Biology of the Isopoda - Workshop and Conference
26-27 June 1990.
Melbourne University

Relationships of the Limnoriidae to several other flabelliferan families

by

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INTRODUCTION

The recently described flabelliferan families Keuphyliidae Bruce, 1980, Lynseiidae Poore, 1987, and Hadromastacidae Bruce and Müller, 1990 were all described by their authors as being similar to the Limnoriidae. Wägele (1989) produced a cladogram showing the possible relationships of the Limnoriidae to these and other flabelliferans. Bruce (1988) discussed the possibility of synonymy of both the Keuphyliidae and Lynseiidae with the Limnoriidae, and originally placed *Hadromastax* in the Limnoriidae. However, the true relationships could not be determined without revision of the Limnoriidae. Such a revision has been recently undertaken (Cookson, 1990), allowing this preliminary examination of the relationships of families similar to the Limnoriidae.

METHODS

The hypothetical primitive isopod is generally considered to be cirolanid-like (Schultz, 1969; Wilson et al., 1976), and for this study the cirolanid *Bathynomus* was used mostly as the outgroup to help determine character state polarity. The following characters were ordered so that 0 is the plesiomorphic state and 1-3 the apomorphic states. Some characters used were similar to those suggested by Wägele (1989).

Characters

1. Body length: less than 2.5 times long as wide (0), more than 2.5 times long as wide (1).

2. Head: fixed to pereonite (0), freely articulating (1).

3. Frontal lamina: present (0), reduced (1), absent (2).

4. Antenna 1 scale: present (0), absent (1).
The pattern of setae found on the limnoriid scale (one brush seta and three simple setae) was also found on another unidentified cirolanid, but without an obvious scale, suggesting fusion rather than scale loss.

5. Number of antennal 1 flagellar articles: more than 5 (0), 5 (1), less than 5 (2).

6. Number of antennal 2 flagellar articles: more than 5 (0), 5 (1), less than 5 (2).

7. Lacinia mobilis of left mandible: large (0), small (1), absent (2).

8. Lacinia mobilis of right mandible: not tubular or with apical perimeter of teeth (0), tubular with apical perimeter of teeth (1).

9. Mandibular palp: present (0), reduced to seta (1), absent (2).

10. Mandibular incisors: without rasp and file (0), with rasp and file (1).

11. Number of spines on outer lobe of maxilla 1: more than 10 (0), 10 (1).

12. Large inner comb seta on inner lobe of maxilla 2: absent (0), present (1).

13. Maxilliped endite: shorter than article 3 of palp (0), longer than palp (*Lynseia*) or article 3 of palp (1).

14. Maxilliped epipod: present (0), absent (1).
Although absent in cirolanids, the retention of this structure may be plesiomorphic.

15. Maxilliped coupling hooks on endite: present (0), absent (1).

16. Pereon with: 7 freely articulating coxae (0), 6 freely articulating coxae (1), 6 partially fused coxae (2).
Although cirolanids have only 6 freely articulating coxae, fusion of the first coxa may be an apomorphy.

17. Propodus of pereopod 1 distoventrally with: no comb seta (0), 1 comb seta (1), 2 comb setae (2).

18. Pereopods 2-5: not markedly tuberculate (0), tuberculate (1).

19. Pereopod 7: of similar size to other pereopods (0), longer than other pereopods (1).

20. Ventral comb seta on carpus: absent on all pereopods (0), found on pereopods 2-7 (1), present but on fewer than 6 pereopods (2).
Possibly this character should be unordered, however work on *Limnoria* and *Paralimnoria* (Cookson, 1990) suggests that state 1 is plesiomorphic to state 2.

21. Pleopod 5 with: 2 rami with setae similar to other pleopods (0), 2 rami with fewer setae than other pleopods (1), 2 rami without plumose setae (2), 1 ramus only, without plumose setae (3).

22. Number of coupling hooks on pleopod 1 peduncle: more than 3 (0), 3 (1), less than 3 (2).

23. Number of coupling hooks on pleopod 2 peduncle: more than 3 (0), 3 (1), less than 3 (2).

24. Peduncle of pleopod 2: broad (0), narrow (1).

25. Appendix masculina articulation: proximal (0), more central (1).

26. Uropod rami: flat and fan-like (0), tubular and circular in crossection, or flattened but oval in crossection (1).

27. Terminal claw on one or both rami: absent (0), present (1).

28. Number of separate sets of brush setae on endopod of uropod: none present (0), 1 (1), 2 (2), 3 (3).

29. Length of uropod exopod (excluding length of any terminal claw): similar to endopod (0), shorter but more than half as long as endopod (1), less than half as long as endopod (2).

30. Articulation of exopod on peduncle of uropod: ventrolateral (0), lateral (1).

31. Uropod endopod directed: longitudinally (0), posteromedially (1).

32. Pleonite 5 length: similar to other pleonites (0), greater than other pleonites (1).

Character state taxon matrix

	Character number						
	00000	00001	11111	11112	22222	22223	33
	12345	67890	12345	67890	12345	67890	12
Bathynomus	00000	00000	00010	10000	00000	00000	00
Paralimnoria	11201	11101	11100	12011	11200	11210	11
Limnoria	11202	21001	11100	12112	21211	11321	01
Lynseia	11212	21010	11101	22112	32211	10321	00
Keuphylia	00102	20120	01000	12001	11200	11120	10
Hadromastax	01212	22000	00111	01002	02210	00001	00

This taxon-character matrix was analysed using the computer program PAUP (Swofford, 1985). Each character was scaled to equal weight. The program was run with the MULPARS and SWAP=GLOBAL options.

RESULTS AND DISCUSSION

PAUP generated one most parsimonious tree (Fig. 1) with a tree length of 47.000 and a consistency index of 0.681. This cladogram supports the removal by Bruce and Müller (1990) of

Hadromastax from the Limnoriidae, and suggests that the Keuphyliidae and Lynseiidae could be synonymised with the Limnoriidae. Further, *Keuphylia* could be placed in a separate subfamily to *Limnoria*, *Paralimnoria* and *Lynseia*. The appropriate diagnoses would be as follows.

HADROMASTACIDAE

Material examined: none (as yet).

Diagnosis. Body semicircular or compressed in crossection. Head circular, freely articulating, pereonite 1 overlaps head posteriorly. Eyes small, lateral. Frontal lamina absent. Clypeus not expanded transversely, labrum small. Pereonites 1-7 with distinct coxal plates. Pleon with 4 segments, 2 only visible dorsally which project dorsally over pleotelson. Pleotelson without lateral crests.

Antenna 1 without scale, flagellum with 3-4 articles. Antenna 2 with 4 flagellar articles. Mandibles without lacinia mobilis, spine row or molar; incisors pointed; triarticulate palp inserted sub-proximally. Maxilla 1 with 8-11 spines on outer lobe, inner lobe with 1 short and 2-3 long flattened setae (only 2 setae in male). Maxilla 2 with 3 setae on outer and middle lobes, inner lobe with 4-5 setae. Maxilliped with pentarticulate palp (articles 4 and 5 reduced in male), without epipod or coupling hooks, endite with 5-7 long pappose setae (fewer in males), endite long, reaching beyond article 3 of palp. Pereopod 7 smaller than other pereopods, not tuberculate, with undivided secondary unguis. Ventral comb seta on carpus absent. Pereopod 1 with 1 blunt spine or comb seta ventrodistally on propodus. Pleopod coupling hook sequence 22222, peduncles without inner projection. Appendix masculina long, articulating distally from inner lobe of endopod. Pleopod 5 similar to other pleopods. Uropods anterolateral, rami flat, without claws, similar size; exopod anterolateral to endopod.

