Terra Nova') Expedition, Zoology* 8: 203–306, figs. 1–37, pls. 1–4.
- Ferrari, F. D. 2000. Patterns of setal numbers conserved during early development of swimming legs of copepods (Crustacea).—*Hydrobiologia* 417: 81–90.
- , and J. W. Ambler. 1992. Nauplii and copepodids of the cyclopoid copepod *Dioithona oculata* (Oithonidae) from a mangrove cay in Belize.—*Proceedings of the Biological Society of Washington* 105: 275–298.
- , and A. Benforado. 1998. Relationships between arthrodial membrane formation and addition of setae to swimming legs 1–4 during development of *Dioithona oculata*, *Ridgewayia klansruetzleri*, *Pleuromamma xiphias*, and *Temora longicornis* (Copepoda).—*Crustaceana* 71: 545–564.
- , and V. N. Ivanenko. 2001. Interpreting segment homologies of the maxilliped of cyclopoid copepods by comparing stage-specific changes during development.—*Organisms, Diversity and Evolution* 1: 113–131.
- Gauld, D. T. 1957. Copulation in calanoid copepods.—*Nature* 180: 510.
- Giesbrecht, W. 1889. Elenco dei Copepodi pelagici raccolti dal Tenente di vascello Gaetano Chierchia durante il viaggio della R. Corvetta 'Vettor Pisani' negli anni 1882–1885 e dal Tenente di vascello Francesco Orsini nel Mar Rosso, nel 1884.—*Atti della Accademia Nazionale dei Lincei, Classe di Scienze Fisiche Matematiche e Naturali Rendiconti* (4) 5, sem 1: 811–815 sem. 2: 24–29.
- . 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte.—*Fauna und Flora des Golfes von Neapel und der Angrenzenden Meeres-Abschnitte*, Herausgegeben von der Zoologischen Station zu Neapel 19: 1–831, pls. 1–54.
- International Code of Zoological Nomenclature. 1985. Articles 62–64. P. 119, in Ride *et al.*, eds, Third Edition. University of California Press, Berkeley. 338 pp.
- Jacoby, C. A., and M. J. Youngbluth. 1983. Mating behavior in three species of *Pseudodiaptomus* (Copepoda: Calanoida).—*Marine Biology* 76: 77–86.
- Katona, S. K. 1975. Copulation in the copepod *Eurytemora affinis* (Poppe, 1880).—*Crustaceana* 28: 89–95.
- Kikuchi, K. 1928. Freshwater Calanoida of middle and south-western Japan.—*Memoirs of the College of Sciences, Kyoto Imperial University, Series B* 4: 65–79, pls. 18–22.
- Krøyer, H. 1849. *Karcinologische Bidrag (Fortsættelse)*.—*Naturhistorisk Tidsskrift*, series 2, 2(6): 561–609, pl. 6.
- Marsh, C. D. 1906. Copepodes. Pp. 175–188, pls. 17–18 in M. Neveu-Lemaire, ed. *Les lacs des hauts plateaux de l'Amerique du Sud*. Mission scientifique G. de Crequi-Montfort et E. Senechal de la Grange. Soudier, Paris. 197 pp., 18 pls.
- Mueller, O.F. 1785. *Entomostraca seu Insecta Testacea, quae in aquis Daniae et Norvegiae reperit, descripsit et iconibus illustravit Otho Fridericus Muller*. F.W. Thiele, Lipsiae & Havniae. 134 pp., index, pls. 1–21.
- Ohtsuka, S., Y. Fukuura, and A. Go. 1987. Description of a new species of *Tortanus* (Copepoda: Calanoida) from Kuchinoerabu Island, Kyushu, with notes on its possible feeding mechanism and in-situ feeding habits.—*Bulletin of Plankton Society of Japan* 34: 53–63.
- , and R. Huys. 2001. Sexual dimorphism in calanoid copepods: morphology and function.—*Hydrobiologia* 453/454: 441–466.
- , and J. W. Reid. 1998. Phylogeny and zoogeography of the planktonic copepod genus *Tortanus* (Calanoida: Tortanidae), with establishment of a new subgenus and descriptions of two new species.—*Journal of Crustacean Biology* 18: 774–807.
- Park, T. 1986. Phylogeny of calanoid copepods.—*Syllogeus* 58: 191–196.

