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Article *in* New Zealand Journal of Marine and Freshwater Research · March 1985

DOI: 10.1080/00288330.1985.9516072

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New Zealand Journal of Marine and Freshwater Research
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tnzm20

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Published online: 29 Mar 2010.

To cite this article: A. D. McKinnon & G. H. Arnott (1985) The developmental stages of Gladioferens pectinatus (Brady, 1899) (Copepoda: Calanoida), New Zealand Journal of Marine and Freshwater Research, 19:1, 21-42, DOI: 10.1080/00288330.1985.9516072

To link to this article: http://dx.doi.org/10.1080/00288330.1985.9516072

New Zealand Journal of Marine and Freshwater Research, 1985, Vol. 19: 21–42 21
0028-8330/85/1901-0021$2.50/0

The developmental stages of *Gladioferens pectinatus* (Brady, 1899) (Copepoda: Calanoida)

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Abstract The developmental stages of *Gladioferens pectinatus* (Brady, 1899) (Copepoda : Calanoida) reared in laboratory culture are described and figured. Features distinguishing *Gladioferens* from 3 other centropagid genera (*Centropages, Boeckella*, and *Calamoecia*) at all stages of development, are presented.

Keywords *Gladioferens pectinatus*; Centropagidae; developmental stages; nauplii; copepodids; description

INTRODUCTION

The calanoid family Centropagidae is well represented in Australasian waters, with stenohaline marine, estuarine, freshwater, and inland saline representatives (Bayly 1964; Bayly & Arnott 1969). To date, a total of 16 species belonging to 7 centropagid genera have been found in the Gippsland Lakes, Victoria (Arnott 1968; Arnott & McKinnon, unpublished data), emphasising the importance of the family in south-eastern Australian estuarine waters. The centropagid *Gladioferens pectinatus* (Brady, 1899) was the dominant planktonic species in the Gippsland Lakes, where it occurred together with 3 of the other 4 species in the genus. The genus has been revised by Bayly (1963). *Gladioferens pectinatus* is a common species in estuaries from eastern Australia at least as far north as the Fitzroy River (Kott 1955; Bayly 1965; Arnott 1968; Arnott & Hussainy 1972; Neale & Bayly 1974; Kennedy 1975, 1978), Tasmania (Nyan Taw & Ritz 1978), and New Zealand (Jillett 1971; Chapman & Lewis 1976; Roper et al. 1983). In Western Australia, *G. imparipes* fulfills a similar ecological role (Rippingale & Hodgkin 1974).

This paper provides a complete description of the developmental stages of *Gladioferens pectinatus* and highlights features that distinguish the genus from other Australasian centropagid genera at all stages of development.

Received 24 April 1984; accepted 22 August 1984

METHODS

'Wild' *G. pectinatus* were collected in August 1980 from a small creek entering the Barwon River at Ocean Grove, Victoria. Ovigerous females were placed in a 2 *l* culture vessel in water of 12×10^{-3} salinity and maintained in a constant temperature room set at 18°C. The prymnesiophyte *Isochrysis galbana* was added as food daily. The adult females were removed after hatching of the egg-sacs, and the nauplii were allowed to develop to maturity. Subsamples of the offspring were periodically taken and preserved in 5–10% formalin. The generation time from egg to adult under these conditions was 17–22 days.

The laboratory-reared developmental stages were cleared in lactic acid and drawn using a Wild M20 phase contrast microscope with the aid of a camera lucida. Body lengths were measured from the anterior end of the body to the base of caudal spines for nauplii and to the end of caudal rami for copepodids and adults. Measurements were made on 10 specimens of stages Nauplius II to adult using an ocular micrometer; means and standard deviations were calculated. Only 2 specimens of Nauplius I were available because of the short life of this stage in *G. pectinatus*; nauplii collected from single family cultures only 2 hours after hatching of the egg sacs were all Stage II. The material has been deposited in the Museum of Victoria, Australia (Reg. nos. J8857–J8870).

For each appendage of a particular developmental stage only the points of difference from the preceding stage are described in the text. Where numbers of setae per segment are presented as a formula, the numbers always begin at the most basal segment. Formulae for armature of swimming legs are presented as outer margin first: Roman numerals, spines; Arabic numerals, setae.

DESCRIPTION OF DEVELOPMENTAL STAGES

Naupliar stages (Fig. 1–30)

Nauplius I (Fig. 1, 2): Mean length 0.09 mm. Ovoid in shape reflecting that of the unhatched embryo. Labrum large and smooth, lying closer to the body than in later stages. Caudal region reflexed along ventral surface of body and yet to fully extend. Caudal armature 2 naked, subequal caudal spines, of which left is slightly longer.

Antennule (Fig. 13) 3-segmented, with 0,3,3 setae. Coxa of antenna (Fig. 19) with 2 setae, basis with 3, endopod with 4, and 1-segmented exopod with 6 setae. Coxa of mandible (Fig. 25) with 1 seta, basis with 2, endopod with 8, and exopod with 5 setae.

Nauplius II (Fig. 3, 4): Mean length 0.13 ± 0.01 mm. Body more elongated than Stage I, posterior end tapering with caudal region now directed backwards. Rostral prominence now present. Labrum in this and all subsequent stages with small spinules on ventral margin. Postero-ventrally there are 3 rows of minute spines. Caudal armature 1 barbed ventral spine larger than half body length on left, and shorter naked dorsal spine on right.

Antennule (Fig. 14) segment 3 with 4 setae. Antenna (Fig. 20) with 1 seta of coxa developed into masticatory seta. Endopod bearing 5 setae, exopod 7 setae, and indications of segmentation on exopod. Exopod of mandible (Fig. 26) 3-segmented, with 2,1,2 setae.

Nauplius III (Fig. 5, 6): Mean length 0.15 ± 0.01 mm. Caudal armature of 4 spines, 1 additional short, naked spine on outer dorsal surface of each caudal ramus.

Antennule (Fig. 15) segment 3 with 7 setae. Coxa of antenna (Fig. 21) with 3 setae (2 masticatory), and basis with 4 setae. Endopod with 7 setae; exopod 5-segmented, with 3,1,1,1,3 setae. Basis of mandible (Fig. 27) with 3 setae, endopod with 10, and exopod with 2,1,3 setae. First appearance of maxillules, each represented by fold in ventral body and 1 long smooth seta, at this stage.

Nauplius IV (Fig. 7, 8): Mean length 0.18 ± 0.01 mm. No change in caudal armature.

Antennule (Fig. 16) segment 3 with 11 setae. Basis of antenna (Fig. 22) with 5 setae, endopod with 8 setae, and exopod segment 1 with 4 setae. Mandible (Fig. 28) with coxa developed into mandibular blade; basis with 5 setae and endopod with 11 setae. Maxillule developed into bilobed flap, outer lobe bearing 3 setae, inner lobe 4 setae.

Nauplius V (Fig. 9, 10): Mean length 0.21 ± 0.01 mm. Caudal armature similar to NIV, but large barbed spine only about 0.4 times body length.

Antennule (Fig. 17) segment 3 with 14 setae. Antenna (Fig. 23) with proximal seta of basis developed into masticatory seta. Endopod bearing 9 setae; exopod segment 1 bearing 5 setae. Basis of mandible (Fig. 29) with 6 setae, exopod 4-segmented, with formula 2,1,1,2. Maxillule developed into separate segment, with 4–5 setae on outer lobe and 11 on inner lobe.

Nauplius VI (Fig. 11, 12): Mean length 0.25 ± 0.01 mm. Caudal armature similar to NV with large barbed spine about 0.4 times body length.

Antennule (Fig. 18) segment 3 with 16 setae. Exopod segment 1 of antenna (Fig. 24) with 6 setae. Basis of mandible (Fig. 30) with 7 setae, and endopod with 12 setae. Maxillule with 6–7 setae on outer lobe and 11 setae on inner lobe. Maxilla, underlying maxillule, consisting of large flap carrying setiform elements on inner margin. Medial and slightly posterior to maxilla is 1-segmented maxilliped bearing 2 terminal setae, outer seta half length of inner seta. Limb buds of first 2 pairs of swimming legs present in place of 2 most anterior rows of postero-ventral spines on body surface of NV. Third row of spines, situated on caudal rami, still present. Leg 1 bearing 7–8 setae, leg 2 bearing 5 setae.

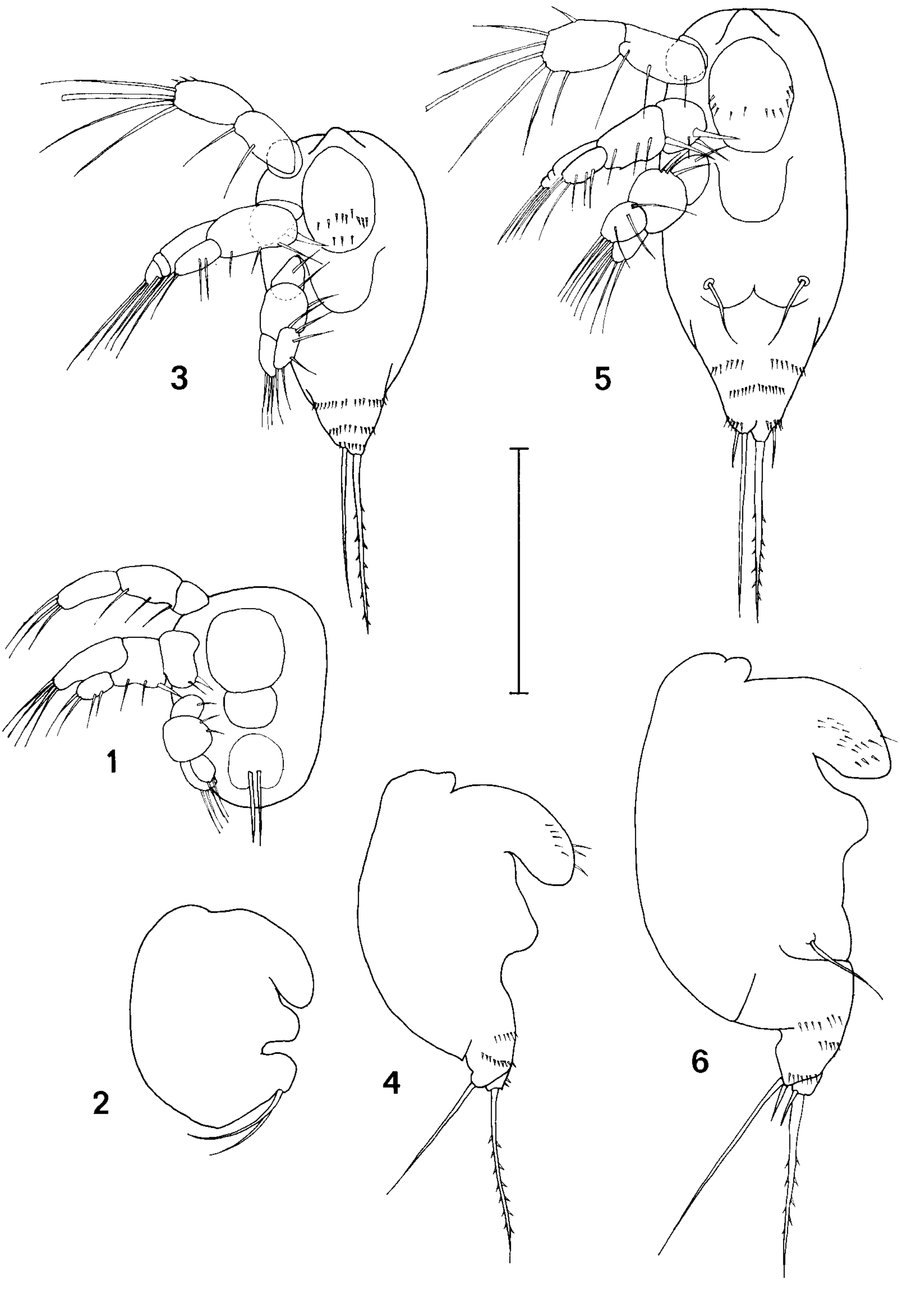

Fig. 1–6 *Gladioferens pectinatus.* Ventral and lateral aspects of Nauplius I to III: 1–2, Nauplius I; 3–4, Nauplius II; 5–6, Nauplius III. Left antennule, antenna, and mandible omitted. Scale bar 0.1 mm.

