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Phylogeny of the Thalestridimorpha Lang, 1944
(Crustacea, Copepoda)

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"Phylogenetic Systematics also aims at contributing to an understanding of the phenomenon of life, to the extent that the nature of life is amenable to scientific investigation"

Willi Hennig (1966)

Contents

1. Introduction

Copepoda are often called the "insects of the sea" considering their body size, abundance, and diversity. They occur in all possible aquatic habitats, from the deep sea to higher mountain ranges (compare Huys & Boxshall, 1991) and play a major role in many ecosystems, as primary consumers in the marine and freshwater plankton, as parasites on a wide range of organisms and as a factor in the remineralisation processes of the marine sediment. Huys & Boxshall quote Sir Alister Hardy (1970, after Huys & Boxshall, 1991) who states, that copepods are the most abundant Metazoa on earth, as far as the number of individuals is concerned. Humes (1994) gives an overview of the estimation of species and individual numbers in general and of the copepods associated with marine invertebrates in particular. The Harpacticoida Sars, 1903 are a subgroup of the Copepoda, and occur predominantly in the marine benthos where they are in the meiofauna communities the second most abundant group as regards to species and individuals after the nematodes. Most species are free-living and marine, but several species also live in freshwater and subterranean waters as well as in association with other organisms as ectoparasites and commensals. Up to now more than 3,000 species have been described. The great majority of species, however, is assumed to be still unknown, mainly because large regions of the earth (e.g. polar regions, Pacific, deep sea) have not yet been extensively sampled. Humes (1994) estimates that not even 50% of all existing species have been registered scientifically.

The basis of all taxonomic and phylogenetic research on harpacticoid copepods until today is the "Monographie der Harpacticiden" by Karl Lang (1948). Besides hypotheses of phylogenetic relationships on the traditional genus, family and suprafamily levels, diagnoses, short descriptions, and keys for all taxonomic levels, even for species, are given (chapters 3 + 8). Chapters on distribution, biology, and anatomy are also included. Lang developed his system of the Harpacticoida, before Hennig (1966, 1982) introduced the method of phylogenetic systematics. Since Lang app. 2,000 new species have been described and more than 300 new supraspecific taxa have been established. Therefore a revision of his system has become necessary. On family and suprafamily level some revisions have already been made, e.g. of the Cletodidae by Por, 1986, the Cylindropsyllidae by Martinez & Moura, 1994, the Miraciidae by Huys & Böttger-Schnack, 1994, the Cancrincolidae by Fiers, 1990. Especially Huys has recently erected many new genera and families and proposed phylogenetic relationships on suprafamily level (Huys, 1988, Cervinoidea, 1990, Laophontoidea, 1990, revision of the Rhynchothalestridae). However, a comprehensive revision of the higher taxa, to which also the Thalestridimorpha belong, has not yet been undertaken.

The revision of the Thalestridimorpha is the first of 3 projects in the AG Zooystematik und Morphologie aiming at a complete revision of Lang's system according to the method of phylogenetic systematics as outlined by Hennig. The significance of this method is briefly discussed in the following.

Systematics, as the oldest biological science, has the major task of managing and classifying the immense species diversity on earth. However, controverse discussions about the method and the criteria of a biological classification system have always existed. A summary of earlier opinions is e.g. given by Hennig (1966, 1982, reprint in German language). Hennig introduced a classification system which is based on the phylogenetic relationships of the organisms. Since the theory of evolution established by Darwin it is known, that organisms are related by phylogeny. On the species level, this relation follows the strict rules of a hierarchy according to Woodger (after Hennig, 1966), contrary to the genealogical relationships between individuals. The concept of species as isolated reproductive communities and splitting of species as the primary process of phylogeny are closely connected. Proceeding from species splitting after the rules of a hierarchy according to Woodger, a clear defined terminology and rules for the procedure of reconstruction of phylogenetic relations between organisms and groups of organisms can be derived. Hennig named his new method "Phylogenetic Systematics". He distinguished very clearly between typological systems, which are based on arbitrary criteria and a phylogenetic system, which tries to reconstruct the real historical processes of phylogeny.

Starting from Hennig's methodology efforts have recently been made to avoid the "evolutionary framework" and to pursue systematics and cladistics with "objective" and "unprejudiced" methods instead: "[...] we will begin with Hennig's explanation, but then slowly move towards the modern cladistic view, which dispenses with the need to rely on any particular theory of evolution for the analysis of systematics" (Kitching et al., 1998, p. 1). The question of whether this procedure is not in fact a step back and without a scientific hypothesis, which explains the relations between organisms à priori (such a hypothesis is the theory of evolution), again generates similar problems as in typological times would be

worth discussing but is beyond the scope of this introduction. Hennig (1966, 1982) has extensively discussed typological concepts and rejected them in favour of phylogenetic systematics, which he considered a definite progress, *exactly because* of its roots in evolutionary theory.

The general perception that knowledge of phylogenetic processes is essential for the explanation of many biological phenomena has in the meantime also been accepted by other biological disciplines outside "pure" systematics. Phylogenetic cladograms play e.g. a role integrated in the quantification of "biodiversity" (Gaston, 1996, Faith, 1994, Warwick & Clarke, 1998). Maddison & Maddison (1992) describe several fictive examples, in which knowledge of the phylogenetic relationships of the respective organisms adds a new dimension to the interpretation of data during examination of various different biological phenomenona.

For the reconstruction of phylogeny the method of Phylogenetic Systematics offers a logical background for an argumentation on the basis of the theory of evolution (in the wider sense of Ax, 1984), with a clearly defined terminology and a precise and logical procedure. Therefore it is preferred in the present study.

Ideally all data available on the organisms under consideration should be included into the phylogenetic analysis, starting from physiology, morphology, developmental biology, etc. For Harpacticoida the adult morphology offers the broadest database available for comparative analysis and therefore it will be considered almost exclusively in the following. More detailed comments on the method can be found in chapter 2. Prior to the actual analysis, results of copepod research are discussed, which contribute additional criteria for the polarisation of characters (chapter 2). A short overview is given on existing systems of Harpacticoida in respect to Thalestridimorpha (chapter 3). The list of characters and the resulting new phylogenetic diagram are presented in chapter 4. Chapter 6 contains an extensive discussion and deduction of groundpattern characters on the different systematic levels. In chapter 7 the topology of the diagram, i.e. the phylogenetic relationships of taxa and the establishment of superordinated higher taxa are discussed in the light of the new system. The relationships within the higher taxon Podogennonta are elaborated (chapter 7.2) as far as possible, and an outlook on the Harpacticoida altogether is given in the light of the new results (chapter 7.3). Further chapters discuss Lang's system (chapter 8) as well as the recent literature (chapter 9) and contributions of postembryonic development (chapter 10).

2. Material and methods

2.1 List of examined species

Abbreviations: m: male, f: female, mm, ff: several males and females, respectively., HT, AT, PT; LT: holotype, allotype, paratype, lectotype, diss.: dissected, Cop.: copepodid stage not further determined, CV: copepodid V.

Parastenheliidae

Parastenhelia spec.	m diss.	Fiji Cam1
Parastenhelia spec.	f diss.	Andros
Parastenhelia spec.	m diss.	Andros
Parastenhelia spec.	m + f	Greece
Parastenhelia megarostrum	Cop, mm + ff,	
	+ f diss.	New Zealand
Karllangia spec.	m diss.	PNG M4

Dactylopusiidae

Dactylopusia spec.	4 ff	Fiji CAM-1
Dactylopusia spec.	m	WBM Seattle
Dactylopusia spec.	f	Chile 7
Dactylopusia spec.	m diss.	Fiji, VL9, Coral Coast
Dactylopusia spec.	CV m diss.	BM Seattle
Dactylopusia spec.	m diss.	PNG M12
Dactylopusia spec.	CVm, 2 CVf	WBM Seattle
Dactylopusia spec.	f diss.	BM Seattle
Dactylopusia spec.	m	AM Seattle
Diarthrodes spec.	m	Fiji CAM-1
Diarthrodes spec.	f	Chile 10
Diarthrodes spec.	f + m, 2 Cop	PNG M11
Paradactylopodia spec.	f diss.	Ant 528/AT
Paradactylopodia spec.	f diss.	Ant 528/AT
Paradactylopodia spec.	ff + m, m diss.	King George Isl, E2/4, 57+58
Paradactylopodia spec.	f	Ant 36

Paradactylopodia brevicornis	f	Chile 1
Paradactylopodia spec.	f diss.	MC 282 Peru trench
Paradactylopdia serrata	m diss., f+m	Museum Stockholm
Paradactylopodia spec.	f	Ant 528/AT
Paradactylopodia spec.	f diss.	Ant 528/AT
Paradactylopodia spec.	f diss.	Ant 33
Paradactylopodia spec.	m diss.	Ant 32
Paradactylopodia spec.	m	Fiji CAM1
Paradactylopodia spec.	f	BU Seattle
Dactylopodella incerta	f diss.	Fiji CAM1
	f diss.	Fiji CAM1
Dactylopusiidae gen. spec.	2 mm diss.	Ant 10/585
Dactylopusiidae gen. spec.	f	Ant 10/585

Rhynchothalestridae

Ambunguipes spec.	f	Sl36 Sri Lanka
Ambunguipes spec.	f diss.	Fiji, 9VL Coral Coast
Ambunguipes spec.	m diss.	SL36 Sri Lanka
Ambunguipes spec.	f diss.	Argentina
Rhynchothalestris spec.	f	Ant 32
Rhynchothalestris tenuicornis	f HT	Hancock Museum

Diosaccidae

Diosaccinae

Amonardia spec.	f	Chile 1
Amonardia spec.	f	AL Seattle
Amonardia spec.	f diss.	AL Seattle
Amonardia spec.	m diss.	AM Seattle
Amonardia spec.	f diss.	Greece
Amphiascoides spec.	2	Andros
Amphiascoides spec.	2	Fiji

Amphiascoides spec.	3	Joao Pessoa Brasil, April 1995, Gisela Moura.
Amphiascoides spec.	m diss. mm + ff	pet shop in Oldenburg
Amphiascoides spec.	m diss.	PNG M12
Amphiascoides spec.n.	m, f	Ant 561
Amphiascopsis spec.	f diss.	PNG M11
Amphiascopsis spec.	m diss.	AM Seattle
Amphiascopsis spec.	m diss.	Greece
Amphiascopsis spec. 1	m + f	SL36 Sri Lanka
Amphiascopsis spec. 2	m (+f?)	SL36 Sri Lanka
Amphiascus 1	f	MC 361 Peru trench
Amphiascus 2	m	MC 276 Peru trench
Amphiascus parvus	m+f diss. copepodids and adults	culture 1
Amphiascus profundus ?	f	MC 292 Peru trench
Amphiascus propinquus	m+f diss. copepodids and adults	culture 2
Amphiascus spec.	f	MC 279 Peru trench
Amphiascus spec.	f	MC 279 Peru trench
Amphiascus spec.	f	MC 282 Peru trench
Amphiascus spec.	f diss.	Ant 6
Amphiascus spec.	f diss.	Fiji CAM1
Amphiascus spec.	f diss.	Fiji CAM1
Amphiascus spec.	m	MC 279 Peru trench
Amphiascus spec.	m	MC 279 Peru trench
Amphiascus spec.	m diss.	MC 295 Peru trench
Amphiascus spec.	m diss.	Fiji CAM1
Amphiascus spec. ?	m diss.	PNG M4
Amphiascus spec. 1	f diss.	Ant 5
Amphiascus spec. 2	f diss.	Ant 33
Amphiascus spec. 3	f diss.	Ant 36

Amphiascus spec. 4	f diss.	Ant 6
Amphiascus spec. 58	m, f	Ant 501 3.11.86 Weddell Sea
Bulbamphiascus spec.	m diss.	Fiji CAM1
Diosaccus spec.	f diss.	SL36 Sri Lanka
Diosaccus spec.	f diss.	WBM Seattle
Metamphiascopsis spec.	m diss.	Greece
Paramphiascella fulvofasciata	m+f diss. copepodids and adults	culture 3
Paramphiascella spec.	m	Andros
Paramphiascopsis ekmani	m diss.	AM Seattle
Paramphiascopsis facialis	m, f	Ant 561, Ant 6
Paramphiascopsis glacialis	m+f	Ant 561
Paramphiascopsis longirostris	m+f diss. copepodids and adults	culture 4
Paramphiascopsis spec.	m	Ant 528
Paramphiascopsis spec.	CV	MC 279 Peru trench
Paramphiascopsis spec.	m diss.	PNG M12
Pseudodiosaccopsis spec.	m diss.	PNG M12
Robertgurneya "similis"	m diss.	Greece
Robertgurneya similis	m + f	Sardinia
Robertgurneya similis	m diss.	Spane, Valencia (1992/93) culture
Robertgurneya spec.	m diss.	PNG M4
Robertgurneya spec.	m+f diss.	Fiji CAM1
Robertgurneya spec.	f diss.	PNG M4
Robertsonia spec.	2 ff	PNG M11
Robertsonia spec.	f diss.	Andros
Robertsonia spec.	f diss.	PNG M12
Robertsonia spec.	m diss.	Bahamas (August 1993, J. Dürbaum)
Robertsonia spec.	m diss.	PNG M11

Schizopera spec.	m + f	Peru, San Bartolo
Schizopera spec.	m + f	Venezuela, Bahia de Plata
Typhlamphiascus spec.	m + f diss.	Bahamas, Andros (August 1993, J. Dürbaum)
Typhlamphiascus spec.	m diss.	Fiji CAM 1
Typhlamphiascus spec.	m diss.	PNG M4
Typhlamphiascus spec.	m diss.	PNG M12
Typhlamphiascus spec.	m+f diss.	Fiji CAM1
Diosaccinae gen.?	f diss.	PNG M12
Diosaccinae gen.?	m diss.	PNG M12
Diosaccinae gen.?	m diss.	PNG M12
Stenheliinae		
Melima spec. n	2 ff	PNG M12
Pseudostenhelia wellsi	f HT, m AT, PT	Mexico 1
St. asetosa	ff PT	USNM cat. no. 169877
St. bermudensis	mm + ff PT	USNM cat. no. 126134
Stenhelia infiernensis	f HT, m AT, PT	Mexico 2
Stenhelia spec. 1	f, m	PNG M11
Stenhelia spec. 2	mm + ff + copepodids	PNG M11
Stenhelia paradivergens	f HT, m AT, PT	Mexico 2
Stenhelia palustris	m	Spiekeroog (North Sea)
Stenhelia peniculata	f	BU Seattle
Stenhelia spec.	CV	Spiekeroog (North Sea)
Stenhelia spec. (cf. *St. bifida*)	f+m diss. mm + ff	South Carolina, USA
Stenhelia spec.	m diss. f + Cop	Bahamas, Andros (August 1993, J. Dürbaum)
Thalestridae		
Eudactylopusiinae		
Eudactylopus spec. 1	m+f	SL36 Sri Lanka

Eudactylopus spec. 2	m diss., f	SL36 Sri Lanka
Eudactylopus spec. 3	m diss.	SL36 Sri Lanka
Eudactylopus spec. 4	f diss.	SL36 Sri Lanka
Eudactylopus spec.	f diss. (damaged) f (frozen)	Maledives, culture
Thalestrinae		
Parathalestris harpactoides	m+f diss. mm+ff,	Helgoland
Parathalestris spec.	m+f diss. copepodids	Concarneau, culture 1
Phyllothalestris spec.	m+f, f diss.	SL36 Sri Lanka
Thalestris longimana	mm + ff, f diss.	Helgoland
	m diss.	red algae, 16.4.86
	Copepodid stages and nauplii	
Thalestris sordida	m	Ant 6
	f	Ant 10/585
	HT	Hancock Museum, Newcastle upon Tyne, UK
	m	14/224 25.1.1989 Weddell Sea
	m	Ant 5
Thalestris gibba	f diss., m diss.	Spitzbergen
Paramenophia chilensis	f diss.	Chile 1
Thalestridae gen. spec.	f diss. (damaged)	Ant 36
Pseudotachidiidae		
Paranannopinae		
Paranannopinae gen. 1, spec. 1.	m diss.	Ant 528/AT
	m	Ant 10
Danielssenia spec.	f diss.	Ant 545
Paradanielssenia spec.	m	Ant 34
Paranannopinae spec. 1	f diss.	Ant 2

Parananopinae spec. 2	mm	AGT 10/560
Parananopus spec.	m + f	Ant V/3 285m D1 12.12.86
		no further declarations

Pseudomesochrinae

Pseudomesochra ? spec.	f	MC 355 1-2 cm Peru trench
Pseudomesochra spec. 1		see Willen, 1996
spec. 2		-“-
Pseudomesochra meridianensis		-“-
Pseudomesochra gertwilleni		-“-
Pseudomesochra spec.		-“-
Pseudomesochra laptevensis		-“-
Pseudomesochra spec. 1		-“-
Pseudomesochra spec. 2		-“-
"*Pseudomesochra gemina*", male		-“-

„Pseudotachidiinae“

Idomene spec.	f	Ant 6
Idomene spec.	f+m	Ant 10/585
Idomene spec.	f	Ant 528/AT
Idomene spec.	f	Ant 230
Idomene spec.	Cop	Ant 571
Idomene spec.	f	Ant 32
Idomene spec.	m	Ant 36
Idomene spec.	mm	Chile 13, Chile 12
Idomene spec.	f	Ant 10/585

„*Pseudotachidius*-lineage“

Pseudotachidiidae gen. 1 spec. 1	m	Ant 1
	f	Ant 36
	f	Ant 10/585
	f	Ant 36
Pseudotachidiidae gen. 1 spec. 2	m diss.	Ant 36

	m diss.	Ant 10/585
	2 mm	Ant 9
Pseudotachidiidae gen. 1 spec. 3	f diss.	Ant 34
Pseudotachidiidae gen. 1 spec. 4	m	Ant 5
Pseudotachidiidae gen. 1 spec. 5	m	Ant 10/585
Pseudotachidiidae gen. 1 spec.	f diss.	Ant 561
Pseudotachidiidae gen. 2 spec. 1	m	Ant 561
	f	Ant 9
	mm	Ant 528
	m, f, CIV	Ant 6
Pseudotachidiidae gen. 2 spec. 2	f diss.	Ant 1
Pseudotachidiidae gen. 2 spec. 3	f diss.	Ant 34
Pseudotachidiidae gen. 2 spec.	f	Ant 528
Pseudotachidius spec. 1	f diss.	AGT 566
Pseudotachidius spec. 2	f diss.	Ant 528
Pseudotachidius spec. 3	f diss.	Ant 528
Pseudotachidius spec. 4	f diss.	labelling illegible, Weddell Sea
Pseudotachidius spec.	f	MC 357 Peru trench
Pseudotachidius jubanyensis	f HT, m AT,	
	m PT diss.	King George Isl. E 1/3 45+46
Pseudotachidius "similis"	f diss.	MC 347 Peru trench
Pseudotachidiidae gen. spec.	m diss.	Ant 36
Pseudotachididae gen. spec.	f	Ant 10

Tisbidae

gen. spec?	f + m	Ant 5
Idyanthe spec.	f	3-285 D1 12.12.86 Weddell Sea
Idyanthe spec.	f	MC 362 Peru trench
Idyanthe spec.	f?	Ant 36
Idyanthinae gen. spec.	f diss.	Ant 10
Idyella spec.	f	3-285 D1 12.12.86 Weddell Sea

Idyella spec.	f	Ant 20
Idyella spec.	f	Ant 34
Idyella spec.	f	Ant 560
Idyella spec.	f diss.	Ant 528
Idyella spec.	f diss.	Ant 528
Idyella spec.	f diss.	Ant 32
Idyella spec.	m	Ant 234
Idyella spec.	m	MC 348 Peru trench
Idyella u.a.	f	Ant 561
Idyellopsis spec.	m diss.	King George Isl.,E2/1 12+13
Marsteinia spec. (Marsteiniidae)	f	MC 348 Peru trench
Scutellidium spec.	m	BU Seattle
Scutellidium spec.	m	BU Seattle
Scutellidium spec.	m diss.	WBM Seattle
Tachidiopsis	f diss.	Ant 560
Tachidiopsis spec		MC 364 Peru trench
Tachidiopsis spec.	f	Ant 528/AT
Tachidiopsis spec.	m	MC 357 Peru trench
Tachidiopsis spec.	m diss.	Ant 528/AT
Tisbe holothuriae	f	course preparation
Tisbe holothuriae	m + f diss.	Dürbaum, culture
Tisbe spec.	f	BU Seattle
Tisbe spec.	f diss.	BU Seattle
Tisbe spec.	m diss.	Ant 32
Tisbe spec.	mm	Ant 36
Tisbidae gen.spec.	CIV	Ant 560
Zosime cf. mediterranea	f diss.	Ant 557
Zosime spec.	f diss.	Ant 545
Tegastidae		
Tegastes spec.	f diss.	Ant 528/AT

Huntemanniidae		
gen.spec.	f	MC 347 Peru trench
Cerviniidae		
gen. spec.	m + f	MC 375 Peru trench
Harpacticidae		
Harpacticidae gen. spec.	2 mm	Ant 5
Harpacticidae gen. spec.	f	Ant 10/585
Harpacticidae gen. spec.	m	Ant 6
Harpacticidae gen. spec.	m	Ant 258
Harpacticus spec.	f diss.	BM Seattle
Harpacticus spec.	m + CI	WBM Seattle
Harpacticus uniremis	m diss.	AM Seattle
Perissocope spec.	m diss.	Ant 561
Perissocope spec.	m diss.	Ant 32
Tigriopus brevicornis	CV m diss.	Concarneau, culture 2
	f diss.	culture 2
	m diss.	Concarneau
	m diss.	Spiekeroog (North Sea)
Tigriopus spec.	Cops	Concarneau, culture 2
Tigriopus? spec:		Chile 9
Zaus spinatus	2 praecopulae	Helgoland
	Praecopula	Helgoland
Tachidiidae		
Tachidius discipes	m diss.	Spiekeroog (North Sea)
Chappuisiidae		
Chappuisius inopinus	ff+mm	groundwater, Aschaffenburg, Karlstein
Ameiridae		
Ameira spec.	f diss.	Ant 32
	Weddell Sea	

Ameiropsis mucronatus	m	Ant 561
Ameiropsis spec. 1	f	Ant 561
Ameiropsis spec. 2	f diss.	Ant 32
gen. spec.	f diss.	Ant 545
gen. spec.	f	Ant 514
gen. spec.	m	MC 361 Peru trench
gen. spec.	f	MC 357 Peru trench
Harpacticoida fam. 1	ff + mm	Weddell Sea, various sites
Protolatiremus sakaguchii	5 ff, 2 mm, diss.	Hokkaido, Japan, Daikokujima Islet, sandy sediment, type material of Itô, 1974

2.2 Further notes on the localities

AGT 566: Weddell Sea, Polarstern expedition, station 566.

Andros: Johannes Dürbaum, August 1993.

Ant 1: Weddell Sea, Polarstern expedition AntV/3, S 73°16,3′, W 21°5,3′, stat. 10-566, 541m depth, AGT, 4.11.1986.

Ant 5: Weddell Sea, Polarstern expedition AntV/3, S 72°53,3′, W 19 ° 30,2′, stat. 10-520, 481m, AGT, 20.10.1986.
Ant 6: Weddell Sea, Polarstern expedition AntV/3, S 74°02,5′, W 24 ° 22,0′, stat. 10-553, 376m depth, AT, 31.10.1986.

Ant 10/585: Weddell Sea, Polarstern expedition AntV/3, S 76°00,9′, W 28°15,9′, stat. 10-585, AGT, 323m depth, 11.11.1986.

Ant 10: Weddell Sea, Polarstern expedition AntV/3, S 75°50,9′, W 27°10,6′, stat. 10-589, 320m depth, AGT, 12.11.1986.

Ant 20: Weddell Sea, Polarstern expedition Ant VII, S 75°07,1′,W 27 ° 59,5′, stat. 14-241, 462m depth, AGT, 1.2.1989.

Ant 32: Weddell Sea, Polarstern expedition AntV/3, S 74°6,09′,W 24°39,73′, stat. 10-539, 541m depth, BG, 25.10.1986.

Ant 33: Weddell Sea, Polarstern expedition AntV/3, S 72°02,0′, W 15°26,5′, stat. AGT 672, 432m depth, 26.11.1986.

Ant 34: Weddell Sea, Polarstern expedition Ant V/3, S 73°33,0′, W 21°50,7′, stat. 10-594, 467-445m depth, ground trawl, 15.11.1986.

Ant 36: Weddell Sea, Polarstern expedition AntV/3, S 73°55,8′, W 23°04,0′, stat. 10-592, 228-235m, ground trawl, 14.11.1986.

Ant 224: Weddell Sea, Polarstern expedition, station 14/224, 25.1.1989.
Ant 230: Weddell Sea, Polarstern expedition AntVII, 75°14,2′S, 026°,59,4′W, stat. AntVII, AGT, 270m depth, 30.1.89.

Ant 258: Weddell Sea, Polarstern expedition Ant VII, 74°41,0′S, 029°28,2′W, stat. 258, 500m depth, multicorer, 9.2.1989.

Ant 514: Weddell Sea, Polarstern expedition AntV/3, 721°40,7′S, 020°05,5′W, stat. 514, 200-500m depth, 18.10.1986.

Ant 528/AT: Weddell Sea, Polarstern expedition AntV/3, S 72°28,0′, W 7°23,5′, 300m, AT, 22.10.1986.

Ant 545: Weddell Sea, Polarstern expedition, Ant V/3, 75o37,6′S, 027o50,1′W, 1. BG, no information about the depth, stat. 10/545, 28.10.86.

Ant 557: Weddell Sea, Polarstern expedition Ant V/3, 73°57,1′S, 024°05,3′W, stat. 557, BG, 625m depth, 1.11.1986.

Ant 560: Weddell Sea, Polarstern expedition Ant VII, 73°57,1′S, 024°49,6′W, stat. 560, 200-500m depth, 2.11.1986.

Ant 561: Weddell Sea, Polarstern expedition Ant V/3, 72°52,5′S, 019°30,2′W, 430m depth, AGT, 3.11.1986.

Ant 571: Weddell Sea, Polarstern expedition AntV/3, S 73°16,0′, W 20°28,3′, stat. 10-571, 393m depth, AGT, 8.11.1986.

Argentina: Atlantic, Rio Negro, Las Grutas, beach rock, tide pools with coarse sand, stones and algae, Gritta Veit-Köhler, 5.2.1997.

Chile 1: Panitao, bay of Reloncavi, near Puerto Montt, fine mixture of sand and calcareous remains, 5m, K.H. George, 21.08.1991.

Chile 9: Playa Huantajaya/Iquique. Rocky zone: digging of deep hole above the watermark, filtration of the collected water. Substrate: fine sand and shell lime, K.H. George, 04.10.1991.

Chile 10: Tocopilla, at the watermark. Substrate: coarse, grey-coloured sand, little shell lime, K.H George 06.10.1991.

Chile 12: La Herradura/Coquimbo, directly at the watermark, K.H George, 17.10.1991.

Chile 13: La Herradura/Coquimbo, rinsing of *Ulva lobata*, K.H George, 17.10.1991.

Conarneau, culture 2: tide pool northwest of Concarneau, 4°00′W, 47°59′N, Th.D. Künnemann, August 1996.

Fiji Cam1: „Grid reference“ 60K XE 4093, Viti Levu, Joske Riff, west of Suva, Fiji Islands, coarse coral sand from 3m depth, H.K. Schminke, 20.08.1984.

Fiji, VL9, Coral Coast: Fiji-Islands, Viti-Lem, Coral Coast near Korotogo, Johannes Dürbaum, Dec. 1993.

Greece: October 1995, Johannes Dürbaum.

Hancock Museum: *Rhynchothalestris tenuicornis*, holotype diss., slide no. 2.4.3.29, Deutsche Südpolarexpedition 1901-1903, Observatory Bay, Kerguelen, determined by G.S. Brady.

Helgoland: "NW-intertidal", collected from small macro algae, H.U. Dahms, 8.5.1986.

King George Isl, E2/4, 57+58: South Shetlands, Antarctic, Potter Cove, Jubany Base, bay entrance, 62°14′ S, 58°40′ W, sandy silt, Gritta Veit-Köhler, 21m depth, 7.1.1995.

King George Isl, E1/3, 45+46: South Shetlands, Antarctic, Potter Cove, Jubany Base, inner bay, 62°14′ S, 58°40′ W, soft bottom, Gritta Veit-Köhler, 29m depth, 6.1.1995.

King George Isl, E2/1, 12 +13: South Shetlands, Antarctic, Potter Cove, Jubany Base, bay entrance, 62°14′ S, 58°40′ W, sandy silt, Gritta Veit-Köhler, 15m depth, 23.11.1994.

Culture 1: North Sea, Helgoland, littoral, whirled up sediment, northwest tidal zone, H.U. Dahms, 10.6.1986.

Culture 2: as culture 1, only 24.5.1986.

Culture 3: Helgoland, collected from *Laminaria hyperborea*, 8-12m depth, H.U. Dahms, 20.7.1983.

Culture 4: as culture 1, only 14.6.1986.

MC 276 Peru trench: Discol 2-expedition, 07°03.62′S, 88°27,06′W, 4,148m depth, multicorer, 11.09.1989.

MC 279 Peru trench: Discol 2-expedition, 07°03,74′S, 88 ° 22,22′W, 4,138m depth, multicorer, 0-6 cm, 12.09.1989.

MC 282 Peru trench: Discol 2-expedition, 07°03,41′S, 88°27,32′W, 4,145m depth, 0-6 cm, multicorer, 14.09. 1989.

MC 292 Peru trench: Discol 2-expedition, 07°07,49′S, 88 ° 26,90′W, 4,186m depth, 20.09.1989.

MC 295 Peru trench: Discol 2-expedition, 07° 04,51′S, 88° 31,57′W, 4,149m depth, multicorer, 22.09.1989.

MC 347 Peru trench: Discol 3-expedition, 07°04,208′S, 88o27,389′ W, 4,167m depth, 08.02.1992.

MC 348 Peru trench: Discol 3-expedition, 07°05,019′ S, 88°26,985′ W, 4,176m depth, 0-1 cm „disturbed“, 08.02.1992

MC 357 Peru trench: Discol 3-expedition, 07°4,406′ S, 88°27,849′ W, 4,135m depth, 2-4 cm, 16.02.1992.

MC 361 Peru trench: Discol 3-expedition, 07°04,453′S, 88°27,621′W, 4,163m depth, multicorer, 0-1 cm, 17.02.1992.

MC 362 Peru trench: Discol 3-expedition,07o04,532′ S, 88o27,611′W, 4,166m depth, 1-2 cm „disturbed“, 17.02.1992.

MC 364 Peru trench: Discol 3-expedition, 07°04,457′S, 88 ° 26,733′W, 4,165m depth, 0-1 cm „disturbed“, 18.02.1992.

MC 375 Peru trench: declaration missing in the cruise report of the Discol 3-expedition (Schriever G. & Hjalmar Thiel, 1992. Berichte aus dem Zentrum für Meeres- und Klimaforschung, Reihe E: Hydrobiologie und Fischereiwissenschaft, Nr.2)

Mexico 1: Ensenada del Pabellón, coastal lagune, Mexico, 24°19′-24°35′N, 10°28′-107°-45′W, sample sites: Atravesado, 23.06.1991, Chapparro, 30.04.1991, Carnevaca, Samuel Gomez, 23.06.1991.

Mexico 2: Sistema Lagunar Altata, Ensenada del Pabellon, Sinaloa, Mexico, 24o19′-24o45′N, 107o28′-107o57′W, sample sites: Isla Infiernillo (*St. infiernensis*), 0-3cm, 3.1.1991, Las Arenitas, 0-3cm, 3.1.1992, Las Ratas, Estero Pericon, 0-3cm, 1.5.1991 (*St. paradivergens*) Samuel Gomez.

Museum Stockholm: Natur Historiska Riksmuseet Stockholm, *Paradactylopodia serrata* Lang, 1965, syntypes, Katalognr. 2221, Tomales Bay, Lawsons landing, muddy sand, K. Lang, 24.08.1960.

New Zealand: Mana Bank in Panatahanui-Inlet, Wellington, Feb.-May 1981.

Peru, San Bartolo: Lima, interstitial, sandy beach, P. Martinez und G. Moura, October 1992.

PNG M4: Papua New-Guinea, Ednago Island (island near Kavieng, New Ireland), excavation, sublittoral sand from app. 1m depth, rinsed, H.K. Schminke, 11.11.1984.

PNG M11: Papua New-Guinea, Motupore Island, mud-flat in front of the marine biological station, dry at low tide, at high tide uppermost mud sand layer collected and rinsed, H.K. Schminke, 21.11.1984.

PNG M12: Papua New-Guinea, Motupore Island, in front of the marine biological station, rinsing of *Zostera* rhizomes and leaf, at low tide, H.K. Schminke, 21.11.1984.

Seattle: Elliot Bay, Seattle, Washington, USA, April 1995, Jeff R. Cordell;
WBM: sand covered with algae.
BM6: cobbles with sand, covered with algae, many Cirripedia.
AM: Rock placed as habitat mitigation, covered with algae, many Cirripedia.
BU: mixture of stones and sand.
AL: Rock placed as habitat mitigation, covered with algae.
BM: cobbles with sand, covered with algae, many Cirripedia.
Spiekeroog (North Sea): Joachim Wiechmann, 6.7.1994

Spitzbergen: macroalgae, 3-10m depth, Ålesund, Kongsfjord, May-June 1997, J. Dürbaum

Sl36 Sri Lanka: Unawatuna, dead corals on an exposed coral reef, intertidal 1m, H.G. Müller, 11. 03. 1993.

South Carolina, USA: type locality of *Stenhelia bifida*, see Coull, 1976, collected by B. Coull, 1.9.1996.

Venezuela, Bahia de Plata: Isla Magarita, P. Martinez and
G. Moura, October 1992.

2.3 Preparation and microscopy

The animals were fixed and conserved either in formol or in alcohol. For examination they were transferred in into glycerine (or in few cases in Zeiss W15 embedding medium). Either whole animals or dissected parts were mounted on slides, surrounded with melted paraffin and cooled down again after adjusting the cover glass. The objects on the slide could again be moved by warming up the paraffin. Permanent preparations can be prepared by sealing the margins of the cover glass with e.g. nail varnish.

Needles armed with tungsten wire served as dissection tools. Dissection was done under a Wild Heerbrugg binocular at maximally 75 x magnification. The needles were sharpened chemically in boiling $NaNo_2$.

The microscopy was done with a Leitz Diaplan Interference microscope with a maximally 1,000 x magnification. The drawings were partly done with the aid of a camera lucida.

2.4 Abbreviations in the text and in the figures

Aes: aesthetasc
A1= antennule
A2= antenna
Md= mandible
Mxl= maxillule
Mx= maxilla
Mxp= maxilliped
P1-P6= peraeopods 1-6
f= female
m= male
gp: groundpattern of the last common stem species
exp, enp: exo- bzw endopod
enp1: 1. segment (counted from proximal) of the endopod
„enp1“: enp1 of an older groundpattern, which can still be identified in the new compound segment
Ro: rostrum

CI-CVI: copepodid stages 1-6

2.5 Notes on the analysis and presentation of the results

The obtained groundpattern characters are based on the analysis of the above-listed material and the literature. In the AG Zoosystematik und Morphologie a catalogue of all original species descriptions of Harpacticoida has been built up, which was included in the analysis. The new system has been worked out according to the methodology of the Phylogenetic Systematics after Hennig (1966, 1982), the further development of which was specified and summarized by Ax (1984, 1995). The method has been elaborated and explained in detail by e.g. Sudhaus & Rehfeld (1992), Ax (1984, 1995, 1999) and Hennig (1966). Wägele (1994) additionally discusses discrepancies and differences compared to methods of computer cladistics.

A clear and strict distinction between"results" and "discussion" was not possible, because the analysis of characters always includes a discussion in connection with other characters.

In many illustrations the characters are already arranged according to the new system for more clarity.

The obtained autapomorphies are included in the text as large, bold numbers, which agree with the respective numbers of the character list (chapter 4.2). References on the respective illustrations and chapters can be inferred from the character list.

The character list contains only short descriptions of the characters, a more detailed discussion and description are given in the stated illustrations and chapters.

The terms "Oligoarthra segment" and "Polyarthra segment", mainly used in chapters 6.1 and 6.2, refer to the respective numbering of homologous segments of the male and female antennule within the Oligoarthra and Polyarthra (compare e.g. figs. 5 + 16).

Only sister taxa have the same systematic rank, when Hennig is followed consequently. However, in the new system the traditional family categories of Lang are retained for the present, to the advantage of communication with other scientists working on Harpacticoida.

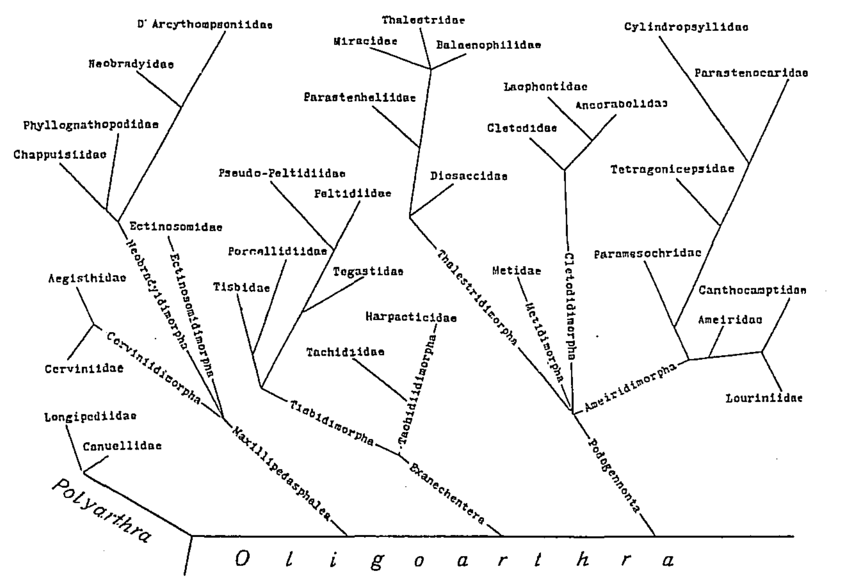
2.6 Notes on the polarisation and analysis of the characters

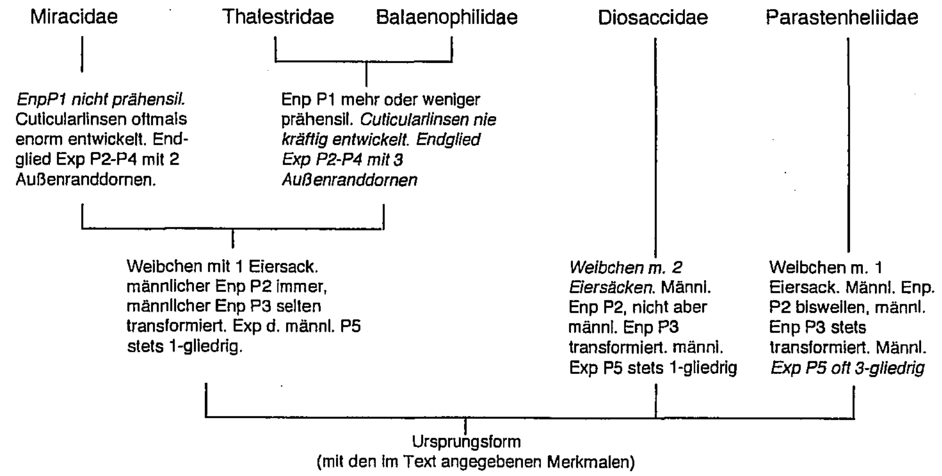
The polarisation is the major difficulty in every phylogenetic reconstruction. Besides the outgroup comparison (see below), other criteria are available for copepods. There is a general consensus among copepodologists, that the evolution of copepods has proceeded primarily towards a reduction of somites and segments of the appendages (by fusion and/or loss) as well as of the setation. It is assumed that the appendages, except for the antennules, were of identical shape in both sexes in the ancestral copepod (Boxshall, et al., 1984, protocol of a discussion on the hypothetical ancestral copepod during the First International Conference on Copepoda in Amsterdam, 1981, Huys & Boxshall, 1991). Huys & Boxshall distinguish at least 2 basic mechanisms: 1. Progressive reduction in the adults, traceable by "intermediate forms", 2. Heterochronic displacement of the development of segments and setae during ontogeny and subsequent loss in the adults (e.g. the female oligoarthran antennule). The same authors deduce the shape of the different appendages of the ancestral copepod from the maximal number of setae and segments actually found in the extant copepod orders. This procedure is confirmed by the obvious homology of the individual setae and segments in all copepod orders. Since several different fusion and reduction patterns, which often show further "qualitative" transformations (e.g. mouthparts of the Siphonostomatoida), occur within different copepod lineages, it can be assumed that each of these different patterns has most probably been formed by convergent reductions from a once multi-segmented and multi-setose groundpattern. This groundpattern is still present to a great extent, e.g. 3-segmented swimming legs with homologous setation in several orders (Platycopioida, Calanoida, Cyclopoida, Harpacticoida). Compared to this view, it is rather improbable, that such a groundpattern has developed from the different fusion and reduction patterns more than once.

3. Earlier classifications of the Harpacticoida

The first classifications of Harpacticoida reach back to the second half of the nineteenth century (Boeck, 1864, 1872, Brady, 1880, Canu, 1892). Lang (1948) gives an extensive summary of all these early attempts. The genera known up to then of what is later called Thalestridimorpha were still distributed among the different higher taxonomic categories. Sars (1903-1911, 1919-1921), in his monograph "Crustacea of Norway", divided the Harpacticoida into 2 sections (I. Achirota, with a "non-prehensile" Mxp and P1; II. Chirognatha with "prehensile" Mxp) and 20 families, most of which are still valid today. To the latter belong the Thalestridae Sars, 1905, Diosaccidae Sars, 1906 and the Balaenophilidae Sars, 1910, which already contained the genera known until then of the later Thalestridimorpha. A subsequent system published by Monard (1927) followed Sars to a great extent.

The most extensive and most important contribution to the phylogeny and systematics of the Harpacticoida is the "Monographie der Harpacticiden" by K. Lang (1944, 1948). Comprehensive diagnoses are given on all systematic levels and relationships between supraspecific taxa are proposed and discussed. Lang's family system (fig. 1) still is the basis for all taxonomic and phylogenetic research today. A short summary of the system was published in advance in 1944 as "preliminary communication". Lang (1944, 1948) established the Thalestridimorpha, which contained the following taxa: Diosaccidae Sars, 1906, Balaenophilidae Sars, 1910, Miraciidae Dana, 1846, Parastenheliidae Lang, 1944, and the Thalestridae Sars, 1905. The latter family had already been revised by Lang in 1936 and had been divided into the 4 subfamilies Pseudotachidiinae, Dactylopusiinae, Thalestrinae and Parastenheliinae. The Parastenheliinae were elevated to family rank only in 1944/1948. A further subfamily, the Rhynchothalestrinae, was also added in 1944/1948. The relationships within the Thalestridimorpha and Thalestridae as proposed by Lang have been the starting points of the present study and are once more depicted in figs. 2 + 3. The complete family system of the Harpacticoida of Lang is again reproduced in fig. 1. A more detailed discussion of the hypotheses of Lang, as far as the Thalestridimorpha are concerned, is given in chapter 8.





EnpP1 nicht prähensil. Cuticularlinsen oftmals enorm entwickelt. Endglied Exp P2-P4 mit 2 Außenranddornen.

Enp P1 mehr oder weniger prähensil. *Cuticularlinsen nie kräftig entwickelt. Endglied Exp P2-P4 mit 3 Außenranddornen*

Weibchen mit 1 Eiersack. männlicher Enp P2 immer, männlicher Enp P3 selten transformiert. Exp d. männl. P5 stets 1-gliedrig.

Weibchen m. 2 Eiersäcken. Männl. Enp P2, nicht aber männl. Enp P3 transformiert. männl. Exp P5 stets 1-gliedrig

Weibchen m. 1 Eiersack. Männl. Enp. P2 bisweilen, männl. Enp P3 stets transformiert. Männl. *Exp P5 oft 3-gliedrig*

Ursprungsform
(mit den im Text angegebenen Merkmalen)

Above: fig. 1: Family system of the Harpacticoida after Lang, 1948.
Below: fig. 2: System of the Thalestridimorpha after Lang, 1948.

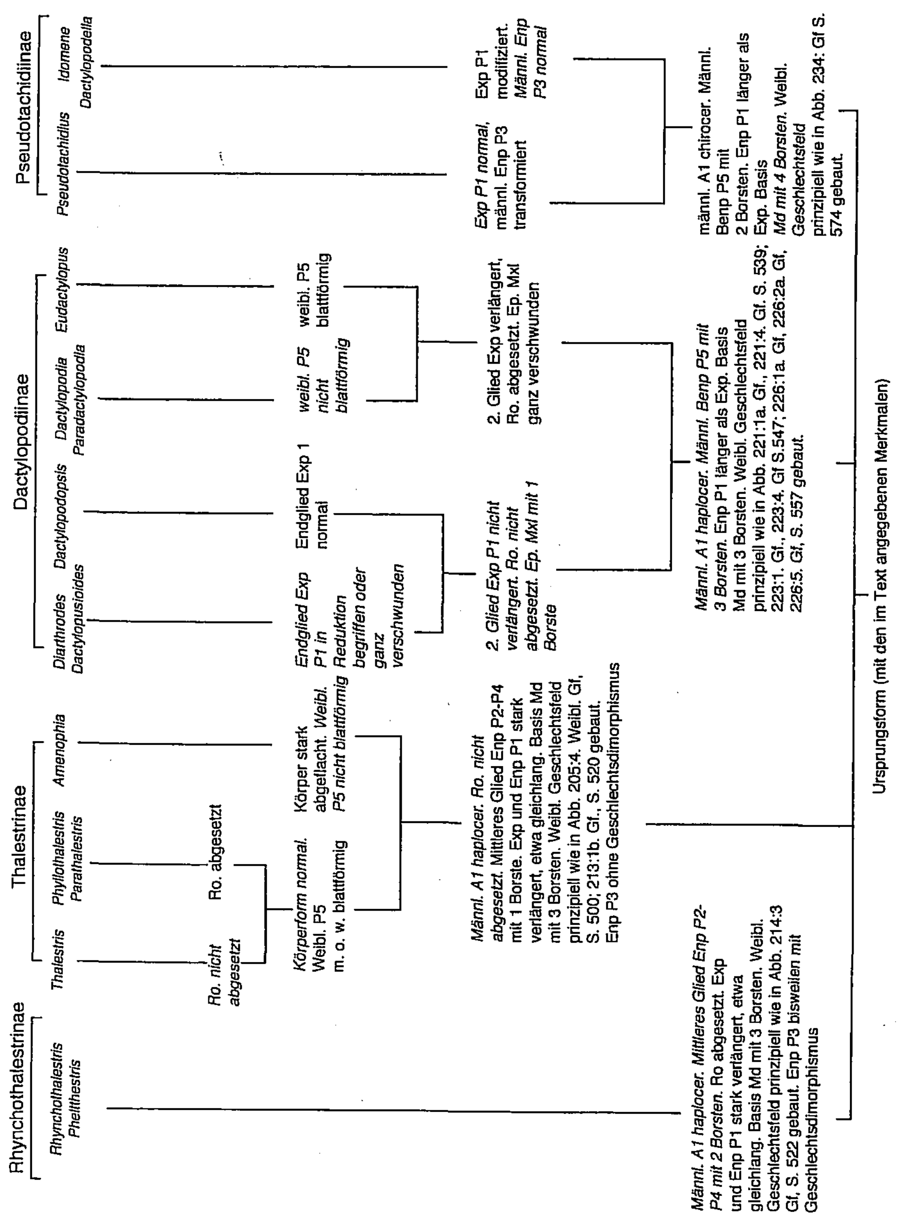


Fig. 3: System of the Thalestridae after Lang, 1948.

4. The new system of the Thalestridimorpha

4.1 Notes on the topology of the phylogenetic cladogram of the Thalestridimorpha

As a start of the phylogenetic analysis of the Thalestridimorpha, the old system of Lang (1948, see figs. 2 + 3) was tested as an ad hoc hypothesis. For the polarisation of characters other taxa within Podogennonta and Oligoarthra as well as the ancestral copepod itself, as reconstructed by Huys & Boxshall (1991), have been used as outgroups. For the taxa Podogennonta and Oligoarthra new autapomorphies confirming their monophyly were found in the course of the present study (compare chapters 6.1, 6.2, 7).

At first the monophyly of the thalestridimorphan subtaxa (figs. 2 + 3) as established by Lang (1948) has been tested. The Thalestridae turned out not to be monophyletic. Synapomorphies have been found only for the Thalestrinae and *Eudactylopus/Neodactylopus* (compare chapters 6, 7.1, 7.2). The Pseudotachiidae were recognised as a monophyletic taxon near the base of the Podogennonta and have been removed from the Thalestridimorpha. The monophyly of the remaining subfamilies sensu Lang, the Rhynchothalestrinae, Dactylopusiinae, and also the Parastenheliidae could be confirmed. The supraspecific taxon *Pseudomesochra* is removed from the Diosaccidae and assigned to the Pseudotachdiidae, within which it is closely related to the Paranannopinae (Willen, 1996). Within the Diosaccidae sensu Lang (1948) a taxon Stenheliinae is recognised, consisting of the supraspecific taxa *Stenhelia*, *Cladorostrata*, *Pseudostenhelia* and *Onychostenhelia*.

Several synapomorphies were found for the "remaining" Thalestridae (=Thalestrinae and *Eudactylopus/Neodactylopus*) plus Diosaccidae. Thus a new taxon Thalestridoidea could be established restricting the number of possible phylogenetic cladograms within Thalestridimorpha considerably. The remaining taxa Rhynchothalestridae, Dactylopusiidae and Parastenheliidae could be characterised by autapomorphies each, but none of them could be combined with any other to a superordinated taxon. The Rhynchothalestridae were recognised as the sistergroup of Thalestrioidea. The Parastenheliidae with several more plesiomorphic characters, turned out to be the sistergroup of the remaining Thalestridimorpha. The Miraciidae could easily be accommodated within the Diosaccidae.

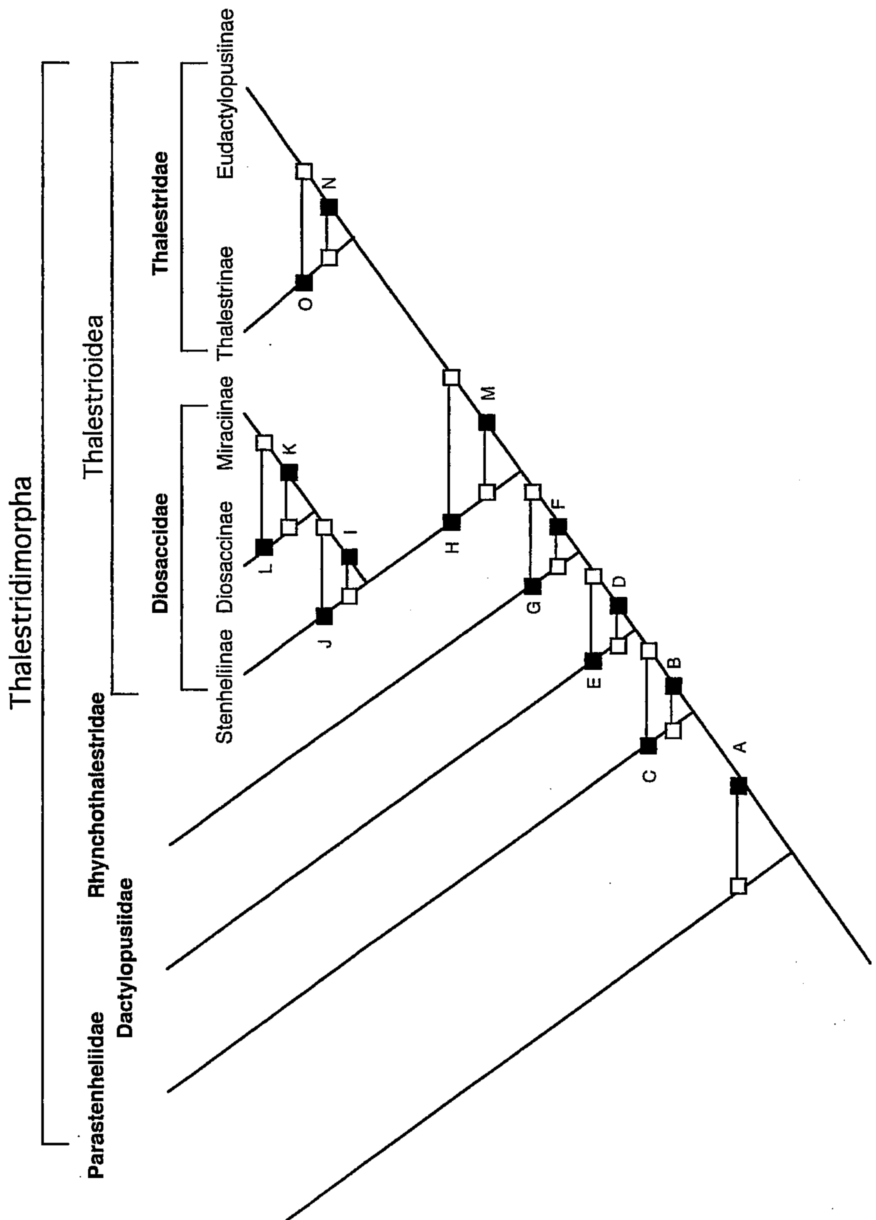


Fig. 4:
Phylogenetic cladogram of the Thalestridimorpha.