LIMNORIIDAE

Diagnosis. Pereonites 2-7 with coxal plates, freely articulating or partially fused. Pleon with 5 free segments. Clypeus transversely elongated. Antenna 1 with scale (except *Lynseia*), scale usually with 1 brush and 3 simple setae. Antenna 2 lateral or ventrolateral to antenna 1. Mandible with incisors pointed, lacinia mobilis, and setal row on right mandible, with or without palp. Molar absent. Maxilla 1 with 2 lobes. Maxilla 2 with 2 setae on outer lobe, 3 on middle lobe, and inner lobe with large inner seta. Maxilliped with epipod. Pereopods with secondary ungui. With ventral comb seta on carpus of pereopods 6 and 7, and often other pereopods. Pereopod 1 with 2 comb setae ventrodistally on propodus. Pleopod 5 with reduced size (even absent) and/or reduced setation, without coupling hooks. Uropod peduncle ventral, rami tubular (oval or circular in crossection), exopod shorter than endopod, endopod with brush setae, rami may possess terminal claw.

KEUPHYLIINAE

Keuphylia

Material examined: 'Pandora" wreck, stns NQ 22, 24, 25.

The specimens examined differ from *Keuphylia nodosa* in several respects, such as the absence of pleopod 5, and so may represent a new species.

Diagnosis. Body dorsoventrally compressed, 1.8 times as long as wide, longitudinally oval-disc shape. Head flat, fixed and surrounded laterally by pereonite 1, anterior margin of pereonite 1 with downward curvature. Eyes dorsal. Antenna 2 lateral to antenna 1. Frontal lamina reduced, visible only from above. Clypeus not reaching lateral margin of antenna 2 articulation. Labrum broad. Pereonites 2-7 with coxae freely articulating. Pleonite 5 similar length to other pleonites, pleonite 1 not extending ventrally as far as other pleonites. Pleotelson elongate and rectangular, surrounded laterally by pleonite 5, without lateral crests.

Antenna 1 with scale, bearing 3 simple setae and 1 brush seta, with 3 flagellar articles. Antenna 2 with 4 flagellar articles. Left mandible with setal row and large lacinia mobilis, right mandible with tubular lacinia mobilis with perimeter of apical teeth; palp absent. Maxilla 1 outer lobe with 11 spines, inner lobe with 3 setae. Maxilliped with pentarticulate palp; endite short, not reaching beyond article 3 of palp, with 1-2 coupling hooks. Pereopods all similar size, not tuberculate, with undivided secondary unguis. Ventral comb seta present on carpus of pereopods 1-7. Pleopod coupling hook sequence 32220, peduncles broad. Appendix masculina articulating proximally. Pleopod 5 absent or present, with 2 rami when present. Ventral uropods posterolateral, rami flattened but tubular, directed posteromedially, endopod curved and with long terminal claw, with 1 set of brush setae. Uropod exopod ventrolateral, without claw, less than half as long as endopod.

LIMNORIINAE

Body semicircular in crossection, elongated, 3-15 times as long as wide. Head circular or oval, freely articulating, mobile. Anterior margin of pereonite 1 directed upwardly or level with body, overlaps head posteriorly. Eyes lateral. Frontal lamina absent. Clypeus reaching lateral margin of antenna 2 articulation. Labrum circular. Pleotelson with lateral crests. Antenna 2 ventrolateral to antenna 1. Mandible with palp or replacement seta, left mandible with small lacinia mobilis. Outer lobe of maxilla 1 with 5 smooth outer spines and 5 serrated inner spines, inner lobe with 1 short and 3 long setae. Maxilliped endite long, reaching beyond article 3 of palp. Pereopod 7 longer than other pereopods. Uropods ventrolateral.

Paralimnoria

Material examined: see Cookson (1990).

Diagnosis. Head circular. Pleonite 5 longer than other pleonites, 0.8-0.9 times as long as pleotelson, with lateral crests. Pleonite 1 not extending ventrally as far as other pleonites. Pleotelson posteriorly semi-circular.

Antenna 1 with large scale, bearing 1 brush and 3 simple setae, with 5 flagellar articles. Flagellum of antenna 2 with 5-6 articles. Left mandible with 3 serrated setae in setal row. Right mandible with tubular lacinia mobilis bearing perimeter of apical teeth. Mandibular palp with 3 articles. Incisors with rasp and file surfaces. Five smooth outer spines on outer lobe of maxilla 1 with 4 similar in length and fifth more than half this length. Maxilliped with pentarticulate palp, endite with 1 coupling hook, apically with 5 curved pappose setae of similar form. Pereopods not markedly tuberculate. Secondary unguis on pereopod 1 trifid, occasionally bifid. Ventral comb seta present on carpus of pereopods 2,3,5,6,7 and sometimes 4. Pleopod coupling hook sequence 32220, peduncle of pleopods 1-4 broad. Appendix masculina articulating proximally. Pleopod 5 nearly as large as other pleopods. Uropod rami directed posteromedially, with long terminal claws, endopod with 2 sets of brush setae. Exopod more than half as long as endopod (claw length not included), ventrolateral. Uropod peduncle with trifurcate pappose setae ventrally.

Limnoria

Material examined: see Cookson (1990).

Diagnosis. Head circular. Pleon with pleonite 5 longest, 0.3-0.9 times as long as pleotelson, with lateral crests. Pleonite 1 not extending ventrally as far as other pleonites. Pleotelson posteriorly semicircular.

Antenna 1 with scale bearing 1 brush (except *L. cristata*) and 3 simple setae, flagellum with 3-4 articles. Antenna 2 flagellum with 3-5 articles. Left mandible with 0-2 serrated setae in setal row. Mandibular palp with 0-3 articles, replaced by seta if lost. Incisors with or without rasp and file. Five smooth outer spines on outer lobe of maxilla 1 with 4 similar in length and 1 less than half this length. Maxilliped with pentarticulate palp, endite with 1 coupling hook, apically with 3 curved pappose setae of similar form. Pereopods usually tuberculate. Secondary unguis present on pereopod 1 at least, pereopod 1 secondary unguis bifid or variable. Ventral comb seta present on carpus of pereopods 6 and 7, and sometimes 2,3,4, or 5. Pleopod coupling hook sequence 32220, 22220 or 33330, peduncle narrow. Appendix masculina articulating near mid-length of endopod. Pleopod 5 nearly as long or smaller than other pleopods, without plumose setae. Uropod exopod with terminal claw (rarely

without claw), endopod with 3 sets of brush setae. Exopod less than half as long as endopod (claw length not included), lateral to endopod. Uropod peduncle without trifurcate pappose setae.

Lynseia

Material examined: type material.

Diagnosis. Body markedly elongate, about 15 times as long as wide. Head longitudinally ovoid. Coxae on pereonites 2-7 partially fused to tergites. Clypeus anteriorly produced. Pleonites all similar in length, tergum of pleonite 1 extending ventrally as far as other pleonites. Pleotelson elongated.

