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On the Relationships of the Normanellidae and the Recognition of Cletopsyllidae grad. nov. (Copepoda, Harpacticoida)

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Abstract. The phylogenetic relationships of the families of the Laophontoidea are re-assessed in the light of new morphological data on the Normanellidae. The taxonomic concept of the latter is restricted to the subfamily Normanellinae which on account of the morphology of antennule, antenna, mandible, P1, P2 and male P6 is regarded as the most primitive lineage within the Laophontoidea. Cladistic analysis has confirmed HUYS' (1990a) phylogenetic scheme for the remaining families.

Both sexes of a new genus and species, *Bathycletopsyllus hexarthra*, are described from 460 m depth off La Réunion. The genus *Cletopsyllus* Willey is reviewed, resulting in the recognition of two new genera *Retrocalcar* and *Isocletopsyllus* which are based on differences in antennule morphology, male leg 5 armature and sexual dimorphism of swimming legs and caudal rami. *Cletopsyllus tertius* Por, 1964 *sensu* POR (1967) and *C. quartus* Soyer, 1966 *sensu* MARCUS (1976) are considered *species inquirendae* in *Isocletopsyllus* whereas *Pseudocletopsyllus* Vervoort is maintained as *genus inquirendum* within the Cletopsyllidae. The major morphological transformations and diagnostic characters of the family are reviewed and a key to genera is presented. Swimming leg sexual dimorphism has proved inappropriate for inferring the evolutionary relationships of the Cletopsyllidae which remain enigmatic at present.

Key words. Phylogeny, systematics morphology.

1. INTRODUCTION

The phylogenetic position of the Normanellidae has not been properly addressed since HUYS & WILLEMS (1989) removed the subfamily Normanellinae from the Laophontidae and upgraded it to family level. At present the family contains two subfamilies, the Normanellinae and the Cletopsyllinae, which were intentionally introduced by HUYS & WILLEMS (1989) in order to reflect its diphyletic status. The Normanellinae has been the subject of recent revision by LEE & HUYS (in press) who redefined the generic concept of the type genus *Normanella* Brady and recognized one new genus. No new information has been published on the Cletopsyllinae since HUYS & WILLEMS' (1989) recognition of the subfamily. The relationships and position of both subfamilies in the harpacticoid classification are yet to be elucidated, however, a close affinity of either of these monophyletic lineages to the superfamily Laophontoidea was ruled out by HUYS (1990a).

HUYS (1990a) excluded the Normanellinae from the Laophontoidea on the basis of the following suite of plesiomorphic character states [laophontoidean alternative (apomorphic) character states are given in square brackets]: (1) antenna with separate basis and proximal endopod segment [with allobasis]; (2) P1 exp-2 with inner seta [without]; (3) P1 exp-3 with 2 geniculate setae and 3 spines [2 spines]; (4) P1 enp-2 with inner lateral seta and 2 distal elements [inner seta absent]; (5) P2 enp-2 with 3 inner setae [at most 2 inner setae]; (6) P3 endopod ♂ without genuine apophysis [with]; (7) P5 baseoendopod ♀ with 6 setae [at most 5 setae]; (8) P6 ♂ symmetrical and with 3 setae [asymmetrical and with 2 setae].

LEE & HUYS' (in press) revision of the Normanellinae has revealed new information of phylogenetic significance, necessitating a review of some of the character states listed above which had been based on erroneous observations in the literature. HUYS' (1990a) phylogenetic scheme of the five laophontoidean families, which was generated by hand, will be re-appraised in the light of these new data.

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2. MATERIAL AND METHODS

The descriptive terminology is adopted from HUYS & BOXSHALL (1991). Abbreviations used in the text are: ae, aesthetasc; P1–P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus. Specimens of *Bathycletopsyllus hexarthra* and *Cletopsyllus secundus* were examined with a Zeiss Axioskop microscope equipped with differential interference contrast.

Phylogenetic relationships between taxa were analysed using the phylogenetic computer package PAUP 3.1 prepared by David L. Swofford of the Laboratory of Molecular Systematics, Smithsonian Institution (SWOFFORD 1993; SWOFFORD & BEGLE 1993). Since evolution within the Copepoda is assumed to proceed typically by oligomerization (HUYS & BOXSHALL 1991), all characters were set irreversible using the CAMIN-SOKAL option. This option suppresses character reversals at the expense of introducing extra convergences and thereby increasing the tree-length. The options employed in the analysis were BRANCH AND BOUND, which guaranteed to find all most parsimonious trees, and the MINF optimisation, which assigns character states so that the f-value is minimized.

3. PHYLOGENETIC POSITION OF NORMANELLIDAE

3.1. Characters

The discovery of *Archilaophonte maxima* by WILLEN (1995) and the recent study of *Normanella* Brady by LEE & HUYS (in press) necessitate an update of the characters used by HUYS (1990a) to define the Laophontoidea in general and the Laophontidae in particular.

Antennule. HUYS (1990a) considered the presence of a spinous process on the posterior margin of the second antennulary segment as a synapomorphy for the Laophontoidea. Within the Laophontidae he regarded the absence of this structure in *Esola* Edwards, 1891 as secondary even though this genus represented the most primitive laophontid known. The presence of a well developed thorn-like process on the antennules of *Archilaophonte* gives further credence to this hypothesis since this genus is even more primitive than *Esola* and appears to belong to the same lineage (WILLEN 1995). The process is absent in all Normanellidae.

Mandible. The mandible of *A. maxima* possesses a well defined exopod allowing unequivocal identification of the setae on the palp in other Laophontidae (WILLEN 1995). This character is a unique plesiomorphy within the Laophontoidea *sensu* HUYS (1990a) but is also found in the Normanellidae.

Maxilliped. The syncoxa of *A. maxima* bears 3 setae which is the maximum recorded in any laophontoidean (including the Normanellidae).

P1 endopod. The absence of an inner seta on the proximal endopod segment was scored as an apomorphy for the Laophontidae by HUYS (1990a). WILLEN (1995) has demonstrated its presence in *A. maxima* since and a study of the *Esola*-group by the senior author revealed that it is also retained in some primitive members of this complex, such as *E. typhlops* Sars, 1908. In fact, already DRZYCIMSKI (1969) had recorded this seta in the latter species but his observation remained unnoticed in subsequent literature.

P3 endopod ♂. The few published records describing the P3 endopod in male Normanellidae usually do not contain the detail necessary for assessing its homology. Often not all the elements are illustrated or the outer apophysis is figured as an articulating spine (NOODT (1955) for *N. mucronata reducta*; KLIE (1950) and PALLARES (1975) for *N. minuta*). In the majority of the species for which the male has been described (SARS 1909; MONARD 1935; LANG 1936, 1965; POR 1959) swimming leg sexual dimorphism has apparently not been recorded. Our observations on a wide range of species has revealed that this alleged absence is based on an error which is further supported by BODIN's (1968, 1972) excellent descriptions of the males of *N. minuta*"?" and *N. aberrans*. Even in the absence of ontogenetic evidence, detailed comparison of the armature pattern of both sexes clearly indicates that the male apophysis represents the homologue of the female outer spine. This homology is identical to that of the families of the Laophontoidea and provides robust evidence for a sistergroup relationship of the Normanellidae. HUYS (1990a) documented the ontogeny of the apophysis in male Orthopsyllidae and the formation of a 3-segmented endopod by separation of the distal half of enp-2. A similar 3-segmented condition has also evolved in the Adenopleurellidae (HUYS 1990b) and many primitive Laophontidae, and it almost certainly represents the plesiomorphic state for the superfamily. In the Cristacoxidae and Laophontopsidae, however, distal secondary subdivision did not occur (HUYS 1990a; HUYS & WILLEMS 1989) and this condition is also displayed by the Normanellidae. This circumstantial congruence is not necessary evidence for common ancestry since the modification of the other elements of the distal endopod segment is significantly different between families. In both Cristacoxidae and Laophontopsidae modification of the male endopod does not affect the two apical setae, but the inner seta (only one is present in these families) is strongly reduced to a minute spinous process (Cristacoxidae) or lost altogether (Laophontopsidae). In the Normanellidae none of the 3 inner setae is transformed, however, both apical setae are strongly reduced and represented by two setule-like elements in the male.

P5 armature ♀. HUYS (1990a) remarked that the ♀ P5 of at least some Normanellidae appeared to have 6 setae

on the endopodal lobe rather than the typical number of 5, characterizing the hypothetical laophontoidean ancestor.This statement was based on LANG's (1965) observations of the fifth leg of the Californian species *Normanella bolini* and *N. confluens* and NOODT's (1964) description of *N. porosa* from the Red Sea. Both authors figure a supernumerary element at the inner distal corner of the endopodal lobe which coincides in position with the tube pore found in a wide range of Normanellidae (LEE & HUYS in press) and in the majority of Orthopsyllidae (HUYS 1990a). BODIN (1972) pointed out the presence of 2 tube pores on the endopodal lobe of *N. minuta?* and further remarked that these structures can also be found on other appendages such as the endopods of P2 and P4. His suspicion that tube pores of this size can be easily misinterpreted as setae seems to be substantiated by LANG'S (1965) descriptions of *N. bolini* and *N. confluens* which show an additional seta on the P4 enp-2, conforming with the tube pore found in the species observed by BODIN (1972) and LEE & HUYS (in press). Consequently, the presence of 5 elements on the endopodal lobe of the female P5 should be regarded as an apomorphy for a larger taxon including at least the Laophontoidea and Normanellidae.

