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Restructuring the Ancorabolidae Sars (Copepoda, Harpacticoida) and Cletodidae T. Scott, with a new phylogenetic hypothesis regarding the relationships of the Laophontoidea T. Scott, Ancorabolidae and Cletodidae

Kai Horst George[1]

1 *Senckenberg am Meer, Abt. Deutsches Zentrum für Marine Biodiversitätsforschung DZMB, Südstrand 44, D-26382 Wilhelmshaven, Germany*

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Corresponding author: Kai Horst George (Kai.George@senckenberg.de)

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Abstract

Uncovering the systematics of Copepoda Harpacticoida, the second-most abundant component of the meiobenthos after Nematoda, is of major importance for any further research dedicated especially to ecological and biogeographical approaches. Based on the evolution of the podogennontan first swimming leg, a new phylogenetic concept of the Ancorabolidae Sars and Cletodidae T. Scott sensu Por (Copepoda, Harpacticoida) is presented, using morphological characteristics. It confirms the polyphyletic status of the Ancorabolidae and its subfamily Ancorabolinae Sars and the paraphyletic status of the subfamily Laophontodinae Lang. Moreover, it clarifies the phylogenetic relationships of the so far assigned members of the family. An exhaustive phylogenetic analysis was undertaken using 150 morphological characters, resulting in the establishment of a now well-justified monophylum Ancorabolidae. In that context, the *Ancorabolus*-lineage sensu Conroy-Dalton and Huys is elevated to sub-family rank. Furthermore, the membership of *Ancorabolina* George in a rearranged monophylum Laophontodinae is confirmed. Conversely, the *Ceratonotus*-group sensu Conroy-Dalton is transferred from the hitherto Ancorabolinae to the Cletodidae. Within these, the *Ceratonotus*-group and its hypothesised sister-group *Cletodes* Brady are combined to form a monophyletic subfamily Cletodinae T. Scott, **subfam. nov.** Consequently, it was necessary to restructure the Ancorabolidae, Ancorabolinae and Laophontodinae and extend the Cletodidae to include the displacement and exclusion of certain taxa. Moreover, comparison of the Ancorabolidae, Cletodidae, Laophontoidea and other Podogennonta shows that the Ancorabolidae and Cletodidae form sister-groups in a monophylum Cletodoidea Bowman and Abele, which similarly has a sister-group-relationship with the Laophontoidea T. Scott. According to the present study, both taxa constitute a derived monophylum within the Podogennonta Lang.

Key Words

meiofauna, crustacea, Podogennonta, Cletodoidea, systematics, taxonomy

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Introduction

> *Um dahin zu gelangen, muß man sich indessen von den früheren Ansichten so weit wie möglich freimachen und so vorgehen, als sei bisher kein System vorhanden gewesen.*
>
> Translation:
> *In order to get there, however, one has to get as far away from the previous views as possible and act as if no system had been in place.*
>
> Karl Lang (1936a: 445)

With an estimated number of > 50,000 species (cf. George et al. 2020 and references therein), the Copepoda (Crustacea) inhabit almost all aquatic habitats. In the marine benthos, they present high abundance values, particularly the order Harpacticoida, which is outnumbered only by Nematoda (Giere 2009), but becoming often the most important taxon with respect to biomass (Wells 1988). The Harpacticoida are of eminent ecological importance both as consumers/recyclers of organic matter and as a food source for other organisms (e.g. Hicks and Coull 1983; Coull 1988; Giere 2009). Their quite successful dispersal over almost all marine habitats is reflected by a striking morphological variability (cf. George et al. 2020), providing numerous characteristics also for systematic studies (e.g. Lang 1948; Huys and Boxshall 1991). However, in phylogenetic research of the Copepoda, molecular approaches combined with computer-aided cladistics have prevailed for more than three decades (cf. Seifried 2003). The inexorable ascent of molecular taxonomy over this time has been matched by a progressive disregard for "traditional", i.e. morphological, taxonomy, irrespective of morphologists' attempts to justify and defend the morphological approach (e.g. Hopkins and Freckleton 2002; Lipscomb et al. 2003; Sudhaus 2007; Zhang 2008; Wheeler 2014). However, in the contribution on hand, morphological taxonomy was the only pragmatic approach owing to the lack of adequate material in sufficient quantities to enable molecular analysis.

The Ancorabolidae Sars, 1909 (Fig. 1) were established to allocate the type genus *Ancorabolus mirabilis* Norman, 1903 and three further monotypic genera (Sars 1909). The systematics of the exclusively marine Ancorabolidae has been the object of increasing interest particularly in the last two decades (George 1998a, b, 2001, 2006a, b, c, 2017, 2018; Conroy-Dalton and Huys 2000; Conroy-Dalton 2001, 2003a, b, 2004; George and Plum 2009; Wandeness et al. 2009; George and Tiltack 2010; Gheerardyn and George 2010; Schulz and George 2010; Gheerardyn and Lee 2012; George and Müller 2013; George et al. 2013; George and Gheerardyn 2015; George et al. 2019; Lee and Huys 2019); a general historical summary of research on the Ancorabolidae was given by George (2006a) and recently updated by Lee and Huys (2019). Species assigned to the family are rarely found and, in sediment samples, they generally occur in very low numbers (e.g. George 1998a; George and Schminke 1998; Conroy-Dalton and Huys 2000; Wandeness et al. 2009). Moreover, samples were historically often fixed with formalin (e.g. George 1998a, b, 2001) and neither the types nor additional material of several species are available (e.g. Conroy-Dalton and Huys 2000; George 2001, 2017, 2018). Morphological species descriptions are available, however and although some may be of limited quality (e.g. *Calypsophontodes latissimus* (Brady, 1918), *Laophontodes antarcticus* Brady, 1918, *Bicorniphontodes hamatus* (Thomson, 1882), *B. ornatus* (Krishnaswamy, 1957), *Patagoniaella vervoorti* Pallares, 1968, *Polyascophorus gorbunovi* (Smirnov, 1946)) (cf. Thomson 1882; Brady 1918; Smirnov 1946; Krishnaswamy 1957; Pallares 1968), most provide many morphological features of relevance for phylogenetic analyses. Thus, in the present study, a morphological taxonomic approach was the only way to resolve the systematics of the Ancorabolidae.

The phylogenetic evaluation presented here provides a completely new hypothesis concerning the systematics of the Ancorabolidae. As a result of that rearrangement, a new systematic concept involving the supposed closely-related Cletodidae T. Scott, 1904 sensu Por (1986) is also presented and discussed in detail.

Methods

This analysis strictly follows the concept of "consequent phylogenetics" (Hennig 1982; Ax 1984, 1988, 1995; Sudhaus and Rehfeld 1992); the characters used are compared and discussed in detail, leading to an intersubjective phylogenetic hypothesis (Ax 1984). No computer-based cladistic analysis was made, so the presented cladogram (Fig. 2) is not a computer-generated one, but simply serves to illustrate the result of the complex phylogenetic analysis.

Morphological comparison was predominantly based on original species (re)descriptions, as well as on Lang (1948, 1965), Huys and Boxshall (1991), Huys et al. (1996), Willen (2000), Seifried (2003) and Boxshall and Halsey (2004). Whenever available, direct comparison of (type) material was included.

General scientific terminology follows a literal translation of Lang (1948) with additional terms from Huys and Boxshall (1991). Phylogenetic terminology is translated from Ax (1984). The terms "telson" and "furca" are adopted from Schminke (1976).

Abbreviations used in the text:

A1: antennule, A2: antenna, cphth: cephalothorax, enp-1–enp-3: endopodal segments 1–3, exp-1–exp-3: exopodal segments 1–3, FR: furcal ramus/rami, md: mandible, mxl: maxillula, mx: maxilla, mxp: maxilliped, P1–P5: swimming legs (= "pereiopods") 1–5, syn.: synonymised names. Outer elements (setae/spines) of the swimming legs are indicated by Roman, inner elements by Arabic numerals.

To facilitate the differentiation between the hitherto existing taxonomic arrangement and the here postulated new arrangement, the following notation was used: "Ancorabolidae" set in quotation marks refers to the previous, while Ancorabolidae ● accompanied by a black dot means the here hypothesised new composition of the taxon. Same applies to "Ancorabolinae"/Ancorabolinae ●, "Laophontodinae"/Laophontodinae ● and "Cletodidae"/Cletodidae ●.

With respect to the number of segments and setae/spines, I adopt the generally accepted principle of oligomerisation (Huys and Boxshall 1991; Seifried 2003), which postulates that a reduction of segments/elements constitutes the relatively more derived state.

When analysing a large number of characters, a remarkable amount of convergences may be expected. That is the case also in the contribution on hand. The supposed convergences are highlighted with grey in Table 1, whereas the respective yellow fields indicate to which taxon the character is explicitly assigned (and discussed correspondingly).

Results

An exhaustive phylogenetic analysis (cf. Methods), based on 150 morphological characters (Table 1), was under-

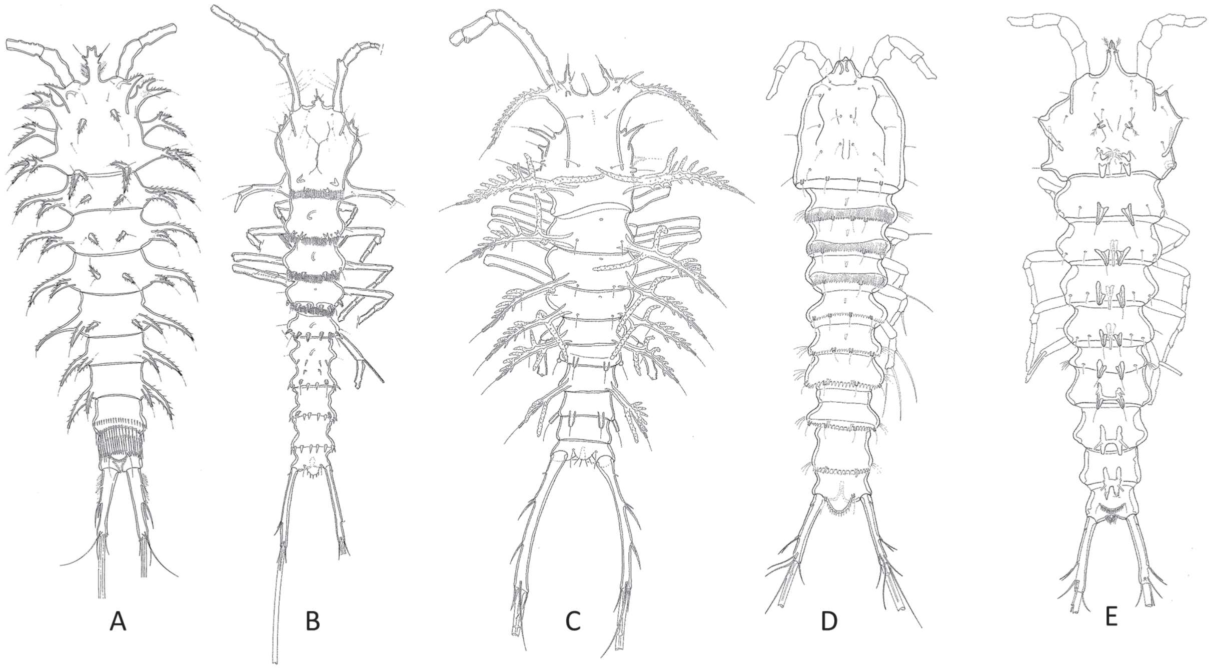

Figure 1. Representatives of "Ancorabolidae" Sars, 1909, **A.** *Ancorabolus ilvae* George, 2001, **B.** *Ancorabolina chimaera* George, 2006, **C.** *Ceratonotus vareschii* George, 2006, **D.** *Laophontodes typicus* T. Scott, 1894, **E.** *Paralaophontodes anjae* George, 2017. Modified from George 2001 (A), 2006a (B), 2006b (C), 2017 (D), 2018 (E). No scales.

taken. It started with a re-examination of the "Ancorabolidae" confirming its polyphyletic status due to the ambiguity of those characters that had so far been assumed as clear apomorphies for the "Ancorabolidae". Consequently, the following changes were made:

1. The *Ceratonotus*-group was excluded from the "Ancorabolidae". Subsequent comparison with the "Cletodidae" revealed that the *Ceratonotus*-group shows closest relationship to the "cletodid" type genus *Cletodes* Brady, 1872. Thus, it was assigned to the Cletodidae ● T. Scott, 1904 sensu Por (1986);
2. The formerly supposed sister-group of the *Ceratonotus*-group, the *Ancorabolus*-lineage, was elevated to sub-family rank and is now redefined as Ancorabolinae ● Sars, 1909;
3. As demonstrated by Lee and Huys (2019), the taxon *Patagoniaella* Pallares, 1968 cannot be retained in the "Ancorabolidae". However, their assignment of *Patagoniaella* to the "Cletodidae" is rejected and the genus is placed as *species inquirenda* in Harpacticoida;
4. Lee and Huys' (2019) assignment of *Ancorabolina* George, 2006 to the "Laophontodinae" Lang, 1944 is here adapted to Laophontodinae ● and phylogenetically substantiated;
5. The assignment of the *Ceratonotus*-group to the Cletodidae ● and its discovered close relationship with *Cletodes* lead to the erection of Cletodinae T. Scott, 1904 subfam. nov. as a distinct monophylum within that family. However, as a detailed phylogenetic analysis of the Cletodidae ● would go beyond the scope of this study, the phylogeny within Cletodidae ● remains unresolved;
6. Ancorabolinae ● and Laophontodinae ● are characterised as sister-groups of the monophylum Ancorabolidae ● Sars, 1909;
7. Ancorabolidae ● and Cletodidae ● form the monophyletic Cletodoidea Bowman & Abele, 1982;
8. Laophontoidea T. Scott, 1904 and Cletodoidea share a sister-group-relationship, building a monophyletic taxon within Podogennonta Lang, 1944, presumably in a clade named "taxon II" by Willen (2000).

The results of the complete phylogenetic analysis are pictured in Fig. 2 and listed in Table 2. The latter summarises the results and presents the studied taxa, their subordinate taxa, the apomorphies (Table 1) justifying the monophyletic states of the respective taxa, indicates the sections in the discussion that provide the detailed phylogenetic argument and identifies the branches in Fig. 2 corresponding to the respective taxa/sections. That clear representation facilitates the detailed phylogenetic treatment as presented in the discussion.

As the phylogenetic analysis lead, in parts, to a remarkable re-ordering of the supra-generic taxa, updated or newly-composed diagnoses were necessary:

Family Ancorabolidae ● Sars, 1909 (modified after Boxshall and Halsey 2004)

Harpacticoida Sars, 1903, Podogennonta Lang, 1944. Body basally elongate, mostly cylindrical, occasionally

Table 1. List of 150 morphological characters used in the phylogenetic analysis. Apomorphic states marked with “*1*”, plesiomorphies [set in square brackets in the first column] marked with “0”; “**1+**” indicates further deviation inside certain taxa. Convergent deviations marked with “***1***”. Interrogation marks: no information available.

No.	Character/taxon (0 = plesiomorphy; 1 = apomorphy; 1+ = further deviation)	*Podogennonta*	*Laophontoidea*	*Tapholaophontodes*	*Algensiella*	*Calypsophontodes*	*Rostrophontodes*	*Laophontodes*	*Bicorniphontodes*	*Ancorabolina*	*Paralaophontodes*	*Lobopleura*	*Probosciphontodes*	*Ancorabolus*-lineage	*Ceratonotus*-group	*Cletodes*	Remaining *Cletodidae*
1	P1 elongation of endopod, longer than exopod, prehensile [P1 enp-1 not longer than exopod, not prehensile]	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
2	P1 enp-2 strongly reduced in size [P1 enp-2 as long as enp-1]	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
3	P1 enp-3 strongly reduced in size [P1 enp-3 as long as enp-1]	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
4	P1 enp-3 element I-en shifted apically [element I-en arising subapically on outer margin]	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
5	P1 enp-3 element I-en transformed into claw [element I-en regular spine]	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
6	P1 enp-3 element 5 geniculated [element 5 non-geniculate seta]	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
7	P1 enp-3 element 4 shortened [element 4 as long as accompanying elements]	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
8	P1 exp-3 element VI geniculated [element VI non-geniculate]	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
9	P1 exp-3 element VII geniculated [element VII non-geniculate]	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
10	P1 exp-3 element 3-ex lost [element 3-ex still present]	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
11	P1 exp-3 element 4-ex lost [element 4-ex still present]	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
12	P1 endopod fusion of enp-1 and -2 = 2-segmented enp [segments not fused = 3segmented enp]	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
13	P1 enp-1 elongated, longer than exopod	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	**1+**	**1+**	**1+**
14	P1 enp-1 element 1 lost	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
15	P1 enp-2 element 4 lost	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
16	A1 female at most 8-segmented [female A1 >8 segments]	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
17	A2 with Allobasis [A2 with basis]	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
18	A2 endopod with only 1 slender seta at distal edge [with 2 slender setae]	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
19	P2, P3 (female) and P4 enp 2-segmented, more slender than exp [3-segmented enps, as broad as exp]	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
20	P1 exp-2 element 2-ex lost [element 2-ex still present]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
21	P1 exp-3 element III lost [element III still present]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
22	Rostrum fused with cphth [rostrum distinct]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
23	A1 female at most 5-segmented [female A1 >5 segments]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
24	A1 female fourth segment very small [segment not much smaller than preceding/following segments]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
25	A1 female third segment (partly) overlapping fourth one [no overlap]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
26	A1 female aesthetasc on third segment [aes on fourth segment]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
27	A2 exp with at most 3 setae [exp with >3 setae]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
28	Md palpus 1-segmented (i.e. without exp and enp) [at least exp still present]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
29	Md palpus with at most 6 setae [palpus >6 setae]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
30	Mxl endopod and exopod fused with basis [at least exp distinct]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
31	Mx endopod with at most 2 setae [enp >2 setae]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
32	Mxp syncoxa with at most 1 seta [syncoxa >1 seta]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
33	P2-P4 enp-2 very slender, cylindrical [enp-2 broad]	0	0	**1+**	*1*	*1*	*1*	*1*	*1*	*1*	*1*	**1+**	**1+**	*1*	*1*	*1*	*1*
34	P2 enp-2 without inner seta [inner seta still present]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
35	P3 female enp-2 with at most 1 inner seta [enp-2 >1 seta]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
36	P2-P4 Enp-1 without inner setae [at least 1 inner seta still present]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
37	P5 female endopod fused with basis = baseoendopod [endopod still separate]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
38	P5 endopodal lobe reduced, narrow [lobe broad, well-developed]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*
39	A2 exopod atrophied, at most knob-like (if not reduced completely) [exp moderate or small, but well-developed]	0	0	**1+**	**1+**	*1*	*1*	*1*	*1*	**1+**	*1*	*1*	*1*	**1+**	**1+**	***1***	0
40	A2 exopod with at most 1 seta [exp >1 seta]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	***1***	***1***	0
41	Mx with at most 2 endites [third endite at least represented by 1 seta]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	***1***	***1***	0
42	Mxp loss of elongate seta accompanying maxillipedal claw [elongate seta still present]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	0	0	0

No.	**Character/taxon (0 = plesiomorphy; 1 = apomorphy; 1+ = further deviation)**	***Podogennonta***	***Laophontoidea***	***Tapholaophontodes***	***Algensiella***	***Calypsophontodes***	***Rostrophontodes***	***Laophontodes***	***Bicorniphontodes***	***Ancorabolina***	***Paralaophontodes***	***Lobopleura***	***Probosciphontodes***	***Ancorabolus*-lineage**	***Ceratonotus*-group**	***Cletodes***	**Remaining *Cletodidae***
43	P2 enp-2 without outer seta [outer seta still present]	0	0	**1+**	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	**1+**	*1*	***1***	0	0
44	P5 female endopodal lobe with at most 4 setae [endopodal lobe >4 setae]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	**1+**	**1+**	0
45	A1 2. segment with cluster of spinules [no spinulose cluster developed]	0	0	*1*	*1*	*1*	**?**	*1*	*1*	*1*	*1*	*1*	*1*	0	0	0	0
46	A2 allobasis abexopodal seta (basal half) reduced = with at most 1 seta [that seta still present = with 2 setae]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	0	0	0	0
47	P1 exopodal element II geniculate [element II non-geniculate]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	0	0	0	0
48	P1 exopodal element IV geniculate [element IV non-geniculate]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	0	0	0	0
49	P5 female baseoendopod at most 2 setae [baseoendopod >2 setae]	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	0	0	0	0
50	P5 endopod completely absorbed into basis [endopodal lobe still discernible]	0	0	**1**	**1**	**1+**	*1*	*1*	*1*	*1*	*1*	*1*	*1*	0	0	0	0
51	Cphth anterolaterally with characteristic „sensillar group I“ [no „sensillar group I“]	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0
52	Cphth anterolaterally with characteristic „sensillar group II“ [no „sensillar group II“]	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0
53	Cphth laterally with characteristic „sensillar group III“ [no „sensillar group III“]	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0
54	Cphth posterolaterally with characteristic „sensillar group IV“ [no „sensillar group IV“]	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0
55	Cphth posterolaterally with characteristic „sensillar group V“ [no „sensillar group V“]	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0
56	Development of cuticular, sensilla-bearing lateral body processes [no lateral body processes developed]	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0
57	Development of characteristic sensilla [such sensilla not developed]	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0
58	A1 female 3-segmented [female A1 > 4 segments]	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0
59	P1 whole basis transversely elongated [basis trapezoid, as long as broad]	0	0	0	0	0	0	0	0	0	0	0	0	*1*	***1***	0	0
60	P1 exopod 2-segmented [exopod 3-segmented]	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0
61	P1 enp-1 element 2-en lost [element 2-en still present]	0	0	0	***1***	***1***	***1***	***1***	***1***	***1***	***1***	***1***	***1***	*1*	***1***	***1***	0
62	P2-P4 exp-3 with 2 outer spines [with 3 outer spines]	0	0	***1***	0	0	0	0	0	0	0	0	0	*1*	***1***	***1***	0
63	P2-P4 bases transversely elongated, surpassing coxal outer margin [bases not elongated transversely]	0	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	***1***	***1***	0	0
64	P2-P4 coxae shortened; at most half as broad as basis [coxae as broad as bases]	0	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	***1***	***1***	0	0
65	Md palp with at most 4 setae [palp >4 setae]	0	0	*1*	0	0	0	0	0	0	0	0	0	0	0	0	0
66	P2 without endopod [endopod at least 1-segmented]	0	0	*1*	***1***	0	0	0	0	0	0	0	***1***	0	0	0	0
67	P4 without endopod [endopod at least 1-segmented]	0	0	*1*	0	0	0	0	0	0	0	0	***1***	0	0	0	0
68	P5 baseoendopod female virtually absent [baseoendopod still discernible]	0	0	*1*	0	0	0	0	0	0	0	0	0	0	0	0	0
69	Mxp endopod fused with claw [endopod and claw still distinct]	0	0	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	***1***	0	0	0
70	P1 basis longitudinally elongated [no longitudinal elongation]	0	0	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	0	0	0	0
71	Mxp without endopodal seta accompanying claw [with at least 1 accompanying seta]	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0	0	0
72	P3 enp-1 lost (= endopod 1-segmented) [enp-1 still developed]	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0	0	0
73	P4 enp-1 lost (= endopod 1-segmented) [enp-1 still developed]	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0	0	0
74	FR slender, at least 3x as long as broad [FR broad, at most 2x longar than broad]	0	0	0	0	0	*1*	*1*	*1*	*1*	*1*	*1*	*1*	***1***	***1***	0	0
75	Rostrum ventrally curved [rostrum not curved]	0	0	0	0	*1*	***1***	0	0	0	0	0	0	0	0	0	0
76	Md palp with at most 5 setae [palp >5 setae]	0	0	**1+**	0	*1*	0	0	0	0	0	0	0	0	***1***	0	0
77	P2-P4 sexual dimorphism in the size [no sexual dimorphism; same size in female and male]	0	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0	0
78	Sexual dimorphism on P4 enp: loss of inner seta in male [if sexual dimorphism, than by loss of inner seta in female]	0	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0	0
79	P5 basis, endopod and exopod fused into single plate [not fused to single plate]	0	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0	0
80	Body slender, virtually cylindrical [body fusiform, clearly tapering posteriorly]	0	0	0	0	0	*1*	*1*	*1*	*1*	0	0	0	0	***1***	0	0
81	P1 coxa elongated longitudinally [no longitudinal elongation]	0	0	0	0	0	*1*	*1*	*1*	*1*	***1***	0	***1***	0	0	0	0
82	A2 exopod at most represented by 1 tiny seta [at least a small, 1-segmented, knob-like exopod present]	0	0	0	0	0	0	*1*	*1*	*1*	0	0	0	**1+**	**1+**	0	0

No.	**Character/taxon (0 = plesiomorphy; 1 = apomorphy; 1+ = further deviation)**	***Podogennonta***	***Laophontoidea***	***Tapholaophontodes***	***Algensiella***	***Calypsophontodes***	***Rostrophontodes***	***Laophontodes***	***Bicorniphontodes***	***Ancorabolina***	***Paralaophontodes***	***Lobopleura***	***Probosciphontodes***	***Ancorabolus*-lineage**	***Ceratonotus*-group**	***Cletodes***	**Remaining *Cletodidae***
83	Cuticula of cphth, pedigerous somites, and genital somite with reticulate surface ornamentation [respective ornamentation absent]	0	0	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0
84	P5-bearing somite, GDS, and first abdominal somite dorsally with curved spinous projections [lacking such projections]	0	0	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0
85	FR setae II (and I?) displaced towards proximal margin [setae II and I arising from middle of FR]	0	0	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0
86	Mxl coxa with only 1 seta [with 2 setae]	0	0	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0
87	Mxp claw with long pinnules along distal half [mxp claw bare]	0	0	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0
88	P1 basis with centred outward elongation [basis cylindrical]	0	0	0	0	0	*1*	0	0	***1***	0	0	0	0	0	0	0
89	P1 enp-2 claw slender and elongate [claw short and robust]	0	0	0	0	0	*1*	0	0	0	0	0	0	0	0	0	0
90	P2 enp-2 with 1 apical seta [with 2 apical setae]	0	0	**1+**	**1+**	0	*1*	0	0	0	0	0	0	0	0	0	0
91	P3 enp-2 with 1 apical seta [with 2 apical setae]	0	0	***1***	**1+**	0	*1*	0	0	0	0	0	0	0	0	0	0
92	Cphth with postero-lateral processes [postero-lateral processes not developed]	0	0	0	0	0	0	0	*1*	*1*	0	0	0	0	0	0	0
93	Cphth medio-laterally with triangular extensions [such extensions not developed]	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0	0	0
94	Hyaline frills of body somites digitate, with rounded tips frills serrate or with spinules]	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0	0	0
95	FR setae I and II displaced subapically [setae I and II arising mid-laterally]	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0	0	0
96	A2 allobasis abexopodal seta (endopodal half) reduced = 0 abexopodal setae [seta still present = 1 abexopodal seta]	0	0	***1***	***1***	***1***	***1***	0	*1*	0	0	0	0	0	0	0	0
97	P2 and P3 exp-3 outer spines unipinnate, comb-like, pinnae long [outer spines bipinnate, pinnae small]	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0	0	0
98	A1 female with elongated, slender segments [segments compact, not elongated]	0	0	0	0	0	0	0	0	*1*	0	0	0	***1***	***1***	0	0
99	A2 enp loss of subapical slender seta [at least 1 subapical slender seta present]	0	0	***1***	***1***	0	**?**	0	0	*1*	0	0	0	0	0	0	0
100	A2 exopod completely lost [at least represented by tiny seta]	0	0	***1***	***1***	0	0	0	0	*1*	0	0	0	***1***	***1***	0	0
101	Thoracic and first 2 abdominal somites laterally extended [no lateral extension of thoracic and first 2 abdominal somites]	0	0	0	0	0	0	0	0	0	*1*	*1*	*1*	0	0	0	0
102	A1 female 4-segmented [female A1 >4 segments]	0	0	0	0	0	0	0	0	0	*1*	*1*	*1*	**1+**	***1***	0	0
103	P1 endopod strongly strengthened, mighty appendage [endopod elongate but slender, rather gracile]	0	0	0	0	0	0	0	0	0	*1*	*1*	*1*	0	0	0	0
104	P3 female enp-2 without inner seta [enp with at least 1 inner seta]	0	0	***1***	***1***	0	0	0	***1***	0	*1*	*1*	*1*	***1***	***1***	0	0
105	P4 female enp-2 without inner seta [enp with at least 1 inner seta]	0	0	***1***	***1***	0	0	0	0	0	*1*	*1*	*1*	***1***	***1***	0	0
106	Cphth antero-laterally with triangular extension [antero-lateral extensions not developed]	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0
107	Cphth postero-laterally with triangular extensions [postero-lateral extensions not developed]	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0
108	Rostral tip distinct [rostral tip not distinct]	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0
109	Cphth dorso-median ridge extended intop 2 backwardly directed processes [such processes not developed]	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0
110	Cphth dorsally with hairy tuft [no hairy tuft developed]	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0
111	P2-P6-bearing somites dorsally with H-like processes [H-like processes not developed]	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0
112	Abdominal somites except telson dorsally with A- or H-like processes [A- or H-like processes not developed]	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0
113	A1 male 5-segmented [male A1 at least 6-segmented]	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0
114	Mxp lacking syncoxal apical seta [at least with 1 apical seta]	0	0	0	0	0	0	0	0	0	*1*	0	0	***1***	0	0	0
115	P1 enp-2 distinctly elongated, half as long as enp-1 [enp-2 small, not reaching half the length of enp-1]	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0	0	0
116	Body dorsoventrally depressed [body rounded in transverse section]	0	0	0	0	0	0	0	0	0	0	*1*	*1*	0	0	0	0
117	Thoracic and first 2 abdominal somites with lateral spinulose lobate processes [such processes not developed]	0	0	0	0	0	0	0	0	0	0	*1*	*1*	0	0	0	0
118	Rostrum narrow at its base [rostrum triangular, with broad base]	0	0	0	0	0	0	0	0	0	0	*1*	*1*	0	0	0	0
119	A1 first segment with highly setulose seta [respective seta bipinnate, pinnae of small size]	0	0	0	0	0	0	0	0	0	0	*1*	*1*	0	0	0	0