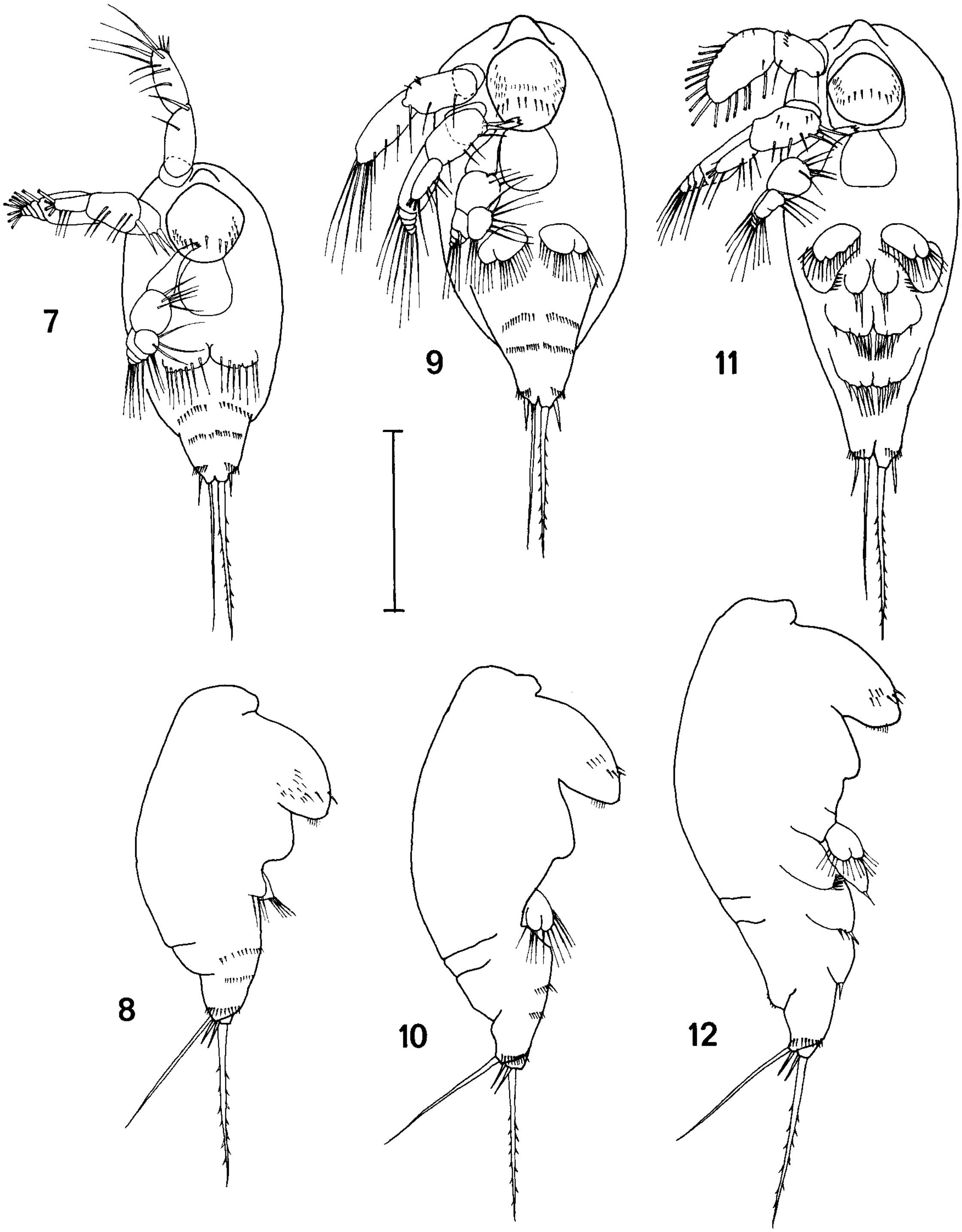

Fig. 7–12 *Gladioferens pectinatus.* Ventral and lateral aspects of Nauplius stages IV to VI: 7–8, Nauplius IV; 9–10, Nauplius V; 11–12, Nauplius VI. Left antennule, antenna, and mandible omitted. Scale bar 0.1 mm.

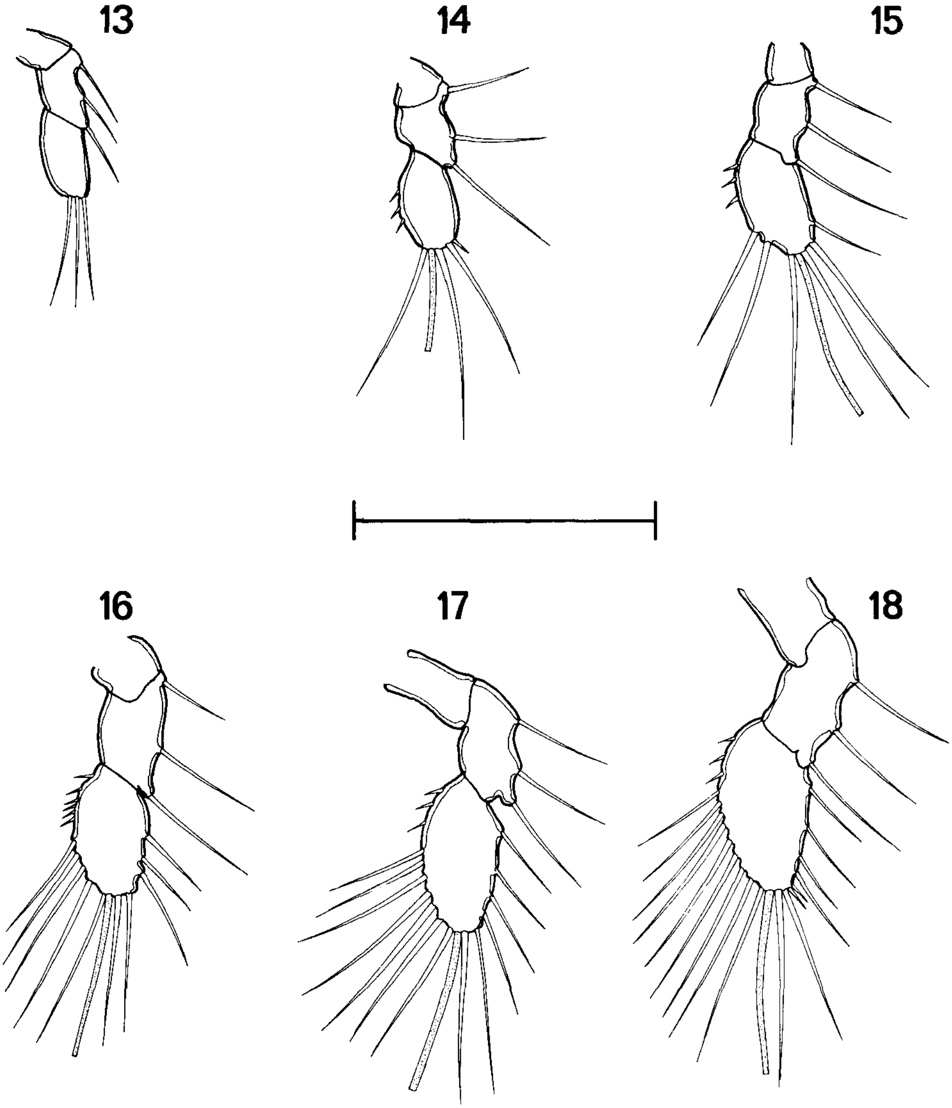

Fig. 13–18 *Gladioferens pectinatus*. Antennule, Nauplius stages I–VI. Scale bar 0.1 mm.

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22 23 24

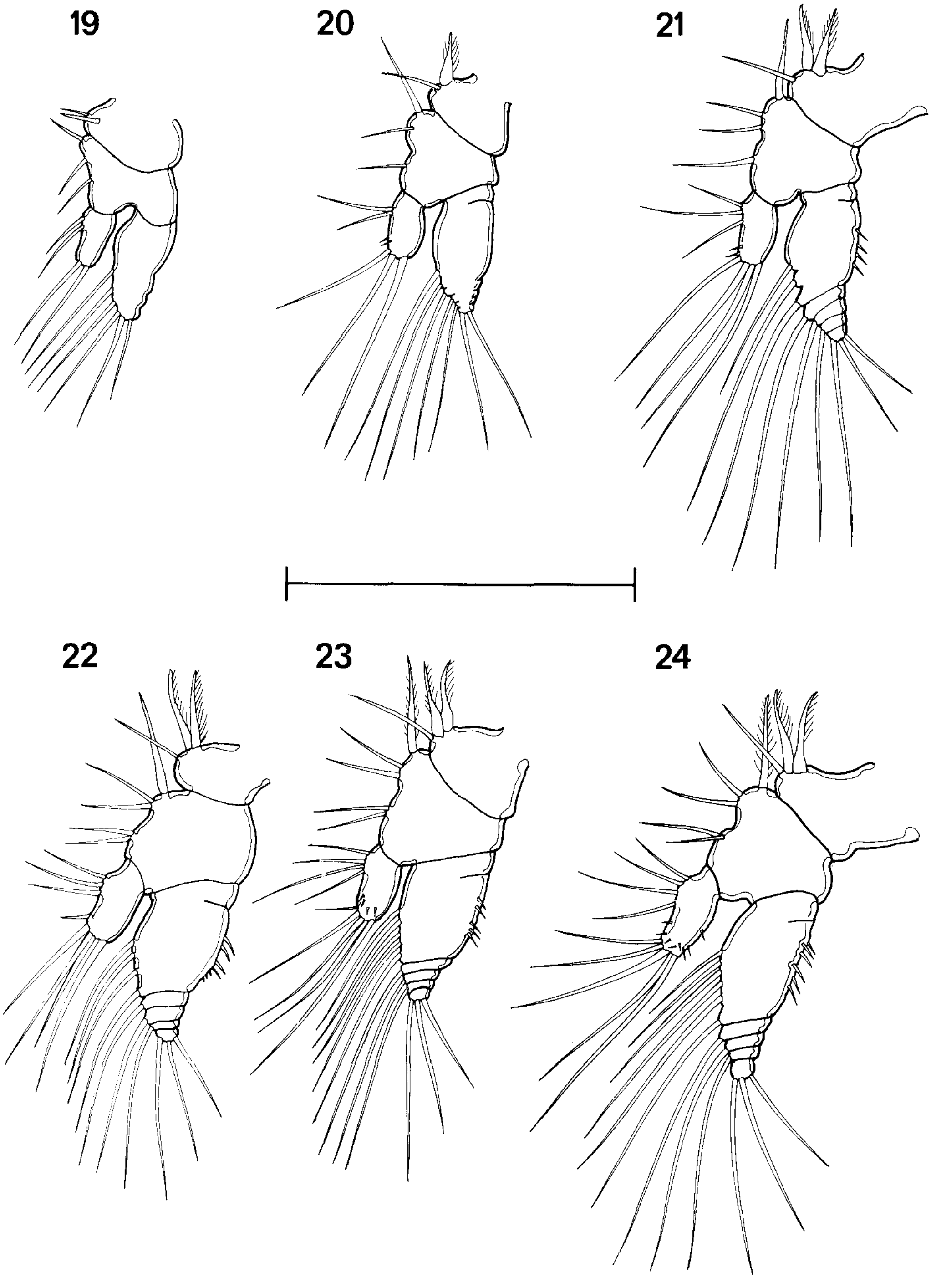


Fig. 19–24 *Gladioferens pectinatus*. Antenna, Nauplius stages I–VI. Scale bar 0.1 mm.