P6 asymmetry ♂. HUYS (1990a) regarded the male P6 as a compound apomorphy supporting the monophyly of the Laophontoidea since the sixth pair of legs is typically asymmetrical (with sinistral and dextral configurations) and has a reduced armature represented by 2 setae. This functional asymmetry has now also been revealed in the Normanellidae (LEE & HUYS in press) although the difference in size between left and right members is not yet expressed, thus resembling the condition found in primitive Laophontidae such as *Esola*. Most Normanellidae possess 3 setae on the male P6, however, secondary loss of one of the elements has resulted in a bisetose condition in *Sagamiella* Lee & Huys.

3.2. Phylogenetic analysis

The characters used in the analysis of phylogenetic relationships between the Normanellidae and the different families of the Laophontoidea are listed in Tab. 1. Apomorphic character states are explained inside square brackets using the multistate system. The scores for each character and taxon are compiled in matrix format in Tab. 2. *Canthocamptus mirabilis* Štěrba (Canthocamptidae) was selected as the outgroup and scores for this species are based on the excellent redescription by ITÔ & TAKASHIO (1980).

A single optimal tree was obtained with tree-length 51 and consistency index 0.667 (Fig. 1). The topology of HUYS' (1990a: fig. 18) hand-generated cladogram of the Laophontoidea is confirmed by the present analysis. The Laophontidae still diverge as the first offshoot of a 5-family clade, a position which is undoubtedly rein-

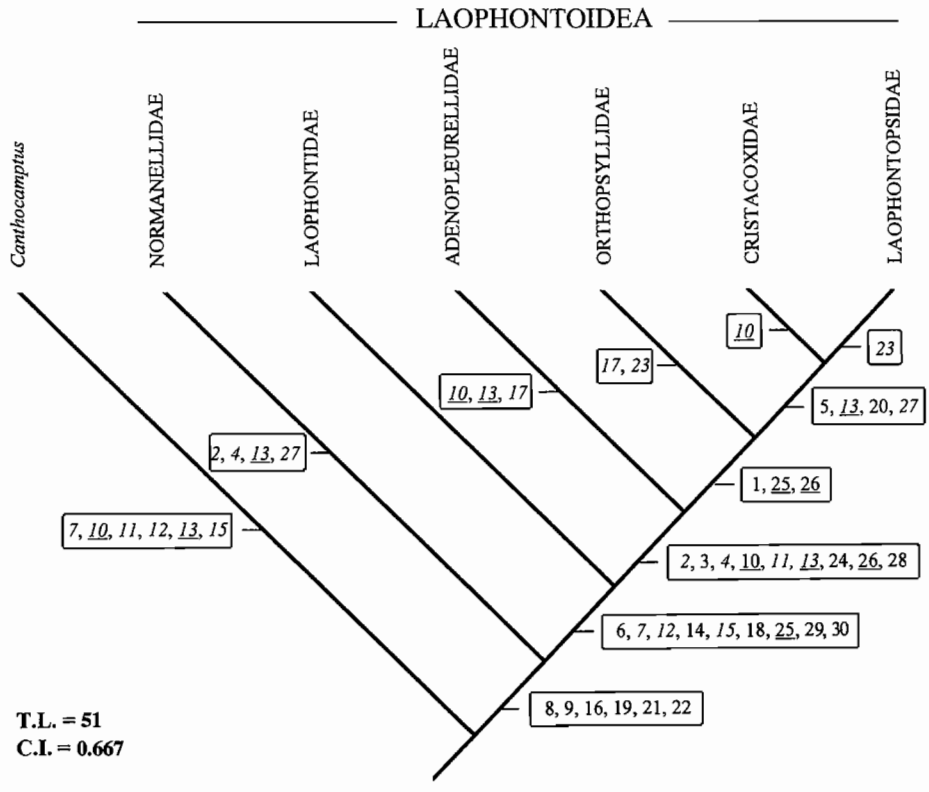

Fig. 1. Cladogram depicting relationships between families of Laophontoidea. Numbers refer to apomorphic states of characters listed in Tab. 2 [underlined numbers refer to multistate characters, italics indicate convergences].

Table 1. Characters used in the phylogenetic analysis. Apomorphic character states are referred to in square brackets. Characters 10, 13, 25 and 26 are multistate characters.

1. Body with clear demarcation between prosome and urosome [body cylindrical]
2. Antennule ♀ segments 3 and 4 free [fused forming double compound segment]
3. Antennule ♀ segments 5–8 free [fused forming triple compound segment]
4. Antennule ♂ segment 4 (= ancestral segment XIII) free [incorporated into segment 5]
5. Antennule segments ♂ distal to geniculation free [fused forming single compound segment]
6. Antennule ♀/♂ without posterior spinous process on segment 2 [process present]
7. Antennary basis and proximal endopod segment free [fused forming allobasis]
8. Antennary basis (or basal component of allobasis) with abexopodal seta [seta absent]
9. Antennary exopod 2-segmented [1-segmented]
10. Mandible with 2 setae on basis [1: with 1 seta; 2: unarmed]
11. Mandible with defined exopod [exopod incorporated into basis or completely absent]
12. Maxillule with free bisetose exopod [exopod fused to basis, with 1 seta]
13. Maxilliped with 3 setae on syncoxa [2: with 2 setae; 1: with 1 seta]
14. P1 exp-2 with inner seta [without]
15. P1 exp-3 with 3 outer spines [with 2 outer spines]
16. P1 enp 3-segmented [2-segmented through fusion of enp-2 and -3]
17. P1 enp-1 with inner seta [seta absent]
18. P1 enp-2 with inner lateral seta [seta absent]
19. P1 enp-3 (or enp-2 when ramus 2-segmented) with 3 distal elements [inner seta absent]
20. P2-P4 exp-3 outer elements spiniform [setiform]
21. P2 endopod 3-segmented [2-segmented; enp-2 and -3 failed to separate]
22. P3 endopod 3-segmented [2-segmented; enp-2 and -3 failed to separate]
23. P2-P4 enp-1 with inner seta [inner seta absent]
24. P2 enp-2 (or enp-3 when endopod 3-segmented; cf. *Canthocamptus*) with outer spine/seta [element absent]
25. P2 enp-2 with 3 inner setae (or enp-3 with 2 inner setae when endopod 3-segmented; cf. *Canthocamptus*) [1: with 2 inner setae; 2: with 1 inner seta]
26. P3 enp-2 with 3 inner setae (or enp-3 with 2 inner seta when endopod 3-segmented; cf. *Canthocamptus*) [1: with 2 inner setae; 2: with 1 inner seta]
27. P3 enp ♂ 3-segmented [2-segmented through failure of secondary separation of enp-2]
28. P3 enp ♂ inner setae of distal segment not modified [reduced]
29. P4 enp-2 with 2 inner setae [with 1 inner seta]
30. P6 ♂ with 3 setae [with 2 elements]

Table 2. Character states of 30 characters listed in Table 1 for outgroup (*Canthocamptus mirabilis*) and 6 laophontoidean families.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Canthocamptus mirabilis	0	0	0	0	0	0	1	0	0	1	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adenopleurellidae	0	1	1	1	0	1	1	1	1	1	1	1	2	1	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1
Cristacoxidae	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	0	1	1	1	1	1	0	1	2	2	1	1	1	1
Laophontidae	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	1	0	1	1	0	1	1	0	0	1	0	0	0	1	1
Laophontopsidae	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	0	1	1	1	1	1	1	1	2	2	1	1	1	1
Normanellidae	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	1	0	0	0	0	1	0	0	0
Orthopsyllidae	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	2	2	0	1	1	1

forced by the discovery of *Archilaophonte*. The common descent of this clade is strongly supported by (a) the presence of a posterior spinous process on the second antennulary segment, (b) the fusion of the antennary basis and proximal endopod segment forming an allobasis, (c) the fusion of the maxillulary exopod to the basis, (d) the presence of only 2 outer spines on P1 exp-3, (e) loss of the inner seta on P1 exp-2, (f) loss of the inner lateral seta on P1 enp-2, (g) P2 enp-2 with 1-2 inner setae (loss of 1 seta), (h) P4 enp-2 with 1 inner seta, and (i) ♂ P6 with at most 2 elements. The Normanellidae occupy a robust sistergroup relationship with this clade which is supported by the following synapomorphies: (a) antennary basis (or basal portion

of allobasis) without seta, (b) 1-segmented antennary exopod, (c) fusion of P1 enp-2 and -3, (d) P1 enp-2 with 2 distal elements (inner seta lost), (e) P2-P3 endopod 2-segmented. This suite of characters in conjunction with the homology of the male P3 endopod (see above) provides a sound basis for the inclusion of the Normanellidae in the Laophontoidea. From this relationship it can be inferred that the typical endopodal armature of leg 1 in the Laophontidae and related families resulted from a 2-step reduction. The canthocamptid basic pattern (as retained in *C. mirabilis*) consists of a 3-segmented endopod with formula [0–1^a;0–1^b;0,3,0] with 1^a and 1^b being the inner seta of enp-1 and -2, respectively. The normanellid condition is derived from this pattern by fusion of enp-2 and -3, and loss of the inner distal element, resulting in a formula [0–1^a;1^b,2,0]. In all other families further reduction has occurred leading to a [0–1;0,2,0] pattern through loss of the inner seta 1^b.
In addition to the apomorphies indicated in Fig. 1, the Normanellidae can also be defined on the basis of the sexual dimorphism on P3 endopod ♂ which includes the failure in separation of the distal segment and the gross reduction of the 2 apical setae.