No.	Character/taxon (0 = plesiomorphy; 1 = apomorphy; 1+ = further deviation)	*Podogennonta*	*Laophontoidea*	*Tapholaophontodes*	*Algensiella*	*Calypsophontodes*	*Rostrophontodes*	*Laophontodes*	*Bicorniphontodes*	*Ancorabolina*	*Paralaophontodes*	*Lobopleura*	*Probosciphontodes*	*Ancorabolus*-lineage	*Ceratonotus*-group	*Cletodes*	Remaining *Cletodidae*
120	Mxl 1 coxal seta reduced in size [mxl with both coxal setae well-developed]	0	0	0	0	0	**1+**	0	0	0	0	*1*	*1*	0	0	0	0
121	Mx endopod with at most 1 seta [enp with or represented by 2 setae]	0	0	0	0	0	0	0	0	0	0	*1*	*1*	0	0	0	0
122	P2-P4 exp-2 without inner setae [with at least 1 inner seta]	0	0	***1***	***1***	***1***	0	0	0	0	0	*1*	*1*	0	0	0	0
123	P2-P4 exp-3 element VII minute [element VII long]	0	0	0	0	0	0	0	0	0	0	*1*	*1*	0	0	0	0
124	P5 basoendopodal setae reduced in size [setae of moderate length]	0	0	0	0	0	***1***	0	0	0	0	*1*	*1*	0	0	0	0
125	P3 male endopod only 2-segmented [male endopod 3-segmented]	0	0	0	0	0	0	0	0	0	0	*1*	0	***1***	0	0	0
126	P4 endopod with 1 apical seta [with >1 seta]	0	0	0	0	0	***1***	0	0	0	0	*1*	0	0	0	0	0
127	P5 baseoendopod represented by minute seta [represented by >1 seta]	0	0	0	0	0	***1***	0	0	0	0	*1*	0	0	0	0	0
128	Development of paired genital system in both sexes [genital system unpaired]	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0	0
129	Cphth medially with well-developed lateral processes [lateral processes not developed]	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0
130	Cphth: posterior corners produced into long lateral lobate processes [no lateral lobate processes developed]	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0
131	Rostrum extremely elongated [rostrum of moderate length]	0	0	0	0	***1***	***1***	0	0	0	0	0	*1*	0	0	0	0
132	Rostrum laterally with rows of long spinules [rostrum laterally without spinules]	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0
133	A2 endopodal distalmost lateral spine strongly reduced in length [spine as long as the accompanying one]	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0
134	Maxillar endites each with 2 setae [endites >3 setae]	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0
135	P3 endopod completely lost in both sexes [endopod still present at least in male]	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0	0
136	P1 enp-1 strongly reduced in size, enp not prehensile [enp-1 elongate, enp prehensile]	0	0	0	0	0	0	0	0	0	0	0	0	0	*1*	*1*	*1*
137	P1 enp-2 elongated, at least as long as enp-1 [enp-2 shorter than enp-1]	0	0	0	0	0	0	0	0	0	0	0	0	0	*1*	*1*	*1*
138	P1 enp-2 element 5: geniculation reformed [element 5 still geniculated]	0	0	0	0	0	0	0	0	0	0	0	0	0	*1*	*1*	*1*
139	P1 enp-2 element I-en reformed into spine [element I-en still a claw]	0	0	0	0	0	0	0	0	0	0	0	0	0	*1*	*1*	*1*
140	Mxp loss of tiny seta accompanying the maxillipedal claw [tiny seta still present]	0	0	0	0	0	0	0	0	0	0	0	0	0	*1*	*1*	*1*
141	P5 baseoendopod with at most 3 setae [P5 baseoendopod with >3 setae]	0	0	**1+**	**1+**	**1+**	**1+**	**1+**	**1+**	**1+**	**1+**	**1+**	**1+**	0	*1*	*1*	0
142	P2-P4-bearing body somites with cuticular, sensilla-bearing dorsal processes [no dorsal processes developed]	0	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0
143	Rostrum small, narrow [rostrum triangular with broad base]	0	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0
144	A1 first segment elongate [first segment compact, not elongate]	0	0	0	0	0	0	0	0	***1***	0	0	0	0	*1*	0	0
145	P1 enp-2 element 3 lost [element 3 still present]	0	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0
146	Basis P2 transversely as long as exopod [basal elongation not reaching length of exopod]	0	0	0	0	0	0	0	0	0	0	0	***1***	0	*1*	0	0
147	Basis P3 transversely as long as exopod [basal elongation not reaching length of exopod]	0	0	0	0	0	0	0	0	0	0	0	***1***	0	*1*	0	0
148	Basis P4 transversely as long as exopod [basal elongation not reaching length of exopod]	0	0	0	0	0	0	0	0	0	0	0	***1***	0	*1*	0	0
149	P1 exopodal element VI lost geniculation [element VI still geniculated]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0
150	P1 exopodal element VII lost geniculation [element VI still geniculated]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0

slightly tapering posteriorly or slightly dorsoventrally compressed, podoplean boundary between pro- and urosoma inconspicuous. Sexual dimorphism in A1, P3, P4 (occasionally), P5 and P6; females with genital double somite due to fusion of last (P6-bearing) thoracic somite with first abdominal (genital) one. Cphth and/or body somites sometimes with lateral, latero-dorsal and/or dorsal cuticular processes of different size and shape carrying a sensillum at their tips; somites often with long tube pores. Rostrum fused with cphth, of variable shape. FR short and squarish or elongate and slender, with 6–7 setae (seta I sometimes missing). Female A1 3–5-segmented, male A1 5–8-segmented, subchirocer or chirocer. A2 with allobasis that bears 0–2 abexopodal setae; exopod

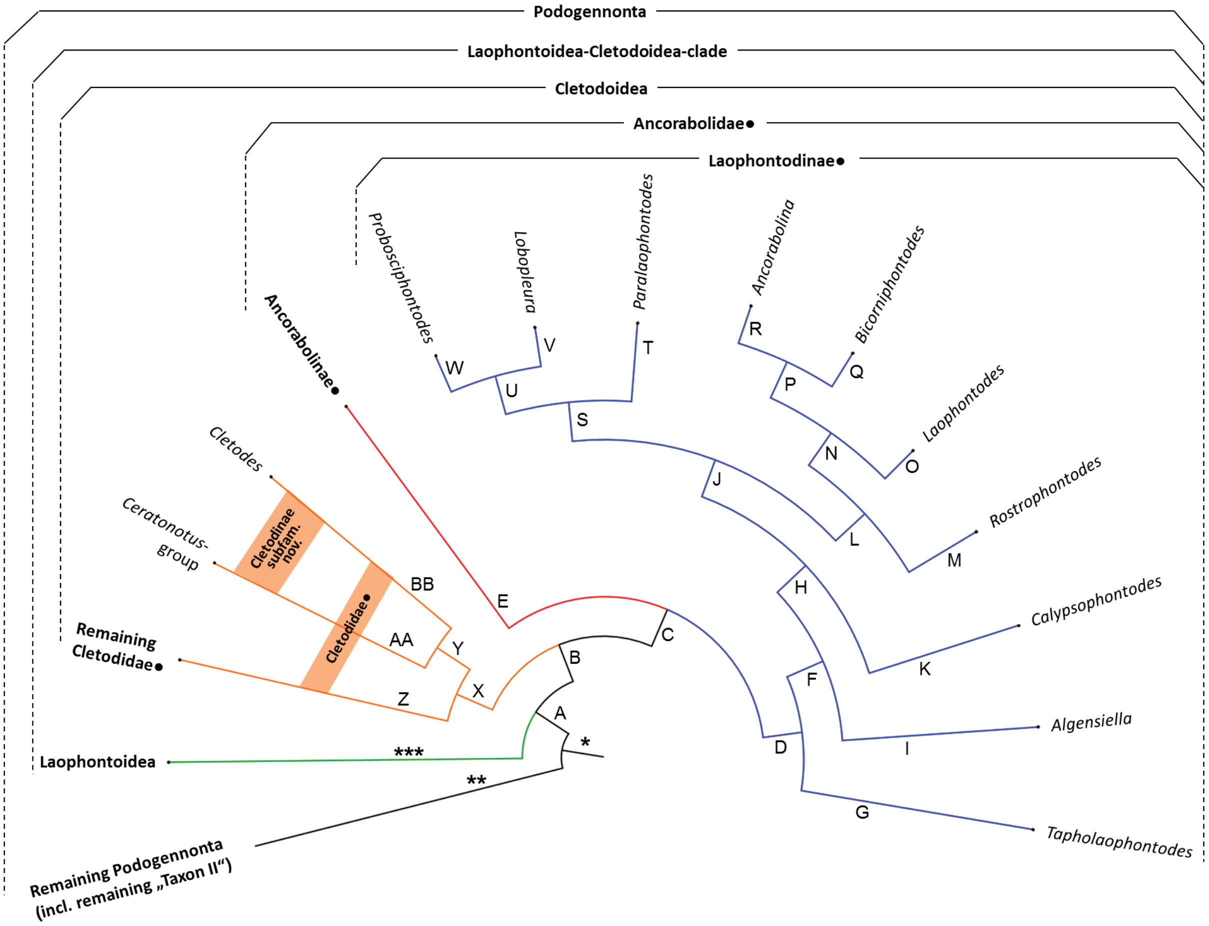

Figure 2. Cladogram visualising the result of the current phylogenetic evaluation. Capitals A–BB refer to the corresponding sections in the text; asterisks (*; **; ***) refer to the respective discussion in Chapters I and II.

small and knob-like with one tiny seta, represented by one tiny seta or absent. Md palp unilobate, with at most six setae. Mxl endo- and exopod incorporated into basis. Mx with two endites, endopod small, with two setae or represented by 1–2 setae. Mxp prehensile (subchelate), syncoxa with 0–1 apical seta, endopod and apical claw fused or distinct with claw accompanied by minute seta. P1 of podogennontan shape, prehensile, basis sometimes longitudinally and/or transversely elongated; endopod 2-segmented, enp-1 elongate, longer than exopod, with or without apical inner seta, enp-2 apically with claw and with or without long seta, subapically with spine or tiny seta; exopod 2–3-segmented, exp-1 with one outer spine, if exopod 3-segmented exp-2 with outer geniculate seta, inner seta absent, exp-3 with four setae, at least apical ones geniculated; if exopod 2-segmented exp-2 with five setae, at least apical ones geniculate. P2–P4 mostly with transversely elongated bases, exopods 3-segmented, exp-1 lacking inner seta, exp-2 with or without inner seta, exp-3 with 0–2 inner setae and 2–3 outer spines; P2 and P4 endopods absent or 1–2-segmented, if present enp-1 small, without setae, enp-2 slender, cylindrical, with 0–1 inner and/or outer seta/spine and 1–2 apical setae; P3 endopods in female as in P2 and P4, in male 2–3-segmented, with apophysis on the second or terminal segment. P5 with baseoendopod, endopodal lobe small or completely absorbed into basal part, with 1–4 setae, exopod fused with baseoendopod (females) or distinct (males), with 3–5 setae/spines. Genital system single (one copulatory pore and fused gonopores); P6 forming a genital operculum in females, asymmetric or absent in males.

Included genera: *Algensiella* Cottarelli & Baldari, 1987, *Ancorabolina* George, 2006, *Ancorabolus* Norman, 1903 (**type genus**), *Arthropsyllus* Sars, 1909, *Bicorniphontodes* George, Glatzel & Schröder, 2019, *Breviconia* Conroy-Dalton & Huys, 2000, *Calypsophontodes* Gheerardyn & Lee, 2012, *Juxtaramia* Conroy-Dalton & Huys, 2000, *Laophontodes* T. Scott, 1894, *Lobopleura* Conroy-Dalton, 2004, *Paralaophontodes* Lang, 1965, *Probosciphontodes* Fiers, 1988, *Rostrophontodes* Lee & Huys, 2019, *Tapholaophontodes* Soyer, 1975, *Uptionyx* Conroy-Dalton & Huys, 2000.

Subfamily Ancorabolinae ● Sars, 1909

Harpacticoida Sars, 1903, Podogennonta Lang, 1944, Ancorabolidae ● Sars, 1909. Body basally elongate, mostly cylindrical, podoplean boundary between pro- and

Table 2. Results of the phylogenetic analysis. The list shows the investigated taxa, their assigned subordinated genera/species, cross-references to the respective Chapter/sections in the discussion and in Fig. 2 and the recognised autapomorphies. Convergent apomorphies are set in bold italics.

Taxon	Assigned subordinated taxa	Discussion: section	Fig. 2: branch	Tab. 1: autapomorphies
Podogennonta Lang, 1944	cf. Willen (2000)	I, II	*	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11; cf. Willen (2000), Seifried (2003)
Remaining Podogennonta (including remaining „Taxon II“	cf. Willen (2000)	I, II	**	cf. Willen (2000)
Laophontoidea-Cletodoidea-clade (L-C-clade)	Laophontoidea T. Scott, 1904	I, II, III/A	A	12, 13, 14, 15, 16, 17, 18, 19
	Cletodoidea Bowman & Abele, 1982			
Laophontoidea T. Scott, 1904	Adenopleurellidae Huys, 1990	I, II	**	cf. Huys (1990), Huys and Lee (1998/99)
	Cristacoxidae Huys, 1990			
	Laophontidae T. Scott, 1904			
	Laophontopsidae Huys & Willems, 1989			
	Normanellidae Lang, 1944			
	Orthopsyllidae Huys, 1990			
Cletodoidea Bowman & Abele, 1982	Ancorabolidae● Sars, 1909	II, III/B	B	20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38
	Cletodidae● T. Scott, 1904 *sensu* Por (1986)			
Ancorabolidae● Sars, 1909	Ancorabolinae● Sars, 1909	I, II, III/C	C	***39***, ***40***, ***41***, 42, ***43***, ***44***
	Laophontodinae● Lang, 1944			
Laophontodinae● Lang, 1944	*Algensiella* Cottarelli & Baldari, 1987	III/D	D	45, 46, 47, 48, 49, 50, ***141***
	Ancorabolina George, 2006			
	Bicorniphontodes George, Glatzel & Schröder, 2019			
	Calypsophontodes Gheerardyn & Lee, 2012			
	Laophontodes T. Scott, 1904			
	Lobopleura Conroy-Dalton, 2001			
	Paralaophontodes Lang, 1965			
	Probosciphontodes Fiers, 1988			
	Rostrophontodes Lee & Huys, 2019			
	Tapholaophontodes Soyer, 1975			
Ancorabolinae● Sars, 1909	*Ancorabolus* Norman, 1903	III/E	E	51, 52, 53, 54, 55, 56, 57, 58, ***59***, 60, ***61***, ***62***, ***63***, ***64***, ***69***, ***74***, ***82***, ***98***, ***100***, ***102***, ***104***, ***105***, ***114***, ***125***
	Arthropsyllus Sars, 1909			
	Breviconia Conroy-Dalton & Huys, 2000			
	Juxtaramia Conroy-Dalton & Huys, 2000			
	Uptionyx Conroy-Dalton & Huys, 2000			
Algensiella-*Probosciphontodes*-clade (A-P-clade)	*Algensiella*	III/F	F	***61***, ***63***, ***64***
	Ancorabolina			
	Bicorniphontodes			
	Calypsophontodes			
	Laophontodes			
	Lobopleura			
	Paralaophontodes			
	Probosciphontodes			
	Rostrophontodes			
Tapholaophontodes Soyer, 1974	2 species	III/G	G	***62***, 65, ***66***, ***67***, 68, ***76***, ***90***, ***91***, ***96***, ***99***, ***100***, ***104***, ***105***, ***122***
Calypsophontodes-*Probosciphontodes*-clade (C-P-clade)	*Ancorabolina*	III/H	H	***69***, 70
	Bicorniphontodes			
	Calypsophontodes			
	Laophontodes			
	Lobopleura			
	Paralaophontodes			
	Probosciphontodes			
	Rostrophontodes			
Algensiella Cottarelli & Baldari, 1987	2 species	III/I	I	***66***, 71, 72, 73, ***90***, ***91***, ***96***, ***99***, ***100***, ***104***, ***105***, ***122***
Rostrophontodes-*Probosciphontodes*-clade (R-P-clade)	*Ancorabolina*	III/J	J	***74***
	Bicorniphontodes			
	Laophontodes			
	Lobopleura			
	Paralaophontodes			
	Probosciphontodes			
	Rostrophontodes			

Taxon	Assigned subordinated taxa	Discussion: section	Fig. 2: branch	Tab. 1: autapomorphies
Calypsophontodes Gheerardyn & Lee, 2012	2 species	III/K	K	***75***, ***76***, 77, 78, 79, ***96***, ***122***, ***131***
Rostrophontodes-Ancorabolina-clade (R-A-clade)	*Ancorabolina* *Bicorniphontodes* *Laophontodes* *Rostrophontodes*	III/L	L	***80***, ***81***
Rostrophontodes Lee & Huys, 2019	*Monotypic*	III/M	M	***75***, 83, 84, 85, 86, 87, ***88***, 89, ***90***, ***91***, ***96***, ***120***, ***124***, ***126***, ***127***, ***131***
Laophontodes-Ancorabolina-clade (La-A-clade)	*Ancorabolina* *Bicorniphontodes* *Laophontodes*	III/N	N	***82***
Laophontodes T. Scott, 1904	13 species	III/O	O	**?**
Bicorniphontodes-Ancorabolina-clade (B-A-clade)	*Ancorabolina* *Bicorniphontodes*	III/P	P	92
Bicorniphontodes George, Glatzel & Schröder, 2019	5 species	III/Q	Q	93, 94, 95, ***96***, 97, ***104***
Ancorabolina George, 2006	6 species	III/R	R	***88***, ***98***, ***99***, ***100***, ***144***
Paralaophontodes-Probosciphontodes-clade (Pa-P-clade)	*Lobopleura* *Paralaophontodes* *Probosciphontodes*	III/S	S	101, ***102***, 103, ***104***, ***105***
Paralaophontodes Lang, 1965	8 species	III/T	T	***81***, 106, 107, 108, 109, 110, 111, 112, 113, ***114***, 115
Lobopleura-Probosciphontodes-clade (Lo-P-clade)	*Lobopleura* *Probosciphontodes*	III/U	U	116, 117, 118, 119, ***120***, 121, ***122***, 123, ***124***
Lobopleura Conroy-Dalton, 2004	3 species	III/V	V	***125***, ***126***, ***127***, 128
Probosciphontodes Fiers, 1988	2 species	III/W	W	***66***, ***67***, ***81***, 129, 130, ***131***, 132, 133, 134, 135, ***146***, ***147***, ***148***
Cletodidae● T. Scott, 1904 *sensu* Por (1986)	Cletodinae T. Scott, 1904 **subfam. nov.** *Acrenhydrosoma* Lang, 1944 *Australonannopus* Hamond, 1974 *Barbaracletodes* Huys, 2009 gen. *incertae sedis* *Dyacrenhydrosoma* Gee, 1999 *Echinocletodes* Lang, 1936	III/X	X	136, 137, 138, 139, 140
Cletodidae● (cont.)	*Enhydrosoma* Boeck, 1872 *Enhydrosomella* Monard, 1935 *Geehydrosoma* Kim et al., 2014 *Intercletodes* Fiers, 1987 *Kollerua* Gee, 1994 *Limnocletodes* Borutzky, 1926 *Miroslavia* Apostolov, 1980 *Monocletodes* Lang, 1936 *Nannopodella* Monard, 1928 *Neoacrenhydrosoma* Gee & Mu, 2000 *Paracrenhydrosoma* Gee, 1999 *Pyrocletodes* Coull, 1973 *Schizacron* Gee & Huys, 1996 *Scintis* Por, 1986 *Sphingothrix* Fiers, 1997 *Spinapecruris* Gee, 2001 *Strongylacron* Gee & Huys, 1996 *Stylicletodes* Lang, 1936 *Triathrix* Gee & Burgess, 1997 *Arthuricornua* Conroy-Dalton, 2001	III/X	X	136, 137, 138, 139, 140
Cletodinae Por, 1986 **subfam. nov.**	*Ceratonotus* Sars, 1909 *Cletodes* Brady, 1872 *Dendropsyllus* Conroy-Dalton, 2003 *Dimorphipodia* Lee & Huys, 2019 *Dorsiceratus* Drzycimski, 1967 *Echinopsyllus* Sars, 1909 *Polyascophorus* George, 1998 *Pseudechinopsyllus* George, 2006 *Touphapleura* Conroy-Dalton, 2001 *Acrenhydrosoma*	III/Y	Y	***39***, ***40***, ***41***, ***44***, ***61***, ***62***, ***141***
Remaining Cletodidae● T. Scott, 1904 *sensu* Por (1986)	*Australonannopus* *Barbaracletodes*(?)	III/Z	Z	**?**

Taxon	Assigned subordinated taxa	Discussion: section	Fig. 2: branch	Tab. 1: autapomorphies
Remaining Cletodidae● (cont.)	*Dyacrenhydrosoma*	III/Z	Z	**?**
	Echinocletodes			
	Enhydrosoma			
	Enhydrosomella			
	Geehydrosoma			
	Intercletodes			
	Kollerua			
	Limnocletodes			
	Miroslavia			
	Monocletodes			
	Nannopodella			
	Neoacrenhydrosoma			
	Paracrenhydrosoma			
	Pyrocletodes			
	Schizacron			
	Scintis			
	Sphingothrix			
	Spinapecruris			
	Strongylacron			
	Stylicletodes			
	Triathrix			
Ceratonotus-group (C-g)	*Arthuricornua*	III/AA	AA	***43***, ***59***, ***63***, ***64***, ***74***, ***76***, ***80***, ***82***, ***98***, ***100***, ***102***, ***104***, ***105***, 142, 143, ***144***, 145, ***146***, ***147***, ***148***
	Ceratonotus			
	Dendropsyllus			
	Dimorphipodia			
	Dorsiceratus			
	Echinopsyllus			
	Polyascophorus			
	Pseudechinopsyllus			
	Touphapleura			
Cletodes Brady, 1872	34 species (plus 1 *nomen nudum*)	III/BB	BB	150, 151

urosoma inconspicuous. Sexual dimorphism in A1, P3, P4 (occasionally), P5 and P6; females with genital double somite due to fusion of last (P6-bearing) thoracic somite with first abdominal (genital) one. Cphth and/or body somites with lateral and sometimes also with dorsolateral and dorsal cuticular processes of different size and shape that carry a sensillum at their tips; sensilla arising like a ball-and-socket joint from cup-shaped tips of processes. Somites often with long tube pores. Rostrum fused with cphth, of variable shape. FR elongate and slender, with 6–7 setae (seta I sometimes missing). Female A1 3-segmented, male A1 7–8-segmented. A2 with allobasis that bears 0–2 abexopodal setae; A2 exopod absent. Md palp unilobate, with at most six setae. Mxl endo- and exopod fused with basis. Mx with two endites, endopod small, with two setae. Mxp prehensile (subchelate), syncoxa lacking apical seta, endopod and apical claw fused, claw accompanied by minute seta. First swimming leg (P1) of podogennontan shape, prehensile, basis transversely elongate; endopod 2-segmented, enp-1 elongate, longer that exopod, without apical inner seta, enp-2 apically with two geniculate setae, subapically with tiny seta; exopod 2-segmented, exp-1 with one outer spine, exp-2 with five setae/spines, 3–4 of which geniculate. P2–P4 with transversely elongated bases, exopods 3-segmented, exp-1 lacking inner seta, exp-2 with or without inner seta, exp-3 no inner setae, two outer spines; P2 and P4 endopods 2-segmented, enp-1 small, without setae, enp-2 slender, cylindrical, with 0–1 inner and two apical setae; sometimes with outer seta/spine; P3 endopods in female as in P2 and P4, in male 2-segmented, with apophysis on second segment. P5 with baseoendopod, endopodal lobe small, with four setae (females) and two setae (males). Exopod distinct, with 3–4 setae/spines. Genital systems single (one copulatory pore and fused gonopores)¸ P6 forming a genital operculum (females), asymmetric or absent in males.

Included genera: *Ancorabolus* (**type genus**), *Arthropsyllus*, *Breviconia*, *Juxtaramia*, *Uptionyx*.