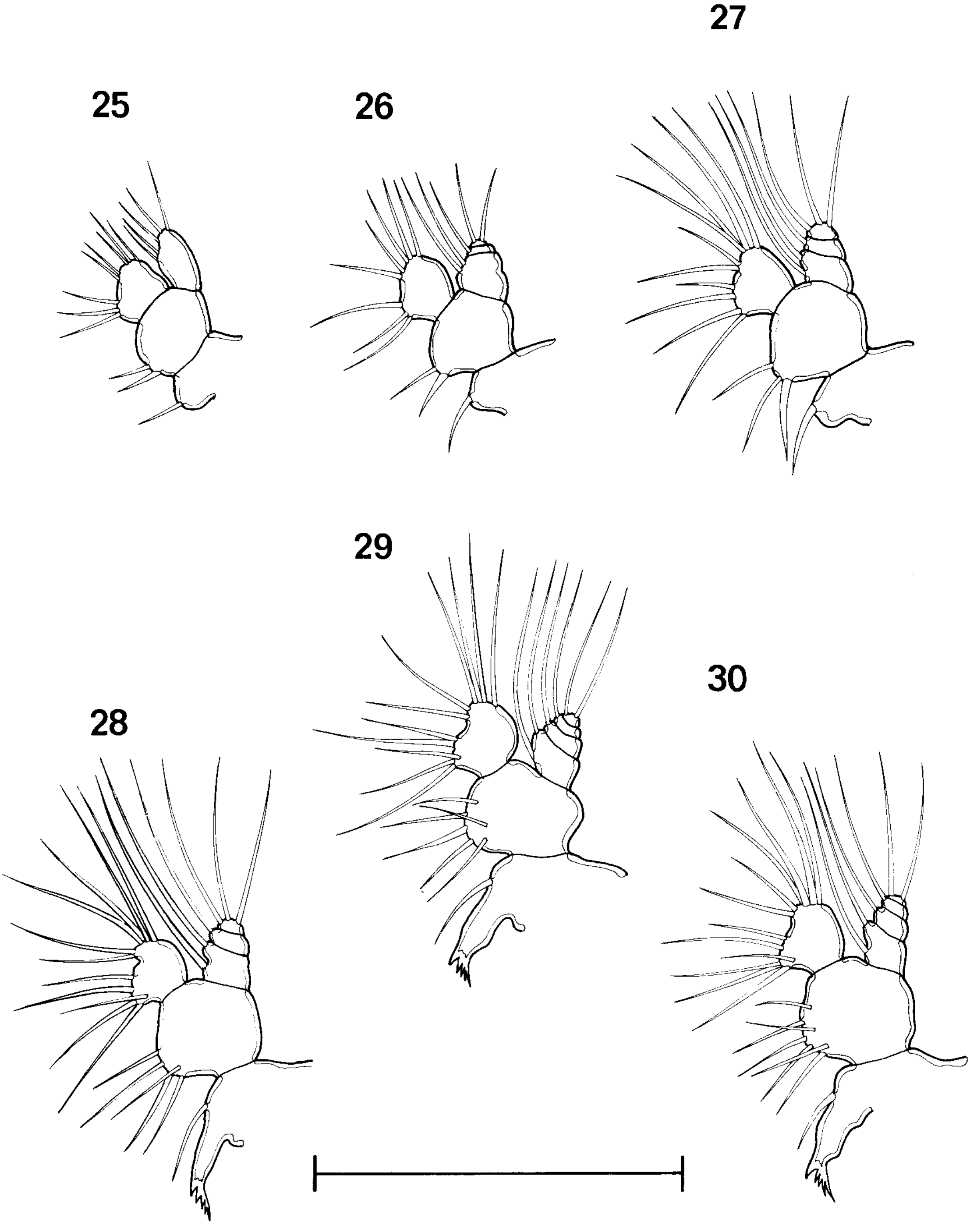


Fig. 25–30 *Gladioferens pectinatus.* Mandible, Nauplius stages I–VI. Scale bar 0.1 mm.

Copepodid stages and adult (Fig. 31–119)

Copepodid I (Fig. 31, 32): Mean length 0.33 ± 0.02 mm. Prosome consisting of cephalosome and 3 metasome segments, urosome of 2 segments. Caudal rami bear 5 setae each.

Antennule (Fig. 47) 10-segmented. Coxa of antenna (Fig. 56) with 1 seta, basis with 2 setae. Endopod 2-segmented with 2,10 setae. Exopod 6-segmented with 4,1,1,1,1,4 setae. Basis of mandible (Fig. 62) with 4 setae. Endopod 2-segmented with 4,6 setae; exopod 3-segmented, with 1,1,4 setae. First outer lobe of maxillule (Fig. 68) with 4 setae, second outer lobe with 1 seta. First inner lobe with 9 setae, second with 3, third with 4 setae. Fused basis and endopod segments bearing 7 setae, and 1 distinct endopod segment bearing 5 setae. Lobe representing exopod bearing 7 setae. Maxilla (Fig. 74) 2-segmented, basal segment of 4 lobes each bearing 3 setae, terminal segment of 2 lobes bearing 3, 7 setae. Maxilliped (Fig. 80) 4-segmented, bearing 5,3,2,4 setae.

Two pairs of swimming legs (Fig. 86, 92) with buds of pair 3 present. Armature:

Leg 1	coxa 0-0	basis 0-0	exopod	III-I-3
			endopod	1-2-3
Leg 2	coxa 0-0	basis 0-0	exopod	III-I-3
			endopod	1-2-3

Copepodid II (Fig. 33, 34): Mean length 0.45 ± 0.02 mm. Prosome consisting of cephalosome and 4 metasome segments, urosome of 2 segments. Caudal rami bearing 6 setae each, as do all subsequent stages.

Antennule (Fig. 48) 13-segmented. Antenna (Fig. 57) similar to CI. Endopod segment 2 of mandible (Fig. 63) with 7 setae, exopod 4-segmented with 1,1,1,3 setae. First outer lobe of maxillule (Fig. 69) with 6 setae, and first inner lobe with 10 setae. Maxilla (Fig. 75) with first lobe of basal segment bearing 4 setae. Maxilliped (Fig. 81) 5-segmented with 7,3,3,1,4 setae.

Three pairs of swimming legs (Fig. 87, 93, 99) and buds of pair 4 present. Armature:

Leg 1	coxa 0-0	basis 0-0	exopod	I-0, II-I-4
			endopod	0-1, 1-2-4
Leg 2	coxa 0-0	basis 0-0	exopod	I-0, II-I-4
			endopod	0-1, 2-2-3
Leg 3	coxa 0-0	basis 0-0	exopod	III-I-3
			endopod	1-2-3

Copepodid III (Fig. 35, 36): Mean length 0.61 ± 0.02 mm. Prosome consisting of cephalosome and 5 metasome segments (as in all subsequent stages); urosome 2-segmented.

Antennule (Fig. 49) 21-segmented. Endopod segment 2 of antenna (Fig. 58) with 13 setae. Exopod of mandible (Fig. 64) 5-segmented with 1,1,1,1,2 setae. First outer lobe of maxillule (Fig. 70) with 8 setae, first inner lobe with 12 setae. Exopod now distinct, and bearing 8 setae. Maxilla (Fig. 76) similar to CII. Maxilliped (Fig. 82) 6-segmented with 9,3,3,1,2,4 setae.

Four pairs of swimming legs (Fig. 88, 94, 100, 105) and buds of pair 5 present. Armature:

Leg 1	coxa 0-1	basis 0-0	exopod	I-1, II-I-4
			endopod	0-1, 1-2-4
Leg 2	coxa 0-1	basis 0-0	exopod	I-1, III-I-5
			endopod	0-1, 2-2-4
Leg 3	coxa 0-1	basis 0-0	exopod	I-0, II-I-4
			endopod	0-1, 2-2-3
Leg 4	coxa 0-0	basis 1-0	exopod	III-I-3
			endopod	1-2-?

Copepodid IV (Fig. 37, 38): Mean length female 0.78 ± 0.02 mm, male 0.77 ± 0.04 mm. Urosome 3-segmented.

Antennule (Fig. 50, 53) 24-segmented and sexually dimorphic, male right antennule slightly more robust than that of female. Endopod segment 2 of antenna (Fig. 59) with 14 setae. Endopod segment 2 of mandible (Fig. 65) with 8 setae. First outer lobe of maxillule (Fig. 71) with 9 setae, second outer lobe with 2 setae. First inner lobe with 13 setae, fused basis and endopod with 8 setae, distinct endopod segment with 6 and exopod with 9 setae. Maxilla (Fig. 77) 4-segmented, the basal segment bearing 3 lobes with 4,3,3 setae, segment 2 with 1 lobe bearing 3 setae, segment 3 with 2 lobes bearing 4,1 setae, and segment 4 bearing 7 setae. Maxilliped (Fig. 83) 7-segmented with 9,3,4,2,1,2,4 setae.

Full complement of 5 pairs of swimming legs (Fig. 89, 95, 101, 106, 111) present. Armature:

Leg 1	coxa 0-1	basis 0-0	exopod	I-1, II-I-4
			endopod	0-1, 1-2-5
Leg 2	coxa 0-1	basis 0-0	exopod	I-1, III-I-5
			endopod	0-1, 2-2-5
Leg 3	coxa 0-1	basis 0-0	exopod	I-1, III-I-5
			endopod	0-1, 2-2-4
Leg 4	coxa 0-1	basis 1-0	exopod	I-0, III-I-5
			endopod	0-1, 2-2-3
Leg 5	coxa 0-0	basis 1-0	exopod	III-I-2
			endopod	0-2-2

Copepodid V (Fig. 39–42): Mean length female 1.08 ± 0.05 mm, male 1.00 ± 0.05 mm. Three urosome segments in female and 4 in male. First segment in female with pronounced ventral bulge, and longer than anal segment. No such bulge in male, and first urosome segment only about half length of anal segment.