4. REVISION OF CLETOPSYLLINAE HUYS & WILLEMS, 1989

Although being recorded from tropical and subtropical zones of all oceans, Cletopsyllinae are extremely rare and individual species are usually encountered in very low numbers. Of the nine species currently allocated to this subfamily four are known from a single female only: *Cletopsyllus papillifer* Willey, 1935 from Bermuda, *C. secundus* Nicholls, 1945 from western Australia, *C. quartus* Soyer, 1966 from Banyuls-sur-mer in France and *Pseudocletopsyllus spiniger* Vervoort, 1964 from the Caroline Islands. With the doubtful exception of *C. tertius* Por, 1964, which has been recorded from both the mediterranean and Red Sea coasts of Israel (Por 1964, 1967), none of the species has been recorded again since its original description. Marcus (1976) claimed a second record of *C. quartus* from the Tanzanian coast but the possibility that she was dealing with a different species is substantial (see below).

4.1. Description of *Bathycletopsyllus hexarthra* gen. et sp. nov.

- ***Bathycletopsyllus* gen. nov.**

Cletopsyllidae. Antennule ♀ 6-segmented; posterior margin of segment 3 smooth, not modified. P4 exp-2 and -3 with unilaterally pectinate spines in ♂; outer spines of P3 exp-3 slightly modified in ♂. P5 exopod of ♂ with 5 setae/spines. Caudal ramus sexually dimorphic, cylindrical; proximal portion with distinct dorsal outgrowth in ♀, bearing a spur-like process posteriorly and a secondary process dorsally.
Type and only species. *Bathycletopsyllus hexarthra* gen. et sp. nov.
Etymology. The generic name is derived from the Greek *bathys*, meaning deep, and refers to the deepest cletopsyllid record known thus far. The species name is derived from the Greek *hex*, meaning six, and *arthron*, meaning joint, and refers to the 6-segmented female antennule.
Type locality. Indian Ocean, off La Réunion; 21°01.40' S, 55°10.3' E; depth 460 m; muddy sand.
Material examined. Holotype ♀ (dissected on 13 slides), paratype ♀ (in alcohol) and paratype ♂ (dissected on 8 slides) deposited in Muséum National d'Histoire naturelle, Paris (reg. nos. MNHN-Cp1498–1500). Additional paratypes (3 ♀♀ and 1 ♂ in alcohol) deposited in The Natural History Museum, London (reg. nos 1998.1064–1067). Collected during MD32 expedition (11 August–10 September 1982) to the deeper waters around the island of La Réunion (R.V. Marion-Dufresne), organized by the TAAF (Terres Australes et Antarctiques Françaises), Paris (chief scientist: Dr. A. Guille). Station DS178, sampled on 08 September 1982 and sorted in CENTOB (Centre National de Tri d'Océanographie Biologique), Brest.
Description.
FEMALE. Body length measured from anterior margin of rostrum to posterior margin of caudal rami: 1210–1250 mm. Cephalothorax bell-shaped, distinctly widening in posterior third; with several swellings laterally; posterior margin with numerous spinous processes, posterolateral margin crenulate (Figs. 2A; 3A). Body somites clearly defined by lateral constrictions; posterior margins with spiniform projections dorsally and laterally; pleural areas of thoracic somites well developed. Integument of somites with minute denticles. Genital and first abdominal somites completely fused forming genital double-somite; original segmentation marked by dorsal transverse ridge bearing series of spiniform projections dorsally and dorsolaterally, and by lateral constrictions. Posterolateral angles of first three urosomites strongly produced into spinous outgrowths bearing few spinules. Ventral posterior margins of abdominal somites serrate; those of second and third abdominal somites with transverse spinule row. Anal somite with long setules ventrally, bordering anal opening; posterolateral angles forming rounded, spinular protuberance; additional spinules around posterior margin ventrally and laterally. Anal operculum rounded, fringed with long setules.
Caudal rami (Figs. 2A; 3B–D) slightly divergent, cylindrical; proximal fifth expanded bilaterally and ventrally and forming large outgrowth proximally. Both inner

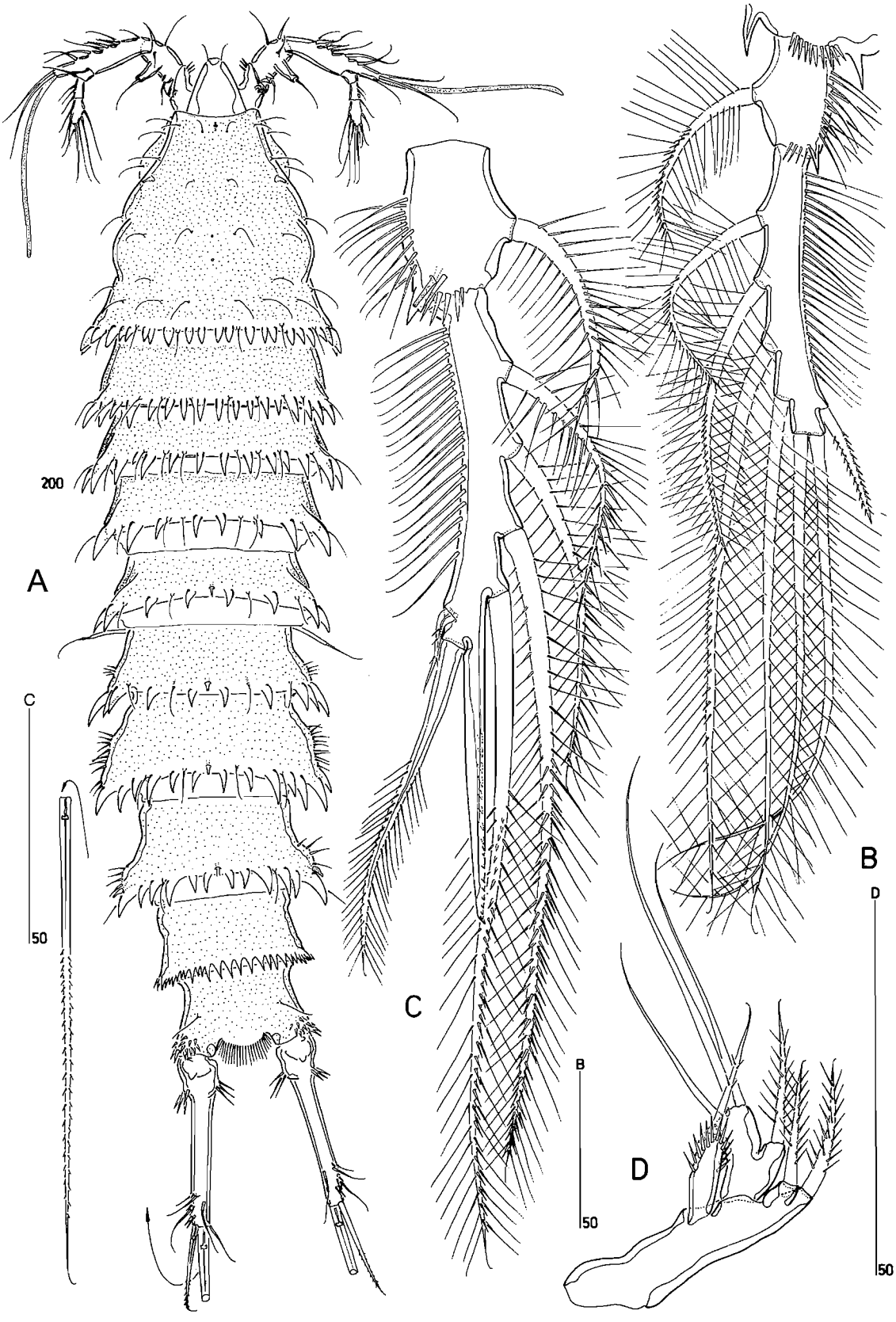

Fig. 2. *Bathycletopsyllus hexarthra* gen. et sp. nov. **A,** Habitus (♀), dorsal; **B,** P2 endopod (♀), anterior; **C,** P2 endopod (♂), anterior. *Retrocalcar secundus* (Nicholls, 1945) comb. nov. **D,** Mandibular palp.