Antenna 1 without scale, flagellum with 3 articles. Antenna 2 flagellum with 1 article. Left mandible without setal row. Mandibular palp lacking, replaced by simple seta. Incisors without rasp and file (as typified in *Limnoria*), left mandible with row of ridges above rasp position. Lacinia mobilis on right mandible absent? Five smooth outer spines on outer lobe of maxilla 1 with 4 similar in length and 1 less than half this length. Maxilliped with single articled palp, endite without coupling hook. Pereopods 2-5 tuberculate. Secondary unguis of pereopod 1 with 2 small ventral branches. Ventral comb seta present on carpus of pereopods 6 and 7. Pleopod coupling hook sequence 22220, peduncles without inner projection. Appendix masculina articulating sub-proximally. Pleopod 5 with 1 ramus, as long as other pleopods (excluding setal lengths), without plumose setae. Uropod rami without terminal claws, endopod with 3 separately positioned brush setae. Exopod less than half as long as endopod, lateral to endopod. Uropod without trifurcate pappose setae.

FIGURES

The drawings of *Bathynomus* were taken from Bruce (1986), *Hadromastax* from both Bruce (1988) and Bruce and Müller (in press), most of *Lynseia* from Poore (1987) and some of *Keuphylia* from Bruce (1980).

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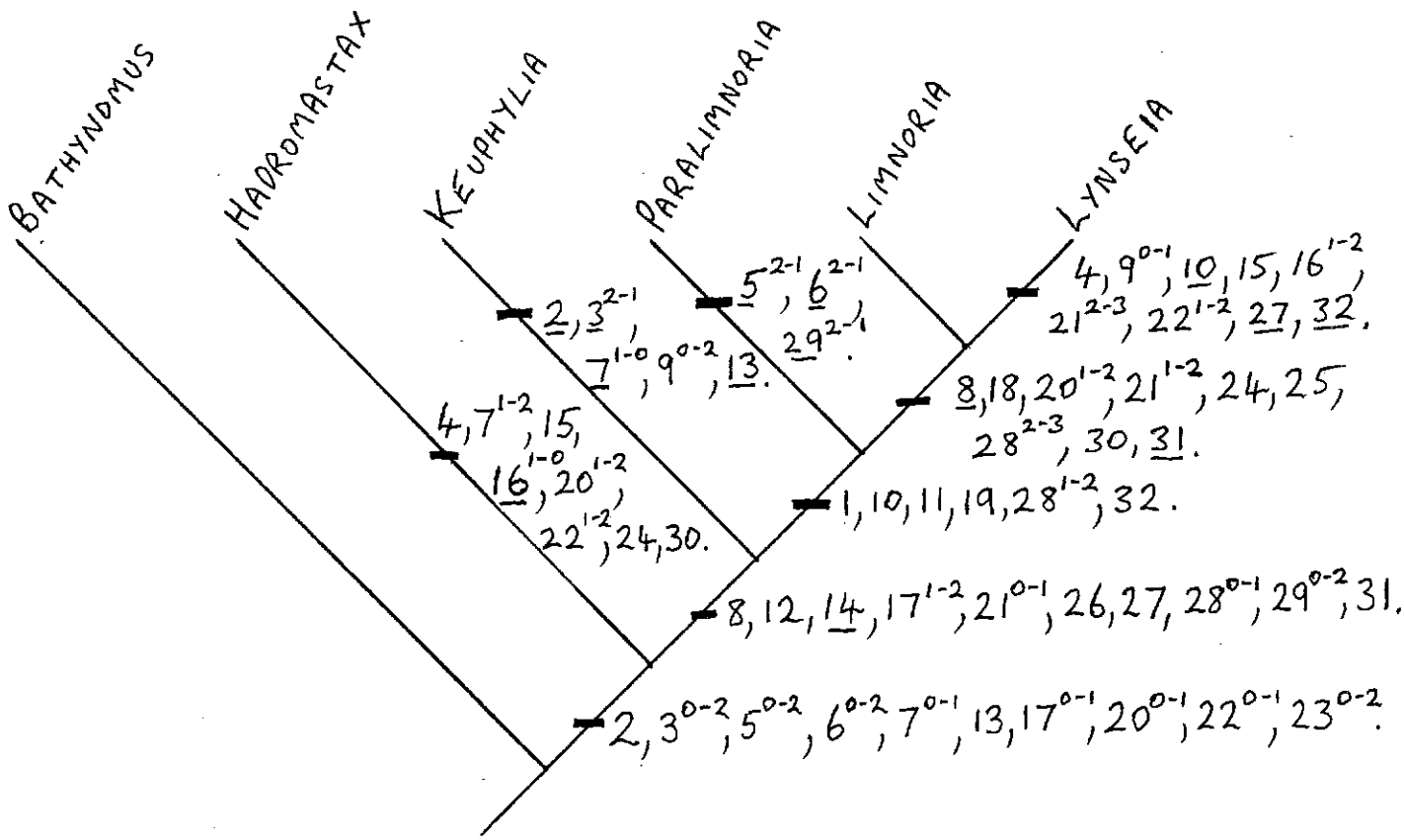
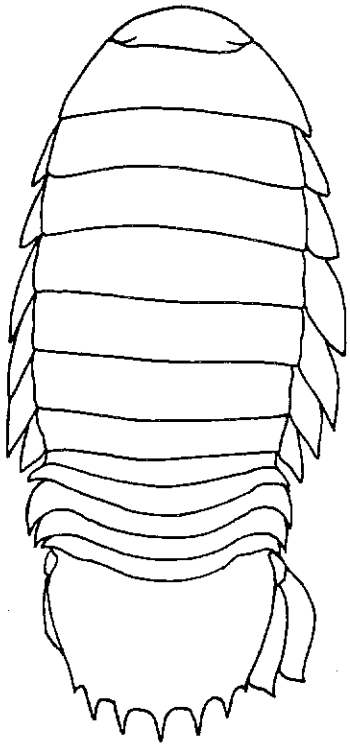
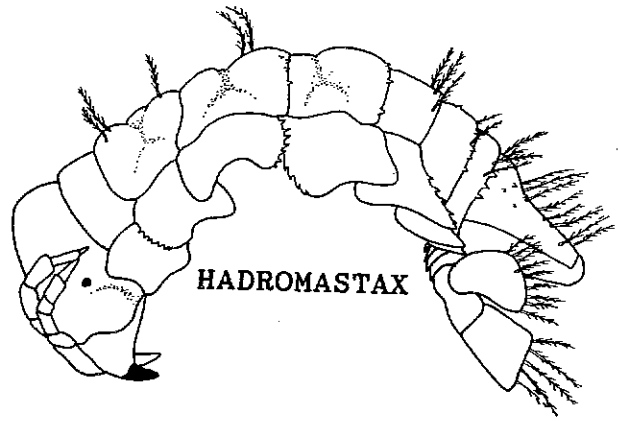


FIGURE 1

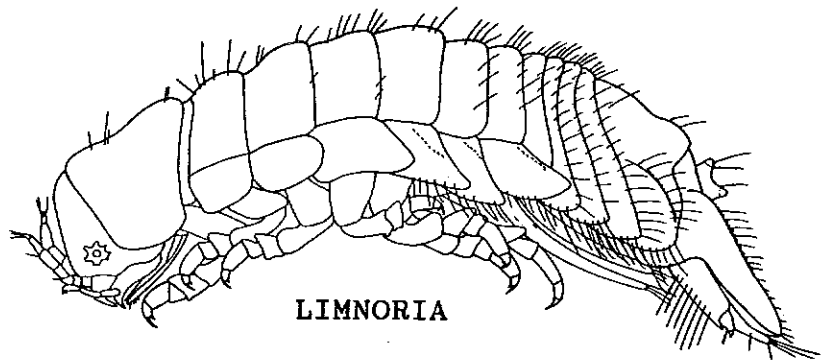
Cladogram generated by PAUP.
Underlined character numbers are reversals.
For multistate characters, superscripts indicate ancestral followed by derived states.