Male right antennule (Fig. 54) more robust than that of female (Fig. 51), with spine-like projection on each of segments 17, 18, and 19. Endopod segment 2 of antenna (Fig. 60) with 15 setae. Exopod

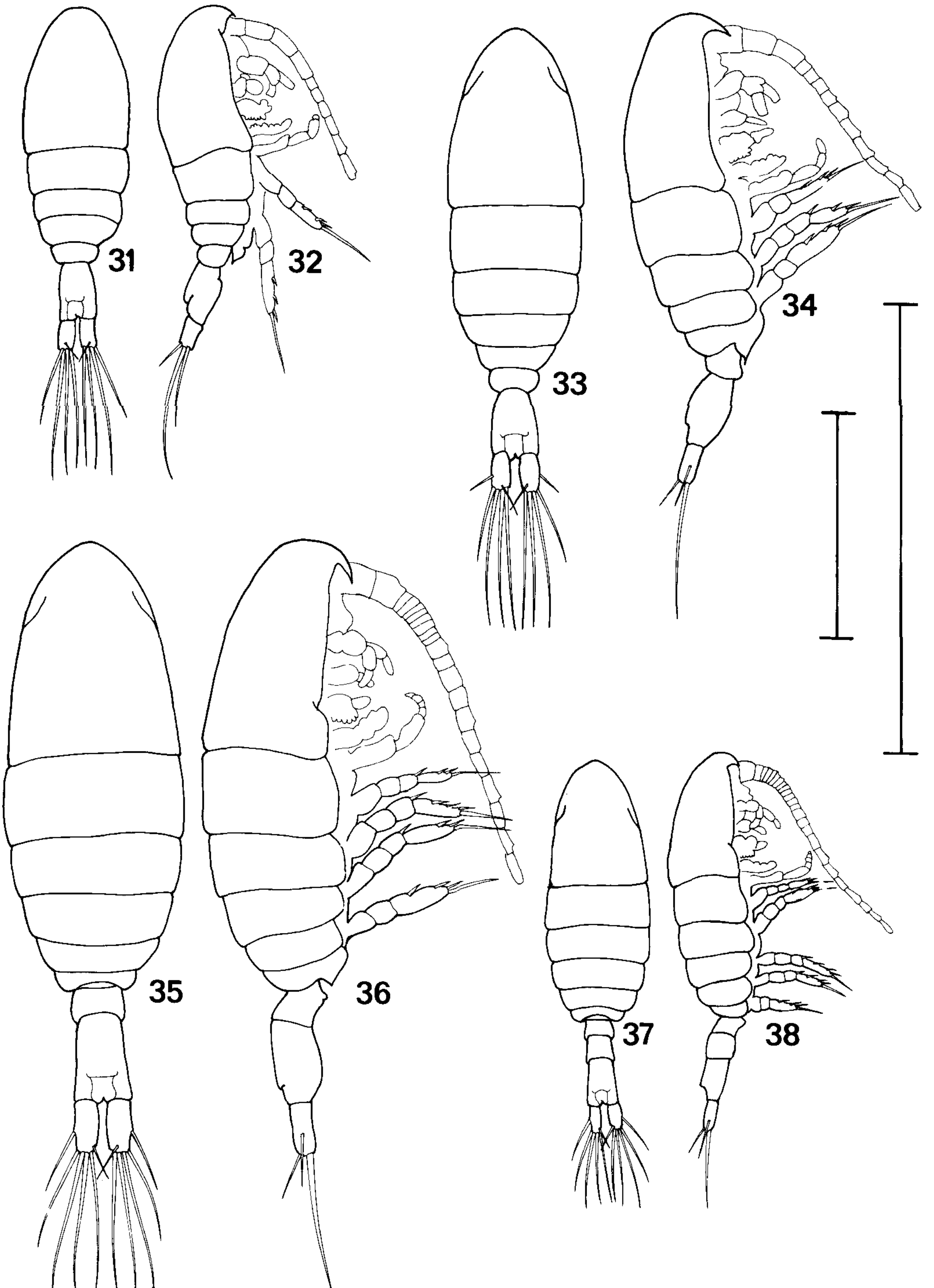


Fig. 31–38 *Gladioferens pectinatus.* Dorsal and lateral aspects of Copepodid stages I to IV: 31–32, Copepodid I; 33–34, Copepodid II; 35–36, Copepodid III; 37–38, Copepodid IV. Scale bars 0.5 mm; small bar Fig. 31–36, large bar Fig. 37–38.

segment 1 incompletely divided adjacent to first seta. Mandible (Fig. 66) similar to that of CIV. Fused basis and endopod of maxillule (Fig. 72) with 9 setae, distinct endopod segment with 7, exopod with 10 setae. Maxilla (Fig. 78) similar to that of CIV. Maxilliped (Fig. 84) with 9,3,5,3,2,3,4 setae.

Formula for armature of swimming legs (Fig. 90, 96, 102, 107, 108, 112, 115):

Leg 1	coxa 0-1	basis 0-0	exopod	I-1, 0-1, II-I-3
			endopod	0-1, 0-2, 1-2-3
Leg 2	coxa 0-1	basis 0-0	exopod	I-1, I-1, II-I-5
			endopod	0-1, 0-2, 2-2-4
Leg 3	coxa 0-1	basis 0-0	exopod	I-1, I-1, II-I-5
			endopod	0-1, 0-2, 2-2-4
Leg 4	coxa 0-1	basis 1-0	exopod	I-1, I-1, II-I-5
			endopod	0-1, 0-2, 2-2-3
Leg 5	coxa 0-0	basis 1-0	exopod	I-0, III-I-2
			endopod	0-0, 0-2-3

Female fourth legs (Fig. 107) asymmetrical with enlarged seta on inner margin of left coxa; male fourth legs identical with normal seta on coxa (Fig. 108). Female fifth legs have a spine-like projection on inner margin of distal exopodite segment (Fig. 112), not present in male (Fig. 115). Male fifth legs slightly asymmetrical with right endopodite and exopodite longer than those on left.

Adult (Fig. 43–46): Mean length female 1.42 $\pm$ 0.04 mm, male 1.28 $\pm$ 0.03 mm. Four urosome segments in female and 5 in male. Female genital segment bearing 2 robust ventro-lateral spines characteristic of species, 2 curved rows of smaller spines on ventral surface anterior to these. Second and third urosome segments in female both bearing row of spines dorsally along posterior margin; no such spines in male. Urosome of ovigerous females typically arched, ovoid egg sac attached ventrally to segment 3. Mean of 30 eggs per sac.

During last moult, segments 6–9, 19–21, and 22–23 of male right antennule fuse, thus reducing the number of segments from 24 to 18. Male right antennule (Fig. 55) hinged between segments 15 and 16, segments 7–9 each having stout spine. Male left antennule and both female antennules (Fig. 52) consist of 24 segments as in CV. Exopod of antenna (Fig. 61) 7-segmented, with 1,3,1,1,1,1,4 setae. Mandible (Fig. 67) and maxillule (Fig. 73) similar to those of CV. Basal segment of maxilla (Fig. 79) bearing 3 lobes with 5,3,3 setae. Maxilliped (Fig. 85) with 9,3,6,4,3,4,5 setae.

Formula for armature of female swimming legs (Fig. 91, 97, 103, 109, 113, 114):

Leg 1	coxa 0-1	basis 0-0	exopod	I-1, 0-1, II-I-3
			endopod	0-1, 0-2, 1-2-3
Leg 2	coxa 0-1	basis 0-0	exopod	I-1, I-1, II-I-5
			endopod	0-1, 0-2, 2-2-4
Leg 3	coxa 0-1	basis 0-0	exopod	I-1, I-1, II-I-5
			endopod	0-1, 0-2, 2-2-4
Leg 4	coxa 0-1	basis 1-0	exopod	I-1, I-1, II-I-5
			endopod	0-1, 0-2, 2-2-3
Leg 5	coxa 0-0	basis 1-0	exopod	I-0, I-0, II-I-2
			endopod	0-0, 0-1, 0-2-2

Male legs 2, 3, 4, and 5 all display some degree of asymmetry. Terminal endopodite segment of left leg 2 highly modified (Fig. 98), large basally-directed process replacing proximal seta on inner margin and next 2 setae both thicker and shorter than rest. Proximal endopodite segment of left leg 3 has stout spine on inner margin in place of usual much longer seta (Fig. 104); similar situation evident for leg 4, although the asymmetry is less obvious and variable. Male fifth legs highly modified (Fig. 116, 117) and some variability in inner marginal projections at junction of proximal and middle segments of right exopodite evident (Fig. 117–119). Female fourth legs asymmetrical with inner margin seta of left coxa greatly enlarged compared with that on right (Fig. 109); both setae are different to normal condition in male (Fig. 110).

A more complete description of *G. pectinatus* adults, including a full discussion of asymmetry and variation in structure, is given by Bayly (1963).

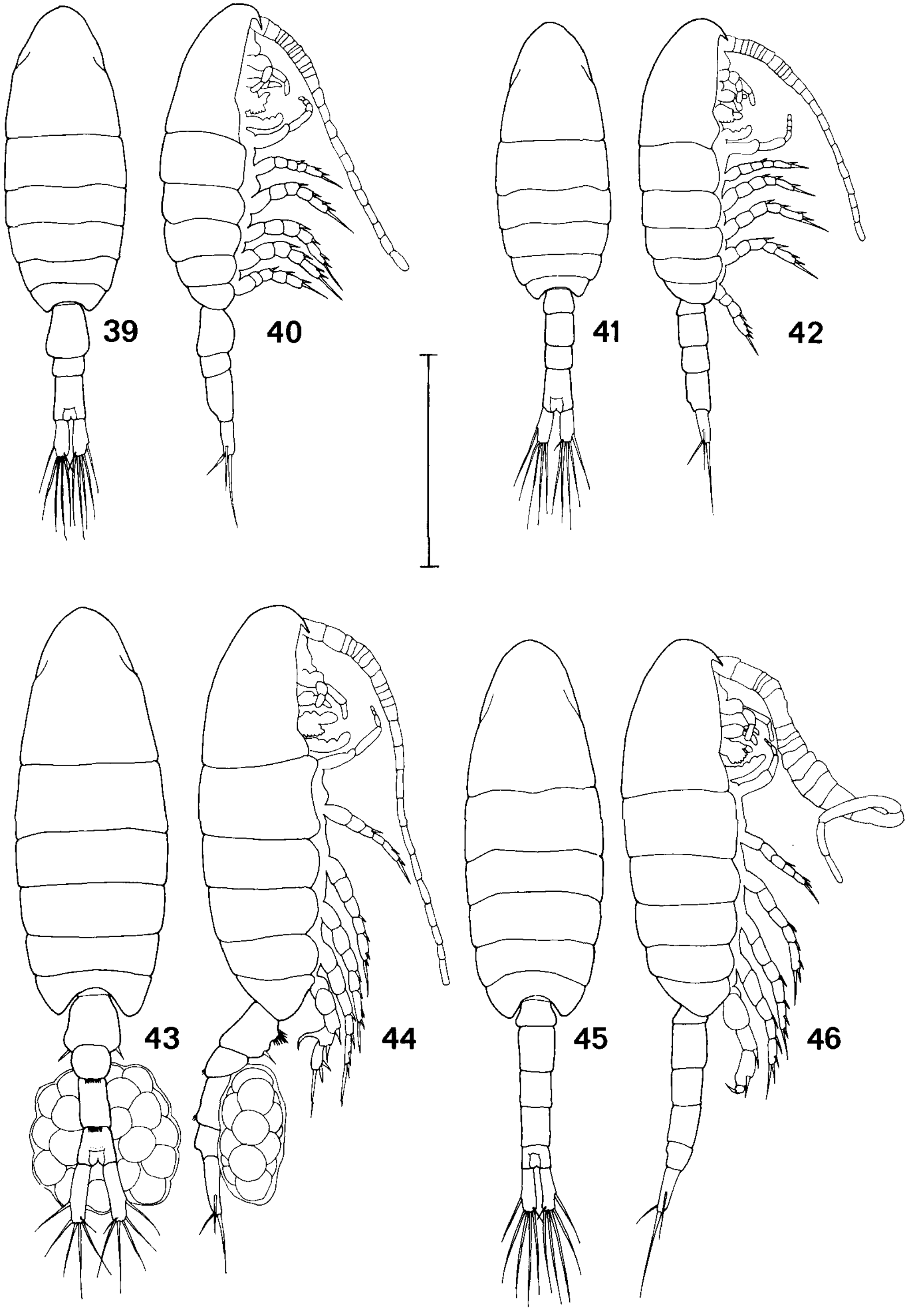
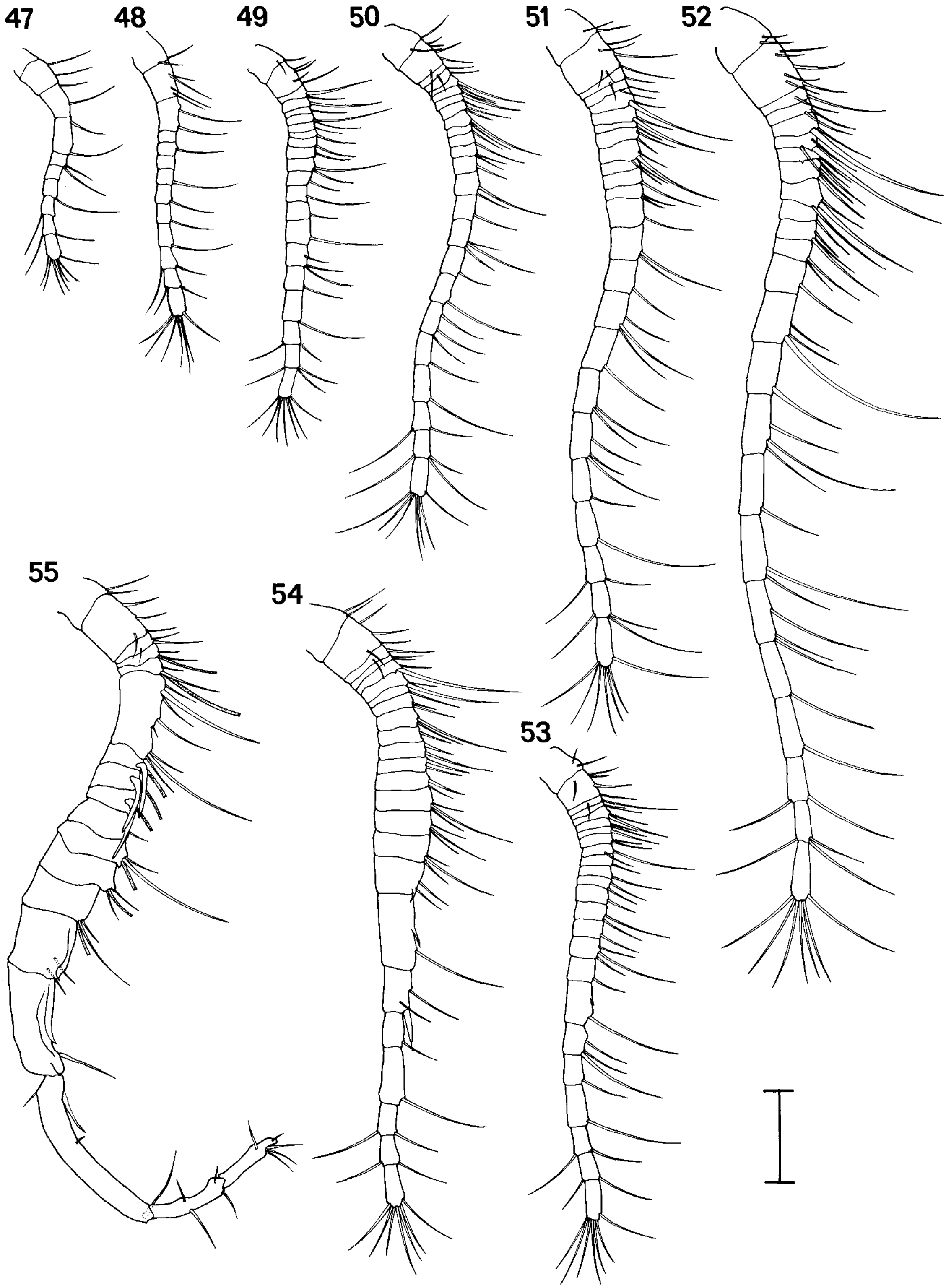