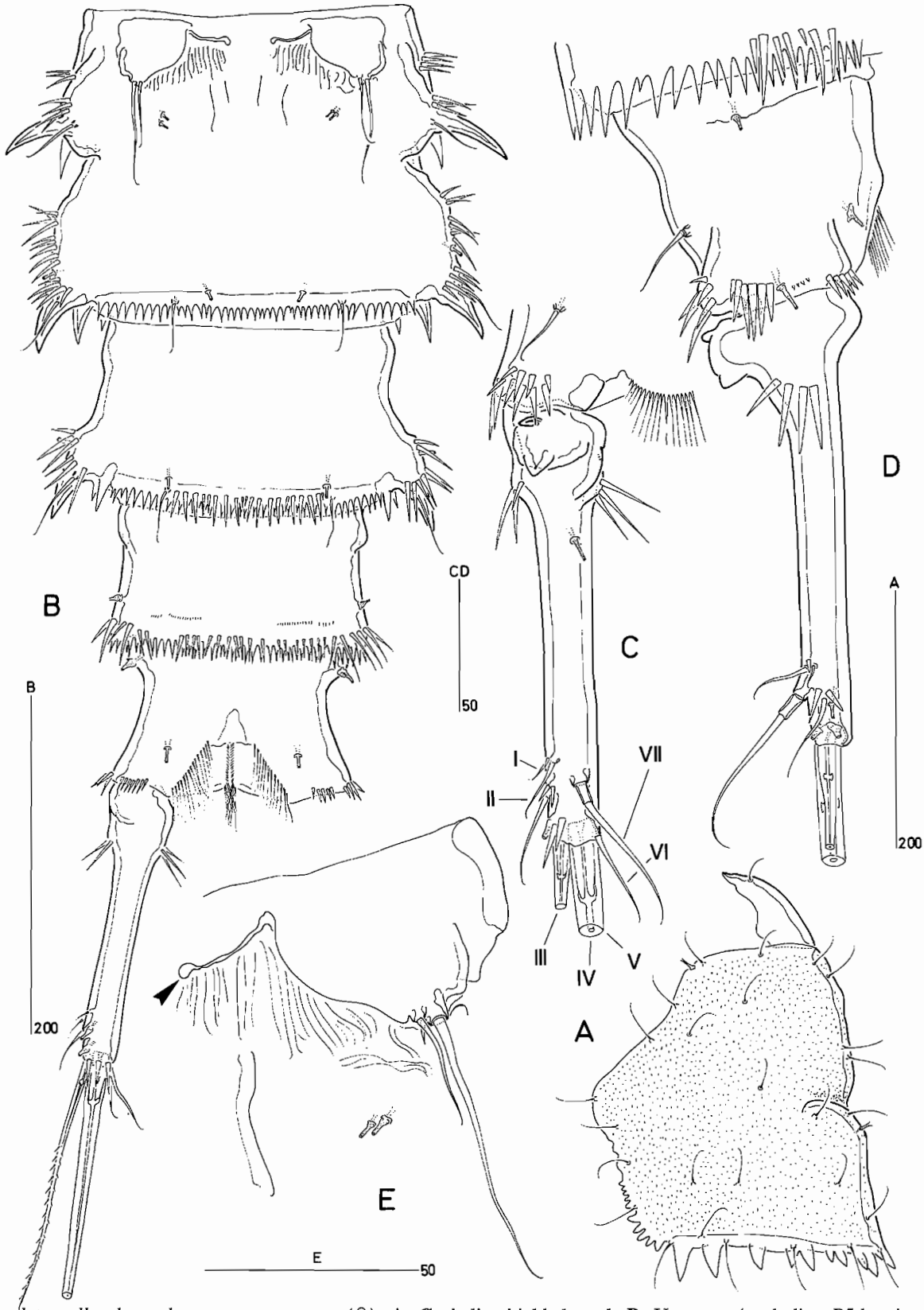

Fig. 3. *Bathycletopsyllus hexarthra* gen. et sp. nov. (♀). **A,** Cephalic shield, lateral; **B,** Urosome (excluding P5-bearing somite), ventral; **C,** Left caudal ramus, dorsal; **D,** Anal somite and right caudal ramus, lateral; **E,** Right genital aperture (copulatory pore arrowed).

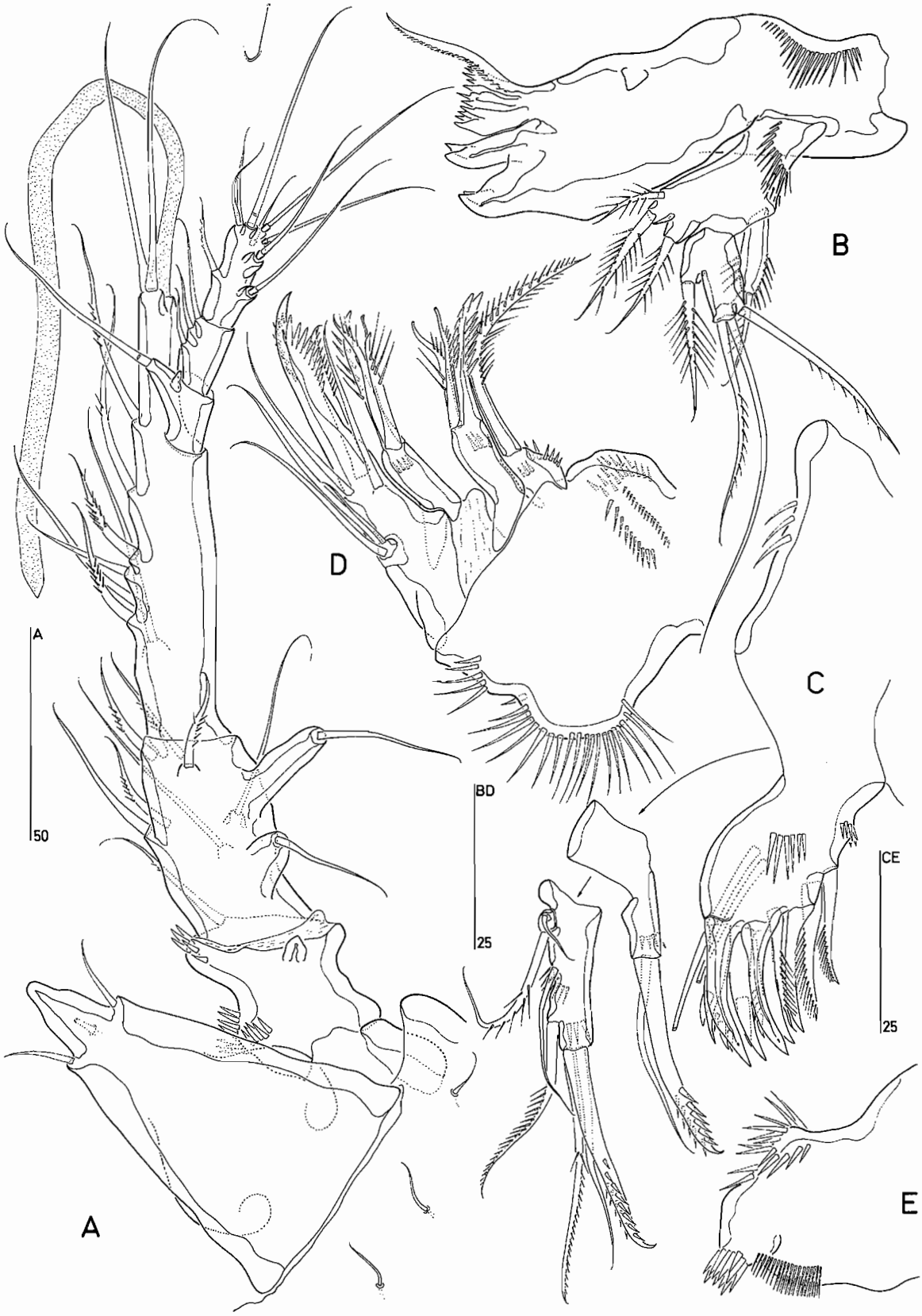

Fig. 4. *Bathycletopsyllus hexarthra* gen. et sp. nov. (♀). **A,** Rostrum and antennule, dorsal; **B,** Mandible; **C,** Maxillule with disarticulated coxa and palp, posterior; **D,** Maxilla, anterior; **E,** Left paragnath.

and outer expansions with few long spinules; dorsal outgrowth with posteriorly directed rounded process and minute secondary process dorsally. All 7 setae located in distal quarter; setae I-II small, closely set; setae IV–V bipinnate, with predesigned fracture planes; seta VI bare; seta VII arising from short process. Tube pores present dorsally near proximal inner margin and along distal outer margin.

Rostrum (Fig. 4A) large, triangular; 1.5 times as long as basal width; apex pointed and ventrally directed (Fig. 3A); paired sensillae located near apex; ventral surface with paired lobate extensions.

Antennule (Fig. 4A) 6-segmented; with small sclerite around base of segment 1. Segment 1 with 2 spinule rows around anterior margin and small dentiform process dorsally near distal margin. Segment 2 with 2 conical processes, distal one longest. Segment 3 longest, with smooth posterior margin; distal portion produced into cylindrical pedestal, reaching beyond distal margin of segment 5. Armature formula: 1-[1 pinnate], 2-[5 + 4 pinnate], 3-[4 + 4 pinnate + (1+ae)], 4-[1], 5-[3], 6-[6 + 1 pinnate + acrothek]. Apical acrothek consisting of 2 small setae.

Antenna (Fig. 5A–B). Coxa with spinule row. Allobasis elongate; original segmentation marked by incomplete surface sutures; abexopodal margin with 2 groups of strong spinules; abexopodal seta minute (arrowed in Fig. 5A), located anterior of distal spinule group. Exopod small, 1-segmented; with long subapical and shorter apical seta (Fig. 5B). Endopod elongate, with spinules along inner margin; lateral armature consisting of 2 pinnate spines and minute seta (arrowed in inset of Fig. 5A); distal armature consisting of 2 apically curved pinnate spines and 3 geniculate setae, the longest of which being fused basally to vestigial seta.

Labrum (Fig. 5C,D). Distal margin pectinate posteriorly and with densely packed setules anteriorly; lateral margins with spinules, gradually increasing in size medially.

Mandible (Fig. 4B) with spinules around base of palp; gnathobase with 2 strong teeth, several multicuspidate blades and 1 pinnate seta at dorsal corner. Palp biramous; basis with 3 pinnate setae and 2 spinule rows; endopod with 1 lateral and 3 distal setae; exopod small, 1-segmented, with 1 apical seta.