Subfamily Laophontodinae ● Lang, 1944

Harpacticoida Sars, 1903, Podogennonta Lang, 1944, Ancorabolidae ● Sars, 1909. Body basally elongate, mostly cylindrical, occasionally slightly tapering posteriorly or slightly dorsoventrally compressed, podoplean boundary between pro- and urosoma inconspicuous. Sexual dimorphism in A1, P3, P4 (occasionally), P5 and P6; females with genital double somite due to fusion of last (P6-bearing) thoracic somite with first abdominal (genital) one. Cphth sometimes with lateral cuticular processes; somites often with long tube pores and sometimes with dorsal cuticular projections. Rostrum fused with cphth, of variable shape. FR short and squarish or elongate and slender, with 6–7 setae (seta I sometimes missing). Female A1 4–5-segmented, male A1 5–7-segmented, subchirocer or chirocer. A2 with allobasis bearing 0–1 abexopodal seta; A2 exopod small and knob-like with one tiny seta, represented by one tiny seta or absent. Md palp unilobate, with at most six setae. Mxl endo- and exopod fused with basis. Mx with two endites, endopod small, with two setae or represented by 1–2 setae. Mxp prehensile (subchelate), syncoxa with 0–1 apical seta, endopod and apical claw fused or distinct, claw accompanied by minute seta. First swimming leg (P1) of podogennontan shape, prehensile, basis sometimes longitudinally and/or transversely elongated; endopod 2-segmented, enp-1 elongate, longer that exopod, with or without apical inner seta, enp-2 apically with claw and with or without long seta, subapically with spine or tiny seta; exopod 2–3-segmented, exp-1 with one outer spine, if exopod 3-segmented exp-2 with outer geniculate seta, inner seta absent, exp-3 with four setae, at least apical ones geniculate, if exopod 2-segmented, exp-2 with five setae, at least apical ones geniculate. P2–P4 mostly with transversely elongated bases, exopods 3-segmented, exp-1 lacking inner seta, exp-2 with or without inner seta, exp-3 with 0–2 inner setae and three outer spines; P2 and P4 endopods absent or 1–2-segmented, if present, enp-1 small, without setae, enp-2 slender, cylindrical, with 0–1 inner and/or outer seta/spine and with 1–2 apical setae; P3 endopods in female as in P2 and P4, in male 3-segmented, with apophysis on the second segment. P5 with baseoendopod, endopodal lobe completely absorbed into basal part, with two (females) or 1–2 setae (males), exopod fused with benp (females) or distinct (males), with 3–5 setae/spines. Genital systems single (one copulatory pore and fused gonopores)¸ P6 forming a genital operculum (females), asymmetric or absent in males.

Included genera: *Algensiella*, *Ancorabolina*, *Bicorniphontodes*, *Calypsophontodes*, *Laophontodes* (**type genus**), *Lobopleura*, *Paralaophontodes*, *Probosciphontodes*, *Rostrophontodes*, *Tapholaophontodes*.

Family Cletodidae● T. Scott, 1904 sensu Por (1986)
(updated after Boxshall and Halsey 2004)

Harpacticoida Sars, 1903, Podogennonta Lang, 1944. Body basally elongate, occasionally cylindrical, podoplean boundary between pro- and urosoma inconspicuous. Sexual dimorphism in A1, P3, P4 (occasionally), P5, P6, FR (sometimes); females with genital double somite due to fusion of last (P6-bearing) thoracic somite with first abdominal (genital) one. Cphth and/or body somites sometimes with latero-dorsal or dorsal cuticular projections of different size and shape that carry a sensillum at their tips; somites occasionally with long tube pores. Rostrum fused with cphth, usually triangular in shape, often bifid at tip, recurved dorsally in some species, narrow and short in others, occasionally completely absorbed into cphth. FR short and pyriform, sometimes elongate, with 6–7 setae. Female A1 4–5-segmented, male A1 6–7-segmented, subchirocer. A2 with allobasis that bears 0–2 abexopodal setae; A2 exopod small, 1-segmented, with 2–3 setae or tiny, knob-like, bearing one seta or absent. Md palp unilobate, with 2–6 setae. Mxl coxa distinct, partially or completely fused to basis; endo- and exopod fused to basis. Mx usually with two2 endites – in some species (*Limnocletodes* Borutzky, 1926), an additional proximal endite is represented by one seta; endopod small, with two setae that are sometimes fused at base or represented by two setae. Mxp prehensile (subchelate), syncoxa with one apical seta, endopod and apical claw fused, claw accompanied by long or minute seta. First swimming leg (P1) not prehensile, basis sometimes transversely elongated; endopod 2-segmented or absent, rarely reaching length of exopod; enp-1 at most as long as enp-2, with or without inner seta; enp-2 apically with 2–3 setae; exopod 2–3-segmented, exp-1 with one outer spine, if exopod, 3-segmented: exp-2 with outer spine, inner seta absent, exp-3 with two outer spines and two apical setae, sometimes geniculate, if exopod, 2-segmented exp-2 with two outer spines and three apical setae, often geniculate. P2–P4 sometimes with transversely elongated bases, exopods 2–3-segmented, exp-1 lacking inner seta, exp-2 with inner seta, exp-3 without inner seta, with 2–3 outer spines and two apical setae; P2 and P4 endopods absent or 1–2-segmented, if present enp-1 small, without setae, enp-2 slender, cylindrical, with 0–1 inner and/or outer seta/spine and 1–2 apical setae; P3 endopods in female as in P2 and P4, in male 2–3-segmented, with apophysis on the second or terminal segment. P5 with baseoendopod, endopodal lobe small or completely absorbed into basal part, with 1–5 setae, exopod distinct or fused with benp, with 3–4 setae/spines. Female genital system with one copulatory pore and fused gonopores¸ P6 forming a genital operculum in females, asymmetric or absent in males.

Included genera: *Acrenhydrosoma* Lang, 1944, *Arthuricornua* Conroy-Dalton, 2001, *Australonannopus* Hamond, 1974, *Barbaracletodes* Huys, 2009(?), *Ceratonotus* Sars, 1909, *Cletodes* Brady, 1872 (**type genus**), *Dendropsyllus* Conroy-Dalton, 2003, *Dimorphipodia* Lee & Huys, 2019, *Dorsiceratus* Drzycimski, 1967, *Dyacrenhydrosoma* Gee, 1999, *Echinocletodes* Lang, 1936, *Echinopsyllus* Sars, 1909, *Enhydrosoma* Boeck, 1872, *Enhydrosomella* Monard, 1935, *Geehydrosoma* Kim, Trebukhova, W. Lee & Karanovic, 2014, *Intercletodes* Fiers, 1987, *Kollerua* Gee, 1994, *Limnocletodes* Borutzky, 1926, *Miroslavia* Apostolov, 1980, *Monocletodes* Lang, 1936, *Nannopodella* Monard, 1928, *Neoacrenhydrosoma* Gee & Mu, 2000, *Paracrenhydrosoma* Gee, 1999, *Polyascophorus* George, 1998, *Pseudechinopsyllus* George, 2006, *Pyrocletodes* Coull, 1973, *Schizacron* Gee & Huys, 1996, *Scintis* Por, 1986, *Sphingothrix* Fiers, 1997, *Spinapecruris* Gee, 2001, *Strongylacron* Gee & Huys, 1996, *Stylicletodes* Lang, 1936, *Triathrix* Gee & Burgess, 1997, *Touphapleura* Conroy-Dalton, 2001.

Subfamily Cletodinae T. Scott, 1904, subfam. nov.

Harpacticoida Sars, 1903, Podogennonta Lang, 1944, Cletodidae ● T. Scott, 1904 sensu Por (1986). Diagnosis generally as for Cletodidae ●, with following amendments: A2 exopod atrophied, at most formed by one small, knob-like segment that carries one tiny seta or completely absent. Mx with two endites only. P1 enp-1 without inner seta, P2–P4 exp-3 with two outer spines. Female P5 with at most four setae.

Included genera: *Arthuricornua*, *Ceratonotus*, *Cletodes* (**type genus**), *Dendropsyllus*, *Dimorphipodia*, *Dorsiceratus*, *Echinopsyllus*, *Polyascophorus*, *Pseudechinopsyllus*, *Touphapleura*.

Discussion

I. General remarks

The historical background regarding the establishment of the taxa "Ancorabolidae", "Ancorabolinae" and "Laophontodinae" was summarised by George (2006a) and recently updated by Lee and Huys (2019). Since the family's erection by Sars (1909), its monophyletic status has been generally accepted, although several authors have raised concerns, particularly at the beginning of the 21st century (e.g. Conroy-Dalton 2003a, 2004; George 2006a; Gheerardyn and George 2010; Gheerardyn and Lee 2012). More recently, George and Müller (2013) presented a detailed discussion on some characteristics indicating the paraphyletic status of the "Ancorabolidae". As shown by these authors (and already indicated by Conroy-Dalton (2004) and George (2006a)), the monophyletic status of the "Ancorabolidae" was questioned by the ambiguity of its presumed autapomorphies. George (2006a) listed three characters as potential "ancorabolid" autapomorphies [plesiomorphic states in square brackets]:

A. Female A1 at most 5-segmented [female A1 at least 6-segmented];
B. Bases of P2–P4 transversely elongated [bases not elongated transversely];
C. P5 exp longitudinally elongated [P5 exp not elongated longitudinally].

A fourth derived character, originally identified by Lang (1948), i.e. the loss of the antennary exopod, was rejected by George (2006a), since several "ancorabolid" species are now known to bear a small, 1-segmented A2 exp.

When discussing the systematic relation of *Echinocletodes* Lang, 1936 with the "Ancorabolidae", George and Müller (2013) qualified characters A–C, confirming their ambiguity – these characters are not exclusively found in the "Ancorabolidae" but widely distributed amongst several harpacticoid families and characters B and C are, in addition, not found in all "Ancorabolidae". Moreover, these authors discussed the complexity of character B, highlighting three distinct features, namely (i) reduction and shortening of P2–P4 endopods; (ii) lateral elongation of the bases themselves, leading to a lateral shift of the exopod; (iii) shortening of the coxae, resulting in a coxa-basis borderline that does not enclose the whole basis. Consequently, George and Müller (2013) rejected the monophyletic status of the "Ancorabolidae".

The extensive phylogenetic analyses of harpacticoid major taxa, provided by Willen (2000) and Seifried (2003), support Lang's (1948) assignment of the "Ancorabolidae" to the Podogennonta Lang, 1944 (Fig. 2, branch *). Although being highly derived if compared with the diagnostic characters of podogennontan groundpattern (cf. Willen 2000; Seifried 2003), the "Ancorabolidae" share apomorphies of the Podogennonta, such as the reduction of the mxp enp-2, with the mxp endopod being 1-segmented (Willen 2000; Seifried 2003). Similarly, in some "Ancorabolidae" ("Laophontodinae"; "Ancorabolinae": *Ancorabolus*-lineage sensu Conroy-Dalton and Huys 2000; *Ancorabolina*), the shape of the P1 corresponds to that of the podogennontan groundpattern. This important affiliation is discussed in detail below (Chapter II).

Within the Podogennonta, however, the position of the "Ancorabolidae" remains uncertain. They yet may be assigned to Willen's (2000) "taxon II", which encloses all Podogennonta except the (?)Harpacticidae Dana, 1846, (?)Latiremidae Bozic, 1969 and Pseudotachidiidae Lang, 1936 (cf. Willen 2000: 198, fig. 82) (altogether pooled in Fig. 2, branch **).

Lang (1948) united the "Ancorabolidae", Laophontidae T. Scott, 1904 and "Cletodidae" in the supra-familiar taxon Cletodidimorpha Lang, 1948, whose name was changed to Cletodoidea Bowman & Abele, 1982 (Bowman and Abele 1982). However, when splitting the "Cletodidae" into several different families, Por (1986) placed the "Ancorabolidae" and Laophontidae into the Laophontoidea T. Scott, 1904, with the "Cletodidae" in its own supra-family Cletodoidea. Subsequently, Huys (1990a) established the Laophontoidea uniting the Adenopleurellidae Huys, 1990, Cristacoxidae Huys, 1990, Laophontidae, Laophontopsidae Huys & Willems, 1989 and Orthopsyllidae Huys, 1990. Huys (1990a) stated that the "Ancorabolidae" does not share any of the laophontoid apomorphies and, therefore, rejected the hypothesis of a closer "Ancorabolidae"–Laophontoidea-relationship. Later, Huys and Lee (1998/99) added the Normanellidae Lang, 1944 to the Laophontoidea (Fig. 2, branch ***), leading to further systematic complications. Although the Laophontoidea is not registered in the World Register of Marine Species (Walter and Boxshall 2020), its validity as a monophylum is generally accepted (e.g. George 2006a; Kihara and Huys 2009; Huys and Kihara 2010). This was also the case for the assumption that the "Ancorabolidae" is more closely related to the "Cletodidae" than to the Laophontoidea (Conroy-Dalton 2003a, 2004). Nevertheless, George (2006a) followed Lang's (1948) and Por's (1986) hypothesis of a close relationship between the "Ancorabolidae" and Laophontidae, extending it to the Laophontoidea. This was based on the shape of the P1 and a re-evaluation of laophontoid apomorphies, concluding that a close relationship between the Laophontoidea and "Ancorabolidae" still holds (George 2006a).

Against the background discussed above, the Laophontoidea and "Cletodidae" were selected as outgroups of the "Ancorabolidae" for this current phylogenetic analysis. Further comparison aimed to uncover the phylogenetic relationships amongst all three groups. A matrix of 150 phylogenetically-relevant morphological characters was created (Table 1), including the presumed "ancorabolid" autapomorphies A–C. This enabled the morphological comparison of all "ancorabolid" species with each other, as well as with the Laophontoidea, "Cletodidae" and other podogennontan taxa (e.g. the Ameiridae, Argestidae and Tetragonicipitidae).

This analysis suggests, as discussed below, that the monophyly of the "Ancorabolidae" cannot be maintained. Thus, Lang's (1936a) suggestion of starting anew was adopted. Confirming George and Müller's (2013) doubts, it is shown that the "Ancorabolidae" forms a polyphylum and neither the "Ancorabolinae" nor "Laophontodinae" are monophyletic. Moreover, the "Ancorabolidae" and "Cletodidae" must be re-ordered: the "Laophontodinae" (plus *Ancorabolina* = Laophontodinae ●) and the *Ancorabolus*-lineage constitute a monophyletic taxon Ancorabolidae ●, whilst the *Ceratonotus*-group sensu Conroy-Dalton (2001) forms part of the Cletodidae ●. Additionally, ancorabolid ●, cletodid ● and laophontoid species together form a well-supported clade within the Podogennonta, as proposed by Lang (1948) and George (2006a). This hypothesis is supported by and based upon Willen (2000) and Seifried's (2003) phylogenetic characterisation of the Podogennonta, particularly the shape and development of the P1.

II. The development of the P1 in the Podogennonta as the origin of the new phylogenetic concept

The shape, size and setation of the first swimming leg is an important indicator of systematic relationships within the Harpacticoida and particularly in the Podogennonta (Willen 2000) and has been the object of significant controversial discussion with regards to ancorabolid taxonomy (e.g. Lang 1948; Huys 1990a; Conroy-Dalton and Huys 2000; Conroy-Dalton 2001; George 2006a). As summarised by George (2006a), there have been two opposite hypotheses, namely (i) the interpretation of a prehensile P1 in the *Ancorabolus*-lineage as a derived stage (Conroy-Dalton and Huys 2000) and (ii) the assumption of the respective P1 as an ancestral state (Lang 1948; George 2006a). The inclusion of the Laophontoidea and "Cletodidae" as outgroups in this current analysis has proved informative to this discussion.

According to Willen (2000) and Seifried (2003), the hypothetical podogennontan ancestor (Fig. 2, branch *) bore a P1 (Fig. 3A) characterised by eleven derived features (Table 1: characters 1–11). The endopod consists of an elongated enp-1 (Table 1, character 1), a small enp-2 (Table 1, character 2) and enp-3 (Table 1, character 3), resulting in a P1 endopod longer than the P1 exopod. Additionally, the outer spine of enp-3 (Fig. 3A, element I-en) was shifted apically (Table 1, character 4) and transformed into a claw (Table 1, character 5); the middle apical seta (Fig. 3A, element 5-en) became geniculated (Table 1, character 6) and the inner apical seta (Fig. 3A, element 4-en) was diminished in size (Table 1, character 7). Thus, the endopod became prehensile. In the exopod, both apical setae of exp-3 (Fig. 3A, elements VI, VII) became geniculated (Table 1, characters 8 and 9), whilst the 2 inner setae (Fig. 3A, elements 3-ex and 4-ex) reduced completely (Table 1, characters 10 and 11). Such a P1 is still retained in several podogennontan taxa, such as the Ameiridae (part.) and Tetragonicipitidae (part.). However, within Willen's (2000) "taxon II", a further development of the P1 can be observed. In this study, the data suggest the following scenario:

1. In the hypothetical ancestor of the Laophontoidea–Cletodoidea-clade (L–C-clade, cf. III/A), the endopod became 2-segmented and enp-1 underwent elongation (Fig. 3B), becoming longer than the whole exopod. Additionally, the proximal seta of enp-1 (Fig. 3B, element 1-en) and the short apical seta of enp-2 (Fig. 3B, element 4-en) were lost (Table 1, characters 12–15).
2. The Laophontoidea (Fig. 2, branch ***) and Cletodoidea (cf. III/B) were separated by further evolution in the Cletodoidea, with the P1 exopod losing the inner element on exp-2 (Fig. 3C, element 2-ex) and the proximal outer spine of exp-3 (Fig. 3C, element III) (Table 1, characters 20 and 21). These elements are still present in the Laophontoidea (Fig. 3B).

Within the Cletodoidea, the ancestor of the Ancorabolidae ● (cf. III/C) retained the P1 condition shown in Fig. 3C, as did the subordinated Laophontodinae ● (cf. III/D), as still detectable in the laophontodin genus *Tapholaophontodes*. The sister-group of the Ancorabolidae ●, the Cletodidae ● (cf. III/V), may be characterised by the following further development of the P1:

3. The formerly elongated enp-1 strongly reduced in size, becoming, at most, as long as exp-1, whilst enp-2 increased in length (Fig. 3D; Table 1, characters 127–130). Overall, the P1 endopod in the Cletodidae ● is shortened considerably in comparison with the podogennontan ancestor. If Willen's (2000) and Seifried's (2003) hypothesis regarding the podogennontan P1 groundpattern is adopted, the P1 of the Cletodidae ● exhibits several supplementary deviations. However, these are ambiguous and await more detailed evaluation, specifically: the enp-2 apical claw (Fig. 3D, element I-en) reverted to an outer pinnate spine in the subapical position; the enp-2 geniculate apical seta (Fig. 3D, element 5-en) reverted to a bipinnate or biplumose seta. Thus, the P1 in the Cletodidae ● lost its prehensile state, being the endopod at most as long as the exopod.

The secondary transformation of highly specialised elements (I-en, element 5) into a more primitive, pre-podogennontan state may sound somewhat implausible. However, as discussed by several authors (e.g. Mayr

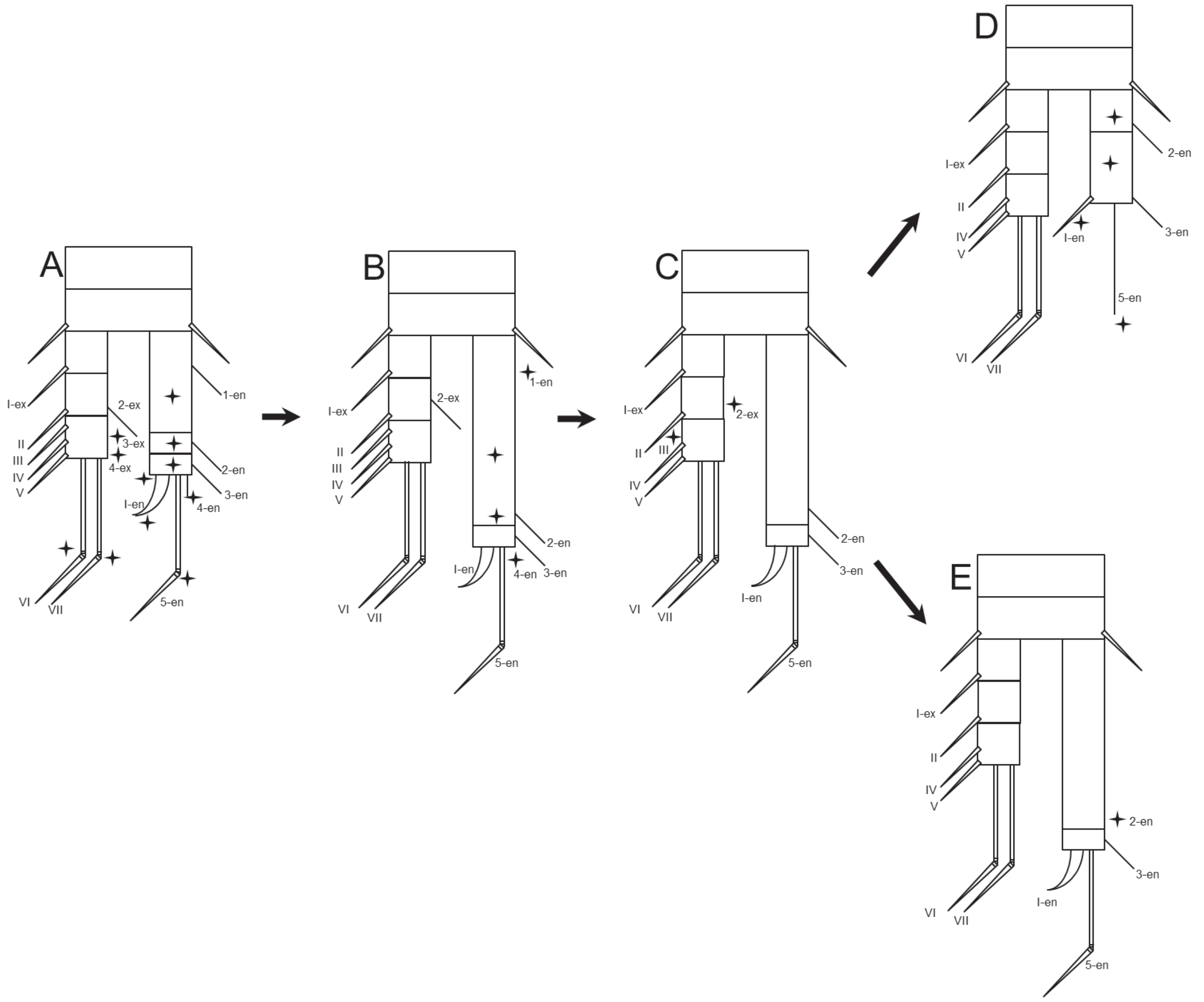

Figure 3. Schematic representation of hypothesised groundpatterns for the shapes of the first swimming leg P1 in each proposed taxon. **A.** Podogennontan (after Willen 2000; Seifried 2003), **B.** Laophontoidea–Cletodoidea-clade, **C.** Cletodoidea, **D.** Cletodidae ●, **E.** Ancorabolidae ●. Black crosses indicate apomorphies; Roman numerals = outer spines, Arabic numerals = inner setae; ex = exopod, en = endopod. Explanations given in the text.

1975; Ferrari 1988; Fiers 1990; Boxshall and Huys 1998; Wägele 2001; Seifried 2003), such reverse transformation may apparently occur, it is in fact:

> *...not simply a regain of the older state, but instead a new state that merely resembles the older plesiomorphic one*. (Seifried 2003: 209/210).

This hypothesis serves as the basis for the secondary transformation of elements I-en and 5-en in the Cletodidae ● presented here. The alternative was that the specialisation of elements I-en and 5-en into a claw (combined with an apical shift) and a geniculated seta, respectively, do not form part of the podogennontan groundpattern as postulated and well-supported by Willen (2000) and Seifried (2003). The rejection of a secondary transformation of a prehensile P1 back to a non-prehensile P1 in the Cletodidae ● would, however, mean that it could no longer be assigned to the Podogennonta, but should be placed between the Podogennonta and the Neobradyidae Olofsson, 1917, if following Seifried's (2003) systematic concept. As shown below, such displacement of the Cletodidae ● would cause a conflict with respect to several other derived characters that are shared with the Ancorabolidae ● (cf. III/A, III/B). It is therefore postulated that the podogennontan groundpattern of the P1 constitutes the evolutionary basis for the Ancorabolidae ● and Cletodidae ●. Consequently, the drastic transformation of the P1 in both the "Cletodidae" and the *Ceratonotus*-group is regarded as an evolutionary novelty that has been inherited from a common ancestor. That premise forms the basis of the here presented new phylogenetic concept.

4. The Ancorabolidae ● splits into two sister-groups, the Laophontodinae ● (cf. III/D) and the Ancorabolinae ● (cf. III/E). The latter is characterised by a further deviation of the prehensile P1, with loss of the distal inner seta (Fig. 3E, element 2-en) of enp-1 (Table 1, character 61). This is evidenced by the retention of element 2-en in *Tapholaophontodes* (La-

ophontodinae ●) and in *Limnocletodes* (Cletodidae ●). However, within two sub-clades–in the A–P-clade (cf. III/F) and the Cletodinae subfam. nov. (cf. III/Y) – element 2-en is subsequently reduced and is considered here as a convergent development.

To summarise, the following conclusions, with respect to P1 development, can be made: (i) the Laophontoidea, the "Ancorabolidae" and the "Cletodidae" evolved from a common ancestor with a P1 characterised by four apomorphies (Fig. 3B; Table 1, characters 12–15); (ii) the "Ancorabolidae" and the "Cletodidae" descend from a common ancestor characterised by two further apomorphies missing from the supposed sister-group Laophontoidea (Fig. 3C; Table 1, characters 20–21); (iii) the "Cletodidae" and the *Ceratonotus*-group share a P1 characterised by four further apomorphies (Fig. 3D; Table 1, characters 137–140), whilst the "Laophontodinae" and the *Ancorabolus*-lineage derive from a common ancestor that retained the P1 as shown in Fig. 3C; (iv) with the loss of element 2-en on P1 enp-1, the ancestor of the *Ancorabolus*-lineage (= Ancorabolinae ●) evolved a further apomorphy (Table 1, character 61), which also occurred convergent in the A–P-clade and in Cletodinae subfam. nov. (Fig. 3D, E).

This scenario provides the foundation for the phylogenetic analysis below, in which a large number of additional derived characters are discussed.

III. Phylogenetic analysis: A new concept for a podogennontan Laophontoidea – Ancorabolidae ● – Cletodidae ● -clade, based on the re-evaluation of morphological characters

Characters 1–11 of Table 1 focus on the derived state of the podogennontan P1 as compared with the remaining Harpacticoida. It is not the aim of this study to evaluate the phylogenetic status of the Podogennonta, which has been done extensively by Willen (2000) and was confirmed later on by Seifried (2003). Thus, characters 1–11 merely illustrate that the here treated taxa–even those that present further deviations–can generally be assigned to Podogennonta.

The phylogenetic evaluation starts with "taxon II" of Willen's (2000) system. Compared with other podogennontan "taxon II" taxa (Ameiridae, Argestidae, Tetragonicipitidae), there is a group formed by the Laophontoidea, "Ancorabolidae" and "Cletodidae".

Remarks: The analysis explicitly excludes two "ancorabolid" taxa, namely *Echinocletodes* Lang, 1936 and *Patagoniaella* Pallares, 1968. *Echinocletodes* has been excluded from "Ancorabolidae" by George and Müller (2013) and is currently assigned to the "Cletodidae" (Walter and Boxshall 2020); it is therefore not further discussed here. The assignment of *Patagoniaella* to the "Ancorabolidae" has been questioned already by George (2006a). Recently, Lee and Huys (2019) suggested its affiliation to the "Cletodidae". Its phylogenetic status is discussed in detail below (cf. III/CC).

A. The Laophontoidea–Cletodoidea-clade (L–C-clade)

The monophyly of the Laophontoidea–Cletodoidea-clade (L–C-clade) clade is supported by eight unambiguous autapomorphies (Table 1, characters 12–19; Fig. 2, branch A). Characters 12–15 refer to the development of the P1 and were discussed above (cf. Chapter II).

Character 16, female A1 at most 8-segmented: according to Seifried (2003), the podogennontan female A1 consists of nine segments. This agrees with the groundpattern of Oligoarthra (Willen 2000), which is now synonymised with Harpacticoida (Khodami et al. 2017). Within Podogennonta, oligomerisation of the female A1 takes place in several taxa. Families such as the Ameiridae Boeck, 1865, Argestidae Por, 1986, Canthocamptidae Brady, 1880, Tetragonicipitidae Lang, 1944 and Thalestridimorpha sensu Willen (2000) include several species whose female antennules have a reduced number of segments, down to a minimum of six segments (cf. Boxshall and Halsey 2004 for overview).