4.2 List of characters

f = female, m = male, [] = plesiomorphic state

1. A1 m+f: segments 7 +8 fused (fig. 7, chapter 6.2.3) [still separated]

2. A1 f: segment 4: as in Thalestrinae (fig. 9, chapter 6.1.3) [complete setation: „2+2+1+[1+aes]“]

3. A1 f: segment 4: setation as in Diosaccinae and Parastenheliidae (fig. 9, chapter 6.1.3) [complete setation: „2+2+1+[1+aes]“]

4. A1 f: segment 4: as in Miraciinae (fig. 9, chapter 6.1.3) [complete setation: „2+2+1+[1+aes]“]

5. A1 f: segment 5: 2 setae (fig. 7, chapter 6.1.3) [3]

6. A1 f: segment 9: setation as in Stenheliinae (fig. 10, chapter 6.1.3) [Oligoarthra groundpattern (figs. 6 + 7)]

7. A1 f: segment 6: elongated, with only 2 lateral setae (chapter 6.1.3) [not elongated, with 3 lateral setae and 1 terminal seta (fig. 6)]

8. A1 f: segments 4 + 5 fused (fig. 8, chapter 6.1.3) [separated]

9. A1 m: segments 2 + 3 fused (fig. 21, chapter 6.2.3) [separated]

10. A1 m: segment 6: with modification of a homologous seta (fig. 22, chapter 6.2.3) [this seta not modified]

11. A1 m: segment 9: with “spinule-row” (fig. 23, chapter 6.2.3) [without “spinule-row”]

12. A1 m: segments 6-9 fused (figs. 17, 19, 21, chapter 6.2.4) [separated]

13. A1 m: loss of setae or aesthetascs on segments 2, 3 + 10 (fig. 21, Miraciinae, chapter 6.2.3) [respective setae and aesthetascs still present]

14. A1 m: aesthetasc of segment 3 missing (fig. 21, chapters 6.2.2-4, 7.3, 11) [present]

15. A1 m: aesthetasc of segment 4 missing (fig. 21, chapter 6.2) [present]

16. A2exp3+4 of Oligoarthra gp fused (fig. 24, chapter 6.3.1) [these segments separated]

17. A2 „enp1“: loss of geniculation and reduction of a homologous seta (fig. 25, chapter 6.3.1) [seta well developed, with geniculation]

18. A2 exp1: proximal seta shortened (fig. 26, chapter 6.3.2) [normally developed]

19. A2 exp1: loss of proximal seta (fig. 26, chapter 6.3.2) [this seta present]

20. A2 exp: 1-segmented, with only 2 setae (fig. 26, chapter 6.3.2) [3-segmented, more than 2 setae]

21. A2 exp: 2-segmented (fig. 26, chapter 6.3.2) [3-segmented]

22. A2 exp: seta „3" (or „4"?) missing (fig. 26, chapter 6.3.2) [present]

23. A2: „exp2" (fusion product of exp2 + 3 of Podogennonta gp, figs. 24+26) shortened, 1 terminal seta lost (fig. 26, chapter 6.3.2) [„exp2" not shortened, terminal seta present]

24. A2 exp3: 1 terminal seta either lost/or miniaturised (fig. 26, chapter 6.3.2) [always present and not miniaturised]

25. Md exp with reduced setation (fig. 27, chapter 6.4.1) [with complete setation of Oligoarthra gp (= 6 setae)]

26. Md exp: of type 1 (figs. 27 + 28, chapter 6.4.2) [Thalestridimorpha gp]

27. Md exp: of type 2 (figs. 27 + 28, chapter 6.4.2) [Thalestridimorpha gp]

28. Md exp: 1-segmented, with at most 3 (4) setae (fig. 28, chapter 6.4.2) [multi-segmented with 4 setae]

29. Md palp: represented by 1 „segment", with 2 setae, modified shape of gnathobase (compare Huys & Böttger-Schnack, 1994) [palp not reduced, gnathobase not modified]

30. Md exp: 1-segmented (exp1-4 of Thalestridimorpha gp fused, fig. 28, chapter 6.4.2) with complete setation (= 6 setae) [2-3-segmented]

31. Md exp: 1-segmented and shortened, with only 2 setae (fig. 28, chapter 6.4.2) [not shortened, with complete setation (= 6 setae)]

32. Md exp: 2-segmented, setae displaced (fig. 28, chapter 6.4.2) [3-segmented, setae not displaced]

33. Md exp4+5 of Oligoarthra gp fused (figs. 27 + 28, chapter 6.4.1) [these segments separated (fig. 27)]

34. Md exp: 2-segmented (fig. 28, chapter 6.4.2) [Podogennonta groundpattern]

35. Md gnathobase: with blunt teeth (fig. 31, chapter 6.4.5) [teeth of „normal" shape]

36. Md „enp1" (enp1 of Oligoarthra gp, in this case fused with enp2, fig. 29): with only 2 setae (proximal seta missing) (fig. 29, chapter 6.4.3) [with 1 proximal seta and 2 distal setae]

37. Md „enp2" (enp2 of Oligoarthra gp, in this case fused with enp1, fig. 29): = Thalestridimorpha gp (fig. 29, chapter 6.4.3-4) [= Podogennonta gp (fig. 29)]

38. Md „enp2": 1 inner apical seta inserting as a single element (fig. 30, chapter 6.4.4) [basally fused with 2 more setae (fig. 30)]

39. Md „enp2": 1 inner apical seta missing (fig. 30, chapter 6.4.4) [present (fig. 30)]

40. Md „enp1": with only 1 seta (fig. 30, chapter 6.4.4) [with 2 setae]

41. Md basis: with 3 setae (chapter 7.3) [with 4 setae]

42. Mxl: with only 1 coxal outer seta (table 1, chapter 6.5.1) [with 4 coxal outer setae]

43. Mxl: coxal outer seta missing (table 1, chapter 6.5.1) [present]

44. Mxl: apical precoxal spines: with „double spinules" (fig. 33, chapter 6.5.2) [without these ornamentations]

45. Mxl basis: with 2+4 setae (table 1, chapter 6.5.1) [with 3+4 setae]

46. Mxl enp: with 3 setae (table 1, chapter 6.5.1) [with 4 setae]

47. Mxl: exp only represented by 2 or 3 setae (table 1, chapter 6.5.1) [exp well developed]

48. Mxl: shape of praecoxa as in Dactylopusiidae (fig. 34, chapter 6.5.2.1) [as in Thalestridimorpha gp (fig. 33)]

49. Mxl: shape of praecoxa as in Parastenheliidae (fig. 34, chapter 6.5.2.1) [as in Thalestridimorpha gp (fig. 33)]

50. Mxl: shape of praecoxa as in Pseudotachidiidae (fig. 35, chapter 6.5.2.2) [as in Podogennonta gp (fig. 33)]

51. Mxl praecoxa: outermost posterior apical spine in *Eudactylopus* slightly reduced and of setal shape, completely missing in Thalestrinae (fig. 34, chapter 6.5.2.1) [present, clearly developed as spine (fig. 33)]

52. Mxl coxa: with at most 4 setae (table 1, chapter 6.5.1) [with 5-6 setae]

53. Mxl coxa: with at most 2 setae (table 1, chapter 6.5.1) [with 4 setae]

54. Mxl exp: with 2 setae (table 1, chapter 6.5.1) [with 4 setae]

55. Mxl: as in the Miraciinae (see Huys & Böttger-Schnack, 1994) [as Thalestridimorpha gp]

56. Mxl: as in Eudactylopusiinae (fig. 34, chapter 6.5.2.1) [as Thalestridimorpha gp]

57. Mxl: posterior „upper" praecoxal spine missing (fig. 34, chapter 6.5.2.1) [present]

58. Mx enp: Pseudotachidiidae gp (figs. 37 + 39, chapter 6.6.2) [Podogennonta gp (fig. 37)]

59. Mx enp: Thalestridimorpha- and Tetragonicipitidae gp (fig. 37, chapter 6.6.2) [Podogennonta gp (fig. 37)]

60. Mx enp: 1-segmented, with only 3 setae (fig. 38, chapter 6.6.2) [Thalestridimorpha gp (figs. 37 + 38)]

61. Mx enp: only represented by 1 seta (fig. 38, chapter 6.6.2) [clearly developed]

62. Mx enp: Thalestridae gp (fig. 38, chapter 6.6.2) [Thalestridimorpha gp (fig. 38)]

63. Mx precoxal endites: as depicted for Thalestridimorpha gp in fig. 40 (chapter 6.6.3) [Podogennonta gp (fig. 40)]

64. Mx praecoxal endites: as in Pseudotachidiidae (fig. 44, chapter 6.6.3) [Podogennonta gp (fig. 40)]

65. Mx praecoxal endites: as in Parastenheliidae (fig. 43, chapter 6.6.3) [Thalestridimorpha gp (fig. 40)]

66. Mx praecoxal endite: single lobe with only 1 seta (fig. 43, chapter 6.6.3) [bilobed, with 2+3 setae (fig. 40)]

67. Mx praecoxal endites: completely missing (chapter 6.6.3, compare Huys & Böttger-Schnack, 1994) [present]

68. Mx praecoxal endites: with 2 setae altogether, distal and proximal part still distinguishable, but fused, with 1 seta each (fig. 42, chapter 6.6.3) [clearly bilobed, with 2 +3 setae (fig. 40)]

69. Mx praecoxal endite: with 2 setae, distal and proximal part not distinguishable any more (fig. 42, chapter 6.6.3) [clearly bilobed, with 2+3 setae (fig. 40)]

70. Mx coxal endites: with characteristic shape of setae (fig. 40, chapter 6.6.3) [setae not modified in this way (Oligoarthra groundpattern)]

71. Mx proximal coxal endite: 1 flagellate seta missing (fig. 41, chapter 6.6.3) [present (fig. 40)]

72. Mx proximal coxal endite: 1 spine-like seta missing (compare Huys & Böttger-Schnack, 1994, S. 247, fig. 25D) [present]

73. Mxp: with only 4 coxal setae, arranged in 2 pairs one beneath the other (fig. 46, chapter 6.7.1) [with up to 7 setae]

74. Mxp: endopodal claw fused with enp (fig. 47, chapter 6.7.2) [separated, enp clearly demarcated (figs. 47 +48)]

75. Mxp: coxal setae arranged in single row along distal segmental margin (fig. 47, chapter 6.7.2) [arrangement pairwise one beneath the other (fig. 47)]

76. Mxp: as in Thalestrioidea gp (figs. 47 + 48, chapter 6.7.2) [Thalestridimorpha gp (figs. 46 + 47)]

77. Mxp: as in Diosaccidae gp (fig. 48, chapter 6.7.2) [Thalestrioidea gp]

78. Mxp: as in Stenheliinae gp (fig. 48, chapter 6.7.2) [Diosaccidae gp]

79. Mxp: as in Miraciinae gp (fig. 48, chapter 6.7.2) [Diosaccidae gp]

80. Mxp: as in Thalestridae gp (fig. 48, chapter 6.7.2) [Thalestrioidea gp]

81. Mxp: as in Parastenheliidae gp (fig. 47, chapter 6.7.2) [Thalestridimorpha gp (figs. 46 + 47)]

82. Mxp: as in Dactylopusiidae gp (fig. 47, chapter 6.7.2) [Thalestridimorpha gp (figs. 46 + 47)]

83. Mxp: as in Pseudotachidiidae gp (fig. 49, chapter 6.7.3) [Podogennonta gp (fig. 46)]

84. Setae on P1enp3 and P1exp3: of characteristic shape (fig. 50, chapter 6.8.1) [shape of setae as in remaining swimming legs]

85. Setae on P1enp3 and P1exp3: shape as in groundpattern of *Protolatiremus sakaguchii* (fig. 52, chapter 6.8.2) [Podogennonta gp (fig. 50)]

86. P1 enp3: with 3 setae (figs. 53 + 54, chapter 6.8.2) [with 4 setae]

87. P1 exp2: elongated (figs. 52-54, chapter 6.8.2) [not elongated (fig. 50)]

88. P1 enp1: inner seta inserting in distal quarter of segment (fig. 54, chapter 6.8.2) [insertion point not reaching beyond first half of inner margin (figs. 50, 53, 54)]

89. P1: as in Miraciinae gp (fig. 54, chapter 6.8.2) [Diosaccidae gp]

90. P1: as in Parastenheliidae gp (fig. 53, chapter 6.8.2) [Thalestridimorpha gp]

91. P1: as in Eudactylopusiinae gp (fig. 54, chapter 6.8.2) [Thalestridimorpha gp]

92. P1: as in Dactylopusiidae gp (fig. 53, chapter 6.8.2) [Thalestridimorpha gp]

93. P1: as in Pseudotachidiidae gp.(fig. 55, chapter 6.8.3) [Podogennonta gp]

94. Intercoxal sclerites of P2-P4: with pair of projections (fig. 59, chapter 6.9.2) [without projections]

95. P2-P4: derived shape of articulation between enp2 + 3 (fig. 58, chapter 6.9.2) [articulation of "normal" shape]

96. P3enp2: with 1 seta (chapter 6.9) [with 2 setae]

97. P4enp2: with 1 seta (chapter 6.9) [with 2 setae]

98. P4enp3: proximal inner seta missing (chapter 6.9) [present]

99. P2enp3: 1 inner seta missing (chapter 6.9) [present]

100. P3enp3: with 2 inner setae (chapter 6.9) [with 3 setae]

101. P2-P4: as in Miraciinae gp (compare Huys & Böttger-Schnack, 1994) [swimming legs of "normal" shape]

102. P5 f: exopodal setae „13" + „14" missing (figs. 61-66, chapter 6.10.1 + 6.10.2) [present (figs. 61, 62)]

103. P5 f: shape of benp and exp as in Parastenheliidae gp (fig. 62, chapter 6.10.2) [of „moderate shape"; compare fig. 61 and chapter 6.10.1]

104. P5 f: as in Pseudotachidiidae gp (fig. 66, chapter 6.10.3) [Podogennonta gp (fig. 61)]

105. P5 f: exp and benp with tendency towards a more extreme foliate shape (fig. 63, chapter 6.10.2) [exp and benp never foliate]

106. P5 f: benp and exp as in Miraciinae gp (fig. 65, chapter 6.10.2) [„moderate shape", compare chapter 6.10.1 and fig. 61]

107. P5 f: shape of benp and exp as in Stenheliinae gp (fig. 65, chapter 6.10.2) [„moderate shape"]

108. P5 f: seta „1" separated either by spatial displacement or by modified shape from 2 (figs. 62, 63, chapter 6.10.2) [„1" and „2" of identical shape, located directly one beneath the other (compare fig. 61)]

109. P5 m: benp with 2 setae (chapter 6.12.1) [with 3 setae]

110. P5 m exp: innermost seta (originating from exp2 of Oligoarthra gp) missing (chapter 6.12.1) [present]

111. P5 m exp: 1-segmented (chapter 6.12.1) [2-3-segmented]

112. P2 m enp: sexually dimorphic as in *Protolatiremus sakaguchii* (fig. 70, chapter 6.11.1, 7.3) [without sexual dimorphism]

113. P2 m enp: 2-segmented (fusion of enp2 +3) (fig. 69, chapter 6.11.1, 7.3) [*always* 3-segmented]

114. P2 m enp: always 2-segmented with modified setae on „enp3" (fig. 69, chapter 6.11.1, 7.2) [setae without modification (compare chapter 7.3 for further explanations and fig. 69)]

115. P2 m enp: sexually dimorphic as in Dactylopusiidae gp (figs. 69, 72-74, chapter 6.11.1) [without setal modifications on „enp3"]

116. P2 m enp: sexually dimorphic as in Thalestrioidea gp (figs. 69, 71, 73, 75, chapter 6.11.1) [without setal modification on „enp3"]

117. P2 m enp: sexually dimorphic as in Rhynchothalestridae gp (fig. 69, chapter 6.11.1) [without setal modification on „enp3"]

118. P2 m enp: sexually dimorphic as in Miraciinae gp (compare Huys & Böttger-Schnack, 1994 and chapter 6.11.1, 7.1) [Thalestrioidea gp]

119. P2 m enp: sexually dimorphic as discussed for Stenheliinae in chapter 7.1 (fig. 76, chapter 6.11.1, 7.1) [Thalestrioidea gp]

120. P2 m enp: sexually dimorphic as in Pseudotachidiidae (fig. 77, chapter 6.11.2) [*without sexual dimorphism*]

121. P1 m: basis with „Nebendornen" (fig. 79, chapter 6.12.2) [without basal sexual dimorphism]

122. P1 m: basis with at most 3 large „Nebendornen" and with „nose-like" segmental projection (fig. 79, chapter 6.12.2) [„multiple Nebendornen", similar to spinule-row, without segmental projection (fig. 79)]

123. P3 m enp2: with segmental projection [without projection]

124. Rostrum: of „stenheliid" shape of (fig. 80, chapter 6.12.3) [of „normal" shape, compare fig. 80 and chapter 6.12.3]

125. Rostrum: with ventrally located, large subapical pores (fig. 11, chapter 7.2) [pores absent]

126. Anal somite: divided (chapter 6.12.4) [not divided (fig. 81)]

127. Caudal seta I (ventrolateral seta): modified spine-like (figs. 81A-C, E, chapter 6.12.4) [not modified (fig. 81G)]

128. Caudal seta I: miniaturised or completely missing, I + II spatially separated (fig. 81F, chapter 6.12.4) [caudal seta I „normally" developed, I +II juxtaposed (figs. 81A-C, E)]

129. Caudal seta I: shortened (fig. 81D, chapter 6.12.4)
[„normal" or spine like (compare chapter 7.1) (figs. 81A-C, E)]

4.3 Arrangement of characters in the phylogenetic cladogram of the Thalestridimorpha and in fig. 82

Podogennonta: 16, 42, 44, 70, 73, 84

Taxon I (Pseudotachidiidae): 1, 8, 12, 24, 34, 43, 45, 46, 50, 58, 64, 74, 83, 93, 96, 97, 102, 104, 109, 111, 120, 123, 125, 126, 128

Taxon II: 14, 17, 36, 41, 59, 63 (or for A?)

Taxon III: 87

Taxon IV (*Protolatiremus sakaguchii*): 25, 85, 112

A: Thalestridimorpha: 33, 37, 63 (or for II?), 94, 113, 127 (or for B?)

B: 102, 111, 114, 127 (or for A?)

C: Parastenheliidae: 3, 5, 11, 15, 18, 21, 28, 45, 47, 49, 60, 65, 74, 81, 86, 90, 96, 97, 99, 100, 103, 109, 129

D: 26

E: Dactylopusiidae: 5, 27, 48, 66, 71, 74, 82, 86, 92, 98, 115

F: Thalestrioidea: 9, 10, 18, 38, 43, 52, 76, 97, 116

G: Rhynchothalestridae: 74, 75, 95, 117

H: Diosaccidae: 19, 54, 77, 86, 88, 99, 109, 110

I: 5, 121

J: Stenheliinae: 1, 6, 32, 35, 78, 107, 119, 124

K: Miraciinae: 1, 4, 7, 13, 15, 20, 29, 55, 61, 67, 72, 74, 79, 89, 101, 106, 118

L: Diosaccinae: 3, 71, 122

M: Thalestridae: 5, 21, 22, 30, 39, 51, 62, 68, 74, 80, 105, 108

N: Eudactylopusiinae: 23, 31, 40, 53, 56, 61, 69, 91, 95

O: Thalestrinae: 2, 46, 57, 96

5. Summary of the groundpattern characters of the discussed taxa

Explanation of the symbols: ♦= symplesiomorphy; ✹= autapomorphy; ⇔= polarisation unclear yet.

Oligoarthra

Rostrum: groundpattern still unknown.

Female A1: ✹ 9-segmented, number and arrangement of setae see figs. 5+6.

Male A1:✹ haplocer, 14-segmented, arrangement and shape of setae see figs. 15 + 16; ✹ ancestral segments I + II with only 1 seta each.

A2: ✹ enp1 with only 1 seta, „enp2“ with 4 primarily unmodified setae, „enp3“ with 7 setae „enp2“ + „enp3“ = enp2); ✹ exp 4-segmented, with 2, 1, 1, 3 setae.

Md: ⇔ basis with 4 setae; ✹ enp 2-segmented, enp1 with 3 (4) setae, enp2 with 3 lateral setae and 2 apical groups of setae with 3+3 (4) setae, each one basally fused (fig. 29); ♦ exp 5-segmented with 1, 1, 1, 1, 2 setae.

Mxl: ♦ basis with 4+4 setae; ♦ coxa with 6 setae; ♦ 4 coxal outer setae; ✹exp with 5 setae; ✹enp with 5-6 setae; ♦ praecoxal arthrite: anterior surface in the outer half with 2 juxtaposed setae, posterior surface with 2 proximal setae, subapical inner margin with 2 plumose setae, apically 2 rows of spines with 3 anterior and 4 posterior spines as well as 1 smaller, flexible seta inserting on the anterior surface (fig. 33).

Mx: ⇔ enp and basis as in fig. 36 (also Polyarthra?); ⇔ praecoxal endite bilobed, with 3+3 setae; ♦ both coxal endites with 3 setae each.

P1: ♦ shape of segments and setation as in the subsequent swimming-legs.

Female P5: ⇔ = Podogennonta groundpattern?

Male P2: ♦ without sexual dimorphism.

Male P5: ⇔ = Podogennonta groundpattern?

Anal somite: ♦ not divided; ♦ anal operculum present.

Caudal rami: ♦ all setae of the Copepoda groundpattern (see Huys & Boxshall, 1991) present and well developed (fig. 81G).

Podogennonta

Rostrum: groundpattern still unknown.

Female A1: ⇔ = Oligoarthra groundpattern, except segment 2 with only 12 setae.

Male A1: ♦ = Oligoarthra groundpattern.

A2: ♦ enp2 subterminal 4 setae of characteristic shape (with geniculate seta, see fig. 25); ✹ exp3+4 of Oligoarthra groundpattern fused (fig. 24); ♦ exp setation of Oligoarthra groundpatterns completely retained (fig. 24).

Md: ⇔ basis with 4 setae; ⇔ enp1+2 of Oligoarthra groundpattern fused; ♦ „enp1“ with 1+2 setae, „enp2“ with 3 lateral and 2 terminal groups of setae, the latter 2 basally fused, and with 3+4 setae, respectively (fig. 29); ⇔ exp 4- or 5-segmented?

Mxl: ✹ basis with 3+4 setae; ♦ coxa with 6 setae; ✹ enp with 4 setae; ⇔ exp with 4 setae; ✹ only 1 coxal outer seta present; ✹ praecoxal arthrite: complete setation of Oligoarthra groundpattern, but the posterior apical spines carry „double spinules“ (fig. 33).

Mx: ⇔ enp1 of Oligoarthra groundpattern (fig. 37) fused with basis (allobasis); ✹ 1 seta each is lost on enp1, 3 + 4 (fig. 37); ✹ praecoxal endites fused, with 3+3 setae, distal part with 2 „flagellate setae“ (fig. 40); ✹ both coxal endites with setae of characteristic shape: anteriorly 1 more claw-like seta, posteriorly 2 strong, mostly unilaterally spinulose setae with subterminal flagellum (fig. 40).

Mxp (fig. 46): ✹ 4 syncoxal setae, arranged in 2 pairs from proximal to distal; ♦ 2 inner basal setae located medially and distally; ⇔ seta 3 in fig. 46 developed as “main claw”; ✹ enp1+2 of the Oligoarthra groundpattern fused, „enp1“ with „main claw“, reduced claw (seta 2 in fig. 46) and 1 seta, „enp2“ only represented by a group of 4 small setae on the anterior surface.

P1 (fig. 50): ✹ of characteristic shape: enp1 elongate, enp2+3 short; enp3 with 1 inner seta, terminally with anterior claw, middle geniculate seta and posterior miniaturised seta; exp3 terminally with 2 „true“ geniculate setae, but never with inner seta.

P2-P4: ♦ setal formula:

	P2	P3	P4
enp	1.2.221	1.2.321	1.2.221
exp	11.11.223	11.11.323	11.11.323

Female P5: ⇔ benp with 6 setae, exp 1-segmented with 8 setae, shape and arrangement of setae characteristic as in fig. 61 (✹ on the level of Oligoarthra or Podogennonta?).

Male P2enp: ♦ as in the female

Male P5: ♦ exp 3-segmented with 7 setae, enp with 3 (4?) setae.

Anal somite: ♦ not divided; anal operculum present.

Caudal rami: ♦ setae not modified, I and II of equal length and well developed.

Pseudotachidiidae

Rostrum: ⇔ large, of more rectangular shape, with 2-4 sensillae, with large, ventrally located, subapical pores (fig. 11).

Female A1: ✹ setation and segmentation see fig. 8.

Male A1: ✹ subchirocer, 10-segmented, setation and segmentation see figs. 17 + 19.

A2: ♦ enp subterminally with geniculate seta = Podogennonta groundpattern; ✹ 1 of the 3 terminal setae on exp3 reduced or completely lost; ♦ segmentation of exp as Podogennonta groundpattern.

Md: ♦ basis with 4 setae; ♦ enp = Podogennonta groundpattern; ✹ exp 2-segmented, with complete set of setae (2+4) of Oligoarthra groundpattern.

Mxl: ✹ basis with 2+4 setae; ✹ coxal outer seta missing; ✹ enp with 3 setae; ♦ exp with 4 setae; ✹ praecoxal arthrite as in Podogennonta groundpattern, except apical spines with swelling and one of the 2 posterior surface setae displaced towards the distal outer margin (see fig. 35).

Mx (fig. 37): ✹ enp 2+3 of the Podogennonta groundpattern fused, setae 6,8 and 9 in fig. 37 lost; ✹ praecoxal endite with 2 basal fused endites, with 1+3 setae, 2 of the latter setae with flagellum; shape as in fig. 44; ⇔ coxal endites are derived from Podogennonta groundpattern, still further modified (fig. 45).

Mxp: ✸ derived from Podogennonta groundpattern as in fig. 49: syncoxa with only 2 setae, only 1 basal seta (probably the distal one) has been retained, enp and claw fused, setation of „enp1“ only represented by the "main claw" (=seta 3 in fig. 46), „enp2“ only represented by 2 setae.

P1: ✸ as Podogennonta groundpattern, except enp1 outer and terminal margin furnished with large spinules and with 1 large pore in the outer distal corner, exp1-3 outer spines unilaterally ornamented with spinules (fig. 55).

P2-P4: ✸ as in Podogennonta groundpattern, except P3enp2 and P4enp2 each with only 1 seta; ♦ intercoxal sclerites without projections.

Female P5: ✸ shape of segments and setae derived from Podogennonta groundpattern: exp small, setae 13+14 of fig. 61 missing, benp with outer constriction between basis and enp, seta 1 of fig. 61 elongate, seta 2 strongly shortened (fig. 66).

Male P2enp: ✸ 3-segmented, homologous setae on enp3 modified (fig. 77).

Male P3enp: ✸ enp2 with segmental projection.

Male P5: ✸ exp 1-segmented; ♦ exp with 7 setae; ✸ enp with 2 setae

Anal somite: ✸ divided; ✸ anal operculum absent, pseudoperculum present.

Caudal rami: ✸ I completely missing or miniaturised (fig. 81).

Taxon II (see fig. 82)

(not all details of the groundpattern have been analysed in the course of this study)

Rostrum: ⇔ = groundpattern still unknown.

Female A1 ♦ = Podogennonta groundpattern.

Male A1 ♦ =Podogennonta groundpattern, except segment 3 without aesthetasc.

A2: ✸ = Podogennonta groundpattern, except A2enp2 subterminal setae: loss of the geniculation of the respective seta (fig. 27).

Md: ✸ basis with 3 setae; ✸ „enp1“ with 2 setae.

Mxl: ♦ = Podogennonta groundpattern.

Mx: ⇔ = Podogennonta groundpattern, except enp seta 1 in fig. 37 miniaturised.

Mxp: ♦ = Podogennonta groundpattern.

P1: ♦ = Podogennonta groundpattern.

P2-P4: ♦ = Podogennonta groundpattern.

Female P5: ✸ = Podogennonta groundpattern.

Male P2enp: ♦ = as in female.

Male P5: ♦ = Podogennonta groundpattern.

Anal somite: ♦ = Podogennonta groundpattern.

Caudal rami: ♦ = Podogennonta groundpattern.

Protolatiremus sakaguchii

(not all aspects of the groundpattern, especially of the mouthparts, have been analysed in detail, as far as they are autapomorphies without influence on the thalestridimorphan system)

Rostrum: ⇔ = tiny, triangular.

Female A1 ♦ 9-segmented.

Male A1 ♦ generally as in Taxon II groundpattern, except ✸ segments 9 + 10 as well as 12 + 13 fused, aesthetasc on 5 lost.

A2: ♦ = taxon II groundpattern, except ✸ exp 2-segmented with 2 + 4 setae.

Md: ✸ basis with 3 setae; ✸ „enp1“ with 2 setae; ✸ exp 4-segmented with 1, 0, 1, 2 setae (fig. 27).

Mxl: ♦ = Podogennonta groundpattern, except ✸ basis with 2 + 4 setae, exp with 3 setae, posterior surface setae on the praecoxal arthrite absent.

Mx: ♦ = Podogennonta groundpattern, except ✸ enp 1-segmented, with 4 setae, basis with claw + 2 setae, praecoxal endite with 3 setae.

Mxp: ♦ = Podogennonta groundpattern, except ✸ syncoxa with 1 seta, enp with reduced setation.

P1: ✸ derived from Podogennonta groundpattern as in fig. 52.

P2-P4: ✸ setal formula:

	P2	P3	P4
enp	1.2.221	1.2.221	1.1.221
exp	11.11.223	11.11.223	11.11.223

Female P5: ♦ = Podogennonta groundpattern.

Male P2enp: ✸3-segmented, enp2 enlarged, outer seta and outer terminal seta modified (fig. 70).

Male P5: ✸ benp with 2 setae, exp with 6 setae, second outermost seta shortened.

Anal somite: ♦ = Podogennonta groundpattern.

Caudal rami: ♦ = Podogennonta groundpattern.

Thalestridimorpha (= Taxon A in fig. 4)

Rostrum: (✸?) shape of an elongate triangle, with pointed tip, large, with 2-8 (*Diosaccus*) sensillae.

Female A1: ♦ = Podogennonta groundpattern.

Male A1: ♦= Podogennonta groundpattern, except segment 3 without aesthetasc.

A2: ♦ subterminal geniculate seta on enp reduced (fig. 25); ♦ exp = Podogennonta groundpattern.

Md: ♦ basis with 3 setae; ♦ enp1+2 of Oligoarthra groundpattern fused; ♦ „enp1" with only 2 setae; ✸ „enp2" laterally without setae, apically with single seta, which has become detached from the outer setal triad (figs. 29, 30); ✸ exp 4+5 of Oligoarthra groundpattern (figs. 27 + 28) fused → exp actually 4-segmented with 1,1,1,1+2 setae.

Mxl: ♦ basis with 3+4 setae; ♦ exp with 4 setae; ♦ enp with 4 setae; ♦ 1 outer seta present; ♦ coxa with 6 setae; ♦ praecoxal arthrite as Podogennonta groundpattern.

Mx: ♦ enp = Podogennonta groundpattern, except seta 1 in fig. 37 miniaturized; ♦ praecoxal endite as Podogennonta groundpattern, except distal part with only 2 setae, one of which „flagellate"; ♦ coxal endite = Podogennonta groundpattern.

Mxp: ♦ = Podogennonta groundpattern.

P1: ♦ = Podogennonta groundpattern, except tendency towards elongation of exp2 present in all subtaxa (compare chapter 7.3).

P2-P4: ♦ = Podogennonta groundpattern, except ✸ intercoxal sclerites with paired, pointed projections.

Female P5: ♦ = Podogennonta groundpattern.

Male P2enp: ✸ sexually dimorphic 2-segmented (compare chapter 7.2 and 6.11, fig. 69).

Male P5: ♦ = Podogennonta groundpattern.

Anal somite: ♦ not divided, anal operculum present.

Caudal rami: ⇔ I modified as spine; (✸?) c.r. not longer than broad.

Parastenheliidae

Rostrum: ♦ = Thalestridimorpha groundpattern.

Female A1: ♦ 9-segmented, Thalestridimorpha groundpattern, but see ✸ setation of segments 2 and 4 (figs. 7 + 9).

Male A1: ✸ see Thalestridimorpha groundpattern, but 12+13 and 6+7 fused; ✸ aesthetasc on segment 4 lost; ✸ segment 9 with „spinule row".

A2: ✸ derived from the Thalestridimorpha groundpattern, but exp2-4 of the Oligoarthra groundpattern fused (fig. 26); ✸ proximal seta on exp1 miniaturised (fig. 26).

Md: ♦ basis with 3 setae; ✸ „enp1" with 2, „enp2" with at most 5 setae (fig. 30); ✸ exp1-4 of Thalestridimorpha groundpattern fused, exp shortened, with only 3, at most 4 setae.

Mxl: ✸ basis with 2+4 setae; ♦ enp with 4 setae; ✸ exp lost, but still represented by 3 setae at most; ♦ coxal outer seta present; ⇔ 5 coxal setae; ✸ shape praecoxal arthrite as in fig. 34.

Mx: ✸ enp1-3 of Podogennonta groundpattern fused, still represented by 3 setae at most; ✸ praecoxal endite bilobed, proximal part much shorter than distal part, with 2+2 setae (fig. 43); ♦ coxal endites = Podogennonta groundpattern.

Mxp: ✸ derived from groundpattern of Podogennonta/Thalestridimorpha as in fig. 47: syncoxa with 3 setae (1 proximal lost), basal setae medially moved together, „enp1" with claw and 1 seta, „enp2" with 3 setae, enp + claw fused.

P1: ✸ derived from Podogennonta groundpattern: enp 2-segmented (enp2+3 of Podogennonta groundpattern fused), enp1 elongate, enp 2 with only 3 setae, the middle geniculate seta developed claw-like, exp3 with characteristic setation (fig. 53).

P2-P4: ✸ = Thalestridimorpha groundpattern, except P3enp2 + P4enp2 each with only 1 seta, P2enp3 with only 1 seta, P3enp3 with only 2 setae.

Female P5: ✸ setation as in Podogennonta groundpattern, except seta 6 in fig. 61 lost, benp small and triangular, only reaching to the first quarter of exp 1, the latter strongly elongated (fig. 62).

Male P5: ♦ exp 3-segmented (= Oligoarthra groundpattern); ✹ benp with 2 setae.

Male P2: ♦ 2- or 3-segmented, without modification of setae.

Anal somite: ♦ not divided, anal operculum present.

Caudal rami: ✹ seta I shortened, II elongated (fig. 81D).

Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea (= Taxon B in fig. 4)

Rostrum: ♦ = Thalestridimorpha groundpattern.

Female A1 ♦ = Thalestridimorpha groundpattern.

Male A1 ♦ = Thalestridimorpha groundpattern.

A2: ♦ = Thalestridimorpha groundpattern.

Md: ⇔ = Thalestridimorpha groundpattern, except „enp1“ with inner seta much shorter than outer seta.

Mxl: ♦ = Thalestridimorpha groundpattern.

Mx: ♦ = Thalestridimorpha groundpattern.

Mxp: ♦ = Thalestridimorpha groundpattern.

P1: ♦ = Thalestridimorpha groundpattern.

P2-P4: ♦ = Thalestridimorpha groundpattern.

Female P5: ✹ = Podogennonta groundpattern, except setae 13+14 in fig. 61 lost.

Male P2enp: ✹ always 2-segmented, enp3 with setal modification (fig. 69).

Male P5: ✹ as Podogennonta groundpattern, except exp always 1-segmented.

Anal somite: ♦ = Thalestridimorpha groundpattern.

Caudal rami: ⇔ I modified as spine (fig. 81 A-C, E).

Dactylopusiidae

Rostrum: ♦ = Thalestridimorpha groundpattern.

Female A1: ✹ = Thalestridimorpha groundpattern, except segment 5 with only 2 setae.

Male A1: ✹ = Thalestridimorpha groundpattern, except segments 6+7 fused.

A2: ♦ enp and exp = Thalestridimorpha groundpattern

Md: ♦ basis with 3 setae; ⇔ enp = Thalestridimorpha groundpattern, except inner single seta missing (fig. 30); ✹ exp1 of Thalestridimorpha groundpattern fused with basis, represented by 1 seta being located on the basis (figs. 27 + 28); ✹ exp3+4 of Thalestridimorpha groundpattern fused (figs. 27 + 28); ♦ exp setation complete (= Oligoarthra groundpattern).

Mxl: ♦ basis with 7 setae; ♦ coxal outer seta present; ✹ exp with 3 setae; ♦ enp with 4 setae; ✹ praecoxal arthrite as in fig. 34.

Mx: ✹ enp2+3 of Thalestridimorpha groundpattern fused, with 1,4 setae (fig. 38); ✹ praecoxal endite long and narrow, with only 1 seta, both lobes fused (fig. 43); ✹ coxal endites as in Podogennonta groundpattern, only in the proximal endite 1 „flagellate seta“ lost (fig. 41).

Mxp: ✹ derived from Podogennonta/Thalestridimorpha groundpattern as in fig. 47: syncoxa with only 2 terminal setae, only proximal basal seta retained, enp and claw fused, „enp1“ with 1 seta + claw, „enp2“ with 2 setae.

P1: ✹ derived from Podogennonta groundpattern: enp3 with only 3 setae, anterior and middle one developed claw-like, exp3 shortened, setation terminad displaced, no “true” geniculate setae developed any more (fig. 53).

P2-P4: ✹ = Podogennonta groundpattern, except P4enp3 with proximal inner seta missing.

Female P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern, except seta 6 in fig. 61 missing.

Male P2enp: ♦ 2-segmented; ✹ setal modifications on enp3 as in figs. 69, 72-74.

Male P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern

Anal somite: ♦ = Thalestridimorpha groundpattern.

Caudal rami: ♦ I modified as spine, c.r. broader than long.

Rhynchothalestridae/Thalestrioidea (=Taxon D in fig. 4)

Rostrum: ♦ = Thalestridimorpha groundpattern.

Female A1: ♦ = Thalestridimorpha groundpattern.

Male A1: ♦ = Thalestridimorpha groundpattern.

A2: ♦ = Thalestridimorpha groundpattern.

Md: ♦ enp = Thalestridimorpha groundpattern; ✹ exp1+2 of Thalestridimorpha groundpattern fused, exp3 + 4 shortened, proximal segment elongate, setation complete (= Oligoarthra groundpattern), compare figs. 27 + 28.

Mxl: ♦ = Thalestridimorpha groundpattern.

Mx: ♦ enp and endites = Thalestridimorpha groundpattern.

Mxp: ♦ = Thalestridimorpha groundpattern.

P1: ♦ = Thalestridimorpha groundpattern.

P2-P4: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Female P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Male P2enp: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Male P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Anal somite: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Caudal rami: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Rhynchothalestridae

Rostrum: ♦ = Thalestridimorpha groundpattern.

Female A1: ✹ = Thalestridimorpha groundpattern, except segment 3 with only 9 setae.

Male A1: ♦ = Thalestridimorpha groundpattern.

A2: ♦ = Thalestridimorpha groundpattern.

Md: ♦ = Rhynchothalestridae/Thalestrioidea groundpattern.

Mxl: ♦ basis with 3+4 setae; ♦ enp and exp each with 4 setae (Podogennonta groundpattern); ♦ coxal outer seta present; ✹ praecoxal arthrite = Thalestridimorpha groundpattern, except posterior proximal surface setae lost (fig. 34).

Mx: ✹ = Thalestridimorpha groundpattern, except enp2+3 of Podogennonta groundpattern fused.

Mxp: ✹ = Thalestridimorpha groundpattern, except enp and claw fused; ✹ coxal setae terminally arranged in one single row.

P1: ⇔ probably as in *Ambunguipes* (compare fig. 53 and chapter 6.8), derived from Thalestridimorpha groundpattern.

P2-P4: ♦ Thalestridimorpha groundpattern, except ✹ peculiar shape of articulation between enp2+3 (fig. 58).

Female P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Male P2enp: ♦ 2-segmented; ✹ modification of setae an enp3 as in fig. 69.

Male P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Anal somite: ♦ = Thalestridimorpha groundpattern.

Caudal rami: ♦ = Thalestridimorpha groundpattern.

Thalestrioidea (= Taxon F in fig. 4)

Rostrum: ♦ = Thalestridimorpha groundpattern.

Female A1: ♦ = Thalestridimorpha groundpattern.

Male A1: ✹ = Thalestridimorpha groundpattern except segments 6+7 fused; ✹ segments 2+3 fused; ✹ homologous seta on segment 6 modified (fig. 22).

A2: ✹ = Thalestridimorpha groundpattern, except proximal seta on exp1 miniaturised (fig. 26).

Md: ✹ enp = Thalestridimorpha groundpattern, except "enp2" with missing seta in inner setal triad (compare fig. 30); ♦ exp = Rhynchothalestridae/Thalestrioidea.

Mxl: ♦ praecoxal arthrite = Thalestridimorpha groundpattern; ♦ enp with 4 setae; ♦ basis with 3+4 setae; ✹ Coxa only with at most 4 setae; ✹ coxal outer seta missing.

Mx: ♦ enp = Thalestridimorpha groundpattern (fig. 38); ⇔ praecoxal endite as Thalestridimorpha groundpattern, except on proximal part with only 2 setae; ♦ coxal endites = Podogennonta groundpattern.

Mxp: ✹ = Thalestridimorpha groundpattern, except "enp2" with only 2 setae (fig. 48).

P1: ♦ = Thalestridimorpha groundpattern.

P2-P4: ✹ Thalestridimorpha groundpattern, except P4enp2 with only 1 seta.

Female P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Male P2enp: ♦ 2-segmented; ✹ setae of "enp3" modified as in figs. 69, 71, 73, 75.

Male P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Anal somite: ♦ = Thalestridimorpha groundpattern.

Caudal rami: ♦ = Thalestridimorpha groundpattern.

Diosaccidae

Rostrum: ♦ = Thalestridimorpha groundpattern.

Female A1: ♦ = Thalestridimorpha groundpattern.

Male A1: ♦ = Thalestrioidea groundpattern.

A2: ✹ = Thalestrioidea groundpattern, except proximal seta on exp1 completely lost (fig. 26).

Md: ♦ = Thalestrioidea groundpattern.

Mxl: ♦ = Thalestrioidea groundpattern, except ✹ exp with only 2 setae.

Mx: ♦ enp = Thalestridimorpha groundpattern; ♦ praecoxal endites = Thalestrioidea groundpattern; ♦ coxal endites = Podogennonta groundpattern.

Mxp: ✹ = Thalestrioidea groundpattern, except "enp2" with only 1 small seta (fig. 48).

P1: ✹ = Thalestridimorpha groundpattern, except inner seta on enp1 inserting in distal quarter of the segment and ✹ enp3 without inner seta (fig. 54).

P2-P4: ✹ = Thalestrioidea groundpattern, except P2enp3 with only 1 inner seta.

Female P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

male P2enp: ♦ 2-segmented; ♦ = Thalestrioidea groundpattern, except former P2enp3 with only 1 inner seta.

Male P5: ✹ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern, except benp with only 2 setae (only exception: *Miracia efferata*); ✹ exp: innermost seta lost (inner seta of „enp2").

Anal somite: ♦ = Thalestridimorpha groundpattern.

Caudal rami: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Stenheliinae

Rostrum: ♦ = Thalestridimorpha groundpattern.

Female A1: ✹ = Thalestridimorpha groundpattern, except segments 7+8 fused and setation on segment 9 modified (fig. 10).

Male A1: ♦ = Thalestrioidea groundpattern.

A2: ♦ = Diosaccidae groundpattern.

Md: ♦ enp = Thalestrioidea groundpattern; ✹ exp3 + 4 fused, complete set of setae present, but apparently displaced (fig. 32); ✹ gnathobase with blunt teeth.

Mxl: ♦ = Diosaccidae groundpattern.

Mx: ♦ = Diosaccidae groundpattern.

Mxp: ✹ = Diosaccidae groundpattern, except 1 distal syncoxal seta missing, basal setae moved together towards distal margin, „enp1" with 1 seta lost, all „enp2" setation completely lost (fig. 48).

P1: ♦ = Diosaccidae groundpattern.

P2-P4: ♦ = Diosaccidae groundpattern.

Female P5: ✹ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern, except exp spread away in a characteristic way and enp flattened (fig. 65).

Male P2enp: ♦ 2-segmented; ✹ modification of setae compare chapter 6.11 and fig. 76.

Male P5: ♦ = Diosaccidae groundpattern.

Anal somite: ♦ = Thalestridimorpha groundpattern.

Caudal rami: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Diosaccinae

Rostrum: ⇔ = Thalestridimorpha groundpattern.

Female A1: ✹ = Thalestridimorpha groundpattern, except segment 4 with homologous setae missing (fig. 9).

Male A1: ♦ = Thalestrioidea groundpattern.

A2: ♦ = Diosaccidae groundpattern.

Md: ♦ basis with 3 setae; ♦ enp as Thalestrioidea groundpattern; ♦ exp as Taxon Rhynchothalestridae/Thalestrioidea groundpattern.

Mxl: ♦ = Diosaccidae groundpattern.

Mx: ✹ = Diosaccidae groundpattern, except on proximal coxal endite 1 „flagellate seta" missing (fig. 41).

Mxp: ♦ = Diosaccidae groundpattern.

P1: ♦ = Diosaccidae groundpattern.

P2-P4: ♦ = Diosaccidae groundpattern.

Female P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Male P5: ♦ = Diosaccidae groundpattern.

Male P2: ♦ = Thalestrioidea groundpattern.

Male P1: ✹ basis with 3 large "Nebendornen" and a "nose-like" chitinous projection (fig. 79).

Anal somite: ♦ = Thalestridimorpha groundpattern.

Caudal rami: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Miraciinae (for illustrations compare Huys & Böttger-Schnack, 1994)

Rostrum: ✹ "thalestridimorph", but directed ventrad (fig. 80).

Female A1: ✹ = Diosaccidae groundpattern, except segments 6+7 fused and loss of setae on almost all segments (fig. 7).

Male A1: ✹ = Thalestrioidea groundpattern, except aesthetasc on segment 4 missing; ✹ segments 10+11 fused; ✹ loss of setae on segments (2+3) + 10 (fig. 21).

A2: ✹ exp 1-3 of Podogennonta groundpattern fused, exp strongly reduced; ✹ exp only with 1 terminal and 1 lateral seta.

Md: ✹ palp consisting only of 1 "segment" with 2 setae.

Mxl: ✹ basis, coxa and enp fused, with totally 3 setae, exp developed as small projection with 1 seta.

Mx: ✹ enp only represented by 1 seta, coxal endites each with only 2 setae, praecoxal endite lost, setation partly thickened and deformed.

Mxp: ✹ Diosaccidae groundpattern and see fig. 48.

P1: ✹ derived from Diosaccidae groundpattern, enp2+3 fused with only 3 terminal setae, exp 3 with only 4 setae, setae and segments deformed (fig. 54).

P2-P4: ✹ derived from Diosaccidae groundpattern, setae and segments deformed and displaced, cf. Huys & Böttger-Schnack (1994).

Female P5: ✹ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern, except seta 6 in fig. 61 missing, benp and exp narrowed (fig. 65).

Male P5: ✹ benp with 3 setae (only in *Miracia efferata*), exp with 6 setae, exp long and narrow.

Male P2: ✹ derived from Thalestrioidea groundpattern, compare figs. 4G, 11E+F, 21G+F, 26D in Huys & Böttger-Schnack (1994).

Male P1: ✹ basis with „spinule-like "Nebendornen" (fig. 79).

Anal somite: ✹ not divided, but anal operculum absent.

Caudal rami: ✹ seta I shortened and thickened; rami elongated and broad (compare figs. 13C-E, 27A-C in Huys & Böttger-Schnack, 1994).

Thalestridae

Rostrum: ♦ = Thalestridimorpha groundpattern.

Female A1: ✹ Thalestridimorpha groundpattern, except segment 5 with only 2 setae.

Male A1: ♦ = Thalestrioidea groundpattern.

A2: ✹ = Thalestrioidea groundpattern, except exp2-4 of Oligoarthra groundpattern fused; ✹ seta 3 (in fig. 26) on „exp2" disappeared (fig. 26).

Md: ♦ basis with 3 setae, ✹ enp = Thalestrioidea, except „enp2" with inner seta missing (fig. 30); ✹ exp1-4 of Thalestridimorpha groundpattern fused, exp shortened, setation complete (= Oligoarthra groundpattern).

Mxl: ✹ = Thalestrioidea groundpattern, ⇔ except posterior '"upper" apical spine already reduced (finally lost in the Thalestrinae (fig. 34); ♦ coxa with only 4 setae.

Mx: ✹ enp2+3 of Thalestridimorpha groundpattern fused (fig. 38), setae 6, 8+9 in fig. 37 lost; ✹ praecoxal endite broad and weakly bilobed, each lobe with 1 seta (fig. 42); ♦ coxal endite = Podogennonta groundpattern.

Mxp: ✹ = Thalestrioidea, except 1 proximal syncoxal seta missing, enp + claw fused ✹ enp as in fig. 48.

P1: ⇔ probably = Thalestridimorpha groundpattern (see fig. 54 and discussion in chapter 6.8).

P2-P4: ♦ = Thalestrioidea groundpattern.

Female P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern, except seta 6 in fig. 61 absent; ✹ tendency towards a foliceaous shape of exp and benp; ✹ seta 1 in fig. 61 spatially or by different ornamentation separated from 2 (fig. 63).

Male P2enp: ♦ 2-segmented; ♦ setal modification as in Thalestrioidea groundpattern.

Male P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Anal somite: ♦ = Thalestridimorpha groundpattern.

Caudal rami: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Thalestrinae

Rostrum: : ♦ = Thalestridimorpha groundpattern.

Female A1: ♦ = Thalestridae groundpattern, except ✸ loss of setae on segment 4 (fig. 9).

Male A1: ♦ = Thalestrioidea groundpattern.

A2: ♦ = Thalestridae groundpattern.

Md: ♦ = Thalestridae groundpattern.

Mxl: ✸ = Thalestrioidea groundpattern, except enp with only 3 setae; ✸ praecoxal arthrite as Thalestridimorpha groundpattern, only posterior proximal surface setae and „upper“ apical posterior spine absent (fig. 34); ⇔ exp with 3(4) setae, coxa with only 4 setae.

Mx: ♦ praecoxal endite and enp as Thalestridae groundpattern; ♦ coxal endites as in Podogennonta groundpattern.

Mxp: ♦ = Thalestridae groundpattern.

P1: ♦ = Thalestridae groundpattern.

P2-P4: ✸ = Thalestridae groundpattern, except P3enp2 with only 1 seta.

Female P5: ♦ = Thalestridae groundpattern.

Male P2enp: ♦ = Thalestrioidea groundpattern.

Male P5: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

Anal somite: ♦ = Thalestridimorpha groundpattern.

Caudal rami: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern, (✸ Caudal seta I modified in a different way as in Thalestridimorpha groundpattern?)

Eudactylopusiinae

Rostrum: ♦ = Thalestridimorpha groundpattern.

Female A1: ⇔ = Thalestridimorpha groundpattern, except for setation in fig. 7.

Male A1: ♦ = Thalestrioidea groundpattern.

A2: ✸ = Thalestridae groundpattern, except exp2 strongly shortened, 1 terminal seta missing (fig. 26).

Md: ♦ basis with 3 setae; ✸ enp as Thalestridae, except „enp1“ with only 1 seta; ✸ exp very small, with only 2 apical setae (fig. 28).

Mxl: ✸ specific spatial arrangement of palp, „twisted“ appearance after preparation, coxa with only 2 setae; ✸ praecoxa see Thalestridae groundpattern, except only 1 of the anterior surface setae present, which is located at outer margin (fig. 34).

Mx: ♦ = Thalestridae groundpattern, except ✸ enp only represented by 1 seta (fig. 38); ✸ praecoxal endite clearly with only 1 lobe (fig. 42).

Mxp: ♦ = Thalestridae groundpattern.

P1: ✸ derived from Thalestridimorpha groundpattern: enp1 elongate, enp2+3 of Podogennonta groundpattern fused, enp (2+3) with only 3 setae (1 inner seta missing), exp3 with only 4 setae in total: 3 outer spines and 1 inner „true“ geniculate terminal seta (fig. 54).

P2-P4: ✸ as Thalestridae, except specific shape of articulation between enp2+3.

Female P5: ♦ = Thalestridae groundpattern.

Male P2enp: ♦ = Thalestrioidea groundpattern.

Male P5: ♦ = Thalestrioidea groundpattern.

Anal somite: ♦ = Thalestridimorpha groundpattern.

Caudal rami: ♦ = Taxon Dactylopusiidae/Rhynchothalestridae/Thalestrioidea groundpattern.

6. Analysis and discussion of the characters used in figs. 4 and 82 and in the character list

6.1 Female antennule

6.1.1 Harpacticoida and Oligoarthra groundpattern

Because of the oligomerisation of the proximal segments a direct homologisation of the female oligoarthran antennule with the ancestral copepod antennule is not possible. Huys & Boxshall (1991) tried to solve this problem by homologising the polyarthran and the oligoarthran female antennule and "completing" the oligoarthran segmentation with the polyarthran (p. 116, table 2). A more convincing approach has been published recently (Huys & Boxshall, 1998). It was tried to establish the segmental homology by analysing the ontogenetic development of antennular segmentation and setation patterns across six copepod orders, which revealed numerous common features. These features were combined to produce a hypothetical general model for ontogenetic antennular development in the Copepoda. This "ancestral" pattern, which is mainly based on calanoids and modified by platycopioids, was conferred upon a representative of the Harpacticoida (*Ambunguipes rufocincta*). The resulting segmental homology of the adult female antennule is again reproduced in fig. 5.

Welche Arbeit

The data published by Boxshall & Huys (1998) allow further interpretations:

- A multisegmented adult antennule is considered plesiomorphic (e.g. Huys & Boxshall, 1991). Generally, ontogenetic antennule development in Copepoda seems to proceed primarily by successive separation of articulations. Compound segments result from failure of expression of articulations separating ancestral segments. Therefore, a delay or suppression of the separation of segments which lead to compound segments can be considered as a derived condition. Apart from this primary process, sexual dimorphic compound segments in the adult male are typically due to secondary fusion during the final moult.
- Comparing the patterns of antennule development in the representatives of the six copepod orders in Boxshall & Huys (1998) a further "basic" common feature can be observed: except for harpacticoids, in all other orders the successive separation of articulation principally results in the same segmental number and homologous compound segments in male and female. The additional compound segments in the adult male are secondary fusions and due to sexual dimorphism (as well as a higher number of aesthetascs). In the case of Oligoarthra, represented by *Ambunguipes rufocincta* in Boxshall & Huys (1998), the complete development of the female antennule is delayed so that it retains a copepodid morphology, whereas in the male it undergoes further formation of segments and setae. This is confirmed by data available for other oligoarthran taxa (compare descriptions of Dahms, 1987, 1989, 1990, 1993a, 1993b). The "new" compound segment XIV-XVI in the adult male is probably also due to secondary fusion. Copepodid characters of the oligoarthran adult female antennule are the failure of separation of ancestral segments II, XIII, XVIII, and XXIII. Furthermore the anteroproximal setae of ancestral segments IX-XI, XVII, XVIII and XX are not developed.

- Thus the segmentation and setation of the male antennule, without the compound segments due to sexual dimorphism, are interpreted here as the original oligoarthran groundpattern. The heterochronic events leading to the paedomorphic female antennule are considered here as an autapomorphy of the Oligoarthra.
- The pattern presented by Boxshall & Huys (1998) cannot be generalised for all Harpacticoida, because the morphological structure of the antennule appears to be quite different in Oligoarthra and Polyarthra (compare e.g. figs. 14 + 15). Even when accepting the monophyly of the Harpacticoida, the oligoarthran antennule does probably not represent their groundpattern:
- Female and male of Polyarthra, apart from sexual dimorphism, generally have more characters in common than with females or males of Oligoarthra and vice versa. This is true e.g. in the arrangement of setae and aesthetascs. In Oligoarthra the number of antennular aesthetascs is sexually dimorphic, i.e. at most 4 in the male and 2 in the female, whereas in Polyarthra there seem to be no such sexual dimorphism.
- According to Dahms (1988, 1989, 1993a) Polyarthra have an "own" copepodid development.
- The polyarthran segment 1 inserts on a segment-like projection, which is armed with characteristic spinule rows along the inner margin making it in most cases identifiable also in the literature ("0" in fig. 14). Such a "pedestal" is not present in Oligoarthra.

- The characteristic arrangement of setae, which in most cases can be identified and homologised in the oligoarthran female and male antennule (see figs. 6 + 15), cannot be recognised in Polyarthra, which show quite a different morphology.
- This is apparent also when attempting to homologise the antennular segmentation of both taxa, see e.g. the previous chapter on the male antennule. The homologisation of the female antennules of Polyarthra and Oligoarthra in Huys & Boxshall (1991, see above, compare fig. 5) is mainly based on the assumed aesthetasc homology, which is not convincingly supported.
- The antennular groundpattern of Polyarthra has still to be reconstructed and data on the development pattern are as yet not available either. Therefore the condition of the harpacticoid antennular groundpattern still remains uncertain at present.

Further observation: In all copepod orders the distal array of setae usually is already established at the CI-stage. Oligoarthra are no exception, since the delay in expressing free segment XXIV only at CV seems to be an autapomorphy of *Ambunguipes rufocincta*. Other data on oligoarthran taxa (compare descriptions of *Tegastes clausi*, *Thalestris longimana*, *Parastenhelia megarostrum* by Dahms, 1989, 1990, 1993a, respectively) show, that they fit well into the general pattern.

6.1.2 Groundpattern of the Thalestridimorpha

The groundpattern of the female A1 of the Thalestridimorpha, with the following setal formula: 1(1); 2(12); 3(10); 4(6+aes); 5(3); 6(4); 7(2); 8(2); 9(7+aes), seems to agree with that of the Oligoarthra (figs. 6 + 7). Within Tisbidae and closely related taxa higher setal numbers occur in segments 2 (maximally 15, e.g. in *Drescheriella glacialis*, according to Dahms & Dieckmann, 1987) and 3 (11 setae in *Altheutha interrupta*, according to Huys & Boxshall, 1991). The Superornatiremidae, also supposed to be related to Tisbidae, show supernumerary setae on the swimming legs. It could be that the occurrence of supernumerary setae is restricted to Tisbidae and related taxa. In that case this phenomenon could be regarded as apomorphic. The antennule groundpattern of Thalestridimorpha would then be in complete agreement with the Oligoarthra groundpattern (fig. 6).

For the reconstruction of this groundpattern, the maximal number of setae and segments, as encountered during examination of the material (chapter 2.1) and analysis of the literature, has been taken into account. The setal arrangement is depicted in fig. 6 from dorsal view. The illustration was compiled as follows: Segment 1 after *Paramphiascopsis facialis* (Diosaccinae), 2-8 after *Ambunguipes* spec. (Argentina), whereby the setation of segment 4 was completed after *Stenhelia* spec. 1 (Papua New Guinea), and segment 9 again after *P. facialis*. All segments carry the maximal number of setae present in the Thalestridimorpha and in the Oligoarthra groundpattern (except maybe segments 2 + 3, see above). Segment 1 and the 3 distalmost segments 7-9 are the phylogenetically "oldest" part of the oligoarthran female antennule. Within Copepoda the terminal segment 9 developed in the Cyclopoida and convergently in the Harpacticoida, Siphonostomatoida and Poecilostomatoida (all 4 taxa belong to the Podoplea), by fusion of the ancestral segments XXVI-XXVIII according to Huys & Boxshall (1991). The Calanoida and Platycopioida still carry 9 setae on the respective homologous segments, whereas Podoplea carry only 8 (including the aesthetasc). This and the quite similar spatial arrangement and shape of the setae (compare Huys & Boxshall, 1991) in the respective taxa may nevertheless be indicative of a homologous development in Cyclopoida and other Podoplea.

The following character complexes have been analysed, as far as the female thalestridimorphan antennule is concerned: 1. Fusion of homologous segments, 2. The occurrence of modifications on homologous setae, 3. The loss of homologous setae.

6.1.3 Female antennule within the Thalestridimorpha and Pseudotachidiidae

6.1.3.1 Segmental fusion

All subtaxa of Thalestridimorpha, except for the Stenheliinae and Miraciinae, have retained the 9-segmented oligoarthran antennule. The respective groundpatterns, reconstructed from analysis of material and literature, are depicted in fig. 7. Segmental fusion occurs nearly always within the subtaxa and plays no major role for systematics of the higher categories, except for the fusion of segments 7 + 8 as autapomorphies for Stenheliinae and Miraciinae, respectively 1. The latter fusion occurs quite frequently, e.g. within all genera of Dactylopusiidae, within Parastenheliidae and Diosaccidae. In Diosaccinae, these segments are still separated, e.g. in *Amonardia*, *Metamphiascopsis*, *Amphiascopsis*, and *Typhlamphiascus*. *Robertsonia* additionally shows a fusion of segments 3 + 4, leaving the proximal aesthetasc on the now secondary third segment. The fusion of segments 3 + 4 and 6-8 (often –9) is an autapomorphy for *Paradactylopodia* within the Dactylopusiidae. The latter fusion is, however, also observed within *Diarthrodes*. In nearly all species 7 + 8 are fused as well. The reconstruction of the pseudotachidiid groundpattern (fig. 8) finally results in a (fusion of 7 + 8) 8-segmented antennule **1**, although no more than 7 segments are ever realised in any subtaxon. Segment 5 is only free in *Pseudomesochra*, 6 only in *Idomene* (fig. 8). The fusions of segments 4 + 5 and 6-8 are present within all lineages identified so far (compare chapter 11.2) and seem to have a common genetic basis **8**, as they do not occur in the outgroups (Oligoarthra). Furthermore, the "*Pseudotachidius* lineage" within Pseudotachidiidae shows a fusion of segments 6-9, which also appears within Paranannopinae (*Paradanielssenia*, *Mucrosenia*).

6.1.3.2 Setal modifications and reductions

Setation of the individual antennule segments is specific and more (distal part) or less (segments 2 + 3) easy to homologise. Losses and modifications of homologous setae are indicative of relationships of taxa. The setal groundpattern of the Thalestridimorpha is depicted in fig. 6. In the case of segments 2 + 3 it was nearly impossible to homologise individual setae by form and position. Segment 4 (figs. 6 + 9) carries at most 7 setae (including the aesthetasc), which are grouped in the arrangement "2-2-1-1+aes". The maximal number of setae has been retained by Stenheliinae, Thalestridae (*Eudactylopus*), Hamonidiidae, and probably in the last common ancestor of Dactylopusiidae. This can be deduced from the combined arrangement of the setae in *Dactylopusia* and *Paradactylopodia* (fig. 9). For *Hamondia*, only the original description (Huys, 1990) was available for comparison. In the taxa analysed for the present study one of the setae inserts ventrally (fig. 9), whereas this is not shown in the description of *Hamondia*. Outside Thalestridimorpha the complete groundpattern of the Harpacticoida is only documented in the original descriptions of *Tachidiopsis parasimilis* by Dinet (1974) and *Tachidiopsis sarsi* by Bodin (1968). The Thalestridimorpha apparently also show the most primitive condition within the Oligoarthra. As illustrated in fig. 9, individual setae have become lost within individual lineages. The figure shows the apomorphies for the respective taxa **2-4** (see also chapters 4 + 7).

The complete setation of segment 5, consisting of 1 terminal and 2 smaller subterminal setae, has been completely retained by all Rhynchothalestridae and Stenheliinae, whereas in the other taxa at least 1 subterminal seta is missing **5**. Outside the Thalestridimorpha the complete setation of segment 5 was nowhere observed, except again in the description of *Tachidiopsis parasimilis* by Dinet, 1974. As already mentioned above, the 8 setae (including the aesthestac) of the terminal segment can be easily homologised (figs 6 + 10), but they are conservative in such a way that, except for the Stenheliinae, no further characters could be obtained. Fig. 10 shows the various setal patterns of segment 9 within the examined representatives of the Stenheliinae and the reconstructed stenheliinid groundpattern, into which the data from the literature were included. Autapomorphies of Stenheliinae **6** are a thickened seta 2 (number of setae according to fig. 10), loss of seta 5, and a tendency towards reduction of the terminal aesthetasc, which has become completely lost in some cases, e.g. in *Stenhelia peniculata*, *St. infiernensis*, *St.* spec. 1 (Papua New Guinea). Seta 4 is probably always missing as well. There are morphological hints (suture in the segment), that the proximal seta 1 belongs to the preceding segment in *Stenhelia paradivergens* (fig. 10). The terminal segment is still further derived in *Stenhelia "bifida"* with the loss of more setae and the displacement of the remaining ones.

Contrary to the Thalestridimorpha, strong setal modifications occur within Pseudotachidiidae, but apparently not in their groundpattern. In different lineages there are (compare chapter 11.2) representatives with exclusively long and smooth setae (*Idomene*, *Pseudomesochra*, Pseudotachidiidae gen. 1, spec. 2, Weddell Sea). Setal modifications together with segmental fusions (figs. 8 + 13) and a transformation row were observed within the "*Pseudotachidius* lineage": a homologous seta on segment 2 is miniaturised (fig. 12, compared to Pseudotachidiidae gen. 1, spec.1, representing the "normal" state), segments 3-6 show modifications of the homologous setae (thickening, shortening and modified spinulose ornamentation). In Pseudotachidiidae gen.1, spec. 1 (Weddell Sea) these apomorphic features are still weak compared to *Pseudotachidius* and its immediate relatives, which show the most derived states (figs. 11 + 13). In these cases segments 6-9 are fused (not completely in the *Pseudotachidius similis* group?), all setae are modified, and the terminal aesthetasc is reduced or completely lost (figs. 11 + 13). An "intermediate state" is present in Pseudotachidiidae gen. 1, spec.1 (Weddell Sea) at the base of this group (fig. 13).

P.61: Fig. 5: Different homology schemes of the female antennule of Oligoarthra, Polyarthra and ancestral copepod.

P. 62: Fig. 6: *Groundpattern of the female antennule of the Thalestridimorpha* (probably also of the Oligoarthra).

P. 63: Fig. 7: Groundpattern of the female antennule in the Thalestridimorpha and Oligoarthra.

P. 64: Fig. 8: Groundpattern of the female antennule in the Pseudotachidiidae and Oligoarthra.

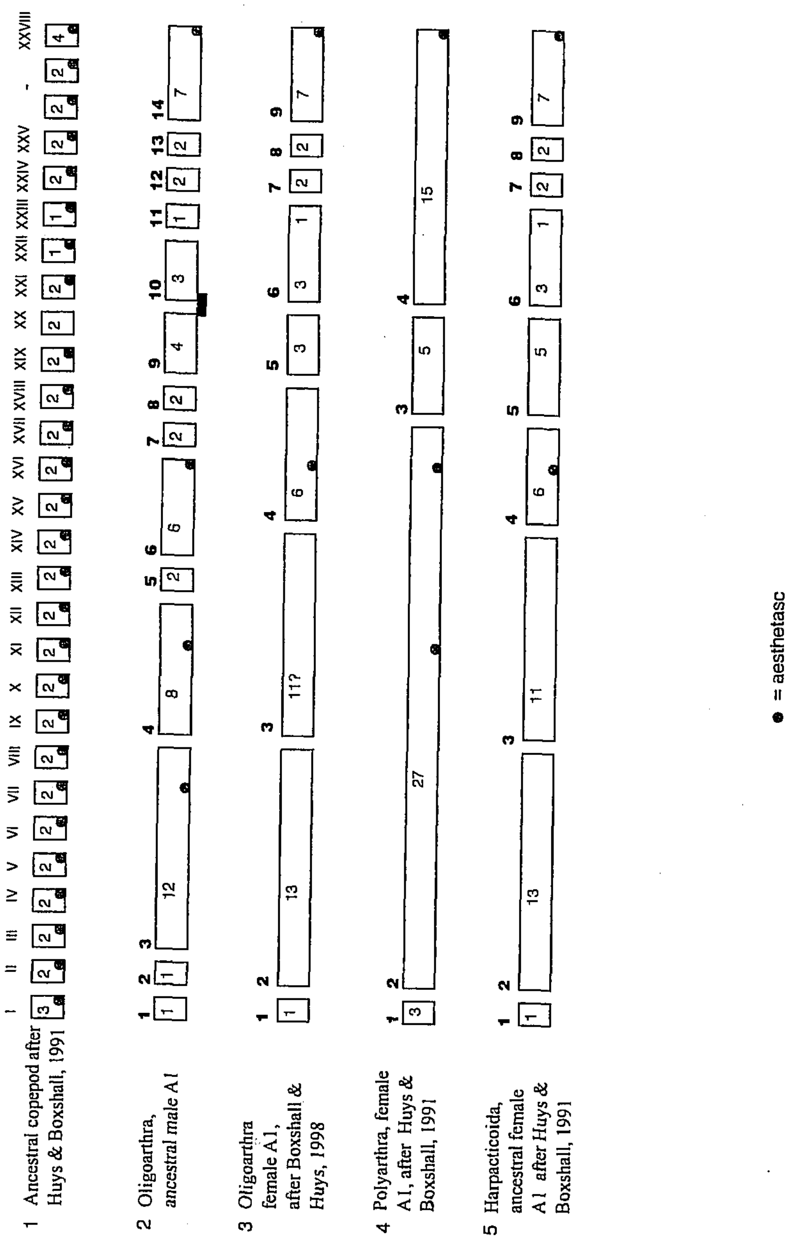
P. 65: Fig. 9: Antennule female segment 4 within the Thalestridimorpha.