Paragnaths (Fig. 4E) well developed lobes with ornamentation as figured.

Maxillule (Fig. 4C). Praecoxal arthrite with 9 setae/spines around distal margin and 2 setae on anterior surface. Coxal endite with 1 seta and 1 bipinnate spine. Basis with 1 bipinnate spine and 2 setae apically, and 1 seta along outer margin. Endopod probably incorporated into basis and represented by 1 seta. Exopod represented by minute knob, partly delimited at base and with 1 small and 1 long seta.

Maxilla (Fig. 4D). Syncoxa with long spinules around outer margin and short spinules medially; with 3 endites: proximal endite smallest, with 1 long, bipinnate spine; middle endite drawn out into pectinate spine and with 2 tube-setae; distal endite with similar armature and surrounded at base by large area of membranous, flexible integument. Allobasis drawn out into pectinate claw; accessory armature consisting of 2 bare setae and 1 bipinnate spine. Endopod represented by a minute rudiment carrying 1 short and 2 long setae.

Maxilliped (Fig. 5E). Syncoxa with 3 pinnate setae and spinular pattern as figured. Basis unarmed; with spinule row along palmar margin and few spinules along outer margin. Endopod represented by apically curved claw, minutely pinnate in distal half; accessory armature consisting of long bare setae and 2 vestigial elements.

P1 (Fig. 5F) with well developed praecoxa. Coxa with complex spinular pattern as figured. Basis with outer bipinnate seta and inner bipinnate spine; inner portion produced into cylindrical pedestal for endopod; anterior surface with tube pore; distal margin with spinous process between exopod and endopod. Exopod 3-segmented; exp-1 with long outer spine; exp-2 inner element short and spiniform; exp-3 with 2 outer spines and 2 geniculate setae apically. Endopod 2-segmented, prehensile; enp-1 nearly 3 times as long as enp-2; inner element of enp-1 distinctly curved, inserting in middle third of segment, with long spinules near base; enp-2 with 2 minute setae along inner margin, and 1 unipinnate spine and 1 geniculate seta distally.

P2-P4 with 3-segmented exopods (Fig. 6A,C) and 2-segmented endopods (Fig. 2B). Ornamentation and armature as in *C. sagamiensis* (cf. Itô 1971). Bases with outer pinnate spine (P2) or naked seta (P3–P4).

Fifth pair of legs (Fig. 8E) not fused medially. Baseoendopod with long triarticulate setophore bearing outer basal seta. Endopodal lobe triangular with stepped inner margin bearing 3 bipinnate setae; distal portion distinctly bilobate with outer lobe spinous and bearing tube pore, and inner lobe rounded and hyaline (see inset Fig. 8E); inner margin with 2 closely set setae; distinct tube pores present around bases of proximal inner seta and outer setophore. Exopod very long, about 12 times as long as wide; with 1 inner, 1 apical and 4 outer setae (proximalmost on small cylindrical process); with 2 tube pores near apex.

Genital field located near anterior margin of genital double-somite (Fig. 3B). Genital apertures paired, comprising gonopore and medially displaced copulatory pore (arrowed in Fig. 3E); each covered by an operculum derived from the sixth legs, bearing long outer and short inner seta plus vestigial element.

MALE. Body length measured from anterior margin of rostrum to posterior margin of caudal rami: 1010–1030 mm. Body (Fig. 7A) slightly more slender than in ♀,

ules. This condition was also found in *C. tertius* and *C. brattstroemi* but in these species it appears to be restricted to the spines of the distal segment only (POR 1964; GEDDES 1981). A less pronounced variant of this modification was recorded by MARCUS (1976) in her Tanzanian specimens of *C. quartus*. In this case the spinules along the outer margin are also enlarged but not fused to the main axis of the spine which retains its essentially bipinnate appearance. It is conceivable that gradations exist between these two conditions and that particularly the slightest modifications have remained unnoticed in some species descriptions. ITÔ (1971) does not mention any swimming leg sexual dimorphism in his description of *C. sagamiensis*, and in a personal communication to GEDDES (1981) confirmed this absence for the exopods. Since ITÔ undoubtedly referred to the pectinate condition of *C. brattstroemi* and not to the pinnate variant of *C. quartus*, we suspect that the P4 exopod is also slightly modified in male *C. sagamiensis*. Exopodal sexual dimorphism is completely lacking in *C. bacescui* and *C. rotundifera* (MARCUS 1976; FIERS 1986) and probably also in the as yet undiscovered male of the closely related *C. papillifer*.

GEDDES (1981) recorded sexual dimorphism in the outer spines of the P3 exopod in *C. brattstroemi* and noted that particularly those of the proximal and middle segments were heavily chitinized. The significance of the unusually modified spine figured by MARCUS (1976) on the proximal exopod segment of this leg in *C. quartus* is difficult to assess. Since none of the other exopodal spines is modified and the proximal spine appears to be deformed it is possible that MARCUS' specimen was teratological. Slight sexual dimorphism was found on P3 exp-3 in *B. hexarthra*, involving the outer and outer apical spines which possess coarser spinules than in the female.

P5 setation ♂. The exopod typically possesses 3 outer spines, an apical seta and an inner seta or spine. Most cletopsyllids share this basic ornamentation pattern, however, the males of *C. bacescui* and *C. rotundifera* have only 4 elements. This apomorphic condition evolved through loss of the middle outer spine.

Caudal rami. Sexual dimorphism in the caudal rami appears to be characteristic for all Cletopsyllidae but its potential as an autapomorphy at the family level should be considered with caution. Although presumably genetically controlled by the same mechanism, caudal ramus sexual dimorphism in this family is expressed in different ways and the homology between the corresponding phenotypes is difficult to interpret. The caudal ramus is typically cylindrical in the male and modified in the female. Four different types of modification can be recognized:

(a) In *C. sagamiensis* and *C. brattstroemi* the female caudal ramus is cylindrical but the outer proximal margin is produced into a lobate expansion bearing a spur-like process posteriorly and a secondary process dorsally. Re-examination of the female holotype (NHM reg. no. 1947.10.7.8) of *C. secundus* revealed similar processes (Fig. 9C) even though the original form of the ramus is obscured as a result of secondary modification. Although essentially cylindrical in structure (as revealed by the internal chitinous ribs) the ramus has developed a largely hyaline, lamelliform extension on the inner margin. This superficial resemblance with the broad and dorsoventrally flattened caudal rami found in *C. papillifer*, *C. bacescui* and *C. rotundifera* led FIERS (1986) to suggest a close relationship between *C. secundus* and these species.

(b) In *Bathycletopsyllus* an analogous modification has taken place in the proximal region of the caudal ramus (Fig. 3C, D). In addition to some bilateral expansion (Fig. 3C) major swelling has occurred along the dorsoventral axis and is clearly discernible in lateral aspect (Fig. 3D). The dorsal outgrowth typically possesses a small, posteriorly directed process and an accessory minor projection. It is conceivable that the condition in *C. sagamiensis* and *C. brattstroemi* evolved from the *Bathycletopsyllus* type by outward rotation or displacement of the dorsal outgrowth.

(c) No real modifications are found in the female caudal ramus of *C. bacescui* and sexual dimorphism is only expressed in the shape. Slight lateral expansion has occurred along both inner and outer margins in the mid-region of the ramus which is dorsoventrally depressed. Since there is close resemblance between the female caudal ramus of *C. bacescui* and *C. papillifer*, we suspect that the same caudal ramus sexual dimorphism applies to the latter.

(d) In *C. tertius* the caudal ramus is cylindrical in both sexes and only weakly sexually dimorphic. In the female there is a small, raised spinulose patch near the inner proximal margin. The male ramus is also markedly longer than in the female.

4.3. Diagnoses of genera

FIERS (1986) recognized two species groups within *Cletopsyllus* on the basis of the morphology of the caudal rami and the armature of the P5 exopod in the male. We have considered additional characters as outlined above and suggest to split up *Cletopsyllus* in three lineages which are accorded generic rank.

- ***Cletopsyllus* Willey, 1935**

Cletopsyllidae. Body somites with crenulate or dentate posterior margin, but without large spinous processes dorsally. Antennule ♀ 4-segmented; posterior margin of segment 3 distinctly crenulate. P3-P4 exopods with-

out sexual dimorphism. P5 exopod of ♂ with 4 setae/spines. Caudal ramus without distinct sexual dimorphism; dorsoventrally depressed in ♀ with inner margin medially produced and convex; outer margin with spinule row between anterior margin and insertion site of setae I–II.

Type species. *Cletopsyllus papillifer* Willey, 1935 [by monotypy]

Other species. *C. bacescui* Marcus, 1976; *C. rotundifera* Fiers, 1986.

Remarks. Marcus (1976) has already pointed out the close similarity between *C. papillifer* and *C. bacescui*. Both species share the distinctly bifid rostrum, the long terminal process on the P5 endopodal lobe in both sexes and the same caudal ramus shape in the female. In *C. rotundifera* the rostrum is clearly not bifid, the terminal process on the P5 is virtually non-existent and the caudal ramus is lamelliform. This species also has only 1 seta on P1 enp-2 whereas its congeners have 2 well developed elements on this segment, and the exopods of the swimming legs have spinous extensions instead of spinules. *C. rotundifera* clearly occupies an isolated position in the genus and future discovery of additional species might well necessitate a reappraisal of its current generic assignment. Fiers (1986) did not mention caudal ramus sexual dimorphism in *C. rotundifera* but it is likely that, in accord with its congeners, at least a slight difference in shape is noticeable between the sexes. Other features requiring confirmation include the presence of only 1 seta on the antennary exopod, the complete separation of the antennary basis and endopod and the absence of the mandibular exopod. The short basal seta in Fiers' illustration of the ♀ P5 is obviously incorrect since the typical bi-articulate setophore is figured in his lateral habitus drawing (his Fig. 16b).