The L–C-clade also reflects such oligomerisation in the A1. In the Cletodoidea, the female A1 consists of at most five segments (e.g. Conroy-Dalton 2004; George 2006a, 2017, 2018; George and Gheerardyn 2015) and the laophontoid Adenopleurellidae, Cristacoxidae, Laophontopsidae and Orthopsyllidae are characterised by a 4-segmented female A1 (Huys and Willems 1989; Huys 1990a, b, c). Nonetheless, as several species of Normanellidae and Laophontidae present female antennules with up to six and eight segments, respectively (e.g. Willen 1992; Huys 1990a; Lee and Huys 1999a; Kihara and Huys 2009), it is concluded that the ancestor of the L–C-clade carried an 8-segmented female A1. Compared with the podogennontan groundpattern, that number of segments is regarded here as deviation.

Character 17, A2 with allobasis: an antennar allobasis is formed by the fusion of the basis and the first endopodal segment (Lang 1948). This derived condition is found in all representatives of the L–C-clade but not in the groundpattern of other "taxon II"-Podogennonta (e.g. Ameiridae, Tetragonicipitidae): exceptions occur in two species of *Normanella* Brady, 1880 (Laophontoidea: Normanellidae), namely *N. bolini* Lang, 1965 and *N. pallaresae* Lee & Huys, 1999, in which the basis and enp-1 are discernible by a transverse suture (Lang 1965; Packmor and Riedl 2016).

Another conspicuous feature of the A2 is the 1-segmented antennar exopod, which is observable in the whole L–C-clade. This might be interpreted as apomorphic character when compared with Ameiridae (cf. Boxshall and Halsey 2004) and Thalestridimorpha (Willen

2000). Nevertheless, a 1-segmented A2 exopod is heterogeneously distributed over the Podogennonta (e.g. Cletopsyllidae Huys & Willems, 1989, Rhizotrichidae Por, 1986, Tetragonicipitidae). Thus, whilst the phylogenetic relationship of the L–C-clade with the remaining "taxon II"-Podogennonta remains unclear, a 1-segmented A2 exopod cannot be used for phylogenetic comparison, as it might indicate a close relationship within the Podogennonta at a higher taxonomic level.

Character 18, A2 endopod with only one slender seta accompanying the two spines at the distal edge: Within the relatively derived Podogennonta (Thalestridimorpha, Tetragonicipitidae; cf. Willen 2000), the A2 endopod still bears, apart from two strong spines, two very slender and fine juxtaposed setae. In the L–C-clade, however, one of these setae is reduced; this is seen as an autapomorphy of that clade compared with the remaining Podogennonta.

Character 19, endopods of P2, P4 and female P3, slender and 2-segmented: In the groundpattern of the Podogennonta, swimming legs have 3-segmented endopods (cf. Willen 2000). However, the Laophontoidea, "Ancorabolidae" and "Cletodidae" show 2-segmented P2, P4 and female P3 endopods. Moreover, the endopods are much more slender than the respective exopods. Additionally, enp-1 becomes shorter than enp-2. In addition to the named taxa, this endopodal shape is also observed in the Argestidae (part.), Cletopsyllidae, Rhizotrichidae (part.) and Tetragonicipitidae. Nevertheless, these latter taxa are considered as distinct monophyla (Kunz 1984; Por 1986; Huys and Lee 1998/99; Corgosinho and Martínez Arbizu 2010; Packmor 2013; Gheerardyn and George 2019), owing to the absence of autapomorphies of the L–C-clade. Thus, the development of slender, 2-segmented P2–P4 endopods in the Argestidae (part.), Cletopsyllidae, Rhizotrichidae (part.), Tetragonicipitidae and in the L–C-clade is regarded as convergence. For the L–C-clade, the development of such endopods forms part of a set of derived characters. It is assumed here that their development took place in the common ancestor of the Laophontoidea, "Ancorabolidae" and "Cletodidae", being synapomorphic for these three taxa.

Remarks: Character 19, along with characters 33, 36, 62, 63, 64, 78, 84, 98, 112, 113, 123, 124 and 143 constitutes a character complex, as it pools the respective character changes (seta reduction, seta/segment elongation or shortening) of three different pairs of swimming legs. However, to date, they have always been observed together; if, in future, new species present morphological changes in only single pairs of swimming legs, they can be split into single characters.

B. Cletodoidea Bowman & Abele, 1982

As stated by Lang (1948), the "Ancorabolidae" and "Cletodidae" form a monophyletic major taxon, shown here to be unambiguously supported by 19 autapomorphies (Table 1, characters 20–38; Fig. 2, branch B). These evolved in a hypothetical common ancestor being exclusively present in "Ancorabolidae" and "Cletodidae" species, but missing in the sister-group Laophontoidea.

Characters 20 and 21 refer to the P1 and have been discussed above (Chapter II).

Character 22, Rostrum: According to Huys and Boxshall (1991), the harpacticoid groundpattern has a distinct rostrum, being defined at its base and this, therefore, represents the ancestral state within the Harpacticoida. While several Laophontoidea still retain this plesiomorphic state (e.g. Huys and Willems 1989; Huys 1990a; Willen 1992, 1995), it is fused to the cephalothorax in all species of the Cletodoidea and interpreted here as an autapomorphy for that taxon.

Characters 23–26, development of the female antennule: The most plesiomorphic female A1 within the "Ancorabolidae" and "Cletodidae" consists of five segments (character 23), being a clear apomorphy compared with the Laophontoidea, which retains an up to 8-segmented female A1 (cf. III/A, character 16). The female A1 in the Cletodoidea is quite characteristic, with segments 1–3 of almost equal length, segment 4 very small (character 24) and (at least partly) overlapped by the acrothek of the previous segment (character 25) and segment 5 of nearly the same length as segments 1, 2 and 3, respectively, but more slender (Fig. 4A–D). Aesthetascs are present on the third (character 26) and fifth segments. The presence of an aesthetasc on the third segment is also found in several laophontoid species (e.g. Normanellidae, Cristacoxidae, Adenopleurellidae; cf. Huys 1990a, b; Huys and Lee 1998/99); however, in several Laophontidae (e.g. *Afrolaophonte chilensis* Mielke, 1985, *Bathylaophonte* Lee & Huys, 1999, *Heterolaophonte minuta* (Boeck, 1872)), the aesthetasc arises from the fourth segment, even if the A1 consists of only five segments, for example, in *Amerolaophontina reducta* (Coull & Zo, 1982) (cf. Mielke 1985; Fiers 1991; Willen 1992; Lee and Huys 1999a). Thus, in the laophontoid groundpattern, the position of the first aesthetasc is on the fourth antennular segment, whilst its location on the third segment occurred later as a convergence.

In the "Cletodidae", the above-described female A1 is found in all genera with the exception of *Intercletodes* (four segments), *Limnocletodes* (four segments), *Scintis* (four segments) and *Sphingothrix* (three segments). In most species, the 5-segmented A1 is rather short and sturdy, as in *Enhydrosoma* (Fig. 4A), although it may be elongated and narrower, as in *Cletodes* (Fig. 4B).

Remarks: An exception is the "cletodid"(?) genus *Barbaracletodes* Huys, 2009. The females of *B. barbara* Becker, 1979 and *B. carola* Becker, 1979 bear a 7-segmented A1 (Becker 1979), being a huge exception within the "Cletodidae". Nevertheless, the systematic status of *Barbaracletodes* is absolutely uncertain. Huys et al. (1996) removed it to the Canthocamptidae, which was adopted by Boxshall and Halsey (2004). Additionally, Gee (1998) stated that *Barbaracletodes* cannot be maintained within the "Cletodidae"; however, like Huys et al.

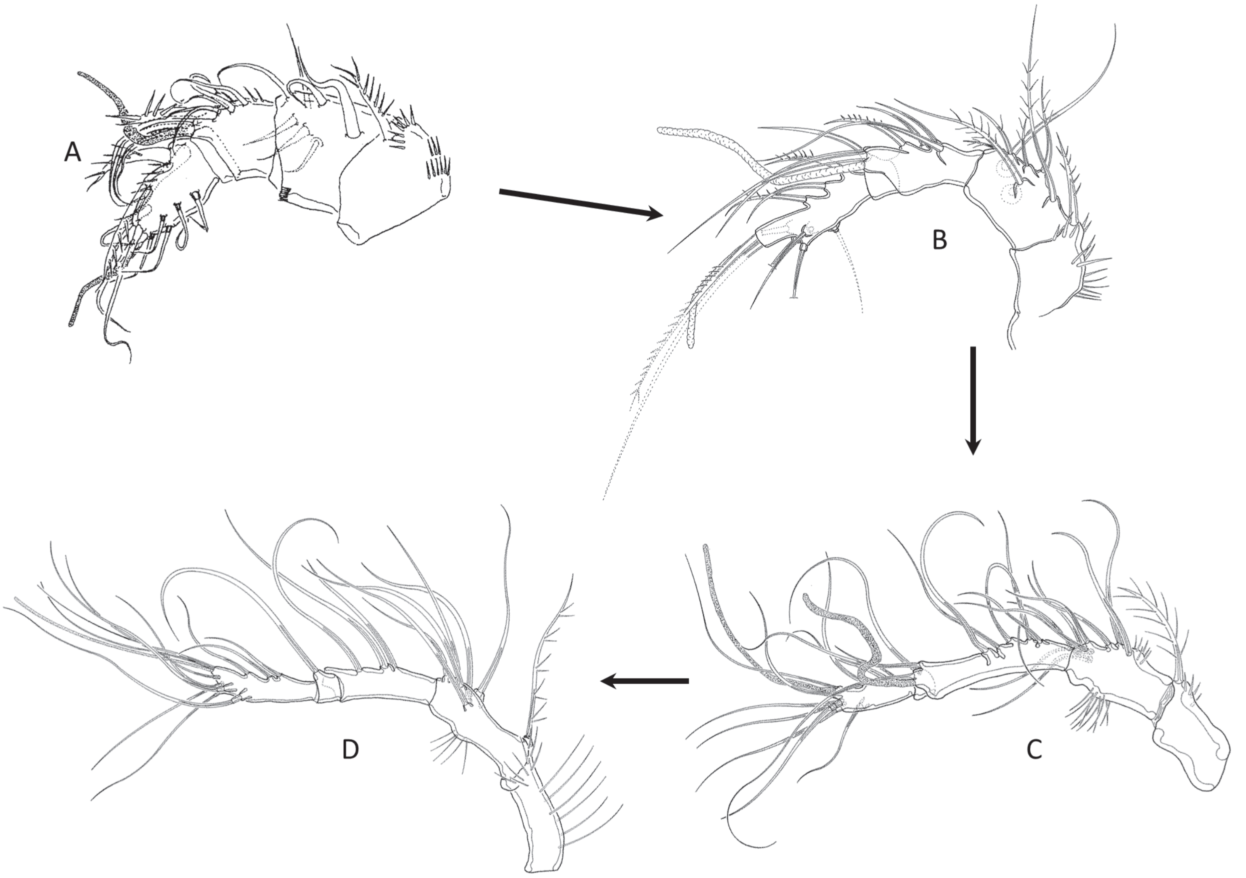

Figure 4. Antennulae (A1) of **A.** *Enhydrosoma parapropinquum* Gómez, 2003, **B.** *Cletodes meyerorum* George & Müller, 2013, **C.** *Bicorniphontodes bicornis* (A. Scott, 1896), **D.** *Ancorabolina divasecunda* Gheerardyn & George, 2010. Arrows indicate gradual elongation. Modified after Gómez 2003 (A), George and Müller 2013 (B), George and Gheerardyn 2015 (C), Gheerardyn and George 2010 (D). No scales.

(1996), he provided no further justification. Therefore, Wells (2007; cf. also Huys 2009) retained the genus in the "Cletodidae" as genus *incertae sedis*. In the present contribution, *Barbaracletodes* is not included in the phylogenetic analysis.

In the "Ancorabolidae", a 5-segmented A1 is found in the subfamily "Laophontodinae", specifically in *Algensiella*, *Ancorabolina* (Fig. 4D), *Bicorniphontodes*, *Laophontodes* (Fig. 4C), *Rostrophontodes*, and *Tapholaophontodes*. Instead, all remaining "Ancorabolidae" bear only four or even three segments in the female A1. Therefore, within the "Ancorabolidae", a 5-segmented female A1 has always been regarded as the ancestral state (e.g. Lang 1936, 1948). As noted for the "Cletodidae", a gradual elongation and cutting-back of the female A1 is also observed in the "Ancorabolidae".

Due to the very specific shape of the female A1 in the "Cletodidae" and "Ancorabolidae", it is considered here to have developed in a common ancestor of both taxa. Comparison with the sister-group Laophontoidea (and even with other Podogennonta) clearly reveals that the reduction towards a 5-segmented A1, in combination with the above-described additional morphological particularities, forms a derived state that is shared only by the "Cletodidae" and "Ancorabolidae", thus constituting a complex synapomorphy for both taxa. The reduction of antennular segments within Laophontoidea (see above) is–analogue to the position of the aesthetasc on the third segment–consequently interpreted here as convergence.

Character 27, A2 exopod with at most three setae: while the hypothetical ancestor of the Laophontoidea is characterised by an A2 exopod bearing four setae (Laophontidae, Normanellidae (part.), Orthopsyllidae; cf. Huys 1990a), the groundpattern of the here-postulated Cletodoidea consists of at most three exopodal setae as documented for the cletodid genus *Limnocletodes* by Gee (1998). This is seen as autapomorphic for the Cletodoidea.

Characters 28 and 29, md palp 1-segmented, with at most six setae: the hypothetical ancestor of the Laophontoidea bore a md palp with both the exopod and endopod well-developed, a condition that is retained in, for example, *Archilaophonte maxima* Willen, 1995 (Laophontidae) and in the Normanellidae, whilst in the Cristacoxidae, the md endopod is retained (cf. Huys 1990a; Willen 1995; Lee and Huys 1998/99). In the Cletodoidea, however, both the endopod and exopod are incorporated into the basis, resulting in a unilobate md palp (character 28). Moreover, at least seven setae are found on the md palp of the ancestral laophontoid (two basal setae, one exopodal and four endopodal setae), as still observed in *Normanella* (cf. Lee and Huys 1998/99; Packmor and Riedl 2016). In comparison, all representatives of the Cletodoidea bear at most six setae on the md palp, which is regarded as autapomorphic for that group.

Character 30, mxl endopod and exopod fused with basis: while in the laophontoid groundpattern, the mxl bears both an endopod and exopod (e.g. *Archilaophonte* Willen, 1995, *Heterolaophonte minuta*, *Bathylaophonte*), these are lost in the Cletodoidea. This is considered as an autapomorphy of that taxon.

Character 31, mx endopod with at most two setae: in the laophontoid groundpattern, the mx bears three endopodal setae (e.g. *Bathylaophonte*, *Normanella*; cf. Huys and Lee 1998/99; Lee and Huys 1999a, b; Packmor and Riedl 2016), whilst all members of the Cletodoidea carry only two setae on the mx endopod. This latter state is regarded as a shared deviation and thus as an autapomorphy for the group.

Character 32, mxp syncoxa with at most one seta: the Laophontoidea present 2–3 apical setae on the mxp syncoxa (e.g. Laophontidae (part.), Normanellidae (part.); cf. Willen 1992, 1995; Huys and Lee 1998/99; Packmor and Riedl 2016), whilst in the Cletodoidea only one seta is retained. This is interpreted as autapomorphy of the taxon.

Character 33, extreme reduction of P2–P4 endopods: the above-discussed development of the P2–P4 endopods (cf. III/A, character 19) suffered a further deviation in the Cletodoidea: the enp-2 is transformed into a relatively slender and cylindrical segment (cf. Figs 5A–D, 6B, C). Although noted in other podogennontan taxa (e.g. Argestidae (part.)), in combination with the additional derived characters of Cletodoidea, this occurs in all known cletodoid species and is, therefore, considered as inherited from their last common ancestor and thus interpreted as an autapomorphy of that suprafamily.

Character 34, loss of inner setae on P2 enp-2: the groundpattern of the Laophontoidea includes the retention of three inner setae at the P2 enp-2, as documented for some normanellid species (*Paranaiara* Kihara & Huys, 2009, *Normanella* (part.)) (cf. Huys and Lee 1998/99; Kihara and Huys 2009; Packmor and Riedl 2016) and is considered to be the plesiomorphic state. In contrast, the Cletodoidea is characterised by the complete loss of all inner setae on P2 enp-2, which constitutes a clear autapomorphy of that group.

Character 35, female P3 enp-2 with at most one inner seta: analogue to character 34, the Laophontoidea retains a plesiomorphic condition as compared with the Cletodoidea: several laophontoid species retain three inner setae on the female P3 enp-2 (e.g. *Archilaophonte maxima*, *Bathylaophonte*, *Normanella dubia* Brady & Robertson, 1880, *N. pallaresae*) (cf. Willen 1995; Lee and Huys 1999a; Packmor and Riedl 2016). In the Cletodoidea, this number is drastically reduced; here, the most plesiomorphic condition of one inner seta is still found in some “Cletodidae” (e.g. *C. bodini* Dinet, 1974, *C. dentatus* Wells & Rao, 1987, *Enhydrosoma littorale* Wells, 1967), as well as in some “laophontodin” species (e.g. *Calypsophontodes macropodia*, *Laophontodes* (part.)), most *Ancorabolina* species and in the *Ancorabolus*-lineage (part.) (cf. Dinet 1974; Wells 1967; Gee and Fleeger 1986; Wells and Rao 1987; Conroy-Dalton and Huys 2000; Gheerardyn and George 2010; George and Gheerardyn 2015). Therefore, character 35 is seen as autapomorphic for the Cletodoidea.

Character 36, P2–P4 enp-1 without inner seta: as commented in III/A, character 19, the P2–P4 enp-1 became shorter than the enp-2. In the Laophontoidea, however, the enp-1 still retains an inner seta (e.g. Cristacoxidae (part.), Laophontidae (part.) and Normanellidae). That seta is lost completely in the Cletodoidea, perhaps as a result of a further diminution of the enp-1, so character 36 forms a clear autapomorphy of the Cletodoidea.

Characters 37 and 38, shape of female P5: contrary to the condition in the supposed laophontoid groundpattern (Fig. 7A), the species of the Cletodoidea present a female P5 with the basis and endopod fused to form a baseoendopod (character 37) (Fig. 7B–D). That fusion is a clear deviation and therefore regarded as autapomorphy for the Cletodoidea. Moreover, the endopodal part becomes narrow (character 38) (Fig. 7B–D) or is lost completely (Fig. 7E, F). This latter state is considered apomorphic when compared with the Laophontoidea.

C. Ancorabolidae ● Sars, 1909

The Cletodoidea splits into two monophyletic taxa that can be characterised each by distinct autapomorphies: the Ancorabolidae ● and the Cletodidae ●. The latter taxon is characterised primarily by the exclusive transformation of the P1 (cf. II, III/X), whilst the Ancorabolidae ● (Fig. 2, branch C) presents a set of six autapomorphies that are not related to further transformation of the P1 (Table 1, characters 39–44).

Characters 39 and 40, A2 exopod reduced, at most knob-like and A2 exopod with at most one seta: within the Ancorabolidae ●, the A2 exopod is most commonly small and knob-like (character 39) bearing one small seta (character 40), as noted for *Calypsophontodes*, *Lobopleura*, *Paralaophontodes* (part.), *Probosciphontodes* and *Rostrophontodes*. Additionally, a further deviation with the exopod represented only by a minute seta, is recorded in *Bicorniphontodes* and *Laophontodes* (part.), whilst in *Algensiella*, *Ancorabolina*, the *Ancorabolus*-lineage, *Laophontodes* (part.) and *Tapholaophontodes*, the A2 exopod may be completely lost. The absence of an exopod is confirmed by highly-detailed species descriptions in *Ancorabolina*, the *Ancorabolus*-lineage and *Tapholaophontodes rollandi* Soyer, 1975; however, it is possible that, in some *Laophontodes* species, *Algensiella* and *Tapholaophontodes remotus* Cottarelli & Baldari, 1987, the presence of an exopod/seta may have been overlooked, as noted for other taxa (cf.

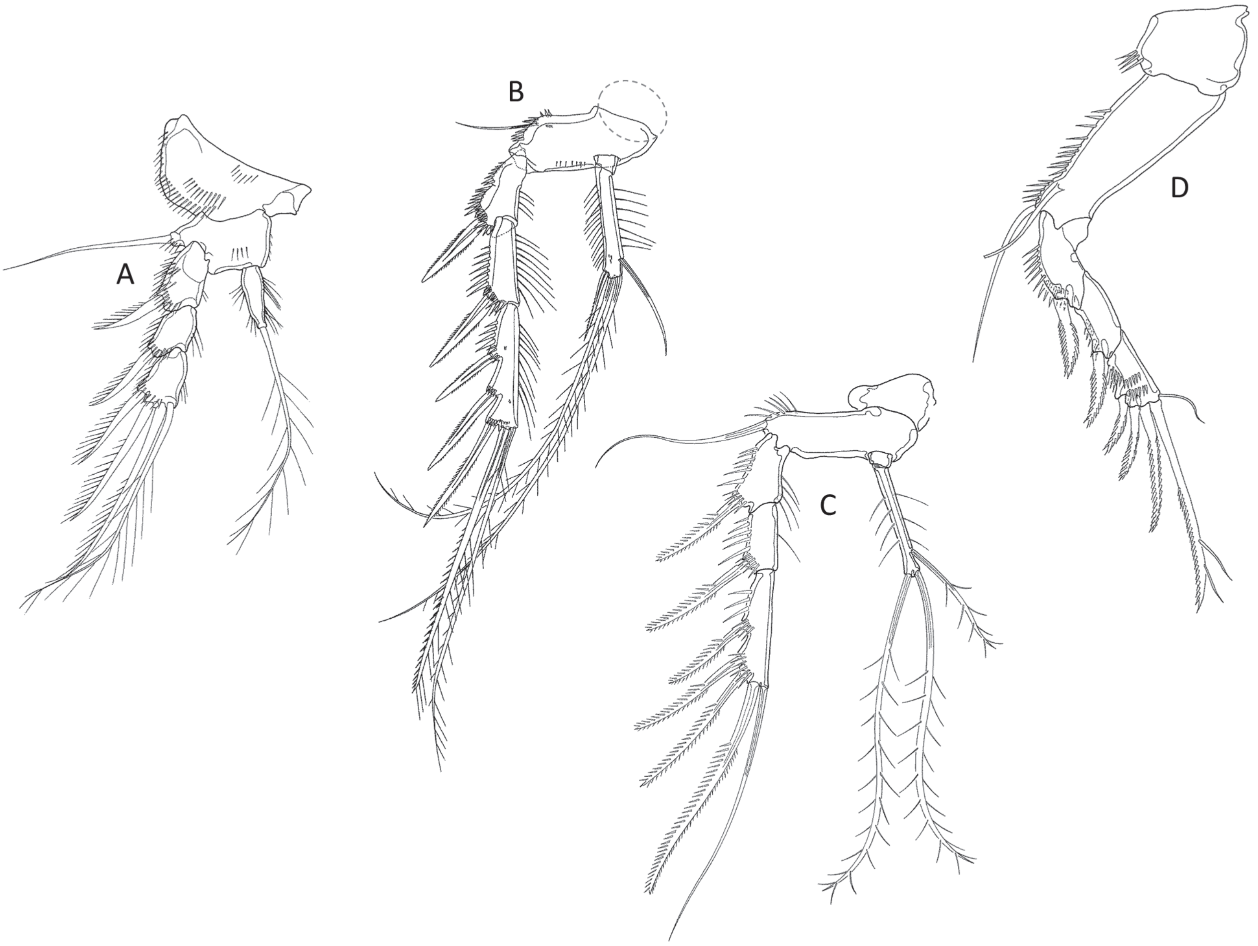

Figure 5. A. P3 of *Tapholaophontodes rollandi* Soyer, 1975, **B.** P3 of *Calypsophontodes macropodia* (Gee & Fleeger, 1986); dotted circle indicates approximate position and size of coxa; **C.** P3 of *Laophontodes sarsi* George, 2018, **D.** P4 of *Probosciphontodes stellata* Fiers, 1988. Modified after Mielke 1985 (A), Gheerardyn and Lee 2012 (B), George 2018 (C), Fiers 1988 (D). No scales.

George 2018). However, since even overlooked exopods can be expected to be small or to bear only one seta, for the context of this analysis, both characters are considered to be autapomorphies for the Ancorabolidae ●.

The convergent presence of both apomorphies, as well as all further convergences, in the Cletodidae ● is discussed below (cf. III/X).

Character 41, mx with at most 2 endites: the complete reduction of the proximal endite in the mx took place in the Ancorabolidae ●, whereas in the Laophontoidea and Cletodidae ● (part.), the proximal endite is at least represented by one seta. Its complete loss is therefore considered as autapomorphic for the Ancorabolidae ●. For its convergent presence in Cletodinae subfam. nov., see section III/Y.

Character 42, mxp claw without elongate accompanying seta: in the Laophontoidea, the claw of the mxp is accompanied by one small and one long seta (*Normanella*, *Sagamiella*, Cristacoxidae (part.); cf. Huys and Lee 1998/99; Huys and Kihara 2010; Packmor and Riedl 2016), the latter being lost in the Ancorabolidae ● and is thus considered an autapomorphy.

Character 43, P2 enp-2 without outer seta: While the P2 enp-2 still retains an outer seta in the groundpattern of the Laophontoidea and Cletodidae ●, it is lost in the Ancorabolidae ● (and convergent in the *Ceratonotus*-group; cf. III/AA).

Character 44, P5 female baseoendopod with at most four setae: whereas in the Laophontoidea (e.g. *Heterolaophonte minuta*, *Laophontopsis borealis* Huys & Willems, 1989, *Normanella mucronata* Sars, 1909, *Sagamiella latirostrata* Lee & Huys, 1999) and in the groundpattern of the Cletodidae ● (*Scintis*, *Enhydrosoma baruchi* Coull, 1975), a female P5 baseoendopod bearing five setae (Fig. 7A) is not uncommon, in the Ancorabolidae ●, the number of baseoendopodal setae never exceeds four (Fig. 7B–F). This is regarded as autapomorphic for the Ancorabolidae ●. A further deviation is present in the Cletodinae subfam. nov. (cf. III/Y), with a female P5 baseoendopod carrying only three setae (Table 1, character 142).