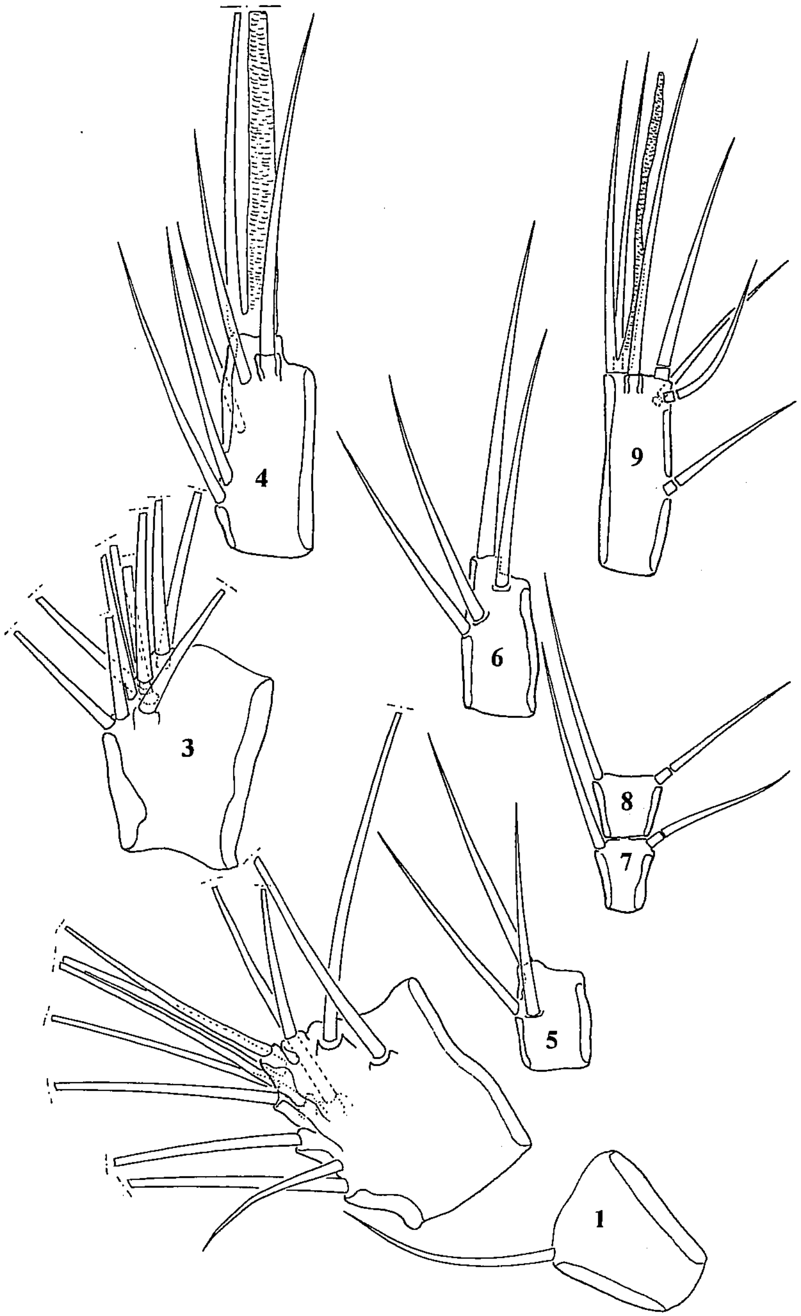
P. 66: Fig. 10: Antennule female segment 9 within the Stenheliinae.

P. 67: Fig. 11: SEM Photographs.

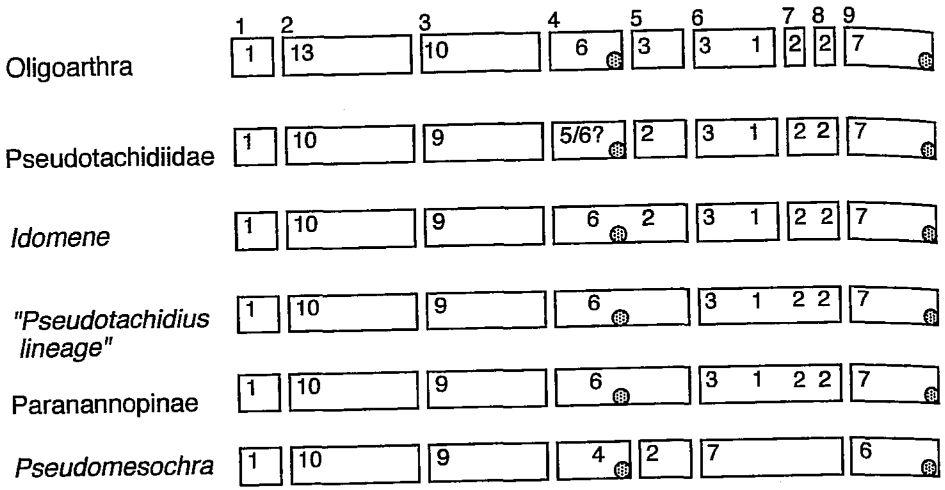
P. 68: Fig. 12: Miniaturised seta on segment 2 of the female antennule within the "*Pseudotachidius lineage*". Pseudotachidiidae gen. 1, spec. 1 still shows a "normally" developed seta, representing the plesiomorphic state.

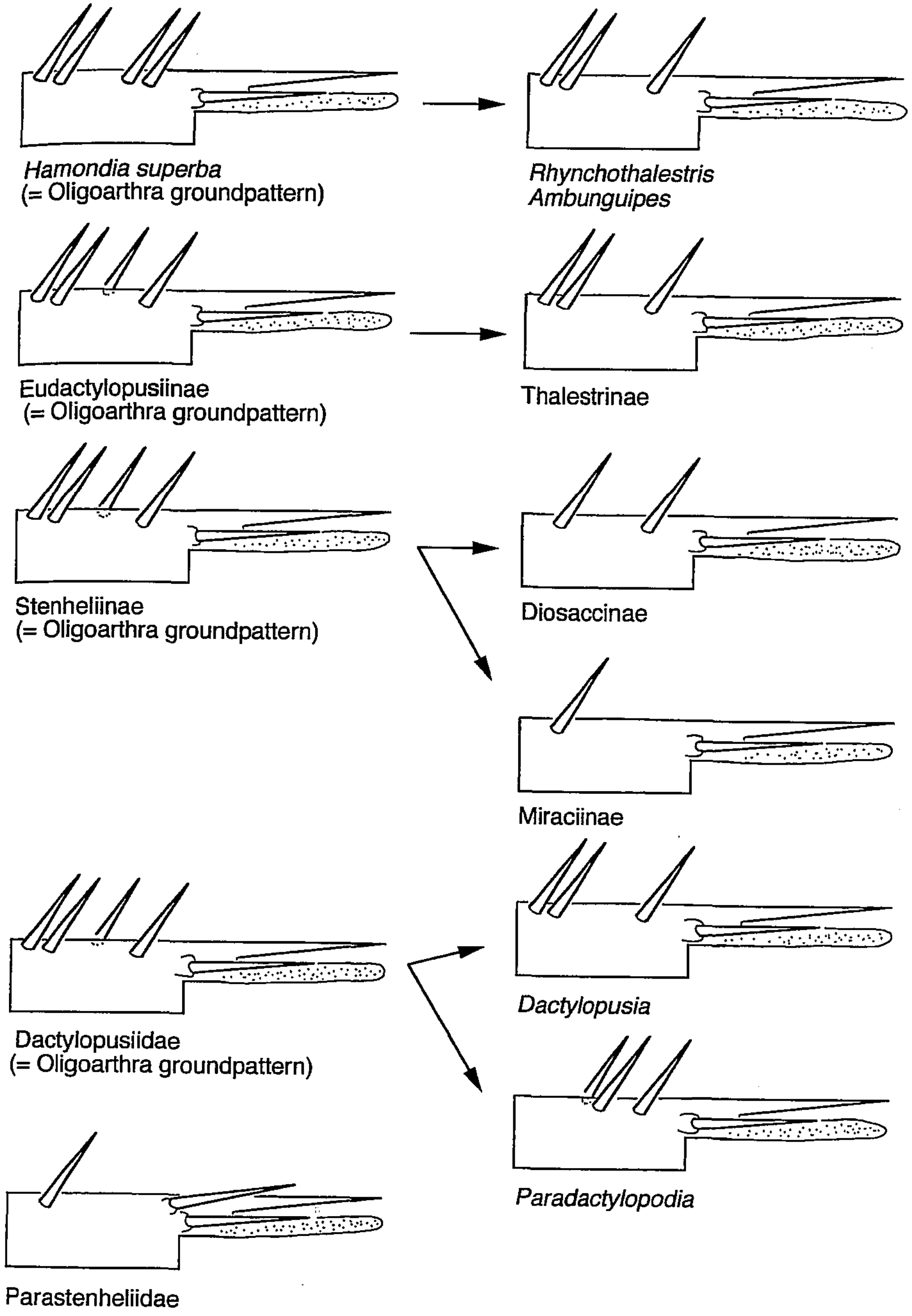
P. 69: Fig. 13: Modified setae on homologous segments of the female antennule within the "*Pseudotachidius* lineage".

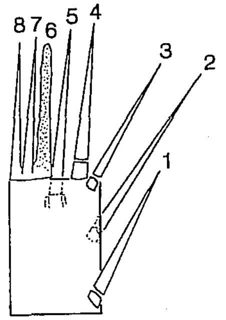




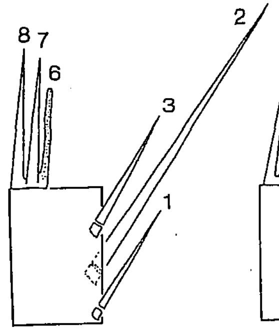
	1	2	3	4	5	6	7	8	9
Oligoarthra groundpattern	1	13	10	6	3	3 1	2	2	7
Parastenheliidae	1	11	9	4	2	3 1	2	2	7
Dactylopusiidae	1	11	10	6	2	3 1	2	2	7
Rhynchothalestridae	1	12	9	6	3	3 1	2	2	7
Ambunguipes	0	12	9	5	3	3 1	2	2	7
Hamondia superba	0	11	8	6	3	3 1	2	2	7
Thalestridimorpha Podogennonta Taxa B, D, F, O, M,	1	12	10	6	3	3 1	2	2	7
Eudactylopus sp.	1	11	11	6	2	3 1	2	2	7
Diosaccidae/ Diosaccinae	1	12	9	4	2	3 1	2	2	7
Stenheliinae	1	11	9	6	3	3 1	2 2		5
Miraciinae	1	7	9	3	2	2 1	2		6


1 2 3 4 5 6 7 8 9
Oligoarthra 1 13 10 6 3 3 1 2 2 7
Pseudotachidiidae 1 10 9 5/6? 2 3 1 2 2 7
Idomene 1 10 9 6 2 3 1 2 2 7
"Pseudotachidius lineage" 1 10 9 6 3 1 2 2 7
Paranannopinae 1 10 9 6 3 1 2 2 7
Pseudomesochra 1 10 9 4 2 7 6

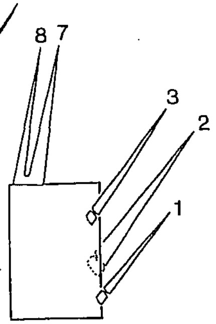

Hamondia superba
(= Oligoarthra groundpattern)
Rhynchothalestris
Ambunguipes
Eudactylopusiinae
(= Oligoarthra groundpattern)
Thalestrinae
Stenheliinae
(= Oligoarthra groundpattern)
Diosaccinae
Miraciinae
Dactylopusiidae
(= Oligoarthra groundpattern)
Dactylopusia
Paradactylopodia
Parastenheliidae



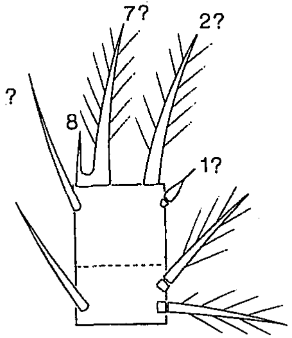
groundpattern Oligoarthra



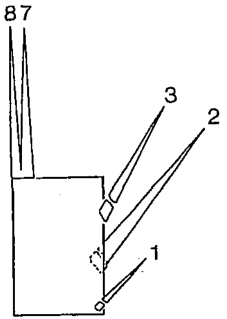
Melima spec.



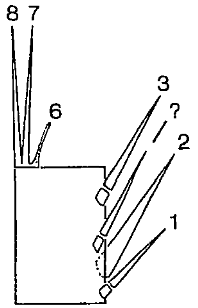
Stenhelia spec



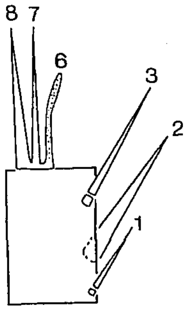
Stenhelia spec. (*bifida*-group)



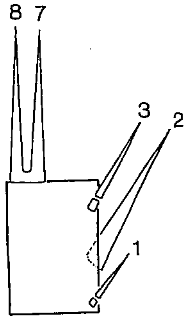
Stenhelia peniculata



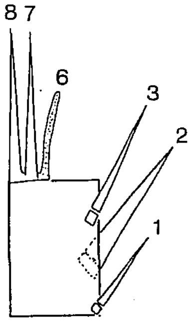
Stenhelia paradivergens



Pseudostenhelia wellsi



Stenhelia spec. (Mexico)



Stenheliidae groundpattern

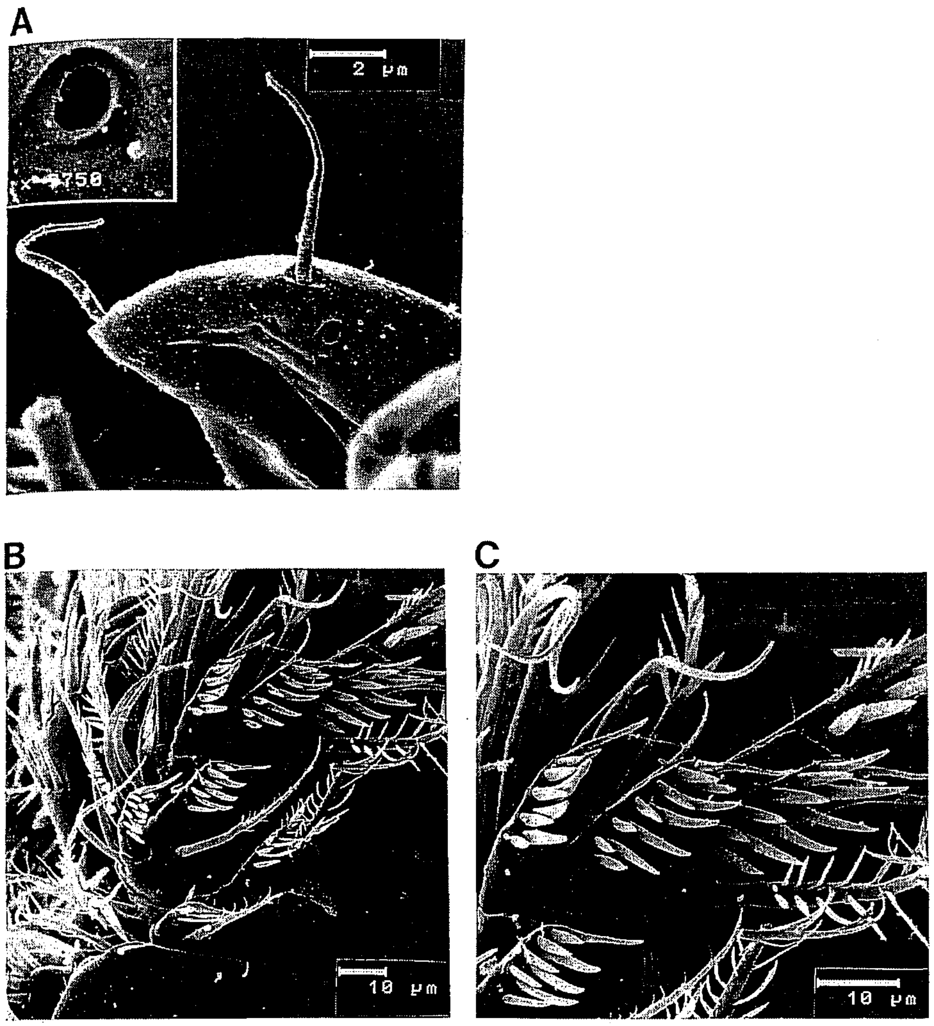
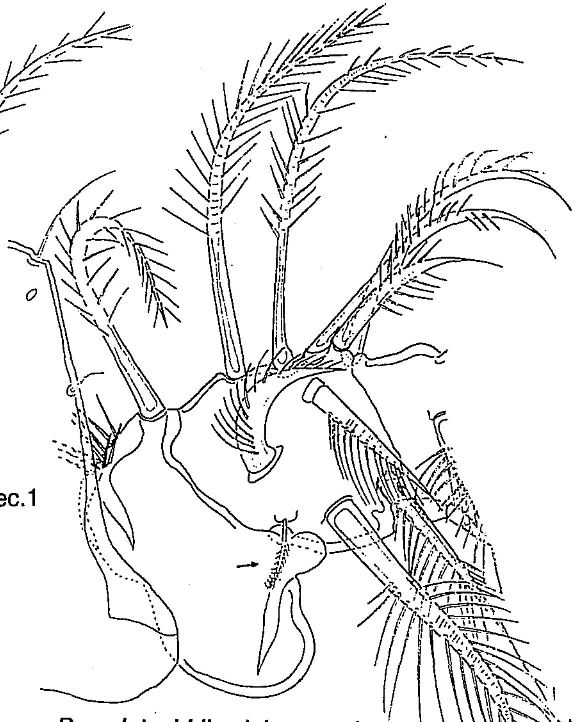
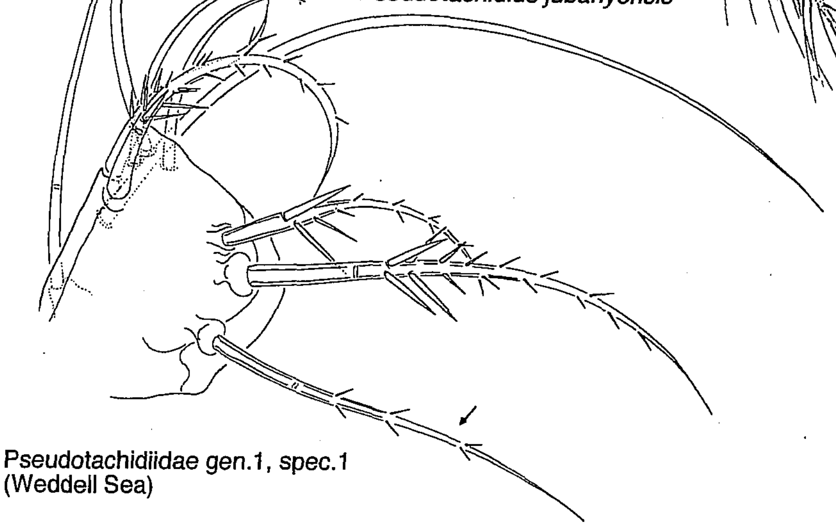


Fig. 11: REM photographs: A: rostrum with ventrally located subapical large pores in *Pseudotachidius jubanyensis*. B: female antennule in a dorsal overview in Pseudotachidiidae gen. 2, spec.. C: distal segments of the female antennule in Pseudotachidiidae gen. 2, spec. ("*Pseudotachidius lineage*") with characteristic spinule ornamentation of setae in detail.

Pseudotachidiidae gen. 2, spec.1
(Weddell Sea)

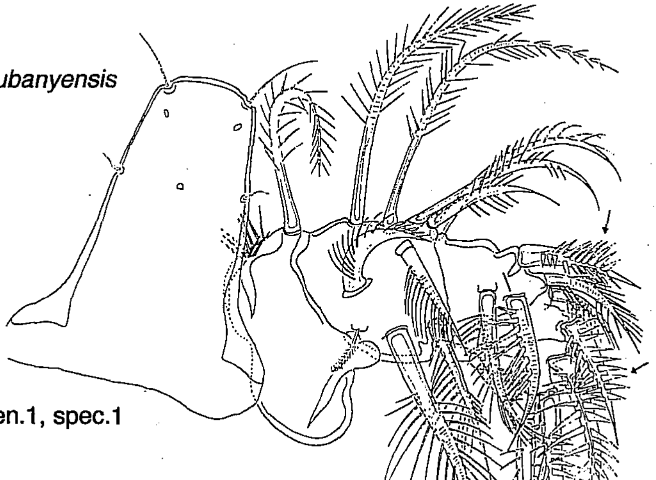


Pseudotachidius jubanyensis



Pseudotachidiidae gen.1, spec.1
(Weddell Sea)

Pseudotachidius jubanyensis



Pseudotachidiidae gen.1, spec.1
(Weddell Sea)

6. 2 Male antennule

6.2.1 Groundpattern of the Harpacticoida

According Huys & Boxshall (1991) the harpacticoid groundpattern of segmentation and setation agrees with the male antennule of *Hamondia superba* (Thalestridimorpha, Rhynchothalestridae). This antennule because of its still complete setation (except for ancestral segments I and II, see fig. 16) makes homologisation of segments with those of the antennule of the ancestral copepod quite reliable. The main geniculation is located between the ancestral segments XX and XXI, which is homologous with that of the other Neocopepoda ("neocopepodan geniculation"). The oligoarthran segments 12 + 13 show the "posterior setae", which are also present in the equivalent ancestral segments. This was verified with the examination of more than 100 species of Harpacticoida (see chapter 2.1) and the literature.

It turned out, that *Hamondia* apparently lacks a modified scale-like seta of segment 9, which has been observed in nearly all oligoarthran taxa (e.g. Diosaccidae, Thalestridae, Neobradyiidae, in the latter developed as seta) and therefore has to be added to the oligoarthran groundpattern (compare figs. 13 + 14). Furthermore, all Thalestridimorpha, and therefore *Hamondia* as well, lack an aesthetasc on segment 3. Such an aesthetasc is widely distributed within the Harpacticoida, e.g. in the Pseudotachidiidae, Harpacticidae (*Perissocope* spec., Weddell Sea), Cerviniidae, Rotundiclipeidae, Aegisthidae, Novocriniidae, and Harpacticoida fam. nov. 1. This, and its position as the outermost element on the ventral side of the segment (the exact homologisation of every individual seta is quite difficult in the proximal part of the antennule in the adult) lead to the assumption, that an asthetasc on this segment belongs primarily to the oligoarthran groundpattern. The question arises of whether the asthetasc in the Thalestridimorpha and in the Paranannopinae and *Protolatiremus* has either simply become lost or modified into a seta. In the examined harpacticoid species the assumed complete setation of segment 3, "12 + aes", was actually never observed, but always either "11 + aes" or 12 setae without aesthetasc. Both alternatives occur within closely related taxa (Paranannopinae, other Pseudotachidiidae). These observations speak in favour of a secondary aesthetasc having developed from the present setal set of the segment.

On the other hand, the following arguments speak in favour of the asthetasc being "primary" and a setation of "12 + aes" in the oligoarthran groundpattern:

- the complete setation of the antennule, excluding the aesthetascs, agrees exactly with that of the ancestral antennule (except for segments 1 and 2 being homologous with the ancestral segments I + II and carrying only 1 seta each = another autapomorphy of the Oligoarthra?). The aesthetasc in question could easily be explained as primary aesthetasc being adopted from the ancestral antennule. Furthermore,
- all other 3 aesthetascs of the male antennule groundpattern are most probably such "primary" aesthetacs:
  - Aesthetasc on segment 4 of the Oligoarthra: this aesthetasc is always the outermost element on the ventral side of the segment. Dahms (1988) followed the ontogenetic development from a certain seta in *Tegastes clausi* (CIV-CVI) and *Thalestris longimana*. In the Oligoarthra groundpattern segment 4 has retained the complete 8 setae of ancestral segments IX-XII and the additional aesthetasc, which therefore originates primarily from the setal set of the ancestral segments and not secondarily from a modified seta (the ontogeny maybe reflects the evolutionary development of the aesthestasc from a seta in the ancestral copepod?). There are a few examples with 9 setae without aesthetasc, viz. *Neobradya pectinifera* (see fig. 18) and *Sentiropsis minuta* (whereas the other Paranannopinae follow the above-mentioned pattern with "8 + aes"). These cases are considered here as derived.
  - Aesthetasc on segment 6: this aesthetasc is also added to the complete set of setae of the equivalent ancestral segments XIV-XVI. The basal fusion with a seta (in both sexes) is maybe an autapomorphy of the Oligoarthra, although there are cases in primitive taxa, in which both elements seem to be still separated, e.g. *Tachidiopsis* spec. (Weddell Sea) and Harpacticoida fam. 1. The "tritheka complex" in *Heterolaophonte minuta* described by Dahms (1989), in which a third seta is added, seems to be an (aut?)apomorphy of the Laophontidae. In this case the single distal seta of the setal "2-2-1" group (compare figs. 13 + 20) is shifted distad towards the aesthetasc/seta complex. However, this phenomenon is not connected in any way with the "tritheka complex" on the male antennulae of the Calanoida after Giesbrecht (according to Dahms, 1989).

- Terminal aesthetasc on the terminal segment: this aesthetasc occurs in addition to 7 setae (the eighth seta of the ancestral groundpattern has apparently become lost within the Podoplea, see also chapter 6.1 and available data from Huys & Boxshall, 1991) and is homologous with the aesthetasc on the ancestral segment XXVIII (terminal location). The question of to which extent the fusion with 2 other setae to a "tritheka" is distributed beyond Harpacticoida remains to be examined.

The aesthetasc on segment 3 is considered here as a primary aesthetasc.

In all copepod orders more aesthetascs and/or other than the above-mentioned ones are present, whereas only the latter have been retained as primary aesthetascs in the Oligoarthra. This could be interpreted as autapomorphy for them within the Copepoda. Within the Cerviniidae also secondary aesthetascs can be observed (fig. 20). However, no male specimens of Cerviniidae have been available for examination in the present study.

For the reconstruction of the ancestral male harpacticoid antennule, Huys & Boxshall did not consider the Polyarthra. In this taxon the antennular segmentation and setation is reduced, compared to the Oligoarthra, not allowing a direct homologisation with the ancestral copepod antennule. The general morphology of the polyarthran antennule, i.e. position and shape of setae as well as proportions and shape of segments differ considerably from those of the Oligoarthra and can in contrast to the more specialised antennule types of the Oligoarthra (compare e.g. fig. 14 with figs. 15, 18, 19 + 20) apparently not be derived from the "qualitative" and "quantitative" oligoarthran groundpattern discussed below. To test the general "compatibility" of the polyarthran antennule with the oligoarthran one an attempt was made to homologise setation and segmentation of both types by analysing the description of *Echinosunaristes bathyalis* by Huys (1995, figs. 14 + 16). Since no own material was available, this description was the only reliable source of detailed information about segmentation and setation of the polyarthran male antennule. A survey of the literature confirmed, that only *Canuellina tuba* Por, 1983 and *Sottolana uxoris* Por, 1969 show the same number of segments in the distal part of the antennule as *Echinosunaristes bathyalis*, the latter therefore probably representing a quite primitive condition with regard to the male antennule.

Different homology constellations are depicted in fig. 16. "Polyarthra A-E" follows Huys & Boxshall (1991) in homologising both proximal aesthetascs present in both sexes of the Polyarthra with the aesthetascs on the male oligoarthran segments 4 and 6 equivalent to ancestral segments XI and XVI. This was supported by the authors only for the aesthetasc on ancestral segment XI in the female Polyarthra antennule, which is followed distad by 12 more setae (= 6 ancestral segments). Otherwise only the preassumed monophyly of the Harpacticoida seemed to be the basis of this decision. With this aesthetasc homology also the proximal part of the polyarthran antennule is defined until ancestral segment XVI (figs. 16 A-E). All subsequent distal segments must therefore be distributed across oligoarthran segments 7-14 (= ancestral segments XVII-XXVIII). In the constellations A + B the Polyarthra segment 5 shows more setae than the equivalent ancestral segments. In C segment 5 is extended by adding ancestral segment XXVI at the expense of segment 6, in D by adding XX at the expense of segment 4. Furthermore, in D the segments XX and XXI forming the proximal and distal part of the "neocopepodan geniculation" in all Neocopepoda would be fused. In constellations A-D the "main geniculation" of the male antennule would not be homologous with the "neocopepodan geniculation" but would be located more distad. An attempt to homologise this geniculation with the "neocopepodan geniculation" (E-F in fig. 16) in spite of all that would result in supernumerary setae on the polyarthran segments 4 + 5, which lie proximally of the geniculation (constellation E), or the aesthetasc homology with the oligoarthran antennule falls apart (F). The constellations probably being the most compatible solutions are C, D + F. An argument against C, however, is the presence of 7 setae on segment 6, which was described for *Scottolana dissimilis* by Fiers (1982) and for *Canuellina tuba* by Por (1983), and which would imply the incorporation of at least 3 ancestral segments into segment 6. The consequence would be again the constellations A, B or D. However, in the latter the segments forming the "neocopepodan geniculation" in all other Neocopepoda are not separated but incorporated in segment 5, which would be absolutely unique within the Copepoda. Moreover, the morphology of segment 4 (compare fig. 14) suggests an incorporation of more than 2 segments. In constellation F the preassumed aesthetasc homology with the oligoarthran antennule would fall apart. These considerations lead to the consequence that the groundpattern of an assumed monophylum Harpacticoida has to be different from that postulated by Huys & Boxshall. Their hypothesis represents only the groundpattern of the Thalestridimorpha.

Another question arises concerning the homology of polyarthran segment 1, which carries at most 3 setae. It is located on a segment-like projection, which is armed on the inner margin with characteristic spinule rows making it in most cases identifiable also in the literature ("0" in fig. 14). According to Huys (1995) this structure is no real segment but a pedestal, from which segment 1 arises. However, there are indications in the literature that "0" is carrying a seta and therefore is a real segment (in *Longipedia weberi* Itô, 1980, described in the female, which is, however, homologous with the male in this part of the antennule, *Parasunaristes cucullaris* Fiers, 1982 female, *Scottolana glabra* Fiers, 1982, female and male). This would lead to a further shift of the homologies in fig. 16, the former segment 1 with the 3 setae being a fusion product at least of ancestral segments II + III (more than 2 setae), whereas the first 2 segments are clearly equivalent to the free ancestral segments I + II in the Oligoarthra.

A thorough revision of the Polyarthra with the purpose of reconstructing a male antennule groundpattern is necessary, before final statements are possible. There are e.g. also indications of a further separation of segment 2 (*Longipedia coronata* Wells, 1980, *Canuella paenelantica* Fiers, 1982, *Brianola elegans* Hamond, 1973) in the literature. These indications are summarized as follows:

- The male A1 of the Polyarthra shows a morphological structure "qualitatively" and "quantitatively" different from the Oligoarthra (compare also the female antennule), not easily derivable from the groundpattern of the latter.
- The "not compatible" constellations A-E in fig. 16 suggest, that the aesthetasc homology of Oligoarthra and Polyarthra assumed by Huys & Boxshall (1991) is questionable.
- Assuming the monophyly of the Harpacticoida and thus a common male antennule groundpattern, the latter would have to be completely different from the one proposed by Huys & Boxshall (1991) which was based only on the Oligoarthra (probably with more aesthetascs, different setation and segmentation). The male A1 of the Polyarthra would have to be considered as a strongly derived appendage, with a secondary "main geniculation".

6.2.2 Groundpattern of Oligoarthra and Podogennonta

The groundpattern of these taxa agrees with the segmentation and setation depicted in figs. 15 + 16.

Shape and arrangement of the setae (except for setation of segments 3 + 4 in fig. 15) are specific in such a way ("qualitative groundpattern") that they are still identifiable in more derived types of oligoarthran antennules, e.g. in antennules, in which the segments around the geniculation are fused and/or swollen (subchirocer and chirocer type, e.g. Pseudotachidiidae, figs. 17 + 19 and *Geeopsis incisipes*, fig. 18) or strong alterations of the segmental length proportions occur (*Aegisthus mucronatus*, fig. 18). The male antennules of the cerviniid taxa, which show a secondary loss of the geniculation can nevertheless be traced back to the above-mentioned groundpattern (fig. 20).

There is much uncertainty in the literature about the male antennule types haplocer, subchirocer, and chirocer introduced by Lang (1948), which have led to misinterpretations and misunderstandings. Dahms′ statement (1988), that antennule type, "clasping mode", and taxonomic level are not correlated in any way has been misunderstood by Huys & Boxshall (1991). They write (p. 116), that "Dahms (1988) found no correlation between type of antennule and taxonomic affinities. Within a single genus closely related species exhibiting either chirocer or subchirocer antennules can be found." In the present study it is shown, that the occurrence of homologous segmental fusions, including the formation of chirocer and subchirocer antennules depends quite well on the respective taxon (fig. 21) and the shape of the antennule even offers autapomorphies for the identification of taxa. E.g., a subchirocer or chirocer antennule never occurs in the Thalestridimorpha, whereas a subchirocer antennule is already an apomorphic character of the Pseudotachidiidae groundpattern **12**. The vague definition of the 3 types by Lang (1935, 1948), which has been adopted by Huys & Boxshall (1991) is a problem:

Haplocer: "only weakly developed, the swollen part is just a little thicker than the preceding segments and they carry distalwards of the swelling a variable number of segments."

Subchirocer: occupies an "intermediate position", "sometimes near one type, sometimes near the other. The swollen part is however in most cases stronger developed than in the preceding [haplocer] type, and they carry 2, at most 3 distal segments."

Chirocer: "strongest swelling" "[...], having never more than 1 segment distal of this part." "The swollen part is in most cases formed by fusion of different segments [...]" (Lang, 1948, p. 41/42). The haplocer antennule is considered as the most primitive type.

First of all it has to be taken into account that these characterisations are purely descriptive and for themselves do not allow a statement about homologies and/or phylogenetic relationships. Chirocer and subchirocer antennules can co-occur in closely related taxa, a fact, which was regarded as an indication of independence of the taxononomic level by Huys & Boxshall (see above), because the former can be a further derived state of the latter, as e.g. within the Pseudotachidiidae (see the example of the paranannopinid species below). Huys & Gee (1996) describe the male antennule of *Peltisenia aberrans* (Paranannopinae) as haplocer, and therefore as the more primitive antennule, only because the compound segment preceding the geniculation is not swollen ("*P. aberrans* is the only species in the Paranannopidae [...] to have haplocer antennules", p. 73). Instead, this antennule originates from the subchirocer groundpattern of the Pseudotachidiidae (figs. 17 + 19) being already derived from the Oligoarthra groundpattern, as well as the antennules of *Sentiropsis minuta* and *Afrosenia spinipes*, which are described as chirocer and subchirocer, respectively, in the same publication. In this case the flattened segment in question in *Peltisenia aberrans*, on the basis of the pseudotachidiid groundpattern, has to be regarded as even further derived. Fiers (1982) describes the male antennule of *Scottolana glabra* as "modified as a typical haplocer organ", only because the segment preceding the "main geniculation" is flattened and despite the fact, that this antennule belongs to the above-discussed Polyarthra type, which is not homologous in many aspects.

Dahms (1988) also follows Lang's definition and considers the haplocer type as primitive within Harpacticoida, and additionally presumes that chirocer and subchirocer antennules have developed independently more than once within Oligoarthra. Chirocer/subchirocer antennules occur by all means also convergently in taxa that are not closely related (e.g. *Geeopsis incisipes*, fig. 18, Pseudotachidiidae, fig. 19, Harpacticidae, Laophontidae).

Since it can certainly be of advantage to use these terms as short descriptions with high information content, the following new definitions are proposed (fig. 17):

Haplocer: the segments 6-9 remain separated and segment 10 is at best fused with 11. Therefore the segments before and after the geniculation remain free. This type in its most primitive state agrees with the oligoarthran groundpattern (fig. 15), but still includes the possibility of fusion of single segments.

Subchirocer: segments 6-9 fuse to a "compound segment" and together form the proximal part of the geniculation, whereas all segments in the distal part can remain free in the most primitive state, or are partially fused (figs. 15 + 17).

Chirocer: in this type segments 6-9 are fused and all segments located distally of the geniculation are also fused to one single segment.

This definition is independent of a subjective estimation of a "more" or "less" pronounced swelling of the "middle" segments. Since the Polyarthra show a special type of antennule (see above), the homologies of which are not as clear as in the Oligoarthra, these terms should be used only for the latter. Within the Oligoarthra there are other antennule types, which cannot be characterised by Lang's terms. An example is *Aegisthus mucronatus* (see fig. 18) with strongly modified segmental length proportions. A secondary loss of the geniculation can be observed in certain cerviniid taxa (fig. 20). In *Eucanuella spinifera* the two segments concerned still show the "geniculative" deformation, whereas this is not true any more for *Cervinia plumosa* and *C. magna*. However, in contrast to the Polyarthra, these derived antennules always show morphological evidence, that they can be traced back to the oligoarthran groundpattern (characteristic setation).

6.2.3 Groundpattern of the Thalestridimorpha

The groundpattern is depicted in fig. 21 and has been completely retained by *Hamondia superba* (Rhynchothalestridae). The shape of the male antennule is quite conservative, as far as setation and segmentation are concerned. The complete set of setae is nearly always present. The aesthetasc on segment 4 has been lost in the Parastenheliidae, Miraciinae **15** and within Diosaccinae. Loss of setae occurs mainly on segment 3 (Parastenheliidae, Miraciinae), whereas in the distal part of the antennule the setation is nearly always complete, except for the Miraciinae, which show a pronounced setal reduction in their groundpattern (fig. 21) **13**. A free segment 7 is still present only in very few taxa of Harpacticoida, e.g. in *Hamondia*, *Ambunguipes*, and *Protolatiremus sakaguchii* as representatives of the Podogennonta, in Chappuisiidae (*Chappuisus inopinus* from Karlstein), and in Rotundiclipeidae. Therefore its fusion with segment 6 in almost all taxa of Thalestridimorpha is not a useful character for analysing phylogenetic relationships. Besides 6 + 7, also 12 + 13 are fused in the Stenheliinae.

Segment 2 (= ancestral segment II) is represented in *Parastenhelia megarostrum* and *Karllangia* by a ventrally located, deformed sclerite (fig. 23) bearing 1 apical seta, which inserts on a projection reaching far into the proximal half of segment 3. This specialisation is only present in the above-mentioned taxa, whereas segment 2 is either fused with 3 or has become lost in the remaining Parastenheliidae. Therefore it is difficult to decide on which systematic level this character is autapomorphic. In any case, a free segment 2 still belongs to the groundpattern of the Parastenheliidae. An autapomorphy of the Parastenheliidae is the occurrence of a spinule row on segment 9 **11**. In the Thalestrioidea segment 2 (= ancestral segment II) is clearly fused with segment 3 (the latter bearing 1 additional seta) **9**. A further apomorphic character is the modification of a certain seta on segment 6 **10** (the outermost of the second pair of setae from the seta group "2-2-1-1+aes", see fig. 22).

6.2.4 Groundpattern of the Pseudotachidiidae

The groundpattern of this taxon is depicted in figs. 17, 19, 21. Segments 6-9 are always fused (subchirocer type) **12**. The number of setae agrees with the Oligoarthra groundpattern. Also the chirocer type, with a complete fusion of all segments distal of the geniculation, occurs within the Pseudotachidiidae, e.g. in *Sentiropsis minuta* (Paranannopinae). The Paranannopinae lack the aesthetascs on segment 3 and 4, respectively, and segments 12+13 are always fused.

P. 79: fig. 14: Male antennule of *Echinosunaristes bathyalis* (Polyarthra) after Huys, 1995).

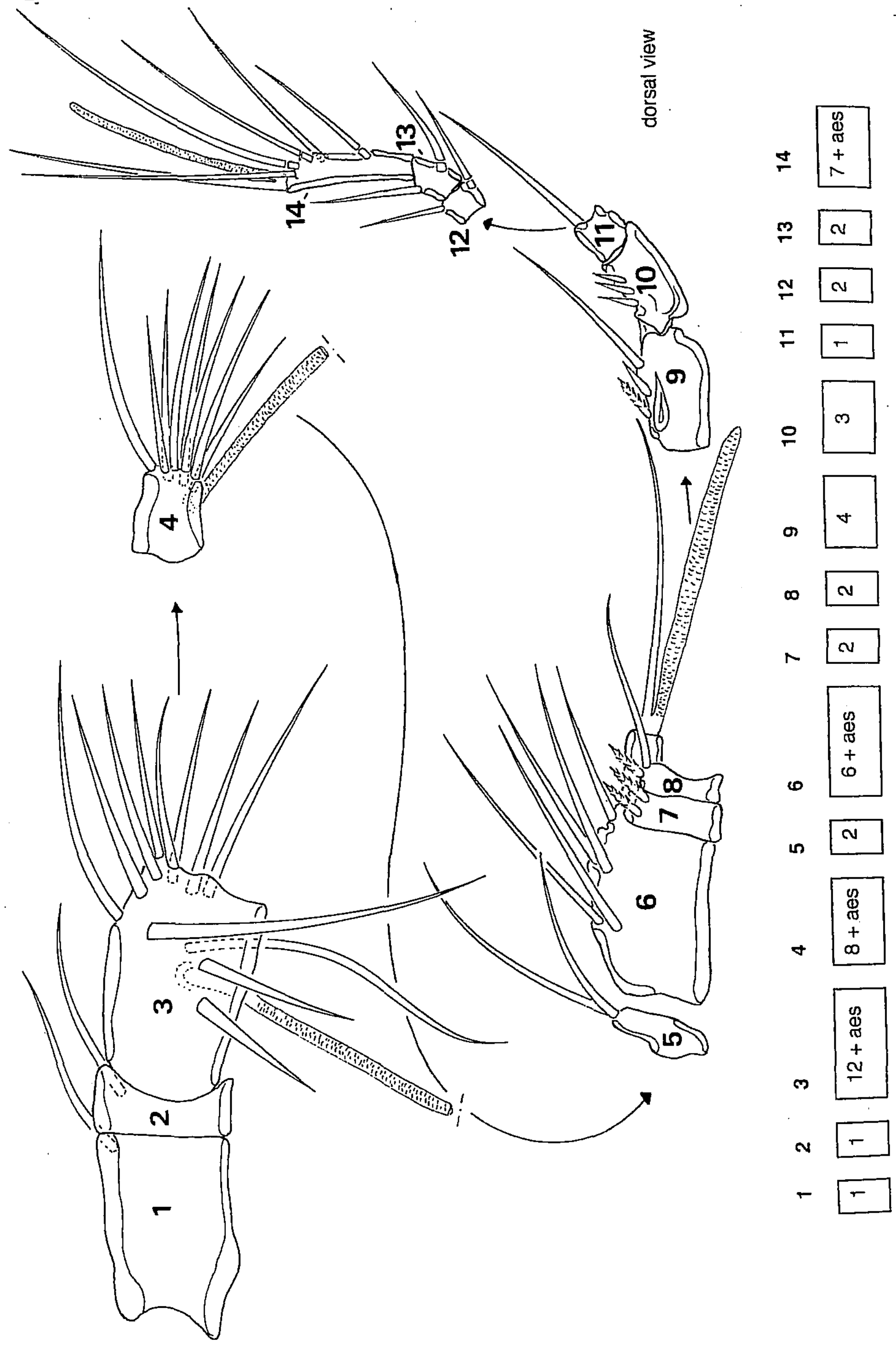
P. 80: fig. 15: Groundpattern of the male antennule of the Oligoarthra and Podogennonta.

P. 81: fig. 16: Attempt of a homologisation of the antennules of Oligoarthra, Polyarthra and ancestral copepod (for further explanation see chapter 5.2.1).

P. 82: fig. 17: Specified definition of Lang's types of oligoarthran male antennules.


Echinosunaristes bathyalis
(illustration of Huys, 1995, Canuellidae)

armature: 0; I(3); II(2 aes + 18); III (1); IV(1 + 3); V(8 + 2); VI(5 + 1)


dorsal view
1
2
3
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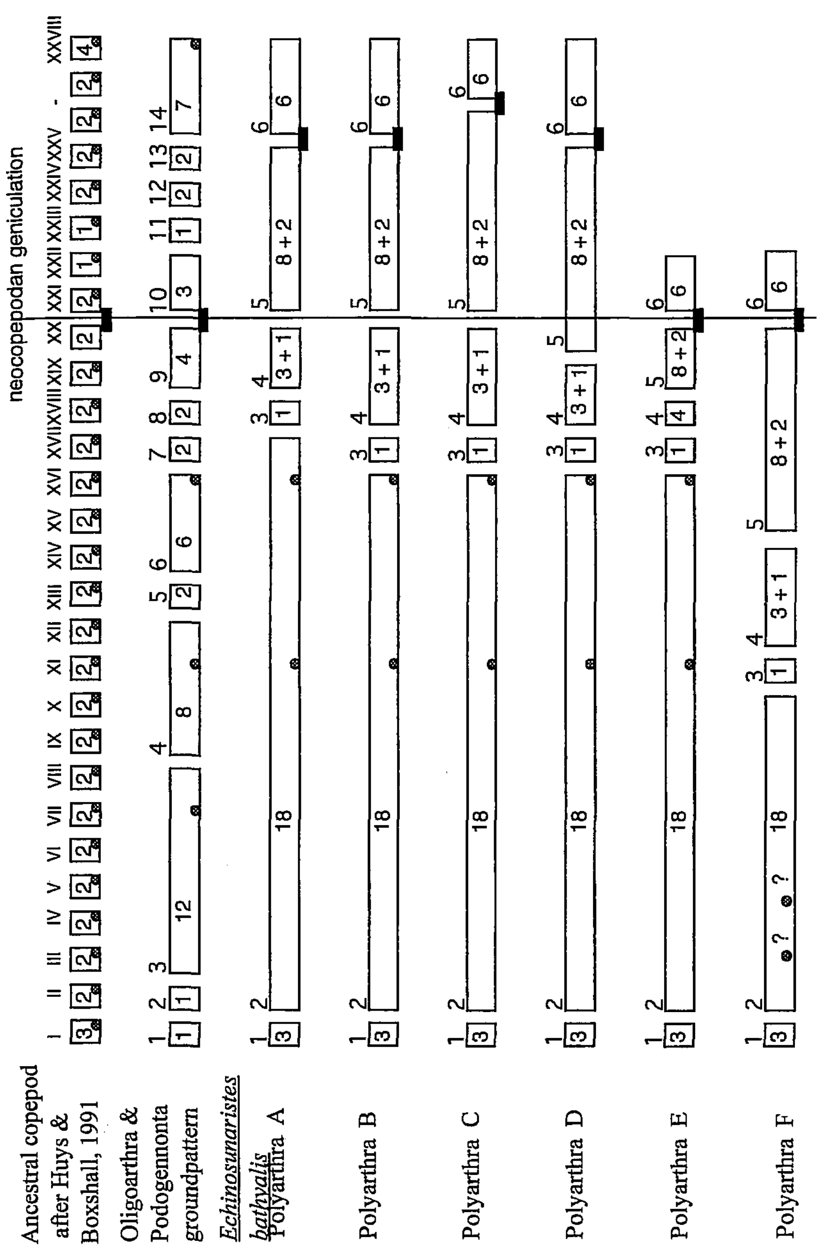
11
12
13
14
1 2 3 4 5 6 7 8 9 10 11 12 13 14
1
1
12 + aes
8 + aes
2
6 + aes
2
2
4
3
1
2
2
7 + aes


neocopepodan geniculation
I II III IV V VI VII VIII IX X XI XII XIII XIV XV XVI XVII XVIII XIX XX XXI XXII XXIII XXIV XXV - XXVIII
Ancestral copepod after Huys & Boxshall, 1991
Oligoarthra & Podogennonta groundpattern
Echinosunaristes bathyalis
Polyarthra A
Polyarthra B
Polyarthra C
Polyarthra D
Polyarthra E
Polyarthra F
12
8
6
7
18
8 + 2
3 + 1
6
?

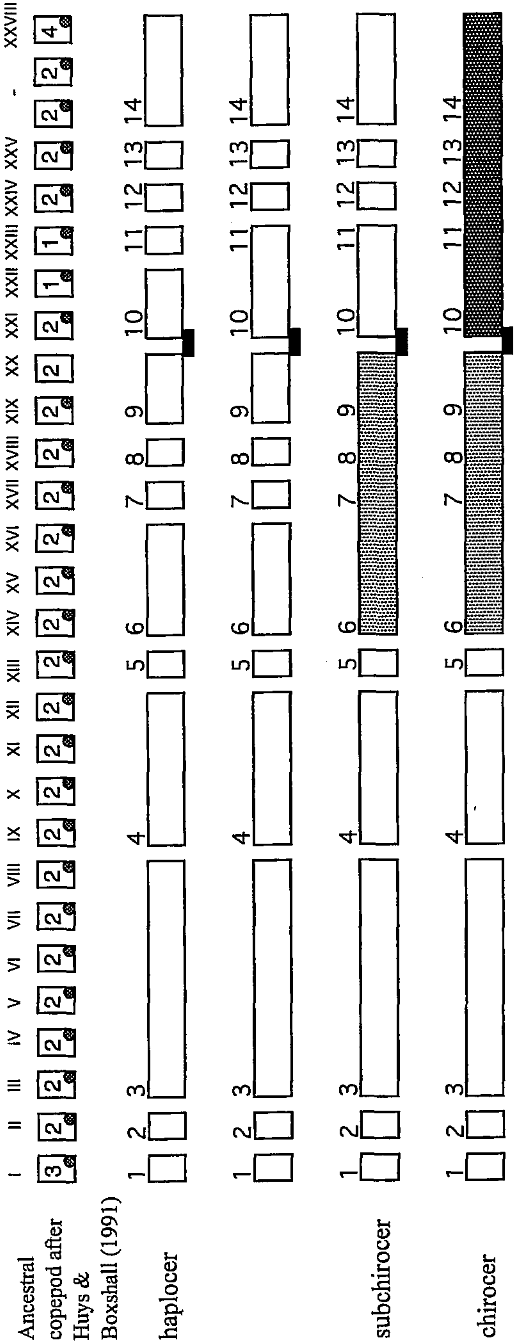


Fig. 18: Different types of male antennule within the Oligoarthra.

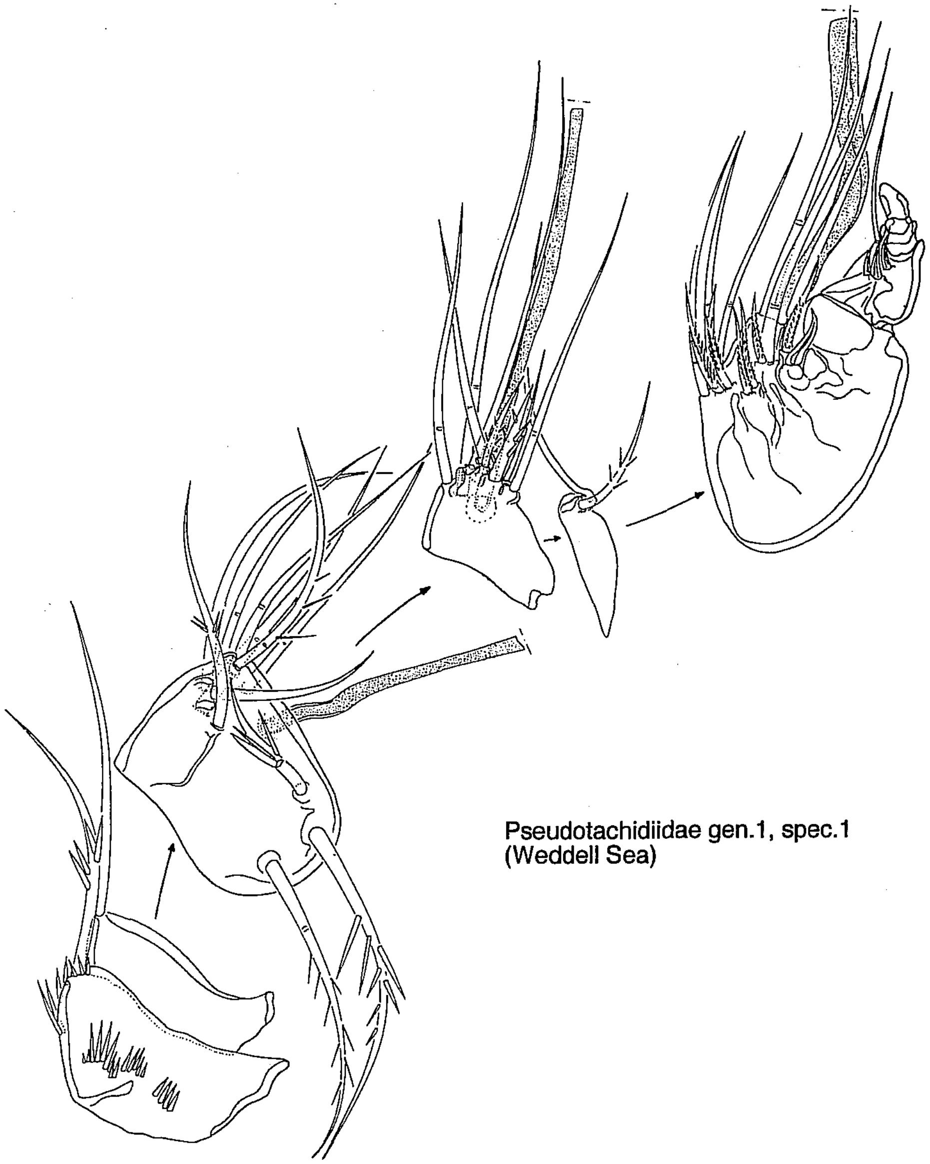
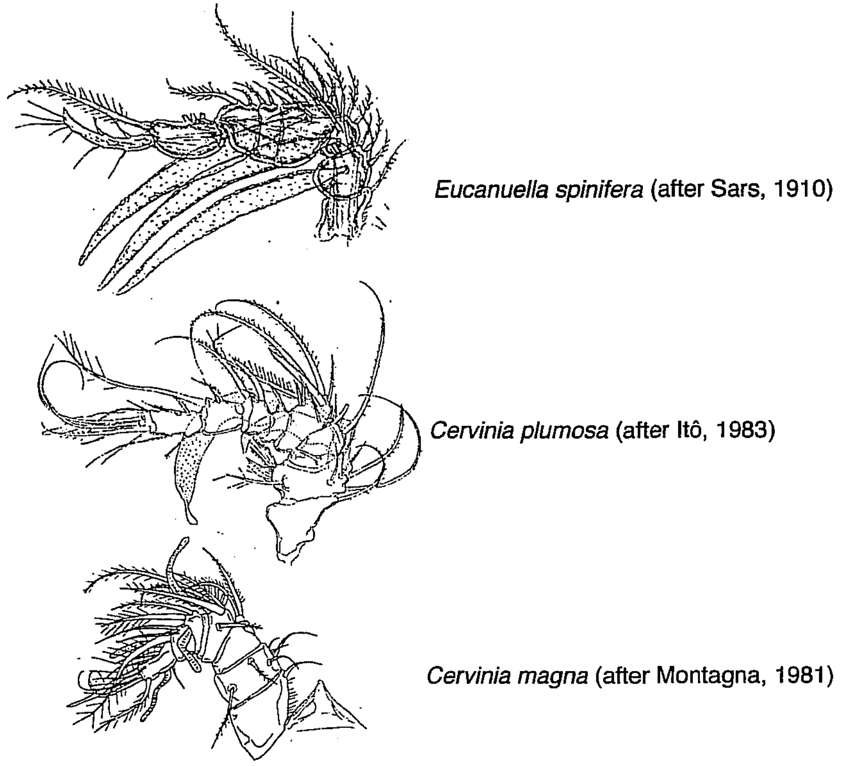


Fig. 19: Subchirocer antennule in the Pseudotachidiidae.


Eucanuella spinifera (after Sars, 1910)

Cervinia plumosa (after Itô, 1983)

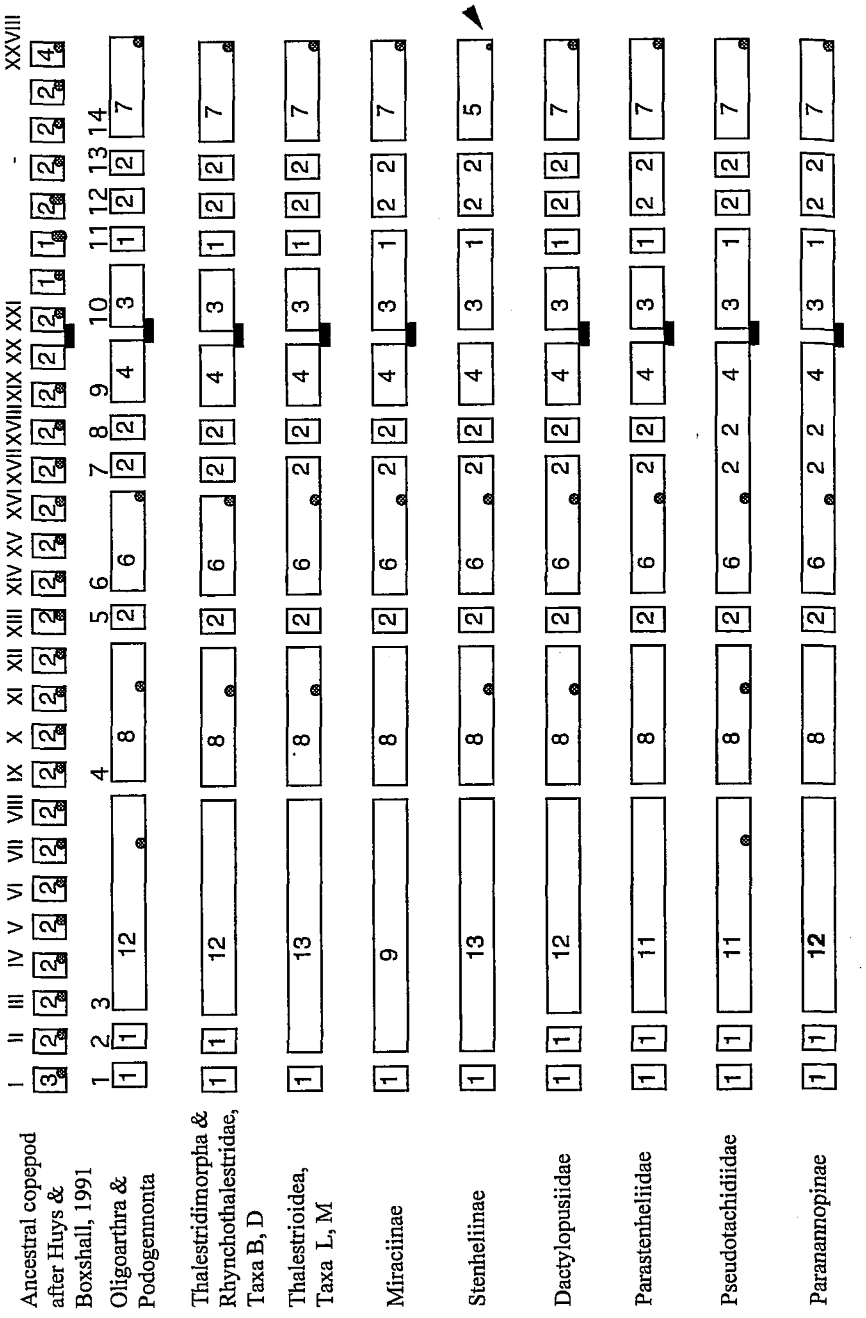
Cervinia magna (after Montagna, 1981)

Fig. 20: Secondary loss of the geniculation and the occurrence of secondary aesthetascs in the male antennule within the Cerviniidae.

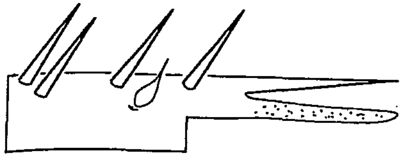
P. 86: fig. 21: Groundpatterns of the male antennule in the Thalestridimorpha and Pseudotachidiidae.

P. 87: above: fig. 22: Male antennule segment 6 in the Thalestrioidea.

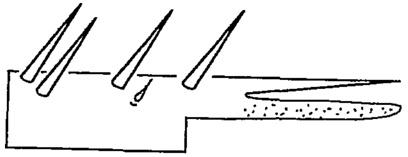
P. 87: below: fig. 23: Male antennule of *Karllangia pulchra* (Parastenheliidae) with the free segment 2 (after Mielke, 1994).



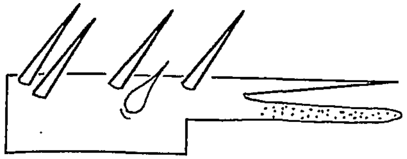
dorsal view



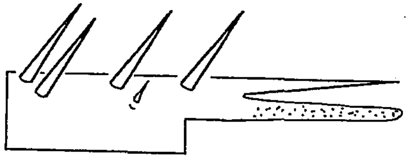
Thalestris longimana



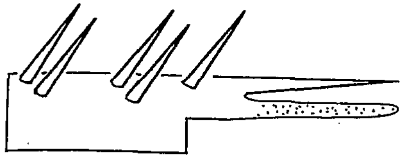
Parathalestris harpactoides



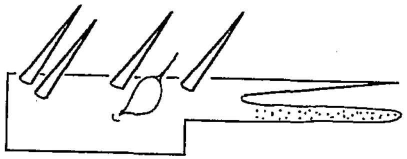
Amphiascopsis spec.