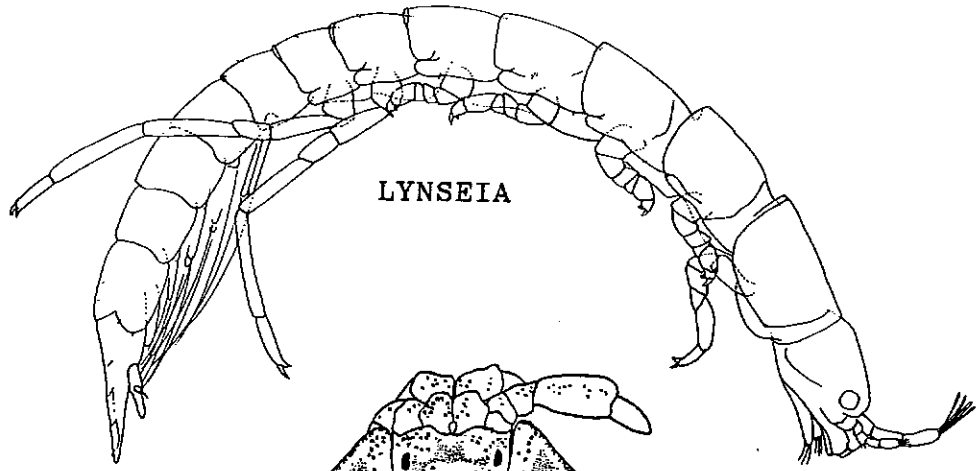
BATHYNOMUS



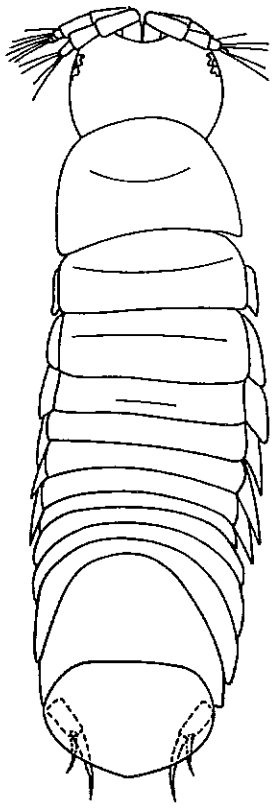
HADROMASTAX



LIMNORIA



LYNSEIA



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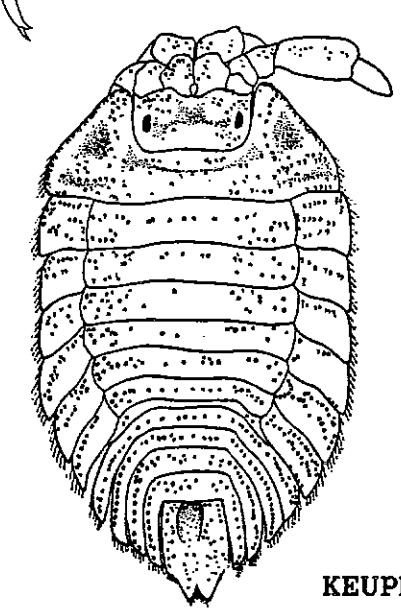
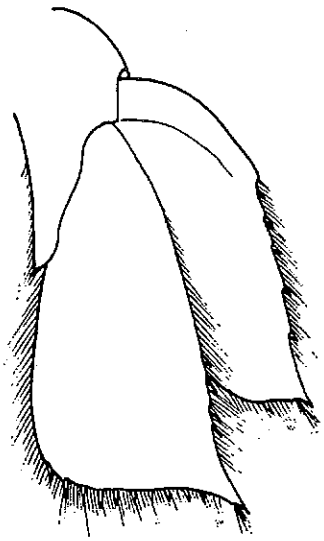


KEUPHYLIA



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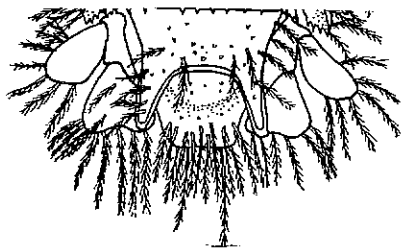
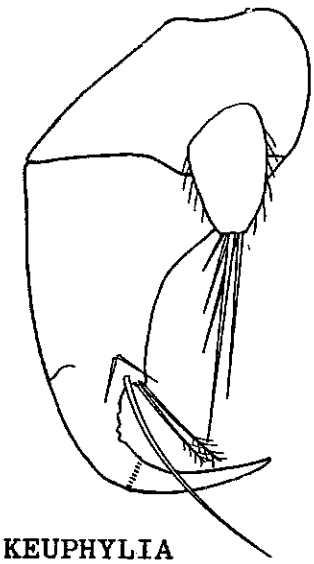


HADROMASTAX



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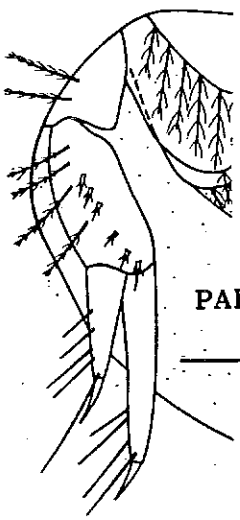