D. Laophontodinae ● Lang, 1944

The Ancorabolidae ● splits into two monophyla, namely the Ancorabolinae ● (cf. III/E) and Laophontodinae ●. The latter comprises the genera *Tapholaophontodes*,

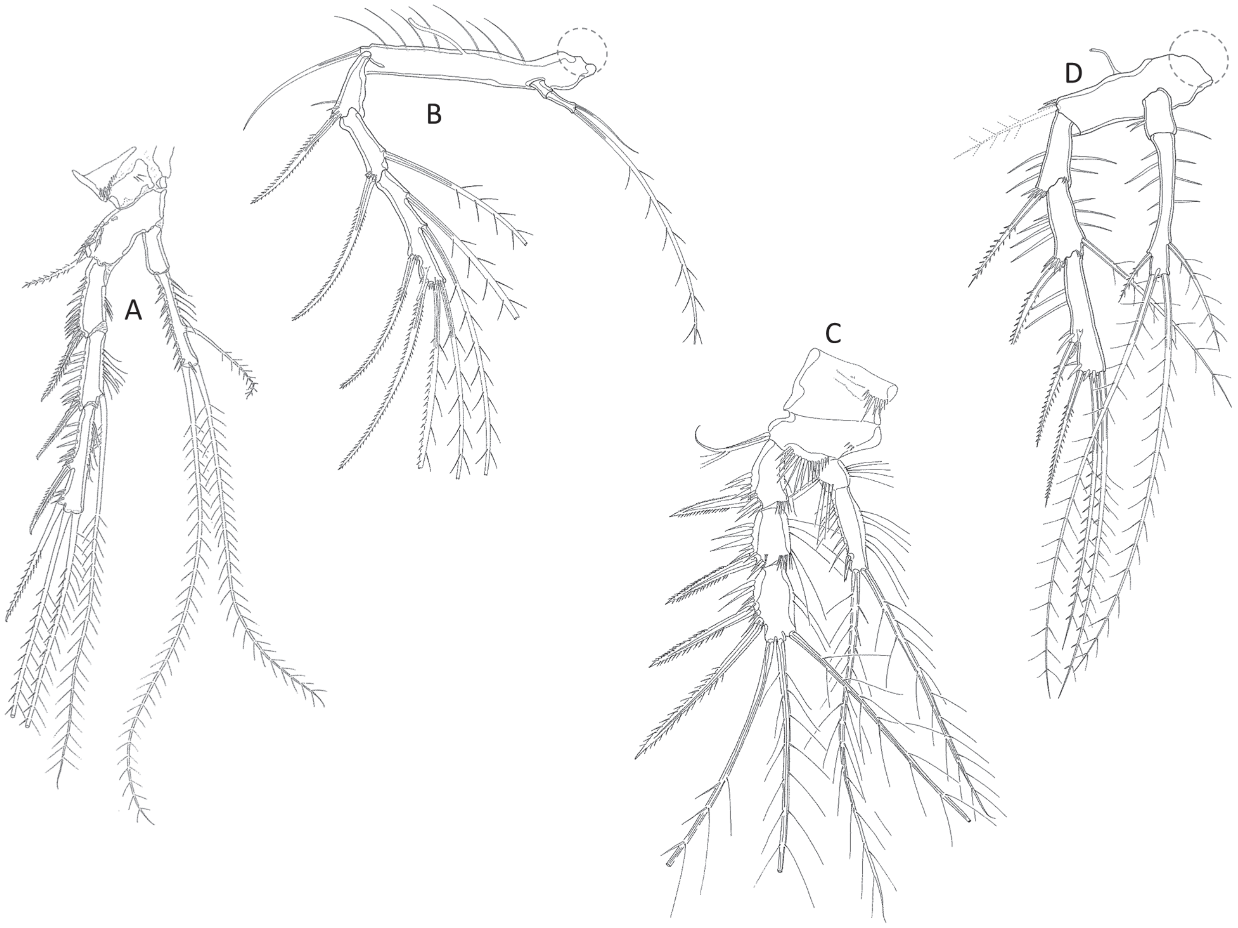

Figure 6. A. P2 of *Arthropsyllus serratus* Sars, 1909, **B.** P2 of *Polyascophorus monoceratus* George, Wandeness & Santos, 2013, **C.** Female P3 of *Enhydrosoma curticauda* Boeck, 1872, **D.** Female P3 of *Cletodes meyerorum* George & Müller, 2013. Dotted circles indicate approximate position and size of coxa. Modified after Conroy-Dalton and Huys 2000 (A), George et al. 2013 (B), Gee 1994 (C), George and Müller 2013 (D). No scales.

Algensiella, *Calypsophontodes*, *Laophontodes*, *Rostrophontodes*, *Bicorniphontodes*, *Ancorabolina*, *Paralaophontodes*, *Lobopleura* and *Probosciphontodes* and is characterised by six unambiguous characters (Table 1, characters 45–50; Fig. 2, branch D).

Character 45, A1 second segment with cluster of spinules at outer margin: all members of the Laophontodinae ● are characterised by several stout or long spinules clustered on the outer margin of the second antennular segment. This is missing in the Ancorabolinae ●, Cletodidae ● and Laophontoidea and is, therefore, interpreted as an autapomorphy of the Laophontodinae ●. A further deviation, detected by Gheerardyn and George (2010), is a rounded, bump-like expansion, from which the spinulose cluster arises. Contrary to the assumption of Gheerardyn and George (2010), which was subsequently adopted by Gheerardyn and Lee (2012), it is not clear if this deviation is apomorphic for the whole Laophontodinae ●. Although such a bump is, in fact, well-developed in most species of that clade, being at least weakly indicated in *Bicorniphontodes bicornis* (A. Scott, 1896), *B. horstgeorgei* (George & Gheerardyn, 2015), *Calypsophontodes macropodia*, *Laophontodes scottorum* George, 2018, *L. sabinegeorgeae* George & Gheerardyn, 2015 and *L. whitsoni* T. Scott, 1912, it is definitely absent in *L. macclintocki* Schizas & Shirley, 1994 and *L. monsmaris* George, 2018 (cf. Schizas and Shirley 1994; Gheerardyn and Lee 2012; George and Gheerardyn 2015; George 2018). Until clarification of the significance of the absence (secondary reduction) of the bump-like expansion in *L. macclintocki* and *L. monsmaris*, it should not be considered indicative of the monophyletic status of the Laophontodinae ● and is, therefore, not considered in the present analysis.

Character 46, abexopodal seta absent from basal part of A2 allobasis: in the groundpattern of the Podogennonta, both the A2 basis and enp-1 bear one abexopodal and one inner seta, respectively (Seifried 2003). As demonstrated above (cf. III/A, character 17), the fused allobasis represents a derived state for the L–C-clade also. However, the allobasis in the L–C-clade retains two abexopodal setae, the proximal seta corresponding to the former basis and the distal to the former enp-1. Thus the loss of the proximal seta in Laophontodinae ● is regarded as autapomorphic for that clade.

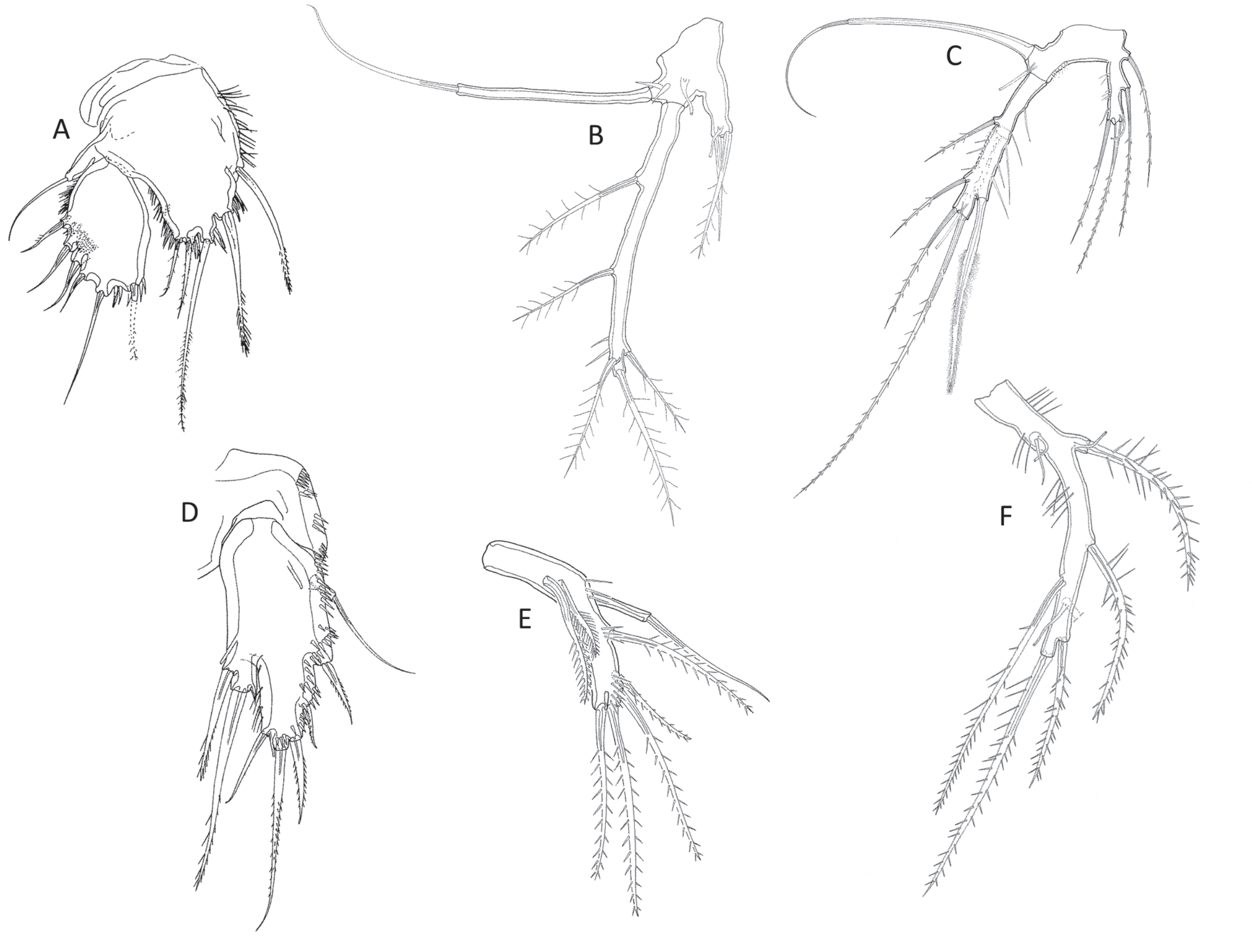

Figure 7. Female P5 of **A.** *Heterolaophonte minuta* (Boeck, 1872), **B.** *Cletodes meyerorum* George & Müller, 2013, **C.** *Ancorabolus chironi* Schulz & George, 2010, **D.** *Calypsophontodes macropodia* (Gee & Fleeger, 1986). **E.** *Laophontodes sarsi* George, 2018, **F.** *Dorsiceratus wilhelminae* George & Plum, 2009. Modified from Willen 1992 (A), George and Müller 2013 (B), Schulz and George 2010 (C), Gheerardyn and Lee 2012 (D), George 2018 (E), George and Plum 2009 (F). No scales.

Characters 47, 48, transformation of P1 exopodal spines II and IV into geniculate setae: in the Podogennonta, Laophontoidea, Cletodidae ● and also in the Ancorabolinae ●, P1 exopodal elements II (character 47) and IV (character 48) are "typical" outer bipinnate spines (cf. Figs 8A, B, D, 9C, D). In contrast, in the species of Laophontodinae ●, these elements are transformed into geniculated setae (cf. Fig. 9A, B), creating a clear autapomorphy for Laophontodinae ●.

Character 49, the female P5 baseoendopod bearing two setae only: all members of the Laophontodinae ● show the reduced number of, at most, two setae (Fig. 7E), while its supposed sister-group Ancorabolinae ● retains four setae (cf. Fig. 7C) as seen in the groundpattern of the Cletodoidea (cf. III/B). However, Character 49, or even a further reduction in the setal number, is also observed in the Cletodinae subfam. nov. (e.g. *Cletodes carthagiensis* Monard, 1935 (two setae), *C. longifurca* Lang, 1948 (two setae), *C. meyerorum* (two setae; Fig. 7B) and the *Ceratonotus*-group (1–2 setae)), although, in the groundpattern of the hypothesised Cletodidae ● (cf. III/X), the female P5 baseoendopod bears three setae (e.g. *Cletodes hartmannae* Lang, 1965, *C. macrura* Fiers, 1991, *Enhydrosoma baruchi* Coull, 1975, *Intercletodes interita* Fiers, 1987) (cf. Lang 1965; Coull 1975; Fiers 1987, 1991). This is seen as an autapomorphy of Cletodidae ● compared with its hypothesised sister-group Ancorabolidae ● (Table 1, character 142). The reduction to, at most, two baseoendopodal setae within the Cletodidae ●, on the other hand, is considered convergent.

Character 50, the complete absorption of the female P5 endopod into the basis: all species of the Laophontodinae ● (except *Calypsophontodes*, cf. III/K) present a female P5 in which the endopodal lobe is completely incorporated into the basis, thus losing its biramous shape (Fig. 7E). Compared with the Ancorabolinae ● and Cletodidae ●, which retain an elongated endopodal lobe in the baseoendopod (Fig. 7C and Fig. 7B, respectively), that state is considered autapomorphic for the Laophontodinae ●. It is noteworthy that although some species in the *Ceratonotus*-group (e.g. Fig. 7F) have similar female P5 swimming legs, this is considered convergent, since other taxa (*Echinopsyllus*, *Pseudechinopsyllus*) retain an endopodal lobe (Conroy-Dalton 2003a; George 2006b, Wandeness et al. 2009).

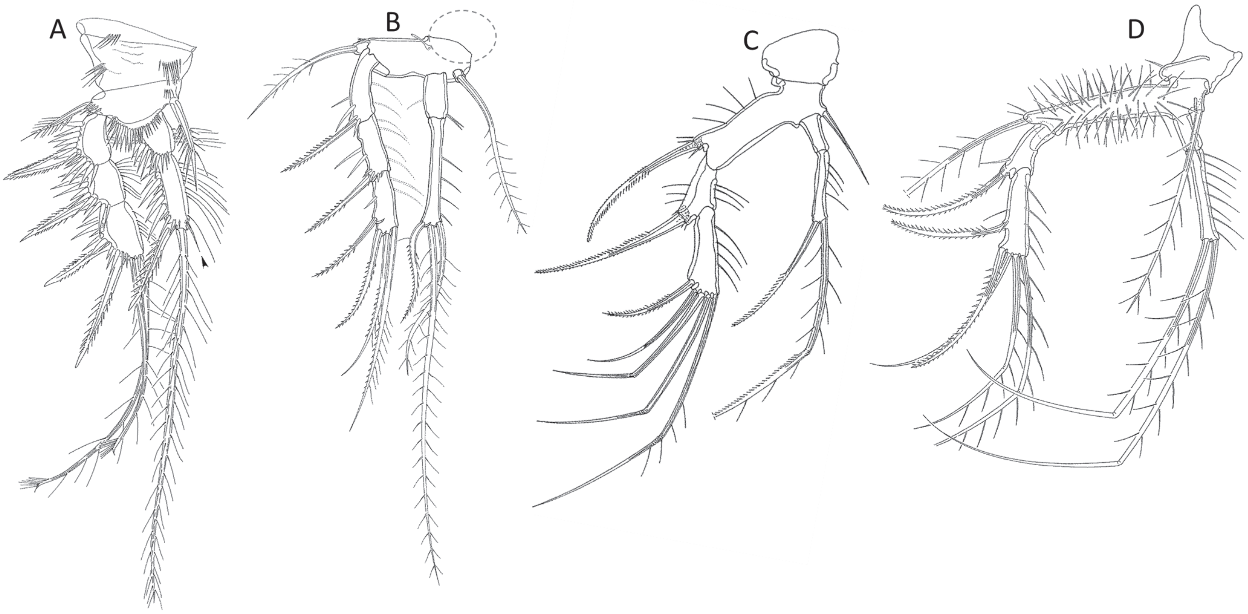

Figure 8. P1 of **A.** *Enhydrosoma curticauda* (Boeck, 1872); arrow points to inner apical seta (element 3), **B.** *Cletodes meyerorum* George & Müller, 2013, **C.** *Touphapleura schminkei* (George, 1998), **D.** *Ceratonotus steiningeri* George, 2006. Modified from Gee 1994 (A), George and Müller 2013 (B), George 1998b (C), George 2006c (D). No scales.

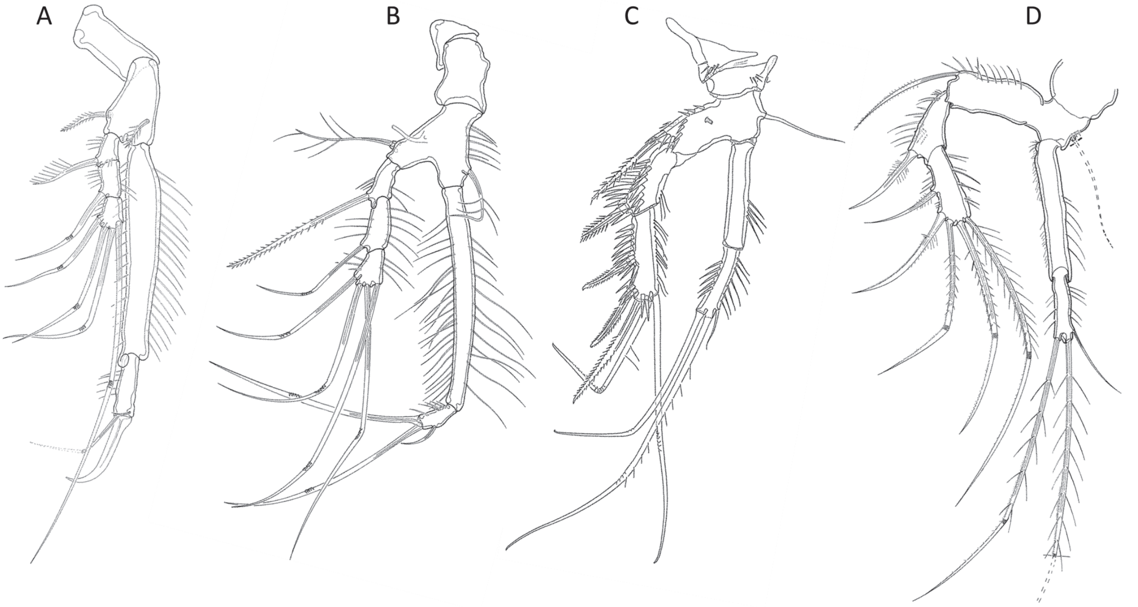

Figure 9. P1 of **A.** *Laophontodes monsmaris* George, 2018, **B.** *Ancorabolina divasecunda* Gheerardyn & George, 2010, **C.** *Arthropsyllus serratus* Sars, 1909, **D.** *Ancorabolus chironi* Schulz and George; 2010. Modified from George 2018 (A), Gheerardyn and George 2010 (B), Conroy-Dalton and Huys 2000 (C), Schulz and George 2010 (D). No scales.

E. Ancorabolinae ● Sars, 1909

Composition: eleven species in five genera:

Ancorabolus Norman, 1903
- *Ancorabolus chironi* Schulz & George, 2010
- *Ancorabolus confusus* Conroy-Dalton & Huys, 2000
- *Ancorabolus hendrickxi* Gómez and Conroy-Dalton, 2002
- *Ancorabolus ilvae* George, 2001 (*species inquirenda*)
- *Ancorabolus inermis* Conroy-Dalton & Huys, 2000
- *Ancorabolus mirabilis* Norman, 1903 (**type species**)

Arthropsyllus Sars, 1909
- *Arthropsyllus serratus* Sars, 1909 (**type species**)

Breviconia Conroy-Dalton & Huys, 2000
- *Breviconia australis* (George, 1998) (**type species**); syn. *Arthropsyllus australis* George, 1998

Breviconia echinata (Brady, 1918) (*species inquirenda*); syn. *Laophontodes echinatus* Brady, 1918

Juxtaramia Conroy-Dalton & Huys, 2000

Juxtaramia polaris Conroy-Dalton & Huys, 2000 (**type species**)

Uptionyx Conroy-Dalton & Huys, 2000

Uptionyx verenae Conroy-Dalton & Huys, 2000 (**type species**)

The *Ancorabolus*-lineage, which is elevated here to the subfamily Ancorabolinae ● (Fig. 2, branch E), was carefully examined in detail by Conroy-Dalton and Huys (2000). They documented a set of derived characters, namely the development of five peculiar "sensillar groups" on the cphth (Table 1, characters 51–55) that are exclusively present in all representatives of that lineage and are not further discussed here. Seven additional apomorphies are presented with regard to the current hypothesis (Table 1, characters 56–62).

Character 56, development of lateral cuticular processes on the free body somites: although the development of lateral and/or dorsal cuticular body processes is widespread in the Harpacticoida (e.g. Idyanthidae Lang, 1944: *Meteorina* George, 2004, *Pseudometeorina* George & Wiest, 2015, *Styracothorax* Huys, 1993; Laophontidae: *Echinolaophonte* Nicholls, 1941; Argestidae: *Mesocletodes* Sars, 1909 (part.); Aegisthidae Giesbrecht, 1893: *Pontostratiotes* Brady, 1883; Tetragonicipitidae: *Laophontella* Thompson and A. Scott, 1903), the development of such processes in the "Ancorabolidae" has been considered a good diagnostic and even phylogenetically-relevant character. The body processes of most "Ancorabolidae" and particularly of those taxa united in the subfamily "Ancorabolinae" seem at first glance to be quite similar: their location on the cephalothorax and body somites is more or less the same in the different species; the processes themselves are of a remarkable length at least in most species; they are often covered by fine spinules and bear a sensillum at their tip. Nonetheless, attempts to homologise the "ancorabolid" processes have been made rarely (Conroy-Dalton and Huys 2000; Conroy-Dalton 2001, 2003a) and careful comparison of "ancorabolid" cuticular body processes actually reveals a variability that includes non-"ancorabolid" taxa.

A detailed homologisation of the cuticular processes in the "Ancorabolidae" requires an extensive study of all corresponding species, including detailed ontogenetic comparison from the first to the last copepodid stage. Such an approach cannot be achieved in the contribution on hand. However, a comparison of the available information already provides relevant and helpful information, so the peculiar and "typical ancorabolid" body processes can be included into the current systematic evaluation.

Within the "Ancorabolidae", sensilla-bearing lateral body processes are restricted to Ancorabolinae ●; neither Laophontodinae ● nor the *Ceratonotus*-group developed them. Thus, their evolution in Ancorabolinae ● is a clear autapomorphy for that taxon. Additionally, this may be accompanied by the derived development of a second set of processes arising latero-dorsally (cf. George 1998a; Conroy-Dalton and Huys 2000). However, inclusion of these latter characters would require a detailed comparison of the respective species and, therefore, it is not considered here.

Character 57, development of special sensilla on the body: there is a second indication contradicting the supposed autapomorphic character of dorsal/dorsolateral cuticular processes for the "Ancorabolinae". Specifically, the shape of the sensilla at the tips of these processes: in the *Ceratonotus*-group, the tip of each process–at least in the supposed original form as seen in *Touphapleura*, *Dimorphipodia*, *Arthuricornua*, *Pseudechinopsyllus* and *Dorsiceratus*–is rather rounded and blunt and from the centre of which a tiny, hair-like sensillum arises (Fig.10A, B). These sensilla strongly resemble those that simply break through the cuticula; they are found in all Harpacticoida and are considered as the ancestral, plesiomorphic, state.

In contrast, in the Ancorabolinae ● (i.e., the former *Ancorabolus*-lineage), even in those species showing the weakest cuticular processes, the process ends in a cup-shaped tip; the terminal sensilla has a base as broad as the cup-shaped tip of the process, inserting like a ball-and-socket joint and tapering distally, as observed in *Breviconia* (Fig. 10C) and *Juxtaramia* (cf. Conroy-Dalton and Huys 2000). This derived sensillar shape is regarded as autapomorphy for the Ancorabolinae ●. Furthermore, in *Uptionyx* and *Ancorabolus*, the sensillum is transformed into a "spiniform main branch bearing a flagelliform lateral branch" (Conroy-Dalton and Huys 2000: 347) (Fig. 10D).

Character 58, female antennule 3-segmented: all females of the Ancorabolinae ● bear a 3-segmented A1, while the groundpattern of the Cletodoidea consists of a 5-segmented A1 (cf. III/B, character 23). A 5-segmented female A1 is retained in most Laophontodinae ● and has therefore also been seen as a laophontodin groundpattern. The 5-segmented A1 also forms part of the groundpattern of the Cletodidae ● (cf. Boxshall and Halsey 2004), so the occurrence of a 3-segmented female antennule in some representatives of the Cletodidae● (*Ceratonotus*, *Dendropsyllus*, *Scintis*) is interpreted here as convergent evolution.

Character 59, basis of P1 transversely elongated: the current hypothesis assumes that. within the Ancorabolidae ●, the classical "Laophontodinae" retained a P1 basis in the ancestral state (i.e. not transversely elongated; Fig. 9A), All Ancorabolinae ● show a longitudinally short but transversely elongated P1 basis (Fig. 9C, D). That derived condition is present also in the *Ceratonotus*-group and has been interpreted as autapomorphy of the "Ancorabolinae" (Lang 1948). In that context, George (2006a) assumed that the moderate transverse elongation in *Ancorabolina chimaera* George, 2006 (cf. Fig. 9B) may constitute an intermediate state between the "Laophontodinae" and "Ancorabolinae" and assigned that species to the "Ancorabolinae", despite some morphological discrepancies. Recently, Lee and Huys

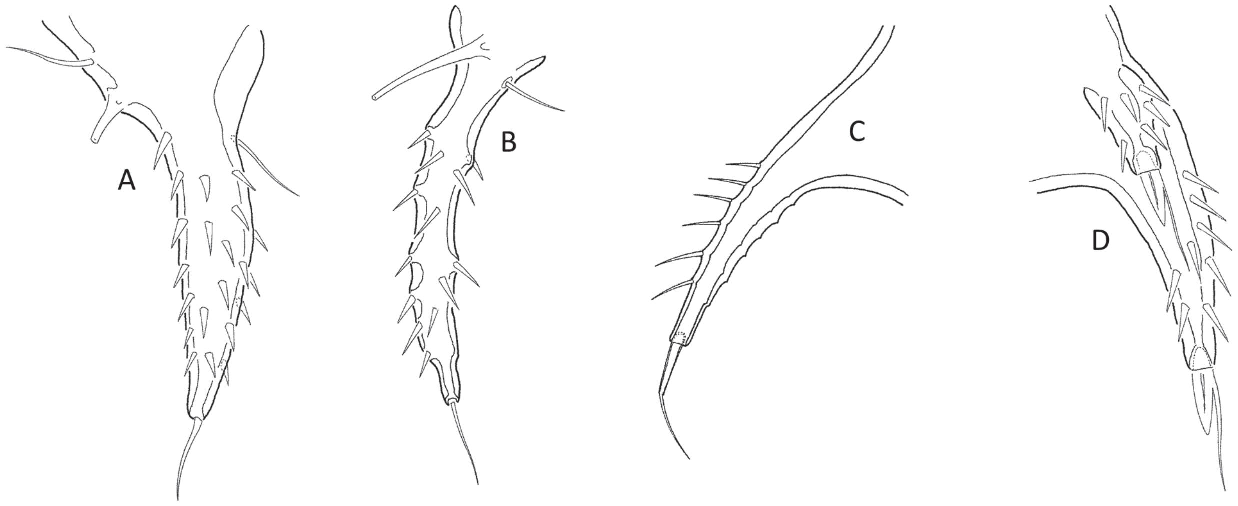

Figure 10. Cuticular body processes of **A.** *Arthuricornua anendopodia* Conroy-Dalton, 2001, **B.** *Dorsiceratus ursulae* George, 2006, **C.** *Breviconia australis* (George, 1998), **D.** *Ancorabolus inermis* Conroy-Dalton & Huys, 2000. Modified after Conroy-Dalton 2001 (A), George 2006b (B), George 1998a (C), Conroy-Dalton and Huys 2000 (D). No scales.

(2019) shifted *Ancorabolina* from the "Ancorabolinae" to the "Laophontodinae". This was done, based (amongst others) on the hypothesis that the transverse elongation of the P1 basis in *Ancorabolina* did not enclose the whole segment as in the "Ancorabolinae", but only its distal part. Simultaneously, according to Lee and Huys (2019), the departure of the endopod suffered a longitudinal elongation, resulting in a P1 basis that formed cylindrical pedestals for both the endo- and the exopod (Lee and Huys 2019). Whilst the phylogenetic position of *Ancorabolina* in the Laophontodinae ● is discussed below (cf. III/L–III/R), here I agree with the hypothesis of Lee and Huys (2019) that the transverse elongation of the P1 basis is not homologous in the Ancorabolinae ● and *Ancorabolina*. For the latter, I hypothesise that, previous to the transverse elongation, a longitudinal prolongation of the P1 basis took place (Table 1, character 70), which is a clear autapomorphy of the laophontodin ● C–P-clade (cf. III/H). The subsequent transverse elongation of the basis within the C–P-clade (*Ancorabolina*, *Rostrophontodes*) is, according to Lee and Huys (2019, interpreted here as independent development and listed in Table 1 as character 89 (cf. III/M). Thus, character 59 is considered as autapomorphic for the Ancorabolinae ●. Its presence also in the *Ceratonotus*-group must be regarded as convergence, as both taxa can be clearly assigned to their respective superordinate taxa and characterised by autapomorphies that are missing from each other.