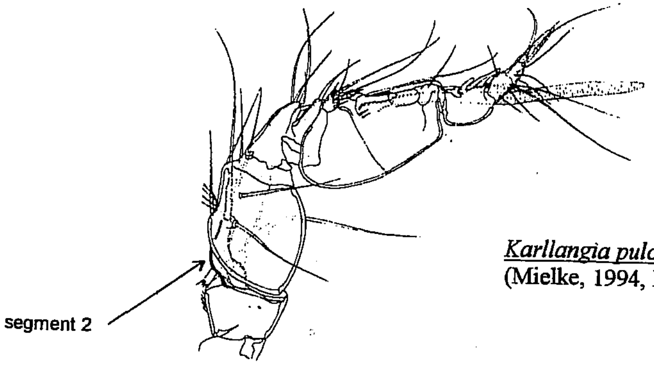
Paramphiascopsis spec.



Dactylopusiidae
(outgroup)



Eudactylopus spec.



Karllangia pulchra
(Mielke, 1994, Parastenheliidae)

6.3 Antenna

6.3.1 Groundpattern reconstruction of the Thalestridimorpha, Podogennonta and Pseudotachidiidae

According to Huys & Boxshall (1991) the A2 exp possesses 4 segments with 2,1,1,3 setae in the Oligoarthra groundpattern. This complete groundpattern (fig. 24) has still been retained in Tisbidae (Idyanthinae, Tisbinae), Cerviniidae and Harpacticoida fam. 1. Martinez & Moura (1998) describe a new taxon *Atergopedia* (Novocriniidae Huys & Iliffe, 1997) from the Barent Sea, in which the distal segment displays a slight constriction. Because of the incomplete setation, however, a homologisation of the potentially 5 segments is not possible. Since the proximal segment in the Thalestridimorpha/Podogennonta also still shows at most 2 setae, their 3-segmented groundpattern has probably developed from the one of the Oligoarthra by fusion of distal segments 3 + 4, while the original setation has been completely retained (fig. 24). The Thalestridimorpha and Pseudotachidiidae are quite primitive representatives of the Podogennonta and their A2 exp most probably also represents the groundpattern of the latter (fig. 24).

According to Huys et al. (1996) a 4-segmented A2 exp occurs in *Tigriopus brevicornis* (Harpacticidae), but this could not be confirmed by own observations.

In the groundpattern of Oligoarthra the A2 enp has 2 segments, the distal one being a fusion product of segments 2, 3 and 4 of the ancestral copepod and segments 2 + 3 of the Polyarthra, according to Huys & Boxshall (1991). The Polyarthra bear 2, 5, 7 setae at most on segments 1, 2 and 3, whereas there are 1 seta on enp1, 4 subterminal (on former enp2) and 7 terminal setae (former enp3) on enp2 in Oligoarthra. The 7 terminal setae are very conservative in shape and number within the Oligoarthra and reveal no characters for the systematics of Thalestridimorpha and Pseudotachidiidae.

This is different for the 4 subterminal enp2-setae. Maximally 4 setae are present in Oligoarthra (with the exception of *Atergopedia*, see below) showing taxon-specific modifications. In Neobradyidae, *Tachidiopsis* and representatives of the Idyanthinae (*Idyanthe*) (fig. 25) these setae are more or less "normal", whereas in Tisbidae (Tisbinae, Idyanthinae (*Idyella Idyellopsis*)), Harpacticidae, Harpacticoida fam. 1, Novocriniidae and Pseudotachidiidae (which are primitive representatives of the Podogennonta) a homologous modification pattern can be found (fig. 25): the setation is differentiated into 2 spine-like setae (the proximal one shorter than the distal one) and 2 juxtaposed setae, the adexopodal of which geniculate and the other one long and slender. In Cervinoidea (Rotundiclipeidae, Styracothoracidae and Cerviniidae) and also *Zosime* (Tisbidae) only 3 setae are left, which are located and shaped in a different way (secondarily or primarily?). Since the Pseudotachidiidae show the above-described pattern, it can be postulated to represent the groundpattern of the Podogennonta as well. In Thalestridimorpha the geniculate seta has lost its geniculation, has become very slender and very often basally fused with the juxtaposed seta **17** (fig. 25). Since this is also present in Tetragonicipitidae, it is apparently no autapomorphy for Thalestridimorpha but for a more inclusive taxon within Podogennonta.

6.3.2 A2 exp differentiation within Thalestridimorpha and Pseudotachidiidae

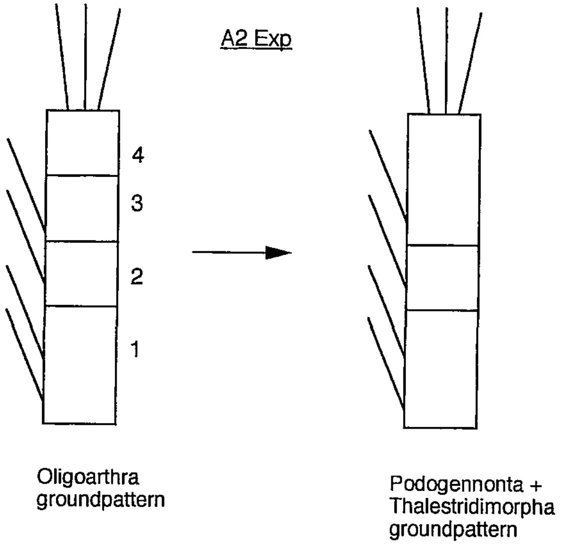
Since the A2 enp, apart from the presence/absence of the seta on enp1, is very conservative within the Thalestridimorpha and Pseudotachidiidae in respect to shape and number of setae, the character analysis was concentrated on the A2 exp. The A2 exopods within Thalestridimorpha are depicted in fig. 26. The complete thalestridimorph/podogennontan groundpattern is retained in the Dactylopusiidae and Rhynchothalestridae. In the Pseudotachidiidae one terminal seta on exp3 is either minute or completely lost **24**. In the Parastenheliidae exp2 +3 are fused but retain complete setation **21**. Additional modifications are the thickened terminal seta on exp3 and the generally sexually dimorphic exp in *Karllangia*. The shortened proximal seta on exp1 ("1" in fig. 26) **18** is probably a remnant of the copepodid phase (compare descriptions of Dahms, 1990, 1993a) and must have been taken over into the adult organisation presumably independently in the Parastenheliidae and Thalestrioidea, respectively.

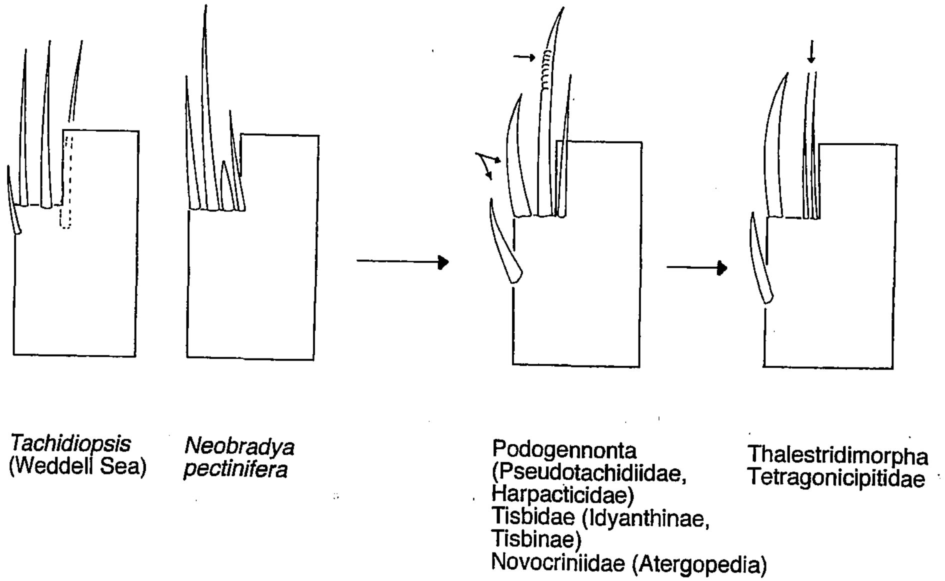
Proceeding from the common groundpattern of the Rhynchothalestridae/Thalestrioidea (= taxon D in fig. 4), this **18** is the only apomorphic feature of the A2exp to be found in the last common ancestor of the Thalestridae and Diosaccidae. In Diosaccidae the proximal seta on exp1 is completely lost **19**. The stem species of Thalestridae also had a 2-segmented exp (by fusion of exp2 + 3 of the Thalestridimorpha/Podogennonta-groundpattern) **21** with one seta lost (probably seta “3” of fig. 24) **22**. Finally, in *Eudactylopus* the actual exp2 (fusion of exp2 +3, see above) is much shorter than exp1 and one terminal seta is lost additionally **23**.

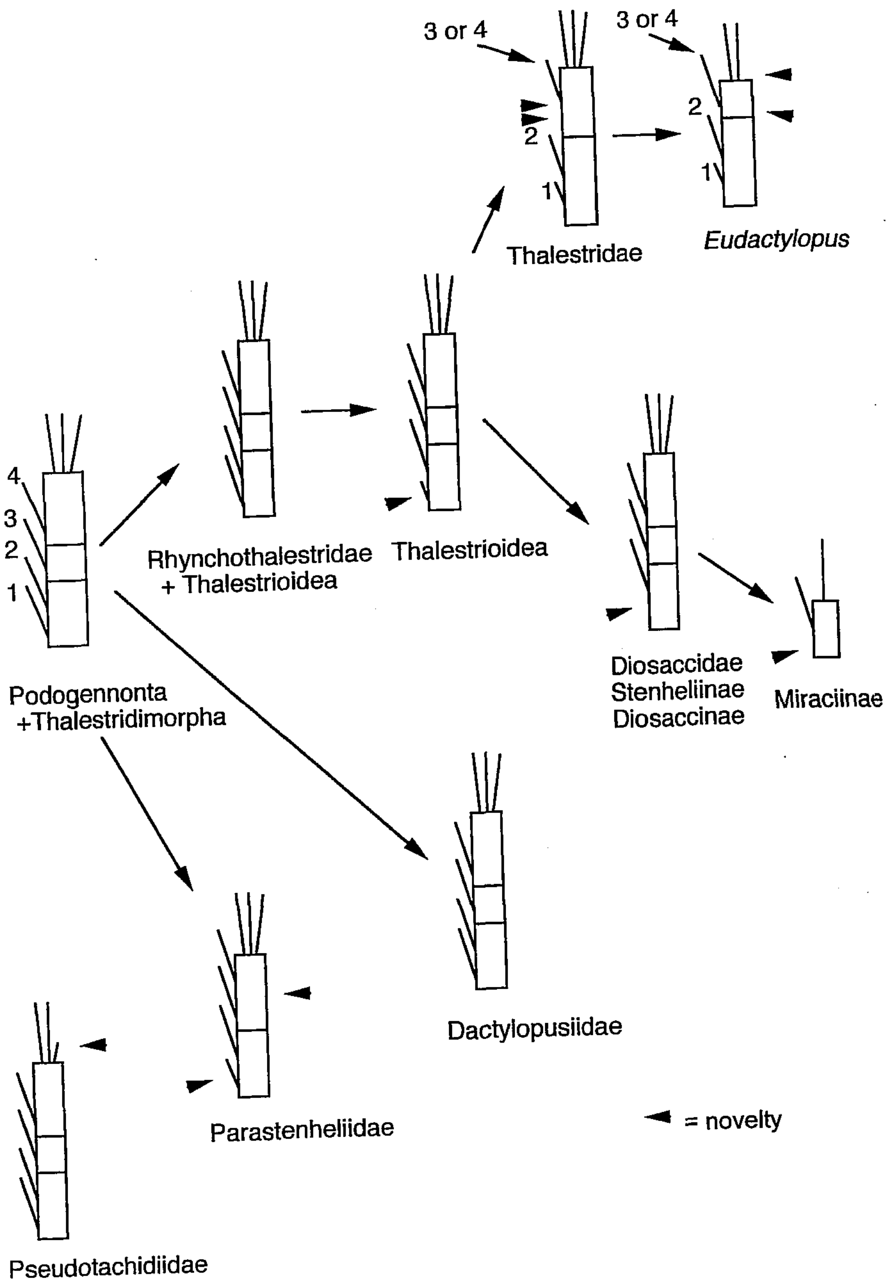
P. 91: above: fig. 24: Groundpattern of antenna exp in Oligoarthra and Podogennonta.

P. 91: below: fig. 25: Subterminal setation of antenna enp1 (=enp2 of Polyarthra) within the Oligoarthra.

P. 92: fig. 26: Groundpattern of antenna exp in the Thalestridimorpha and Pseudotachidiidae.







6.4 Mandible

6.4.1 Reconstruction of the exopod groundpattern in the Thalestridimorpha and Pseudotachidiidae

According to Huys & Boxshall (1991) the Md exp is 5-segmented with 1, 1, 1, 1, 2 setae in the copepod groundpattern. Such an exp must have been present in Polyarthra as well as in the Oligoarthra groundpattern, although it is no longer present in any actual harpacticoid taxon. *Echinosunaristes bathyalis* Huys, 1995 (Polyarthra) still shows a 5-segmented exp with incomplete separation of segments and complete setation. Reconstruction for the Oligoarthra is more difficult. Outside the Podogennonta only the following type occurs: 4-segmented with 2, 1, 1, 2 setae. The proximal segment is a fusion product of the first 2 proximal segments of the copepod groundpattern (fig. 27). Within the Podogennonta, e. g. in *Paradactylopodia* (Dactylopusiidae, Thalestridimorpha), a 2-segmented exp with 1, 4 setae and 1 additional seta located directly on the basis can be observed. Obviously the proximal segment is fused with the basis and only represented by 1 seta, so that an original separation of the 2 proximal oligoarthran segments can be assumed (fig. 27, type 2). Comparing this type with the 3-segmented exp in the groundpattern of the Rhynchothalestridae/Thalestrioidea-lineage (taxon D in fig. 4), the proximal 2 segments of which are fused (type 1 in fig. 27), one can postulate a 4-segmented exp with 1, 1, 1, 3 setae for the Thalestridimorpha groundpattern. The only representative of the Podogennonta directly displaying a 4-segmented exp, *Protolatiremus sakaguchii* Itô, 1974, has an incomplete setation, i.e. setae 1 (or 2?) and 3 of fig. 27 are missing **25**. The presence of an elongate proximal segment (fig. 27), as in the respective taxa of the Oligoarthra and Podogennonta with complete setation (see above), leads to the assumption that this segment is a compound segment resulting from the fusion of exp1 +2 of the oligoarthran groundpattern in *Protolatiremus* as well. The fusion of the last 2 distal oligoarthran segments in both type 1 and type 2 can be interpreted as an autapomorphy for Thalestridimorpha **33**.

Comparing both types of 4-segmented exp, which must have become 4-segmented in at least two different ways within Oligoarthra, a 5-segmented exp with complete setation can also be easily reconstructed for the groundpattern of the Oligoarthra and Podogennonta (fig.

27). The groundpattern of the Pseudotachidiidae consists of a 2-segmented exp (segments 1-2 and 3-5 of Oligoarthra) with 2, 4 setae **34** (fig. 28).

6.4.2 Md exp within the Thalestridimorpha (fig. 28)

Proceeding from the groundpattern, which actually does not appear any more in any extant species (figs. 27 + 28), 2 types can be distinguished: **1.** 3-segmented, with 2, 1, 3 setae, proximal segment being almost twice as long as both distal segments together **26** (figs. 27 +28). This type still can be observed completely unchanged in Rhynchothalestridae and in the groundpattern of Diosaccidae and Diosaccinae (actually e. g. in *Paramphiascopsis* and *Amphiascopsis*). Further reduced states are found in Thalestridae **30** and Stenheliinae **32** (fig. 28). In the former all segments are fused to form one single compound segment, while all 6 setae have been retained **30**. In Eudactylopusiinae only 2 setae on a small segment are left **31** (fig. 28).

2. originally 3-segmented with 1, 1, 4 setae, the distal segment being longer than the proximal one, the proximal segment of the Thalestridimorpha groundpattern being only represented by one seta located on the basis (figs. 27 + 28). This type occurs only in Dactylopusiidae (*Paradactylopodia*, *Dactylopusia*), with further reduced setation in most of the species. The additional fusion of the third segment of the Thalestridimorpha groundpattern with the distal one is an autapomorphy for Dactylopusiidae **27** (figs. 27+28). In Parastenheliidae the exp is only 1-segmented, with at most 4 setae **28**. It is not possible at present to assign it to any of the two types described above. In fig. 28 the different states are arranged according to the new system.

6.4.3 Md enp within the Harpacticoida (fig. 29)

In the "ancestral harpacticoid" of Huys & Boxshall (1991) the Md enp has 2 segments at most with 3 + 9 setae. This Md enp is still shown by the Polyarthra. The Oligoarthra display almost the same groundpattern as regards the number of setae and segments (fig. 29). A 2-segmented enp is found in the Paramesochridae (according to Mielke, 1984 and Huys & Boxshall, 1991) and in *Drescheriella* (Tisbidae, according to Dahms & Dieckmann, 1987). In most taxa enp1 and 2 are fused, 3 setae on "enp1" still occur in a number of taxa, such as Tisbidae (Idyanthinae, Tisbinae, Cholidyinae), Ectinosomatidae, Harpacticidae, Cerviniidae, Paramesochridae and Pseudotachidiidae. Mielke (1984) describes a fourth minute seta in *Diarthrodella neotropica* (Paramesochridae). Maximally 9 setae are present on "enp2" e. g. in Harpacticidae (*Harpacticus uniremis*) and Pseudotachidiidae. In 2 species of Pseudotachidiidae gen. 1 even 10 setae have been found. In most taxa a division into 2 (in case of reduced setation) or 3 groups of setae can be observed: one lateral one, consisting of 3 lateral setae and two apical ones, each with a group of 3 (or 4 in Pseudotachidiidae gen. 1) basally fused setae (fig. 29). Setal and segmental reductions often seem to be connected with the disintegration of this arrangement and the fusions (e. g. Cerviniidae, Dactylopusiidae). In the Paramesochridae even all setae are basally fused together, forming a secondary third segment (Mielke, 1984, Huys & Boxshall, 1991, see fig. 29). Since the above-described arrangement is found in many (all?) taxa with a more primitive enp (Neobradyidae, Tisbidae, Harpacticidae, Cerviniidae (*Eucanuella rostrata* Itô, 1983), Thalestridimorpha) it probably belongs to the Oligoarthra groundpattern as an autapomorphic character. This groundpattern can therefore be described as follows: 2-segmented, with 3 (or 4?) setae on enp1 and 3 (laterally) + 3 + 4 (apically) on enp2, the latter two groups of setae being basally fused, respectively (fig. 29). The complete setation of enp1 occurs in Pseudotachidiidae gen. 1, a 2-segmented enp in *Drescheriella* (after Dahms, 1987) and the Paramesochridae. In Thalestridimorpha the enp is always 1-segmented, with only 2 setae on "enp1" (inner seta always shorter than outer one). The situation in the "enp2" of Thalestridimorpha (figs. 29 + 30) is more complicated. With two exceptions (*Hamondia superba* Huys, 1990, *Stenhelia* with 7 setae) 6 setae at most in 2 setal triads are present. One seta of the outer triad is separated as a single element and in the Thalestrinae is even situated on a projection **37** (figs. 29 + 30). There are sporadic "character reversals", e.g. in single species of *Robertgurneya* (Diosaccinae) this seta is still part of the outer triad, being fused with the other setae, thus making its homologisation possible.

This groundpattern, i. e. 6 setae (+ 1 single lateral seta in *Hamondia* and *Stenhelia*) arranged in one triad, one single seta and one pair of basally fused setae, was directly observed in almost all taxa of Thalestridimorpha (figs. 29 + 30). The situation in the Parastenheliidae, which show only 5 setae (fig. 30) is at least derivable from it. The only representatives of

Podogennonta, except the Thalestridimorpha and Harpacticidae displaying a comparably primitive Md enp are *Protolatiremus* and the Tetragonicipitidae. In the former, three pairs of setae (basally fused?) and 1 lateral seta are present (fig. 29). In those Tetragonicipitidae available for examination the characteristic arrangement of the Thalestridimorpha groundpattern was not observed (fig. 29). Therefore the latter is interpreted as autapomorpic for the Thalestridimorpha **37**.

6.4.4 Md enp within the Thalestridimorpha

The above-described groundpattern of the Thalestridimorpha can be directly observed in all taxa (figs. 30 + 32), except Parastenheliidae, which have only 5 setae. Nevertheless, the enp of the Parastenheliidae can be easily derived from this groundpattern (fig. 30). In the Thalestrioidea one seta of the inner triad is missing (fig. 30); the homology of the single inner apical seta remains unclear **38**. In the *Paramphiascella/Amphiascoides* lineage within the Diosaccinae the number of setae is reduced and both apical seta groups are spatially separated. The complete number of setae of the Oligoarthra groundpattern occurs in one of the examined species of *Amphiascopsis* (Diosaccinae), which is interpreted here as "character reversal". In the Thalestridae one seta of the inner triad is missing, and in *Eudactylopus* an additional seta is lacking on enp1 **40** (fig. 30). Within the Dactylopusiidae a trend towards a reduction of the setation and the distinction of "enp1" and "enp2", which is still clearly visible in more primitive states, can be observed (fig. 30).

6.4.5 Md enp within the Stenheliinae

Within the Stenheliinae the whole Md is dramatically modified (figs. 31 + 32). The basis is strongly enlarged (twice the length of the enp in *Melima*). The also elongated enp is folded back onto the basis (compare figs. 31 + 32) in extreme case and one or two of the apical setae are strongly modified (thickened and extremely elongated). The coxa is very compact and the teeth of the gnathobase are small, stout and blunt **35**. A lot of transitional states of the Mdenp can be observed. However, in the Stenheliinae groundpattern (fig. 32) the Md enp and its setation seem to be still unmodified. The setation of *Pseudostenhelia wellsi*, e.g., still agrees completely with the Thalestrioidea-groundpattern, while the enp itself is already slightly deformed. In *Stenhelia bifida* Coull, 1976, basis and enp are not at all elongated and Coull (1976) even described at least 9 endopodal setae. Unfortunately, the material of the type locality kindly provided by Dr. Coull turned out to belong to a different species, which is closely related to *S. bifida*. This new species displayed a strongly reduced setation which prevented a reexamination of the original setation.

The deformation of the enp and the displacement of the setae makes a homologisation of the modified elements with the Thalestrioidea groundpattern almost impossible. Comparing different species which show the extreme type, it appears to be most probable that always the homologous setae are modified (figs. 31 + 32).

P. 98: fig. 27: Groundpattern of the mandible exp in the Oligoarthra, Podogennonta, Thalestridimorpha and *Protolatiremus*.

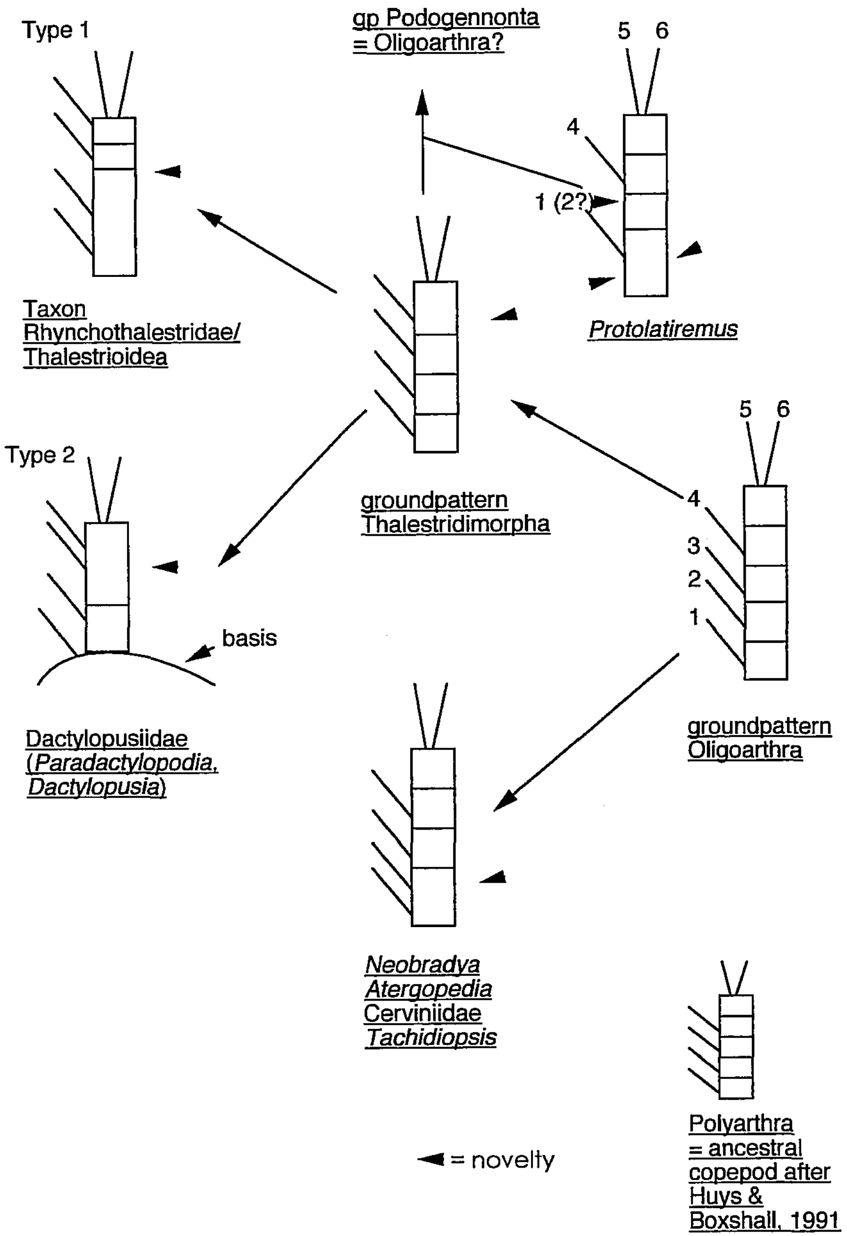
P. 99: fig. 28: Groundpattern of the mandible exp within the Thalestridimorpha and in the Pseudotachidiidae.

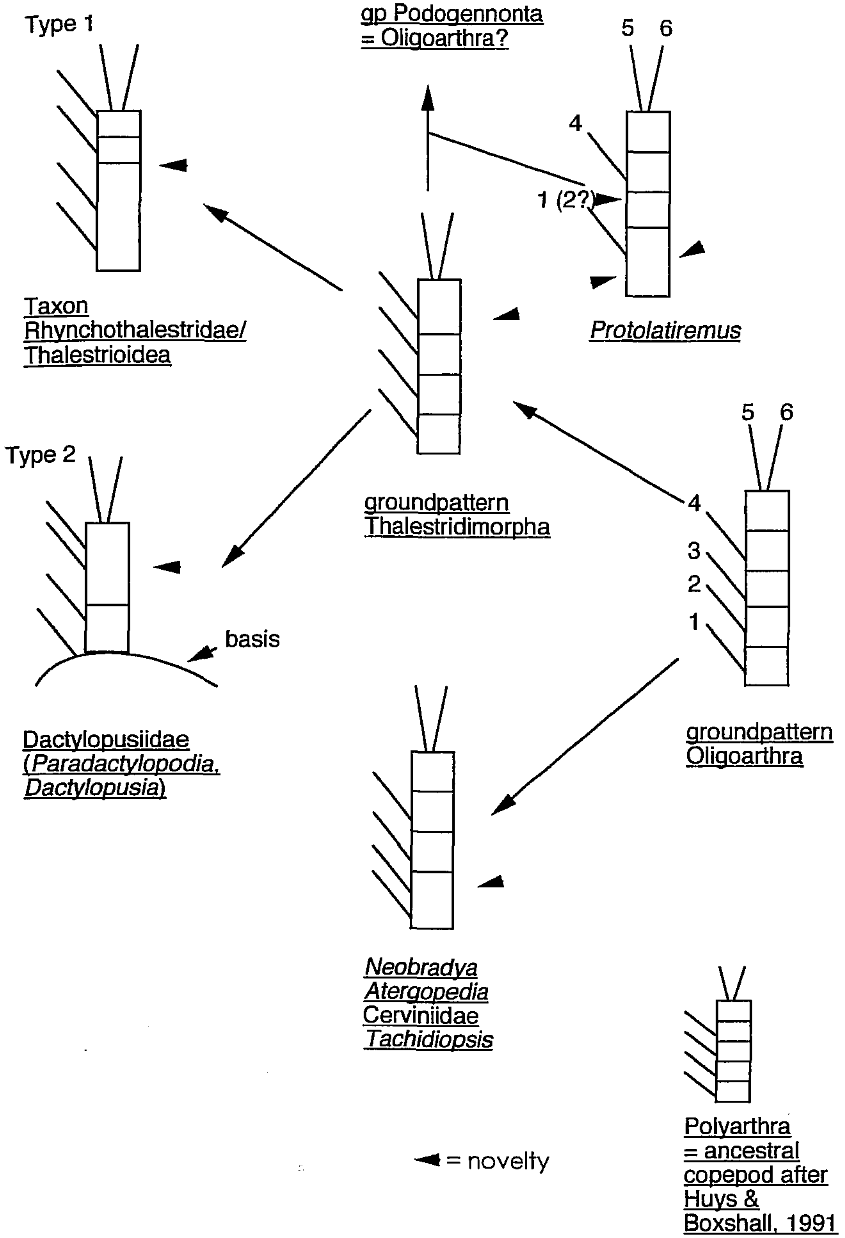
P. 100: fig. 29: Mandible enp within the Harpacticoida.

P. 101: fig. 30: Mandible enp within the Thalestridimorpha.

P. 102: fig. 31: Mandible within the Stenheliinae.

P. 103: fig. 32: Mandible exp and enp within the Stenheliinae.


Type 1
gp Podogennonta
= Oligoarthra?
5 6
4
1 (2?)
Taxon
Rhynchothalestridae/
Thalestrioidea
Protolatiremus
5 6
Type 2
groundpattern
Thalestridimorpha
4
3
2
1
basis
Dactylopusiidae
(Paradactylopodia,
Dactylopusia)
groundpattern
Oligoarthra
Neobradya
Atergopedia
Cerviniidae
Tachidiopsis
= novelty
Polyarthra
= ancestral
copepod after
Huys &
Boxshall, 1991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= Oligoarthra?
5 6
4
1 (2?)
Taxon
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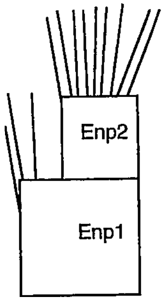
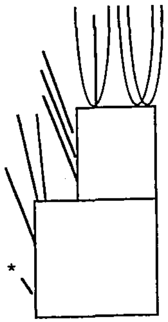
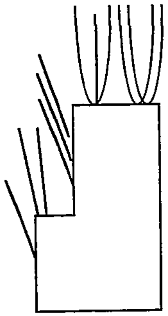
Thalestrioidea
Protolatiremus
5 6
Type 2
groundpattern
Thalestridimorpha
4
3
2
1
basis
Dactylopusiidae
(Paradactylopodia,
Dactylopusia)
groundpattern
Oligoarthra
Neobradya
Atergopedia
Cerviniidae
Tachidiopsis
= novelty
Polyarthra
= ancestral
copepod after
Huys &
Boxshall, 1991



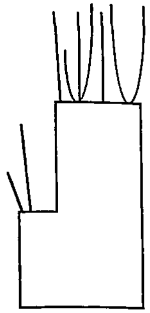
groundpattern
Polyarthra



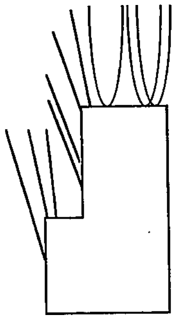
gp Oligoarthra



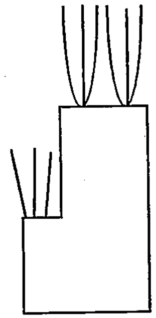
gp
Podogennonta



gp
Thalestridimorpha

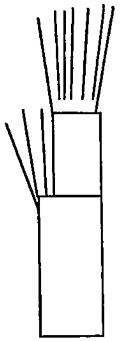


Pseudotachidiidae
gen. spec.
(Weddell Sea)

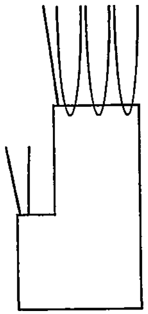


Tisbe
holothuriae

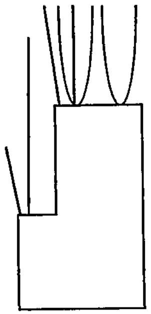
Tetragonicipitidae
gen. spec.
(Weddell Sea)



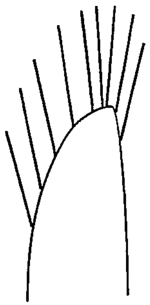
Diarthrodella
parorbiculata
pacifica
Mielke, 1984



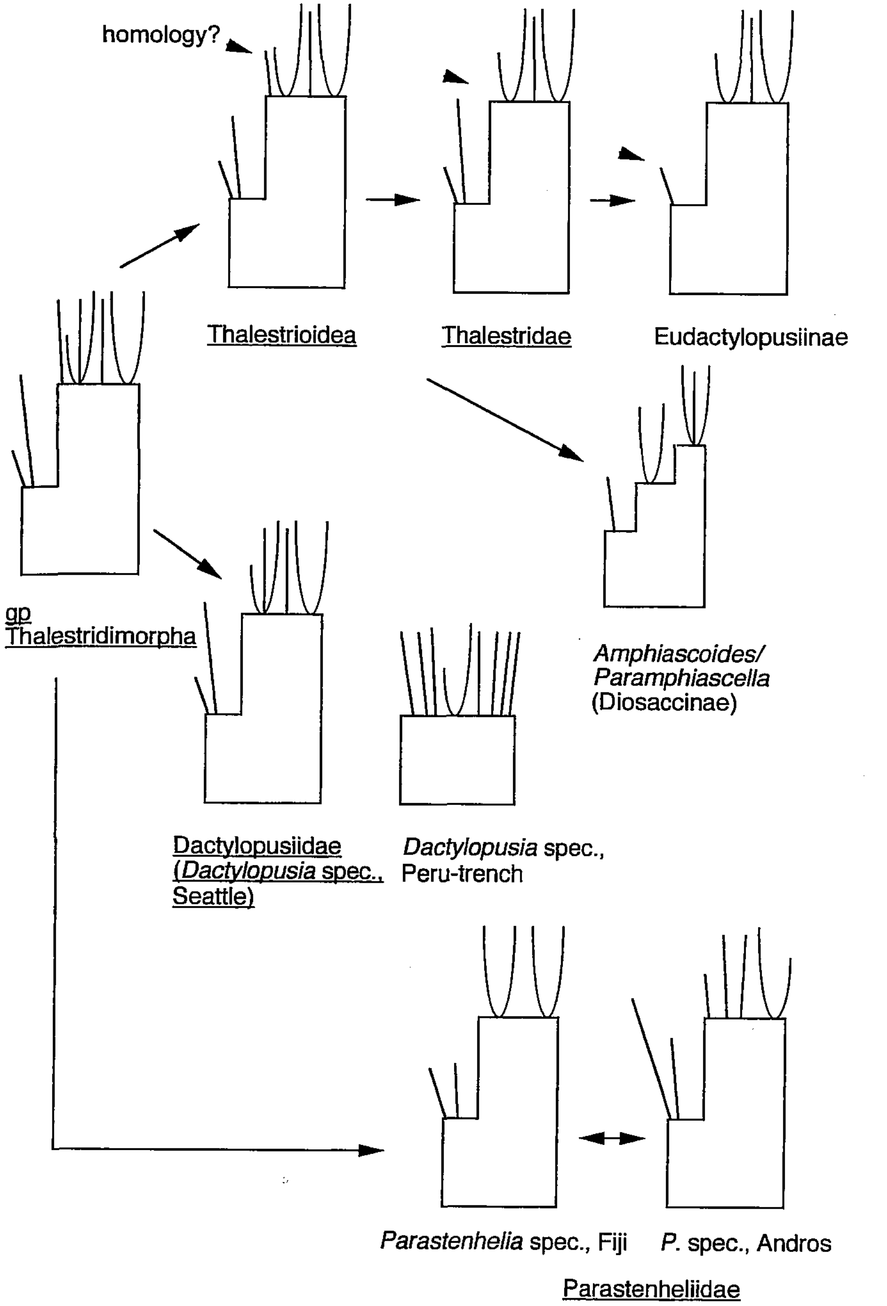
Protolatiremus
sakaguchii
(after Itô, 1974)

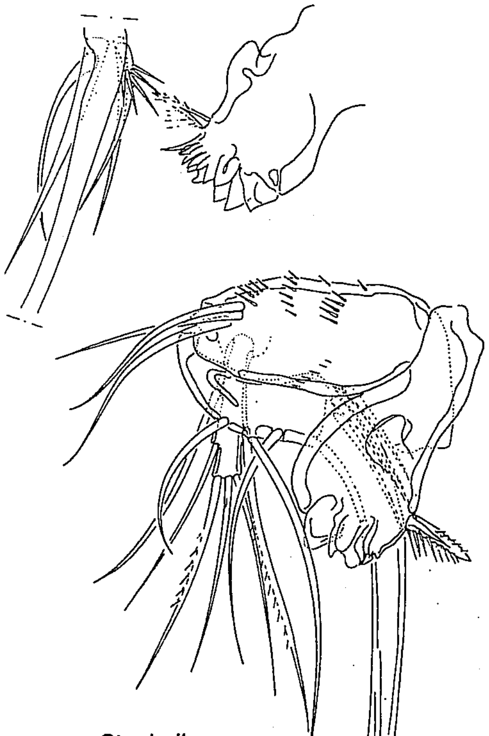


Neobradya
pectinifera

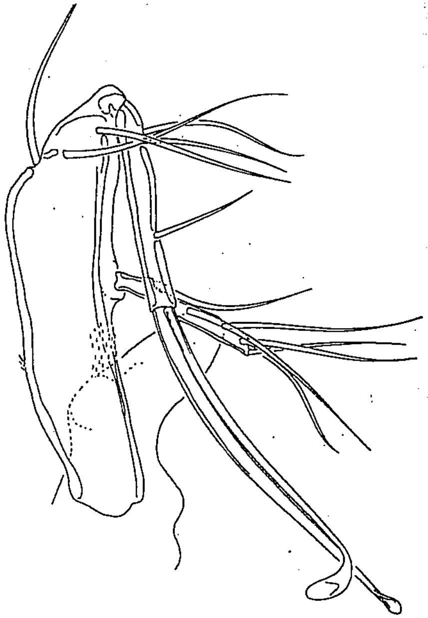


Hemicervinia
stylifera
(after Huys et.al.,
1996)

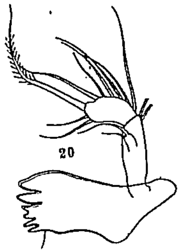




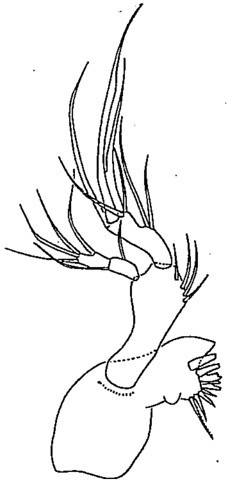
Stenhelia spec.



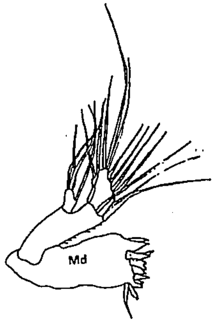
Melima spec.



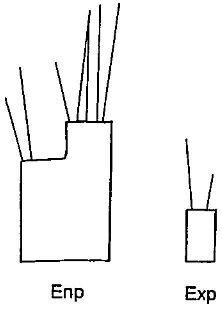
Cladorostrata brevipoda (Shen & Tai, 1963)



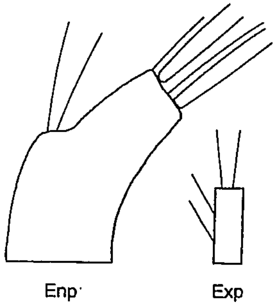
Stenhelia coineauae (Soyer, 1971)



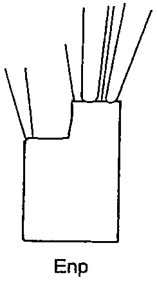
Stenhelia bifida (Coull, 1976)



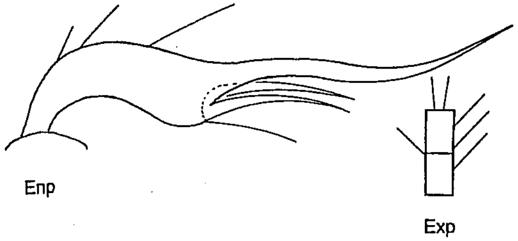
Stenhelia cf. *bifida*



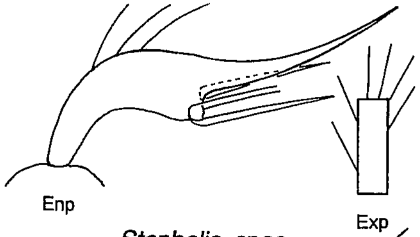
Pseudostenhelia wellsi (Mexico)



Stenheliinae groundpattern

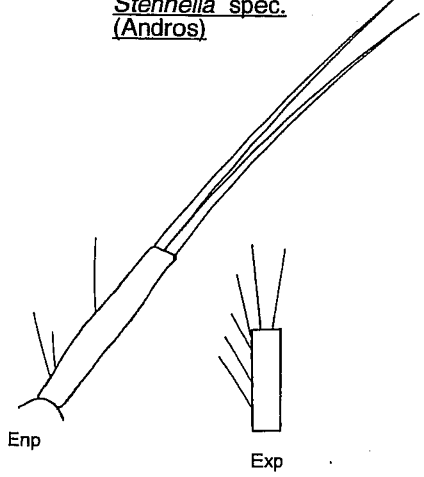


Stenhelia spec. (Mexico)



Stenhelia spec. (Andros)

Stenhelia paradivergens (Mexico)



Melima spec. (Papua New Guinea)

6.5 Maxillula

6.5.1 Basis, coxa, endo- and exopod

The maximal number of setae (= groundpattern) is listed in tab. 1 for the respective taxa. The groundpattern of Thalestridimorpha agrees with that of the Podogennonta and is surprisingly primitive within Oligoarthra. Four setae on the inner basal and 6 on the coxal endite have even been retained of the ancestral copepod as reconstructed by Huys & Boxshall (1991).

Thalestridimorpha and Pseudotachidiidae

Losses of setae on basis, enp and exp yield characters which are depicted in tab.1. It was not always possible to exactly determine the number of coxal setae. Six coxal setae are still present in Rhynchothalestridae and Pseudotachidiidae. Except for the Parastenheliidae with 2 + 4 basal setae **45** and *Ambunguipes/Hamondia* with 6 setae and fused endites within the Rhynchothalestridae, all taxa of the Thalestridimorpha show in their groundpattern the maximal number of 3 + 4 on both still distinguishable basal endites (tab. 1). The Pseudotachidiidae bear 2 + 4 basal **45**, 3 endopodal **46**, and 4 (3 in Paranannopinae) exopodal setae. Maximally 3 endopodal setae are present in the Thalestrinae **46**, whereas all other Thalestridimorpha have 4. The Dactylopusiidae and Parastenheliidae show at most 3 exopodal setae, in the latter the exp itself is lacking and only represented by the setae **47**. The Diosaccinae and Stenheliinae have only 2 setae on the exp **54**. The outer coxal seta, retained in the Thalestridimorpha groundpattern from the Podogennonta groundpattern, is missing in all taxa of Thalestrioidea (tab. 1) **43**.

6.5.2 Praecoxal arthrite

The maximal number of 14 setae within the Harpacticoida (according to Huys & Boxshall, 1991) is found in *Longipedia* (Polyarthra) and still in the Thalestridimorpha and therefore in the groundpattern of the Podogennonta. On the praecoxal arthrite in both Poly- and Oligoarthra there are 12 apical and 2 juxtaposed setae on the anterior surface. These 2 juxtaposed surface-setae also occur within Podoplea in Misophrioida, which possess 15 praecoxal setae altogether (compare *Archimisophria squamosa* after Huys & Boxshall, 1991 and *Archimisophria bathylaptevensis* after Martinez-Arbizu & Seifried, 1996). In all other podoplean orders less setae are present (Gelyelloida, Cyclopoida) and/or the maxillule is strongly reduced (Siphonostomatoida, Poecilostomatoida and Mormonilloida) or completely lost (Monstrilloida). Except for Harpacticoida and Misophrioida no trace of the 2 juxtaposed surface setae is found in these taxa (compare Huys & Boxshall, 1991).

Shape and arrangement of the apical setae appear to be different in Poly- and Oligoarthra, respectively (for the Polyarthra compare Huys & Boxshall, 1991, p. 132, fig. 2.4.12). The Oligoarthra groundpattern can be described as follows (fig. 33): On the posterior side there are a row of 4 apical spines, 2 plumose setae on the inner subapical margin and 2 slender setae, located subapically in the inner half of the posterior surface. On the anterior side 3 apical spines, 1 slightly subapically located shortened seta, and 2 long juxtaposed surface setae are present. Arrangement and shape of setae look quite different from those in Polyarthra (compare Huys & Boxshall, 1991, p. 132, fig. 2.4.12), but can be found again in Misophrioida (compare Martinez & Seifried, 1996). The Thalestridimorpha and therefore also the Podogennonta as the superordinated taxon have retained this special arrangement but the 4 apical posterior spines show an additional pair of "double-spinules" each (fig. 33), which are interpreted here as an evolutionary novelty and therefore as autapomorphic for the Podogennonta (and as symplesiomorphic for the Thalestridimorpha) **44**. The complete podogennontan groundpattern is still realized e.g. in theTetragonicipitidae and *Metamphiascopsis* (Diosaccinae). As in many Oligoarthra, the 2 posterior slender surface setae are missing in the Harpacticidae. In several oligoarthran taxa (Tisbidae, Laophontidae, Novocriniidae, etc.) the praecoxal spines are still further modified by reduction and different arrangement. However, the wide distribution of the above described praecoxal shape, especially in the more primitive taxa (e.g. *Tachidiopsis*) and even beyond the Harpacticoida in the Misophrioida, is an argument to polarize it as plesiomorphic within Oligoarthra.

6.5.2.1 Thalestridimorpha (fig. 34)

The complete podogennontan groundpattern is retained only in *Metamphiascopsis*. The 2 posterior slender surface setae are missing in all taxa of Thalestridimorpha except the Parastenheliidae (fig. 34, *Parastenhelia megarostrum*) and *Metamphiascopsis* (Diosaccinae). In the Diosaccinae changes of the groundpattern are otherwise very rare (e.

g. "stiletto"-shape in *Typhlamphiascus* spec. from the Fiji-Islands). The "upper" apical praecoxal spine is always missing in the Thalestrinae **57**. A very derived maxillule is shown by *Eudactylopus*. A special spatial arrangement of the palp gives it a characteristic "twisted" shape after preparation, the"upper" apical praecoxal spine is reduced to a plumose seta **56** (fig. 34).

A derived praecoxa is also found in the Dactylopusiidae and Parastenheliidae. In both taxa the apical spines are displaced, giving the arthrite a more slender appearance. A homologous displacement pattern can be detected within the Dactylopusiidae: the "upper" posterior spine is thickened and slightly shifted downwards, the third spine arising from the "upper" (= outer) margin is more strongly plumose or ornamented, the tips of all spines are slightly rounded **48** (fig. 34). Although a displacement of the apical spines has also taken place in the Parastenheliidae **49** (fig. 34), the recognition of a homology pattern is hardly possible, not least due to the smallness of the objects.

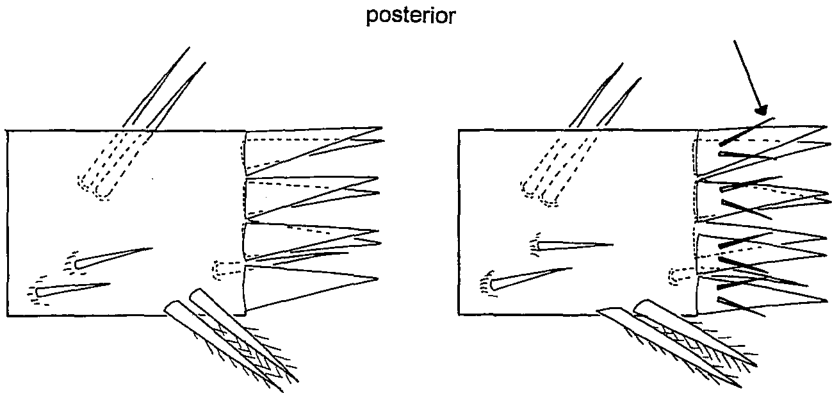
6.5.2.2 Pseudotachidiidae (fig. 35)

The groundpattern exhibits at least one speciality: the 3 anterior apical spines show a dent (fig. 35) **50**. One of the posterior surface setae is still present in "Pseudotachidiinae" being displaced "upwards" and characteristically ornamented (fig. 35). Whether this seta is already a part of the Pseudotachidiidae groundpattern, is not yet clear, because it lacks completely in the Paranannopinae and Pseudomesochrinae. There are transitions in the degree of dents on the anterior apical spines and the degree of sclerotisation of all apical spines between the taxa (fig. 35). In the Paranannopinae/Pseudomesochrinae the dentation is only moderate and the ornamentation variable. In *Idomene* and other representatives of "Pseudotachidiinae" the dent is large and more distally located. Additionally, the spine bears spinules and on the anterior side there are 2 elongated spinules which insert always at the same site. The "*Pseudotachidius* line" shows an even stronger sclerotisation and "spreading" of the apical spines (fig. 35).

Table 1:
Maximal setation of the maxillule palp within the Harpacticoida

	OS*	**Basis** Endites outer↔inner side	**Enp**	**Exp**	**Coxa**	**cox. OS**
Ancestral copepod (after Huys & Boxshall, 1991)	2	5 + 4	6, 4, 7	11	6	9
Polyarthra (after Huys & Boxshall, 1991)	1	4 + 4	5 + 6	11	6	5
Oligoarthra		4 + 4	5-6	5	6	4
Podogennonta		3 + 4	4	4	6	1
Thalestridimorpha		3 + 4	4	4	6	1
Rhynchothalestridae		3 + 4	4	4	6	1
Diosaccinae/ Stenheliinae		3 + 4	2 + 2	2	4	-
Thalestrinae		3 + 4	3	4	4	-
Eudactylopusiinae		3 + 4	4	3	2	-
Parastenheliidae	Pore	2 + 4	4	✹	5	1
Dactylopusiidae		7	4	3	5	1
Pseudotachidiidae		2 + 4	3	1 + 3	6	-
Paranannopinae		2 + 4	3	1 + 2	6	-

*OS= outer setae; ✹ = exp only represented by 2-3 setae



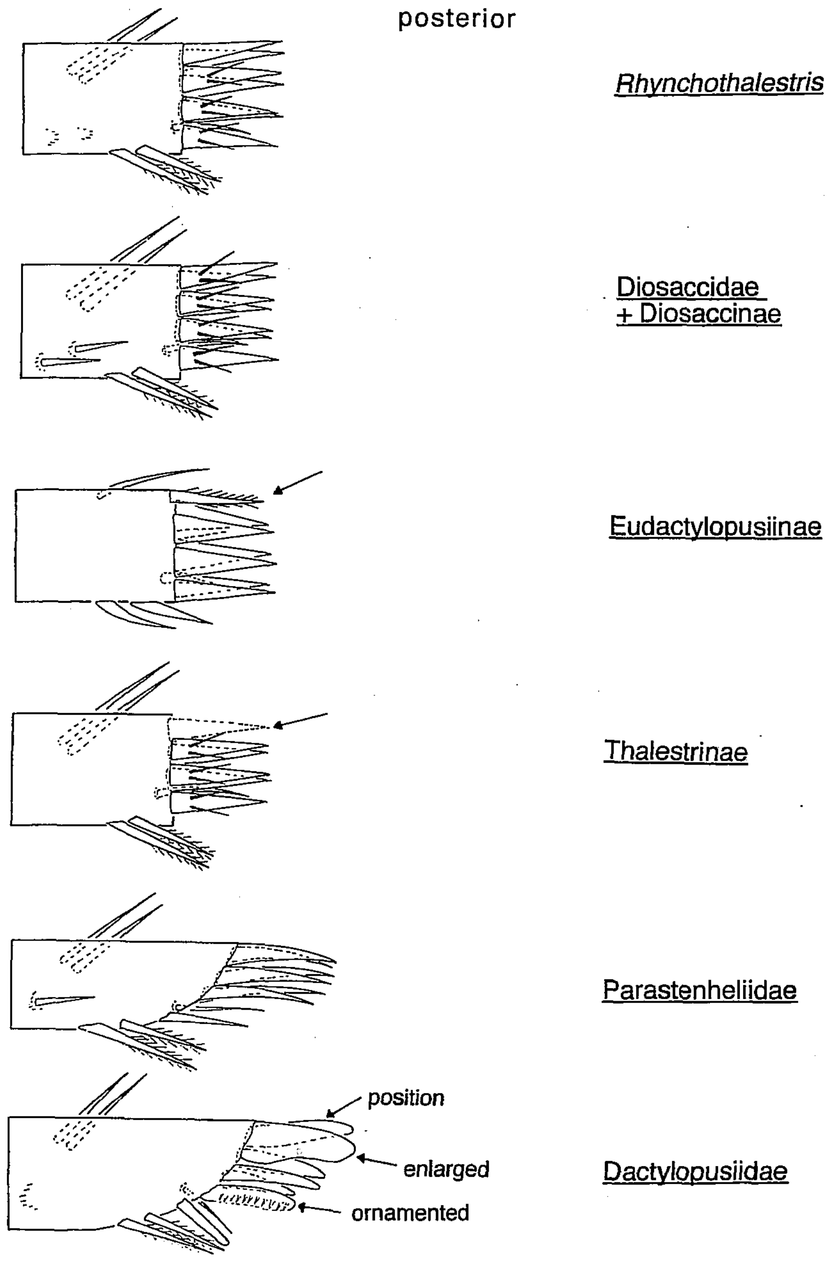
groundpattern
Oligoarthra

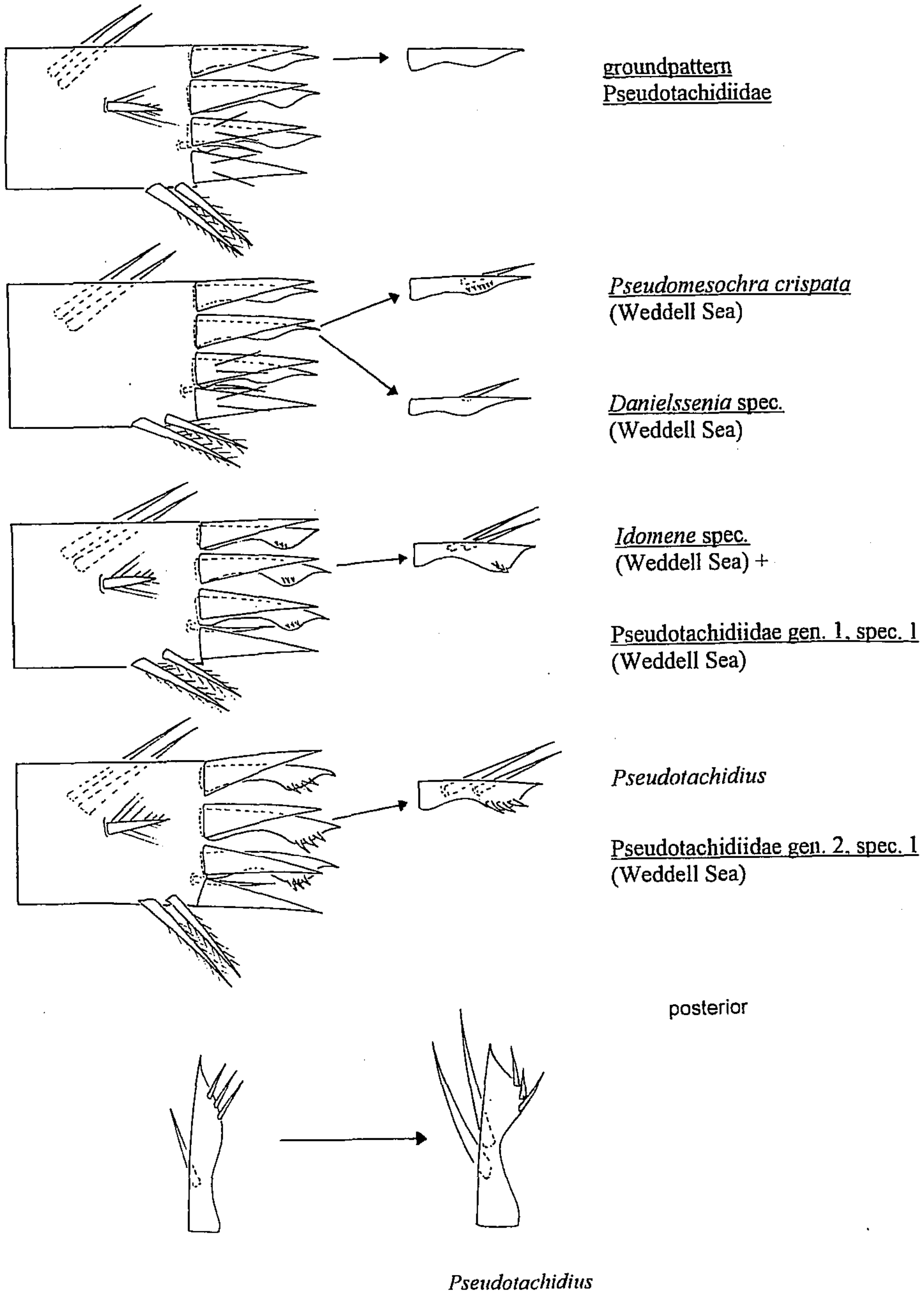
groundpattern
Podogennonta +
Thalestridimorpha

Fig. 33: Groundpattern of the maxillule praecoxal arthrite in the Oligoarthra, Podogennonta and Thalestridimorpha.

P. 109: fig. 34: Groundpatterns of the maxillule praecoxal arthrite within the Thalestridimorpha.

P. 110: fig. 35: Maxillule praecoxal arthrite in the Pseudotachidiidae.





6.6 Maxilla

6.6.1 Harpacticoida groundpattern

For the harpacticoid groundpattern Huys & Boxshall (1991) postulate a separation of coxa and praecoxa (Polyarthra), with the maximal number of 6, 3, 3, 3 setae on the respective endites, 4 setae on the basis and an enp completely demarcated from the basis with 4 segments and 3, 2, 2, 4 setae (fig. 36). For the latter, however, no actual example is given. In most Harpacticoida the proximal enp-segment is fused with the basis to form an allobasis. Seta "A" (fig. 36) is modified as a claw and fused with the basis in Polyarthra (fig. 2.4.13 in Huys & Boxshall, 1991) as well as in most Oligoarthra. Seta "D" (fig. 36) on the anterior side of the basis is also claw-like in both taxa and may be an autapomorphy of the Harpacticoida.

6.6.2 Mx endopod: groundpattern of Podogennonta, Thalestridimorpha and Pseudotachidiidae

In Thalestridimorpha there are at most 3 free endopod segments (e.g. in *Paramphiascopsis glacialis*, Diosaccinae), the proximal one is fused with the basis (= allobasis). The number of basal setae corresponds with that of the ancestral copepod. The third, distal segment bears 2 apical setae and 1 subapical geniculate seta (No. 4, 5, 6 in fig. 37). The second, middle segment has 1 geniculate seta located on the anterior side (No. 3 in fig. 37). The setation of the proximal (= first) segment is more difficult to assess. Setae 2 + 7 are clearly located on segment 1. Seta 1 inserts at the border between basis and enp1, seta 8 on a small projection on the basis (fig. 37). Comparing this with the harpacticoid groundpattern of Huys & Boxshall (1991), at most two setae belong to segment 1 (setae 2 + 7) and 1 + 8 to the allobasis. Seta 9 is displaced onto the basal endite and is still present in *Rhynchothalestris helgolandica* (after the description of Huys, 1990). At the same position a tube pore was observed in *Ambunguipes* and some Diosaccinae (derivate of seta?). The Pseudotachidiidae have retained only 2 free endopod segments (fusion of enp2 and 3 of the podogennontan groundpattern) and only seta 1 is left of the setae of the proximal segment of the harpacticoid groundpattern (figs. 37 + 45). During the fusion of enp2 and 3 one seta (probably no. 6) has become lost **58**. Setal homology in Thalestridimorpha and Pseudotachidiidae was deduced from the arrangement of the setae on the anterior or posterior sides as well as from the presence of geniculate setae and their position in the respective setal pattern. Geniculate setae are also found in several other oligoarthran taxa and are apparently homologous (compare Huys & Boxshall, 1991, fig. 2.4.14, *Tachidiopsis cyclopoides* and fig. 37). From the above-discussed enp groundpatterns of Thalestridimorpha and Pseudotachidiidae the Podogennonta groundpattern was reconstructed (fig. 37), which corresponds largely with the Thalestridimorpha groundpattern. The only difference is the miniaturisation of seta 1 in the Thalestridimorpha (as well as in the Tetragonicipitidae), however, being "normally" developed in the Pseudotachidiidae, thus representing an autapomorphy either for both former taxa or a still more inclusive taxon within the Podogennonta **59**. The Pseudotachidiidae show the following autapomorphies derived from the Podogennonta groundpattern (compare fig. 37): fusion of enp2 + 3, loss of seta 4 (or 6?), loss of the endopodal setae on the allobasis **58**. An autapomorphy of the Podogennonta derived from the harpacticoid groundpattern (enp-setation 3, 2, 2, 4) is the loss of 1 seta on each of the free segments enp2 + 3, respectively. It remains unclear whether seta 1 in the examined Thalestridimorpha and Pseudotachidiidae belongs to the allobasis or actually to enp1. REM-photographs of Pseudotachidiidae gen. 2 (fig. 45) and observations with light microscopy in representatives of the Thalestridimorpha point towards the latter possibility. Therefore the allobasis would carry 2 instead of 3 setae, which would conflict with the harpacticoid groundpattern of Huys & Boxshall. Within the Pseudotachidiidae (fig. 39) the enp becomes 1-segmented (e.g. in *Idomene*) with reduced setation (*Pseudotachidius*). A 2-segmented enp is retained in species of Pseudotachidiidae gen. 1 and gen. 2. The enp in *Pseudomesochra* and the Parannopinae is 1-segmented with only 4 setae. The same spatial arrangement of the setae (fig. 39) in both taxa indicates that the reduction may be homologous. In one lineage within Paranannopinae (Gee & Huys, 1991, 1994, 1996) setae of the Mx enp and of other mouthparts as well are modified into "claviform aesthetascs".