Fig. 39–46 *Gladioferens pectinatus*. Dorsal and lateral aspects of Copepodid V and adult: 39–40, Copepodid V, female; 41–42, Copepodid V, male; 43–44, adult female; 45–46, adult male. Scale bar 0.5 mm.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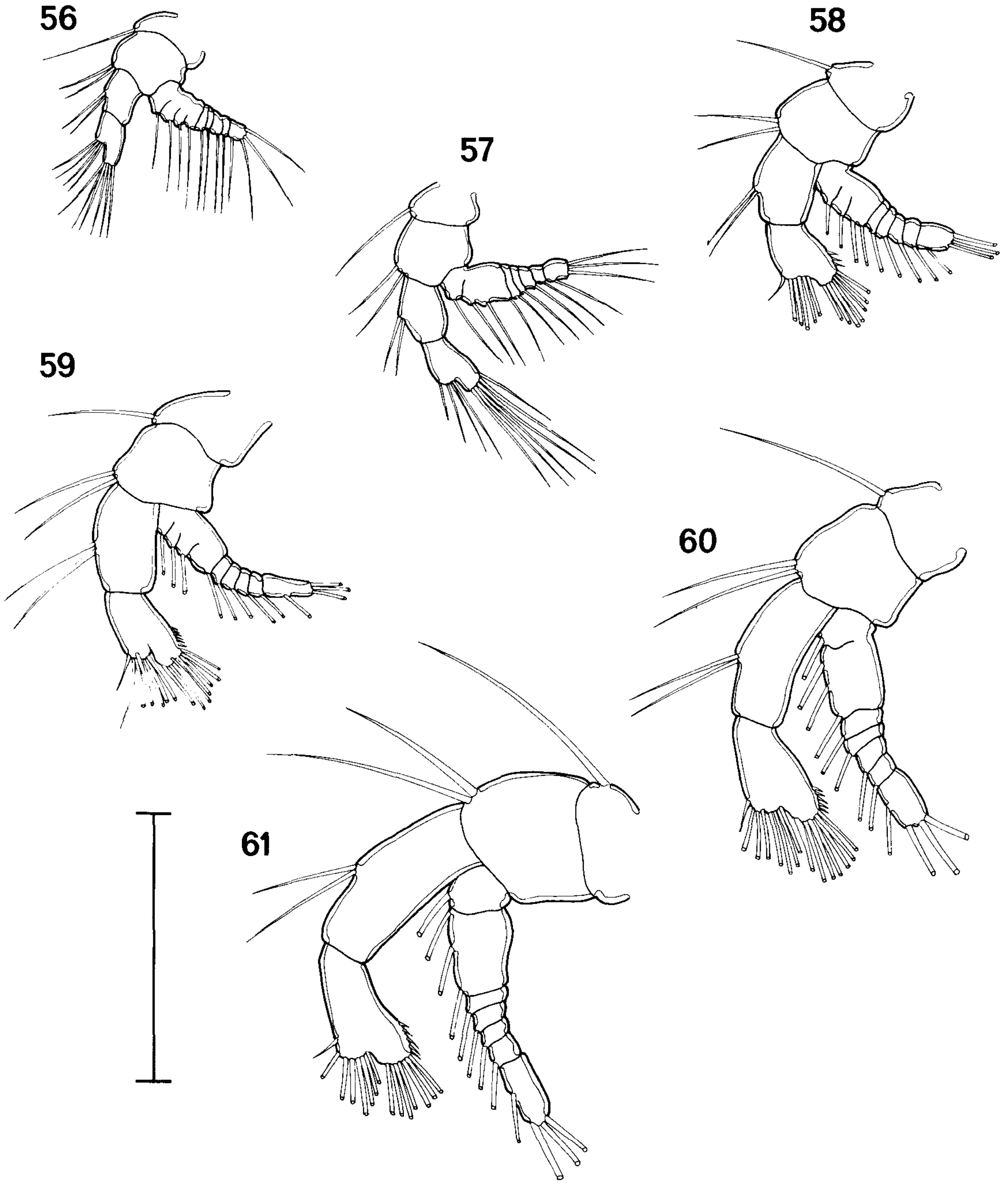


Fig. 56–61 *Gladioferens pectinatus*. Antenna, Copepodid stages I–V and adult. Scale bar 0.1 mm.

Fig. 47–55 (*opposite*) *Gladioferens pectinatus*. Right antennule: 47–49, Copepodid stages I–III; 50–52, Copepodid stages IV–V and adult, female; 53–55, Copepodid stages IV–V and adult, male. Scale bar 0.1 mm.

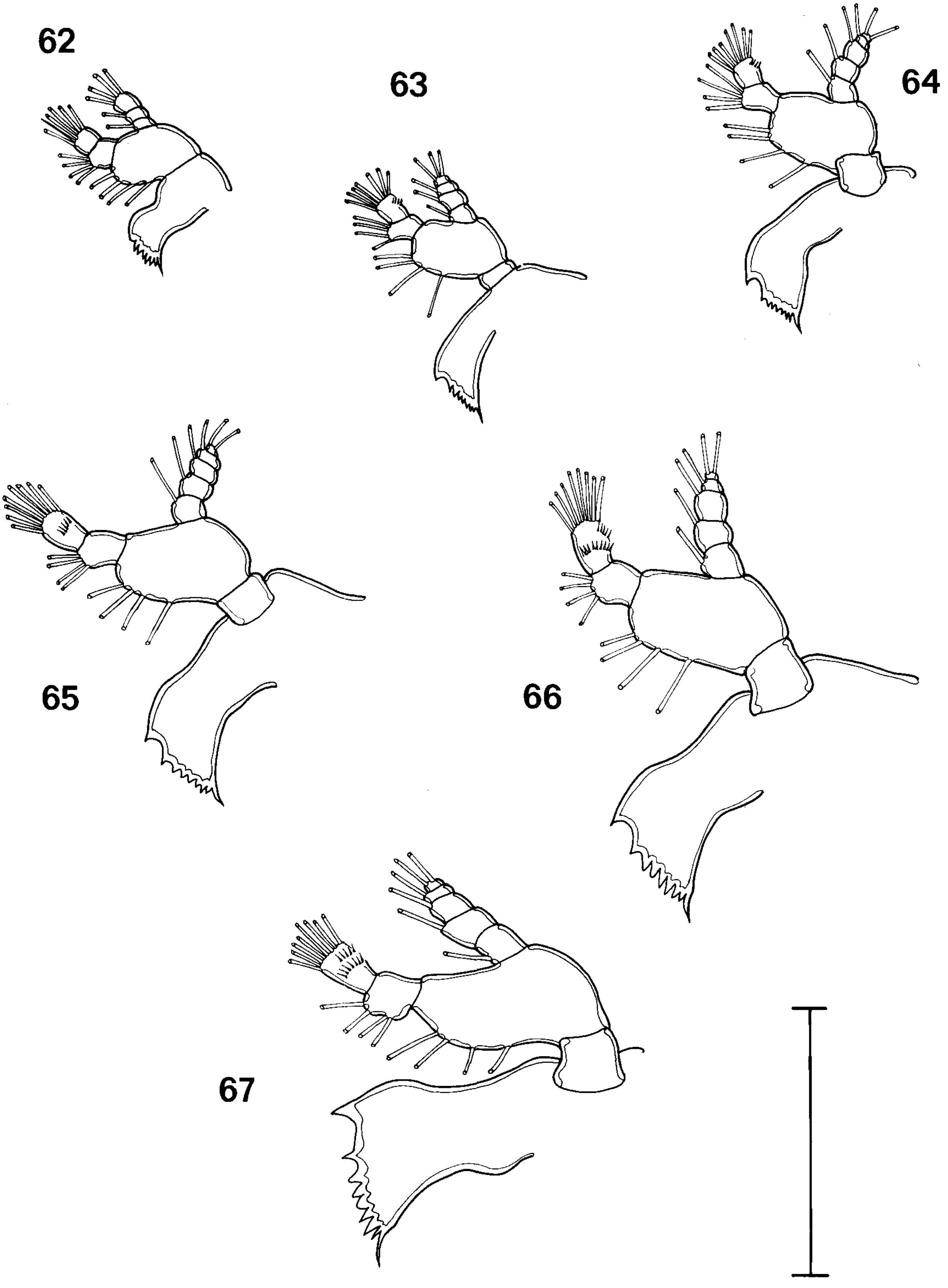


Fig. 62–67 *Gladioferens pectinatus*. Mandible, Copepodid stages I–V and adult. Scale bar 0.1 mm.

