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 Diaptomoidae, 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 copepods (Table I). We use this order, or pattern, to infer homologies of limb segments and to discuss possible synapomorphies for the superfamly. 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 the proximal edge of the distal ramal segment.

We conclude with a discussion of the implications of the analysis for synapomorphies of the superfamly. METHODS AND TERMINOLOGY

The superfamily name Centropagoidea Andronov (1974) is used here; changes proposed by Andronov (1991), including Diaptomoidae 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 I 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.

<table>
<thead>
<tr>
<th>Species and Family</th>
<th>Location and Date</th>
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<tbody>
<tr>
<td><em>Centropages abdonimalis</em> Sato, 1913</td>
<td>Auke Bay, Alaska; US; 10-V-1985</td>
</tr>
<tr>
<td><em>Boeckella poopoensis</em> Marsh, 1906</td>
<td>Mar Chiquita, Argentina; 17-V-1986</td>
</tr>
<tr>
<td><em>Sinocalanus texellus</em> (Kikuchi, 1928)</td>
<td>Isahaya Bay, Nagasaki, Japan; 28-VIII-1987</td>
</tr>
<tr>
<td><em>Euplagonus japonicus</em> (Burckhardt, 1913)</td>
<td>Lake Kiba-ga, Ishikawa; 24-X-1999</td>
</tr>
<tr>
<td><em>Enycrypta affinis</em> (Poppe, 1885)</td>
<td>Chesapeake Bay, Virginia, US; 02-II-1997</td>
</tr>
<tr>
<td><em>Temora longicornis</em> Mueller, 1785</td>
<td>Wadden Sea, Netherlands, in culture; 06/11/1993</td>
</tr>
<tr>
<td><em>Pontella citrinella</em> Giesbrecht, 1889</td>
<td>Maizura Bay, Kyto, Japan; 10-IX-1975</td>
</tr>
<tr>
<td><em>Labidocera pavo</em> Giesbrecht, 1889</td>
<td>Ine Harbor, Kyoto, Japan; 12-IX-1978</td>
</tr>
<tr>
<td><em>Acartia erythraea</em> Giesbrecht, 1889</td>
<td>Nagasaki, Japan; 28-VIII-1987</td>
</tr>
<tr>
<td><em>Torticellia chromatica</em> Chen and Zhang, 1965</td>
<td>San Pablo Bay, California, US; VI-IX-1998</td>
</tr>
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Table 1. Species and families of centropagoidean copepods studied in order of presentation.

Centropages abdonimalis Sato, 1913.—Left and right leg 5 present at CIII as bilobed 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) setae. Proximal endopodal segment with 1 ventral seta and denticles; middle segment with 1 ventral seta and denticles; distal segment with 2 dorsal, 2 terminal, and 2 ventral (6) setae and denticles.

CVI male (Fig. 1E, F): proximal segment of left exopod with 1 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 poopoensis 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.

CVI 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; B, copepodid IV, C, copepodid V; D, adult female. E, adult male, left basis and rami; F, 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 arthrodial membrane of the proximal exopodal segment in the following copepodid stage; stippling on E and H indicates broad arthrodial membrane. b = basis; star next to ventral attenuation of middle exopodal segment. Scale bars represent 0.1 mm.
Eodiptomis japonicus (Burckhardt, 1913).—Left and right exopodal segment with 1 ventral seta; middle segment with 1 ventral seta; distal 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 midventral (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.

CIV 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 setae. Proximal endopodal segment without setae; distal segment with 2 dorsal, 2 terminal, 3 ventral (7) setae.

CIV 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.

CIV 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.

CIV 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.

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.

CIV 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.

CIV 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.

CIV 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.

CIV 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, copepodid III, left limb. Female: B, copepodid IV; C, copepodid V; D, adult (large arthrodial membrane stippled). Male: E, copepodid IV; F, copepodid V; G, adult (large arthrodial membrane stippled; dotted line weakly contrasted arthrodial membrane); H, adult, left leg, medial view. Thin, incomplete line within F indicates position of distal arthrodial membrane of proximal exopodal and endopodal segment in the following copepodid stage; stippling on D and G indicates broad arthrodial 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. *Eurystemora 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 proximal denticule. 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 denticule 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 denticule.