Several different groundpatterns can be described for subtaxa of Thalestridimorpha (fig. 38). The one of the Diosaccidae agrees with that of Thalestridimorpha except for the loss of seta 9. In the Rhynchothalestridae enp2 + 3 are fused, but setation remains complete. Homologisation of setae and segments is just possible in Thalestridae (fig. 38): primarily the enp is 2-segmented, setae 5 (or 6?), 8, and 9 are lacking, no geniculate setae are present (*Parathalestris harpactoides*) **62**. The enp is 1-segmented and well developed in species of *Thalestris*, but in *Phyllothalestris* represented only by the setation, which is nevertheless complete for the Thalestridae. In *Eudactylopus* only one single seta is left (fig. 38) of the enp **61**. In the Parastenheliidae and Dactylopusiidae the Mx enp is too reduced to allow homologisation of setae. The former have a 1-segmented enp with maximally 3 setae **60**. Within the Dactylopusiidae endopods are also mainly reduced: 1-segmented with 3 setae in *Paradactylopodia* and Dactylopusiidae gen. spec. (Weddell Sea) or only represented by 1 or 2 small setae (*Paradactylopodia*, *Diarthrodes*).

6.6.3 Mx syncoxa: groundpattern of Podogennonta, Thalestridimorpha and Pseudotachidiidae

Praecoxa and coxa of the maxilla are fused to form a syncoxa in all Podogennonta. The coxal endites carry the maximal number of 3 setae each (= ancestral copepod after Huys & Boxshall, 1991). The following characteristic setal pattern on both coxal endites is widely distributed in several different taxa of Podogenonnta (Thalestridimorpha, Laophontidae, Tetragonicipitidae, Harpacticidae, further derived in Pseudotachidiidae) (fig. 40): one slender, slightly spine-like seta is located on the anterior and 2 strong setae on the posterior side. The latter setae are mostly unilaterally ornamented with characteristic spinules and subapically furnished with a whip-like flagellate spinule ("flagellate seta "). This remarkable pattern is undoubtedly already a character of the Podogennonta groundpattern as well as that of the Thalestridimorpha. It probably is an autapomorphy of the Podogennonta (+ *Zosime*?) **70**. In Pseudotachidiidae one or both (Pseudotachidiidae gen. 2) flagellate setae are modified further (fig. 45): the respective setae are naked, except for 2 median large spinules. This modification is less pronounced in *Idomene* and Paranannopinae but very prominent in the *Pseudotachidius* lineage, in which the setae are short and of massive appearance. REM photographs of Pseudotachidiidae gen. 2 (fig. 45) revealed that the flagellum of the seta consists of a hollow tube with secretive activity. Whether this is the case in all taxa possessing flagellate setae remains to be examined. "Tubular setae" have already been described in several Paranannopinae, such as *Prionos ornata* and *Anapophysia* *borealis* after Huys & Gee, 1996, *Psammis longipes* after Huys & Gee, 1993. In all cases all flagellate setae of all coxal endites have been concerned.

Shape and setation of the proximal coxal endite yield autapomorphies for subtaxa within the Thalestridimorpha (fig. 41): in the Diosaccinae one of the flagellate setae is missing, and convergently also in the Dactylopusiidae **71**, in *Rhynchothalestris* the proximal flagellate seta is enlarged.

The praecoxal endites are shaped quite individually within the Podogennonta and also within the Thalestridimorpha and are difficult to be traced back to a common groundpattern. Only the maximal number of setae could be reconstructed as groundpattern characteristic by comparison with more primitive representatives of Podogennonta, Thalestridimorpha, and Pseudotachidiidae (fig. 40). Accordingly both endites, which are not completely separated, carry 3 setae each. The distal endite shows a flagellum on one or two of the setae. An autapomorphy either for the Thalestridimorpha or maybe for a rather more inclusive taxon is the loss of a seta on the distal endite **70**. In the Pseudotachidiidae 2 setae are missing on the proximal endite (see also below) **64**. Compared to the harpacticoid groundpattern according to Huys & Boxshall (1991) consisting of 6, 3 setae, the proximal endite lacks 3 setae in Podogennonta. Shape and pattern of the setation of the praecoxal endites yield several autapomorphies for subtaxa within the Podogennonta and Thalestridimorpha (fig. 42-44). The groundpattern of the latter, as far as number of setae is concerned, is represented by *Rhynchothalestris* carrying 2, 3 slender setae (in all other taxa at most 2, 2 setae) (fig. 43). In the Parastenheliidae the proximal endite is remarkably shorter than the distal one (fig. 43) **65** and in the Dactylopusiidae only 1 single endite (fusion product?) with only 1 seta is left (fig. 43) **66**. *Ambunguipes/Hamondia* show a strongly enlarged and characteristically ornamented seta, (additionally directed downwards according to Huys, 1990) on the distal endite (fig. 43). The Diosaccidae bear 2, 2 spinule-ornamented setae, the outermost of which with a flagellum (*Metamphiascopsis*) (fig. 42). The Thalestridae display primarily (*Thalestris*) a single bilobed praecoxal endite with 2 setae lying far apart from each other. This endite is probably a fusion product of the two original endites still carrying 1 seta each (fig. 42) **68**. In *Parathalestris* the endite is indistinctly bilobed, the inner seta is characteristically ornamented (fig. 42). In *Eudactylopus* the endite is long and slender, no more bilobed, but still with 2 setae (fig. 42) **69**.

Shape and pattern of the setation are also very characteristic in the Pseudotachidiidae **64** (fig. 44): the distal endite carries 2 flagellate setae, the outer one short and modified (see fig. 44), the inner one larger and furnished with a higher density of spinules, and with 1 small spine-like seta. The proximal endite is armed with a strong, spinous seta basally which is accompanied by very long spinules. The praecoxal endite of the Paranannopinae can be easily derived from this pattern (fig. 44): both original endites are clearly fused, the spine-like seta on the original distal endite is lost and the seta on the original proximal endite is remarkably enlarged.

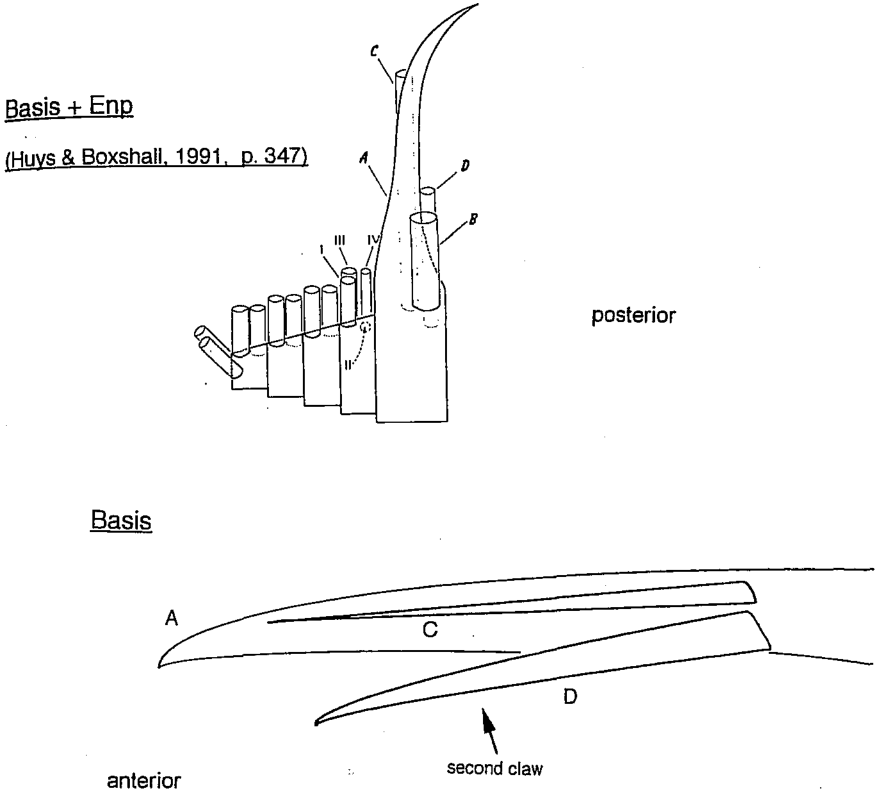
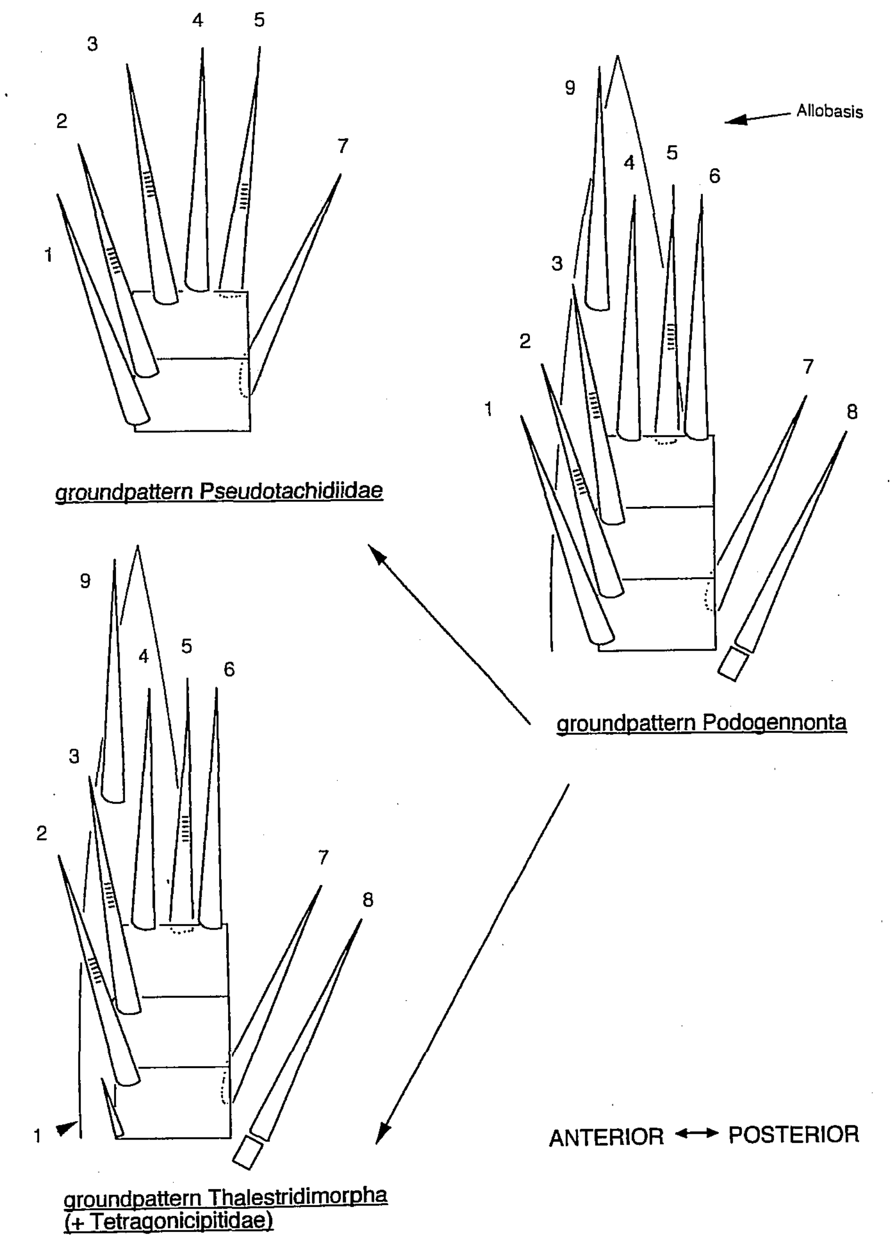


Fig. 36: Groundpattern of the maxilla enp and the maxilla basis in the Harpacticoida after Huys & Boxshall (1991).

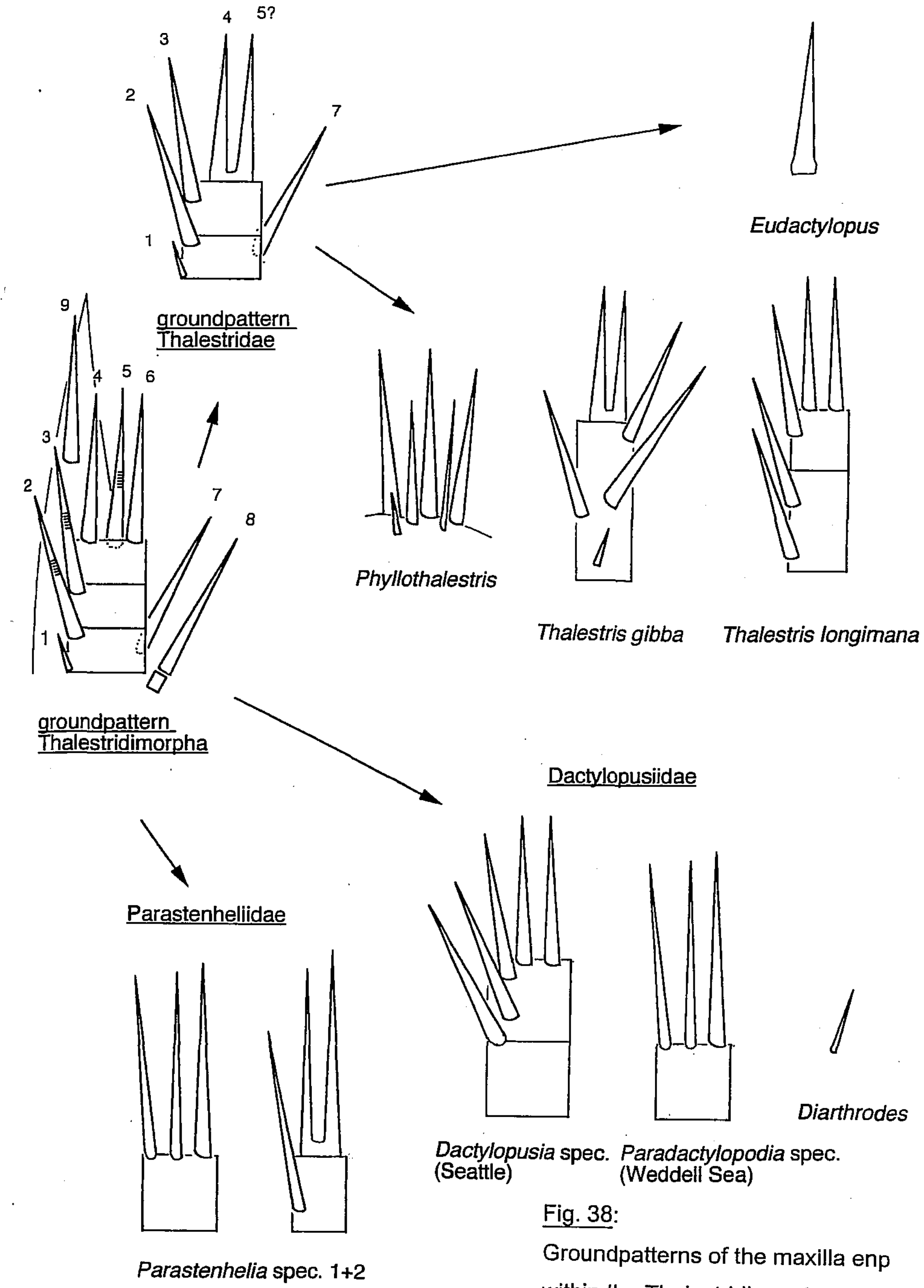


groundpattern Pseudotachidiidae

groundpattern Podogennonta

groundpattern Thalestridimorpha (+ Tetragonicipitidae)

Fig. 37:
Groundpattern of the maxilla enp in the Podogennonta, Pseudotachidiidae and Thalestridimorpha.



groundpattern Thalestridae

Eudactylopus

groundpattern Thalestridimorpha

Phyllothalestris

Thalestris gibba

Thalestris longimana

Dactylopusiidae

Parastenheliidae

Parastenhelia spec. 1+2

Dactylopusia spec. (Seattle)

Paradactylopodia spec. (Weddell Sea)

Diarthrodes

Fig. 38:
Groundpatterns of the maxilla enp within the Thalestridimorpha.

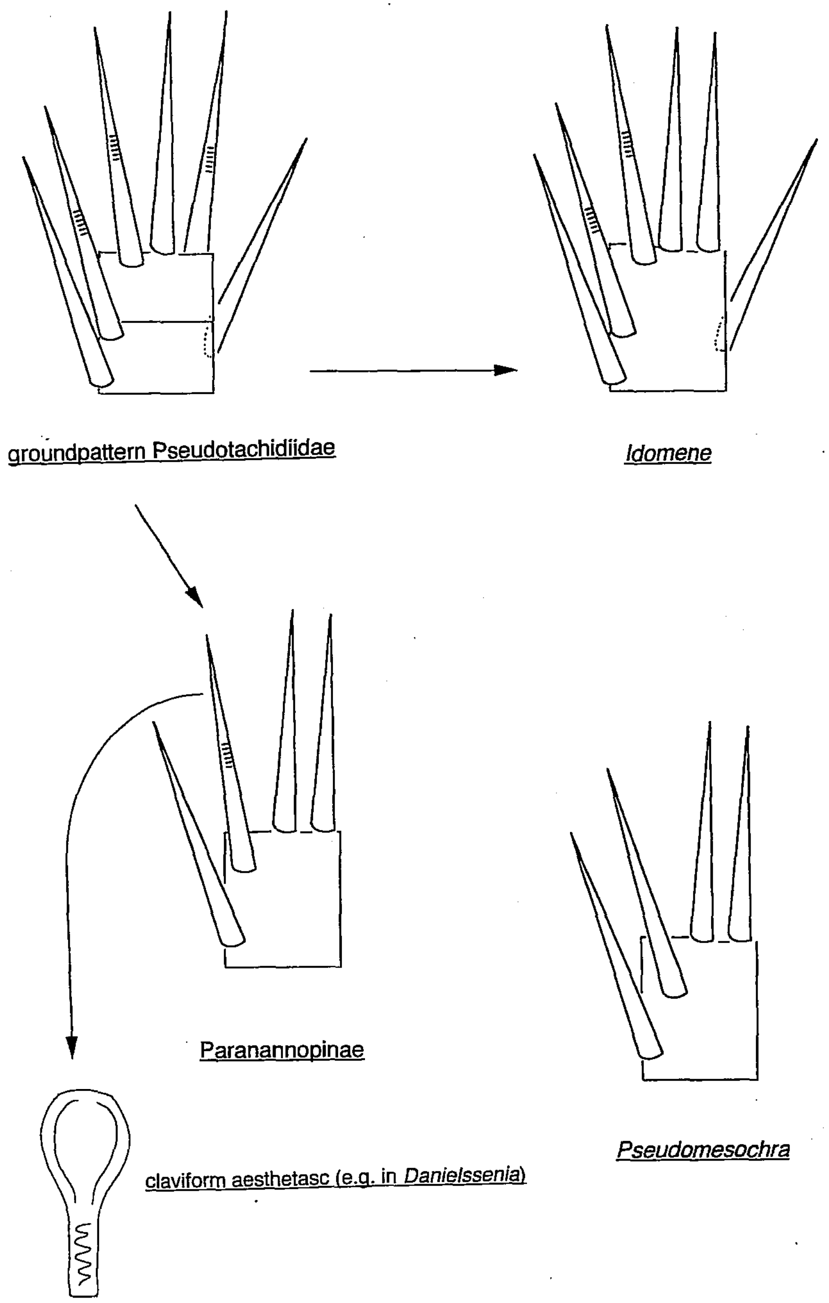


Fig. 39: Groundpatterns of the maxilla enp within the Pseudotachidiidae.

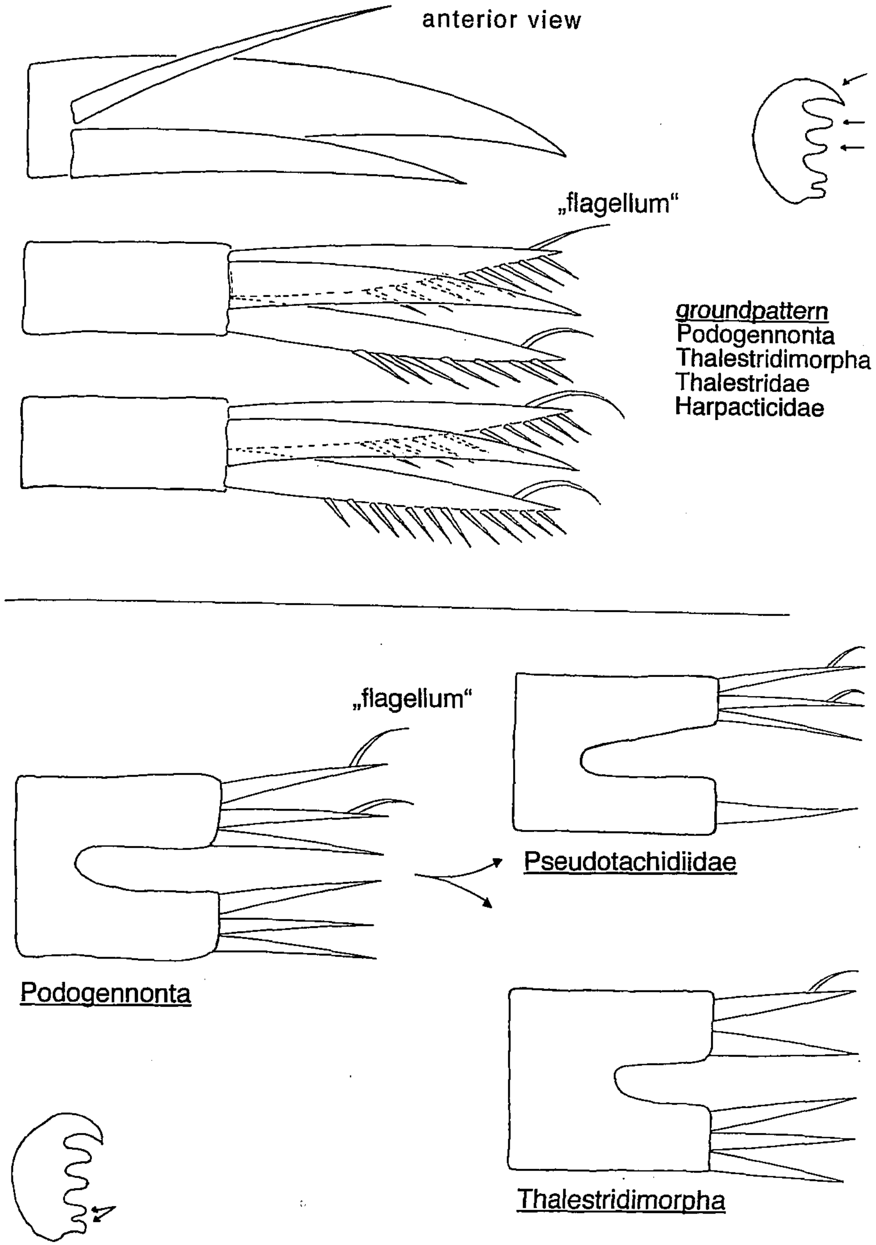


Fig. 40: Groundpattern of the maxilla coxal endites in the Podogennonta and *Thalestridimorpha* (above) and of the praecoxal endites in the Podogennonta, Thalestridimorpha and Pseudotachidiidae (below).

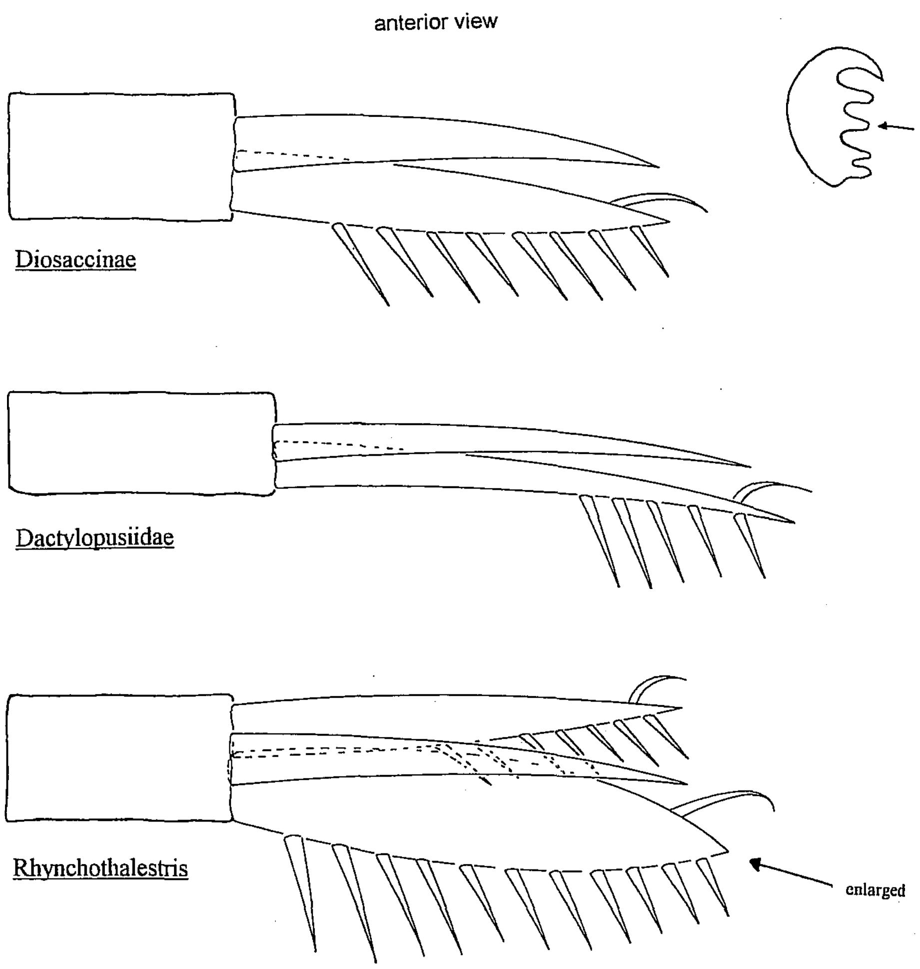


Fig. 41: Proximal maxilla coxal endite in the Diosaccidae, Dactylopusiidae and *Rhynchothalestris*.

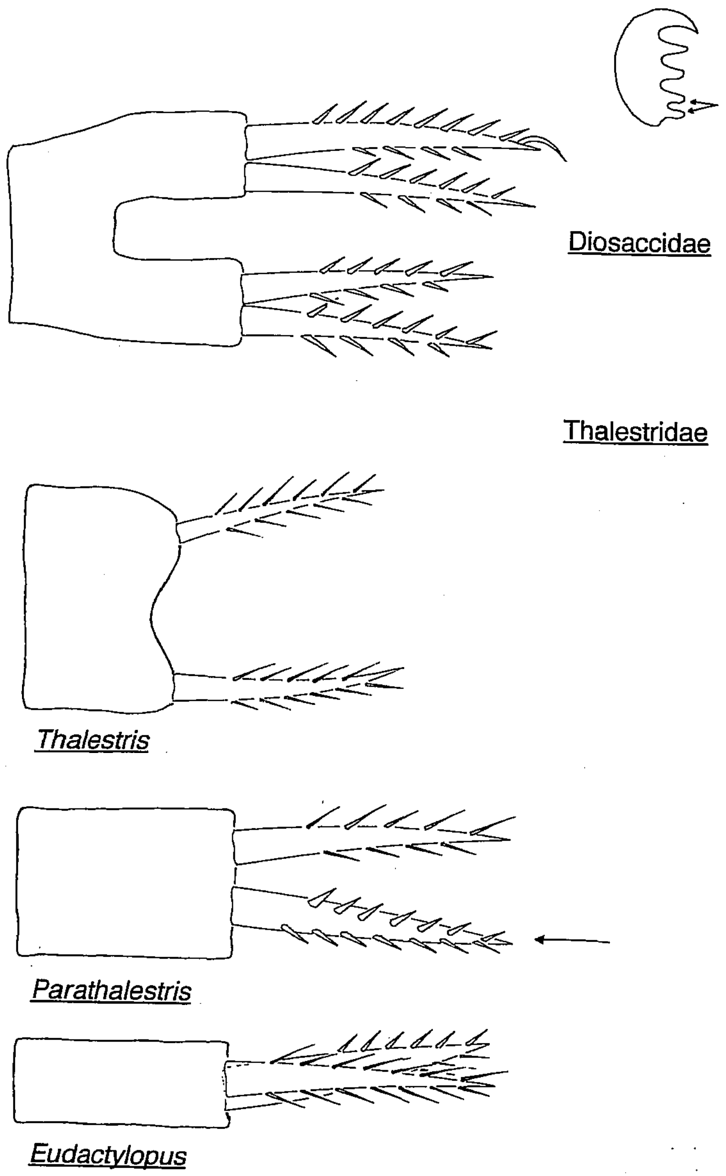
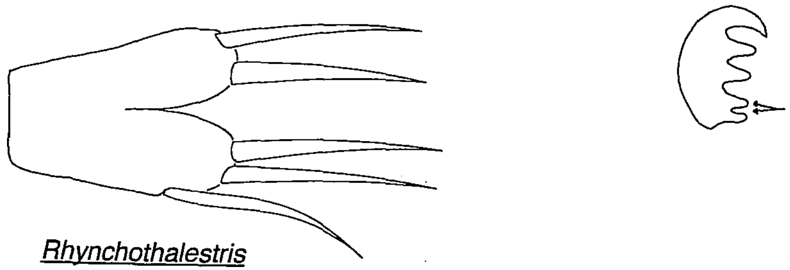
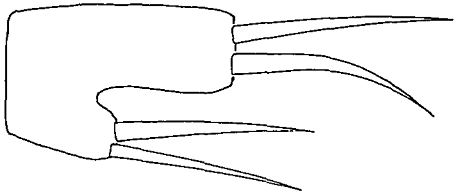


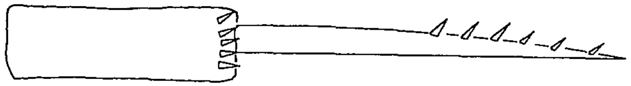
Fig. 42: Maxilla praecoxal endite in the Diosaccidae and Thalestridae.



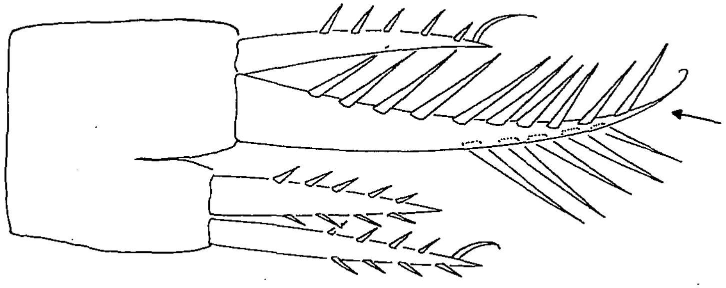
Rhynchothalestris



Parastenheliidae

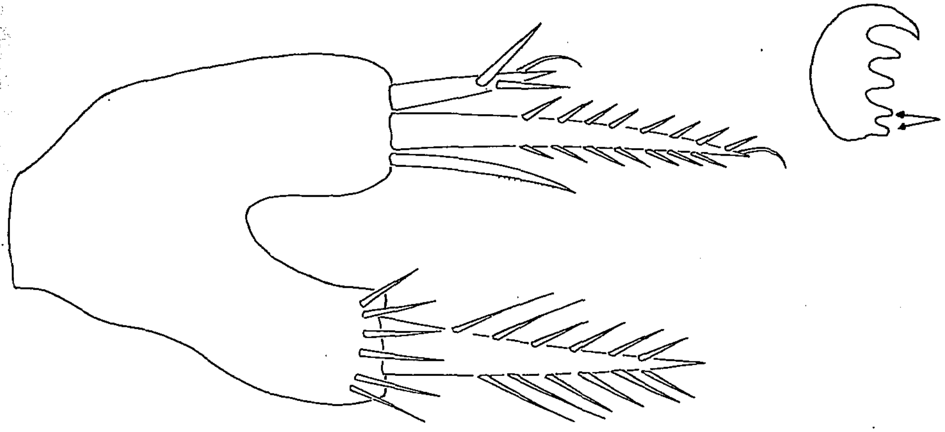


Dactylopusiidae

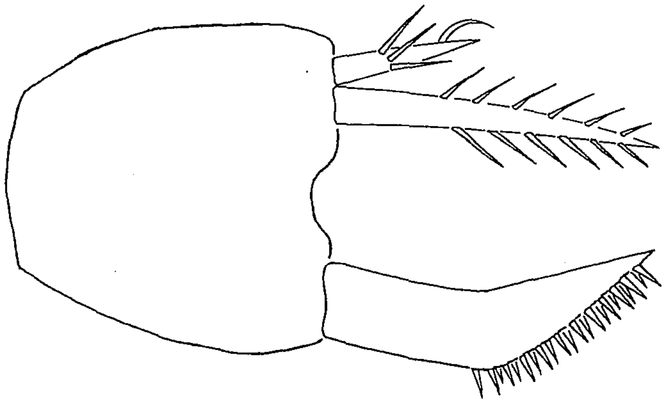


Ambunguipes/Hamondia

Fig. 43: Maxilla precoxal endites in the Dactylopusiidae, Parastenheliidae and Rhynchothalestridae.



Pseudotachidiidae



Paranannopinae + *Pseudomesochra*

Fig. 44: Maxilla praecoxal endites in the Pseudotachidiidae.

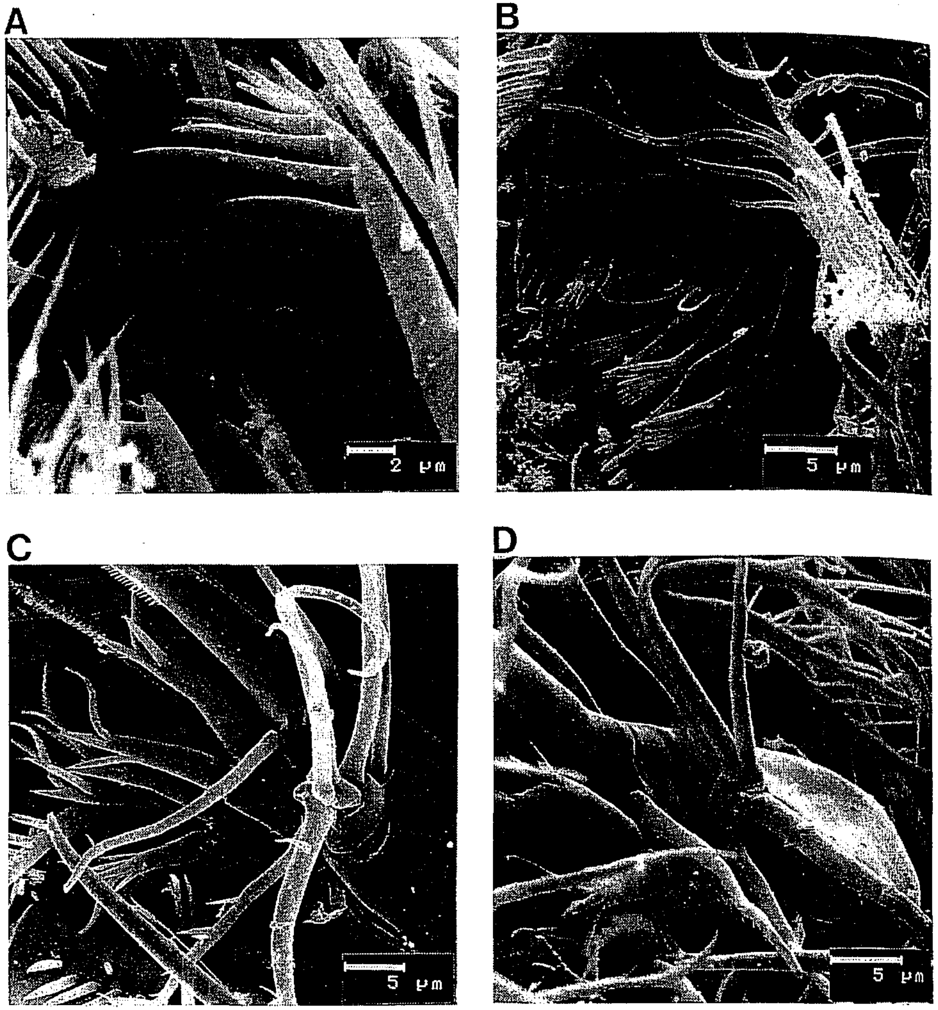


Fig. 45: REM photographs: A+B: Maxillula praecoxal arthrite in *Pseudomesochra* spec. (female, Pseudotachidiidae). Depicted are the posterior "double spinules" on the posterior apical spines (Podogennonta groundpattern) and the dentation of the anterior spines (Pseudotachidiidae groundpattern). C+D: maxilla in Pseudotachidiidae gen. 2, female. Among others, the maxilla enp and the coxal endites with the flagellate setae, the latter of which represent hollow tubes are depicted.

6.7 Maxilliped

6.7.1 The "prehensile" maxilliped within the Oligoarthra

According to Huys & Boxshall (1991) the maxillipedal groundpattern of the Harpacticoida, reconstructed on the basis of primitive characters of Polyarthra, is as follows: the protopodite is still (unclearly) separated into praecoxa and coxa, bearing 1 + 2, 4, 3 setae on the respective endites. The basis bears at most 2 setae (copepod groundpattern), the endopod is 2-segmented, the proximal segment resulting from fusion of the ancestral copepod segments 1-5, and carrying 1 outer seta and 5 + 5 more setae.

The groundpattern characters of the Oligoarthra are based on own material and on the literature. Praecoxa and coxa are still separated, even in several taxa of Thalestridimorpha (see figs. 47 + 48). The praecoxa remains asetose, whereas the coxa bears at most 7 setae (Cerviniidae). The basis carries 2 setae, the enp is 2-segmented, enp1 with no more than 3 and enp2 with no more than 4 setae (Cerviniidae, Idyanthinae, Neobradyiidae, Podogennonta (Thalestridimorpha)). The endopodal setae are unmodified, e.g. in Cerviniidae, but in most Oligoarthra the Mxp is "prehensile", i.e., a more or less developed grasping claw, representing an endopodal seta, is present on the enp. The origin of this claw is difficult if not impossible to assess in most cases, because the remaining setation and segmentation are strongly reduced. Certain taxa of Thalestridimorpha, however, have retained the complete setation of the Mxpenp, making a homology hypothesis possible. Looking at outgroup taxa with still 2-segmented enp, complete setation and "prehensile" claw, which can be found mainly within the more primitive Tisbidae (Idyanthinae), 2 types can be distinguished (fig. 46). Both types probably show a common ancestral state, the arrangement and shape of homologous segments and setae described below being an autapomorphy for a taxon including the taxa in question. Type 1 is represented by *Tachidiopsis cyclopoides* (compare fig. 2.4.15 in Huys & Boxshall, 1991) and *Tachidiopsis* spec. (Weddell Sea Ant/10/560). Enp1 and enp2 are still clearly separated, enp2 is already reduced in size. Enp1 carries 3 setae altogether, 1 small seta at the outer margin (no. 3 in fig. 44) and 2 posterior setae at the inner margin, the distal one of which is claw-like (no. 2 in fig. 44), the proximal one long and slender (no. 1). Enp2 carries 2 long, geniculate setae terminally and one minute seta at the outer margin. The presence of these 2 terminal geniculate setae is widespread among Oligoarthra, e.g. in Tisbidae (Idyanthinae, Tisbinae (*Scutellidium*)), Paramesochridae, Superornatiremidae, and Novocriniidae (see chapter 7.3). The type 2 Mxp is also present within Idyanthinae (*Idyanthe*), Podogennonta (Thalestridimorpha), but also in Tisbinae (*Scutellidium*). In *Idyanthe*, representing the example for type 2 in fig. 46, the Mxp has principally the same shape as in *Tachidiopsis*. Differences are found in the shape of seta no. 3, which is minute and slender in *Tachidiopsis*, but a large claw reaching posteriorly beyond enp2 in *Idyanthe*. In Thalestridimorpha/Podogennonta (fig. 46) seta no.3 has become the "main claw", which is located terminally on the single compound enp segment. In many taxa (Pseudotachidiidae, Thalestridae and more) the terminal claw is fused with the enp segment. The remaining setae of the former enp1 insert posteriorly. The second claw (=seta no. 2) is reduced to a fine and very slender spine-like seta (still visible in *Metamphiascopsis* (Diosaccinae), *Ambunguipes* (Rhynchothalestridae)). Enp2 is totally incorporated into enp1, but is still represented by the complete set of 4 setae (4 setae are only present in *Rhynchothalestris helgolandica* according to the description of Huys, 1990), which are of reduced size and located in a patch on the anterior surface of the segment (fig. 46). A complete setation of the Mxpenp can also be observed in *Scutellidium* (Tisbinae, according to own observations and see illustration of Itô, 1976 in fig. 46), making a homologisation possible (fig. 46). It turned out, that the "main claw" is homologous with the one in the Thalestridimorpha/Podogennonta and that the Mxp belongs to type 2. The Superornatiremidae, for which there are good arguments for a closer relationship with Tisbinae (compare Huys, 1996), have a Mxp which despite reduced setation and segmentation, can probably be assigned to type 1 (posterior position of the proximal and anterior position of the subsequent distal seta at the outer margin, which indicates the origin from enp1 and enp2, respectively; seta no. 2 representing the "main claw"; compare description of Huys, 1996, e.g. fig. 29, p. 534). This would speak in favour of an independent development of type 2 in *Scutellidium* and Thalestridimorpha/Podogennonta, respectively. A thorough revision of Tisbidae, especially of the position of the primitive *Idyanthe* as representative of type 2, has to be done, before final conclusions can be drawn about how often type 2 has developed within Oligoarthra and about whether type 1, being clearly present in *Tachidiopsis* and Novocriniidae, represents the plesiomorphic state of type 2 or maybe even a more derived state (miniaturisation of seta no. 3). In most Oligoarthra the setation is reduced such that direct assignment to one of these two types is impossible.

Further characters of the groundpattern of Podogennonta/Thalestridimorpha are the presence of a demarcated praecoxa (e.g. in *Melima*, Stenheliinae) and of 2 basal setae as well as at most 4 coxal setae being arranged in pairs, which seems to be an autapomorphy of Podogennonta **73**. Outside Thalestridimorpha only maxillipeds with further reduced setation occur within Podogennonta. It cannot be excluded that a "prehensile" Mxp has developed more than once independently.

6.7.2 Maxilliped within the Thalestridimorpha

Starting from the above-described groundpattern the shape of the Mxp yields several useful characters relevant for the systematics within Thalestridimorpha (figs. 47 + 48). The Rhynchothalestridae (fig. 47) retain the enp-setation of the groundpattern (*Rhynchothalestris helgolandica*, after Huys, 1990 seems to be the only species having retained 4 setae on Mxpenp2 -the other species carry 3-), enp and claw are fused **74**. A further autapomorphy of this family is the position of the 4 coxal setae, which are arranged in a terminal row instead of the plesiomorphic pairwise arrangement **75**. The Parastenheliidae lack 1 coxal, 1 enp1- and 1 enp2-seta, respectively, endopod and claw are fused, the basal setae are medially approximated to one another **81**. A separation of enp and claw has been described for the Dactylopusiidae in the literature (*Dactylopusia vulgaris*, Lang, 1965). This could not be confirmed by the study of own material. In the Dactylopusiidae only 2 terminally located coxal setae are present (in *Paradacylopodia* the outer seta is much shorter than the inner one) and one elongated inner seta on the basis. The setation of enp2 consists only of a short "pin" and 1 long seta, on enp1 one seta is missing **82**. The last common ancestor of Thalestrioidea still possessed the complete coxal and basal setation (fig. 48), the endopodal segment was well developed and demarcated from the claw (Diosaccidae). Only 2 enp2-setae are still present, the inner one very short, the other one longer **76**. The Diosaccinae and Miraciinae (= groundpattern Diosaccidae, fig. 48) have only retained 1 enp2-seta inserting terminally on the endopod segment (its homology with either the long or the short seta of the Thalestrioidea groundpattern has to remain open) **77**.

Enp and claw are separated, coxal and basal setation are complete (groundpattern Podogennonta/Thalestridimorpha). In the Miraciinae basis and enp/claw are strongly deformed **79**. In Stenheliinae the complete enp2 setation is lost, the 2 basal setae are approximated to one another near the distal inner margin and 1 seta is missing of the distal coxal pair of setae **78**. The Thalestridae deviate from the Thalestridoidea groundpattern by the loss of a seta of the proximal coxal pair of setae, the loss of 1 seta of enp1, and by the enp segment itself being fused with the claw **80**.

6.7.3 Maxilliped within the Pseudotachidiidae (fig. 49)

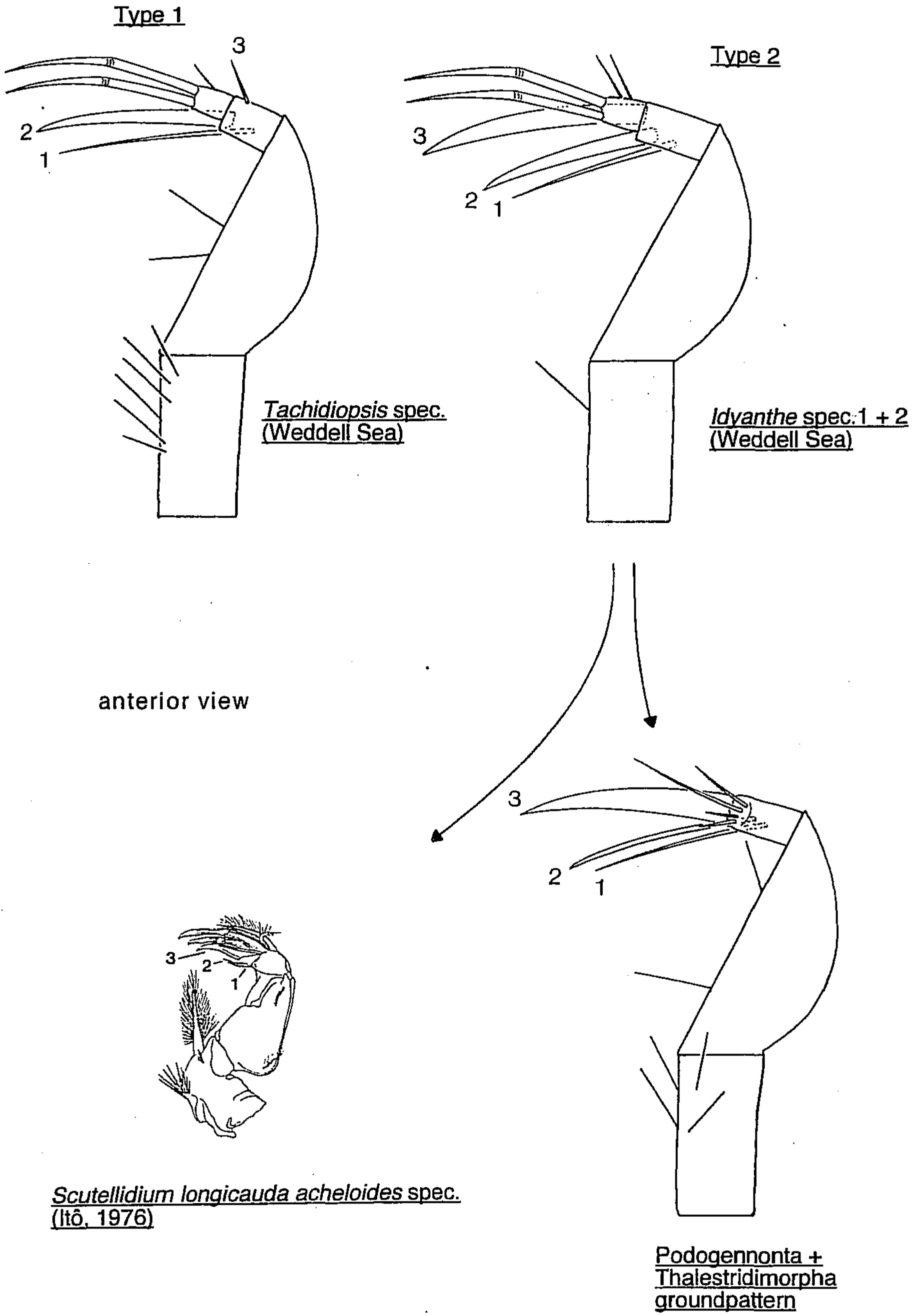
In all subtaxa the complete enp1 setation is lost, except for the endopodal claw. One very short and 1 long, well developed seta remain of the enp2 setation. The basis carries a characteristically shaped seta (it is long and unmodified only in *Pseudomesochra*, *Danielssenia* spec. (Weddell Sea), *Peltisenia aberrans*, and some species of *Idomene*), the syncoxa bears 2 setae, the proximal of which is well developed and strongly spinulose, the distal one smaller (in *Pseudomesochra* the proximal seta is only longer than the plumose distal one) **83**. Outside the Paranannopinae only *Idomene rufocincta* (after Lang, 1965) has retained 2 syncoxal setae, whereas in the other species only the extremely elongated seta remains. The homologies in fig. 49 have been deduced from the Thalestridimorpha/Podogennonta groundpattern (fig. 46).

P. 129: fig. 46: "Prehensile" maxilliped types within the Tisbidae and Podogennonta/Thalestridimorpha.

P. 130: fig. 47: Maxilliped groundpatterns within the Thalestridimorpha.

P. 131: fig. 48: Maxilliped groundpatterns within the Thalestrioidea.

P. 132: fig. 49: Maxilliped groundpatterns in the Pseudotachidiidae.

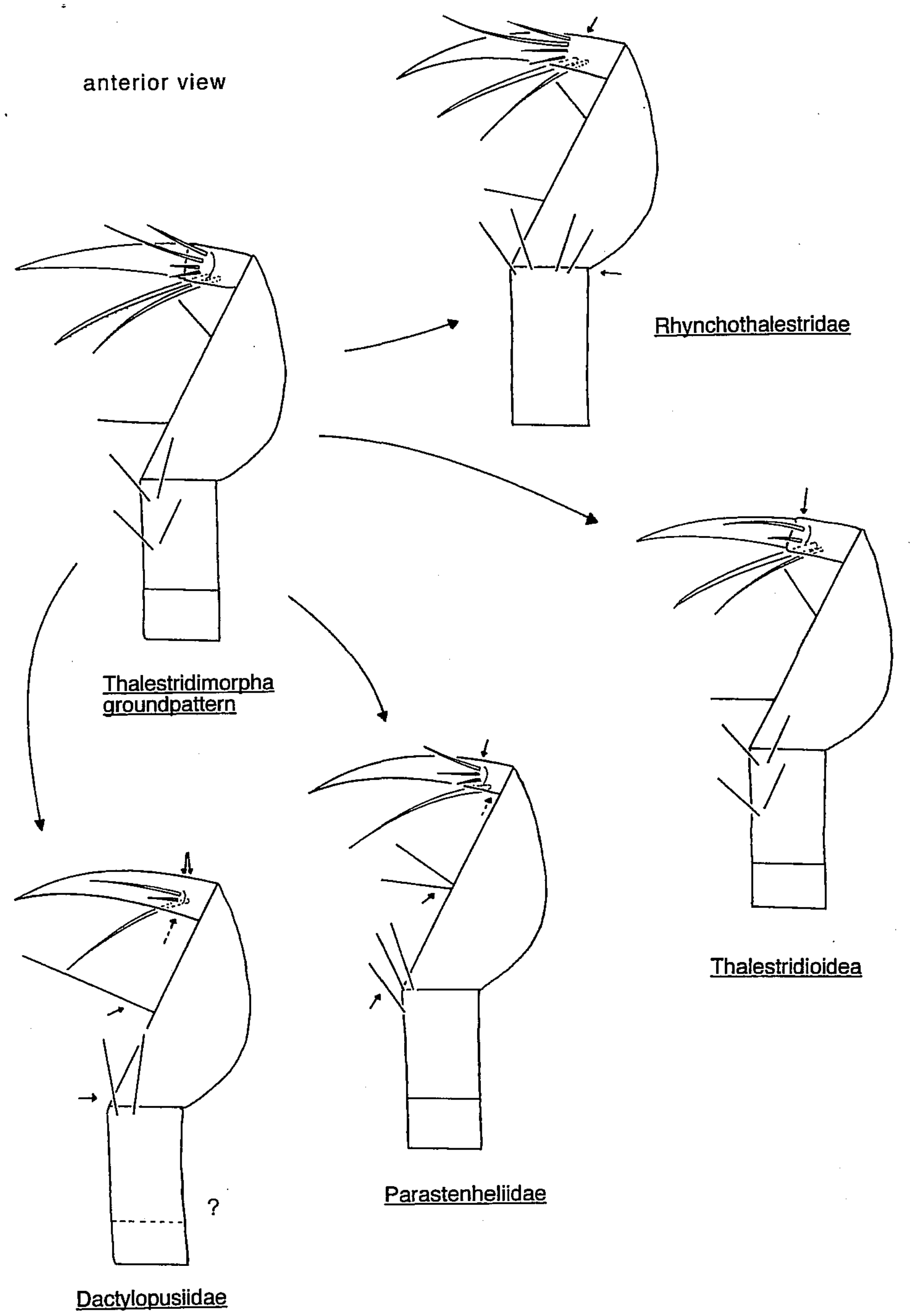


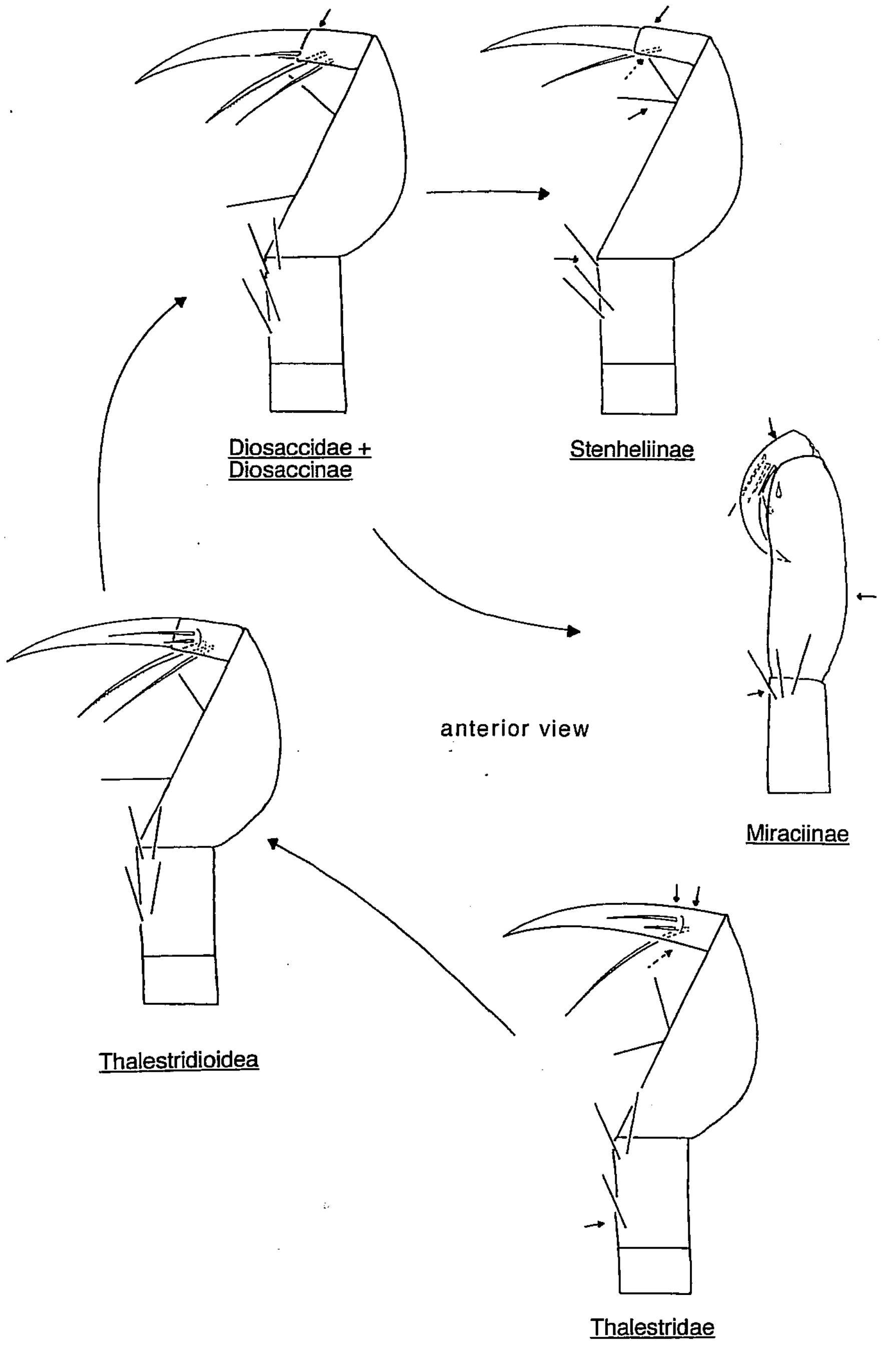
Tachidiopsis spec. (Weddell Sea)

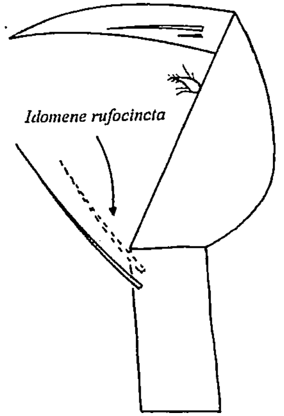
Idyanthe spec. 1 + 2 (Weddell Sea)

Scutellidium longicauda acheloides spec. (Itô, 1976)

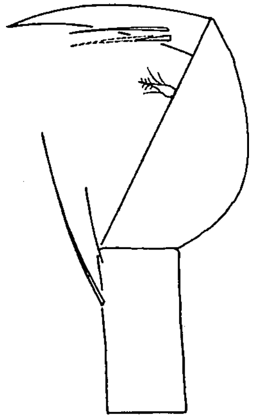
Podogennonta + Thalestridimorpha groundpattern


anterior view
Rhynchothalestridae
Thalestridimorpha groundpattern
Thalestridioidea
Parastenheliidae
?
Dactylopusiidae

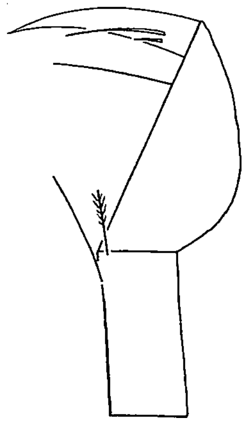

Diosaccidae + Diosaccinae
Stenheliinae
Miraciinae
anterior view
Thalestridioidea
Thalestridae



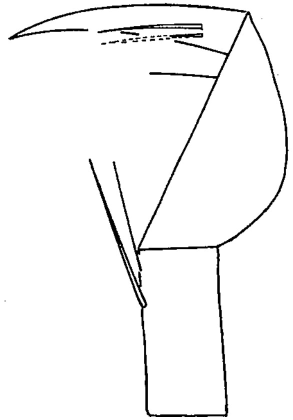
Idomene
„*Pseudotachidius* lineage“



Paranannopinae



Pseudomesochra



Pseudotachidiidae
groundpattern

anterior view

6.8 P1

6.8.1 P1 of the Podogennonta

The shape of the P1 is the most distinctive autapomorphy of Podogennonta. The groundpattern can be described as follows (fig. 50): coxa unarmed, basis with 1 outer and 1 inner seta, respectively; enp and exp 3-segmented, enp1 at least as long as exp1 and 2 together and with 1 inner seta; enp2 and 3 short, enp2 with 1 inner seta, enp3 with 4 setae altogether. Shape and position of the terminal and outer setae of enp3 are quite characteristic: due to a spatial displacement, the setae have become superimposed. The outer claw-like seta lies on the anterior side, behind it there is the now geniculate outer terminal seta and on the posterior side the miniaturised inner terminal seta. In some taxa an within Thalestridimorpha and Pseudotachidiidae, also an additional inner seta is present. A kind of socket joint is often developed between enp1 and 2. The exp is shorter than the enp, exp1 carries 1 outer spine, exp2 one outer spine and 1 inner seta, exp3 bears 3 outer spines but never an inner seta, both terminal setae are primarily modified as true geniculate setae (see below) **84**. In some genera or species (e.g. *Pseudotachidius similis* group, *Parameiropsis*, *Proameira echinipes*, “Canthocamptidae” gen. spec., Weddell Sea) all endopodal segments are of equal length. There also are alternative types of exp3 setation (fig. 50): the outer terminal seta is either again a normal spine (*Paramphiascopsis*, *Robertsonia* (Diosaccinae)) or the inner seta is continuously geniculate (as in *Ameiropsis* spec. 1 and *Ameiropsis mucronatus*). An exp3 with all setae geniculate occurs e.g. within the Tetragonicipitidae, Ancorabolidae, Stenocopiinae and Pseudotachidiidae. However, as the above-described constellation with an elongate enp1 and 2 geniculate terminal setae on exp3 has the widest distribution in many – including non-related - taxa (Diosaccidae, also within *Paramphiascopsis* (*P. glacialis*), Thalestridae, Cletodidae (*Cletodes*), Ancorabolidae, “Laophontoidea”, “Canthocamptidae”, Parastenocarididae, Ameiridae, Tetragonicipitidae, Cancrincolidae, Leptastacidae), it is interpreted here as the plesiomorphic condition and as a groundpattern character of Podogennonta.