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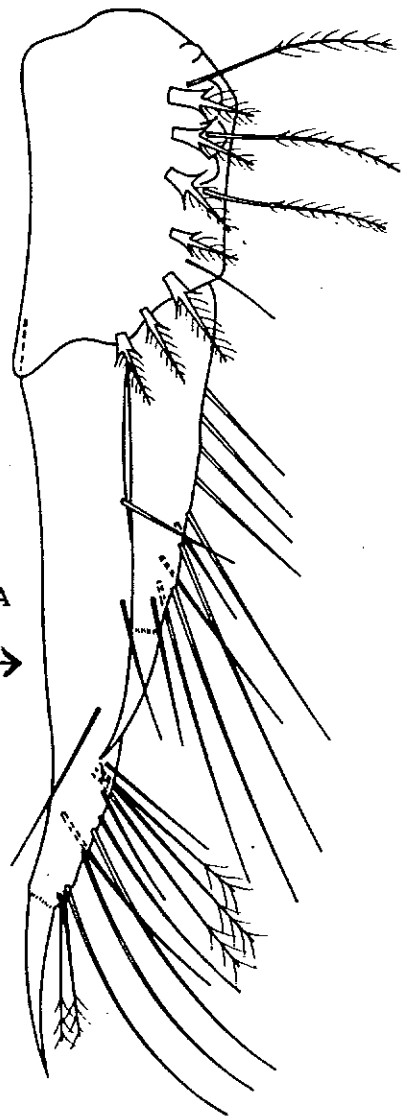
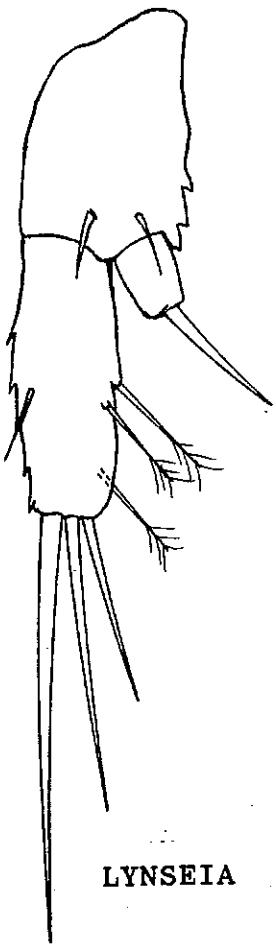
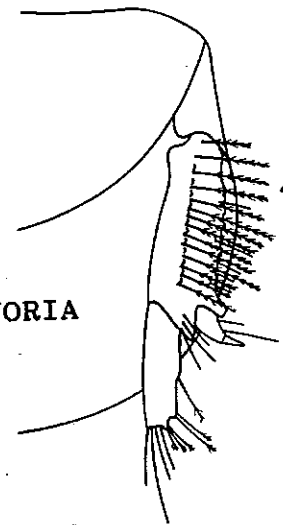
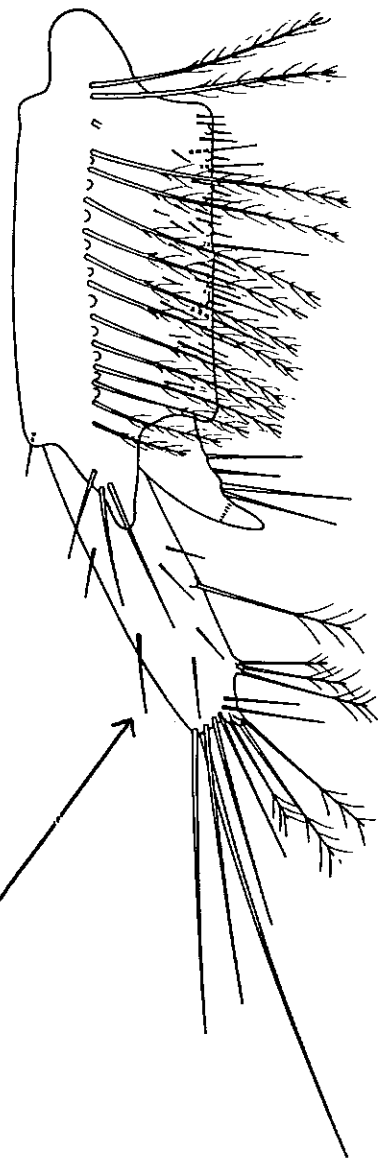




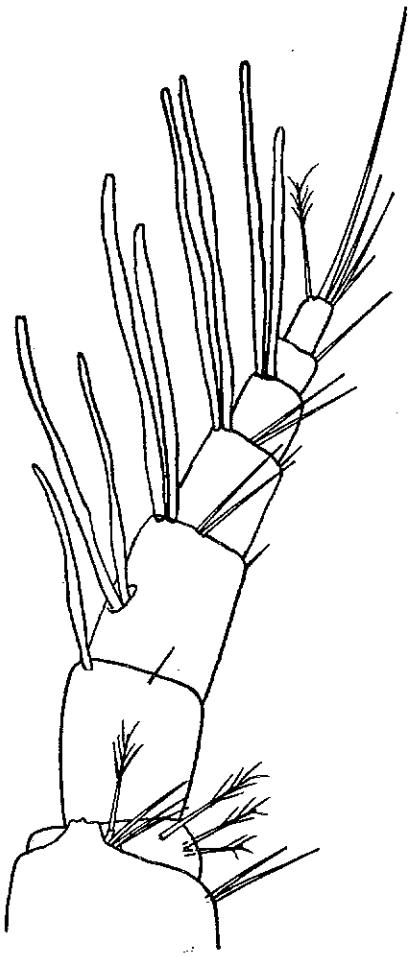
LYNSEIA



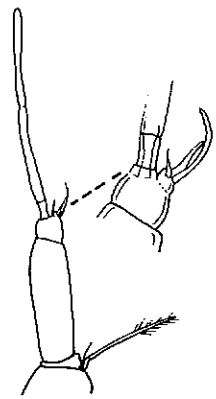
LIMNORIA



Uropods

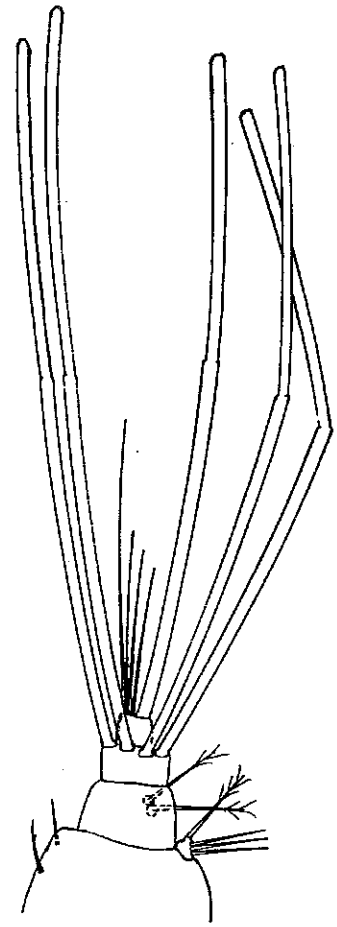


CIROLANID



HADROMASTAX

BATHYNOMUS



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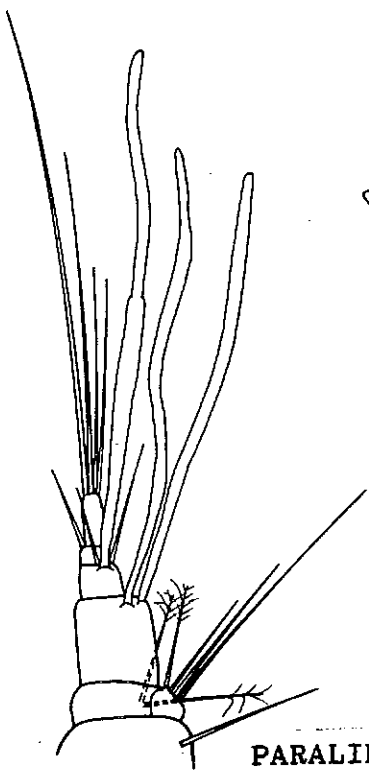
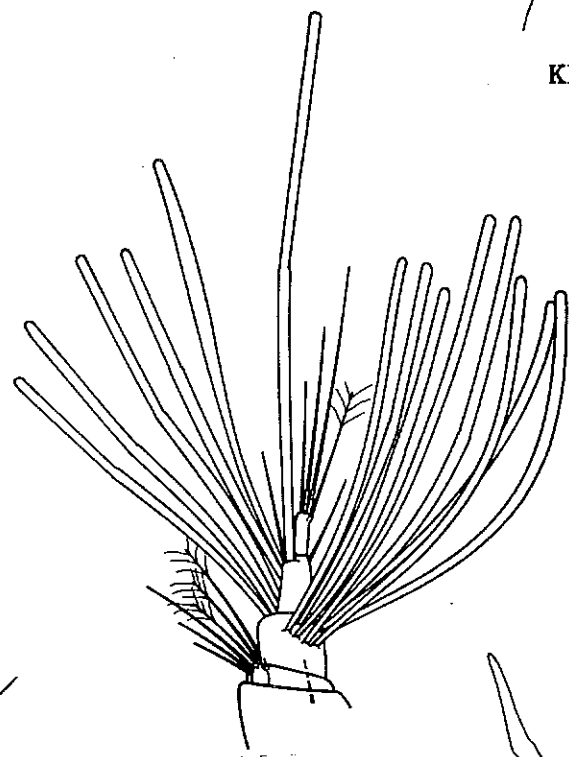
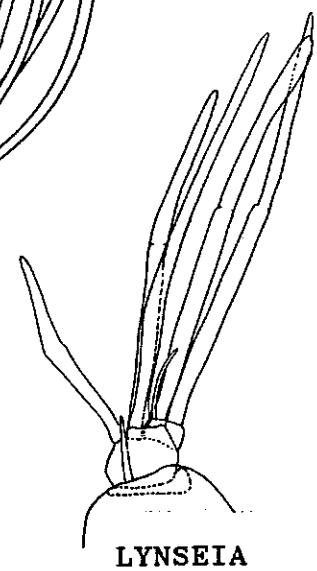