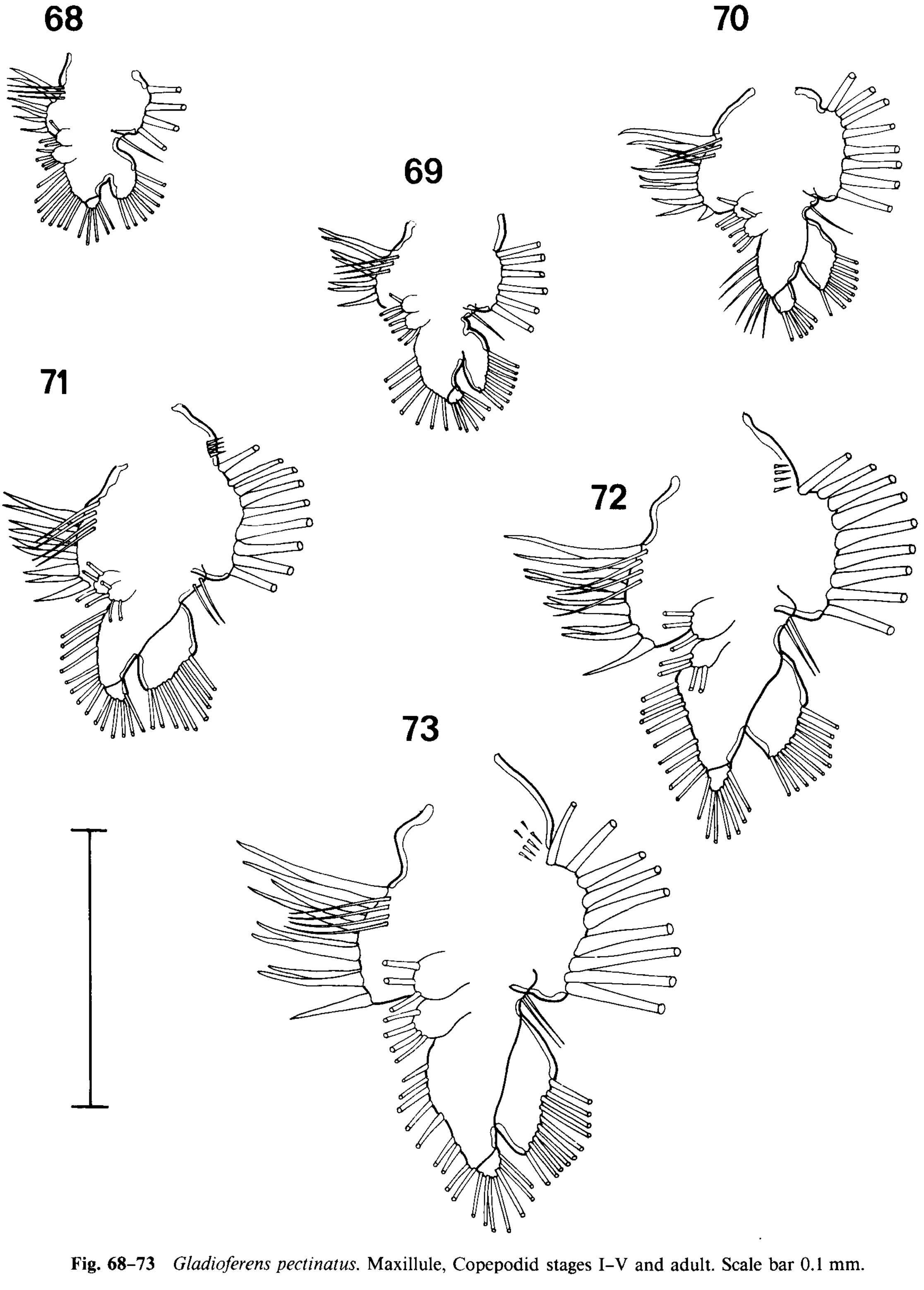


Fig. 68–73 *Gladioferens pectinatus*. Maxillule, Copepodid stages I–V and adult. Scale bar 0.1 mm.

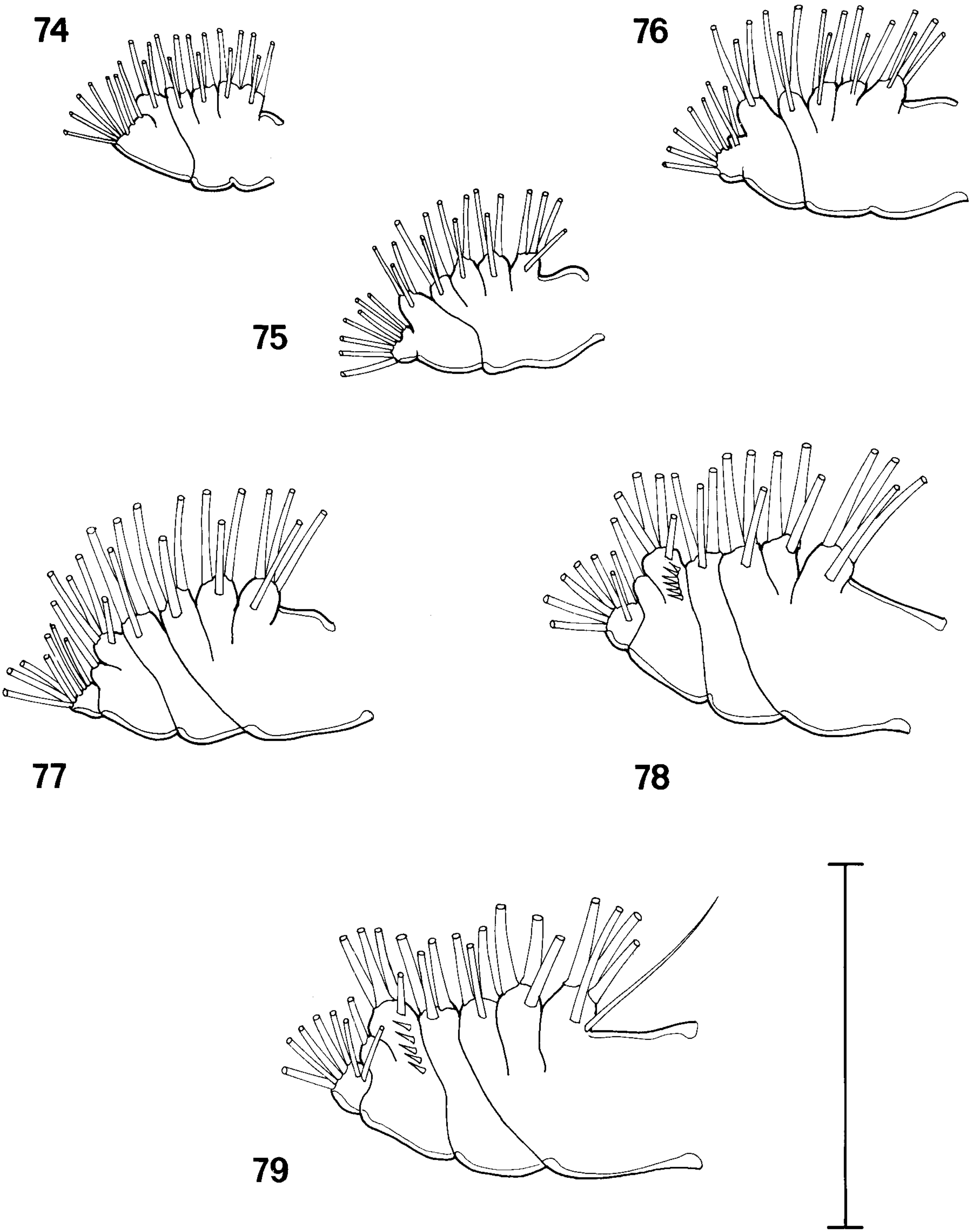


Fig. 74–79 *Gladioferens pectinatus.* Maxilla, Copepodid stages I–V and adult. Scale bar 0.1 mm.

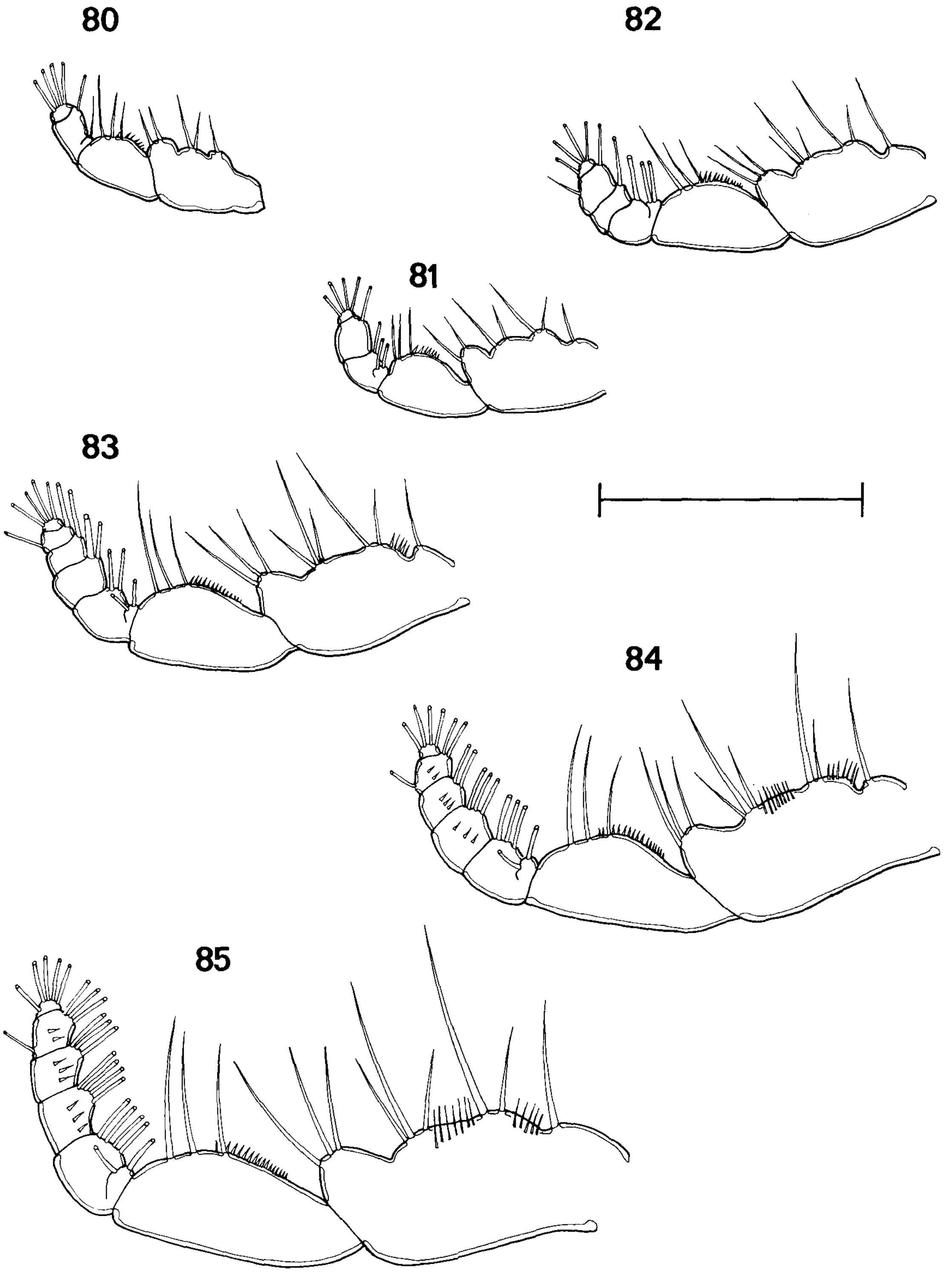


Fig. 80–85 *Gladioferens pectinatus.* Maxilliped, Copepodid stages I–V and adult. Scale bar 0.1 mm.