C. papillifer has traditionally been distinguished from the other species by the presence of 3 instead of 2 inner setae on P4 exp-3 (e.g. Soyer 1966; Marcus 1976). We suspect that the importance of this character might have been overstated since the P4 in Willey's only specimen was aberrant on one side (his Fig. 81) and the supernumerary third seta proved to be absent in the more primitive genus *Bathycletopsyllus*. Pending the discovery of new material of *C. papillifer* we prefer to ignore this feature as a species discriminant in identification keys. Similarly, Marcus' (1976) claim that the inner seta on P1 exp-2 is absent in *C. bacescui* is also doubtful.

Key to species.

1. P5 endopodal lobe of both sexes with long curved terminal process; P1 enp-2 with 2 inner setae; rostrum with bifid apex 2
   P5 endopodal lobe without (♂) or with short rounded (♀) terminal process; P1 enp-2 with 1 inner seta; rostrum with rounded apex .... *C. rotundifera*
2. Insertion point of P1 enp-1 inner seta situated at 55% of segment length; P5 endopodal lobe ♀ elongate rectangular; caudal ramus ♀ with slightly convex outer margin ..... *C. bacescui*
   Insertion point of P1 enp-1 inner seta situated at 66% of segment length; P5 endopodal lobe ♀ short triangular; caudal ramus ♀ with concave outer margin (due to swelling in anterior quarter) ... *C. papillifer*

• ***Retrocalcar* gen. nov.**

Cletopsyllidae. Body somites with dentate posterior margin, but without large spinous processes dorsally. Antennule ♀ 4-segmented; posterior margin of segment 3 smooth, not modified. P4 exp-3 with unilaterally pectinate spines in ♂; P3 exopod sometimes sexually dimorphic. P5 exopod of ♂ with 5 setae/spines. Caudal ramus sexually dimorphic, cylindrical; outer proximal margin in ♀ produced into a lobate expansion bearing a spur-like process posteriorly and a secondary process dorsally.

Type species. *Cletopsyllus brattstroemi* Geddes, 1981 = *Retrocalcar brattstroemi* (Geddes, 1981) comb. nov.

Other species. *C. secundus* Nicholls, 1945 = *Retrocalcar secundus* (Nicholls, 1945) comb. nov.; *C. sagamiensis* Itô, 1971 = *Retrocalcar sagamiensis* (Itô, 1971) comb. nov.

Etymology. The generic name is derived from the Latin prefix *retro*, meaning backward, behind, and *calcar*, meaning spur, and refers to the posteriorly directed spur-like processes on the female caudal rami. Gender: masculine.

Remarks. As pointed out by Geddes (1981) there is an undeniable relationship between *C. sagamiensis* and *C. brattstroemi*, primarily being supported by the morphology of the female caudal ramus. Neither Geddes nor Itô (1971) recognized a similarity with *C. secundus* which, on account of its lamelliform caudal rami, was placed by Fiers (1986) in a group containing *C. papillifer*, *C. bacescui* and *C. rotundifera*. Re-examination of the holotype of *C. secundus* has not only revealed the true morphology of the caudal ramus (see above) but also allowed updating Nicholls' (1945) description of the antenna, mandible and P5. The antenna has a bisetose exopod as in other members of the family and the allobasis possesses a minute abexopodal seta (arrowed in Fig. 9A). The alleged absence of the exopod was unjustly used as a diagnostic character by several authors (Soyer 1966; Marcus 1976; Fiers, 1986). The mandible has 3 apical setae on the endopod (Fig. 2D) and the morphology of the other mouthparts is as in *B. hexarthra*. The detailed morphology and ornamentation

of the P5 are illustrated in Fig. 9B. The anal operculum (Fig. 9C) is not spinulose but bears a fringe of very long setules.

ITÔ (1972) described the copepodid V of *R. sagamiensis* and updated the original description of the adult mandible and subsequently (*in litt.* to GEDDES 1981) also of the male P2 endopod.

Key to species.

1. P1 enp-2 with 1 inner seta; caudal rami ♀ lamelliform, only slightly longer than anal somite, inner margin with distinct hyaline extension ..... *R. secundus*
   P1 enp-2 with 2 inner setae; caudal rami ♀ cylindrical with wide proximal portion, at least 1.5 times as long as anal somite; inner margin straight 2
2. Caudal ramus 3.6 (♀) and 6.5 (♂) times as long as greatest width; outer spines of P3 exp-3 modified in ♂ ..... *R. brattstroemi*
   Caudal ramus 5.3 (♀) and 9 (♂) times as long as greatest width; outer spines of P3 exp-3 not modified in ♂ ..... *R. sagamiensis*

• ***Isocletopsyllus* gen. nov.**

Cletopsyllidae. Body somites with dentate or crenulate posterior margin, but without large spinous processes dorsally. Antennule ♀ 4-segmented; posterior margin of segment 3 smooth, not modified. P4 exp-3 with unilaterally pectinate spines in ♂. P5 exopod of ♂ with 5 setae/spines. Caudal ramus weakly sexually dimorphic, cylindrical; in ♀ with small, raised spinulose patch near inner proximal margin; ♂ ramus markedly longer than in ♀.

Type species. *Cletopsyllus tertius* Por, 1964 = *Isocletopsyllus tertius* (Por, 1964) comb. nov.

Other species. *C. quartus* Soyer, 1966 = *Isocletopsyllus quartus* (Soyer, 1966) comb. nov.

Species inquirendae. *C. tertius* Por, 1964 *sensu* POR (1967); *C. quartus* Soyer, 1966 *sensu* MARCUS (1976).

Etymology. The generic name is derived from the Greek *isos*, meaning equal, and alludes to the slightly developed sexual dimorphism in the caudal rami. Gender: masculine.

Remarks. Both *C. tertius* and *C. quartus* have been the subject of taxonomic confusion. POR (1964) described both sexes of *C. tertius* from off the Israeli mediterranean coast and discovered the first male of the genus. SOYER (1966) described *C. quartus* on the basis of a single female from Banyuls-sur-mer. Although both species are clearly closely related, females can be readily distinguished by a number of morphometric characters such as the length of the caudal rami, the length:width ratio of the P5 exopod and the shape of the 2nd and 3rd antennulary segments. SOYER (1966) also listed differences in the antennule, antenna and mouthparts but these are undoubtedly based on deficiencies in the original description of *C. tertius*. POR (1967) discovered additional material of *C. tertius* in the Gulf of Elat and asserted that the holotype ♀ from the Levant was teratological in the trifid rostrum and the short and broad caudal rami. His subsequent decision to sink *C. quartus* as a junior subjective synonym is disputable for three reasons: (a) POR (1967) did not examine additional females from the Levant, only a male, and his assertion about the aberrant condition of the holotype is deduced from a comparison of two ecologically and geographically remote "populations", the specific identity of which had not been thoroughly verified;(b) even if this assertion is correct, it does not account for the other differences found in e.g. the P5 exopod; (c) the differences in ♀ antennule (slenderness, length of processes on segment 2, etc.) and P5 (exopod length ♀, endopodal lobe length ♂) in conjunction with the discrepancy in caudal ramus length and shape strongly suggest that the Elat material is not *C. tertius* but a different species. We therefore re-instate *C. quartus* as a valid species and regard *C. tertius sensu* POR (1967) as a *species inquirenda* in *Isocletopsyllus*.

MARCUS (1976), apparently unaware of POR's (1967) paper, attributed male specimens from the Tanzanian coast to *C. quartus*. The caudal rami of these males are markedly shorter than those of the female from Banyuls. If MARCUS' identification is correct it implies that *C. quartus* shows an opposite trend in caudal ramus sexual dimorphism since in the closely related *C. tertius* males have much longer caudal rami than females (POR, 1964). We regard this discrepancy within a single genus unlikely and consider *C. quartus sensu* MARCUS (1976) as *species inquirenda* in *Isocletopsyllus*. The slightly bilaterally constricted caudal rami and P5 morphology in the Tanzanian males are reminiscent of those in male *C. tertius* from the Gulf of Elat and this similarity might well be indicative of conspecificity.

4.4. Status of *Pseudocletopsyllus* Vervoort, 1964

VERVOORT 1964) proposed this genus for a new species *P. spiniger*, the description of which was based on a single specimen collected in sponge washings from the Ifaluk lagoon (Caroline Islands). The author identified the holotype as an adult female, however the description by ITÔ (1972) of the fifth copepodid of *C. sagamiensis* has provided indirect evidence that VERVOORT was dealing with a juvenile specimen. ITÔ (1972) already pointed out the stumpy appearance of the swimming legs, the undifferentiated nature of the P5 (with baseoendopod and exopod still fused) and the incomplete abdominal segmentation in *P. spiniger*. Additional

evidence is found in the structure of the caudal ramus and the P1.