PARALIMNORIA



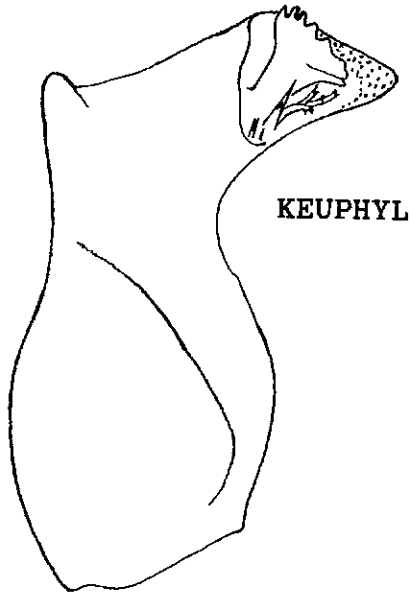
LIMNORIA



LYNSEIA

Antenna 1 flagellum

BATHYNOMUS



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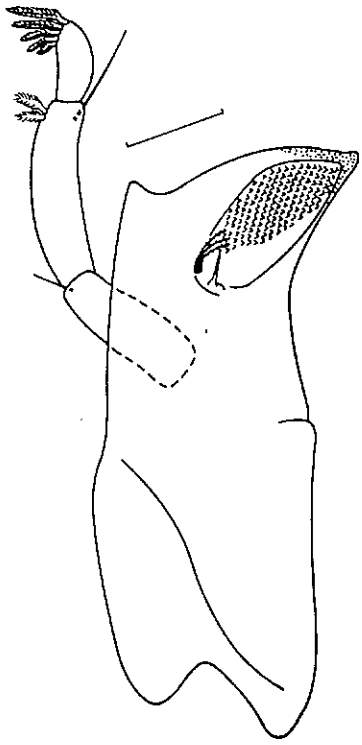
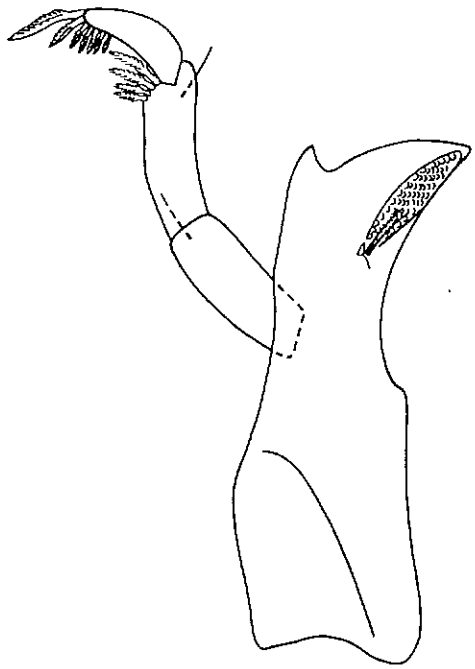


PARALIMNORIA



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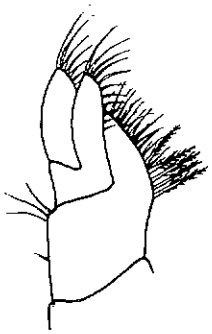
LYNSEIA

Left mandibles



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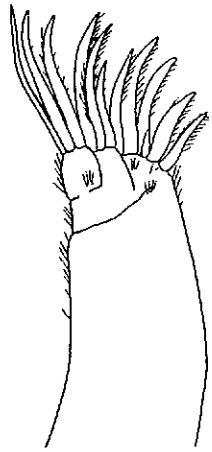

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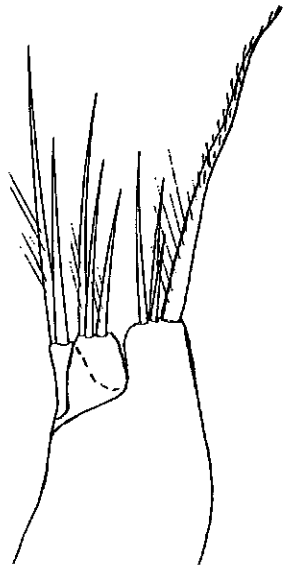

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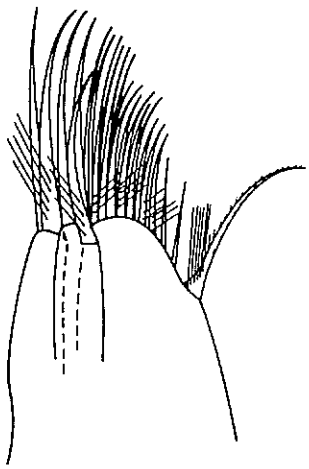

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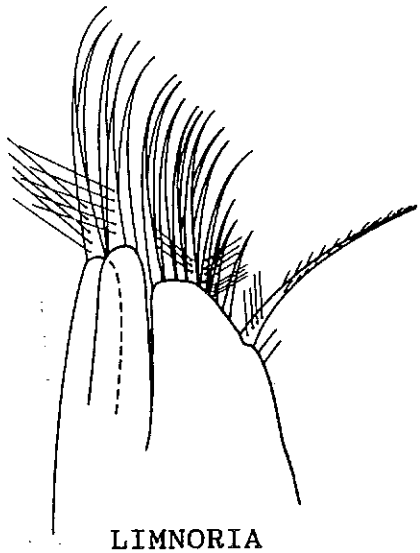

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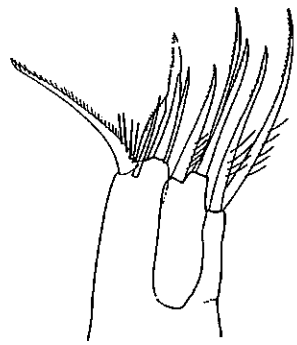

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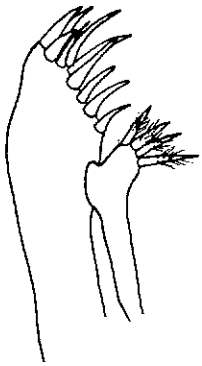

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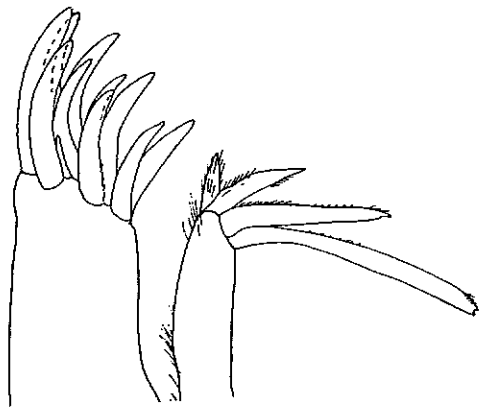