The Cletodidae ● also exhibits elongation of the P1 basis in a few species, particularly a slight transverse elongation can be observed in the genus *Cletodes* (Fig. 8B), being greater in the *Ceratonotus*-group (Fig. 8C, D) and reaching a maximal length in derived taxa such as *Arthuricornua* Conroy-Dalton, 2001, *Ceratonotus* (Fig. 8D), *Echinopsyllus* and others. This is also seen as convergent, both for *Ancorabolina* and the Ancorabolinae ●, owing to several derived characters observed in the Cletodidae ●, but absent from *Ancorabolina* and the Ancorabolinae ● (cf. III/V), which are similarly characterised by apomorphies lacking in the Cletodidae ●.

Character 60, P1 exopod 2-segmented: all members of the Ancorabolinae ● bear a 2-segmented P1 exopod. This deviation is considered to be inherited from a common ancestor and thus an autapomorphy. However, a 2-segmented P1 exopod is also found in several members of the *Ceratonotus*-group (e.g. *Arthuricornua*, *Ceratonotus*, *Dendropsyllus*, *Dimorphipodia*, *Dorsiceratus* (part.), *Polyascophorus*, *Pseudechinopsyllus* and *Touphapleura*), but, since some taxa of that group still retain a 3-segmented P1 exopod (*Dorsiceratus* (part.), *Echinopsyllus*), it cannot be seen as autapomorphic of the *Ceratonotus*-group or as a potential synapomorphy shared with the Ancorabolinae ●; instead, it must be regarded as convergent development. Likewise, the presence of a 2-segmented P1 exopod in some Laophontodinae ● (e.g. *Ancorabolina* (part.), *Paralaophontodes* (part.)) is regarded as convergence, as most representatives of that subfamily retain a 3-segmented P1 exopod.

Character 61, P1 enp-1 element 2-en lost: as discussed in Chapter II, the loss of the inner distal seta on P1 enp-1 occurred independently in both the Ancorabolinae● and Laophontodinae ●, with the exception of *Tapholaophontodes*. Such convergent loss took place a third time in a common ancestor of *Cletodes* and the *Ceratonotus*-group, for which it can be seen, however, as synapomorphy (cf. III/Y).

Character 62, P2–P4 exp-3 with two outer spines: the species of the Ancorabolinae● are characterised by the possession of only two outer spines on P2–P4 exp-3. That character state is considered as derived, because, in the Copepoda, the original condition is the presence of three outer spines on the respective segments (Huys and Boxshall 1991; Willen 2000; Seifried 2003). Three outer spines are also retained in the Laophontodinae ● (except *Tapholaophontodes*) and, thus, this derived loss of one outer spine can be considered apomorphic for the Ancorabolinae ●. However, the loss of one outer spine also occurs in the *Ceratonotus*-group and was regarded as a characteristic supporting the monophyly of the "Ancorabolinae" that included both the *Ancorabolus*-lineage (= Ancorabolinae ●) and the *Ceratonotus*-group (Lang 1948; see also Conroy-Dalton and Huys 2000; George 2006a). Comparison with the "Cletodidae" revealed, however, that *Cletodes* also shares that deviation and, therefore, convergence is more likely. *Cletodes*, the remaining "Cletodidae" and the *Ceratonotus*-group share derived characters 138–142 supporting their close phylogenetic relationship (cf. III/X) and suggesting character 62 is convergent for the Cletodinae subfam. nov. and Ancorabolinae ●, rather than synapomorphic. Assuming a synapomorphic relationship would also mean that the complex development of P1 which took place in the Cletodinae subfam. nov. was the result of convergent development in *Cletodes* and the *Ceratonotus*-group, whilst in this new taxonomy both the Ancorabolinae ● and the *Ceratonotus*-group are well-embedded in their respective super-ordinated clades.

F. The *Algensiella–Probosciphontodes*-clade (A–P-clade)

This clade (Fig. 2, branch F) comprises the genera *Algensiella*, *Calypsophontodes*, *Laophontodes*, *Rostrophontodes*, *Bicorniphontodes*, *Ancorabolina*, *Paralaophontodes*, *Lobopleura* and *Probosciphontodes*. Apart from the convergent development of character 61 on P1 (cf. II, III/E), they all share two derived features that are not present in their supposed sister-group *Tapholaophontodes* (Table 1, characters 63 and 64).

Character 63, P2–P4 bases transversely elongated, surpassing coxal outer margin: the transverse elongation of the bases of swimming legs 2–4 has always been seen as a derived character for the "Ancorabolidae" (e.g. Lang 1948, George 2006a, George and Müller 2013). The elongation is such that the swimming legs stick out laterally, leading to the "spider-like" habitus attributed to representatives of that family (e.g. Huys and Boxshall 1991). Within the Podogennonta, such elongation is rare, being seen in a similar form in only one genus of Ameiridae, *Stenocopia* Sars, 1907 and certain members of Argestidae (*Anoplosomella* Strand, 1929, *Malacopsyllus* Sars, 1911) and Idyanthidae (e.g. *Meteorina*, *Pseudometeorina*). However, as these latter taxa are considered monophyletic (cf. Seifried 2003; Corgosinho and Martínez Arbizu 2010; Gheerardyn and George 2019), each presenting a set of apomorphies that are not shared with the A–P-clade, a closer relationship can be rejected.

In the Ancorabolidae ●, the bases of P2–P4 exhibit gradual transverse elongation. However, although this is considered characteristic for the Ancorabolidae ●, it is not universally recorded in all species. Both species of *Tapholaophontodes*, *T. remotus* and *T. rollandi* show absolutely no transverse elongation of the P2–P4 bases (Fig. 5A).

The weakest transverse elongation in the Laophontodinae ● is seen in *Calypsophontodes macropodia* (Gee & Fleeger, 1986) (cf. Gee and Fleeger 1986; Gheerardyn and Lee 2012) (Fig. 5B), followed by *Laophontodes* (Fig. 5C), within which different states of elongation occur. Strongest transverse elongation is present in *Lobopleura*, *Paralaophontodes* and *Probosciphontodes* (Fig. 5D).

In the "Ancorabolinae", the weakest transverse elongation is observed in *Arthropsyllus serratus* Sars, 1909 (*Ancorabolus*-lineage, now Ancorabolinae ●) (Fig. 6A) (cf. Sars 1909; Conroy-Dalton and Huys 2000), whereas the strongest elongations are present in the representatives of the *Ceratonotus*-group (Fig. 6B).

A transverse elongation of the P2–P4 bases also occurs in the "Cletodidae". In most cletodid species, however, it is slightly indicated by a shortening of both lobes, combined with a slightly outward shift of the exopod (Fig. 6C). Particularly, in the type-genus *Cletodes* all species, with the exception of three (*C. hartmannae* Lang, 1965, *C. longicaudatus* (Boeck, 1872), *C. spinulipes* Por, 1967), present an increasing transverse elongation of the P2–P4 bases (Fig. 6D) (cf. Sars 1909; Lang 1965; Por 1967). Nevertheless, this character is considered as autapomorphic for the A–P-clade owing to the lack of elongated bases in *Tapholaophontodes*, which is regarded as a sister-group of the A–P-clade, with which it shares unambiguous synapomorphies 45–50 (cf. III/D).

Furthermore, it is assumed that this basal elongation occurred independently several times and is not a shared deviation inherited from a common ancestor of "ancorabolid" species. Synapomorphy of this character for the A–P-clade and for the Ancorabolinae ● would mean that the more complex characters 45–50 result from convergent development in the A–P-clade and *Tapholaophontodes*. This is rather implausible and, combined with the occurrence of basal elongation in P2–P4 in other harpacticoid taxa, indicates the convergent evolution of this character (63). Convergent development is also assumed for the *Ceratonotus*-group and in *Cletodes* owing to their shared derived characters which are not seen in the A–P-clade or the Ancorabolinae ● (cf. III/Y).

Character 64, P2–P4 coxae remarkably shortened, width at most half of the width of the respective bases: the shortening of the P2–P4 coxae seems to be linked to the transverse elongation of the basis (e.g. Figs 5B–D, 6A, B, D). In the harpacticoid and podogennontan groundpatterns, the coxa is a large segment, at least as broad as the respective basis (cf. Huys and Boxshall 1991; Willen 2000; Seifried 2003). That state is retained in the Laophontoidea and also in *Tapholaophontodes* (cf. Fig. 5A) and most "Cletodidae" (e.g. Fig. 6C). A shortened coxa and transversely elongate basis is also observed in the Ancorabolinae ● and in other harpacticoid taxa (e.g. Argestidae (part.), Idyanthidae (part.), *Stenocopia*). It is concluded here that character 64 forms an autapomorphy for the A–P-clade, while having developed convergently in the other above named taxa.

G. *Tapholaophontodes*

Composition: two species:
Tapholaophontodes Soyer, 1975
Tapholaophontodes remotus Cottarelli & Baldari, 1987
Tapholaophontodes rollandi Soyer, 1975 (**type species**)
Tapholaophontodes (Fig. 2, branch G) presents 5 derived characters (Table 1, characters 62, 65–68), two of which (65, 68) are exclusive to this taxon.

Character 62, P2–P4 exp-3 with two outer spines: within the Laophontodinae ●, *Tapholaophontodes* is the only taxon showing the derived loss of one outer spine on P2–P4 exp-3. As discussed above (cf. III/E), this is also seen in the comparatively-distant taxa Ancorabolinae ● and in the Cletodinae subfam. nov. (cf. III/Y), which do not share any other derived characters with *Tapholaophontodes*. Thus, the loss of one outer spine is interpreted as convergent development in these taxa.

Character 65, md palp with only four setae: in the groundpattern of the Cletodoidea, the md palp carries six setae (Table 1, character 29). That setal number is retained in most representatives of that taxon. Nevertheless, within the Cletodoidea, a reduction of setae on the md palp is recorded. Some taxa present a palp with five setae (Table 1, character 77, cf. III/K), whilst *Tapholaophontodes* is characterised by the further deviation of a md palp bearing only four setae. This is interpreted as autapomorphic for *Tapholaophontodes*.

Characters 66 and 67, P2 and P4 without endopod: the complete loss of endopods in the swimming legs is widely and quite heterogeneously distributed amongst the Harpacticoida. In the "Ancorabolidae", several, not closely related, species show such endopodal loss at least in the P2 and including up to all pereiopods (e.g. *Algensiella* (P2), *Arthuricornua* (P2), *Ceratonotus* (part.; P2), *Dendropsyllus* (P2), *Dimorphipodia* (P2), *Echinopsyllus* (P2), *Lobopleura* (P2), *Paralaophontodes* (part; P2, P3, P4), *Polyascophorus* (P2), *Probosciphontodes* (P2, P4)), thus indicating convergent development. In the groundpattern of the Laophontodinae ●, all swimming legs still bear endopods, that condition being retained in the sister-group of *Tapholaophontodes*, the A–P-clade; their subsequent loss within the latter (in *Lobopleura*, *Paralaophontodes* (part.) and *Probosciphontodes*) is regarded here as convergent. In that context, characters 66 and 67 are interpreted as autapomorphies of a monophylum *Tapholaophontodes*.

Character 68, female P5 endopodal lobe completely lost: as discussed above (cf. III/D, character 50), the Laophontodinae ● is characterised by a female P5 whose endopodal lobe is completely absorbed into the basal part. Nonetheless, it is still represented by at least 1–2 setae (often accompanied by 1–2 tube pores). In *Tapholaophontodes*, even these setae have been lost completely. Thus, the P5 of *Tapholaophontodes* is unilobate, carrying solely the exopodal armour, as well as the outer basal seta; no endopodal remnants are detectable (cf. Soyer 1975; Mielke 1985; Cottarelli and Baldari 1987). That condition is unique to *Tapholaophontodes* and is therefore considered autapomorphic.

In addition to autapomorphies 65–68, the loss of one seta on the FR might be also considered a derived character for *Tapholaophontodes*: the original armour of the furcal rami in the Harpacticoida consists of seven setae (Huys and Boxshall 1991). This is quite a conservative state. It is present in most harpacticoid species and is also the common state for the taxa treated here. However, in their description of *Tapholaophontodes remotus*, Cottarelli and Baldari (1987) list only six furcal setae, as does Mielke (1985) in the re-description of *T. rollandi*. In contrast, Soyer (1975) shows seven furcal setae in the description of *T. rollandi*, but provided a dorsal and a lateral illustration of the FR (Soyer 1975: 1217, fig. 21B, C) which contradict each other with respect to the location of the setae and also differ from Mielke's (1985) re-description. Thus, this character warrants re-evaluation and re-inspection of *T. rollandi*.

H. The *Calypsophontodes*–*Probosciphontodes*-clade (C–P-clade)

The C–P-clade (Fig. 2, branch H) comprises the genera *Calypsophontodes*, *Laophontodes*, *Rostrophontodes*, *Biconiphontodes*, *Ancorabolina*, *Paralaophontodes*, *Lobopleura* and *Probosciphontodes*. It can be supported by two apomorphies (Table 1, characters 69 and 70):

Character 69, mxp endopod and apical claw fused: for the groundpattern of the Laophontodinae ●, a separation between the mx endopod and the apical claw is assumed, based on the presence of that plesiomorphic state in rather basal taxa, i.e. *Tapholaophontodes* and *Algensiella*. Instead, in all members of the C–P-clade, the apical claw is fused with the mx endopod, which is considered autapomorphic for the C–P-clade. The presence of that deviation also in the *Ancorabolus*-lineage (= Ancorabolinae ●) is interpreted as convergence, as both the Laophontodinae ● (that includes the C–P-clade) and the Ancorabolinae ● are clearly separated and well-supported by characters 45–50 and 51–62, respectively. Future studies may discover further apomorphies for the C–P-clade.

It can be argued that, within *Paralaophontodes*, the importance of character 69 remains uncertain. While most species (*P. anjae* George, 2017, *P. armatus* (Lang, 1936), *P. elegans* Baldari & Cottarelli, 1986, *P. exopoditus* Mielke, 1981 and *P. robustus* (Bŏzić, 1964)) unambiguously show a fusion of the mxp endopod with the claw, Soyer (1975, fig. 19E) clearly describes the endopod being separated from the claw in *P. psammophilus* (Soyer, 1975) and Lang (1965, fig. 301g) shows a fine line in the mxp of *P. hedgpethi* (Lang, 1965), interpreting it as borderline between the endopod and the claw. Fiers (1986) did not describe the mouthparts of *P. echinata* (Willey, 1930), pointing to their similarity with *P. hedgpethi*. Nonetheless, as *P. anjae* still presents a fine suture that may correspond to the former borderline between endopod and claw, the same may be the case in *P. hedgpethi*/*P. echinata* (and even in *P. psammophilus*). A re-examination of this material is necessary to define their status. In the meantime, I postulate that, in *Paralaophontodes*, the mxp endopod and claw are fused together.

Character 70, P1 basis longitudinally elongated: all members of the C–P-clade present a longitudinally elongated P1 basis, a condition that is absent in all remaining members of the Cletodoidea. This further increases the already elongated swimming leg (Fig. 9A, B), which is additionally strengthened in some species by an elongation of the coxa (cf. III/L, character 82). An elongated P1 basis is regarded as autapomorphic for the C–P-clade.

I. *Algensiella*

Composition: two species:
Algensiella Cottarelli & Baldari, 1987
Algensiella boitanii Cottarelli & Baldari, 1987 (**type species**)
Algensiella laurenceae (Bodiou & Colomines, 1988); syn. *Tapholaophontodes laurenceae* Bodiou & Colomines, 1988
Algensiella (Fig. 2, branch I) may be characterised by four autapomorphies (characters 71–74), all being unambiguous.

Character 71, mxp without tiny seta accompanying the mxp claw: all representatives of the Ancorabolidae ● have a mxp claw accompanied by one short seta (cf. III/C, character 42). In *Algensiella*, however, this short seta is absent. This loss is thus considered as autapomorphic for *Algensiella*. Nonetheless, as noted for the A2 exopod (cf. III/C, character 40), it is possible that such tiny mxp setae may have been overlooked (cf. George 2018). Therefore, character 71 should be treated carefully and requires confirmation by re-examination of new material of *Algensiella*.

Characters 72, 73, loss of P3 and P4 enp-1: as clearly shown in the descriptions of *Algensiella boitanii* and *A. laurenceae* (Cottarelli and Baldari 1987; Bodiou and Colomines 1988), the P3 and P4 endopods lack the small enp-1, having only one elongate, slender segment. This is almost unique and similar descriptions given for species, such as *Calypsophontodes latissimus* (Brady, 1918), *Laophontodes antarcticus* Brady, 1918, *L. propinquus* Brady, 1910 and *Bicorniphontodes ornatus* (Krishnaswamy, 1957) (cf. Brady 1910, 1918; Krishnaswamy 1957) may be errors in observation rather than true morphology. For the descriptions of the *Algensiella* species, these doubts do not exist, so the complete loss of the P3 and P4 enp-1 is considered autapomorphic of the genus.

J. *The Laophontodes–Probosciphontodes*-clade (La–P-clade)

The La–P-clade (Fig. 2, branch J) unites *Laophontodes*, *Rostrophontodes*, *Bicorniphontodes*, *Ancorabolina*, *Paralaophontodes*, *Lobopleura* and *Probosciphontodes* and is characterised by a single autapomorphy (Table 1):

Character 74, FR slender, at least 3 times longer than broad: it is assumed that this derived state is the result of convergent development in both the Ancorabolinae ● and the *Ceratonotus*-group. This assumption is supported by autapomorphies 51–62 that characterise the Ancorabolinae ● and the unambiguous characters 45–50 (cf. III/D, Table 1) that characterise the Laophontodinae ●, in which the La–P-clade is embedded. In addition, the *Ceratonotus*-group is seen to branch off much earlier than the La–P-clade, sharing a set of derived characters with the "Cletodidae", which is considered here to be a sister-group of the Ancorabolidae ● (cf. III/C). That phylogenetic relationship is discussed in detail in section III/X below. Consequently, character 74 is regarded as autapomorphic of the La–P-clade. Future investigation may uncover further morphological deviations supporting that hypothesis. However, compared to the basal laophontodin taxa, namely *Tapholaophontodes*, *Algensiella* and *Calypsophontodes*, which each bear short and stout FR (considered the plesiomorphic condition: Gheerardyn and Lee 2012), the long, slender FR in the La–P-clade is a plausible autapomorphy.

K. *Calypsophontodes*

Composition: two species:
Calypsophontodes Gheerardyn & Lee, 2012
Calypsophontodes latissimus (Brady, 1918); syn. *Laophontodes latissimus* Brady, 1918
Calypsophontodes macropodia (Gee & Fleeger, 1986) (**type species**); syn. *Laophontodes macropodia* Gee & Fleeger, 1986

After *Paralaophontodes* and *Lobopleura* (Lang 1965; Conroy-Dalton 2004), *Calypsophontodes* was the third genus formerly assigned to *Laophontodes* (Gheerardyn and Lee 2012). Whilst Gee and Fleeger (1986) noted uncertainty in the taxonomic position of *Laophontodes latissimus* and *L. macropodia*, it was not until Gheerardyn and Lee (2012) undertook a detailed re-description of *C. macropodia*, accompanied by a detailed systematic appraisal, that both species were displaced into a newly-erected genus *Calypsophontodes*. The monophyly of *Calypsophontodes* was supported by two autapomorphic characters, namely (i) sexual dimorphism in P4 enp-2 and (ii) sexual dimorphism in size of the P2–P4 swimming legs. Beside these characters, careful comparison revealed three additional autapomorphies. Thus, *Calypsophontodes* may be characterised as monophylum by five autapomorphies (Table 1, characters 75–79; Fig. 2, branch K):

Character 75, rostrum ventrally curved: in *Calypsophontodes*, the rostrum suffered a remarkable elongation (cf. III/W, Table 1, character 131), combined with a ventral curvature and a strong tapering towards its tip. That rostral shape is quite derived if compared with most Laophontodinae ●, whose rostrum is short, triangular in shape and not curved. It is therefore regarded as autapomorphy of *Calypsophontodes*. However, a very similar rostral shape is present also in *Rostrophontodes*, *Ancorabolina anaximenesi* Gheerardyn & George, 2010 and *A. galeata* Gheerardyn & George, 2010. However, despite the striking similarity, no closer relationship between the named taxa is hypothesised, due to their unambiguous characterisation as, respectively, their affiliation to other genera is based on distinct apomorphies.

Remarks: As discussed below (cf. III/AA, character 143), the rostral shape and size varies remarkably within the Cletodoidea. In particular, the length of the rostrum ranges from a longitudinal diminishing (e.g. *Arthuricornua*, *Dimorphipodia*, *Polyascophorus*, *Touphapleura*) towards its complete absence (*Ceratonotus*, *Dendropsyllus*) over the supposed ancestral condition of a small, triangular rostrum (e.g. *Algensiella*, *Bicorniphontodes*, *Cletodes*, *Laophontodes*, *Tapholaophontodes*) towards its longitudinal elongation (e.g. *Ancorabolina*, *Ancorabolus*, *Calypsophontodes*, *Lobopleura*, *Rostrophontodes*). Such variability in rostral length is often combined with a remarkable narrowing (e.g. *Ancorabolus*, *Dorsiceratus*, *Paralaophontodes*, *Probosciphontodes*). It is, therefore, assumed here that the development of similar rostral shape in different cletodoid species is, in most cases, the result of convergent evolution.

Character 76, md palp with five setae: While the groundpattern of the La–P-clade (cf. III/J) retains the plesiomorphic six setae on the md palp (Table 1, character 29), *C. macropodia* bears only five setae (not described for *C. latissimus* by Brady (1918)). More specifically, all genera of the La–P-clade, except *Ancorabolina*, include species with five setae on the md palp (*Bicorniphontodes*: *B. horstgeorgei*; *Laophontodes*: *L. sarsi*, *L. scottorum*, *L. spongiosus*, *L. whitsoni*; *Lobopleura*: *L. ambiducti*; *Probosciphontodes*: *P. ptenopostica*) (cf. Schizas and Shirley 1994; Conroy-Dalton 2004; George and Gheerardyn 2015; George 2018). Thus, the reduction of one seta in *Calypsophontodes* is interpreted as an autapomorphy for that genus, but convergent where it occurs in single species of the remaining genera. Additional note: *Laophontodes mourois* Arroyo. George, Benito & Maldonado, 2003 was incorrectly described by Arroyo et al. (2003) as having seven setae on the md palp; in fact, it bears six setae in total as two apical, one inner and one outer subapical and two outer lateral setae (George, pers. obs.).

Character 77, P2–P4 with sexual dimorphism expressed in size: that character is absent in all remaining species, so I agree with the assumption of Gheerardyn and Lee (2012) and regard that character as autapomorphic for *Calypsophontodes*.

Character 78, sexual dimorphism in the P4 endopod: in addition to sexual dimorphism in the P3 and P5, several "ancorabolid" species also show sexual dimorphism in the P4 (e.g. *Arthropsyllus serratus* Sars, 1909, *Ceratonotus tauroides* George, 2006, *Dorsiceratus octocornis* Drzycimski, 1967, *Juxtaramia polaris* Conroy-Dalton & Huys, 2000, *Laophontodes monsmaris* George, 2018, *L. whitsoni* T. Scott, 1912) (cf. Drzycimski 1967; Conroy-Dalton and Huys 2000; George 2006b, c, 2018; George and Gheerardyn 2015). It arises as differences in the shape and size of endopodal segments and setae/spines. Usually, sexual dimorphism in the P4 endopod is expressed as the loss of one seta in the female. However, in *Calypsophontodes macropodia*, it is the male that has lost one seta. This condition is found exclusively in *Calypsophontodes* and is regarded here as autapomorphy, as proposed by Gheerardyn and Lee (2012).

Character 79, P5 basis, endopod and exopod fused to a single plate: as pointed out by Gheerardyn and Lee (2012), the P5 in both the female and male of *Calypsophontodes* differs remarkably from all *Laophontodes* species and, in fact, from all Cletodoidea. The characteristic shape of the P5 in the Cletodoidea consists of an elongated exopod that is often separated from the baseoendopod in females, but fused with it in males (cf. Fig. 7B, C, E, F), combined with a reduced endopodal lobe, becoming narrow and short (Fig. 7B, C) or even completely lost (Fig. 7E, F). In contrast, the P5 of *Calypsophontodes* is comparatively broad and ovoid (Fig. 7D). However, it fits with characters 37, 38 and 49 (cf. III/B, III/D)–the endopod is fused with the basis (37), it is small and slender (38) and it carries two setae only (49)–clearly supporting the affiliation of *Calypsophontodes* to the Cletodoidea and down to the C–P-clade. Therefore, it is hypothesised that the P5 of *Calypsophontodes* suffered a transformation into a broad, ovoid appendage by retaining its narrow endopodal lobe, but widening the exopodal lobe (Fig. 7D). This deviation is unique within the Cletodoidea and is, therefore, considered as autapomorphy for *Calypsophontodes*.

L. *The Rostrophontodes–Ancorabolina*-clade (R–A-clade)

The La–P-clade (cf. III/J) splits into two monophyletic taxa considered as sister-groups, the R–A-clade and the Pa–P-clade (cf. III/S). The R–A-clade (Fig. 2, branch L) encloses the genera *Rostrophontodes*, *Laophontodes*, *Bicorniphontodes* and *Ancorabolina* and can be characterised by two unambiguous autapomorphies (characters 80–81):

Character 80, body slender, virtually cylindrical: as stated by Gheerardyn and Lee (2012: 279), *Laophontodes* species "*…exhibit a narrow and elongated body shape with virtually cylindrical body somites…*" (cf. also George and Gheerardyn 2015; George 2018). In contrast, *Algensiella*, *Tapholaophontodes*, *Calypsophontodes*, *Lobopleura*, *Probosciphontodes* and even *Paralaophontodes* (i.e. *P. elegans* Baldari & Cottarelli, 1986) show a more robust and fusiform or dorsoventrally-flattened body (cf. Baldari and Cottarelli 1986; Gee and Fleeger 1986; Cottarelli and Baldari 1987; Bodiou and Colomines 1988; Fiers 1988; Conroy-Dalton 2004). In fact, this latter state is found in many "Cletodidae" and in the Laophontoidea and is quite common in the Harpacticoida. Thus, it is regarded as plesiomorphic, whilst the narrow and elongate body shape of *Laophontodes*, which is also found in *Rostrophontodes*, *Bicorniphontodes* and *Ancorabolina* (George 2006a; Kornev and Chertoprud 2008; George and Tiltack 2009; Gheerardyn and George 2010; George et al. 2019), is interpreted as autapomorphic for the R–A-clade. The presence of a narrow and elongate body in the *Ceratonotus*-group is seen as convergence (cf. III/AA).

Character 81, longitudinal elongation of the P1 coxa: as indicated in the discussion of the longitudinal elongation of the P1 basis (C–P-clade, cf. III/H, character 70), some representatives of that clade also show a longitudinal elongation of the coxa. This applies for all members of the R–A-clade and two genera of the Pa–P-clade, namely *Paralaophontodes* and *Probosciphontodes*. However, both clades can be distinguished clearly by their own apomorphies, which are not expressed in the other taxon. For instance, neither *Paralaophontodes* nor *Probosciphontodes* (cf. III/S) share R–A-clade-apomorphy 80, but present a set of shared deviations missing in the R–A-clade. Thus, character 81 is seen as autapomorphy for the R–A-clade and also its presence in the other two genera is interpreted as convergence.