In *C. sagamiensis* there is a marked difference in the shape and structure of the caudal ramus between the copepodid V and the adult female. In the former the ramus has a lobate spinulose process along the proximal inner margin but no differentiations along the outer margin. In the adult the ramus is distinctly longer, the inner margin is straight and smooth, and the outer margin has a large angular expansion proximally. This transformation obviously occurs at the last moult and is clearly associated with precopulatory mate guarding during which the male holds the adult female by the caudal rami. The caudal ramus in *P. spiniger* is remarkably short and clearly corresponds to the copepodid V condition found in *C. sagamiensis*.

VERVOORT (1964) claims that the inner seta of P1 exp-2 is absent in *P. spiniger*. ITÔ's (1971, 1972) descriptions of *C. sagamiensis* show that this seta is typically minute in the copepodid V stage and might therefore be easily overlooked.

Since it seems impossible to identify adult *P. spiniger* on the basis of VERVOORT's (1964) description, the genus *Pseudocletopsyllus* is regarded here as *genus inquirendum* in the Cletopsyllidae.

4.5. Diagnostic features and relationships of Cletopsyllidae

Antennules. The female antennules are highly distinctive by the presence of two long conical processes on the posterior margin of the second segment. The presence of an apical seta on these processes indicates that they are not homologous with the non-setiferous hook-like processes commonly found in the families of the Laophontoidea (HUYS 1990a) and the Tetragonicipitidae. Additional processes are found on segment 1 but these are smaller, usually spinous and appear to vary in number between species.

The apical acrothek found on the terminal segment in both sexes consists of 2 basally fused setae only, implying that the accessory aesthetasc is secondarily lost in the Cletopsyllidae.

The male antennules are constant in segmentation and are typically subchirocer with the geniculation located between segments 5 and 6. All species possess a proximal spinous outgrowth on the posterior margin of segment 2. Comparison of the setal patterns between both sexes indicates that this structure is homologous with the proximal conical process of female.

Antenna. All species have an allobasis with the original segmentation marked by incomplete superficial sutures on either surface. Some authors have misinterpreted these sutures as a functional articulation (SOYER 1966; POR 1967; FIERS 1986). The exopod, which was overlooked in NICHOLLS' description of *C. secundus*, is typically small and bisetose. FIERS (1986) figured only 1 seta on the exopod of *C. rotundifera* but a subapical scar indicates that the second seta was dislodged. The abexopodal seta on the allobasis is often minute (arrowed in Figs. 5A; 9A) and since it usually attains the size of a setule or spinule we suspect that it was overlooked in all previous descriptions except for WILLEY (1935).

Mouthparts. The mandible, maxillule and maxilla are very conservative in the family and characters based on these appendages are significant primarily at the species level. Variations can be found in for example the number of setae on the mandibular basis, however other characters such as the absence of the mandibular exopod in *C. papillifer* and *C. rotundifera* need confirmation.

Maxilliped. All species have 3 setae on the syncoxa, none on the basis and a long seta accompanying the endopodal claw. One or 2 accessory elements can be found on the endopod but these have rarely been figured.

P1. The morphology of the P1 is conservative throughout the family and not very useful at the species level except for the number of inner setae on enp-2. The exopod typically has an inner seta on exp-2 and 4 elements on exp-3. There is evidence for the presence of a fifth element in FIERS' (1986) drawing of leg 1 in *C. rotundifera* but it is more likely that a spinule was figured. The 2-segmented endopod inserts on a characteristic pedestal formed as a cylindrical outgrowth of the basis. The distal endopod segment has 2 apical elements and typically 2 setae along the inner margin. Only in *C. rotundifera*, *R. secundus* and *I. tertius* 1 seta is found. The setal pattern on this segment in conjunction with the position of the 2 spinule rows provide evidence for its compound origin, suggesting that the cletopsyllid P1 endopod is derived from a 3-segmented ramus.

P2–P4. The presence of 4 inner setae on P2 enp-2 clearly indicates that this segment is compound and that the 2-segmented condition of the P2-P4 endopods arose from collective failure of separation of the middle and distal segments.

P2. The sexual dimorphism of the P2 endopod is among the most diagnostic characters of the family. The inner distal corner of enp-2 in the male is typically produced into a straight or curved (in *C. rotundifera* only) apophysis. The apophysis is completely fused at the base except for the male of *C. bacescui* in which it was described as a simple spine (MARCUS 1976). This observation, however, requires confirmation. The apophysis can be identified as the homologue of the inner distal seta in the female. Additional elements on enp-2 which are transformed in the male include the outer distal seta which is usually shorter and the outer

spine which is reduced in some species such as *B. hexarthra*. The complete absence of the latter in the male of *R. brattstroemi* is unique within the family, however, we suspect that this element is probably vestigial in this species and therefore being overlooked in GEDDES' (1981) description. The apophysis has a bifid apex in *R. brattstroemi* and MARCUS' (1976) male of *C. quartus*. The sexually dimorphic P2 endopod was overlooked in the description of *I. tertius* (POR 1964) and initially also by ITÔ (1971) in his description of *R. sagamiensis* (see ITÔ in GEDDES 1981).

P5. The baseoendopod in both sexes is characterized by an extremely long extension bearing the outer basal seta. This setophore is typically tri-articulate and composite, comprising a long styliform part bearing spinules or setules, and a short distal part. The alleged absence of this setophore in the female of *C. rotundifera* is an error. An articulate, elongate setophore is characteristic of several deepwater genera such as *Malacopsyllus* Sars, 1911 and *Anoplosoma* Sars, 1911. Within the "canthocamptoid complex" this structure is found in the majority of the Ancorabolidae and in some Cletodidae such as *Cletodes* Brady, 1873 and *Enhydrosoma* Boeck, 1873. There is little doubt that it has arisen convergently and as such its homoplasious occurrence is not indicative of phylogenetic affinity. Its functional significance is unknown, however we speculate that the outer basal seta is an important mechanoreceptor and that elongation of the setophore is a functional adaptation aiding to maintain sensory performance in forms which are either dorsoventrally flattened such as the Hamondiidae (HUYS 1990c) or which typically accumulate large amounts of foreign particles on the body surface such as the Ancorabolidae and Cletopsyllidae. Copepods typically create feeding currents to entrain water over their sensory receptors and through their feeding appendages, with the generated flow field creating a hydrodynamic disturbance around the copepod's body. Elongation of setophores may therefore allow their mechanoreceptive setae to detect external hydrodynamic signals in a region where the intensity of those signals is greater than the self-generated disturbance within the flow field (FIELDS & YEN 1993).

Genital field. The arrangement of the female genital apertures in the Cletopsyllidae is unusual. On each side the genital aperture comprises a gonopore (the oviduct opening) and a copulatory pore, covered by an operculum derived from the sixth legs. Each copulatory duct leads via a short copulatory duct into a seminal receptacle (which is presumably unpaired). This paired arrangement is the most primitive state displayed within the Harpacticoida and resembles the condition found in the canuellid genera related to *Canuellina* Gurney (HUYS & BOXSHALL 1991).

P6 ♂. The sixth pair of swimming legs is asymmetrical with one member fused to the somite and the other member articulating and closing off the single functional gonopore. Within a species or population this asymmetry of the male reproductive system can be expressed in both sinistral and dextral configurations, according to whether the testis and vas deferens on the left or right side is developed. Each leg has only 1 seta.

Relationships. LANG (1944) placed *Cletopsyllus* in the Normanellinae on account of the defined rostrum, the presence of an inner seta on P1 enp-1 and 1 claw plus a long seta on enp-2, the 2-segmented ♂ endopod, the well developed endopodal lobe of the ♂ P5 and the precopulatory mate guarding mode involving the male grasping the female's caudal setae. This combination of characters which coincides with LANG's (1944) diagnosis of the subfamily is based solely on plesiomorphies. HUYS & WILLEMS (1989) recognized the polyphyletic status of the subfamily by defining three distinct lineages: (1) *Laophontopsis* Sars, 1908 was designated as the type of a new family Laophontopsidae, (2) *Cletopsyllus* and *Pseudocletopsyllus* were transferred to a new subfamily Cletopsyllinae, (3) *Normanella* was retained as the only genus in the Normanellinae. The relationship of the Laophontopsidae and Normanellidae (as defined above) to the other families of the Laophontoidea are well supported (HUYS 1990a; present account). The phylogenetic position of the Cletopsyllinae, however, is less clear. Apart from the fact that the subfamily does not share any of the synapomorphies of the superfamily Laophontoidea, there are also three characters which exclude it from a larger lineage comprising the Cletodidae, Ancorabolidae, Canthocamptidae and the families of the Laophontoidea (named hereafter the "canthocamptoid complex").