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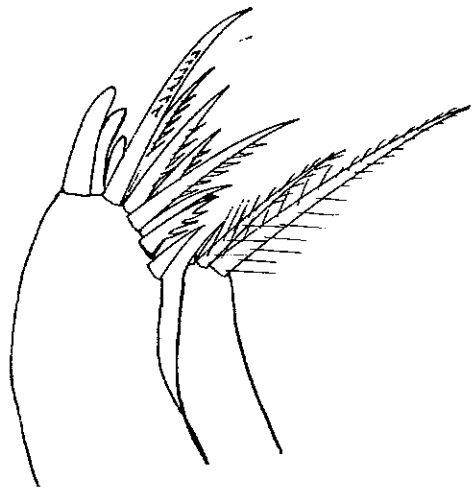

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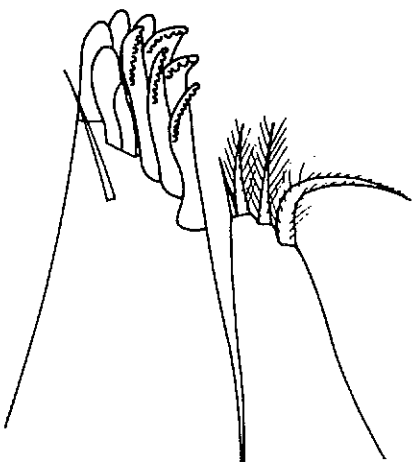

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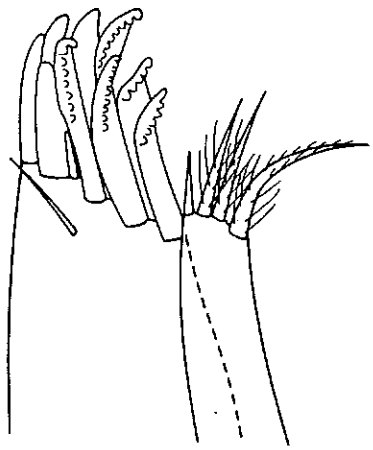

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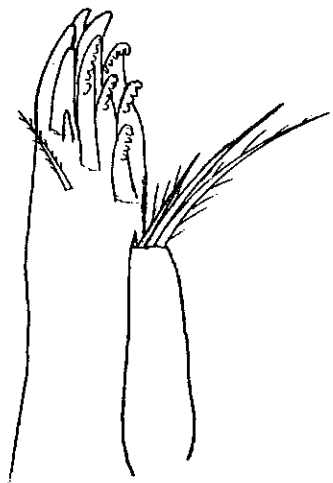

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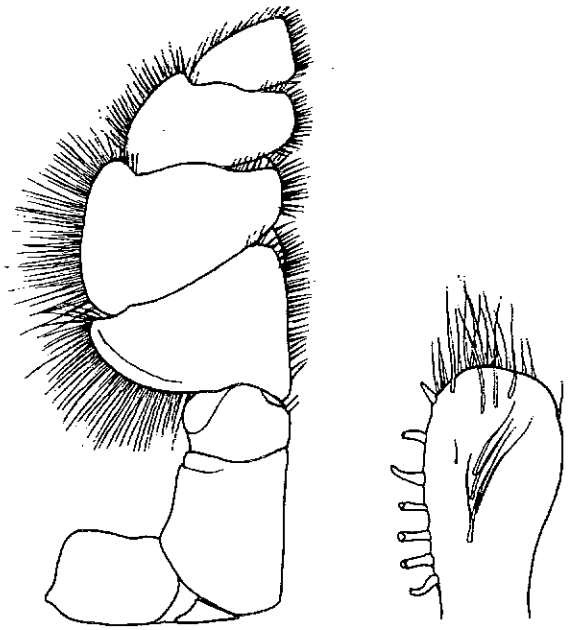

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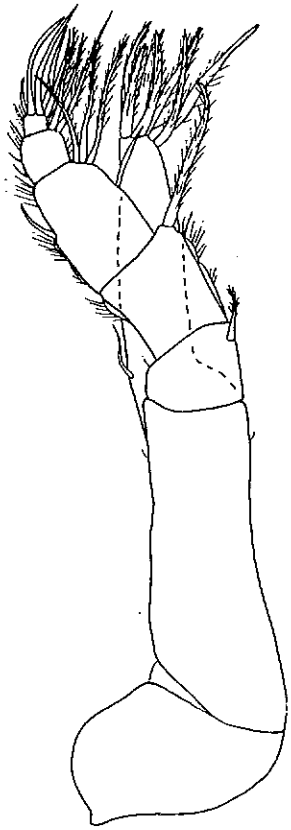

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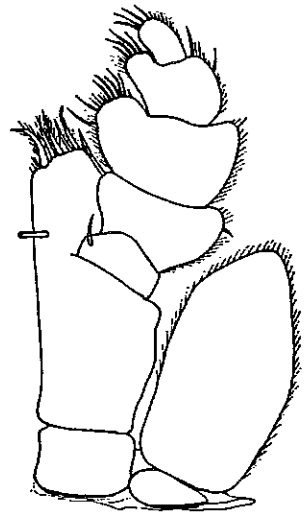

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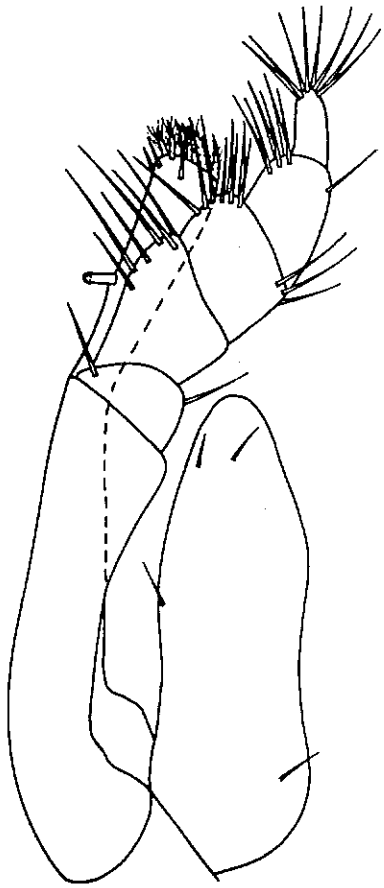

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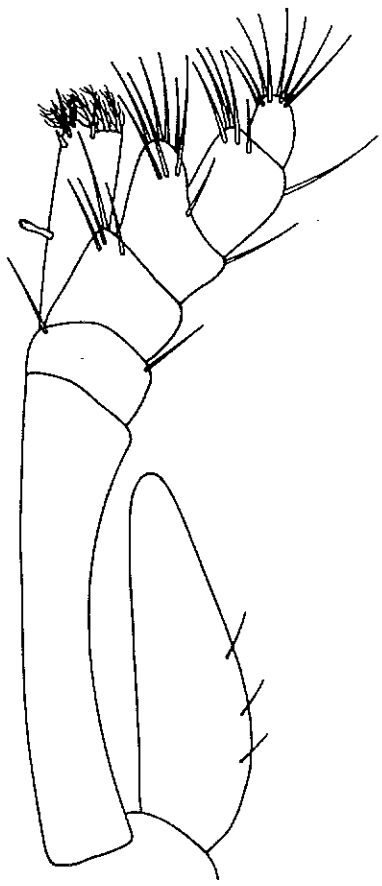