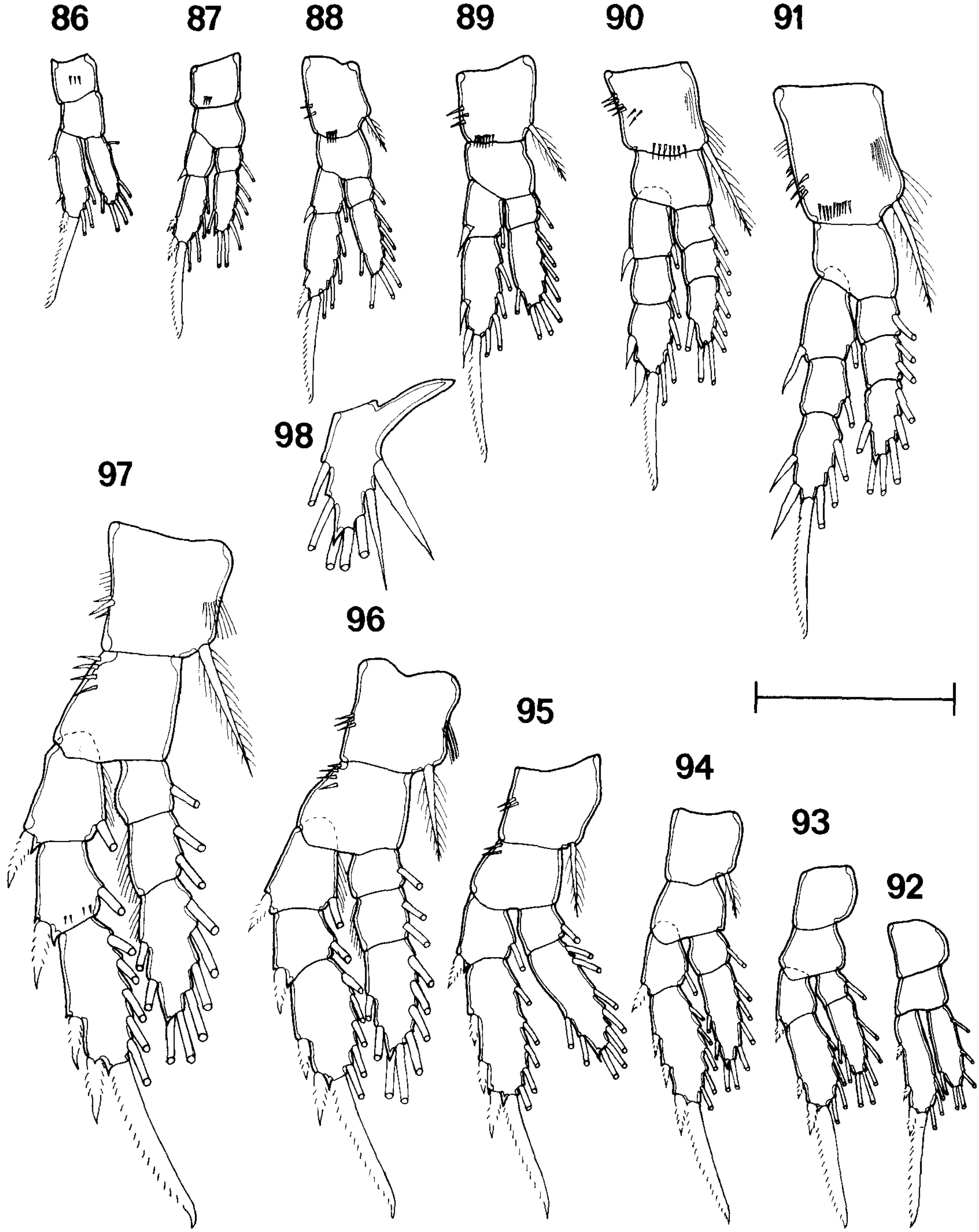
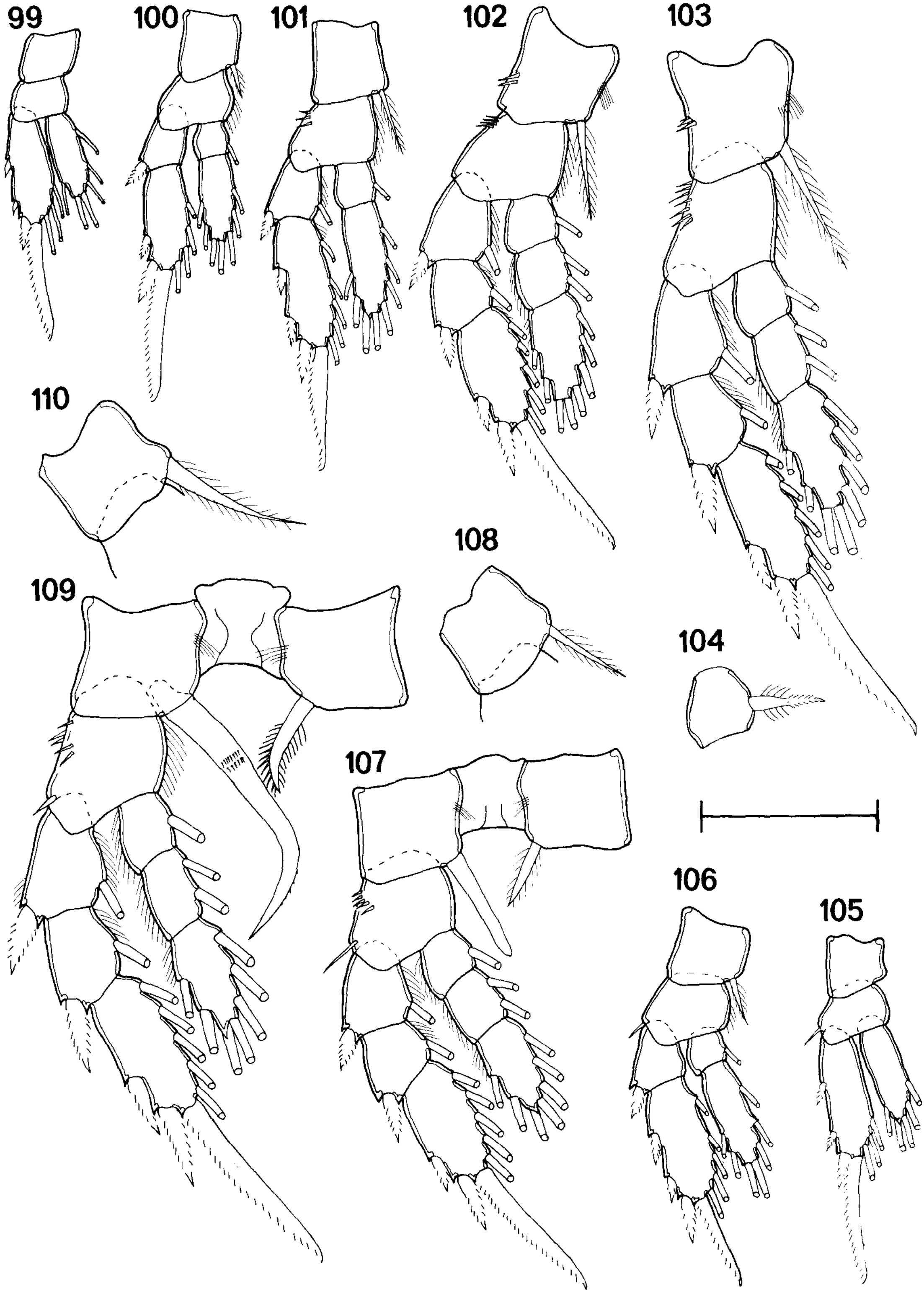


Fig. 86–98 *Gladioferens pectinatus.* 86–91; Leg 1, Copepodid stages I–V and adult; 92–96, Leg 2, Copepodid stages I–V; 97, Leg 2, adult female; 98, left terminal endopod segment of Leg 2, adult male. Scale bar 0.1 mm.

Fig. 99–110 (*opposite*) *Gladioferens pectinatus.* 99–103, Leg 3, Copepodid stages II–V and adult; 104, first endopod segment of male left Leg 3; 105–106, Leg 4, Copepodid stages III–IV; 107, Leg 4, Copepodid V, female; 108, coxa of left Leg 4, Copepodid V, male; 109, Leg 4, adult female; 110, coxa of left Leg 4, adult male. Scale bar 0.1 mm.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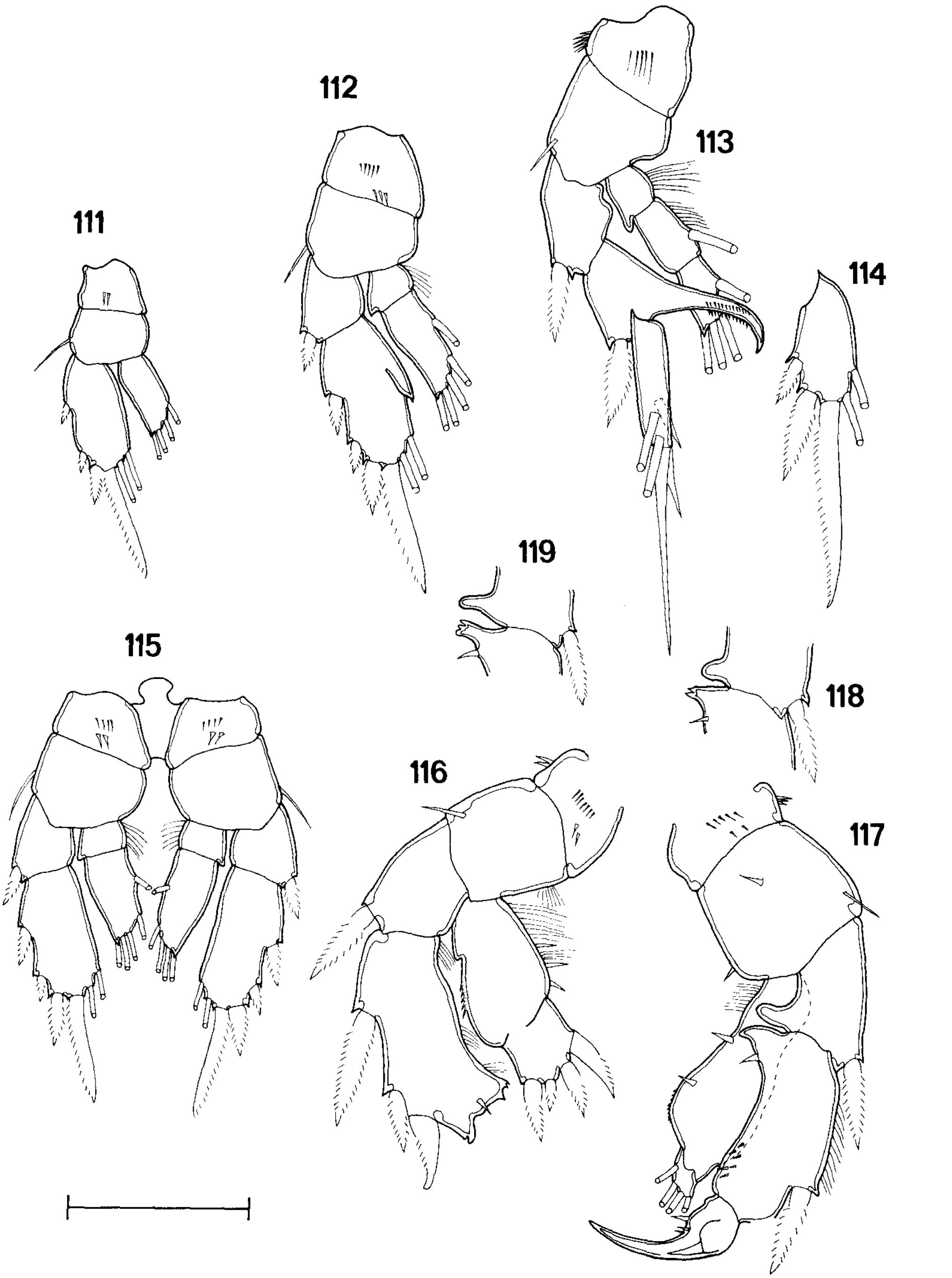

Fig. 111–119 *Gladioferens pectinatus.* Leg 5: 111, Copepodid IV; 112–113, Copepodid V and adult, female; 114, terminal segment of exopod, adult female; 115, Copepodid V, male; 116–117, left and right legs of adult male; 118–119, variation in inner marginal projections of right exopod, adult male. Scale bar 0.1 mm.