First, members of the Cletopsyllinae lack sexual dimorphism on the male P3 endopod. This is a robust apomorphy defining the monophyly of the "canthocamptoid complex" and although controversy exists over the homology of this sexual dimorphism in certain lineages (GEE 1994; FIERS 1996) a detailed study has shown that the modification of the male P3 endopod in the various families of the "canthocamptoid complex"can plausibly be derived from a single ancestral pattern (HUYS, unpubl.). Second, all Cletopsyllinae possess an inner seta on P3–P4 exp-1. The loss of this element on P2–P4 exp-1 is a synapomorphy for the "canthocamptoid complex". Finally, the presence of 4 inner setae on P2 enp-2 indicates that this segment is compound, representing the fused middle and distal segments, and that its armature [1,2,4] is derived from either a [0-2;1,2,2] or, more likely, a [0–1;1,2,3] pattern. Either alternative derivation would exclude the Cletopsyllinae from the "canthocamptoid complex" since none of its members dis-

playing a 3-segmented P2 endopod (e.g. *Canthocamptus* Westwood, 1836) possesses 2 inner setae on the middle segment or 3 inner setae on the distal segment.
The presence of 3 setae on the syncoxa of the maxilliped is another exceptional character within the "canthocamptoid complex". Within this group it is found only in some primitive Laophontidae such as the genus *Archilaophonte* Willen, 1995 (WILLEN 1995). The presence of 3 setae on the endopodal lobe of the male P5 is a character that excludes the family from the Laophontoidea.
The foregoing comparison, which is admittedly based on the principle of elimination, provides evidence that the Cletopsyllinae represent a separate lineage within the Harpacticoida which cannot be accommodated under the broader taxonomic concept of the "canthocamptoid complex". Since the subfamily cannot be placed in any of the other harpacticoid families either it is accorded family rank herein as Cletopsyllidae grad. nov.
Swimming leg sexual dimorphism is often informative in revealing relationships at the subfamily or family level (e.g. HICKS 1988; HUYS 1990b–c). In the Cletopsyllidae sexual dimorphism is typically expressed on the P2 endopod and the most significant feature is the apophysis on the distal segment. This process can be identified as the positional homologue of the inner apical seta in the female. Sexual dimorphism on the P2 endopod is found in a wide range of families, including the Tetragonicipitidae, Thalestridae, Harpacticidae, Hamondiidae, Ambunguipedidae, Diosaccidae, Miraciidae, Porcellidiidae, Paranannopidae and the Idyanthinae (Tisbidae). The sexual dimorphism displayed in the Harpacticidae and most Paranannopidae is largely restricted to the middle endopod segment (i.e. formation of a mucroniform process) and is not relevant here. The Tachidiidae show a variety of modifications of the P2 endopod, involving different segments and elements (LANG 1948; HUYS et al. 1996). Since there is no unifying pattern for the Tachidiidae as a whole, these modifications are not considered here. The modifications found in the other families can be attributed to one or a combination of the following patterns:
(1) reduction in number of setae on enp-3 without modification
In the Porcellidiidae sexual dimorphism involves a reduction in the number of setae from four in the female to two in the male. There are no additional modifications of individual elements (e.g. HICKS & WEBBER 1983).
(2) modification of the outer spine of enp-3
The outer spine is often fused to the segment or modified in a variety of ways in the Paranannopidae (e.g. GEE & HUYS 1991; HUYS & GEE 1993, 1996) and two subfamilies within the Thalestridae, i.e. the Pseudotachidiinae (e.g. HICKS 1989) and the Donsiellinae (HICKS 1988). This element is also modified in the Idyanthinae and often the whole segment becomes transformed with loss of one or several setae.
(3) modification of the outer apical seta of enp-3
In the Miraciidae the terminal spinous process on the distal endopod segment is homologous with the outer apical seta in the female and the inner apical seta is strongly reduced (HUYS & BÖTTGER-SCHNACK 1994). Similarly, in male Diosaccidae the outer apical element is profoundly modified (as is the outer spine) and the inner apical seta does not take part in the gross modification of the endopod (except in some genera such as *Amphiascopsis* Gurney where it became secondarily modified; cf. LANG (1965)). In both these families transformation of the P2 endopod also involves the fusion of enp-2 and -3.
(4) modification of the inner apical seta of enp-3
The inner apical seta in the Ambunguipedidae is transformed into a strongly modified stout appendix with bifid apex in the male (HUYS 1990c). In the thalestrid subfamilies Thalestrinae, Dactylopusiinae and Rhynchothalestrinae the inner apical seta is strongly reduced in males and usually replaced by a setule. FIERS (1995) pointed out that all Tetragonicipitidae have two swollen elements and a short, slender unarmed seta on the distal margin of P2 enp-2 in the male. The swollen elements are often fused to the segment and represent the homologues of the outer spine and the outer apical seta of the female. The short accessory seta on the male endopod is homologous with the inner apical seta and is always articulating with the segment.
In conclusion, a comparative study of P2 endopod sexual dimorphism within the Harpacticoida fails to reveal any indications of phylogenetic affinity between the Cletopsyllidae and other families. The cletopsyllid type is probably closest to that exhibited by the Ambunguipedidae but the apparent absence of such a modification in its sistergroup, the Hamondiidae (HUYS 1990c), indicates that the modification of the inner apical seta has evolved convergently in the Ambunguipedidae and Cletopsyllidae and hence is an autapomorphy for both.
The relationships of the Cletopsyllidae have to remain enigmatic and we suspect the discovery of new missing links rather than an in-depth analysis of the known families to shed light on their phylogenetic position. The family has retained some plesiomorphic character states on both the mouthparts (3 setae on the mandibular basis and maxillipedal syncoxa; maxillary syncoxa with 3 endites) and thoracopods (e.g. P1 exp-2 with inner seta; P5 ♂ with 3 setae on baseoendopod) but at the same time displays significant reductions in other appendages such as the antennule, antenna, maxillule and endopodal segmentation of P2–P4. This mosaic of

characters may indicate that the Cletopsyllidae is an ancient but isolated branch which either remained relatively unsuccessful or has survived as a low number of relicts.
Unique apomorphies for the Cletopsyllidae include the presence of conical processes on segment 2 of the antennule, the sexual dimorphism on the male P2 endopod and the presence of only 1 seta on the male P6.

Family diagnosis.

Harpacticoida. Body elongate, tapering posteriorly; somites well defined with crenulate or dentate posterior margins. Rostrum large, defined at base. Cephalothorax bell-shaped. Genital and first abdominal somites fused in ♀ forming genital double-somite. Urosomites with well developed, posteriorly directed pleural areas. Anal operculum rounded, spinulose or setulose. Sexual dimorphism in antennule, P2 endopod, P5, P6, genital segmentation and caudal ramus; sometimes also in P3–P4 exopod (outer and distal spines of exp-2 and/or exp-3).
Antennule ♀ 4- or 6-segmented; posterior margin of segment 2 with 2 distinct conical processes. Antennule ♂ 7-segmented; subchirocer with geniculation between segments 5 and 6; posterior margin of segment 2 with proximal spinous and distal cylindrical process. Apical acrothek in both sexes represented by 2 setae only.
Antenna with allobasis and minute abexopodal seta; exopod 1-segmented and bisetose; endopod with 3 lateral and 6 distal elements. Mandible with biramous palp; basis with 2–3 setae; exopod 1-segmented and unisetose; endopod 1-segmented with 4 setae. Maxillule without epipodite; basis with 4 elements; rami reduced and incorporated into palp, endopod represented by 1 seta, exopod represented by minute bisetose knob. Maxilla with 3 endites on syncoxa; allobasis with 3 accessory elements and endopod represented by 3 setae. Maxilliped subchelate; syncoxa with 3 setae; basis unarmed; endopod represented by claw with long accessory seta and 1–2 vestigial elements.
P1–P4 with 3-segmented exopods and 2-segmented endopods. P1 basis forming distinct pedestal for endopod; exopod with inner seta on exp-2 and 2 spines plus 2 geniculate setae on exp-3; endopod prehensile, with inner seta on enp-1 and 2 distal (1 claw, 1 geniculate seta) and 1–2 lateral elements on enp-2. P2–P4 with outer spine (P2) or seta (P3–P4) on basis. Armature formula:

	coxa	basis	exopod	endopod
P2	0–0	1–0	I–0;I–1;III,I+1,1	0–1;I,2,4
P3	0–0	1–0	I–1;I–1;III,I+1,2	0–1;I,2,3
P4	0–0	1–0	I–1;I–1;III,I+1,2	0–1;I,2,3

P2 endopod ♂ sexually dimorphic; enp-2 inner apical seta modified into basally curved or styliform spine; outer apical seta markedly shorter than in ♀; outer spine sometimes reduced.
P5 with separate exopod and baseoendopod in both sexes; medially fused in ♂. Baseoendopod with elongate, triarticulate setophore; endopodal lobe triangular with 5 setae/spines in ♀, trapezoid with 3 setae in ♂. Exopod elongate, rectangular, with 6 setae in ♀ and 4-5 setae in ♂.
Genital apertures ♀ paired, each comprising gonopore and copulatory pore; closed off by opercula derived from P6, bearing 3 elements. Sixth pair of legs ♂ asymmetrical with dextral and sinistral configurations; each with 1 seta.
Caudal rami with 7 setae, all located in distal quarter; setae I-III closely set.
One egg-sac.
Marine, free-living.
Type genus: *Cletopsyllus* Willey, 1935.
Other genera: *Bathycletopsyllus* gen. nov.; *Isocletopsyllus* gen. nov.; *Retrocalcar* gen. nov.
Genus inquirendum: *Pseudocletopsyllus* Vervoort, 1964.

4.6. Key to genera.

1. Antennule ♀ 6-segmented ..... *Bathycletopsyllus* gen. nov.
   Antennule ♀ 4-segmented 2
2. Antennule ♀ segment 3 with crenulate posterior margin; P5 exopod ♂ with 4 setae/spines ..... *Cletopsyllus* Willey, 1935
   Antennule ♀ segment 3 with smooth posterior margin; P5 exopod ♂ with 5 setae/spines 3
3. Caudal ramus ♀ with outer proximal margin produced into lobate expansion bearing a spur-like process posteriorly and a secondary process dorsally .. *Retrocalcar* gen. nov.
   Caudal ramus ♀ without outer lobate expansion; ramus markedly longer in ♂ . *Isocletopsyllus* gen. nov.

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