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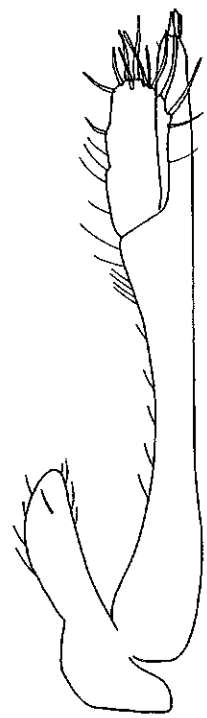

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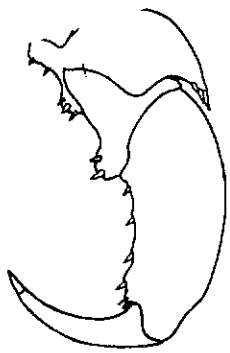
Maxillipeds



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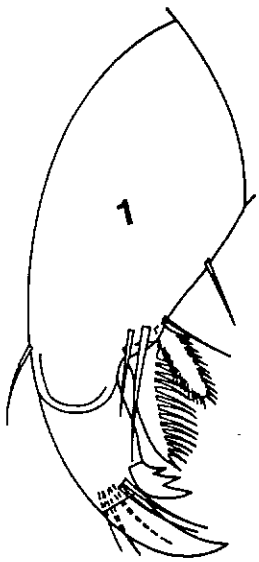

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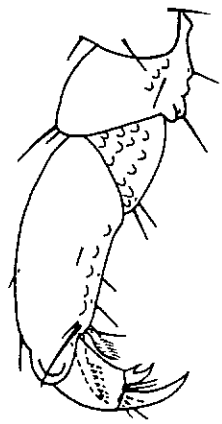

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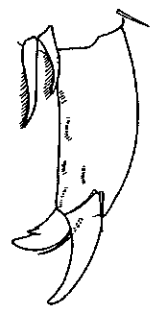

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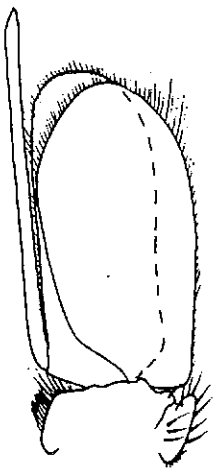
Pereopod 1



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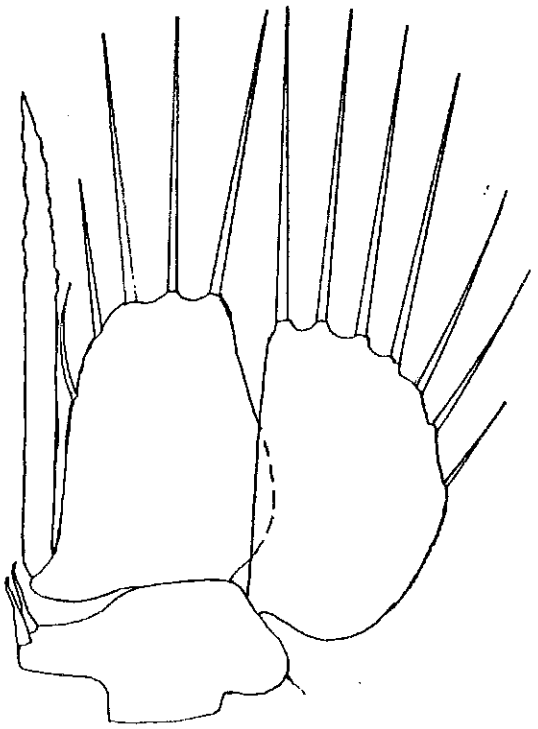

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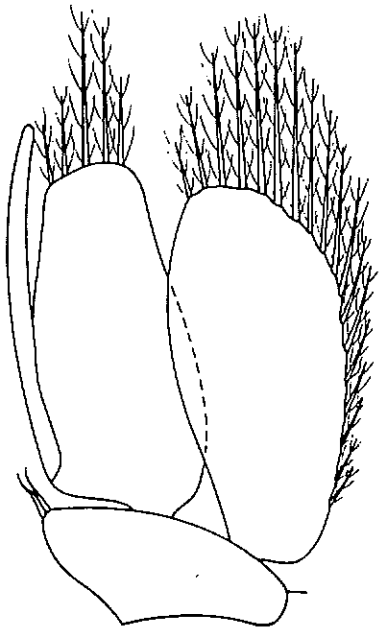

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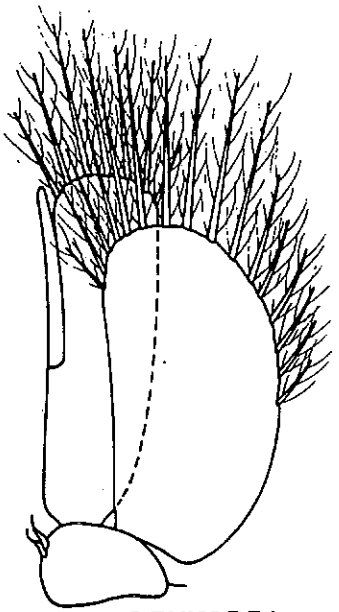

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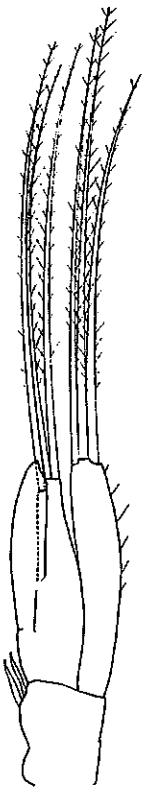

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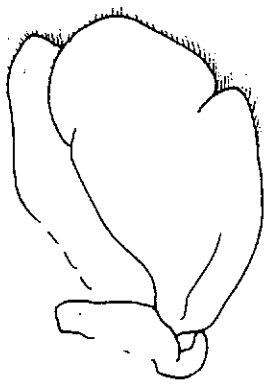

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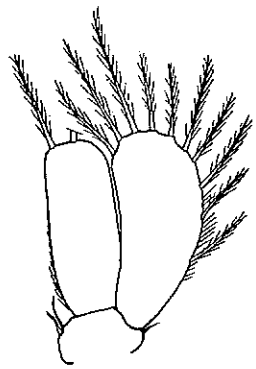

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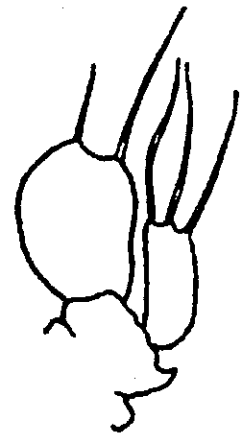

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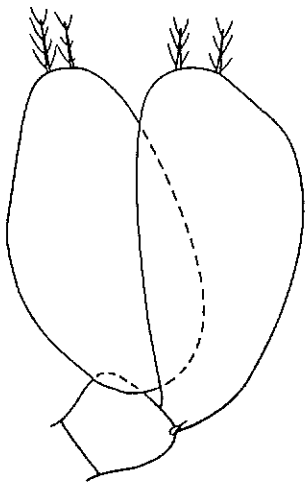

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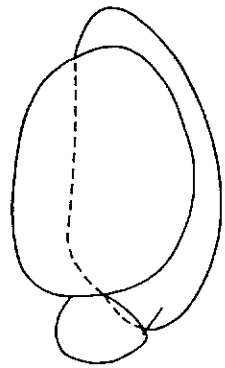

LIMNORIA

LYNSEIA

Pleopod 5