Proceeding from this condition many further modifications can be found within the Podogennonta. The ones present in *Protolatiremus sakaguchii*, Thalestridimorpha, and Pseudotachidiidae are discussed in more detail below. The following autapomorphic features of Podogennonta pertaining to the P1 can be summarised: elongate enp1, characteristic setation of enp3 (see above and fig. 50A), lack of the inner seta on exp3 and the presence of "true" geniculate setae. A "true" geniculation in this case is a single articulation with only a few distinctive articulation rings, in contrast to a continuous articulation, in which no single articulation ring can be clearly distinguished (e.g. Tisbidae, Ameiridae, fig. 50B). A further special case are the "rat-tail setae" in *Pseudomesochra* (Pseudotachidiidae, compare Willen, 1996), which possess a continuous articulation consisting of clear articulation rings ornamented with hairs.

When comparing this "podogennontan" P1 with that of other Harpacticoida, more taxa can be found which have a P1 indicative of phylogenetic relationships with the Podogennonta (fig. 51). There is no inner seta on exp3 present in the Harpacticidae and the shape of the enp agrees with the Podogennonta groundpattern except for the shortness of the middle geniculate seta on enp3. In species of the Paramesochridae the P1 strongly reminds of that of Podogennonta (elongate enp1, geniculate setae on enp3, e.g. in *Paramesochra mielkei*, Huys, 1987, species in Mielke, 1984). The presence of an inner seta on exp3 (e.g. in *Diarthrodella parorbiculata pacifica* Mielke, 1984), however, distinguished them from the Podogennonta, which are without such a seta in all of its taxa. Latiremidae probably are true podogennonts (compare, fig. 51). There is no inner seta on exp3 and despite the modified enp, elements of the podogennontan groundpattern can be found: elongate enp1, short enp2, and one geniculate claw on enp3. True geniculate setae on exp3 have been described for *Delamarella galateae* and *Latiremus eximius* by Cottarelli (1971) and Bozic (1969), respectively (fig. 51). It has to remain open until further revision to which taxon within the Podogennonta they could be assigned.

6.8.2 P1 of the Thalestridimorpha and *Protolatiremus sakaguchii*

Within every subtaxon on traditional family level there is an often extremely elongate exp2. This is unique for the Harpacticoida **79**. This character is also shared by *Protolatiremus sakaguchii* Itô, 1974 (fig. 52), indicating a closer relationship with the Thalestridimorpha (compare chapter 7 for a more elaborate discussion). The shape of the setae on enp3 (short, geniculate claw instead of long and slender seta), their slightly altered position compared with the Podogennonta groundpattern (compare fig. 50A) and the shape of the setae on exp3 (dwarfed proximal outer spine, next outer spine geniculate, distal one not geniculate; inner terminal seta thoroughly geniculate and slightly claw-like, compare fig. 52) are autapomorphies of *Protolatiremus* **85**.

The individual shape of the P1 yields further autapomorphies and diagnostic characters for certain taxa. In the following the characteristics for the respective taxa, starting from the Podogennonta groundpattern, will be described. The Parastenheliidae (fig. 53) show a 2-segmented enp with an often extremely elongate enp1, the inner seta of which inserts in the proximal half of the segment. Enp2 and 3 are fused and the inner setae of both segments are lost. Terminally the setation consists of an anterior claw, a geniculate claw (with few large articulation rings) and of a posterior small, slender seta. The exp is 3-segmented with exp3 carrying only 4 setae (the proximal outer spine is missing), the outer terminal seta being always geniculate, the inner one sometimes (*Parastenhelia costata* after Mielke, 1990) **90**. Exp2 is extremely elongate in several species of *Parastenhelia* (compare fig. 53). In the Dactylopusiidae (fig. 53) the shape of the P1 is quite uniform. Enp1 is elongate, enp2 is almost always asetose (a seta could be observed only in *Dactylopusia euryhalina* after Monchenko, 1967 and *Dactylopusia* spec., Seattle, respectively). Enp3 lacks an inner seta, terminally there are 2 non-geniculate claws, of which the anterior one is smaller, the middle one larger, and there is 1 posterior small seta. Exp2 is clearly elongate, in total the exp remains shorter than the enp. Exp3 is slightly shortened, all setae insert terminally. The inner terminal seta is long and often thoroughly geniculate **92**.

Reconstruction of the rhynchothalestrid groundpattern is more difficult. *Ambunguipes* and *Hamondia* are, well supported by strong synapomorphies (Huys, 1990), more closely related to each other than to *Rhynchothalestris*. Nevertheless, the P1 of *Hamondia* (with the only species *H. superba*) is quite aberrant compared with the other two taxa, containing plesiomophic as well as apomorphic characters (fig. 53): the whole enp, especially enp1, and both terminal claws on enp3 are massive and broad. Exp2 is slightly elongate. Contrarily, the species of *Ambunguipes* show a slender, long enp with the complete setation of the Podogennonta groundpattern. Enp3 bears 2 terminal claws, of which the anterior is half as long as the more posterior one, and 1 small posterior seta. Exp2 is strongly elongate, exp3 bears from the outer to the inner side 2 shorter, slender outer spines, 2 stronger claws and 1 slender seta. The P1 of *Rhynchothalestris* can be easily derived from this pattern and shows only the following slight differences: the enp is 2-segmented, inner terminal seta and proximal outer spine on exp3 are extremely shortened, the outer terminal claw is elongate. The aberrant shape of the P1 of *Hamondia* is surely connected with the generally unusual morphology and way of living, being therefore apomorphic within Rhynchothalestridae. The P1 of *Ambunguipes* probably represents the groundpattern of the whole taxon.

The groundpattern of the Thalestrioidea (fig. 54) agrees with that of the Podogennonta and is still conserved in the Diosaccidae, except for the inner seta lacking on enp3 **86**. An autapomorphy of Thalestrioidea is the insertion of the inner seta in the distal quarter of enp1 **88**. In the Miraciinae, both rami are elongate, the enp is 2-segmented, the original differentiation of the terminal setae is lost and on exp3 shape and position of the setae are altered compared with the Podogennonta groundpattern **89** (fig. 54). Within the Diosaccinae further derived forms occur, e.g. an elongate enp3 in *Typhlamphiascus*, *Amphiascopsis*, and *Amonardia* show convergently the same shape of P1 as the Dactylopusiidae, some *Diosaccus* species the same as the Rhynchothalestridae.

The Thalestrinae show convergently a P1 similar to *Ambunguipes* (compare figs. 53 + 54). Shape and length of the terminal claws are very variable within genera and species. In *Thalestris* and *Phyllothalestris*, for example, the anterior claw and homologous setae of exp3 are shortened (fig. 54), in *Thalestris sordida* both terminal claws are not superimposed but secondarily juxtaposed, with a gap in between. The other subfamily Eudactylopusiinae (fig. 54) shows a 2-segmented enp, which lacks 2 inner setae on the distal segment (= fusion product of enp2 + 3 of Podogennonta groundpattern). The terminal armature consists of 2 claws, of which the anterior is shorter than the posterior one, and there is 1 minute posterior seta. Exp2 is not as strongly elongated as in Thalestrinae. Because one outer spine is missing exp3 carries only 4 setae/spines, of which only the inner terminal seta shows a "true" geniculation **91**.

A new, still undescribed species, of which only one damaged female specimen was detected in samples from the Weddell Sea (Thalestrinae gen. 1, spec. 1) and which was determined as a member of the Thalestrinae, has still retained the typical 2 truly geniculate terminal setae of the Podogennonta groundpattern (fig. 54), which can therefore also be postulated as a groundpattern character of Thalestridae (interpretation of the terminal enp setation was difficult, geniculate seta located anteriorly?!). Nevertheless, the attempt to reconstruct the P1 groundpattern of Thalestridae has not been successful. A great variability of the shape of the terminal endopodal claw within Thalestrinae and the P1 of Eudactylopusiinae derived in many aspects makes polarisation of characters and reconstruction of a common groundpattern very difficult.

6.8.3 P1 within the Pseudotachidiidae

The Pseudotachidiidae groundpattern is derived in the following autapomorphic characters from that of Podogennonta (fig. 55): enp1 furnished with spinules on inner and distal margin and with a large pore on distal half of anterior surface, outer exopodal spines unilaterally fringed with long spinules. Both characters are still realised within all taxa along with more derived states, therefore probably being part of the Pseudotachiidae groundpattern itself **93**. Proceeding from this groundpattern, several derived states can be observed within the subtaxa (fig. 55): *Idomene* has an elongate and "trapezoid"-shaped enp1, whereas enp2 + 3 are short and narrowed. The shape of the terminal claws seems to be variable on the species level. The exp appears much shorter than the enp and inserts directly beneath the outer basal seta. A broadened coxa, reaching far beyond the basis on the outer side, is also present in other taxa, however, not always clear and continuously, but together with the "normal" shape (Paranannopinae). Therefore it is not a clear groundpattern character of the Pseudotachidiidae. In the groundpattern of the "*Pseudotachidius*-lineage" the distal exp segment is narrowed and the setation displaced terminally (convergently also in the Dactylopusiidae, see above). The outer terminal seta is thoroughly geniculate, whereas the inner one is genuinely geniculate. The groundpattern –with moderately elongate enp1- is almost completely retained in Pseudotachidiidae gen. 2, spec. 1 from the Weddell Sea and in *Pseudotachidius peruanus* Becker, 1974. In Pseudotachidiidae gen. 1, spec. 1 additionally the outer distal spine is geniculate. A strongly shortened enp1 occurs in Pseudotachiidae gen. 2, spec. 2 and in all species of *Pseudotachidius* described up to now, except *for P. peruanus* and *P. horikoshii*. In the species of the *Pseudotachidius-similis* group all endopodal segments are of the same length and the differentiation of the terminal setae on enp3 and exp3 is lost. The P1 of the *Pseudotachidius-coronatus* group is very specialised (compare Veit-Köhler & Willen, 1999 and fig. 55): the enp is massive, slightly inclined, enp2 and 3 are both half as long as enp1, inner, outer terminal and outer seta on enp3 are massively developed, without the podogennontan differentiation, the inner terminal seta is miniaturised. The exp inserts very "high" beneath the basal seta and does not reach beyond enp1. The respective setae on exp3 are not geniculate. The species of the "*Pseudotachidius* lineage" show a modified basal outer seta, the distal half of which is furnished with very strong spinules.

The enp of the Paranannopinae is 2-segmented (fusion of enp2 + 3), the distal segment carries only 3 setae terminally (representing former enp3). Most species do not retain the podogennontan differentiation of the setae, but there are exceptions, e.g. *Telopsammis* and *Micropsammis* (fig. 56). A still undescribed and more primitive species from the Weddell Sea (Paranannopinae gen. 1., spec. 1) displays a more elongate enp1 and the outer exopodal spines are unilaterally fringed with strong spinules. Many autapomorphic characters can be observed in the P1 of the Pseudomesochrinae (compare Willen, 1996 and fig. 57).

P. 139: fig. 50: A. P1 groundpattern of the Podogennonta. B. Different types of setal ornamentation on exp3 within the Podogennonta.

P. 140: fig. 51: "Podogennont" shape of P1 within the Oligoarthra.

P. 141: fig. 52: P1 of *Protolatiremus sakaguchii*. Scale bar: 20µm.

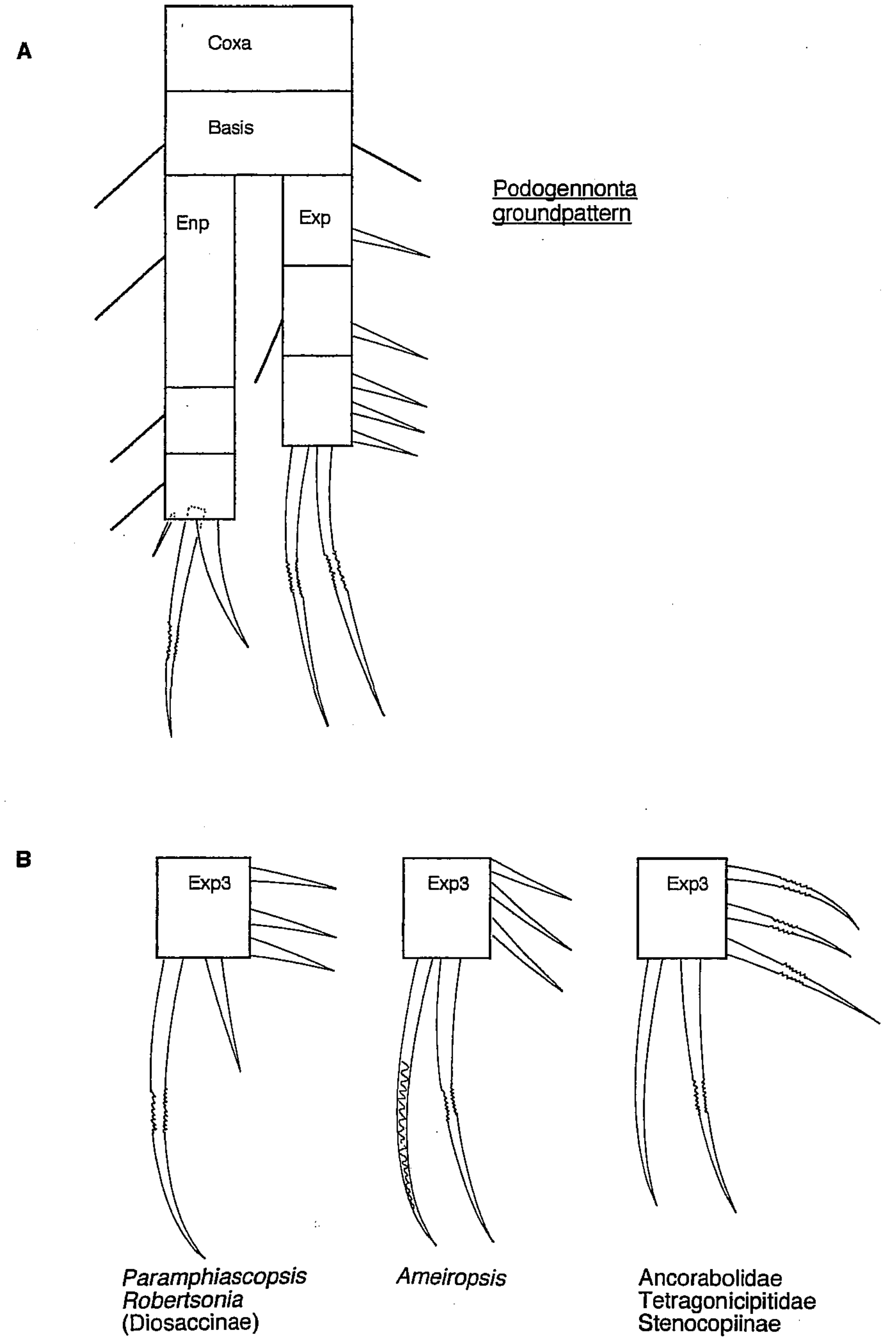
P. 142: fig. 53: P1 groundpatterns within the Thalestridimorpha (excluding the Thalestrioidea).

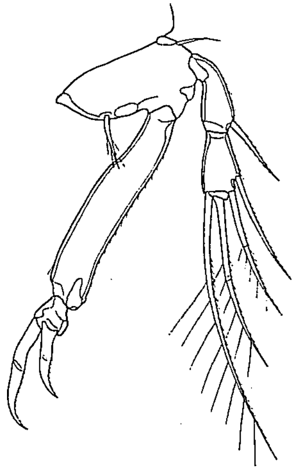
P. 143: fig. 54: P1 groundpatterns within the Thalestrioidea.

P. 144: fig. 55: P1 groundpatterns within the Pseudotachidiidae.

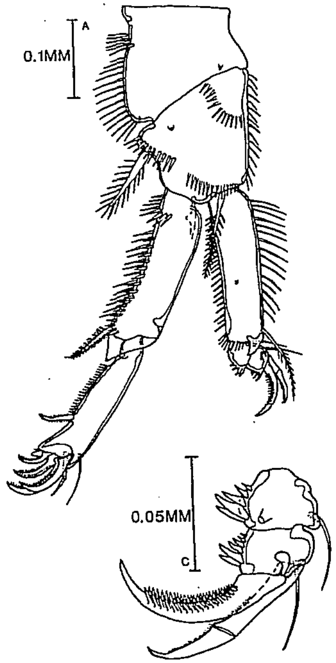
P. 145: fig. 56: P1 groundpatterns within the Paranannopinae.

P. 146: fig. 57: P1 groundpattern of the Pseudomesochrinae.

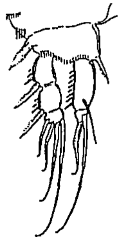




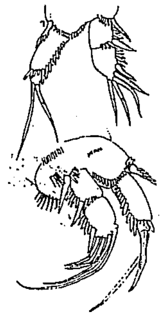
Kliopsyllus unguiseta (Paramesochridae)
(Mielke, 1984)



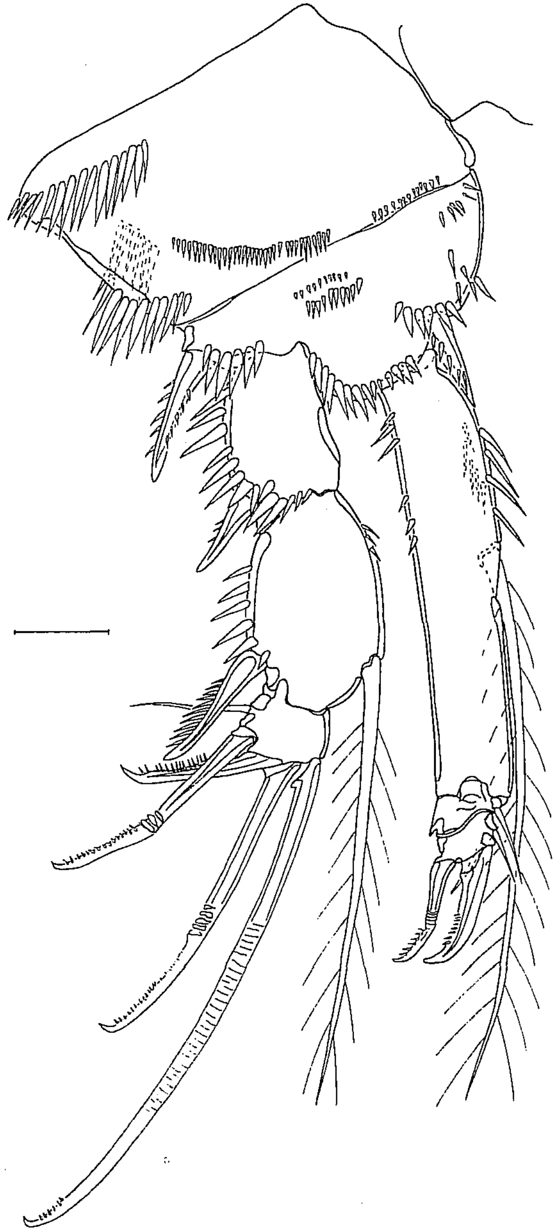
Harpacticus septentrionalis (Harpacticidae)
(Huys et. al., 1996)

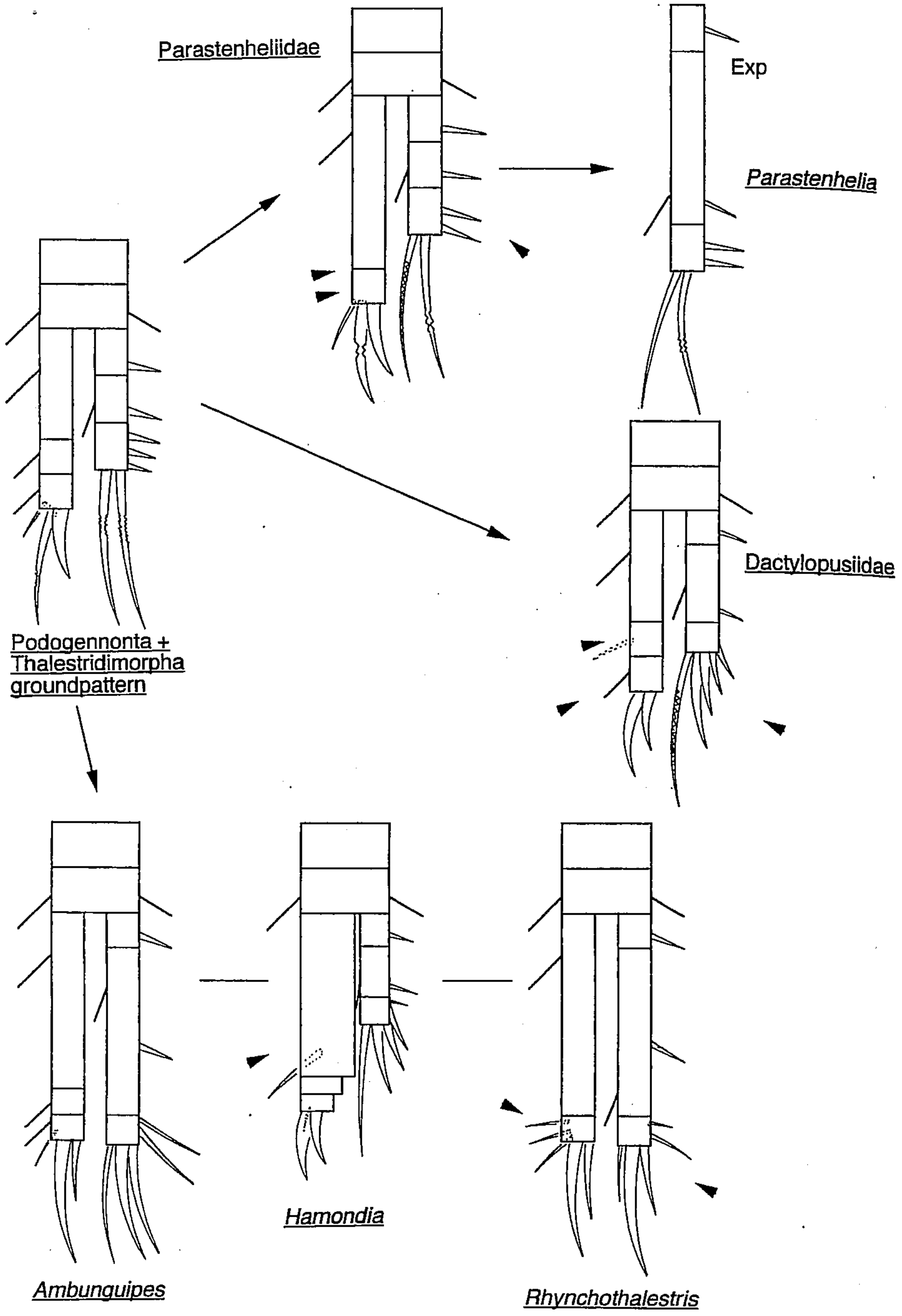


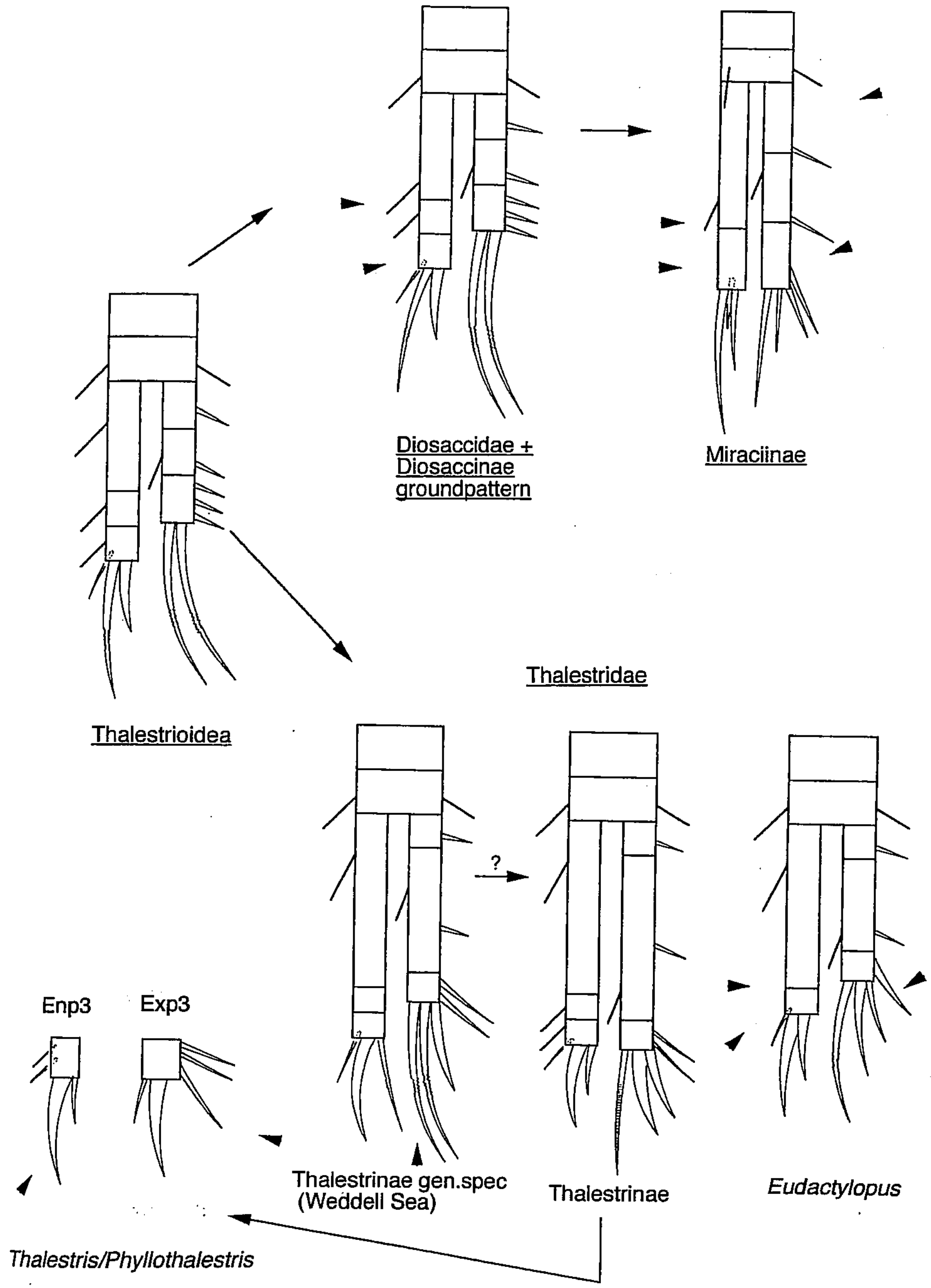
Latiremus eximius (Latiremidae)
(Bozic, 1969)

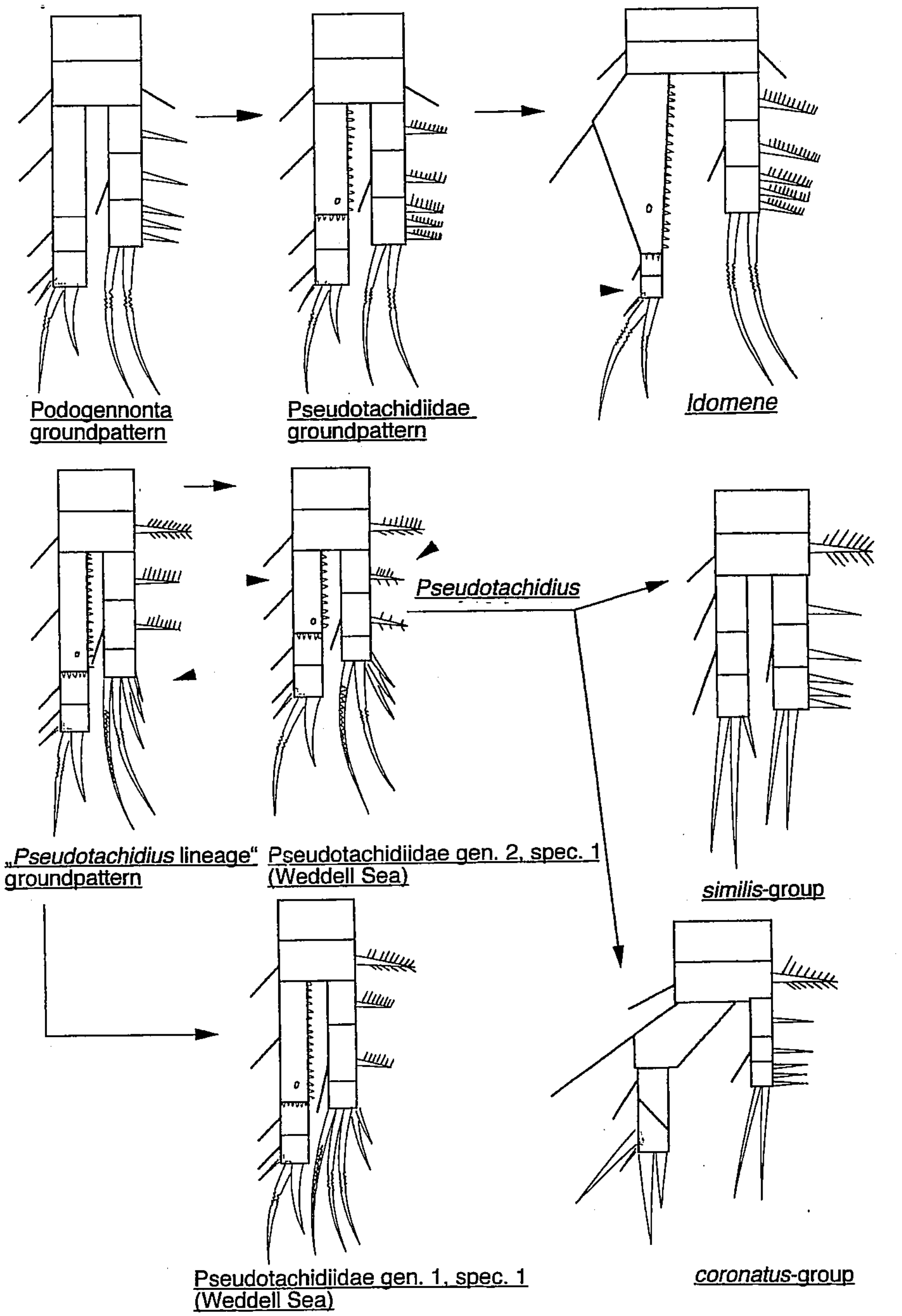


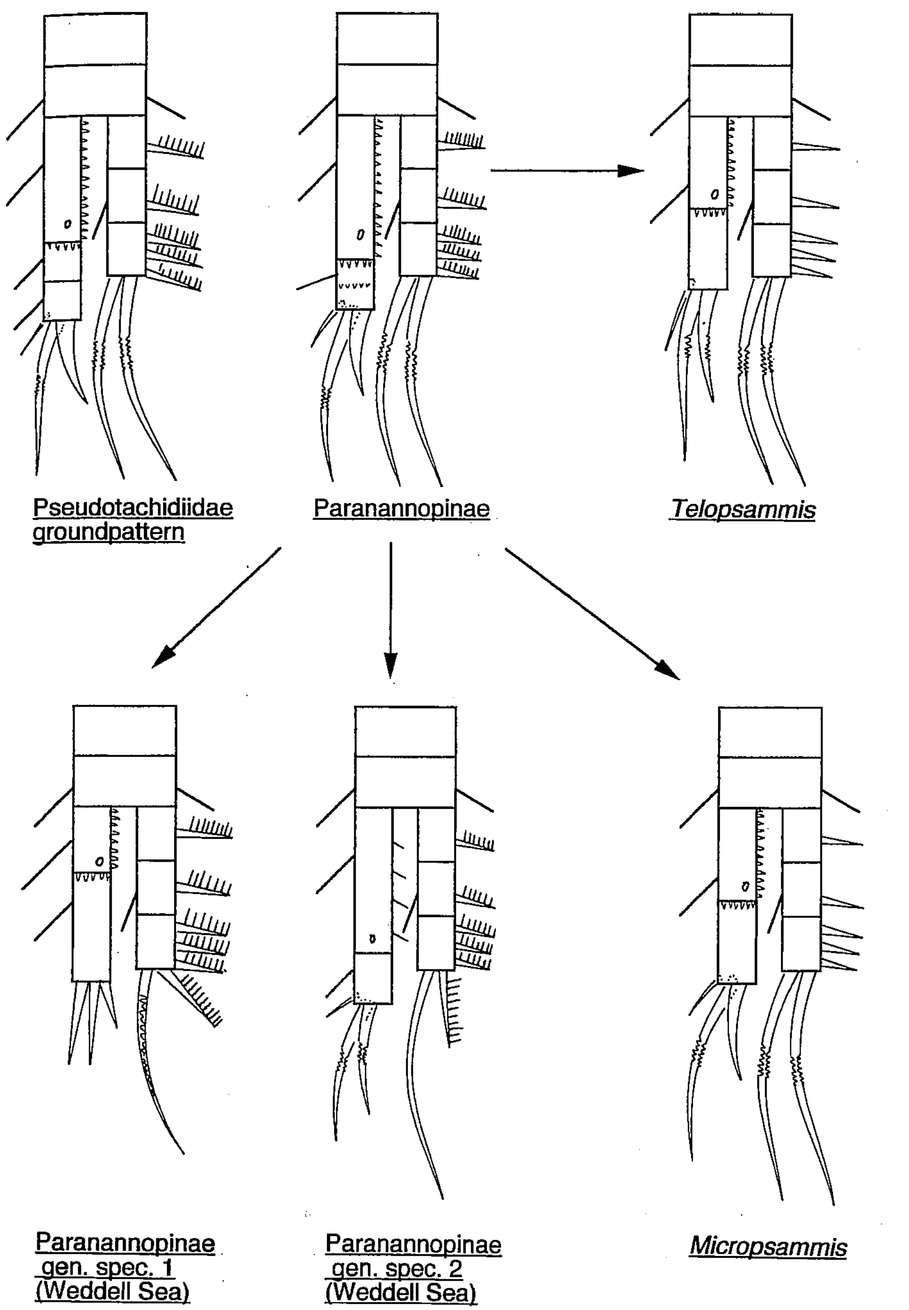
Delamarella galatae (Latiremidae)
(Cottarelli, 1971)

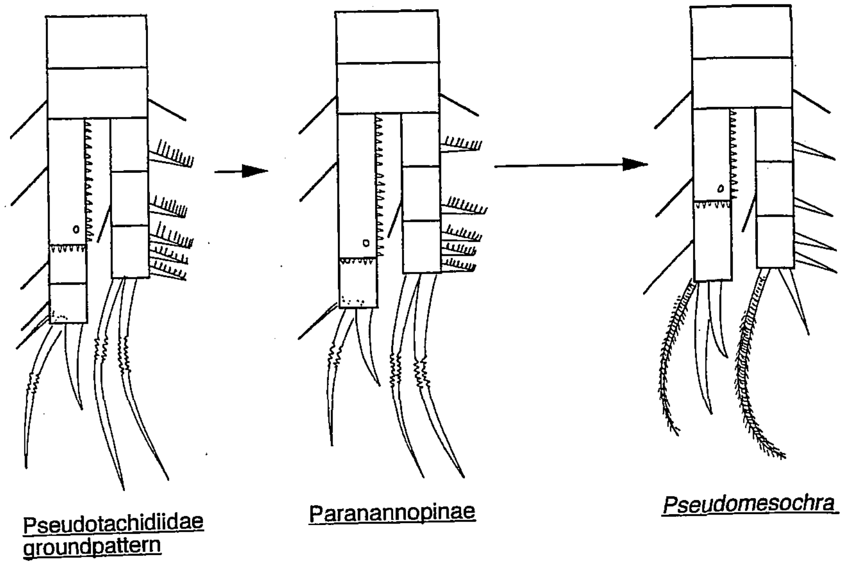



Parastenheliidae
Exp
Parastenhelia
Podogennonta + Thalestridimorpha groundpattern
Dactylopusiidae
Ambunguipes
Hamondia
Rhynchothalestris


Diosaccidae + Diosaccinae groundpattern
Miraciinae
Thalestrioidea
Thalestridae
?
Enp3
Exp3
Thalestrinae gen.spec (Weddell Sea)
Thalestrinae
Eudactylopus
Thalestris/Phyllothalestris


Podogennonta groundpattern
Pseudotachidiidae groundpattern
Idomene
„*Pseudotachidius* lineage“ groundpattern
Pseudotachidiidae gen. 2, spec. 1 (Weddell Sea)
Pseudotachidius
similis-group
Pseudotachidiidae gen. 1, spec. 1 (Weddell Sea)
coronatus-group


Pseudotachidiidae groundpattern
Paranannopinae
Telopsammis
Paranannopinae gen. spec. 1 (Weddell Sea)
Paranannopinae gen. spec. 2 (Weddell Sea)
Micropsammis



6.9 P2-P4

6.9.1 Copepoda groundpattern

In the Copepoda, the peraeopods 2-4 are paired and primarily biramous, with praecoxa, coxa and basis in the protopod and 3 segments each in exo- and endopod. The pairs of legs are functionally connected by an intercoxal sclerite. The setation can be homologised by number, shape, position, and ornamentation. The actual number of setae can be summarized with the aid of a setal formula, for which two possibilities were proposed by Huys & Boxshall (1991): 1. After Sewell, 1949. The setae of each segment are counted from the outside to the inside, and the number of the outer exopodal spines is designated by Roman letters. This method is preferred by the authors. 2. After Lang, 1934. The setae are simply counted from the inside to the outside, without taking any differentiation into account. Since this method is widely used and established in the literature and since it is sometimes difficult to define the terminal outer spine on exp3 unambiguously as spine (Roman letter after 1.) or seta (Latin number after 1.), the setal formula after Lang will be used in the following.

6.9.2 Thalestridimorpha

The setal formula of the groundpattern of the Thalestridimorpha and also Podogennonta is identical with that of the Harpacticoida (after Huys & Boxshall, 1991), except for the lack of coxal setation:

	P2	P3	P4
Enp	1,2,221	1,2,321	1,2,221
Exp	11,11,223	11,11,323	11,11,323
Basis	0,1	0,1	0,1
Coxa	0	0	0

The complete groundpattern has been retained only by the Rhynchothalestridae. The constant lack of homologous setae yields autapomorphies for certain taxa. The Dactylopusiidae lack the proximal inner seta on P4enp3 **98** and the Thalestrioidea and Parastenheliidae 1 inner seta on P4enp2 **97**. In the Diosaccidae 1 (the distal?) inner seta on

P2enp3 is missing and convergently also in the Parastenheliidae **99**. Furthermore, the latter carry only 2 inner setae on P3enp3 **100**. The Thalestrinae lack 1 inner seta on P3enp2 **96**. For the systematics on species and genus level the lack of further setae is of even greater importance.

A good autapomorphy for the Thalestridimorpha as a whole is the shape of the intercoxal sclerite (fig. 59), which has 2 pointed projections ventrally **94**. In several taxa these projections are secondarily reduced, e.g. in species of *Parathalestris, Eudactylopus, Phyllothalestris, Thalestris*, and *Rhynchothalestris*. However, since they are present in every subtaxon of Thalestridimorpha, they probably already belong to the groundpattern this taxon.

In *Rhynchothalestris* and *Ambunguipes* within the Rhynchothalestridae there is a special shape of the articulation between enp2 and enp3 which is depicted in fig. 58 **95** (*Hamondia* shows "normal" swimming legs, but see chapter 6.8). This specialised shape can also be observed in other phytal taxa, such as *Phyllothalestris* (Thalestrinae), *Eudactylopus* (Eudactylopusiinae), and *Metamphiascopsis* (Diosaccinae), but not in the groundpattern of the respective superordinated taxon, thus being convergently developed. Strongly distorted segments or a reduced segmental number of exp and/or enp (e.g. as in the Laophontidae) never occur within Thalestridimorpha, except in connection with sexual dimorphism (P2 and P3 enp in the male).

6.9.3 Pseudotachidiidae

This taxon always lacks 1 inner seta on P3enp2 **96** and P4enp2 **97**, respectively. In the Pseudomesochrinae several setae are missing: one inner seta on P2-P4exp1, 1 inner seta each on P2-P4enp2, and 1 inner seta on P3enp3. The spinulous ornamentation of enp1 and the setae of exp3 are autapomorphic characters of the "*Pseudotachidius*-lineage" (*Pseudotachidius* and related genera): in contrast to their outgroups they show an outer spine on exp3 furnished with long spinules and a "spinule-patch" on the outer margin of enp1 (fig. 60).

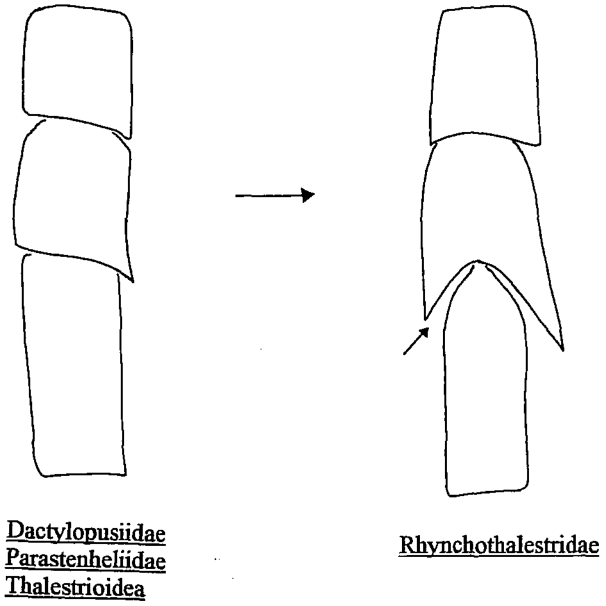
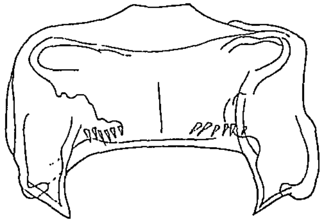


Fig. 58: Specialised shape of articulation between enp2 and enp3 of the swimming legs P2-P4 in the Rhynchothalestridae.

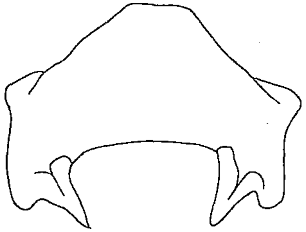
P. 150: fig. 59: Intercoxal sclerite of swimming legs P2-P4 (the P3 is depicted here as an example) in the Thalestridimorpha.

P. 151: fig. 60: Swimming legs P2-P4: specialised spinule ornamentation of exp3 and enp1 within the "*Pseudotachidius lineage*".

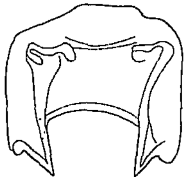
P3



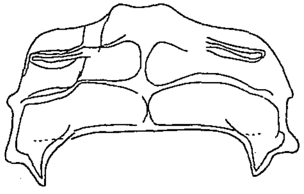
Paramphiascopsis spec.
Diosaccinae, (Weddell Sea)



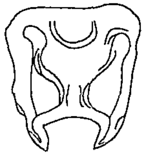
Distioculus minor
Miraciinae (after Huys & Böttger-Schnack, 1994)



Stenhelia spec.
Stenheliinae (Papua New Guinea)

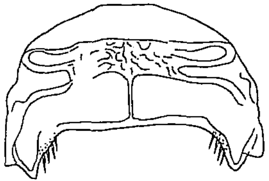


Paradactylopodia spec.
Dactylopusiidae (Weddell Sea)

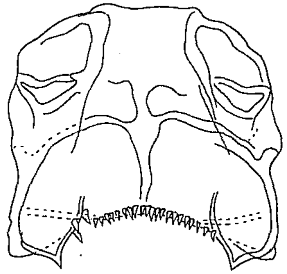


Parastenhelia spec.
Parastenheliidae (Andros)

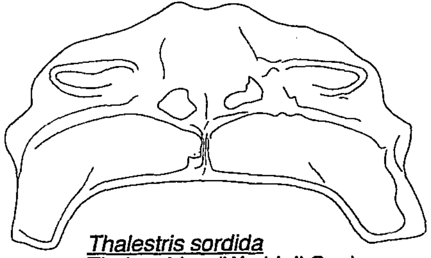
Karllangia spec.
Parastenheliidae (Papua New Guinea)



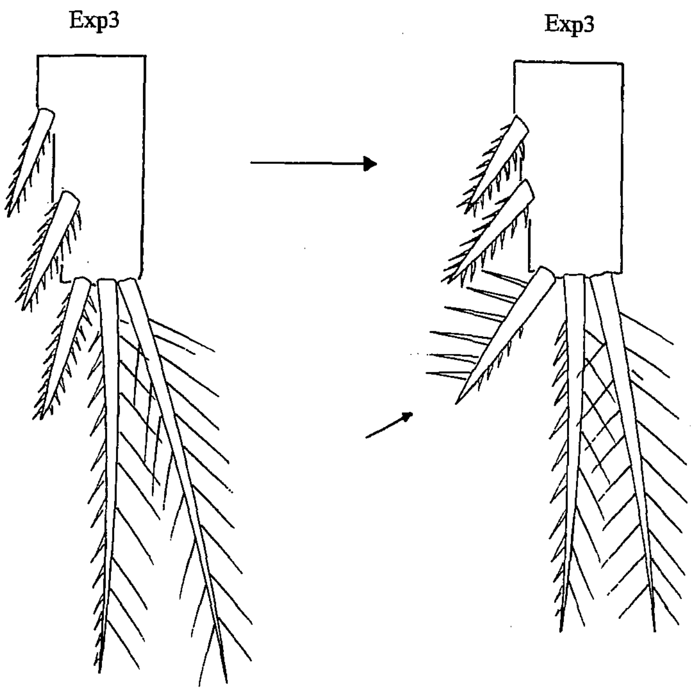
Thalestrinae gen. spec.
Thalestridae (Weddell Sea)

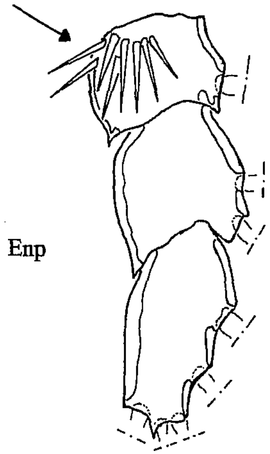


Ambunguipes spec.
Rhynchothalestridae (Argentinia)



Thalestris sordida
Thalestridae (Weddell Sea)





6.10 Female P5

6.10.1 Harpacticoida and Podogennonta groundpattern

In most Harpacticoida (except for *Longipedia minor* with separated enp) basis and enp are fused to form a baseoendopod, and enp and exp are always 1-segmented. The maximal number of 6 setae on the enp (fig. 61) occurs in *Mesochra* ("Canthocamptidae"), Louriniidae, and *Cletocamptus*. The maximal exopod setation of 8 is present only in Parastenheliidae (8 setae occur secondarily also in *Antiboreodiosaccus* (Diosaccinae), see below). Except for *Longipedia minor* all mentioned taxa belong to the Podogennonta,. Outside the Podogennonta a trend towards a reduction of the setation both in benp and exp can be observed (exceptions: Thompsonulidae, benp of *Eupelte villosa*, Peltidiidae, after Dahms, 1992). In several taxa the benp setation is strongly reduced, e.g. in Tisbidae, Aegisthidae, Cerviniidae, Neobradyidae, Tachidiidae). At least within Podogennonta a regular pattern of shape and position of setae can be recognised, making their homologisation possible (fig. 61). Whether this pattern extends beyond Podogennonta can only be assumed, because the setation is often reduced in other taxa (see above). A positive indication is the shape of the benp in *Eupelte villosa* (Peltidiidae, description of Dahms, 1992) and in Tegastidae (after Huys et al., 1996, both of which have retained the complete setation.

The setation groundpattern at least for Podogennonta and also for Thalestridimorpha can be described as follows (fig. 61): innermost 2 setae (Nos. 1 + 2 in fig. 61) on benp stand out against the other setae by identical size (shortened) and ornamentation. They are followed from inner to outer side by inner seta 3 and terminal setae 4 + 5, the latter being always shorter than seta 4. Within Thalestridimorpha the small outer seta 6 is present in at least 2 species of *Rhynchothalestris* (*R. helgolandica* after Huys, 1990 and *R.* spec. from the Weddell Sea) and in *Antiboreodiosaccus* (Diosaccinae), and outside Thalestridimorpha in e.g. *Mesochra*, Louriniidae, and *Cletocamptus*. The exp carries 3 inner setae (No. 12, 13, 14 in fig. 61), which have been retained completely only in *Parastenhelia*, it also carries 2 slender, long and presumably primarily smooth setae inserting terminally on a projection (No. 10 + 11) and 3 outer setae (No. 7, 8, 9). The latter are homologous to certain outer exopodal outer spines of the other swimming legs (which ones?) and are primarily shorter, curved and stronger spinulose compared with the other exopodal setae. Benp and exp are well developed, the former is foliated. This "moderate basic shape" (compare fig. 61) can be found, apart from the Thalestridimorpha, also in Harpacticidae, Laophontidae and "Canthocamptidae", which is a positive argument for its presence in the groundpattern of the Thalestridimorpha and Podogenonnta. The more derived forms within the subtaxa of the Thalestridimorpha will be discussed below.

6.10.2 Thalestridimorpha

The modifications of the above-described groundpattern yield autapomorphies for certain subtaxa. Within the Rhynchothalestridae *Ambunguipes* still shows the "moderate ground shape" which is retained from the podogennontan groundpattern in that of Rhynchothalestridae (fig. 62). In *Rhynchothalestris* (fig. 64) the exp is elongate and the enp shortened, only reaching into the proximal third of the exp. Seta 1 (or 2?) is missing whereas seta 6 is still present. *Hamondia* shows an autapomorphy with its strongly derived P5 (compare Huys, 1990).

The Diosaccidae (fig. 62, 65) still show nearly the complete thalestridimorphan/podogennontan groundpattern, except for the loss of setae 13 + 14 **102**. *Antiboreodiosaccus crassus* (after Giesbrecht, 1902 and Pallares, 1970) has 8 setae on the exp, however, there are 2 supernumerary outer spines present instead of the inner setae 13 + 14 of the groundpattern (fig. 65). Therefore these additional setae are an autapomorphic character for the genus. Seta 6 is located at the "correct" position, completing the Diosaccidae groundpattern. In the Miraciinae the shape of the rami and the setation is slightly derived **106** (fig. 65). The Stenheliinae show a strongly specialised female P5: the exp is spread out and the benp is flattened **107** (fig. 64). The groundpattern of the Thalestridae (fig. 62) is characterised by the spatial and/or ornamental separation of seta 1 in relation to seta 2 **108**. Only within the Thalestridae there are more or less extremely foliated baseoendopods and exopods besides the "moderate basic shape", e.g. in *Phyllothalestris* and *Eudactylopus* (in the former the exopodal setae are shifted closely together), but also within *Parathalestris* **105**. Further derived forms can be found in *Amenophia*, *Paramenophia* and *Thalestris sordida* (fig. 63). Besides an elongate exp, the Parastenheliidae show a shortened, almost triangular benp **103** (fig. 62).

6.10.3 Pseudotachidiidae

The groundpattern (fig. 66) shows several autapomorphic features. The exp is very small, the outer setae have taken the form of spinulose spines and the benp displays a peculiarity in the setation pattern: seta 1 is extremely elongate, whereas 2 is strongly shortened **104**. This kind of benp can be observed in all subtaxa (*Idomene borealis, I. cookensi, I. pectinata, Jonesiella, Archisenia, Fladenia*, Pseudotachidiidae gen. 1, Pseudotachidiidae gen. 2, *Dactylopodella*, even in the strongly derived Donsiellinae, e.g. *Oligoxylora cooksoni*, after Hicks, 1988). The complete exp and benp setation (fig. 66) has only been retained within *Idomene* (enp with seta 6 present: *I. borealis* and *I. scotti*; exp: *I. parasimulans, I. pectinata, I. simulans*). In the Parananopinae, "Pseudotachidiinae" and several species of *Idomene* one of the terminal setae (10 or 11?) is always missing. In the species of the "*Pseudotachidius*-lineage" the distal outer spine of the exp (seta 9 in fig. 66) is smooth, without any spinules. Since the loss of seta 10 (or 11?) occurs in all subtaxa within the Pseudotachidiidae, even in most species of *Idomene*, it probably represents rather an "underlying synapomorphy" in the groundpattern of the whole taxon than a synapomorphy of the Parananopinae and the other Pseudotachidiidae without *Idomene*.

An evidence, that the P5 of the Pseudotachidiidae had to be derived from the Podogennonta groundpattern is the unaltered occurrence of it in the benp of *Psammis* (description of Huys et al., 1996). This is interpreted here as a "character reversal", since it is only present in this one taxon.

Within *Idomene*, a modificaton of the pseudotachidiid groundpattern towards shortened/thickened baseoendopodal setae of equal length and enlargement of the benp itself can be observed (fig. 67). A downright transformation row towards the strongly modified P5 of *Pseudotachidius* can be directly traced within species of the "*Pseudotachidius* lineage" (fig. 68): starting from the groundpattern, which is still retained in Pseudotachidiidae gen. 1, seta 1 becomes short (in Pseudotachidiidae gen. 2). The next step consists in an elongation of the benp towards the inner lateral side as e.g. in *Pseudotachidius peruanus* Becker, 1974 and finally the benp is even more elongate, seta 1 is lost and the exopodal setae gain their characteristic relative length proportions in the *Pseudotachidius-coronatus* group (fig. 68). Within the *Pseudotachidius-similis* group further modifications such as total fusion of benp and exp and fusion of both pairs of legs occur together with a further reduction of setae.

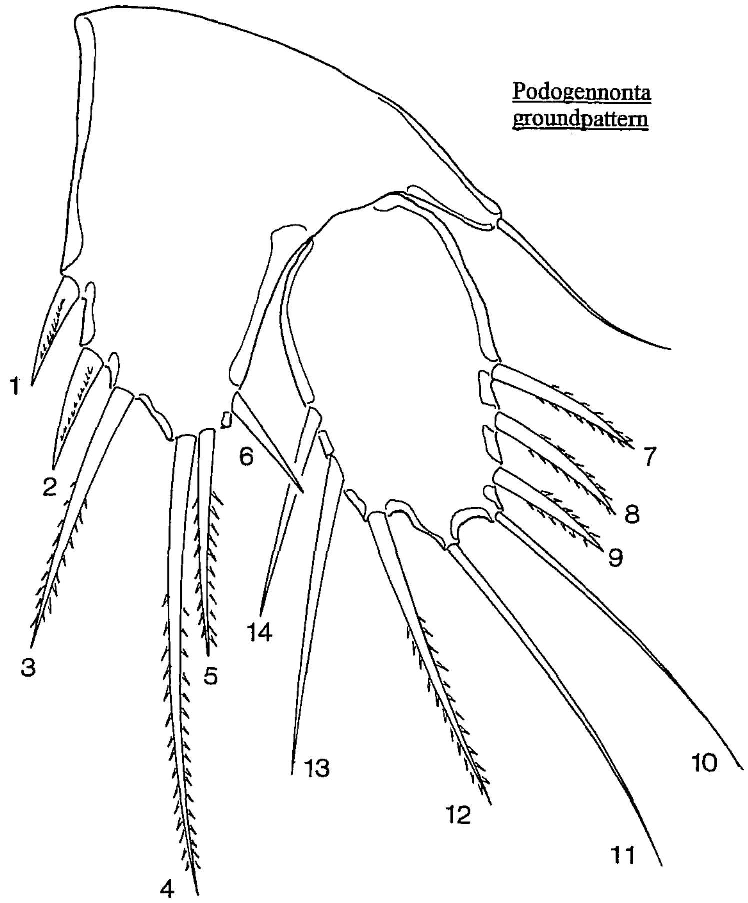
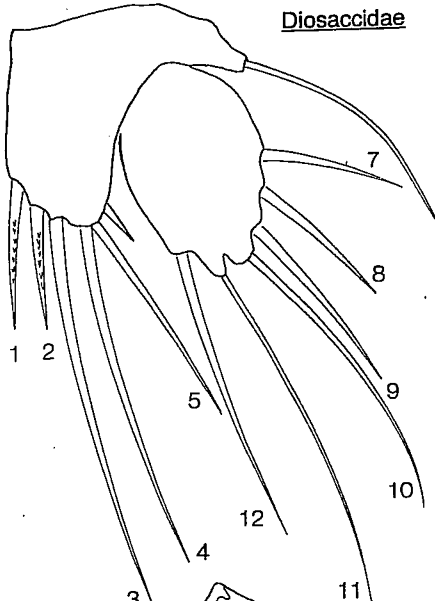


Fig. 61: Female P5 groundpattern of the Podogennonta.

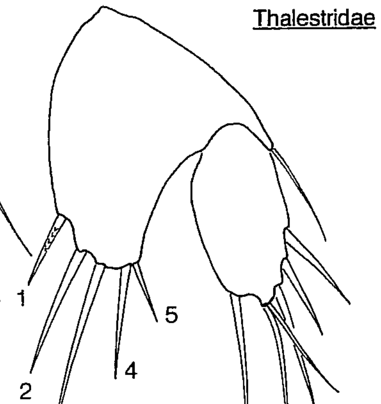
P. 156: fig. 62: Female P5 groundpatterns in the Thalestridimorpha.