M. *Rostrophontodes*

Composition: monotypic:
Rostrophontodes Lee & Huys, 2019
Rostrophontodes gracilipes (Lang, 1936), syn. *Laophontodes gracilipes* Lang, 1936

Lee and Huys (2019) established the genus *Rostrophontodes* (Fig. 2, branch M) to accommodate the species *Laophontodes gracilipes*. They listed eight supposed autapomorphies, (1) a very large rostrum that is sharply pointed towards its tip and recurved ventrally; (2) the cphth, as well as the pedigerous body somites and the anterior half of the GDS (genital somite in males) with a reticulate surface ornamentation; (3) the presence of paired spinous projections dorsally on the P5-bering somite, GDS and first free abdominal somite; (4) mxp claw with long pinnules on distal half; (5) P1 basis transversely elongated in distal half; (6) P1 enp-2 with apical claw being slender and almost as long as adjacent geniculate seta; (7) P2–P4 enp-2 with one instead of two apical setae; (8) furcal seta II (and possibly also seta I) located in proximal third of FR.

From Lee and Huys' (2019) above listed characters five (2–4, 6 and 8) are adopted here without further discussion and listed in Table 1 as characters/character complexes 83 (2), 84 (3), 87 (4), 89 (6) and 85 (8). As discussed by Lee and Huys (2019), they are unique and derived if compared with remaining *Laophontodes* species. I agree with these authors, considering these characters as autapomorphies of *Rostrophontodes*. Character (1) is restricted to the ventral curvature of the rostrum, which is seen as autapomorphy for *Rostrophontodes*, but also occurred convergently in *Calypsophontodes* and *Ancorabolina* (part.). It is listed in Table 1 as character 75 and discussed in section III/K. Character (5) (Table 1, character 88) is interpreted in a different way by Lee and Huys (2019) and discussed below. Character (7) is split into three characters: whilst the reduction of one apical seta in P2 and P3 is listed as characters 90 and 91, respectively (Table 1), the reduction of one apical seta in P4, which occurs convergently in *Lobopleura*, is listed in Table 1 as character 126 and discussed in section III/V. Besides these ten autapomorphies, another deviation was detected:

Character 86, mxl coxa with only one seta: as shown by Kornev and Chertoprud (2008, fig. 5.192.E), the maxillular coxal endite bears one strong unipinnate seta. This is regarded as autapomorphic, because all remaining Ancorabolidae ● bear two setae.

Character 88, P1 basis transversely elongated: as discussed above (cf. III/E), the transverse elongation of the P1 basis in the Ancorabolinae● and *Rostrophontodes* (and *Ancorabolina*) is not considered as convergent development. In *Rostrophontodes* (and *Ancorabolina*), the P1 basis underwent a longitudinal elongation (Table 1, character 70) previous to its transverse elongation. That longitudinal elongation of the P1 basis constitutes a clear autapomorphy of the laophontodin● C–P-clade (cf. III/H). Thus, the subsequent transverse elongation in *Rostrophontodes* (and *Ancorabolina*) is interpreted here as a distinct deviation and is regarded as autapomorphic for *Rostrophontodes*. It evolved convergently in *Ancorabolina* that can, however, clearly be separated from *Rostrophontodes* (cf. III/R).

Remarks: Lee and Huys (2019) hypothesise that the transverse elongation in both *Rostrophontodes* and *Ancorabolina* is restricted to the distal part of the P1 basis. If their statement is interpreted correctly, the transverse elongation of the distal part of the P1 basis was accompanied by a simultaneous longitudinal elongation of the inner apical part, resulting in the formation of cylindrical pedestals for both the exopod (lateral pedestal) and the endopod (apical pedestal). I do not agree with that assumption. As the P1 basis had previously suffered a remarkable longitudinal elongation (cf. III/H, Table 1, character 70), the subsequent further development of an apical pedestal for the endopod is considered here as rather implausible. Instead, I assume that the transverse elongation started with a lateral outgrowth on the outer basal margin of the longitudinally elongated P1 basis, as already indicated in several members of the C–P-clade, such as, for example, in *Bicorniphontodes*, *Calypsophontodes* and *Laophontodes* (part.) (cf. Thomson 1882; Lang 1934; Gheerardyn and Lee 2012; George and Gheerardyn 2015; George 2018; George et al. 2019). In *Rostrophontodes gracilipes* and particularly in *Ancorabolina*, that lateral outgrowth–rather centred than distally–may already be interpreted as transverse elongation, reaching its maximal expression in *Ancorabolina chimaera*, *A. divasecunda* and, especially, in *A. galeata* (cf. George 2006a; Kornev and Chertoprud 2008; Gheerardyn and George 2010).

Characters 90 and 91, P2 and P3 enp-2 with one apical seta: in the groundpattern of the Laophontodinae ●, both the P2 and P3 enp-2 are equipped with two apical setae, a condition that is retained in *Ancorabolina*, *Bicorniphontodes*, *Calypsophontodes*, *Laophontodes* and *Paralaophontodes hedgpethi* (Lang, 1965). Instead, *Rostrophontodes* lost one apical seta in the respective endopodal segments, being autapomorphic for that taxon. With respect to the P3 enp-2, a convergent loss of one apical seta is hypothesised for *Tapholaophontodes*, the basal taxon of Laophontodinae●.

Remarks: Lee and Huys (2019) based their establishment of *Rostrophontodes* on the detailed re-description of *R. gracilipes* (as *Laophontodes gracilipes*) provided by Kornev and Chertoprud (2008). In the meantime, additional material was collected from Anaximenes Seamount (eastern Mediterranean) by George et al. (2018). Although resembling *R. gracilipes* in several derived features (shape of rostrum, body with reticulate surface ornamentation, P2–P4 enp-2 with only one apical seta), the Anaximenes material (two females, one male) differs from *R. gracilipes* in other characters. For instance, both the female and male A1 bear a spinulose "bump" on the second antennular segment; the maxillipedal claw carries spinules along the inner margin, but these are not enlarged on the distal part of the claw; the penultimate abdominal somite is spinulose on its posterior margin, but, contrary to the condition described for *R. gracilipes*, in the Anaximenes material, these spinules are strong and low in number; the FR are longer than in *R. gracilipes* and furcal setae I and II originate from half of the rami, not from the proximal third as in *R. gracilipes* (George, pers. obs.). This suggests that the Anaximenes material probably does not belong to *R. gracilipes* as supposed by George et al. (2018), but belongs to another species of *Rostrophontodes*. That has consequences for both the phylogenetic characterisation of the genus, as well as for its systematic relationships with other supraspecific taxa. For instance, the apomorphies assigned to the genus *Rostrophontodes* by Lee and Huys (2019) (see above) may at least partly turn into apomorphies of *R. gracilipes* only, which would consequently lead to changes in the phylogenetic constellation within the R–A-clade. An ongoing evaluation (George, in prep.) that includes even further material from the Arctic, may elucidate the phylogenetic status of *Rostrophontodes* and the species therein.

N. The *Laophontodes–Ancorabolina*-clade (La–A-clade)

The La–A-clade (Fig. 2, branch N) encloses the genera *Laophontodes*, *Bicorniphontodes* and *Ancorabolina*. So far, that clade can be characterised by one autapomorphy (Table 1):

Character 82, A2 exopod represented by tiny seta: as discussed in section III/C for characters 39 and 40, the Ancorabolidae ● is characterised by having at most a 1-segmented, knob-like A2 exopod bearing one small seta. That state is retained in the Pa–P-clade (cf. III/S), but in the La–A-clade, the endopodal segment is completely lost and the A2 exopod is represented by a single seta only (which is also lost in *Ancorabolina*, cf. III/R). This character is interpreted as autapomorphic for the La–A-clade. It is noteworthy that George and Gheerardyn (2015) erred when re-describing the A2 exopod of *Laophontodes whitsoni* as knob-like carrying a bare seta: re-examination of available material revealed that what George and Gheerardyn (2015) considered to be a tiny exopod, was, in fact, the remarkably sclerotised insertion of the seta (George, pers. obs.). Thus, the derived state of character 82 can be assigned, without exception, to all representatives of the La–A-clade.

O. *Laophontodes*

Composition: thirteen species:
Laophontodes T. Scott, 1894
- *Laophontodes antarcticus* Brady, 1918 (species *incertae sedis*)
- *Laophontodes georgei* Lee & Huys, 2019, syn. *Laophontodes norvegicus* George, 2018
- *Laophontodes gertraudae* George, 2018
- *Laophontodes macclintocki* Schizas & Shirley, 1994
- *Laophontodes monsmaris* George, 2018
- *Laophontodes mourois* Arroyo, George, Benito & Maldonado, 2003
- *Laophontodes propinquus* Brady, 1910
- *Laophontodes sabinegeorgeae* George & Gheerardyn, 2015
- *Laophontodes sarsi* George, 2018
- *Laophontodes scottorum* George, 2018
- *Laophontodes spongiosus* Schizas & Shirley, 1994
- *Laophontodes typicus* T. Scott, 1894 (**type species**)
- *Laophontodes whitsoni* T. Scott, 1912

The phylogenetic evaluation of the monophyletic status of *Laophontodes* (Fig. 2, branch O) remains unproven until today and remains the weakest part of the phylogenetic concept presented here. *Laophontodes* is regarded as the type genus of "Laophontodinae", since, when "Laophontodinae" was established by Lang (1944, 1948), *Laophontodes* was its only genus.

Compared with the remaining "Laophontodinae" and despite the description of several new *Laophontodes* species since the establishment of that genus (cf. Lang 1948; Schizas and Shirley 1994; Arroyo et al. 2003; George and Gheerardyn 2015; George 2018), it cannot yet be characterised by even a single autapomorphy. Yet detailed re-description of several species (George and Gheerardyn 2015; George 2018), as well as careful morphological comparison, did not enable the detection of any morphological deviations shared by all *Laophontodes* species. Thus, it can only be hoped that future research on *Laophontodes* (Table 2) will resolve this unsatisfying taxonomy.

P. The *Bicorniphontodes–Ancorabolina*-clade (B–A-clade)

The striking morphological similarity of *Ancorabolina* and *Bicorniphontodes bicornis* was addressed by Gheerardyn and George (2010), who noted that:

> …*the very first examinations of* Ancorabolina chimaera *(mis-)lead to the assumption of it being a somewhat derived* Laophontodes bicornis. (Gheerardyn and George 2010: 53).

However, these authors subsequently listed 10 differences between these two species, concluding that they belong to different genera. Nonetheless, the current phylogenetic evaluation reveals a sister-group relationship between *Ancorabolina* and *Bicorniphontodes*, the latter having been characterised in more detail, due to the recent description of *B. horstgeorgei* (George & Gheerardyn, 2015) and *B. clarae* George, Glatzel & Schröder, 2019 (George and Gheerardyn 2015; George et al. 2019). The B–A-clade is defined by a single, but phylogenetically, highly relevant autapomorphy (Fig. 2, branch P):

Character 92, postero-lateral cuticular processes on the cephalothorax: more or less similar processes are present in some genera of the distantly-related *Ceratonotus*-group (e.g. *Echinopsyllus* Sars, 1909, *Polyascophorus* George, 1998, *Pseudechinopsyllus* George, 2006) (cf. Sars 1909; George 1998b, 2006b; Conroy-Dalton 2003a). They are absent in the Ancorabolinae●, which exhibits completely different processes in some representatives (cf. III/E). Therefore, their presence in both *Ancorabolina* and *Bicorniphontodes* may be attributed to their development in a hypothetical common ancestor; thus, character 92 must be considered synapomorphic for *Bicorniphontodes* and *Ancorabolina*, i.e. as an autapomorphy of the B–A-clade.

Remarks: Lee and Huys (2019) suggest a close relationship of *Ancorabolina* with *Rostrophontodes*, based on four potential synapomorphies; (1) presence of spinules along the inner margin of the maxillipedal claw; (2) P1 basis bilaterally expanded on distal half, forming distinct pedestals for both the endo- and the exopod; (3) apical claw of P1 enp-2 turned into a slender element; (4) body somites dorsally with spinous processes.

As pointed out by Lee and Huys (2019), the presence of spinules on the inner margin of the maxillipedal claw (1) is also present in species of other genera. In particular, the C–P-clade (cf. III/H) encloses species of different genera bearing such spinules, besides *Rostrophontodes gracilipes* and *Ancorabolina* spp., as well as, for example, *Bicorniphontodes horstgeorgei*, *Calypsophontodes macropodia*, *Laophontodes mourois* and *L. whitsoni* (cf. Arroyo et al. 2003; George 2006a; Kornev and Chertoprud 2008; Gheerardyn and George 2010; Gheerardyn and Lee 2012; George and Gheerardyn 2015). Thus, the assumption of a derived feature shared by *Rostrophontodes* and *Ancorabolina* is only weakly founded and therefore rejected here. With respect to character (4), Lee and Huys (2019) themselves qualify its significance, as the presence and shape of spinous processes vary in the different species of *Ancorabolina* inhibiting an unambiguous characterisation. However, characters (2) and (3) may indeed indicate a closer relationship of *Ancorabolina* with *Rostrophontodes*. A remarkably-narrowed claw on P1 enp- 2 is also shared by *Laophontodes whitsoni*, but this might be a convergence. Otherwise, if characters (2) and (3) supported a close relationship of *Ancorabolina* with *Rostrophontodes*, the here-postulated synapomorphy of *Ancorabolina* and *Bicorniphontodes*, character 92, would represent a convergence for these species. Based on the argumentation given above (cf. III/M), the here-proposed sister-group *Bicorniphontodes–Ancorabolina* is tentatively maintained until an unambiguous characterisation of *Rostrophontodes* is presented.

Q. *Bicorniphontodes*

Composition: five species:
Bicorniphontodes George, Glatzel & Schröder, 2019
- *Bicorniphontodes bicornis* (A. Scott, 1896) (**type species**); syn. *Laophontodes bicornis* A. Scott, 1896
- *Bicorniphontodes clarae* George, Glatzel & Schröder, 2019
- *Bicorniphontodes hamatus* (Thomson, 1882); syn. *Merope hamata* Thomson, 1882, *Laophontodes hamatus* Lang, 1934
- *Bicorniphontodes horstgeorgei* (George & Gheerardyn, 2015); syn. *Laophontodes horstgeorgei* George & Gheerardyn, 2015
- *Bicorniphontodes ornatus* (Krishnaswamy, 1957), syn. *Laophontodes ornatus* Krishnaswamy, 1957

With *Laophontodes hamatus*, Thomson (1882) described the first *Laophontodes* species carrying postero-lateral processes on the cphth. A second species, *L. bicornis*, was described by A. Scott (1896), which was later on re-described by Sars (1909) and again by George and Gheerardyn (2015). Krishnaswamy (1957) reported and partly described *L. ornatus*. It was then more than 50 years before another species bearing postero-lateral cephalothoracic processes was described: *Laophontodes horstgeorgei* was presented as a new representative alongside the first review of the systematic relationship of all above-named species (George and Gheerardyn 2015). It was noted that all four species had a potentially closer relationship, owing to two shared derived characters, namely (i) the presence of backwardly directed postero-lateral processes on cphth and (ii) free body somites with special hyaline frills, whose tips end in tiny round lappets. However, due to the inadequate descriptions of *L. hamatus* and *L. ornatus*, George and Gheerardyn (2015) felt unable to provide a more detailed phylogenetic discussion. Recently, the description of *Bicorniphontodes clarae* George, Glatzel & Schröder, 2019 enabled a deeper analysis (George et al. 2019), yielding six derived characters that support a monophyletic status for *L. bicornis*, *L. hamatus*, *L. horstgeorgei*, *L. ornatus* and *B. clarae.* In addtion to characters (i) and (ii) listed above, these are: (iii) cphth with medio-lateral triangular extensions, (iv) furcal setae I and II displaced subapically, (v) A2 allobasis lacking abexopodal seta on the endopodal half and (vi) outer spines of P2 and P3 exp-3 unipinnate and comb-like, with extremely long pinnae set widely apart from each other. Consequently, George et al. (2019) transferred the four above-listed species into *Bicorniphontodes*. As shown above (cf. III/P), character (i) is regarded as synapomorphic for *Ancorabolina* and *Bicorniphontodes* (Table 1, character 92), but the remaining characters (ii–vi) can be considered autapomorphic (Table 1, characters 93–97) for *Bicorniphontodes* (Fig. 2, branch Q) (see George et al. (2019) for a detailed discussion of these characters and justification for the erection of *Bicorniphontodes*). The abexopodal seta is also absent from the endopodal half of the A2 allobasis in *Tapholaophontodes*, *Algensiella* and *Calypsophontodes*; however, this is considered convergent due to the mutual differences between these taxa and *Bicorniphontodes* as confirmed by the respective autapomorphies (cf. III/G, I, K).

R. *Ancorabolina*

Composition: six species:
Ancorabolina George, 2006
  Ancorabolina anaximenesi Gheerardyn & George, 2010
  Ancorabolina belgicae Gheerardyn & George, 2010
  Ancorabolina cavernicola George & Tiltack, 2009
  Ancorabolina chimaera George, 2006 (**type species**)
  Ancorabolina divasecunda Gheerardyn & George, 2010
  Ancorabolina galeata Gheerardyn & George, 2010

With respect to its supposed sister-group *Bicorniphontodes*, *Ancorabolina* can be characterised by four autapomorphies (Table 1, characters 88, 98–100; Fig. 2, branch R):

Character 88 has been discussed in section III/M.

Character 98, female A1 segments slender, elongated: whilst *Bicorniphontodes* still retains the characteristic shape of the A1, as described for the Cletodoidea (cf. III/B, characters 23–26), the A1 of *Ancorabolina* exhibits a further deviation, being elongated and comparatively slender. This is found in all known *Ancorabolina* species and is, therefore, regarded as autapomorphic for that genus.

Character 99, small seta on distal edge of A2 endopod absent: as discussed above (cf. III/A, character 18), the L–C-clade lost one of two slender setae that accompany the two spines on the distal edge of the A2 endopod in the Podogennonta. Considered autapomorphic for the L–C-clade, that state (presence of only one slender seta) turns into a plesiomorphy at advanced taxonomic levels within the L–C-clade. It is retained, at least in the groundpattern, of several "ancorabolid" genera (e.g. the *Ancorabolus*-lineage, *Calypsophontodes*, the *Ceratonotus*-group, *Laophontodes*, *Lobopleura*, *Paralaophontodes*, *Probosciphontodes*), in *Bicorniphontodes* (cf. Conroy-Dalton and Huys 2000; Conroy-Dalton 2001, 2003a, b, 2004; George 2006b, c, 2017, 2018; Gheerardyn and Lee 2012; George and Gheerardyn 2015; Gómez and Díaz 2017; George et al. 2019) and in the groundpattern of the "Cletodidae" (e.g. *Cletodes*, *Enhydrosoma* Boeck, 1872, *Limnocletodes*, *Neoacrenhydrosoma* Gee & Mu, 2000, *Thriatrix* Gee & Burgess, 1997; cf. Gee and Huys 1996; Gee and Burgess 1997; Gee 1998; Gee and Mu 2000; George and Müller 2013). Conversely, all *Ancorabolina* species share the derived loss of that seta (cf. George 2006a; George and Tiltack 2009; Gheerardyn and George 2010) and this is, therefore, considered autapomorphic for the genus. *Algensiella* and *Tapholaophontodes* are also thought to lack that seta (Soyer 1975; Mielke 1985; Baldari and Cottarelli 1986; Cottarelli and Baldari 1987), although this may be the result of inaccurate observation rather than the absence of the seta itself (cf. George 2018). Unfortunately, the type material for both *Algensiella* and *Tapholaophontodes* is not available and, therefore, it has not been possible to confirm this character state for these genera. Nevertheless, even the absence of that seta is irrelevant in this instance, since both genera branch off much earlier, rendering this character convergent for these genera.

Character 100, A2 exopod absent: as discussed above (cf. III/C), the Ancorabolidae ● can be characterised by an atrophied, knob-like A2 exopod carrying one tiny seta (Table 1, characters 39 and 40). This is retained in the groundpattern of the La–P-clade, whilst in the groundpattern of the La–A-clade, the A2 exopod is represented by a tiny seta only (cf. III/N, character 82). *Ancorabolina* presents a further derived state with the complete loss of even that tiny seta. This state is regarded as autapomorphic for *Ancorabolina*; it is regarded as convergent where it is seen elsewhere in other related taxa (*Algensiella*, Ancorabolinae ●, *Ceratonotus*-group, *Laophontodes* (part.?), *Paralaophontodes* (part.), *Tapholaophontodes*).

S. The *Paralaophontodes–Probosciphontodes*-clade (Pa–P-clade)

The Pa–P-clade (Fig. 2, branch Q) encloses the genera *Paralaophontodes*, *Lobopleura*, and *Probosciphontodes*. It can be characterised by five autapomorphies (Table 1, characters 101–105), of which two (characters 101, 103) are unique to that clade:

Character 101, free thoracic and first two abdominal somites laterally extended: in the La–B–A-clade (the supposed sister-group of the Pa–P-clade, III/L), the free body somites run more or less longitudinally towards their posterior margins. In the Pa–P-clade, however, the free thoracic and first two abdominal somites are laterally extended. This is most weakly expressed in *Paralaophontodes* (cf. George 2017), whilst the longest lateral development is seen in *Probosciphontodes* (cf. Fiers 1988; Conroy-Dalton 2004). This deviation is regarded as autapomorphic for the Pa–P-clade.

Character 102, female A1 4-segmented: all genera in the Pa–P-clade are characterised by a 4-segmented female A1, whereas the remaining taxa assigned to the superordinate Laophontodinae ● (cf. III/D) retain the 5-segmented female A1 which arose in the Cletodoidea (Table 1, character 23). Thus, character 102 is seen as autapomorphic for the Pa–P-clade. The 4-segmented female A1, observed in the Cletodidae ●, is seen as convergent.

Character 103, P1 endopod reinforced: the representatives of the Pa–P-clade share the presence of a greatly-strengthened P1 endopod, such as it forms a powerful appendage. This marks a clear deviation from the remaining members of the Laophontodinae ●, whose P1 remain rather slender and delicate. George (2017) assumed that the derived state was autapomorphic for the monophylum *Paralaophontodes* (character 15 in George 2017); however, since *Lobopleura* and *Probosciphontodes* also exhibit a thickened P1, it is regarded here as synapomorphic for the three taxa.

Characters 104, 105, female P3 and P4 enp-2 without inner seta: whilst the loss of an inner seta on the P2 enp-2 is a derived character shared by all members of the Cletodoidea (cf. III/B, character 34), the cletodoid groundpattern for the P3 and P4 enp-2 still bears one inner seta. That condition is retained in the groundpattern of the C–P-clade (and still observable in *Calypsophontodes*), although a reduction of the inner seta took place independently in both sub-ordered clades (R–A-clade and Pa–P-clade). Nonetheless, in the R–A-clade, some species of *Ancorabolina* and *Laophontodes* (P4 enp-2: also in *Bicorniphontodes*) still retain that seta, suggesting that characters 104 and 105 evolved independently within these genera. However, since these characters are shared by *Lobopleura*, *Paralaophontodes* and *Probosciphontodes*, they can be interpreted as autapomorphies for the Pa–P-clade, having evolved in the Pa–P-clade ancestor.

Remarks: In addition to the taxa discussed here, the reduction of the inner endopodal setae in the female P3 and P4 is also present in *Tapholaophontodes*, *Algensiella*, the Ancorabolinae● and the *Ceratonotus*-group and, as such, represent multiple convergences.

T. *Paralaophontodes*

Composition: eight species:
Paralaophontodes Lang, 1965
- *Paralaophontodes anjae* George, 2017
- *Paralaophontodes armatus* (Lang, 1936), syn. *Laophontodes armatus* Lang, 1936
- *Paralaophontodes echinatus* (Willey, 1930) (**type species**), syn. *Laophonte echinata* Willey, 1930
- *Paralaophontodes elegans* Baldari & Cottarelli, 1986
- *Paralaophontodes exopoditus* Mielke, 1981
- *Paralaophontodes hedgpethi* (Lang, 1965), syn. *Laophontodes hedgpethi* Lang, 1965
- *Paralaophontodes psammophilus* (Soyer, 1975), syn. *Laophontodes psammophilus* Soyer, 1975
- *Paralaophontodes robustus* (Bŏzić, 1964), syn. *Laophontodes robustus* Bŏzić, 1964

The monophyletic status of *Paralaophontodes* (Fig. 2, branch T) was unambiguously confirmed by George (2017) who identified 16 autapomorphic characters for this genus and elucidated the systematic relationships within that taxon (George 2017). Character 15 discussed by George (2017) is here regarded as synapomorphic for *Paralaophontodes*, *Lobopleura* and *Probosciphontodes* (section III/S, character 102). However, the remaining 15 characters are confirmed as autapomorphic for *Paralaophontodes*. These are united to characters/character complexes 106–115 (see George (2017) for further discussion). The simultaneous lack of an apical seta on the mxp syncoxa (character 114) in the Ancorabolinae ● is interpreted as convergence.

U. The *Lobopleura–Probosciphontodes*-clade (Lo–P-clade)

The probable sister-group relationship of *Lobopleura* and *Probosciphontodes* (Fig. 2, branch U) has been discussed in detail by Conroy-Dalton (2004), who listed 10 synapomorphies (characters a–j) for the taxon. Of these, eight characters (a–c, e–g, i, j) are adopted here (Table 1, characters 116–121, 123 and 124) (see Conroy-Dalton (2004) for further discussion). Character (d), the 4-segmented female A1, is not restricted to *Lobopleura* and *Probosciphontodes*, but also present in the supposed sister-group of the Lo–P-clade, *Paralaophontodes* and is, therefore, not apomorphic for the Lo–P-clade (see discussion above (cf. III/S, character 102)). Conroy-Dalton's (2004) character (h), a 3-dimensional appearance of the P5, is set aside in the current analysis owing to lack of material available for observation and confirmation. One additional autapomorphic character was detected for the Lo–P-clade:

Character 122, P2–P4 exp-2 lacking inner seta: whilst an inner seta on the second exopodal segment of P2–P4 is retained in the groundpattern of *Paralaophontodes* (*P. hedgpethi* (Lang, 1965)), it is absent in both *Lobopleura* and *Probosciphontodes*. This is interpreted as a synapomorphy of both taxa and, thus, as an autapomorphy for the Lo–P-clade.

V. *Lobopleura*

Composition: Three species:
Lobopleura Conroy-Dalton, 2004
- *Lobopleura ambiducti* Conroy-Dalton, 2004 (**type species**)
- *Lobopleura expansa* (Sars, 1908), syn. *Laophontodes expansus* Sars, 1908
- *Lobopleura multispinata* (Kornev & Chertoprud, 2008), syn. *Laophontodes multispinatus* Kornev & Chertoprud, 2008

The phylogenetic characterisation of *Lobopleura* (Fig. 2, branch V) was discussed and confirmed by Conroy-Dalton (2004) by means of four autapomorphies. They are unambiguous and thus included in the present evaluation without further discussion of characters 125 (male P3 endopod 2-segmented), 126 (P4 endopod with one apical seta) and 127 (P5 benp represented by one minute seta). The fourth character, namely the display of a paired genital system in both sexes, was considered as a secondary development for *Lobopleura* (Conroy-Dalton 2004) and is included as character 128 (Table 1).