- Poppe, S. A. 1885. Die freilebenden Copepoden des Jadebusens I.—*Ahhandlungen des Naturwissenschaftlichen Vereins zu Bremen* 9: 167–206, pls. 4–7.
- , and J. Richard. 1890. Description du *Schmackeria forbesi* n. gen. et sp., Calanide nouveau recueilli par M. Schmaecker dans les eaux douces des environs de Shanghai.—*Memories de la Societe Zoologique de France* 3: 396–403.
- Ranga Reddy, Y. 1994. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World. 5. Copepoda, Calanoida, Diaptomidae: key to the genera *Heliodyptomus*, *Allodyptomus*, *Neodyptomus*, *Phylloidyptomus*, *Eodyptomus*, *Arctodyptomus* and *Sinodyptomus*. SPB Academic Publishing bv, The Hague. 221 pp.
- Sars, G. O. 1863. Oversigt af de indenlandske Ferskvandcopepoder.—*Forhandlinger i Videnskabs-Selskabet i Christiana, Aar 1862*: 212–262.
- . 1904. Description of *Paracartia grani*, G.O. Sars, a peculiar calanoid occurring in some of the oysterbeds of western Norway.—*Bergens Museums Aarbog 1904* (4): 1–16.
- Sato, C. 1913. Fuyusei-Tokyakurui. (1) [Free-swimming Copepoda. (1)].—*Hokkaido Fisheries Research Laboratory, Investigation Reports* 1: 1–82, pl. 8. [In Japanese.]
- Scott, A. 1909. The Copepoda of the *Siboga* Expedition. Part I. Free-swimming, littoral and semi-parasitic Copepoda.—*Siboga Expedition* 29: 1–323, 69 pls.
- Smirnov, S. S. 1935. K faune Copepoda Amurskogo limana. Zur Copepodenfauna des Amur-Limans.—*Issledovaniya Morei SSSR* 22: 41–53.
- Soh, H. Y., H. L. Suh, S. Ohtsuka, Y. H. Yoon, and S. D. Choi. 2001. Taxonomic studies on brackish copepods in Korean waters—II. Ontogeny and phylogeny of appendages in copepodid stages of *Tortanus derjugini* Smirnov, 1935 (Copepoda, Calanoida).—*Journal of Plankton Research* 23: 1137–1169.
- Steuer, A. 1932. Copepoda (6). *Pleuromanima* Giesbr. 1898 der Deutschen Tiefsee Expedition. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition 'Valdivia' 24: 1–119.
- Suarez-Morales, E., and T. M. Iliffe. 1996. New superfamily of Calanoida (Copepoda) from an anchialine cave in the Bahamas.—*Journal of Crustacean Biology* 16: 754–762.
- Tanimura, A. 1992. Postembryonic development of *Paralabidocera antarctica* (L.C. Thompson) (Copepoda, Calanoida) from the fast ice near Syowa Station, Antarctic.—*Hydrobiologia* 245: 109–128.
- Thompson, I. C. 1898. Report on a small collection of Antarctic plankton from the neighbourhood of the South Shetland Islands, collected by the staff of a Dundee Whaler in 1892–3.—*Transactions of the Liverpool Biological Society* 12: 291–297 pl. 18.
- Vilela, M. H. 1972. The developmental stages of the marine calanoid copepod *Acartia grani* Sars bred in the laboratory.—*Notas y Estudios do Instituto de biologia maritima Lisboa* 40: 1–38.
- Walter, T. C., S. Ohtsuka, S. Puchakarn, K. Pinkaew, and S. Chullasom. 2002. Redescription of two species of *Pseudodyptomus* from Asia and Australia (Crustacea: Copepoda: Calanoida: Pseudodyptomidae) with discussion of the female genital structure and zoogeography of Indo-West Pacific species.—*Proceedings of the Biological Society of Washington* 115: 650–669.
- Wheeler, W. M. 1901. The free-swimming copepods of the Woods Hole region.—*Bulletin of the United States Fish Commission, 1899*, 19: 157–192.
- Wolf, E. 1905. Die Fortpflanzungsverhältnisse unserer einheimischen Copepoden.—*Zoologische Jahrbucher, Abteilung für Systematik* 22: 101–280.

RECEIVED: 21 September 2004.

ACCEPTED: 21 January 2005.