P. 157: fig. 63: Female P5 groundpatterns in the Thalestridae.

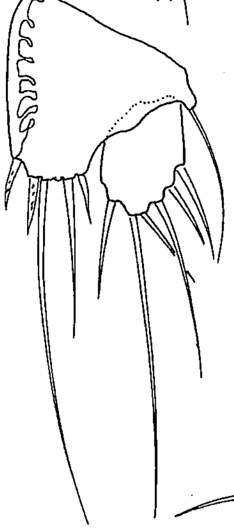
Diosaccidae

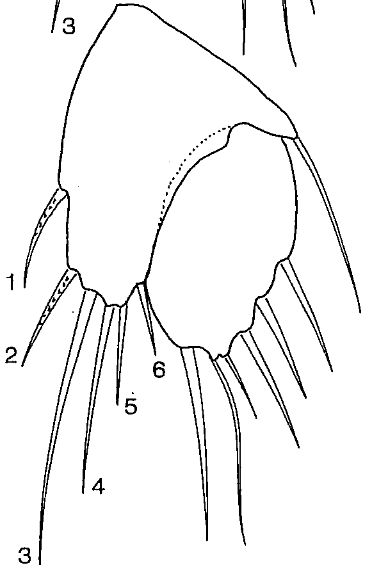


Thalestridae

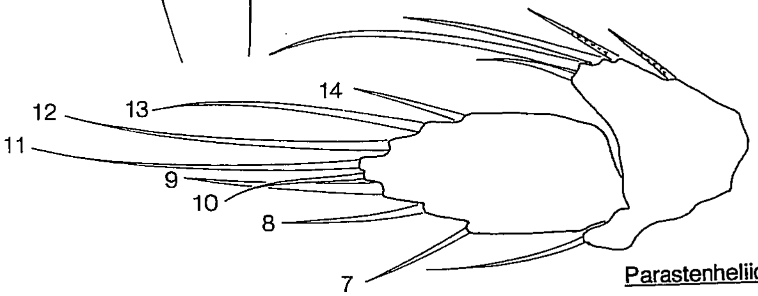


Dactylopusiidae

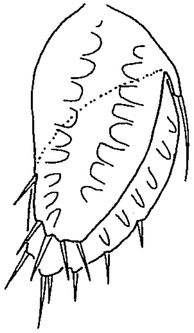




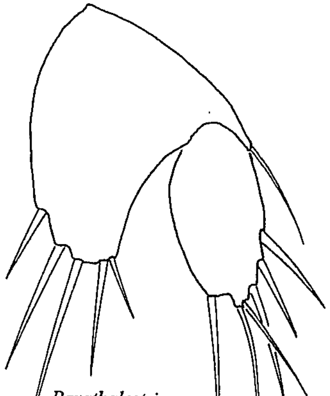
Rhynchothalestridae



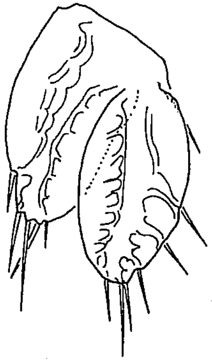
Parastenheliidae



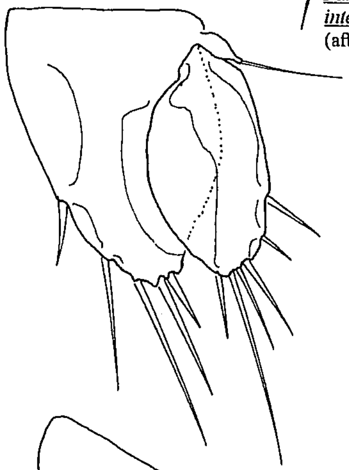
Thalestris gigas
(after Chislenko, 1980)



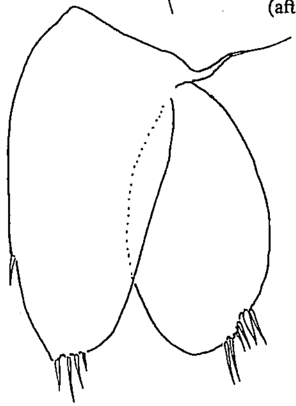
Parathalestris intermedia
(after Mielke, 1975)



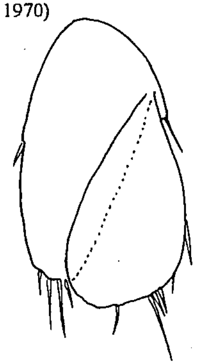
Parathalestris verrucosa
(after Itô, 1970)



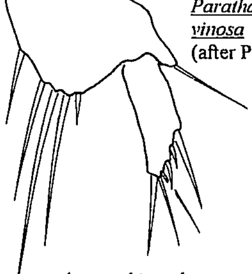
Parathalestris vinosa
(after Pallares, 1975)



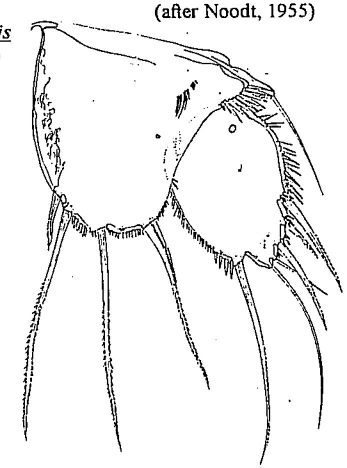
Phyllothalestris mysis
(after Geddes, 1969)



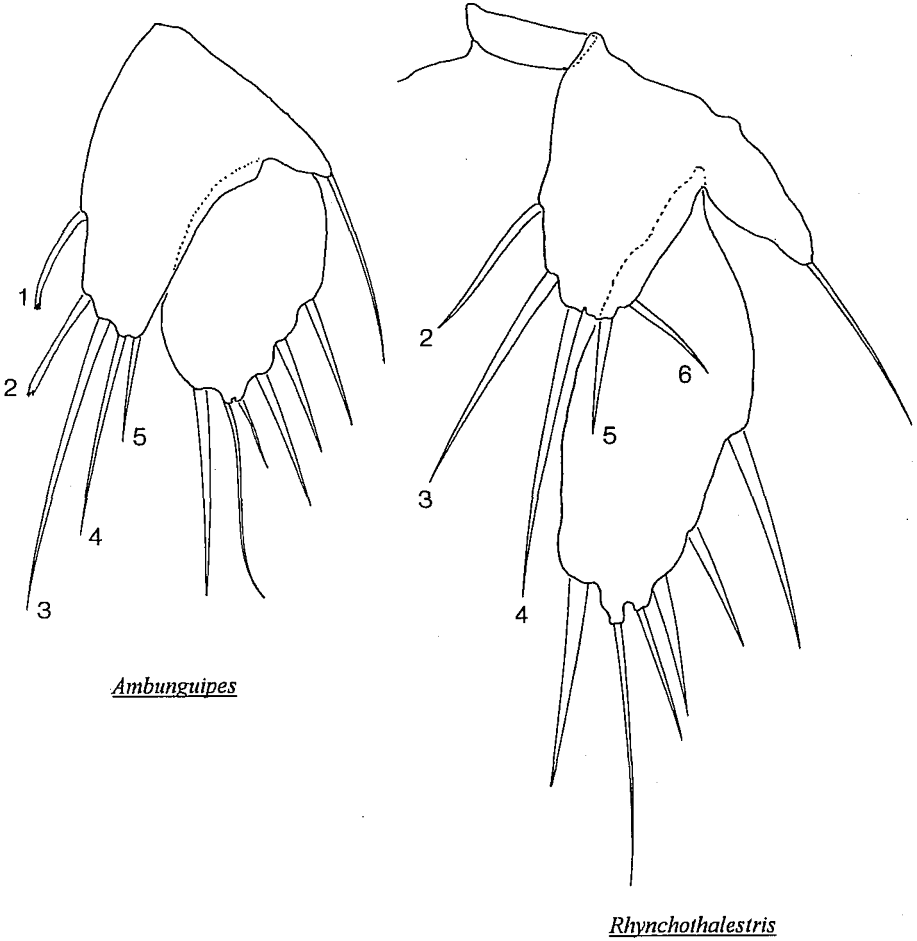
Eudactylopus latipes
(after Noodt, 1955)



Amenophia peltata
(after Sars, 1906)



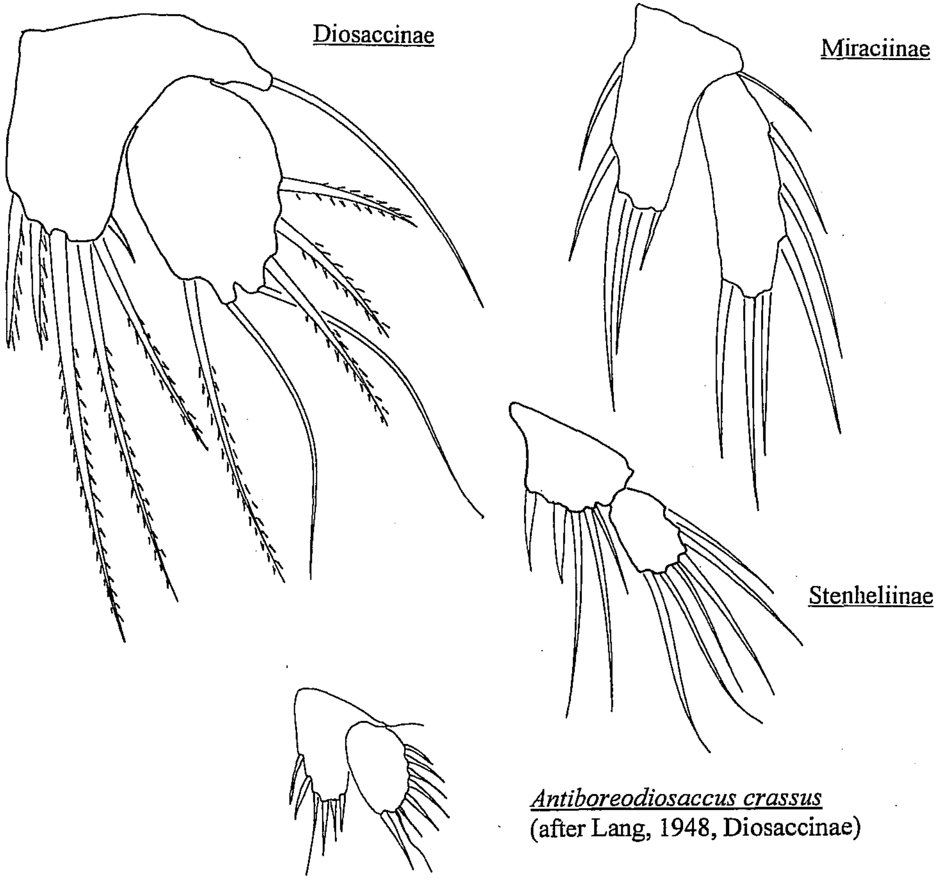
Thalestris sordida
(Weddell Sea)



Ambunguipes

Rhynchothalestris

Fig. 64: Female P5 within the Rhynchothalestridae.



Diosaccinae

Miraciinae

Stenheliinae

Antiboreodiosaccus crassus
(after Lang, 1948, Diosaccinae)

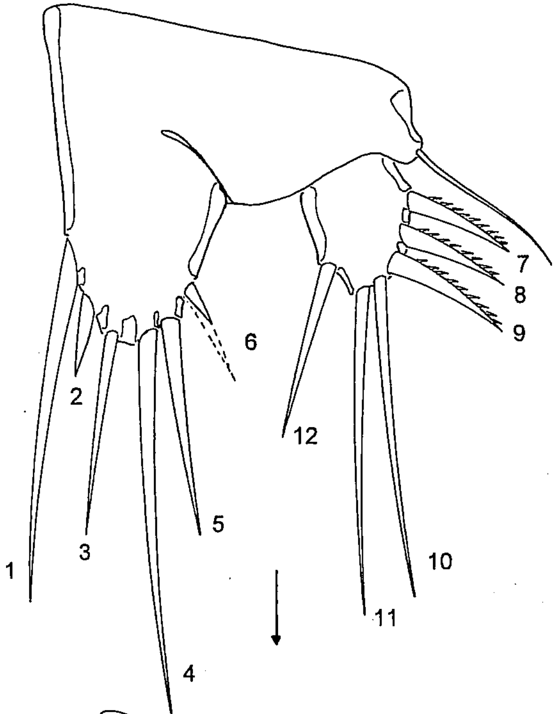
Fig. 65: Female P5 within the Diosaccidae.

P. 160: fig. 66: Female P5 groundpatterns in the Pseudotachidiidae and Parananopinae.

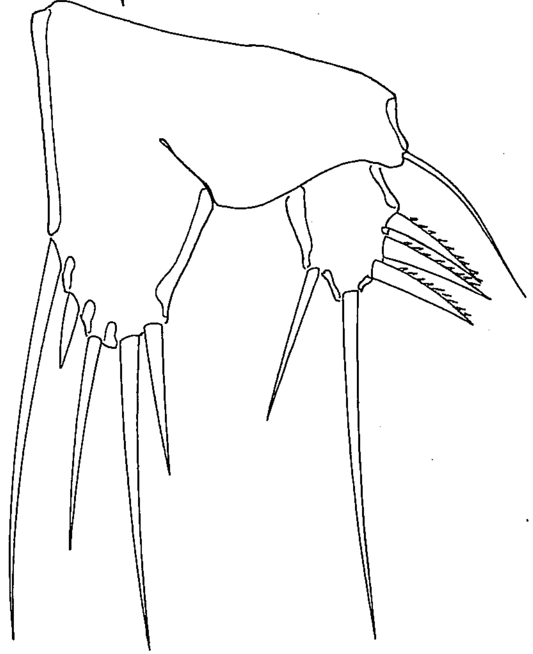
P. 161: above: fig. 67: Transformation row of the female P5 within *Idomene*.

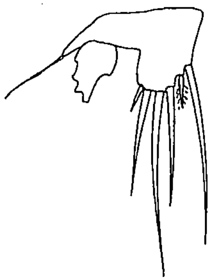
P. 161: below: fig. 68: Transformation row of the female P5 within the "*Pseudotachidius* lineage".

Pseudotachidiidae groundpattern

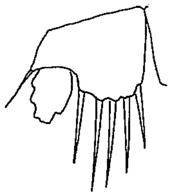


Paranannopinae

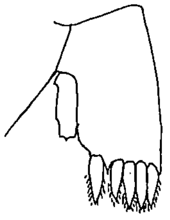




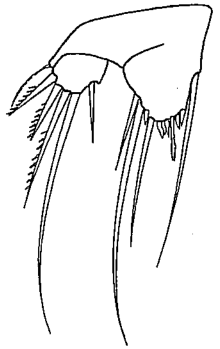
Idomene borealis (after Sars, 1911)



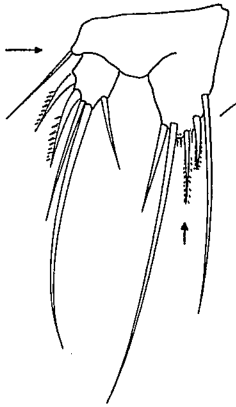
Idomene forficata (after Sars, 1906)



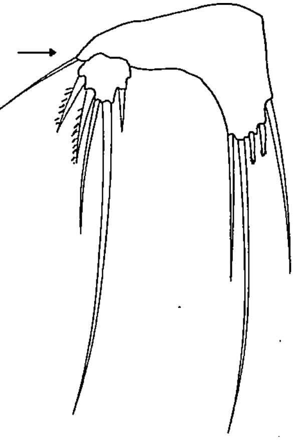
I. laticaudata (after Thompson & Scott, 1903)



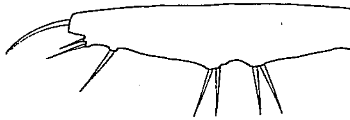
Pseudotachidiidae gen. 1 , spec. 1 (Weddell Sea)



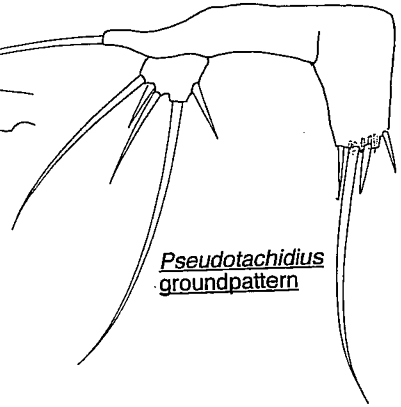
Pseudotachidiidae gen. 2 , spec. 1 (Weddell Sea)



Pseudotachidius peruanus (after Becker, 1974)



Pseudotachidius bipartitus (after Montagna, 1980)



Pseudotachidius groundpattern

6.11 Male P2enp

Most Thalestridimorpha and Pseudotachidiidae show a sexually dimorphic P2enp, the presence of which had also been taken into account by Lang (1948) in his diagnosis of the Thalestridimorpha. However, it turned out, that the individual modifications found in the subtaxa are not always homologous, but revealed autapomorphies for certain more inclusive taxa. In the following the different types of male P2enp are discussed.

6.11.1 Thalestridimorpha

The simplest sexually dimorphic modification is found in Parastenheliidae. The majority of the species show only a simple fusion of enp2 + 3 in the male without any further modification or loss of setae. However, in some species the unaltered 3-segmented female condition is still found, e.g. in *Parastenhelia minuta* (after Pallares, 1982*), Parastenhelia megarostrum*, and all species of *Karllangia* (except for *Karllangia tertia*, which should be placed into *Parastenhelia*, see chapter 11.2). This phenomenon is interpreted here as secondary. A seeming "reversal" back to the groundpattern without sexual dimorphism occurs (e.g. *Hamondia superba*, *Idomene rufocincta*) in single species within well supported taxa. In all of these cases the next related species show the group specific modification and the secondary nature of the "reversal" is quite obvious.

In the potentially most closely related outgroups of Thalestridimorpha the endopods of all swimming-legs are either 2-segmented, and therefore the 2-segmented male P2enp is not caused by sexual dimorphism (Tetragonicipitidae), or all swimming-leg endopods, including male P2 enp, always remain 3-segmented (*Protolatiremus*, compare fig. 70 and chapter 7). Assuming a monophyly of Thalestridimorpha (see chapters 4 + 7), the sexual dimorphic 2-segmented condition of the male P2 enp within Parastenheliidae and other Thalestridimorpha is regarded here as homologous and as an additional autapomorphy for Thalestridimorpha as a whole **113**. The absence of this sexual dimorphism in the above-mentioned outgroups as well as in e.g. Harpacticidae, Pseudotachidiidae, Cletodidimorpha, and Ameiridimorpha sensu Lang, 1948 (in their respective groundpatterns) as congeners within Podogennonta supports this interpretation. The probable secondary condition of the 3-segmented P2enp within Parastenheliidae can also be explained without assuming "character reversal" by developmental delay ("postdisplacement" or late onset) during the copepodid phase. Generally the full complement of setae of enp3 is already present in CIV, and the sexually dimorphic modification in Thalestridimorpha is in many cases already visible in male CV, of which the P2enp is still 3-segmented, and completed during the final moult to the adult. In the males of the respective *Parastenhelia* species a temporal delay of the modification during development could have resulted in retaining the "normal" condition in the adult male. There is no sexually dimorphic modification of the male P2enp3-setation in Parastenheliidae, whereas various setae are always modified in a taxon-specific way in the other taxa (fig. 69) **114**.

In the Rhynchothalestridae a 2-segmented P2enp with the modified homologous setae 2 + 3 (numbering of setae according to fig. 69) of the former P2enp3 can be found (type 2 in fig. 69). In this case seta 3 is shortened and thickened and seta 2 is reduced in size and length **117**. In *Hamondia superba* which is morphological strongly specialised there is a P2enp without sexual dimorphism, but the close relationship with *Ambunguipes* within the Rhynchothalestridae is well supported by several characters as pointed out by Huys (1990).

Another type of male P2enp is depicted in figs. 69, 71, 73 and 75 (type 4) which occurs in the Thalestridae (Thalestrinae and Eudactylopusiinae), Diosaccinae and further derived in the Miraciinae **116**. In this case the setae 1 + 2 are strongly thickened and shifted proximad into a juxtaposed position. Seta 3 is shortened compared with that of the female. Besides this groundpattern, a more derived form is present within *Eudactylopus* (fig. 71). Several further modified forms occur also within the Diosaccinae (e.g. in *Amphiascopsis*, *Amphiascoides*/*Paramphiascella*, *Diosaccus*).

The Dactylopusiidae represent the next type of male P2enp (type 3 in figs. 69, 72-74). In it, one seta is missing compared to the female. According to Huys (1990) this type has to be derived from type 4 by fusion of setae 1 + 2. An "intermoult stage" of a male CV specimen of *Dactylopusia* spec., beneath which the adult was already visible, supports another hypothesis. This CV stage still shows a 3-segmented enp and the complete setation as in the female. After the final moult, seta no. 2 would become lost in the adult (figs. 74 + 75). Comparing the CV stages of both types 3 + 4 (fig. 73), in which those setae that are modified in the adult can already be recognised, it can be seen that setae 1 + 2 are already thickened in type 4, whereas in type 3, setae 1, 3 + 4 are the ones to be already modified. Seta 2, which is lost in the adult, is not at all altered. These different ontogenetic patterns speak against a homology of both types of modification, but for the interpretation that type 3 is an autapomorphy of Dactylopusiidae **115**, which cannot be derived from type 4.

It can be summarised, that in Dactylopusiidae setae 1, 3 + 4 are modified (thickened, shortened and spatially displaced) and seta 2 is lost during the final moult to the adult male (figs. 72, 74). An even further derived state occurs in *Paradactylopodia*, but generally the strong setal reduction and the deformation of the segments conceal a clear homology (fig. 72). In samples from King George-Island an unknown species of *Paradactylopodia* was discovered showing a male P2enp (fig. 72), which still agrees with the type 3 groundpattern in many aspects (except for the fusion of seta 1 with the segment as a first step towards the *Paradactylopodia* type).

A special case that needs to be discussed is the male P2enp of Stenheliinae. The latter, on the basis of other characters can be clearly placed into the Thalestrioidea and further into the Diosaccidae. However, the P2enp of the Stenheliinae cannot be derived morphologically from Thalestrioidea groundpattern (type 2, figs. 69, 71, 74). Even within the Stenheliinae themselves at least 3 different types exist, which cannot be traced back to a common groundpattern (fig. 76). The most common type occurring in most species is depicted in fig. 76 in the right upper line (examples *Stenhelia* spec. (Papua Newguinea) and *St. aemula*). Compared with the female, 2 setae are missing. Examining a still unpublished species from Mexico (the type material was kindly made available by Samuel Gomez) a hypothesis for this type could be established. The hypothetical transformation series is depicted in fig. 76, in which the arrows do not reflect the actual relationships of the respective taxa. A paratype specimen of *Stenhelia infiernensis* from Mexico displays an aberrant male P2enp with the complete setation as in the female, but with miniaturised setae 2 + 3 and the segmental border between enp2 + 3 still clearly distinguished. The further derived forms can easily be reconstructed by the assumed loss of setae 2 + 3 (compare *Stenhelia* spec. and *St. aemula* in fig. 76). This type of male P2 occurs in both the subgenera *Stenhelia* and *Delavalia*, casting doubt on this subgeneric distinction, which is only due to the P1enp being 2- or 3-segmented (Lang, 1948). The male of *Stenhelia* (*Delavalia*) *bermudensis* has retained the full complement of setae as compared with the female, but setae 3 + 4 are strongly modified (see fig. 76 below on the left). In *Pseudostenhelia* only seta 1 is fused with the distal segment in the male (fig. 76, below on the right). Within Thalestridimorpha, the Stenheliinae can clearly be well characterised as a monophylum (see chapter 7.1) by several autapomorphies. This speaks against an interpretation of the different male P2 types to be indicative of a non-monophyly of the Stenheliinae. Another possibility is to interpret the fact that several new and different types of male P2 have become possible within a well supported taxon, which in turn is part of an equally well supported superordinated taxon (Thalestrioidea), as an autapomorphy of Stenheliinae **119** (compare also chapter 7.1 for further discussion). In fig. 69 the groundpatterns of all types of male P2 within the Thalestridimorpha are depicted in an overview. It can be summarised, that the respective shape of the male P2enp is an autapomorphy of the Thalestrioidea **116**, Dactylopusiidae **115**, and Rhynchothalestridae **117**. The Parastenheliidae do not show any setal modifications.

6.11.2 Pseudotachidiidae

Constellation of taxa within Pseudotachidiidae could not be clarified sufficiently as yet. No good autapomorphy was found (chapter 11) especially for "Pseudotachidiinae". In the following the subtaxa, which can already be characterised are compared in order to reconstruct a common groundpattern of the male sexual dimorphism on the P2enp. The most widely distributed type is depicted in fig. 77 above on the right as hypothetic groundpattern of Pseudotachidiidae. It is present in almost all subtaxa which can be characterised as monophyletic, and can be described as follows:

The P2enp remains 3-segmented, the outer, outer terminal and inner terminal setae on enp3 are modified (setae 1, 2, 3 in fig. 77) **120**. In *Idomene*, Pseudotachidiidae gen. 1 and *Pseudotachidius* seta 3 is stronger and/or longer, but not in Paranannopinae. In *Idomene* also a -probably secondarily- unmodified P2enp occurs besides the modified sexually dimorphic groundpattern, e.g. *I. purpurocincta* (after Lang, 1965). Pseudotachidiidae gen. 1, of which several species from the Weddell Sea have been examined, shows incompletely fused enp2 and enp3 (anteriorly fused, posteriorly separated, see fig. 78). Pseudotachidiidae gen. 1 belongs to the "*Pseudotachidius* lineage", which comprises several taxa being more closely related to *Pseudotachidius*. Deviations from the groundpattern are also found within this taxon. The males of most of the *Pseudotachidius* species are still unkown. Only one male of the *Pseudotachidius similis*-group, *P. vikingus* Drzycimski, 1968, has been collected in the Weddell Sea samples (fig. 78, Pseudotachidiidae gen. 2). Its P2, with a deformed enp3 which seems to be fused with the outer seta, is quite aberrant.

In the *Pseudotachidius coronatus*-group (fig. 78) a fusion and/or reduction of the 3 modified setae (in *P. brevisetosus*, after Montagna, 1980) takes place, there is a non-modified P2 (in *P. bipartitus* after Montagna, 1980) and only one seta is modified (in *P. jubanyensis* Veit-Köhler & Willen, 1999) as compared with the above described groundpattern (in *Ps. coronatus*, after Drzycimski, 1969). Since *Pseudotachidius* and the "*Pseudotachidius* lineage" can be clearly characterised as monophyla, all of these variations can somehow be derived from the common groundpattern of the Pseudotachidiidae, which is still present in *Pseudotachidius* as well as in the other taxa (= potential outgroups). The same is true for Paranannopinae (fig. 77), which show as autapomorphy an additional pronounced elongation of the segmental outer margin on the male P2enp2.

The male P2 of *Dactylopodella flava* and *Dactylopodella* spec. (fig. 78) is 2-segmented, whereas it is still 3-segmented in *D. rostrata* and has only 1 modified seta ("No. 1"). A complete revision of this genus has to be awaited before further discussion.

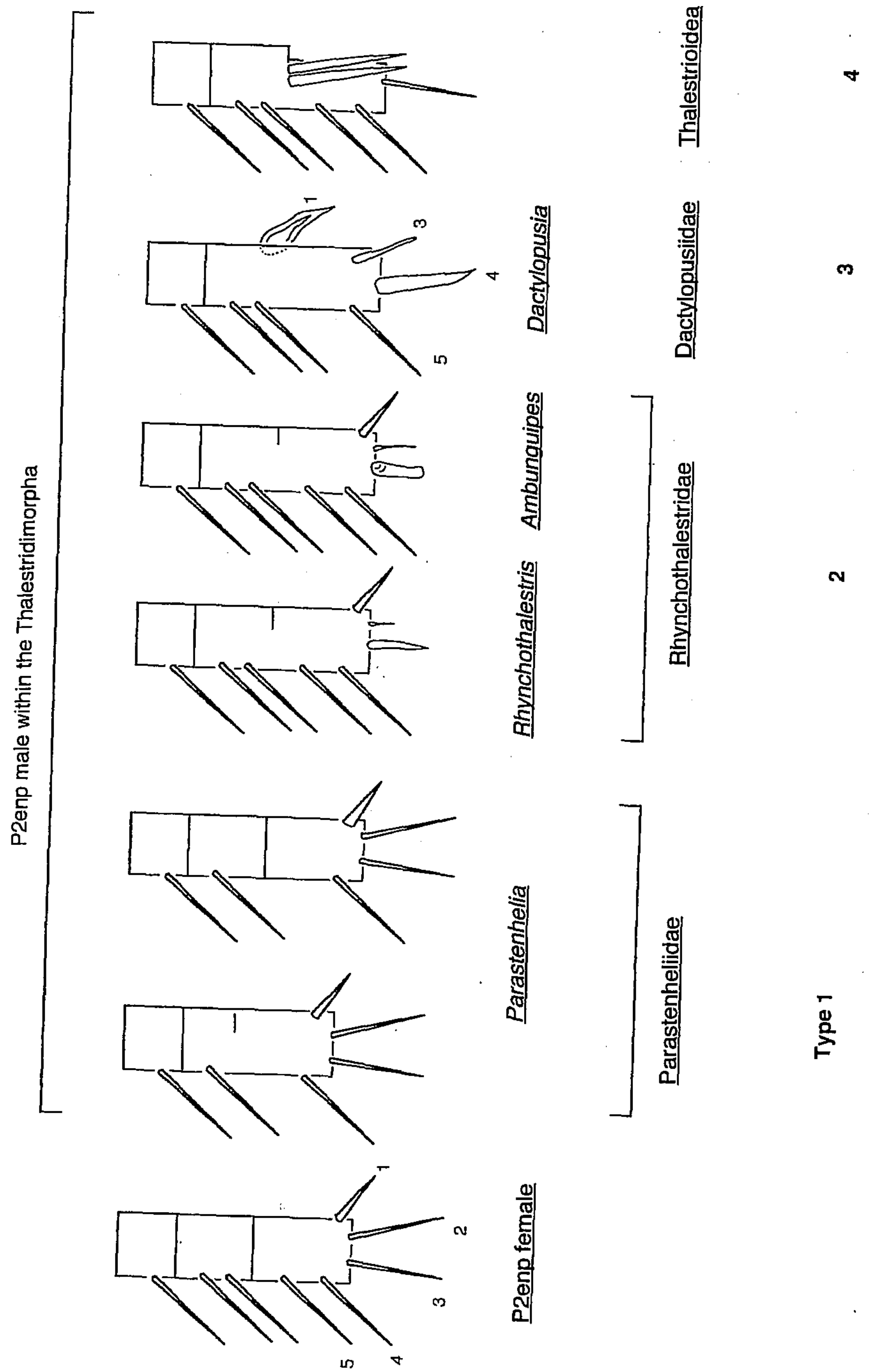
P. 167: fig. 69: Different types of male P2enp within the Thalestridimorpha.

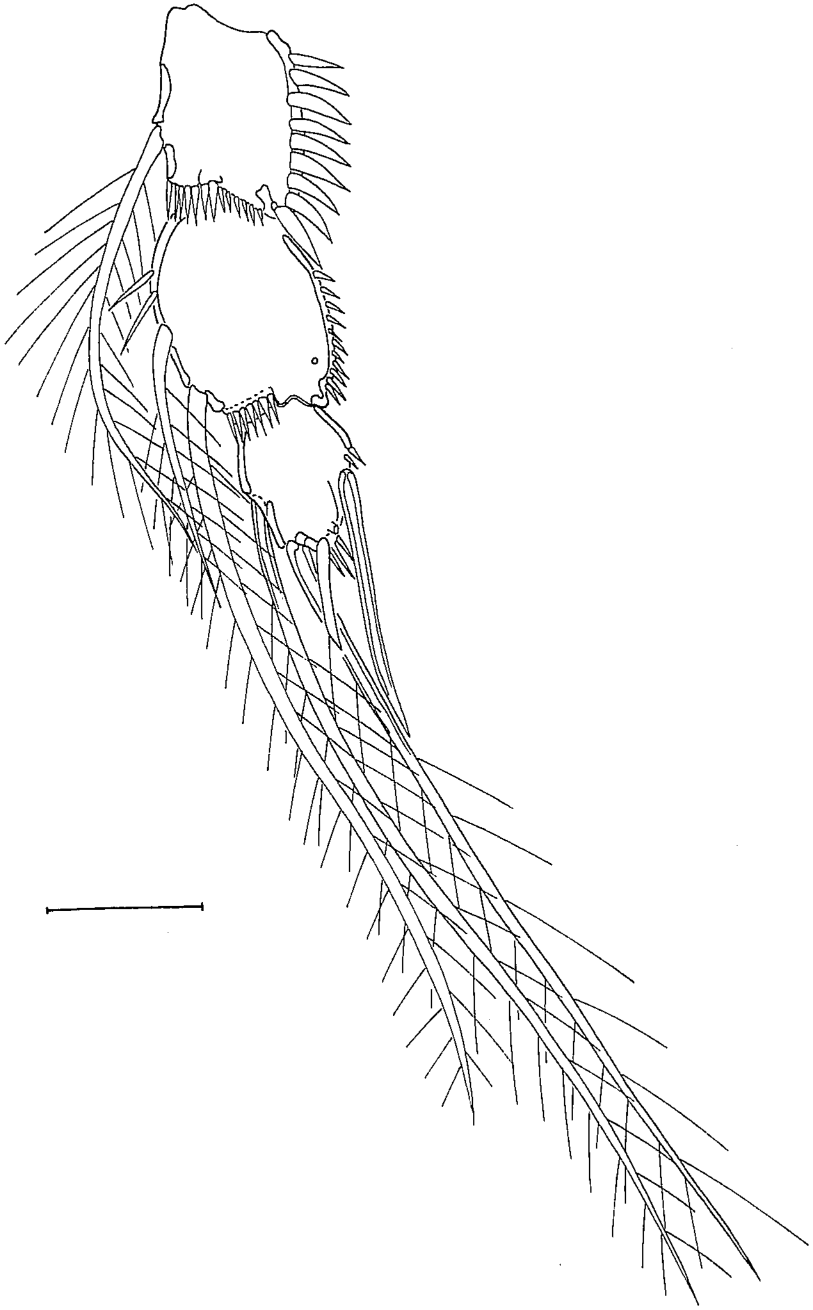
P. 168: fig. 70: Male P2enp in *Protolatiremus sakaguchii*.

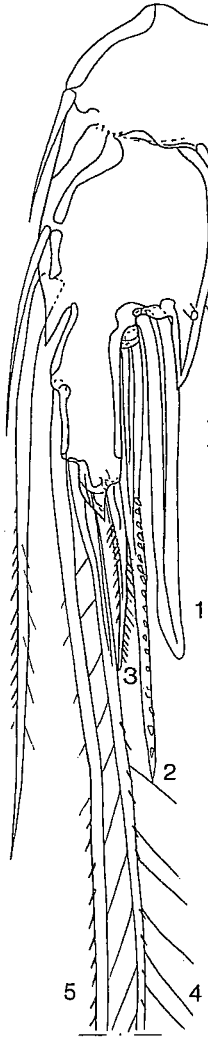
P. 169: fig. 71: Male P2enp within the Thalestridae.

P. 170: fig. 72: Male P2enp within the Dactylopusiidae.

P. 171: fig. 73: Male P2 endopods of CV stages in the Dactylopusiidae (type 3, "intermoult stage") and Diosaccinae (type 4).

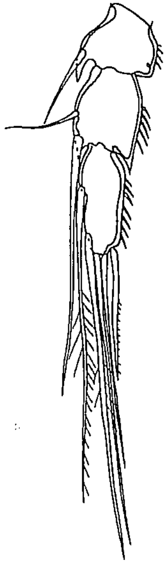




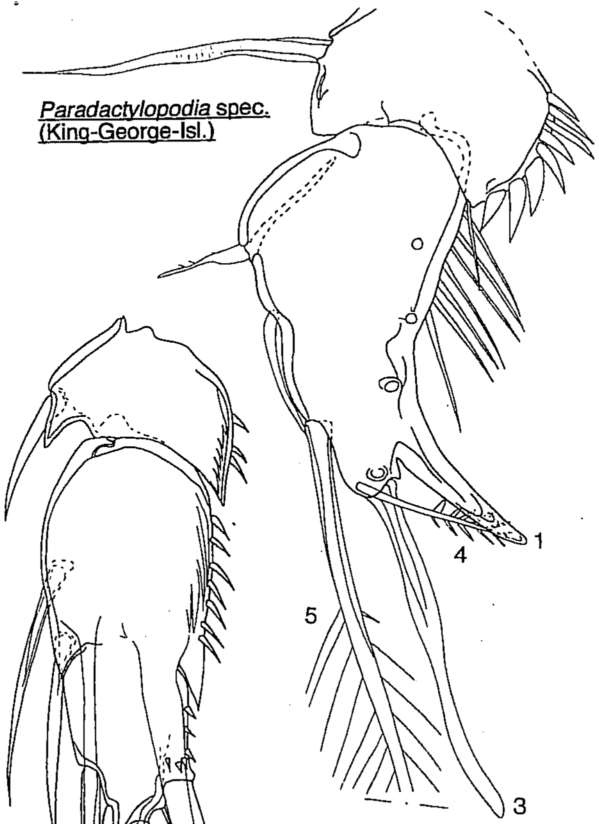


Phyllothalestris spec. (Sri Lanka)

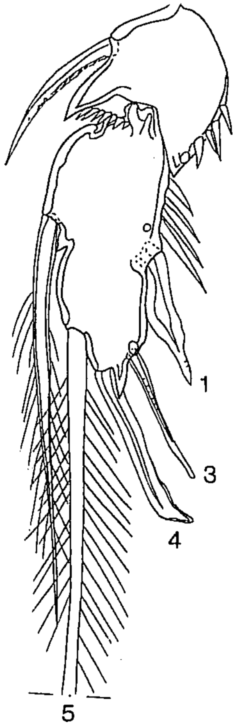
Eudactylopus spec. (Sri Lanka)



unmodified groundpattern (female)

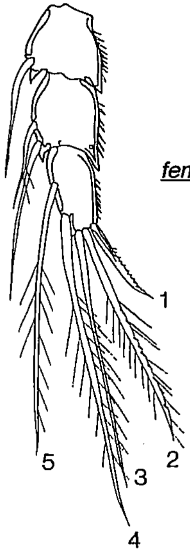


Paradactylopodia spec.
(King-George-Isl.)

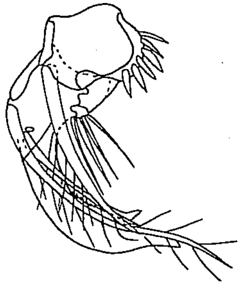


Dactylopusia spec.
(Papua New Guinea

Dactylopusia spec., male CV,
„intermoult“ stage, Seattle



female

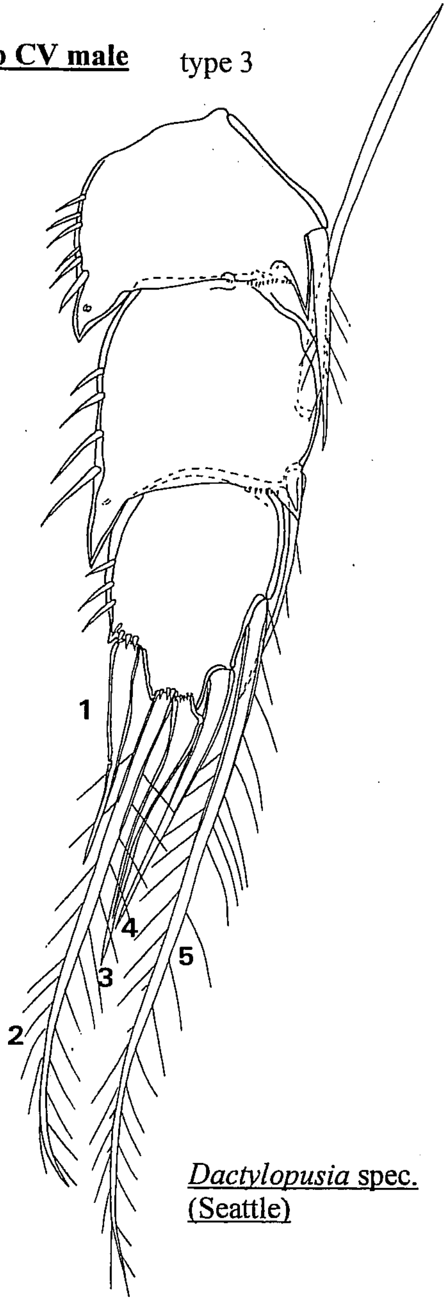


Paradactylopodia spec.
(Fiji Isl.)

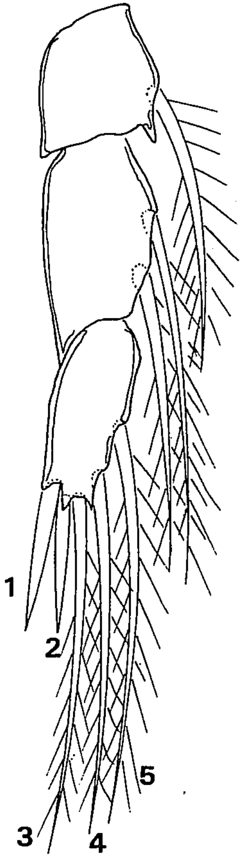
P2enp CV male

type 3

type 4



Dactylopusia spec.
(Seattle)



Paramphiascopsis spec.
(Weddell Sea)

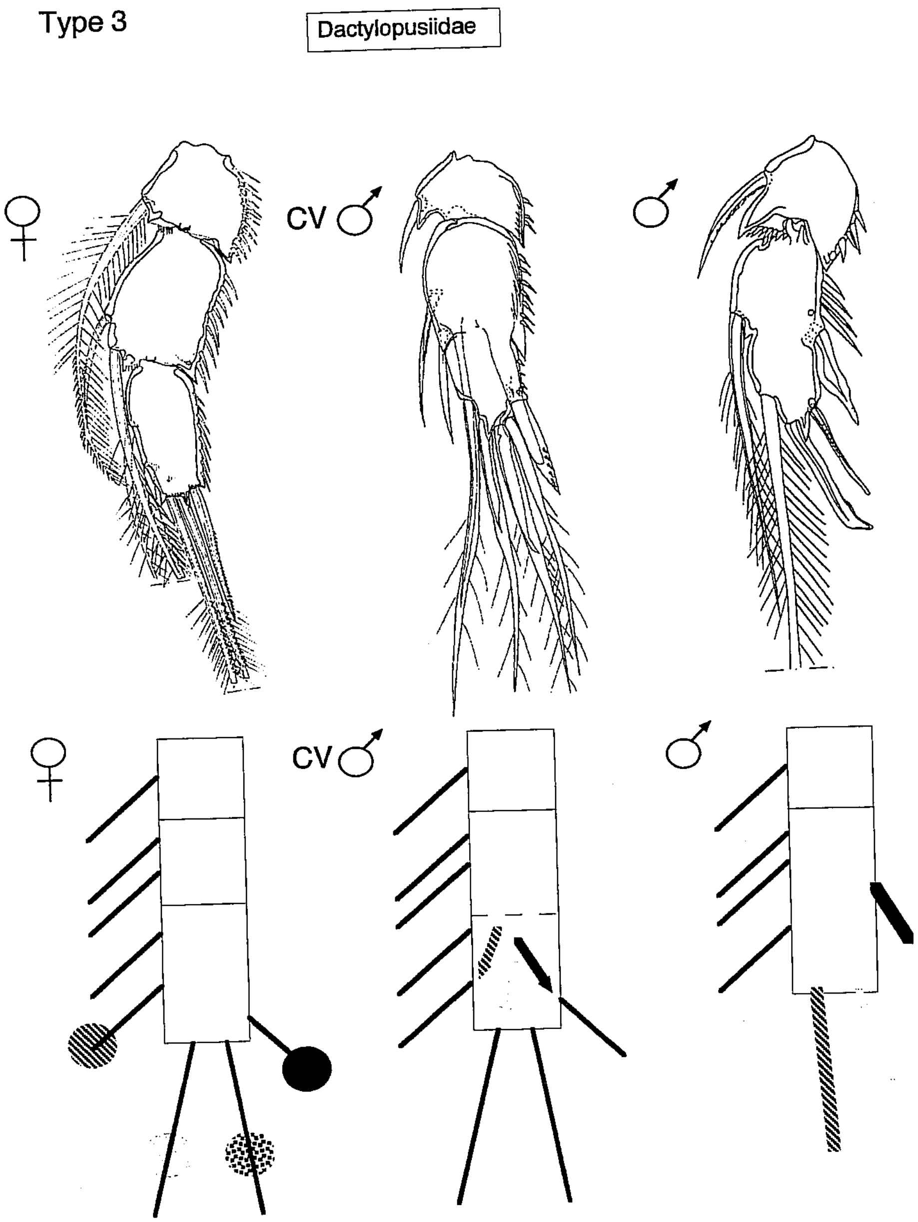


Fig. 74: Setal homology of the sexual dimorphic male P2enp in the Dactylopusiidae (type 3).

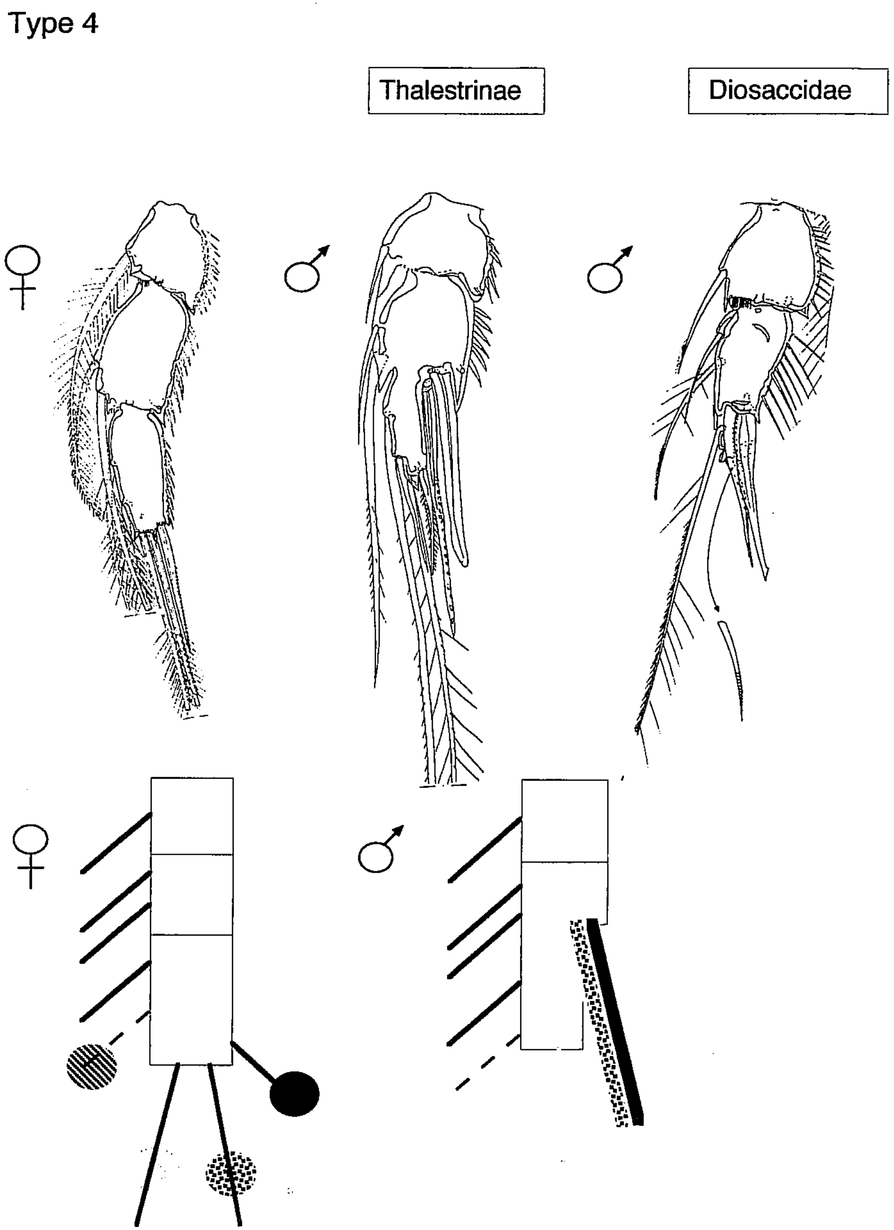
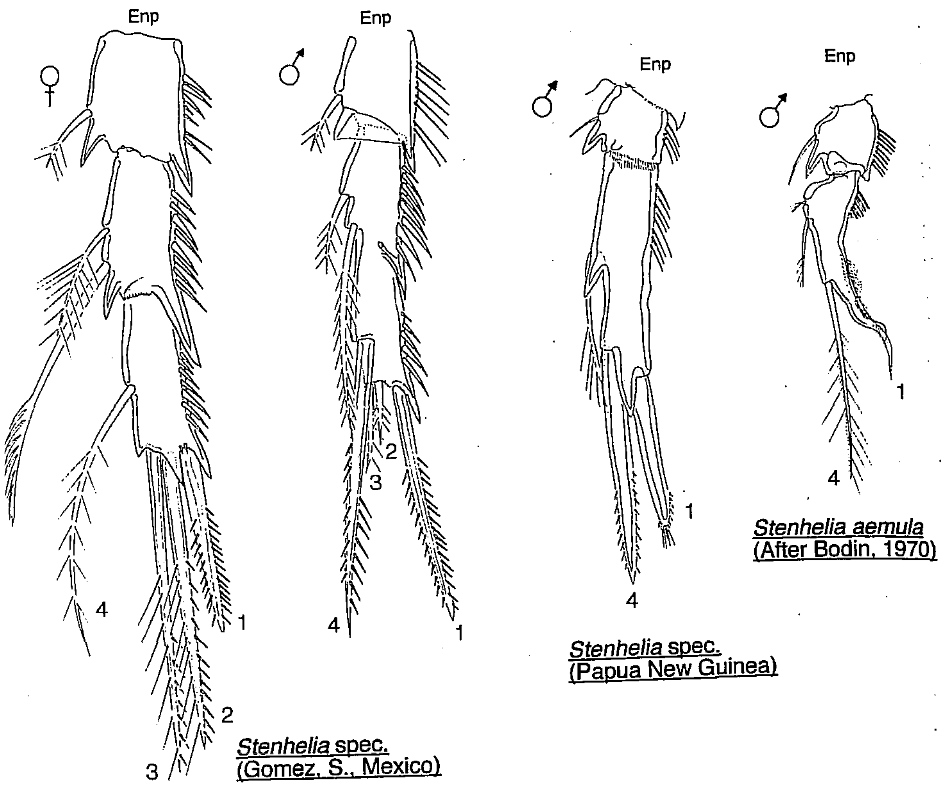


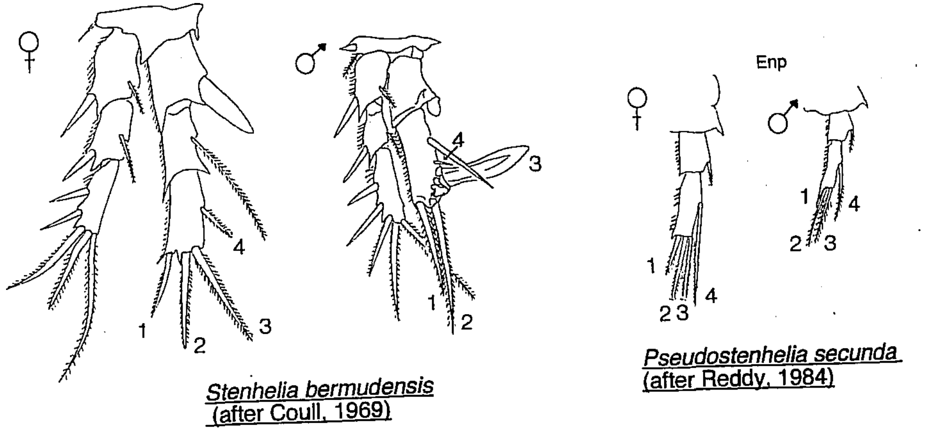
Fig. 75: Setal homology of the sexual dimorphic male P2enp in the Thalestrioidea (type 4).



Stenhelia spec.
(Gomez, S., Mexico)

Stenhelia spec.
(Papua New Guinea)

Stenhelia aemula
(After Bodin, 1970)

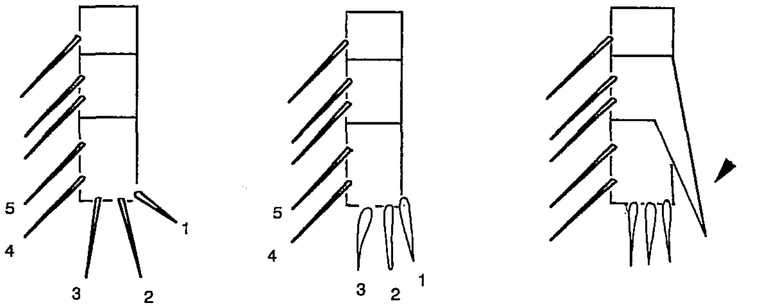


Stenhelia bermudensis
(after Coull, 1969)

Pseudostenhelia secunda
(after Reddy, 1984)

Fig. 76: Male P2enp in the Stenheliinae.

Male P2enp within the Pseudotachidiidae

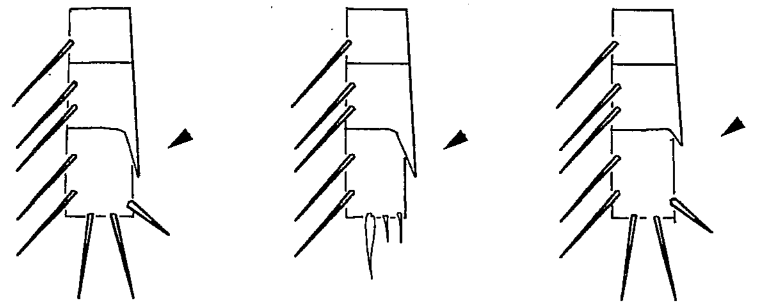


unmodified condition
(female)

male groundpattern

Paranannopinae
male groundpattern

Idomene

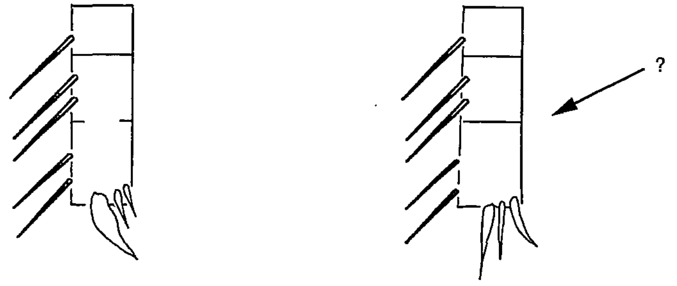


unmodified condition
(female)

male groundpattern

male of *I. purpurocincta*
(after Lang, 1965)

"*Pseudotachidius*-lineage"



Pseudotachidiidae gen.spec
(Weddell Sea), male

Idomene antarctica, male
(after Dahms & Schminke, 1992)

Fig. 77: Male P2enp within the Pseudotachidiidae

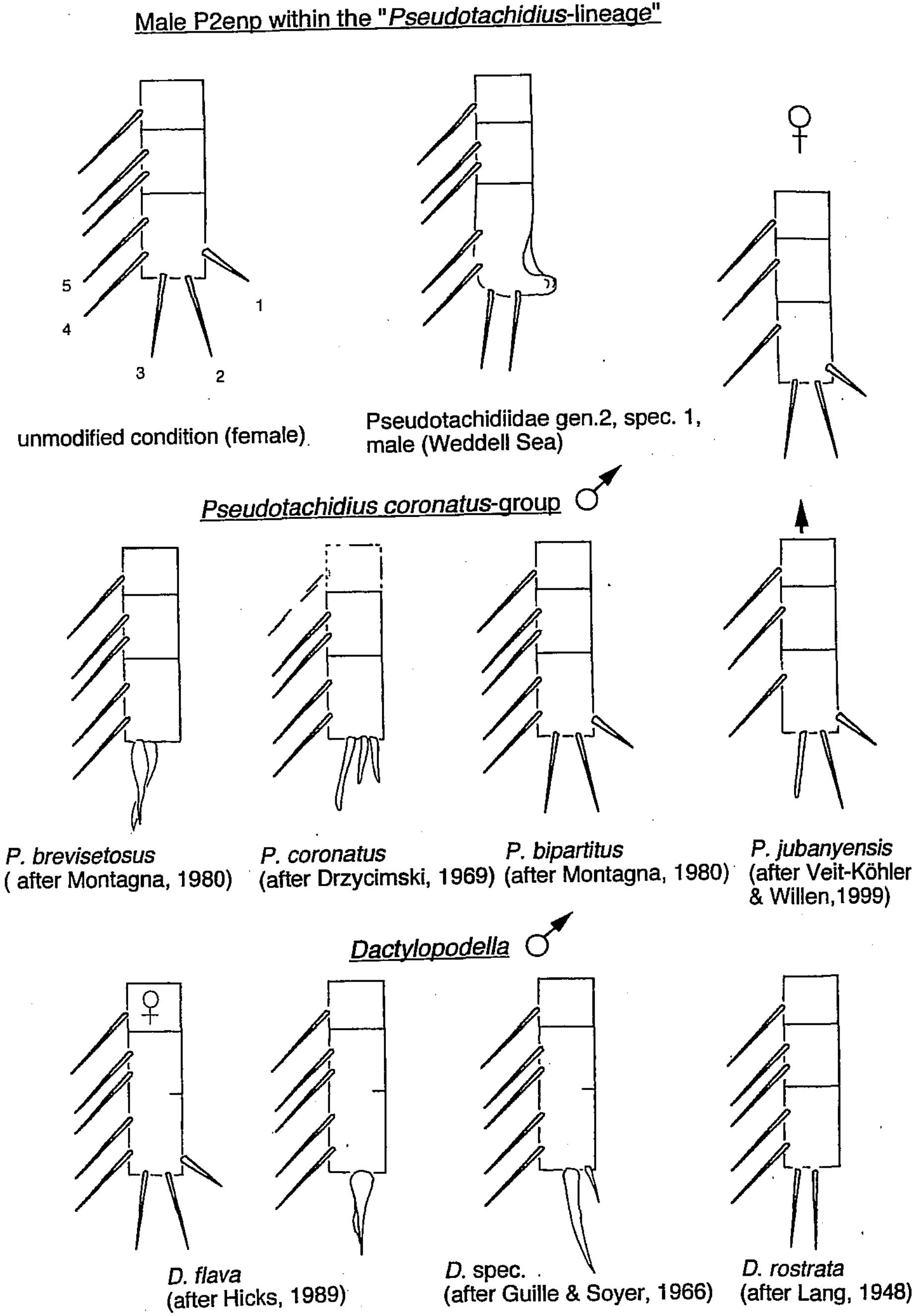


Fig. 78: Male P2enp within the "*Pseudotachidius* lineage".

6.12 Other characters

6.12.1 Male P5

Almost the complete groundpattern of the Oligoarthra has still been retained in the Parastenheliidae (exp) and can be described as follows: the exp is 3-segmented with 0,1; 1,1; and 1,1,2 setae. In the other Thalestridimorpha the exp is 1-segmented with still complete setation. The loss of the inner seta on the original "exp2" is an autapomorphy of the Diosaccidae **110**. Multisegmented exopods also occur within other Oligoarthra, e.g. in Tetragonicipitidae and Neobradyiidae.

The enp carries at most 3 setae (Thalestridimorpha, "Canthocamptidae", Tetragonicipitidae). Huys & Boxshall (1991) even observed an additional inner seta in an undescribed new species of a new family collected at the Great Barrier Reef. Only 2 terminal setae are present in the Parastenheliidae **109**, Diosaccidae, with the only exception of *Miracia efferata* (compare description of Huys & Böttger-Schnack, 1994) and in Pseudotachidiidae **109**. The latter still show the complete exopodal setation in their groundpattern.

6.12.2 Sexual dimorphism in the male P1 (fig. 77)

The sexual dimorphism in the male P1 will be discussed in detail in chapter 7.

6.12.3 Rostrum

Shape and ornamentation of the rostrum appear to be taxon-specific within the Oligoarthra. The rostrum in the Thalestridimorpha is rather large and has an acute-angled shape, whereas it is tiny e.g. in Ameiridae and broad, rectangular with rounded tip in Pseudotachidiidae. It is, however, not clear as yet, which form represents the apomorphic or plesiomorphic state. A detailed, comparative ultrastructural analysis would be useful to make additional anatomic character complexes accessible. A start had been made by Hosfeld (1997) with the examination of the rostrum of *Canuella perplexa* (Polyarthra). Hosfeld believes the divided rostrum with paired frontal filaments, as it exists in the Calanoida within Copepoda but also in other Maxillopoda and Crustacea, to be plesiomorphic within the Copepoda. The thread-like filaments are (at least in the examined examples) associated with the SPX-organ (complex of sensory receptors). An undivided rostrum, as in *Canuella perplexa* and almost all other harpacticoids, would therefore be an apomorphic state. A bipartite rostrum occurs also within Stenheliinae (fig. 80 d-f). The dorsal part is a continuation of the cuticula of the cephalothorax, whereas the ventral parts are of a cuticular structure, which is deeply divided apically (fig. 80 d-f). Such a "composed" rostrum can also be assumed for the Thalestridimorpha as a whole (maybe for all Oligoarthra?) because of the presence of a median ventral suture (compare fig. 80 h, i, k, l, m). Within the Stenheliinae the dorsal part is receding and therefore the ventral part becomes exposed. This phenomenon is interpreted here as secondary and derived for the following reasons:

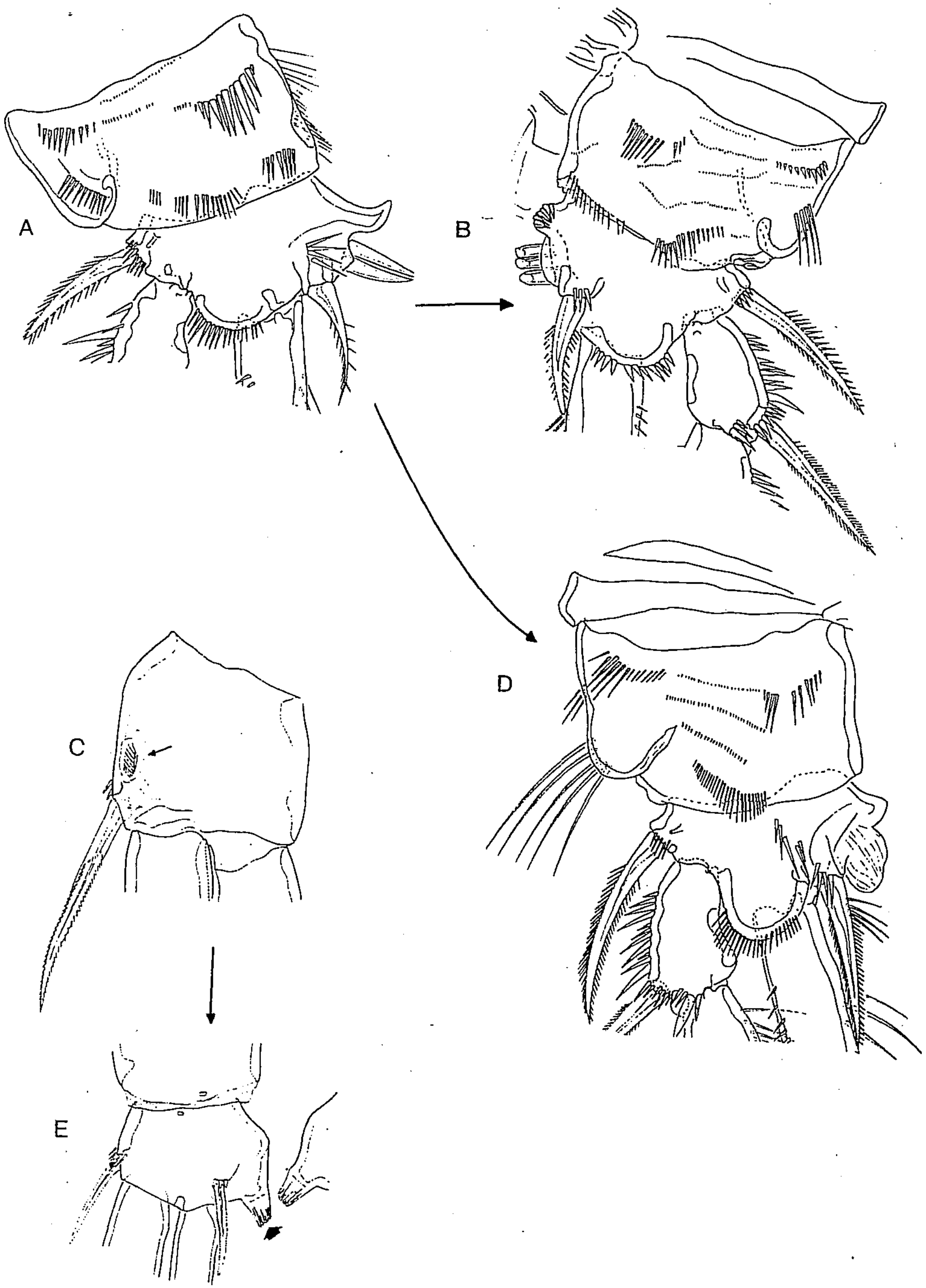
- It seems to be restricted to Stenheliinae within Oligoarthra without exception.
- The apically divided structure does not consist of thread-like filaments as in Calanoida and Metidae (compare Hosfeld, 1997) but is strongly cuticularised and rigid. A possible association with the SPX organ still has to be verified by ultrastructural analyses.
- Occasionally the rostral sensillae are located ventrally (*Melima*, fig. 80 d) and the dorsally in other cases (*Stenhelia bifida*, fig. 80 f, *Cladorostrata*, fig. 80 e).