DISCUSSION

As a consequence of its wide salinity range (< 0.5–34.8×10^{-3} in the Gippsland Lakes), *G. pectinatus* co-occurs in estuaries with representatives of 5 other centropagid genera, namely *Centropages, Isias, Gippslandia, Boeckella*, and *Calamoecia* (Arnott 1968; Arnott & McKinnon unpublished data). Complete descriptions of the developmental stages of centropagids are available for only 3 other Australasian genera. Detailed illustrations of marine species are provided for *Centropages hamatus, C. typicus*, and *C. furcatus* by Oberg (1906), Lawson & Grice (1970), and Björnberg (1972) respectively, and an additional photographic treatment of *C. hamatus* is provided by Klein Breteler (1982). Koga (1960, 1970) illustrated the nauplii only of *C. abdominalis* and *C. tenuiremis* (as *C. yamadai*). Complete descriptions of freshwater species are given by Fairbridge (1945a, 1945b) for *Boeckella opaqua* and *Calamoecia tasmanica subattenuata* (as *Brunella subattenuata*). Chapman & Burns (1976) examined the copepodid stages (particularly stages IV and V) of *Boeckella propinqua, B. hamata, B. dilatata, B. triarticulata*, and *Calamoecia lucasi*. Nothing is available for the estuarine genera *Isias* or *Gippslandia*. *Gladioferens* can be distinguished at all stages of development from *Centropages, Boeckella*, and *Calamoecia*, though some caution must be exercised until further data is available on the variation between species of the same genus.

Significant differences in naupliar structure between genera are apparent in the setation of the antennules. The first segment in NI–NVI has no setae in *Gladioferens* or *Centropages*, but 1 seta is present in both *Boeckella* and *Calamoecia*. The second segment in NI–NVI bears 3 ventral setae in *Gladioferens* and 2 ventral setae in *Boeckella, Calamoecia*, and 4 of the 5 species of *Centropages* (note *C. typicus* has an additional small lateral seta in NIV–NVI). No setae were observed on segment 2 in *Centropages furcatus*, but the apparently variable setation in segment 3 suggests that this species may require further critical examination.

Differences also occur between genera in both the number and structure of the naupliar caudal spines. All genera have 2 terminal spines in NI–NII and an additional 2 lateral spines in NIII–NV, but only *Boeckella* and *Calamoecia* produce a further 2 short medial spines in NVI. *Gladioferens* differs from the other genera in that one of the terminal spines (the left) is barbed in NII–NVI, whereas the 2 lateral spines are smooth in all stages in which they occur. Both *Gladioferens* and *Centropages* possess rows of minute spines postero-ventrally on the body in NII. Although these remain present to NV in *Gladioferens* (2 rows replaced by limb buds in NVI), some are lost in later stages in *Centropages* and are replaced by 1 or 2 pairs of caudal hooks. No postero-ventral spines are figured for *Calamoecia*, and only 1 row is present at the base of caudal rami in NIII–NVI in *Boeckella*.

The naupliar stages of *Boeckella* and *Calamoecia* show a strong similarity indicating that they are probably very closely related (Fairbridge 1945b). *Gladioferens* nauplii are more similar in structure to those of *Centropages*, although the relationship is not as close as between *Boeckella* and *Calamoecia*.

Copepodid stages I–IV can be readily distinguished for all centropagids by counting the number of pairs of well-developed swimming legs (2 to 5 respectively). Stages IV and V both have 5 pairs of swimming legs but can be separated by body length, the number and/or relative size of urosome segments, and for the males by the relative development of the right antennule. *Gladioferens* copepodids can be distinguished from those of other genera through examination of legs 1. Comparative numbers of outer edge spines on the terminal segment of the exopod in copepodids I–V are as follows: *Gladioferens* 3,2,2,2,2; *Calamoecia* 2,1,1,1,1 (Fairbridge 1945b); and *Centropages* and *Boeckella* 4,3,3,3,3 (Fairbridge 1945a; Lawson & Grice 1970). *Calamoecia* also differs in retaining a 1-segmented endopod in leg 1 in copepodids II–V.

The earliest stage at which the sexes can be separated varies between centropagid species. Chapman & Burns (1976) found it impossible to distinguish between male and female stage IV copepodids of *Boeckella* and *Calamoecia* at magnifications used for routine sorting of zooplankton. Although the sexes could be distinguished for the larger species of *Boeckella* in stage V, this was not so for the small *B. propinqua* and for *C. lucasi*. Fairbridge (1945b) found the urosome of the male stage IV of *C. tasmanica subattenuata* to be "indistinctly" 4-segmented, in contrast to the 3-segmented condition of other centropagids described. *Gladioferens pectinatus* resembles *Centropages typicus* (Lawson & Grice 1970) in that the sexes are recognisable at stage IV because of the more robust right antennule in the male. At higher magnifications, sexual differences have been observed in the structure of the fifth legs in CIV copepodids of *B. hamata* (Chapman & Burns 1976), *B. opaqua*, and *C. tasmanica subattenuata* (Fairbridge 1945a, 1945b). However, such differences are only apparent in Copepodid V for *G. pectinatus, Centropages typicus* (Lawson & Grice 1970), *Calamoecia lucasi*, and 3 other species of *Boeckella* (Chapman & Burns 1976). Obvious sexual differences in the structure of the fourth legs are also evident in Copepodid V of *G. pectinatus*.

ACKNOWLEDGMENTS

We thank Mr Murray Smith for culturing the animals used in this study, and Dr G. W. Brand for his helpful comments on the draft manuscript.

REFERENCES

Arnott, G. H. 1968: An ecological study of the zooplankton of the Gippsland Lakes with special reference to the Calanoida. Unpublished BSc(Hons) thesis, Monash University, Australia.

Arnott, G. H.; Hussainy, S. U. 1972: Brackish-water plankton and their environment in the Werribee River, Victoria. *Australian journal of marine and freshwater research 23*: 85–97.

Bayly, I. A. E. 1963: A revision of the coastal water genus *Gladioferens* (Copepoda : Calanoida). *Australian journal of marine and freshwater research 14*: 194–217.

——— 1964: A new species of *Isias* (Copepoda : Calanoida) from the Brisbane River estuary, and a comparison of the Australasian centropagid genera. *Australian journal of marine and freshwater research 15*: 239–247.

——— 1965: Ecological studies on the planktonic Copepoda of the Brisbane River estuary with special reference to *Gladioferens pectinatus* (Brady) (Calanoida). *Australian journal of marine and freshwater research 16*: 315–350.

Bayly, I. A. E.; Arnott, G. H. 1969: A new centropagid genus (Copepoda : Calanoida) from Australian estuarine waters. *Australian journal of marine and freshwater research 20*: 189–198.

Björnberg, T. K. S. 1972: Developmental stages of some tropical and subtropical planktonic marine copepods. *Studies on the fauna of Curacao and other Caribbean islands 40*: 1–185.

Chapman, M. A.; Burns, C. W. 1976: Sexual and other differences in copepodite stages of some New Zealand *Calamoecia* and *Boeckella* spp. (Copepoda : Calanoida). *New Zealand journal of marine and freshwater research 10*: 131–137.

Chapman, M. A.; Lewis, M. H. 1976: An introduction to the freshwater crustacea of New Zealand. Auckland, Collins.

Fairbridge, W. S. 1945a: West Australian fresh-water calanoids (Copepoda). I. Three new species of *Boeckella*, with an account of the developmental stages of *B. opaqua* n. sp. and a key to the genus. *Journal of the Royal Society of Western Australia 29*: 25–65.

——— 1945b: West Australian fresh-water calanoids (Copepoda). II. Two new species of *Brunella*, with an account of the developmental stages of *B. subattenuata* n. sp. *Journal of the Royal Society of Western Australia 29*: 67–89.

Jillett, J. B. 1971: Zooplankton and hydrology of Hauraki Gulf, New Zealand. *New Zealand Oceanographic Institute memoir 53*: 103 p.

Kennedy, G. R. 1975: Plankton of the Fitzroy River Estuary, Queensland: (1) The upper reaches. *Proceedings of the Royal Society of Queensland 86*: 163–169.

——— 1978: Plankton of the Fitzroy River Estuary, Queensland. *Proceedings of the Royal Society of Queensland 89*: 29–37.

Klein Breteler, W. C. M. 1982: The life stages of four pelagic copepods (Copepoda : Calanoida), illustrated by a series of photographs. *Netherlands Institute for Sea Research publication series 6*: 32 p.

Koga, F. 1960: The nauplius larvae of *Centropages abdominalis* Sato. *Bulletin of the Japanese Society of Scientific Fisheries 26*: 877–881.

——— 1970: On the nauplius of *Centropages yamadai* Mori, Copepoda. *Journal of the Oceanographical Society of Japan 26*: 195–202.

Kott, P. 1955: The zooplankton of Lake Macquarie, 1953–1954. *Australian journal of marine and freshwater research 6*: 429–442.

Lawson, T. J.; Grice, G. D. 1970: The developmental stages of *Centropages typicus* Krφyer (Copepoda, Calanoida). *Crustaceana 18*: 187–208.

Neale, I. M.; Bayly, I. A. E. 1974: Studies on the ecology of the zooplankton of four estuaries in Victoria. *Australian journal of marine and freshwater research 25*: 337–350.

Nyan Taw; Ritz, D. A. 1978: Zooplankton distribution in relation to the hydrology of the Derwent River Estuary. *Australian journal of marine and freshwater research 29*: 763–775.

Oberg, M. 1906: Die metamorphose der planktoncopepoden der Kieler Bucht. *Wissenschaftliche Meeresuntersuchungen der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere, Kiel 9*: 37–103.

Rippingale, R. J.; Hodgkin, E. P. 1974: Predation effects on the distribution of a copepod. *Australian journal of marine and freshwater research 25*: 81–91.

Roper, D. S.; Simons, M. J.; Jones, M. B. 1983: Distribution of zooplankton in the Avon-Heathcote Estuary, Christchurch. *New Zealand journal of marine and freshwater research 17*: 267–278.