Remarks: A 2-segmented male P3 endopod (character 125) is also observed in the Ancorabolinae ● (cf. Conroy-Dalton and Huys 2000) and certain taxa of the Laophontoidea (cf. Huys and Willems 1989; Huys 1990a; Huys and Lee 1998/99; Conroy-Dalton 2004) and in the "Cletodidae" (cf. Gee 1994, 1997, 1999). Nevertheless, it is shown in the overall phylogenetic discussion that the Ancorabolinae ● (cf. III/E) and *Lobopleura* are not closely related. Therefore, a 2-segmented male P3 endopod in these other taxa is considered as convergent, as also found for other characters in different laophontoid and cletodid taxa.

W. *Probosciphontodes*

Composition: two species:
Probosciphontodes Fiers, 1988
  Probosciphontodes ptenopostica Fiers, 1988
  Probosciphontodes stellata Fiers, 1988 (**type species**)

Conroy-Dalton (2004) presented an exhaustive discussion on *Probosciphontodes*, providing seven autapomorphies for that taxon (Conroy-Dalton 2004, characters 1–7). Of these, character (5) is not considered here, owing to insufficient explanation ("maxillule without elements representing distal endite"). Characters 1–4, 6 and 7 are considered (Table 1, characters 129/130–133, 134 and 135, respectively), with character (1) divided into character 129–extreme lateral extension of the median expansion on cphth–and character 130–extreme lateral extension of the posterior expansion on cphth.

The extreme rostral elongation (Table 1, character 131) evolved as convergence also in *Calypsophontodes*, *Rostrophontodes* and some species of *Ancorabolina* (Gheerardyn and George 2010; Gheerardyn and Lee 2012; Lee and Huys 2019).

X. Cletodidae ● T. Scott, 1904

Composition: The Cletodidae● comprises the family "Cletodidae" T. Scott sensu Por (1986), which includes 25 genera (Walter and Boxshall 2019) and the *Ceratonotus*-group (cf. III/AA), previously assigned to the "Ancorabolinae".

As discussed in Chapter II, the development of the podogennontan first swimming leg (P1) and its subsequent deviations provide the main basis for the new phylogenetic concept presented here and, consequently, the reorganisation of the "Ancorabolidae". It is hypothesised that Cletodoidea (cf. III/B) split into two subordinated taxa, namely the Ancorabolidae ● (cf. III/C) and its supposed sister-group, the Cletodidae ●. The phylogenetic justification for the hypothesis of the Ancorabolidae ● and all its sub-ordinated clades/genera as well-characterised monophyla was given in sections C–W in Chapter III. The relationship between the family "Cletodidae" and the *Ceratonotus*-group forming a monophyletic taxon is discussed here. Primarily the cletodid ● type genus *Cletodes* and the *Ceratonotus*-group are considered, whilst the remaining Cletodidae ● play a role in a basal phylogenetic evaluation. This is due to the unclear relationships within the Cletodidae ●, which deserve a more detailed phylogenetic analysis, but which is beyond the scope of the current study.

The Cletodidae ● (Fig. 2, branch X) can be characterised by five unambiguous characters (Table 1, characters 136–140), four of which (133–139) relate to the P1 development. These four characters have been discussed in detail in Chapter II.

Character 140, tiny seta accompanying mxp claw lost: as discussed in III/C, the Laophontoidea retains the plesiomorphic condition of the presence of one long and one tiny seta accompanying the mxp claw. It was further proven that the sister-group of the here-reordered Cletodidae ●, i.e. the Ancorabolidae ●, lost the long seta (cf. III/C, character 42). The opposite occurred in the Cletodidae ●, with the tiny seta lost and the long seta retained. This assumed evolutionary pathway is supported by the presence of a long seta in species, such as *Cletodes meyerorum*, *Enhydrosoma curticauda* Boeck, 1872, *Neoacrenhydrosoma zhangi* Gee & Mu, 2000 and *Pseudechinopsyllus sindemarkae* George, 2006 (cf. Gee 1994; Gee and Mu 2000; George 2006b; George and Müller 2013). Within the Cletodidae ●, a tiny seta is present in, amongst others, *Ceratonotus*, *Cletodes* (part.), *Dendropsyllus* and *Enhydrosoma* (part.). However, this is considered to be the secondarily shortening of the long seta retained in the Cletodidae ● rather than the homologue short seta present in the Ancorabolidae ●. This assumption is justified by the observation of the seta gradually decreasing in length across some cletodid ● species (e.g. ranking between the longest and the smallest type: *Arthuricornua anendopodia* Conroy-Dalton, 2001, *Echinopsyllus nogueirae* Wandeness, George & Santos, 2009, *Polyascophorus monoceratus* George, Wandeness & Santos, 2013) (cf. Conroy-Dalton 2001; Wandeness et al. 2009; George et al. 2013). Therefore, the loss of the tiny mxp seta is regarded as autapomorphic for the Cletodidae ●.

Y. Cletodinae T. Scott, 1904, subfam. nov.

The Cletodidae ● splits into two taxa, regarded here as sister-groups: the Cletodinae subfam. nov., comprising the cletodid type genus *Cletodes* and the *Ceratonotus*-group and the remaining Cletodidae● (cf. III/Z). Unlike the Cletodidae ●, the characterisation of its subordinated taxon Cletodinae subfam. nov. (Fig. 2, branch Y) is somewhat ambiguous. All but one of the apomorphies, recognised for the Cletodinae subfam. nov., are present as convergences in other clades discussed here. As in the Ancorabolidae ● (cf. III/C), the Cletodinae subfam. nov. is characterised by characters 39–41, 44, 61 and 62 (Table 1). However, since the Cletodidae ● (cf. III/X) is well-justified by its exclusive development of the P1 (characters 138–141), a convergent development of characters 39–41, 44, 61 and 62 in the Cletodinae subfam. nov. must be assumed. These latter characters are not present in the groundpattern of the Cletodidae ●, having evolved in the sub-ordinated clades/taxa. Moreover, characters 39–41, 44, 61 and 62 treat the reduction of setae, which (a) is considered to be a simple deviation compared with the complex transformation of a prehensile P1 endopod into a non-prehensile one and (b) occurs quite frequently and independently amongst the Harpacticoida, assuming a synapomorphic status of these characters in the respective (subordinated) clades would inevitably lead to the assumption of a convergent development of the P1. This is refuted here, as discussed in Chapters II, III/C (characters 39–41 and 44) and III/E (characters 61 and 62).

One further unambiguous deviation is shared by all members of the Cletodinae subfam. nov.:

Character 141, female P5 baseoendopod with three setae (Table 1): Ancorabolidae ● could be characterised by a female P5 baseoendopod with four setae (cf. III/C, Table 1, character 44). Conversely, all *Cletodes* species and all members of the *Ceratonotus*-group are characterised by a female P5 baseoendopod carrying at most three setae, whilst the remaining Cletodidae ● retain five setae (cf. III/C, character 44). This deviation is, therefore, seen as autapomorphic for the Cletodinae subfam. nov.

Z. Remaining Cletodidae●

The remaining Cletodidae ● (Fig. 2, branch Z) enclose all cletodid ● genera except *Cletodes* and the *Ceratonotus*-group (cf. Results, family diagnosis of the Cletodidae ●).

The most recent list of nine potential autapomorphies of the supposed monophyletic Cletodidae was proposed by Gee (1998, characters i–ix). However, most of these are invalid, characters (i) to (v) being present in the whole Cletodoidea rather than restricted to the Cletodidae, i.e. (i) rostrum fused to the cephalothorax (cf. III/B; Table 1, character 22); (ii) 4–5-segmented female A1 (Table 1, character 23); (iii) A2 exopod bearing at most three setae (Table 1, character 27); (iv-a) unilobate md palp (Table 1, character 28) and (iv-b) unilobate mxl basis (Table 1, character 30); and (v) P1 exp-3 without inner setae, with two apical and two outer elements only (cf. Chapter II; Table 1, characters 8, 9 and 21). Similarly, characters (vi–ix), presented by Gee (1996), are pooled and mixed deviations that are all included in Table 1, characterising taxonomic clades at a higher level than the "Cletodidae". The phylogenetic status of the remaining Cletodidae ● is, therefore, set with a question mark in Table 2 and a phylogenetic characterisation of the Cletodidae ● is still pending, as stated above (cf. III/X).

AA. The *Ceratonotus*-group (C-g)

Composition: 29 species in 9 genera:
Arthuricornua Conroy-Dalton, 2001
  Arthuricornua anendopodia Conroy-Dalton, 2001 (**type species**)
Ceratonotus Sars, 1909
  Ceratonotus coineaui Soyer, 1964
  Ceratonotus concavus Conroy-Dalton, 2003
  Ceratonotus elongatus Gómez & Díaz, 2017
  Ceratonotus pectinatus Sars, 1909 (**type species**)
  Ceratonotus steiningeri George, 2006
  Ceratonotus tauroides George, 2006
  Ceratonotus thistlei Conroy-Dalton, 2003
  Ceratonotus vareschii George, 2006
Dendropsyllus Conroy-Dalton, 2003
  Dendropsyllus antarcticus (George and Schminke 1998), syn. *Ceratonotus antarcticus* George and Schminke 1998
  Dentropsyllus californensis Gómez & Díaz, 2017
  Dendropsyllus kimi Lee & Hus, 2019
  Dendropsyllus magellanicus (George & Schminke, 1998), syn. *Ceratonotus magellanicus* George & Schminke, 1998
  Dendropsyllus thomasi Conroy-Dalton, 2003 (**type species**)
Dimorphipodia Lee & Huys, 2019
  Dimorphipodia changi Lee & Huys, 2019 (**type species**)
Dorsiceratus Drzycimski, 1967
  Dorsiceratus dinah George & Plum, 2009
  Dorsiceratus octocornis Drzycimski, 1967 (**type species**)
  Dorsiceratus triarticulatus Coull, 1973
  Dorsiceratus ursulae George, 2006
  Dorsiceratus wilhelminae George & Plum, 2009
Echinopsyllus Sars, 1909
  Echinopsyllus brasiliensis Wandeness, George & Santos, 2009
  Echinopsyllus grohmannae Wandeness, George & Santos, 2009
  Echinopsyllus nogueirae Wandeness, George & Santos, 2009
  Echinopsyllus normani Sars, 1909 (**type species**)
Polyascophorus George, 1998
  Polyascophorus gorbunovi (Smirnov, 1946), syn. *Echinopsyllus gorbunovi* Smirnov, 1946, *Ceratonotus gorbunovi* Soyer, 1964
  Polyascophorus martinezi George, 1998 (**type species**)
  Polyascophorus monoceratus George, Wandeness & Santos, 2013
Pseudechinopsyllus George, 2006

Pseudechinopsyllus sindemarkae George, 2006 (**type species**)

Touphapleura Conroy-Dalton, 2001

Touphapleura schminkei (George, 1998) (**type species**), syn. *Polyascophorus schminkei* George, 1998

For the phylogenetic characterisation of the *Ceratonotus*-group (Fig. 2, branch AA), Conroy-Dalton (2001: 182) listed seven autapomorphies: (1) body somites virtually cylindrical; (2) P2–P4-bearing somites with paired backwardly-produced processes dorsally; (3) rostrum small, narrow; (4) first A1 segment elongate; (5) P1–P4 endopods reduced; setae/spines of terminal segment apical; (6) male P3 endopod 3-segmented, with apophysis on enp-2; (7) P5 endopod absorbed into basis, with at most two setae.

Characters 1–4 are adopted here; Conroy-Dalton's (2001) character (1) has been discussed in Chapter III/L, as a derived state in the R–A-clade (Table 1, character 80). It is hypothesised that this development is convergent for the *Ceratonotus*-group and the R–A-clade, as both clades are phylogenetically set widely apart and embedded in clearly-defined super-ordinated clades that can be characterised unambiguously by distinct autapomorphies.

Conroy-Dalton's (2001) character (2) is listed in Table 1 as:

Character 142, P2–P4-bearing body somites with cuticular, sensilla-bearing (latero-)dorsal processes: it was Conroy-Dalton (2001) who pointed towards a convergent evolution of the (latero-)dorsal cuticular body processes in both the *Ancorabolus*-lineage (= Ancorabolinae ●) and the *Ceratonotus*-group. She argued that both groups enclose taxa without such body processes, but that they had developed gradually within the respective groups. In the Ancorabolinae ●, dorsal cuticular processes are virtually absent in *Arthropsyllus* and *Uptionyx* Conroy-Dalton & Huys, 2000 (cf. Conroy-Dalton and Huys 2000), small in *Breviconia* Conroy-Dalton & Huys, 2000 and *Juxtaramia* Conroy-Dalton & Huys, 2000 (George 1998a; Conroy-Dalton and Huys 2000) and reach their maximum size in *Ancorabolus* Norman, 1903 (Conroy-Dalton and Huys 2000). In the *Ceratonotus*-group, *Touphapleura* Conroy-Dalton, 2001 shows small cuticular processes, whilst they gradually increase in size and complexity through *Arthuricornua*, *Pseudechinopsyllus*, *Dorsiceratus*, *Echinopsyllus*, *Polyascophorus* George, 1998 and *Ceratonotus* (George 1998b; Conroy-Dalton 2001, 2003a, b; George 2006b, c; Wandeness et al. 2009; George et al. 2013; Gómez and Díaz 2017). Conroy-Dalton (2001) concluded that the hypothetical ancestor of the Ancorabolinae ● lacked these processes, whereas those seen in the *Ceratonotus*-group evolved in their hypothetical ancestor, probably as observed in *Touphapleura* and this seems correct.

Conroy-Dalton's (2001) character (3) is included in Table 1 as:

Character 143, rostrum small, narrow: as discussed above (cf. III/B, character 22), the rostrum fused to the cphth in all representatives of the Cletodoidea, but is distinct in the Laophontoidea. Although fused, the rostrum of the Cletodoidea maintains its original triangular shape with a broad base and a tapering tip (e.g. *Algensiella*, *Cletodes*, *Enhydrosoma* (part.), *Laophontodes* (part.), *Limnocletodes*) (cf. Cottarelli and Baldari 1987; Gee 1998; Gómez 2003; George and Müller 2013; George and Gheerardyn 2015), whilst some exhibit a range of transformations, from a remarkable elongation (e.g. *Ancorabolina* (part.), *Lobopleura*, *Probosciphontodes*), sometimes combined with a bifurcation (*Ancorabolus*) (cf. Fiers 1988; Conroy-Dalton and Huys 2000; George 2001; Conroy-Dalton 2004; Gómez and Conroy-Dalton 2002; George and Tiltack 2009; Schulz and George 2010), a ventral bending and tapering (*Ancorabolina* (part.), *Calypsophontodes macropodia* and *Laophontodes gracilipes* (cf. Lang 1936; Gheerardyn and George 2010; Gheerardyn and Lee 2012) or an upward-bending (e.g. *Schizacron*, *Triathrix*) (cf. Gee and Huys 1996; Gee and Burgess 1997). In the *Ceratonotus*-group, however, a remarkable diminution of the rostrum is observable. In *Pseudechinopsyllus sindemarkae* and *Polyascophorus monoceratus*, it is narrowed, whilst in the remaining *Polyascophorus* species, as well as in *Dorsiceratus*, *Echinopsyllus*, *Touphapleura* and *Arthuricornua*, it gradually reduces in length, until it is completely absorbed into the cphth in *Ceratonotus* and *Dendropsyllus* (cf. George 1998b; 2006b, c; Conroy-Dalton 2001, 2003a, b; Wandeness et al. 2009; George et al. 2013). That rostral diminution is here considered autapomorphic for the *Ceratonotus*-group.

Conroy-Dalton's (2001) character (4) is listed in Table 1 as:

Character 144, A1 first segment elongate: as discussed in Chapter III/B, the Cletodoidea developed a characteristic (female) A1 (Table 1, characters 23–26), with subsequent additional deviations within the clade (Table 1, characters 58 and 98). However, in the Cletodidae ●, the A1 is generally compact and robust, as shown in Fig. 4A. Nonetheless, the hypothetical ancestor of the *Ceratonotus*-group is presumed to have an A1 with enlarged segments (Table 1, character 98), particularly the first segment (cf. George 1998b, 2006b, c; Conroy-Dalton 2001, 2003a, b; Wandeness et al. 2009; George et al. 2013), resulting in an elongate and slender shape. This is regarded as an autapomorphy of the *Ceratonotus*-group compared with the remaining Cletodidae ● and *Cletodes*. A similarly-shaped A1 is seen in *Ancorabolina* and the Ancorabolinae ● and is considered convergent.

Conroy-Dalton's (2001) remaining three characters (5–7) are not considered here. Characters (5) and (7) combine several different characters that have been at least partly considered in earlier discussion above. Character (6), as described by Conroy-Dalton (2001), is found in almost all representatives of the L–C-clade (cf. III/A) and even in other Podogennonta and, therefore, is interpreted here as a plesiomorphic state.

Two more apomorphies can be assigned to the *Ceratonotus*-group: character 59 (Table 1), transverse elongation of the P1 basis and character 100 (Table 1), loss of the A2 exopod. Both characters have been discussed above (cf. III/E and III/R, respectively) and it has been stated that they evolved as convergence in *Ancorabolina*, the Ancorabolinae● and the *Ceratonotus*-group. This is justified by the unambiguous monophyletic status of all three taxa by their respective autapomorphies. However, if compared with the supposed sister-group *Cletodes*, characters 59 and 100 are interpreted here as autapomorphies of the *Ceratonotus*-group, because they are missing in *Cletodes* and all the remaining Cletodidae ●.

Four additional derived characters can be defined for the *Ceratonotus*-group:

Character 145, P1 enp-2 element 3 lost: the inner apical seta on the P1 enp-2 (Fig. 3E, element 3-en) is lost in all members of the *Ceratonotus*-group. That seta is retained in the groundpattern of the remaining Cletodidae (cf. Gee 1994; Gee and Huys 1996; Gee and Burgess 1997) including *Cletodes* (cf. George and Müller 2013) and, thus, regarded as autapomorphy of the *Ceratonotus*-group.

Characters 146–148, remarkable elongation of P2–P4 bases: as discussed in detail for the A–P-clade (cf. III/F), its congeners are characterised by a transverse elongation of the P2–P4 bases, accompanied by a simultaneous shortening of the respective coxae (Table 1, characters 63 and 64). It is assumed that such elongation, which is also observed in the Ancorabolinae ● and at least already indicated in the Cletodidae ●, developed independently several times (cf. III/F). Within the latter taxon, the *Ceratonotus*-group is characterised by strongly-elongated P2–P4 bases that may equal the length of the whole exopod. Compared with the remaining Cletodidae ● and *Cletodes*, that elongation is interpreted as an autapomorphy for the *Ceratonotus*-group. Elongation to a similar extent is present in *Probosciphontodes* only (cf. Fiers 1988; Conroy-Dalton 2004) and must be seen as convergent evolution.

BB. *Cletodes*

Composition: According to Walter and Boxshall (2019), the taxon *Cletodes* encloses 34 species (**type species**: *C. limicola* Brady, 1872) plus one species (*C. exiguus* Sars, 1927) considered as *nomen nudum*.

The characterisation of a monophylum *Cletodes* (Fig. 2, branch Z) causes similar problems as described above for *Laophontodes* (cf. III/O). The most recent phylogenetic discussion of the genus, provided by Gee (2001: 41), concluded that *Cletodes* "…as presently constituted, is ill-defined…". Gee (2001) named two derived characters potentially justifying a monophyletic status of the genus: (a) the small, 1-segmented A2 exopod bearing one seta and (b) P3 and P4 exp-3 being elongate and carrying two outer spines and two apical setae.

A reduced, at most knob-like, 1-segmented A2 exopod (Table 1, character 39) carrying only one seta (Table 1, character 40) has been hypothesised as autapomorphy for Ancorabolidae ● (cf. III/C) and, as a convergent development, also for the groundpattern of Cletodinae subfam. nov. (cf. III/Y). Thus, Gee's (2001) character (a) cannot be maintained as autapomorphy of *Cletodes*. Similarly character (b), which is–including the P2–listed as character 62 in Table 1, has been discussed in detail in Chapter III/E as an autapomorphy of the Ancorabolinae ●. Moreover, it evolved as convergence in the Cletodinae subfam. nov. (cf. III/Y) and, therefore, cannot be autapomorphic for *Cletodes*.

Nonetheless, *Cletodes* may be characterised by 2 autapomorphies referring to the shape of the apical elements of P1 exp-3:

Characters 149, 150, loss of geniculation of setae VI and VIII on P1 exp-3: in the groundpattern of the remaining Cletodidae ● (cf. *Echinocletodes voightae* George & Müller, 2013) (George and Müller 2013), as well as in the *Ceratonotus*-group, the geniculate setae VI and VII on the third exopodal segment of P1 are retained. As shown in Chapter II, the development of geniculation of these elements has been hypothesised as apomorphies in the podogennontan P1 groundpattern by Willen (2000) and Seifried (2003). In contrast, all *Cletodes* species present these setae without geniculation. As it would be quite implausible to assume that only *Cletodes*, as a derived member of Podogennonta, retained the pre-podogennontan state, questioning Willen's (2000) and Seifried's (2003) hypothesis of the podogennontan P1 groundpattern, it is most likely that, in *Cletodes*, both setae VI and VII subsequently lost this geniculation. Consequently, characters 149 and 150 are seen as an autapomorphy of a monophylum *Cletodes*.

CC. The status of *Patagoniaella* Pallares, 1968

Composition: monotypic, *Patagoniaella vervoorti* Pallares, 1968 (**type species**)

When Pallares (1968) described *Patagoniaella vervoorti*, she assigned that species to the "Laophontodinae", based on the absence of a transversely-elongated P1 basis and the presence of three outer spines on P2–P4 exp-3. However, Pallares' (1968) description of *P. vervoorti* is of rather poor quality and partly contradictory, both in the text and in the illustrations. For instance, in the generic diagnosis, Pallares (1968: 462) described the female A1 as 4-segmented ("A1 de la hembra lleva cuatro artejos"), but in the species description (both text and illustration), the female A1 is described as 5-segmented

(Pallares 1968: 465, Lámina I.1). Unfortunately neither the type material nor any other material of that species is available and re-examination could not be done. Consequently, the discussion here must be based on Pallares' (1968) paper.

A comparison of *P. vervoorti* with the Laophontoidea, Ancorabolidae ● and Cletodidae ●, based on Table 1 characters, does suggest its affiliation to the L–C-clade (cf. III/A), owing to the number of shared characters (Table 1, characters 12–19). Only character 18 is not exhibited by *P. vervoorti*. However, this reflects the species description–it cannot be discerned if a slender seta accompanies the two spines at the distal edge of the A2 (Pallares 1968: 465, Lámina 1.4)–rather than a definite character state.

The allocation of *P. vervoorti* to the Cletodoidea (cf. III/B) also seems unproblematic, as *P. vervoorti* shares the derived states of characters 20–38 (cf. Table 1). Beyond this taxonomic level, however, the assignment of *P. vervoorti* to any of the sub-ordinated clades is uncertain. Its placement in the Ancorabolidae ● (cf. III/C), which includes the "Laophontodinae", is problematic, because the shape of the P1 (Pallares 1968: 465, Lámina 1.10) is most similar to that of the Cletodidae ●: it is not prehensile and the enp-2 is elongated, reaching almost the length of enp-1 (cf. Table 1, characters 137, 138). Lee and Huys (2019: 362) assumed an affinity of *Patagoniaella* with the "Cletodidae" because of morphological similarities, such as the short, 5-segmented female A1, the moderate transverse P1–P4 basis elongation and the segmentation/shape of the P1–P4 endopods and the shape of the P5. Additionally, the authors supposed that the setae of the P1 as drawn by Pallares (1968) may end in brush-like tips, which are present in some "cletodid" genera, being of circumstantial evidence for a relationship between *Patagoniaella* and the "Cletodidae". Therefore, the authors provisionally assigned *Patagoniaella* to the "Cletodidae". I do not agree with these conclusions. Firstly, in her written description, Pallares (1968: 466) described the setal tips of the P1 as ending in hooklets ("presentando todas terminación en ganchillo"), but not as brush-like. Moreover, *P. vervoorti* also differs from the Cletodidae ● with the P1 basis not transversely, but longitudinally elongated, which, instead, corresponds to a deviation hypothesised here as autapomorphic for the laophontodin ● C–P-clade (cf. III/H; Table 1, character 70). Such heterogeneity can be observed throughout the characters listed in Table 1; *P. vervoorti* presents a mixture of characters that may be attributed to the Ancorabolidae ● (or to particular sub-ordinated clades within) or to the Cletodidae ●. This is furthermore complicated by the quality of the illustrations provided by Pallares (1968), which impede any detailed comparison of character states and the written description, which is sometimes vague and imprecise. Thus, despite superficial appearances, the allocation of *P. vervoorti* to the Cletodoidea is complex.

Nonetheless, two features described for *P. vervoorti* necessitate its exclusion from both Cletodoidea and the L–C-clade:

A. Mxl with two setae on the coxal epipodite: Pallares (1968: 464) explicitly described the coxal epipodite armed with two setae ("epipodito representado por 2 Sd"). However, in the groundpattern of the Podogennonta, the coxa is characterised by the presence of only one single epipodal seta (Willen 2000; Seifried 2003), whilst two setae are found in the Aegisthidae (Seifried 2003). Thus, the presence of two epipodal setae on the mxl coxa in *Patagoniaella* should immediately exclude that taxon from the Podogennonta.
B. The body shape: The habitus of *Patagoniaella vervoorti* is cyclopiform, with a broad prosoma and a significantly narrower urosoma (Pallares 1968: 464). This does not correspond with the L–C-clade, which is characterised by a slender, more or less fusiform or cylindrical habitus with an inconspicuous or even the absence of a demarcation between pro- and urosoma (cf. Boxshall and Halsey 2004). The body shape of *P. vervoorti* is found in other Podogennonta, but it is the only "ancorabolid" species showing a cyclopiform body shape. Thus, this body shape may be an apomorphy of the species, particularly considering Seifried's (2003) hypothesis that, in the groundpattern of Harpacticoida ("Oligoarthra"), no difference between pro- and urosoma is expressed. However, the combination of characters (A) and (B) further suggests that *P. vervoorti* should be excluded from the L–C-clade.

Consequently, *Patagoniaella vervoorti* is herewith excluded from the Laophontoidea–Cletodoidea-clade and placed in Harpacticoida as *species inquirenda* until specimens of that species can be studied to provide a detailed re-description and to perform a subsequent phylogenetic evaluation.

Conclusions

The exhaustive phylogenetic analysis presented here showed that the previously-recognised "Ancorabolidae" constitutes a polyphylum. Comparison of the Laophontoidea, the "Ancorabolidae" and the "Cletodidae" revealed that, in their current composition, both "ancorabolid" subfamilies, i.e. the "Ancorabolinae" and the "Laophontodinae", are artificial constructs. Using the podogennontan P1 development as a starting point, with all further characters being sub-ordinated, it must be concluded that both "Ancorabolidae" and "Cletodidae" have to be restructured. As a result:

1. The *Ancorabolus*-lineage is given full subfamiliar as Ancorabolinae ● and united with Laophontodinae ● to Ancorabolidae ●;
2. Adopting the inclusion of *Ancorabolina*, suggested by Lee and Huys (2019) and excluding *Patagoniaella*, the monophyletic status of the Laophontodinae ● is confirmed;

3. The *Ceratonotus*-group is included into the "Cletodidae" constituting the Cletodidae ●;
4. Within the Cletodidae ●, the *Ceratonotus*-group is the sister-group of *Cletodes*; both taxa are united as Cletodinae subfam. nov.;
5. The Ancorabolidae ● and Cletodidae ● are hypothesised as sister-groups forming the suprafamilial monophylum Cletodoidea;
6. The Cletodoidea is the sister-group of the Laophontoidea;
7. A monophyletic Laophontoidea–Cletodoidea-clade forms part of a podogennontan branch named as "taxon II" in Willen (2000).

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