*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.

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

CIV 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.

*Acartiya 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 chierchiae, 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 arthrodial 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 arthrodial membrane of the proximal exopodal segment in following copepodid stage; stippling on D indicates broad arthrodial 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 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

CVI female (Fig. 9C): attenuated section of exopod longer, poorly distinguished from rounded section.
terminal setae 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 dextrilohatus_ Chen and Zhang, 1995.—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 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 arthrodial membrane separating the proximal segment from the distal segment is formed at CIV (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 arthrodial 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 arthrodial membrane separating the proximal segment from the distal segment is formed at CIV (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 arthrodial membrane is added at CVI (Fig. 1D). The proximal dorsal seta is allocated to a new segment of the distal complex; the arthrodial 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 arthrodial 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 arthrodial 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 arthrodial membrane separating the proximal exopodal and endopodal segment is present initially at CV, although the eventual location of this arthrodial membrane can be observed through the cuticle of CIV (Fig. 1B). The arthrodial 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 arthrodid membrane. b = basis. Scale bar represents 0.1 mm.
the female. An arthrodial 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 arthrodial 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). Arthrodial 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 arthrodial 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 arthrodial membrane fails to form and separate a proximal and a middle exopodal segment of the female at CV (Fig. 5C). An arthrodial 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 centropagoidans 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 arthrodial 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 setae 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*. Arthrodial 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 arthrodial 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. Arthrodial 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 arthrodial 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 arthrodial 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, 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. Arthrodial 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. Arthrodial membranes separating the proximal segment of left and right exopod from the distal segment are delayed until CVI. An arthrodial 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). Arthrodial 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. Arthrodial membranes separating the proximal segment of left and right exopod from the distal segment are delayed until CVI; arthrodial 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 dextrilibatus.*—The female leg 5 lacks attenuations and setae; arthrodial 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 arthrodial membrane separating the proximal segment of the right exopod from the distal segment forms at CV, but fails to reform CVI. An arthrodial 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 arthrodial 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 arthrodial 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 augaptiloidean 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's urosome in order to position the male during copulation by three species (Jacoby and Youngbluth, 1983). The function of the male leg 5 subchela 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 augaptiloidean 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 in order to position the male during copulation by three species (Jacoby and Youngbluth, 1983).
proximal and distal exopodal segment [left leg of Temora longicornis] or the moveable part is a 1-segmented exopod [right leg of Tartarus 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 Tartarus longipes whose chela is found on the side opposite that of 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 proximal, middle, and distal exopodal segments [Boeckella poopoensis, Undiacutes japonicus, and Acracia erythraea], on the basis of proximal and distal exopodal segments [Sinocalanus tenerus, Eunystena aufinius, and Tartarus dextrilobatus]. However, both chela and subchela should provide useful phylogenetic information for analyzing relationships within the superfamy.

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, Sinocalanus tenerus, and Boeckella poopoensis at CV (Figs. 1C, 2C, 3C), but is allocated to the middle segment when the arthrodial 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 Eunystena aufinius (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 arthrodial 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 Acracia 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 CV; 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., Tartanus (Atortus) erubicans (Ohtsuka, Fukuura, and Go, 1987, or Tartanus (Acutum) 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 posses 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 preservative genital complex present in the adult. Our unpublished observations include CV-VI females of Candaciidae [Candacia pachyacantha (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 Acracia erythraea, the anterior somite and the somite posterior to it fuse during the molt to CV, 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 augaptiloid families (e.g., Heterorhabdidae, Lucicutiidae, 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 *Foss Hageni 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 (Fosshegen, e-mail of 07 Oct 2004 to PDF). *Foss Hageni ferrarii* is not a member of the Centropagoidea and should be retained in the Fosshegenioidea.

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