The extreme, divided condition is not realised in all Stenheliinae. Nearly all other species have a rostrum shaped like an equilateral triangle with a bifid tip, which represents the apical part of the ventral part (see above). However, the extreme, divided condition occurs in different phylogenetic lineages (compare fig. 80 a-g). Both states appear to coexist within *Melima*, which can be clearly characterised as a monophylum. The genetic basis for such a rostrum somehow seems to be present in the stenheliniine groundpattern. Thus, the special shape of the rostrum is regarded here as an autapomorphy of Stenheliinae **124**. The other Thalestridimorpha show a large rostrum shaped like an acute-angled triangle. In the probably most closely related Tetragonicipitidae and *Protolatiremus* it is small and in the Tetragonicipitidae of different shape, depending on the subtaxon (compare e.g. Fiers, 1995). The large triangular rostrum may still be used as a diagnostic character for the Thalestridimorpha rather than a precisely comprehensible autapomorphy at present.

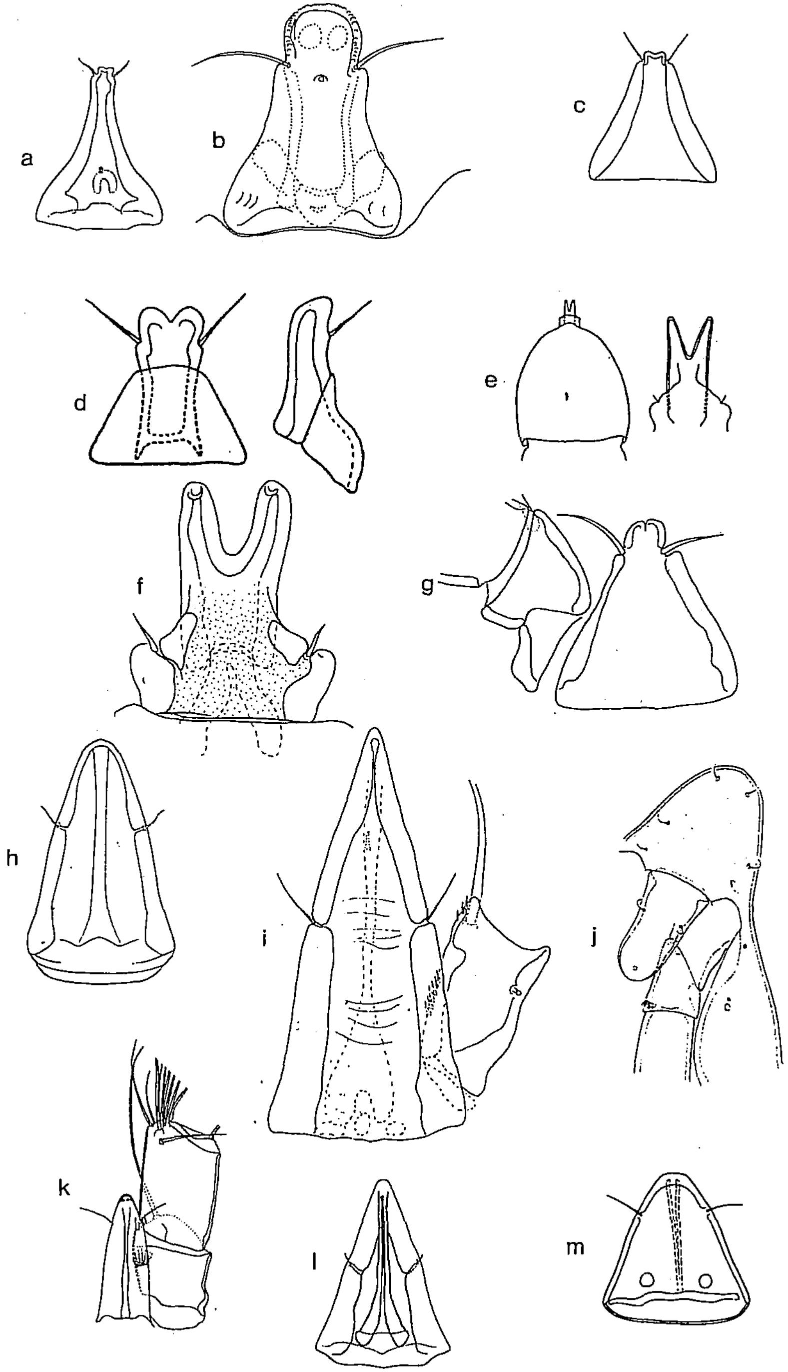
telson and additional abdominal somites. A telson should, of course, not be named a somite. However, the term "anal somite" is established among copepodologists (Huys & Boxshall, 1991) and will therefore be used in the following. In the groundpattern of the Copepoda the anal somite is a coherent section, with a dorsally located anus being covered by a semicircular anal operculum. In the Pseudotachidiidae the anal somite is completely divided longitudinally, while the anal operculum is missing and replaced by a pseudoperculum consisting of the frill of the preceding somite **126**. Within Oligoarthra, a divided anal somite occurs also in the Ectinosomatidae and Neobradyiidae.

The caudal setation can be homologised within the Copepoda (compare Huys & Boxshall, 1991). There are 7 setae of characteristic shape or/and position (fig. 81 G). In the Thalestridimorpha the ventrolateral seta I is modified thorn-like as compared with the groundpattern **127** (compare fig. 81 A, B, C, D, E + G). Seta I is miniaturised in the Parastenheliidae (fig. 81 D) **129**. Whether this can be traced back to an already thorn-like state or to the groundpattern cannot be verified at the moment. Character **127** is therefore either an autapomorphy of Taxon A or only of Taxon B (fig. 4). A thorn-like seta I was not observed in the most closely related outgroups (compare e.g. fig. 81 F, I, H). In the Pseudotachidiidae (fig. 81 F) seta I is either miniaturised or completely lost and also spatially separated from seta II **128**. In the groundpattern of the Podogennonta both setae are situated closely together and juxtaposed (compare fig. 81 G). In most Thalestridimorpha the caudal rami are broader than long. Together with the large triangular rostrum, this may serve as a rough diagnostic character.

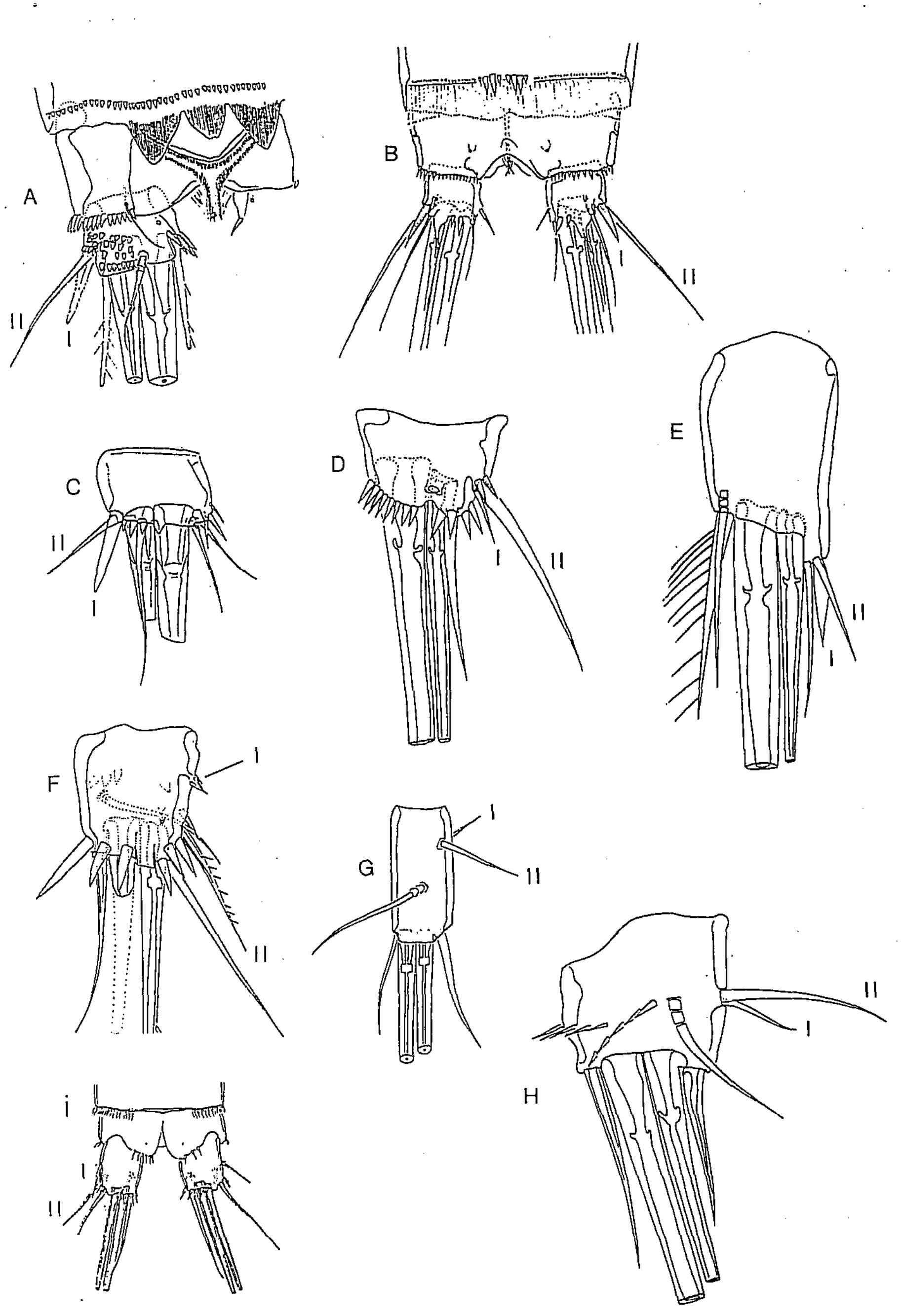
P. 180: <u>fig. 79</u>: Sexual dimorphism of the male P1 basis. A: *Paramphiascopsis facialis* (Weddell Sea, Diosaccinae), B: *P. glacialis* (Weddell Sea, Diosaccinae), C: *Miracia efferata* (Huys & Böttger-Schnack, 1994, Miraciinae), D: *Paramphiascopsis* spec. (Weddell Sea, Diosaccinae), E: *Distioculus minor* (Huys & Böttger-Schnack, 1994, Miraciinae. A fusion of the "Nebendornen" occurs within the Miraciinae as well as within the Diosaccinae.



P. 182: fig. 80: Rostrum in the Stenheliinae and other representatives of the Thalestridimorpha. a: *Onychostenhelia falcifera* (Itô, 1979), b: *Melima* spec. (Papua New Guinea), c: *Stenhelia peniculata* (Lang, 1965), d: *Melima indica* (Wells & Rao, 1987), e: *Cladorostrata brevipoda* (Shen & Tai, 1963), f: *Stenhelia "bifida"* (South Carolina), g: *Stenhelia* spec. (Papua New Guinea), h: *Eudactylopus latipes* (Lang, 1965), i: *Paramphiascopsis* spec. (Weddell Sea), j: *Macrosetella gracilis* (Huys & Böttger-Schnack, 1994), k: *Parastenhelia costata* (Mielke, 1990), l: *Parathalestris bulbisetosa* (Lang, 1965), m: *Dactylopusia vulgaris* (Lang, 1965).



P. 183: fig. 81: Setation of the caudal rami: A: *Ambunguipes rufocincta* (Huys, 1990, Rhynchothalestridae), B: *Paramphiascopsis* spec. (Weddell Sea, Diosaccinae), C: *Dactylopusia decostata* (after Pallares, 1975, Dactylopusiidae), D: *Parastenhelia* spec. (Andros, Parastenheliidae), E: *Eudactylopus* spec. (Malediven, Thalestridae), F: Pseudotachidiidae spec. (Weddell Sea), G: Copepod groundpattern (Huys & Boxshall, 1991), H: *Protolatiremus sakaguchii* (type material of Itô), I: *Harpacticella paradoxa* (Itô & Kikuchi, 1977).



7. Discussion of the newly established hypotheses on phylogenetic relationships

7.1 Discussion of the new phylogenetic system of Thalestridimorpha (fig. 4)

References to the chapters discussing the mentioned characters in detail are listed in the character table (chapter 4.2).

Within the Oligoarthra, for which new autapomorphies have been found in the course of this study (compare chapters 6.1, 6.2, 7.3, 5), a monophylum Podogennonta can be characterised by the following autapomorphies: **16** A2exp3+4 of Oligoarthra groundpattern are fused (compare fig. 24), **42** Mxl with only 1 outer coxal seta, **44** posterior apical spines of the Mxl praecoxal arthrite with "double-spinules" (fig. 33), ✱ derived setation of Mxenp (figs. 36 + 37) (this character is not listed in the character table), **70** setation of the coxal endites of the Mx of characteristic shape (fig. 40), **73** only 4 coxal setae present on the Mxp, arranged in pairs (fig. 46), **84** characteristic shape of the P1enp3- and P1exp3-setation (fig. 50).

All of these characters have been retained in the groundpattern of the Thalestridimorpha, which therefore are a lineage within the Podogennonta. Autapomorphies of Thalestridimorpha (= taxon A in fig. 4 + 82) are the segmentation of the Mdexp, in which exp4 and 5 of Oligoarthra groundpattern are fused (fig. 27) **33**, the special arrangement of the setae on Md"enp2" (fig. 29), which was not observed in the probably most closely related Tetragonicipitidae and *Protolatiremus* (fig. 29) **37**, and the intercoxal sclerites of P2-P4, which show paired, pointed projections (fig. 59) **94**. Three more characters have to be discussed as autapomorphies. On the distal part of the Mx praecoxal endite 1 seta of Podogennonta groundpattern is missing (fig. 40) **63**. Since all Podogennonta which retain a more primitive maxillar setation do not show more than 2 setae (except for the Pseudotachidiidae) it is also possible that this character is already apomorphic on a higher systematic level within Podogennonta (taxon II in fig. 82). Male P2 sexual dimorphism occurs in many taxa within the Oligoarthra, e.g. in the Tisbidae, Pseudotachidiidae, within the Canthocamptidae sensu Lang, 1948, within the Laophontidae, etc. In the

Thalestridimorpha the male P2 enp is 2-segmented, except for a 3-segmented condition in some species within the Parastenheliidae (e.g. *Parastenhelia megarostrum*, *P. minuta* after Pallares, 1982, *P. reducta* after Apostolov, 1975, *Karllangia*) which is interpreted here as secondary (see chapter 6.11.1). In the most closely related outgroups of the Thalestridimorpha the endopods of all swimming-legs are either 2-segmented and therefore the 2-segmented male P2enp is not caused by sexual dimorphism (Tetragonicipitidae), or all swimming-leg endopods, including male P2 enp, always remain 3-segmented (*Protolatiremus*, compare fig. 70 and chapter 7.2). Assuming a monophyly of Thalestridimorpha because of the characters discussed above, the sexually dimorphic 2-segmented condition of the male P2 enp within the Parastenheliidae and in the other Thalestridimorpha is regarded here as homologous and as an additional autapomorphy of the Thalestridimorpha as a whole **113**. The absence of this sexual dimorphism in the above-mentioned outgroups supports this interpretation. No sexual dimorphic modification of the male P2enp3 setation is present in the Parastenheliidae, whereas several different setae are always modified in a taxon specific way in the other taxa (fig. 69) **114**. Except for the Parastenheliidae, the ventrolateral caudal seta I is spine-like modified (fig. 81) **127** in all Thalestridimorpha. In the Parastenheliidae this seta is miniaturised (whereas caudal seta II is elongate and slender). It is difficult to decide, whether character **127** has been present already in the groundpattern of the Thalestridimorpha (in this case being secondarily altered in the Parastenheliidae) or only in taxon B (being an autapomorphy only for taxon B). A large, triangular rostrum and caudal rami being broader than long are preliminarily regarded here as rough diagnostic characters, but not as convincing autapomorphies (compare chapter 6.12.4).

The Parastenheliidae even though strongly derived in many aspects are the sister group of all other Thalestridimorpha (= taxon B in fig. 4). At first sight they seem to share characters with the Thalestrioidea and some of their subtaxa. Characters **18** (A2exp1 with proximal seta shortened) and **97** (loss of 1 seta on P4enp2) are present convergently in the groundpattern of the Parastenheliidae and of Thalestrioidea. In the groundpattern of the latter the complete swimming-leg setation is retained, except for the above mentioned seta on P4enp2, whereas the Parastenheliidae have lost a lot more swimming-leg setae (on

P3enp3 **100**, P2enp3 **99** and, P3enp2 **96**, respectively). This supports a convergent loss of the P4enp2 seta, because loss of a swimming-leg seta is a rather common event in the Parastenheliidae, whereas in the Thalestrioidea it has happened only once. The other autapomorphies of the Thalestrioidea discussed below are not shared by the Parastenheliidae and vice versa. In the Parastenheliidae there is an agreement of characters with certain subtaxa of Thalestrioidea: **21** (A2 2-segmented, fig. 26) and **96** (P3enp2 with only 1 seta) agree with the Thalestrinae, **28** (Mdexp 1-segmented, fig. 26) with the Eudactylopusiinae, **99** (P2enp3 with only 2 setae) and **109** (male P5 benp with only 2 setae) with the Diosaccidae. However, none of these characters is already part of the Thalestrioidea groundpattern.

Since the Mdexp is reduced to one segment with only few setae in the Parastenheliidae, these can at present not be assigned neither to the Dactylopusiidae **27** nor to taxon D **26** (compare fig. 27, 28, chapter 6.4). The occurrence of several quite primitive characters (female P5 setation, see chapter 6.10, 3-segmented male P5exp, see chapter 6.12, both are characters of the Oligoarthra groundpattern!), the plesiomorphic state of the sexually dimorphic male P2enp compared with other Thalestridimorpha (chapter 6.11) as well as some primitive naupliar characters (chapter 10) speak in favour of a position at the basis of the Thalestridimorpha. Important autapomorphies of the Parastenheliidae, besides the characters mentioned above, are the spinule row on segment 9 of the male A1 **11**, the loss of a seta on the Mxl basal endite **45** and on the Mxlenp (tab. 1) **47**, the shape of the Mxl praecoxa (fig. 34) **49**, of the Mx praecoxal arthrite (fig. 42) **65**, of the Mxp (fig. 47) **81**, of the P1 (fig. 53) **90** and of the female P5 (fig. 62) **103**.

Autapomorphies for taxon B are the lack of the exopodal setae 13 + 14 (compare fig. 61-64) of the female P5 **102**, the only 1-segmented male P5exp **111**, the male P2enp provided with modified setae (fig. 69, chapter 6.11) **114** and maybe (or in Thalestridimorpha?) the thorn-like modification of caudal seta I (fig. 81 and chapter 6.12.) **127**.

The next branch of the cladogram are the Dactylopusiidae, formerly a subfamily of Thalestridae now elevated to full family rank. Besides the morphology of the Mdexp **27** discussed in more detail below, they show several more autapomorphies: the shape of P1 (fig. 53) **92**, the male P2enp (figs. 69, 72, 74) **115** and the Mxl praecoxa (fig. 33) **48**, the loss of 1 seta on P4enp3 **98** and the shape of the Mx praecoxal endite (fig. 43) **66**. Character **71** (loss of 1 flagellate seta on the proximal Mx coxal endite, fig. 41) occurs convergently also in the Diosaccinae within Thalestrioidea, however, the homology of the respective setae remains unclear. The Dactylopusiidae are neither closely related with the Diosaccinae nor with the Thalestrioidea, i.e. they do not share any of their autapomorphies. In contrast to the Diosaccinae, there is a strong tendency towards reduction of segmentation and setation in their mouthparts. However, in single species (e.g. of *Dactylopusia*) the respective thalestridimorphan groundpattern is still preserved (see e.g. chapter 6.4).

For taxon D, the sistergroup of Dactylopusiidae, only one single autapomorphy can be found so far **26**. In all Rhynchothalestridae and some Diosaccinae (e.g. *Paramphiascopsis*, *Amphiascopsis*), a 3-segmented Mdexp was observed, in which both proximal segments of the Oligoarthra groundpattern are fused (fig. 27 + 28, chapter 5.4.1). The proximal segment of this exopod is more than twice as long as both distal segments together, which in addition appear even shortened (fig. 27). The Dactylopusiidae on the other hand show a maximally 2-segmented Mdexp, of which the distal segment is a fusion product of the 3 distal segments of Oligoarthra groundpattern (fig. 27 + 28) **27**. The seta belonging to the original proximal segment of the latter is not located on the exp itself but on the basis **27**. Assuming that the respective segment has become fused with the basis and that it is still represented only by the single basal seta, the following hypothesis can be proposed (compare fig. 27): Starting from the Oligoarthra groundpattern, the Mdexp of taxon D and Dactylopusiidae have developed differently. Both types have retained the complete setation. In taxon D, exp1 and 2 of the Oligoarthra groundpattern have become fused, whereas in the Dactylopusiidae this is the case for exp3-5 (or exp3-4 of the Thalestridimorpha groundpattern) (fig. 27). Exp1 of the Oligoarthra groundpattern seems to be completely fused with the basis in the Dactylopusiidae and only represented by one single seta, whereas exp2 is well developed and demarcated. A separation of exp1 and 2 can be still assumed also for the Thalestridimorpha groundpattern (fig. 27).

Within taxon D the Rhynchothalestridae are the sister group of the Thalestrioidea. The Rhynchothalestridae unite those taxa originally belonging to the thalestrid subfamily Rhynchothalestrinae with Hamondiidae Huys, 1990. The Ambunguipedidae Huys, 1990, which also include some taxa of the original Rhynchothalestrinae, have been reunited with the Rhynchothalestridae. The Rhynchothalestridae show quite a primitive setation and segmentation of all appendages within Thalestridimorpha. Autapomorphies of this taxon are the arrangement of the Mxp syncoxal setae (fig. 47) **75**, the shape of the male P2enp (fig. 69) **117** and the shape of the articulation between enp2 + 3 of P2-P4 (fig. 58) **95**, which occurs convergently also in the Eudactylopusiinae within Thalestrioidea. Character **95** can be observed within the Thalestrinae (*Phyllothalestris*) as well, but it is not part of the groundpattern of the Thalestridae itself. The Rhynchothalestridae show the more plesiomorphic conditions for all characters that are apomorphic in the Thalestrioidea, thus excluding them from the latter taxon.

The Thalestrioidea comprise the sister groups Diosaccidae and Thalestridae. This new taxon appears well-founded by the following characters: **9** male A1 with segments 2 and 3 fused, fig. 21, **43** loss of the outer coxal seta on Mxl, tab. 1, **18** proximal seta on A2exp1 shortened, fig. 26, **10** homologous seta on segment 6 of the male A1 modified, fig. 22, **116** shape of the male P2enp, figs. 69, 71, 75. Further characters can be derived from the groundpatterns of the Mxp (fig. 47, 48) **76** and of the Mdenp (fig. 30) **38**. The two main lineages within Thalestrioidea are the Diosaccidae, with the subtaxa Stenheliinae, Diosaccinae, and Miraciinae, and the Thalestridae with the remaining subfamilies Thalestrinae and Eudactylopusiinae.

The combination of the characters **99** loss of an inner seta on P2enp3, **19** loss of the proximal seta on A2exp1, fig. 26, **54** Mxlexp with only 2 setae, tab. 1, and **88** inner seta of P1enp1 inserting in the distal quarter of the segment, characterises the Diosaccidae. Character **110** (male P5exp with inner seta missing) is present in all Diosaccidae, except for one species, *Miracia efferata* (Miraciinae). Because of their highly specialised mode of life (secondarily planktonic), which most likely influenced the strong reduction and modification of segments and setation of the appendages (= many autapomorphies, not all of them have been listed in the new system), the Miraciinae were at first difficult to assign to any thalestridimorphan taxon. The shape of the male P2enp **118**, which is easily derivable from the Thalestrioidea groundpattern (compare p. 215, fig. 4 G + H in Huys & Böttger-Schnack, 1994 with figs. 69, 71, 75), the loss of an inner seta on P4enp2 **97**, and the fusion of segments 2 + 3 of the male A1 (fig. 21) **9** allow their assignment to the Thalestrioidea, and finally characters **88**, **99** as well as the setation of the Mxpenp **77** (=exactly as in the Diosaccinae, compare fig. 48) show them to belong to the Diosaccidae. The presence of sexually dimorphic basal "Nebendornen" on the male P1 (fig. 79 C + E) **121** suggests, that within Diosaccidae the Miraciinae are more closely related to the Diosaccinae than to Stenheliinae.

In contrast to the Miraciinae, the Diosaccinae have retained a quite primitive segmentation and setation of the appendages. As differentiating autapomorphies they show a characteristic shape and constant number of "Nebendornen" as well as the presence of a nose-like "Chitinzapfen" on the male P1 basis (fig. 79 A + B) **122**. The development of 3 large single "Nebendornen", in contrast to a more spinule row-like appearance in the Miraciinae, is here interpreted as the derived state. Within the Miraciinae (see Huys & Böttger-Schnack, 1994) as well as within the Diosaccinae (e.g. *Amphiascoides*/*Paramphiascella*) fusion of the "Nebendornen" results in the formation of a single "Zapfen" (fig. 79 E + D, chapter 6.12.2). A further autapomorphy of the Diosaccinae is the loss of one flagellate seta on the proximal coxal endite of the Mx (fig. 41) **71**. The Miraciinae on the other hand seem to have lost the anterior spine-like seta at the same site (compare fig. 27D, p. 247 in Huys & Böttger-Schnack, 1994) **72**. It remains unclear, whether characters **3** + **4** (setal pattern of female antennule segment 4, fig. 9) already belong to the groundpattern of taxon i (= Diosaccinae + Miraciinae), in which case **4** has to be derived from **3**, or whether instead they are autapomorphies of the Diosaccinae **3** and Miraciinae **4**, respectively. The latter possibility is believed here to be more likely. In the Miraciinae the loss of setae on the appendages is a rather common event, whereas in the Diosaccinae it is quite unusual. However, the possibility that the Miraciinae arose within the Diosaccinae cannot be excluded completely. Further investigations of the relationships within the Diosaccidae are necessary to answer this question.

The Stenheliinae are characterised by the shape of the Mxp (fig. 48) **78**, which can be easily derived from the groundpattern of the Thalestrioidea, the shape of the female P5 (fig. 65) **107**, the female and male A1 **1**, **6** (figs. 6 + 10), and the shape of the rostrum (fig. 80) **124**. With the complete setation of segments 4 and 5, the female A1 is quite primitive within Oligoarthra. Together with the retention of the flagellate seta on the proximal coxal endite of the Mx and the lack of sexual dimorphism on the male P1 basis, this places the Stenheliinae outside of the Diosaccinae, even though they share naupliar characters (chapter 10). A peculiar phenomenon is the non-homologous shape of the male P2enp in several subtaxa of Stenheliinae. There is not even a common groundpattern, to which all these types could be traced back and there is no morphological evidence to derive them from the superordinated Thalestrioidea groundpattern either (compare fig. 69 + 76). The latter has to be interpreted as a strong synapomorphy of the Thalestridae and Diosaccidae. The Stenheliinae show all the other apomorphic characters, thus indicating that they are members of the Thalestrioidea and Diosaccidae, respectively. Two alternative explanations can be deduced from this: 1. Because of their special non-homologous male P2enp the Stenheliinae have to be removed from both superordinated taxa, which would have the consequence, that all autapomorphies of the Thalestrioidea and Diosaccidae would have to be viewed as having developed at least twice independently, or 2., the fact itself, that several different modifications have evolved within the Stenheliinae, of which the monophyly is well supported, could be interpreted as an additional autapomorphy **119** of this taxon. This second alternative is accepted here. Moreover, there is no evidence to assign the Stenheliinae to any other taxon of the Thalestridimorpha.

The revised Thalestridae are the sister group of the Diosaccidae. The Rhynchothalestrinae and Dactylopusiinae, the former subfamilies sensu Lang, cannot be placed into the Thalestrioidea, because they do not share any of the autapomorphies of the latter, but show the plesiomorphic states in these characters (the Pseudotachidiinae have to be removed entirely from Thalestridimorpha). Thus only the subfamily Thalestrinae and the closely related genera *Eudactylopus*/*Neodactylopus* (united here as Eudactylopusiinae), which have been removed from the Dactylopusiinae sensu Lang, remain in the revised Thalestridae. The Thalestrinae can be characterised by the shape of the A2exp (fig. 26) **21**, **22**, the Mxp (fig.

48) **80**, the setation of the female P5 (fig. 63) **108** the Md"enp2" (fig. 30) **39** and by a 1-segmented Mdexp (fig. 28) **30**. In the Thalestridimorpha, an extremely foliate female P5 (benp + exp) is restricted to the Thalestrinae and Eudactylopusiinae (fig. 63). Thus, this character **105** is regarded here as an additional autapomorphy of Thalestridae. Further characters can be deduced from the reconstruction of the groundpattern of the Mx praecoxal endites (fig. 42) **68** and the Mxenp (fig. 38) **62**. The groundpatterns of the Thalestridae are still realised in the Thalestrinae in these cases, but are further derived in the Eudactylopusiinae (figs. 38, 42) **61**, **69**. Fusion of maxillipedal claw and enp occurs quite often within the Thalestridimorpha, e.g. in the Parastenheliidae, Miraciinae (but not in the groundpattern of Diosaccidae), Thalestridae (but not in the groundpattern of Thalestrioidea), Dactylopusiidae, and Rhynchothalestridae and is not a very specialised character of Thalestridae and the other taxa concerned. The same is true for character **5** (segment 5 of female antennule with only 2 setae, fig. 7), which is even present in most Oligoarthra. Besides numerous reductions of mouthpart setation and segmentation (**23**, **31**, **40**, **61**), above all the shape of P1 (fig. 54) **91**, and of the Mxl (fig. 34) **56** are strong autapomorphies of the Eudactylopusiinae. The Thalestrinae are more primitive in many aspects (mouthparts), but can be characterised as a monophylum by the setal pattern on segment 4 of the female A1 (fig. 9) **2**, in contrast to the complete setation in the sister taxon Eudactylopusiinae, by the setation of the Mxl praecoxa (fig. 34) **57**, the lack of a seta on P3enp2 **96** and on Mxlenp (also exp?) **46**.

7.2 Discussion of the phylogenetic relationships within Podogennonta (fig. 82)

The Pseudotachidiidae, which have been removed from the Thalestridae and Thalestridimorpha, do not appear to be the sister group of Thalestridimorpha within the Podogennonta. They rather seem to branch off at the basis of the Podogennonta. This is also supported by primitive naupliar characters (chapter 10). The numerous autapomorphies of Pseudotachidiidae include a pronounced segmental projection on male P3enp2 **123**,

segments 4 + 5 of female A1 fused **8**, the special shape of the Mxl praecoxa **50**, a subchirocer male A1 **12**, loss of a terminal seta on A2exp3 **24**, shape of Mx praecoxa **64**, shape of Mxp **83**, shape of the female P5 **104**, presence of large, subapically and ventrally located rostal pores (fig. 11) **125**. The shape of the P1 is clear evidence that they belong to the Podogennonta (see chapter 6.8). All characters mentioned above are also shared by the Paranannopidae Por, 1986, which therefore have to be placed into Pseudotachidiidae of which they are part as a monophyletic subtaxon Paranannopinae.

Within Podogennonta, a taxon II (fig. 82) can be distinguished, which shows the following autapomorphies: aesthetasc on segment 3 of male A1 missing **14**, reduction of the geniculate seta on A2"enp1" (compare fig. 25) **17**, Md"enp1" with only 2 instead of 3 setae **36**, Md basis with only 3 instead of 4 setae **41**, distal part of praecoxal endite of Mx with only 2 instead of 3 setae **63** (see also chapters 4.3 and 7.1). The Pseudotachidiidae show the plesiomorphic state in all these characters and are therefore excluded from this taxon.

On the contrary, the Thalestridimorpha, Tetragonicipitidae, *Protolatiremus sakaguchii*, and probably also the "classic" families of Metidimorpha, Ameiridimorpha, and Cletodidimorpha are members of taxon II according to Lang (1948). The latter are, however, far more derived in their mouthpart morphology than the first 3 taxa mentioned, which makes the further analysis more difficult. At least character **14** can be directly observed in all taxa assigned to taxon II above.

The Tetragonicipitidae share the miniaturised seta 1 of the maxillar enp (compare fig. 37) **59** with the Thalestridimorpha, but apparently no further specialised characters. The exploitation of new character complexes will be necessary for further hypotheses. In *Robertgurneya* (Diosaccinae) the ultrastructure of an "epicopulatory bulb" at the female genital field was examined which seems to be connected with a specialised mode of sperm transfer (Bensien, 1998). A kind of "epicopulatory bulb" can be observed in all taxa of Thalestridimorpha. In descriptions of tetragonicipitid species (Fiers, 1995, Mielke, 1989) similar structures have been illustrated, but their homology is uncertain as yet. There are no data on the distribution of such a structure within Oligoarthra and no detailed, comprehensive ultrastructural analyses available for the moment.

In *Protolatiremus* and in the above-mentioned "classic" family groups, the Mxenp is represented only by a few setae. It is therefore possible, that **59** belongs already to the groundpattern of taxon II.

A possible candidate for the sister group position of Thalestridimorpha is *Protolatiremus*. This monotypic genus was placed into Thalestridae by its first author Itô (1974). However, except for one character, it does not share any of the autapomorphies either of the Thalestridae or of Thalestridimorpha as a whole. This exception is the elongate P1exp2, which could be interpreted as a synapomorphy of Thalestridimorpha and *Protolatiremus* (taxon III in fig. 82, compare figs. 52-54) **87**. An elongate P1exp2 is not realised in all species of Thalestridimorpha (not in some species of *Parastenhelia* and Diosaccinae, not in Miraciinae and Stenheliinae), but it is clearly present in all subtaxa identified as monophyletic, and the genetic basis for such an elongation seems to exist. It is also a character which is quite unique within Oligoarthra. It was not observed outside of *Protolatiremus* and Thalestridimorpha. However, since this character is the only one to support the sister group relationship between both taxa at present, further data are necessary to confirm a taxon Thalestridimorpha/*Protolatiremus*. Autapomorphies of *Protolatiremus* are e.g. **85** the shape of the setae on P1exp3 and enp3 (compare fig. 52), **112** the unique sexual dimorphism on male P2enp (fig. 70) and **25** the reduced setation of Mdexp (fig. 27).

Harpacticidae and Latiremidae in the course of the present study are placed into Podogennonta, but are not further discussed here. In any case they belong outside of taxon II. To specify their position within Podogennonta, the relationships with Pseudotachidiidae would have to be analysed.

7.3 Outlook on the system of Harpacticoida

There are authors, who argue against a monophyly of Harpacticoida. Tiemann (1984) analysed the diagnosis of Lang (1948) in detail applying the criteria of the phylogenetic systematics according to Hennig (1966, 1982) and did not find a single autapomorphy. According to Dahms (1993) the monophyletic nature of Polyarthra and Oligoarthra together cannot be demonstrated on the basis of naupliar characters.

Within their new system of Copepoda, Huys & Boxshall (1991) listed the following characters in support of a taxon Harpacticoida: the specific fusion pattern of the ancestral segments (of the ancestral copepod) of the female and male antennule, respectively, P1enp2 with only 1 seta, P2exp3 with only 3 inner setae, and a 2-segmented Mxpenp, enp1 representing ancestral segments 1-5 and enp2 ancestral segment 6. The latter character, however, is the result of an analysis of species of Polyarthra only (p. 118 and p. 135, figs. 2.3.15 A+E, *Canuella perplexa* and *Sunaristes dardani*). The present study (chapter 6.1.1) shows that the above-mentioned antennule fusion pattern in both sexes does not represent the harpacticoid groundpattern, but an alternative homologisation with the ancestral antennule (according to Boxshall & Huys, 1998), reveals autapomorphies only for Oligoarthra. The general morphological structure of the antennule of both sexes is quite different in Oligoarthra and Polyarthra, respectively. Assuming Harpacticoida to be monophyletic, their antennule groundpattern would be different from and more primitive than that proposed by Huys & Boxshall (compare chapter 6.1.1). The only autapomorphies of Harpacticoida according to Huys & Boxshall left are therefore the loss of the above-mentioned swimming leg setae. During this study, the following characters were found to be potential autapomorphies of Harpacticoida: "3+9" setae on the Mdenp (compare chapter 6.4), "12+2" setae on the Mxl praecoxa, in contrast to "13+2" in Misophrioida (compare Huys & Boxshall, 1991) and the claw-like appearance of basal seta "D" of the Mx in both Polyarthra and Oligoarthra (see fig. 36 and chapter 6.6.1). A comprehensive analysis of whole Copepoda will be necessary to decide on the monophyly of Harpacticoida.

The monophyly both of Oligoarthra (see Martinez & Moura, 1998) and Polyarthra (see Dahms, 1993) on the other hand seems to be well supported. Further autapomorphies of Oligoarthra, as worked out in the present study, are the fusion pattern of the female antennule, resulting from paedomorphic events during ontogeny (chapter 6.1.11), the shape of setation (chapter 6.2 and fig. 15), and the fusion pattern of segments (fig. 16) of the male antennule.

Within Oligoarthra, the Podogennonta Lang, 1948 turned out to be a monophyletic taxon.

During the present study, the following autapomorphies have been found: shape of P1, with characteristic shape of setae on enp3 and exp3, the latter always without inner seta **84**, presence of "double spinules" on the posterior apical praecoxal spines of the Mxl **44**, the special shape of the maxillar coxal endites. Further -not so specialised- characters are setation and segmentation of A2exp **16**, the Mxenp and maybe of the Mxp (chapters 6.3, 6.6, 6.7, not all of these characters are included in the character table). All above mentioned characters are also present in the Harpacticidae, which according to Lang (1948) belong to the Exanechentera but should be placed into the Podogennonta instead.

Descriptions of *Latiremus eximius* Bozic, 1969 and *Delamarella galatae* Cottarelli, 1971, which belong to the Latiremidae, show "true" geniculate setae on P1exp3 and a P1enp, which can be derived from the podogennontan groundpattern (fig. 51). These are arguments for the inclusion of the Latiremidae into the Podogennonta.

Several taxa, within the Podogennonta (Ameiridae, Parastenheliidae, Thalestridae, Dactylopusiidae, Pseudotachidiidae, Metidae) show a sexually dimorphic basal spine on P1. Such a sexually dimorphic spine can also be observed in the genus *Darcythompsonia* T. Scott, 1906 (after Huys et al., 1996) within the Darcythompsoniidae Lang, 1936. This could be regarded as indicative of an affinity with the Podogennonta.

The specialised shape of the 4 setae on A2enp1 (fig. 25, chapter 6.3), which are modified into 2 curved, spine-like setae as well as into 1 geniculate and 1 long and slender seta, connects the Podogennonta (within which this pattern is present in the Pseudotachidiidae and the Harpacticidae) at least with the Tisbidae (Idyanthinae and Tisbinae), Novocriniidae, Chappuisiidae, and Harpacticoida fam. 1. These taxa are probably part of a common higher taxon within the Oligoarthra. In *Tachidiopsis* and *Neobradya pectinifera* (fig. 25), e.g., the respective setae are still unmodified. The Cerviniidae show only 3 obviously unmodified setae. Within the Podogennonta this pattern is even further modified by reducing the geniculate seta, forming a pair of slender, often basally fused setae together with the juxtaposed inner seta (fig. 25) **17**. This is so in Thalestridimorpha, *Protolatiremus* and Tetragonicipitidae. However, in the "classic" families of Podogennonta sensu Lang, 1948, such as Cletodidae, Laophontidae, and Canthocamptidae, only the 2 spine-like setae and one of the slender setae are still present (e.g. in *Archilaophonte*, cf. Willen, 1995). Thus the question of whether character **17** is already part of the groundpattern of taxon II remains unanswered. The same applies to the character polarisation concerning the shape of the Mxenp, which is further specialised at least in the Thalestridimorpha and Tetragonicipitidae **59** (cf. fig. 37) and to characters **36, 41, 63**.

The "prehensile" shape of the Mxpenp in the thalestridimorphan groundpattern can be homologised with that of *Idyanthe* (fig. 46). Since there are only few representatives of Oligoarthra showing the complete setation, it is still impossible to decide, whether such a Mxp has developed several times or only once. The 2 large terminal, geniculate setae on Mxpenp2 which can be found in Tisbinae, Idyanthinae, *Tachidiopsis*, Paramesochridae, Chappuisiidae, Novocriniidae and Superornatiremidae, are homologous and probably autapomorphic for a higher taxon within the Oligoarthra consisting of these groups and the Podogennonta.

Lang (1948) placed the Metidimorpha with the only family Metidae close to the Thalestridimorpha because of "[...] mehrerer Merkmale, von denen [das] wichtigste [das] zu sein scheint, daß die Basis des 1. Beins denselben Geschlechtsdimorphismus wie bei diesen aufweist" (p. 1485). As mentioned above (chapter 8), a sexually dimorphic inner basal spine on P1, as described e.g. for *Metis ignea* (after Lang, 1948), is present in several not always closely related taxa of Podogennonta, and is therefore no clear evidence for a closer relationship to the Thalestridimorpha. Studying the literature, which includes very detailed descriptions (Fiers, 1992, Mielke, 1989), no further indication for such a relationship could be found. The habitus of *Lauberia tercera* Fiers, 1992 on the other hand strongly reminds of representatives of Laophontoidea sensu Huys, 1990 in the shape and armature of the somites and especially the "pitted" ornamentation of the cephalothorax (cf. *Lauberia tercera*, figs. 4c, 1a+b in Fiers, 1992 with *Laophontopsis borealis* figs. 1a+b and 7a in Huys & Willems, 1989 or *Cristacoxa petkovskii*, fig. 1a+b in Huys, 1990). Edwards (1891, after Lang, 1948, fig. 315.2) illustrated a male P3enp of *Metis holothuriae* showing the typical sexual dimorphism of this suprafamily. However, the latter was not confirmed by the other available descriptions and Lang (1948) and also Mielke (1989) are doubtful about the correctness of this figure.

Suitable candidates for the sistergroup of Thalestridimorpha are at present only the Tetragonicipitidae and *Protolatiremus sakaguchii* Itô, 1974. The former share the shape of the Mxenp (fig. 37) and the characters of taxon II (fig. 82) with the Thalestridimorpha, but no more. In the other "classic" families of Podogennonta the Mxenp is reduced such that it cannot be excluded that the type of Mxenp depicted in fig. 37 could even be a character for a more inclusive taxon within Podogennonta. *Protolatiremus sakaguchii* had been placed into Thalestridae by Itô (1974) because of the "segmentation as well as principal ornamentation of the first pair of legs and some other characters". In Bodin's catalogue (1997) it is listed among Latiremidae. Itô assumed a relationship with the genus

Rhynchothalestris within the Thalestridae sensu Lang, 1948, but gave as evidence only plesiomorphic characters: 9-segmented female antennule, setal formula of the swimming legs, A2 with basis. However, with its slightly elongated P1exp2 (fig. 52) and the modified setae 1 + 2 on the male P2enp, which is nevertheless still 3-segmented, (fig. 70), *Protolatiremus* shares derived characters with Thalestridimorpha. On the other hand, it lacks the paired projections on the intercoxal sclerites of the swimming legs and the 2-segmented male P2enp. *Protolatiremus* cannot be placed into any of the thalestridimorphan taxa and may therefore be their sister group within Podogennonta. To verify this, more analyses are necessary.

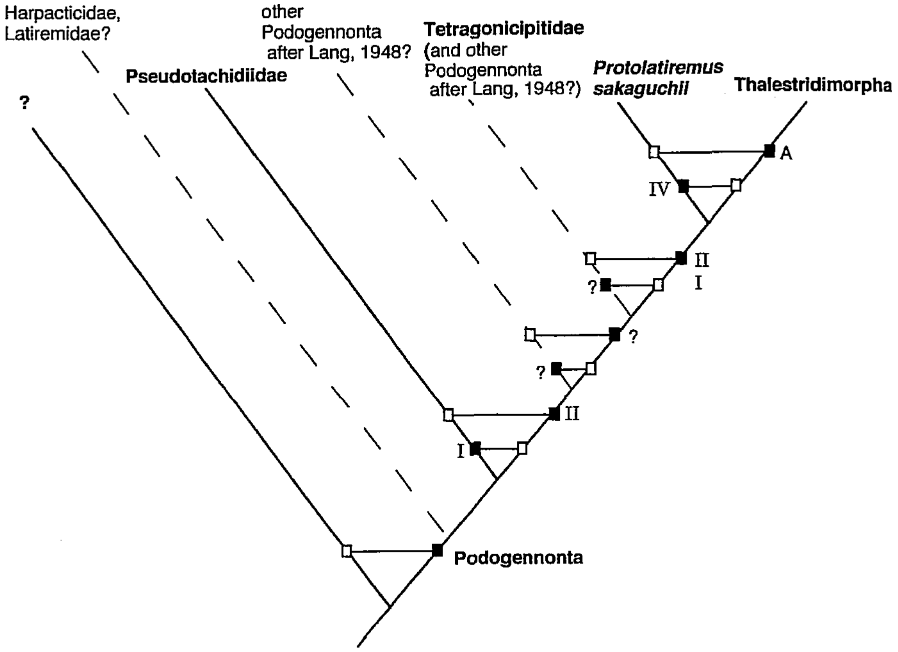


Fig. 82: Hypothesized phylogenetic relationships within the Podogennonta.

8. Discussion of the Thalestridimorpha system according to Lang (1948)

Lang (1944, 1948) established his family system of Harpacticoida, before Hennig's theory of phylogenetic systematics (1966, 1982) started to dominate phylogenetic research. He classified his taxa according to their morphological similarity, without distinguishing apomorphies and plesiomorphies. In the meantime, not only new character complexes (from molecular techniques, ultrastructural analysis) have become amenable to analysis but also a much higher standard of light microscopical observation and description of copepod morphology has been introduced (compare e.g. Huys & Boxshall, 1991), making morphological details available for analysis, which had been overlooked before. Thus, correct homologisation and assessment of characters could be improved considerably. It must also be kept in mind that since Lang 17 new families, 295 new genera and more than 2,000 new species of Harpacticoida have been described (Bodin, 1997). In the following those parts of Lang's system pertaining to the Thalestridimorpha will be discussed in the light of the new system (compare figs. 1, 2, 3, 4, 82).

The diagnoses of Thalestridimorpha and its subtaxa as given by Lang are rather indeterminate and vague, only rarely allowing for a characterisation of taxa by clear autapomorphies. Nevertheless, most of these subtaxa and the Thalestridimorpha themselves could be confirmed as monophyla, although arranged in a different constellation and with a different composition of genera within the new system (see chapters 4 + 7).

Lang's diagnosis of Thalestridimorpha (1948, p. 491) is very unspecific (" [...] Mundteile von wechselndem Aussehen und Bau, [...] Enp [P1] mehr oder weniger umgewandelt, [...], weiblicher P5 in der Regel wohlentwickelt") and partly, even considering the knowledge of that time, incorrect: e.g. the inner basal seta on the male P1 is not "always" modified. It is not, for example, modified in most Diosaccinae, *Eudactylopus*, and in Miraciinae. The only common apomorphic character mentioned is the "transformed" (except for Parastenheliidae) and 2-segmented (except for Pseudotachidiidae) male P2enp. Nevertheless, after the exclusion of the Pseudotachidiinae, several autapomorphies were found suitable for Thalestridimorpha for the new system (**35**, **78**, **85**, **118**, **103**, see chapters 4, 6, 7). The only apomorphic character left of Lang's diagnosis of Thalestridae (p. 491/92) is the "always transformed and mostly 2-segmented male P2enp". Hence, in the new system the

Thalestridae as composed according to Lang have no justification any more (compare figs. 3 + 4). Lang considers Thalestrinae and Rhynchothalestrinae most closely related because of the "same" genital field and the shape of the male P2enp, but because of the sexually dimorphic P3enp in the latter he excludes a direct ancestor-descendant relationship. The same argument is used to refuse a close relationship between Rhynchothalestrinae and Dactylopusiinae. In the Pseudotachidiinae and Dactylopusiinae, the "Enp P1 is developed much more strongly than in the both subfamilies mentioned before" (i.e. Thalestrinae and Rhynchothalestrinae). The differences between them, especially as regards the "primary and secondary sex characteristics" are, however, considered substantial. Finally, Lang presents his system of Thalestridae, which is depicted in fig. 3. In all subfamilies, Lang gave particular weight to the shape of the female genital field. However, it turned out in the meantime, that the latter is quite complex and the possibilities to correctly identify and homologise the visible structures by light microscopy are very limited. A morphological analysis by electron microscopy is only just beginning (e.g. Bensien, 1998) so that in the lack of comparative and comprehensive data for the Thalestridimorpha, a further discussion has to be postponed.

In the following only those characters of the scheme in fig. 3, which are not plesiomorphic within the Thalestridimorpha, are discussed. For the Rhynchothalestrinae sensu Lang these characters are the strongly elongate and equally long rami of P1 and the sexual dimorphism, which "sometimes" occurs on the male P3enp. The latter is actually present only in *Ambunguipes* and *Hamondia* within the Rhynchothalestridae (= Rhynchothalestrinae sensu Lang). The difficulties in reconstructing the P1 groundpattern and also its apomorphic characters are discussed in chapter 6.8.

The Thalestrinae sensu Lang can be confirmed as a monophyletic taxon. However, Lang himself gives no specific character, except for the strongly elongate rami of the P1, which have probably been developed only within the taxon (a demarcated rostrum is present in *Parathalestris*). In his diagnosis of the Dactylopusiinae Lang refers to the special shape of the P2enp. As indications for a closer relationship of *Dactylopusia*/*Paradactylopodia* and *Eudactylopus*, the elongate P1exp2 and the missing outer coxal seta of the Mxl are mentioned. In fact, the former occurs in all subtaxa of Thalestridimorpha and within the Dactylopusiinae; the latter is lost only in *Eudactylopus*, which, together with other characters, places *Eudactylopus* into the Thalestrioidea. The subchirocer male antennule is an autapomorphy of the Pseudotachidiidae also in the new system. The male P3enp2 is primarily equipped with a pronounced segmental projection in all of its genera, not only in *Pseudotachidius*.

All subfamilies of Thalestridae sensu Lang are retained in principle as taxa, however, they are either removed from the Thalestridae (Rhynchothalestrinae, Dactylopusiinae) or from the Thalestridimorpha as a whole, or, like the Eudactylopusiinae, remain in the Thalestridae. This division of the Thalestridae sensu Lang has severe consequences for the constellation of the thalestridimorphan taxa. In Lang's system (fig. 2) the Parastenheliidae are placed at the basis because of their 3-segmented P5exp and their sexually dimorphic P3enp. Together with the Diosaccidae, which carry 2 egg sacs as a plesiomorphic character they are regarded as relatively primitive. The characters connecting Miraciidae, Thalestridae, and Balaenophilidae are quite unspecific ("male P5exp always 1-segmented", "female with 1 egg-sac"). In the new system on the other hand the revised Thalestridae (Thalestrinae + Eudactylopusiinae), Diosaccinae, Stenheliinae, and Miraciinae (and Balaenophilidae, see chapter 7) together form the taxon Thalestrioidea, which in turn is the sister group of the Rhynchothalestridae. The Parastenheliidae are the sister group of Thalestrioidea/Dactylopusiidae (see chapters 4 + 7).

9. Discussion of the more recent literature

In the course of a revision of the Donsiellinae, which were removed from Laophontidae and placed into Thalestridae as close relatives of the Pseudotachidiinae, Hicks (1988) presents a scheme of the relationships within a part of the Thalestridae, which is not explicitly phylogenetic. It is not differentiated between apo- and plesiomorphies. The main branches consist of the Pseudotachidiinae and Donsiellinae on the one hand and of the remaining thalestridan subfamilies sensu Lang (1948) on the other. The listed characters are, however, either quite unspecific ("P5 male with 2 or less setae"), or they are plesiomorphic characters and thus unsuitable to characterise a taxon: "male A1 chirocerate, Md coxa-basis with 4 setae, male P5benp with 2 or less setae" for the Pseudotachidiinae and Donsiellinae, and "male P5benp as a rule with 3 setae, male A1 haplocer, Md coxa-basis with 3 remaining setae" for the 3 remaining subfamilies. Nevertheless, the descriptions and the discussion show, that the strongly specialised Donsiellinae indeed share characteristic autapomorphies with the Pseudotachidiidae, e.g. apophysis on the male P3enp2 **123**, shape of the male P2enp **120**, of the female P5 **104**, divided anal somite **126**, etc., and can therefore be assigned to this taxon.

A quite detailed revision of the Rhynchothalestrinae, together with a description of a new monotypic family Hamondiidae was made by Huys (1990). The genus *Rhynchothalestris* can be divided into 2 species-groups. One of these shows autapomorphic agreement with the Hamondiidae and is given the status of a new family, Ambunguipedidae Huys, 1990. The taxon Hamondiidae/Ambunguipedidae is well supported by 6 apomorphic characters stated by Huys. Huys emphasises the numerous differences between this taxon and *Rhynchothalestris*, which he regards as counter-evidence against a closer relationship of both groups. However, these differences are only autapomorphies of the respective taxa and do not necessarily exclude a phylogenetic relationship between them. In the present study at least 3 autapomorphies have been found to justify the unification of the taxa in question to a family Rhynchothalestridae (**70**, **88** + **109**, see chapters 4 + 7). In his discussion on the relation of the Rhynchothalestrinae with the other thalestrid subfamilies sensu Lang, Huys recognised a transformation series within the different sexually dimorphic male P2 endopods. He considered the P2 of Thalestrinae (type 4 in fig. 69) to be the most primitive form, from which that of the Dactylopusiinae has been derived by fusion of setae 1 + 2 (compare figs. 69, 72, 74), and which in turn is further modified by the loss of setae in *Paradactylopodia* (compare fig. 72). Huys also argued that the P2 of the Rhynchothalestrinae is not homologous with these forms and considered the Thalestrinae and Dactylopusiinae to be much more closely related to each other than to any other subfamily within the Thalestridae sensu Lang. A further argument is the presence of a sexually dimorphic inner basal spine on male P1 in the Thalestrinae/Dactylopusiinae, but not in the Rhynchothalestrinae.

However, in the present study it could be shown that the male P2enp of the Thalestrinae and Dactylopusiinae, respectively, are not homologous either, for there are different setae involved in the modification and instead of a fusion of setae 1 + 2, a loss of seta 2 has taken place during the final moult from male CV to the adult (chapter 6.11.1 and figs. 69, 71-75). Therefore, contrary to Huys′ view, the different types of male P2 are autapomorphies for *Rhynchothalestris/Ambunguipes/Hamondia* (= Rhynchothalestridae of the new system), for the Dactylopusiidae, and Thalestridae/Diosaccidae (=Thalestrioidea), respectively (fig. 69). The presence of a sexually dimorphic inner basal spine on male P1 is no "novel character", but probably an "old" character of the Podogennonta, because it occurs in many subtaxa of the latter (compare chapter 7.3). During this study it could be observed in *Parastenhelia* spec., several Thalestrinae, Dactylopusiidae (see material and methods), and Diosaccinae (e.g. *Robertgurneya*, *Amphiascopsis*, *Amonardia*), as well as outside the Thalestridimorpha in Pseudotachidiidae gen. 1 and Ameiridae. In the literature it is described for the Darcythompsoniidae (Huys et al, 1996) and Metidae (Lang, 1948). Therefore a sexually dimorphic basal spine on P1 is interpreted here rather as a symplesiomorphic phenomenon for Thalestrinae and Dactylopusiidae.

Huys & Böttger-Schnack (1994) published an extensive revision of Miraciidae with very detailed redescriptions of all 4 species known up to now and proposed a new system. For the Miraciidae as a whole no autapomorphy was listed.

Hosfeld (1997) studied the ultrastructure of various harpacticoid species for the first time. This investigation is very promising but a larger data base would be necessary for pertinent phylogenetic conclusions. The results can be summarised as follows:

- The male genital system is a promising character complex, however, there are not many data available as yet.

- In 3 examined species of the Diosaccinae the testes are displaced into the urosome and a strong enlargement and increased complexity of the gonad was observed (= potential autapomorphy of the Diosaccinae or Diosaccidae?).
- The harpacticoid spermatophores studied are morphologically so variable that conclusions about phylogenetic relationships are not possible.
- The investigation of the ultrastructure of the spermatozoa revealed two elongated successively arranged mitochondria in Thalestridae (2 species of the Thalestrinae had been examined) and also in Diosaccinae, which could be an autapomorphy of the Thalestrioidea.
- Two species of the Diosaccinae agreed in sperm ultrastructure.
- For the analysis of position and distribution of podocytes for phylogenetic purposes, more species of Harpacticoida have to be investigated.

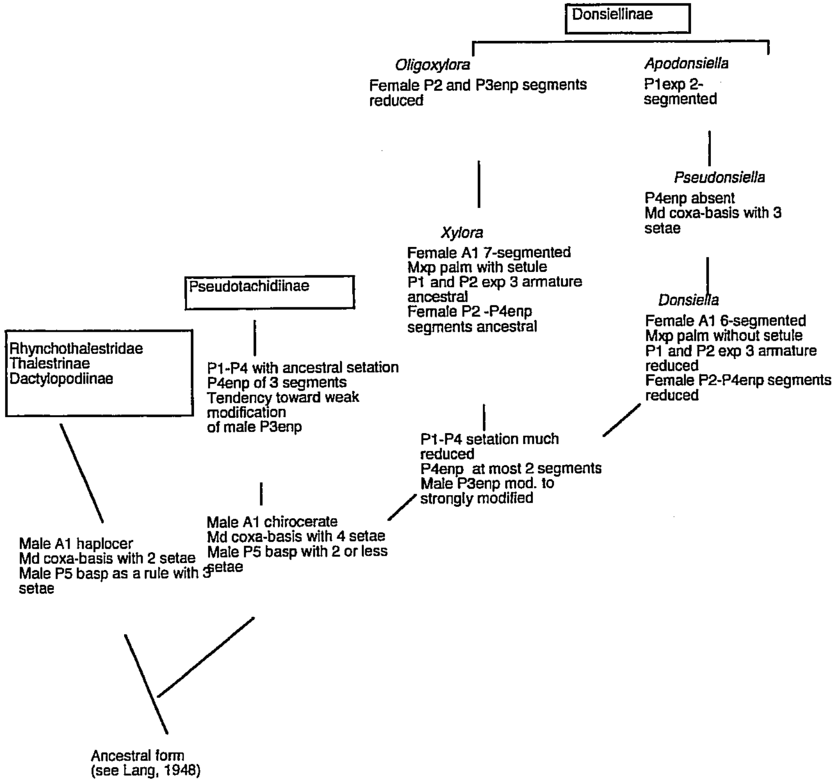


Fig. 83: Relationships within the Thalestridae after Hicks, 1988.

10. Postembryonic development

Detailed descriptions of complete series and single stages of nauplii of several taxa of Harpacticoida have been published by Dahms (1987, 1990a + b, 1993a). These data give first insights into general patterns of larval development on different systematic levels. Some phylogenetic interpretations of these data (Dahms, 1990a) speak in favour of hypotheses presented here, others do not.

Part of the material investigated by Dahms (NI of *Thalestris longimana*, NI of *Parathalestris harpactoides*, 3 NII of *Diarthrodes nobilis* and an unknown Thalestridae (identified by Dahms as *Thalestris brunnea*) as well as the complete nauplius series of *Parastenhelia megarostrum* have kindly been made available by him for re-examination.

The following characters are in accordance with the system presented here (compare chapter 4 + 7) (after Dahms and own examinations):

- A foreshortened shape of the nauplii appears to be restricted to taxa, which belong to the Thalestrioidea (Thalestrinae, Stenheliinae, Diosaccinae). In Diosaccinae and Stenheliinae (*Stenhelia palustris* and *Pseudostenhelia wellsi*), as representatives of Diosaccidae, an inability to swim and sideways locomotion are further specialisations. The exceptional position of *Amonardia* and *Amphiascopsis* within Diosaccinae, with plesiomorphic elongated body shape of the nauplius and several autapomorphies can also be confirmed by adult characters, while the assignment to the Diosaccinae is out of question (maxillar coxal endite with homologous seta missing **71**, characteristic "Nebendornen" and "Chitinzapfen" on the male P1 basis **122**).

- *Diarthrodes nobilis* (Dactylopusiidae, ex-Thalestridae) shows the plesiomorphic elongated body shape besides several autapomorpic features.

- Two groups of nauplii can be distinguished within the Thalestridae sensu Lang, 1948. The Pseudotachidiinae (with *Pseudotachidiius* spec. and *Idomene* spec. as species examined by Dahms, 1990a) and the remaining Thalestridae differ in the following characters (Pseudotachidiinae/Thalestridae): A2exp 3-5-segmented /2-segmented; Mdexp 2-segmented/1-segmented; A1 3-segmented/1-segmented. This is in accordance with the separation of the Pseudotachidiinae from the Thalestridimorpha in the system proposed here.

- The Mdexp of *Dactylopusioides macrolabris* is 1-segmented with 4 setae, the 3 distal ones being elongated, as in *Diarthrodes cystoecus* and *D. nobilis*. All these 3 taxa can be placed into the Dactylopusiidae. The high number of A2exp-segments in the examined Pseudotachidiinae (3-4 in *Idomene* spec. and even 5 in *Pseudotachidius* spec., which is the maximal number within the Oligoarthra) is in agreement with the position of the Pseudotachidiidae at the basis of the Podogennonta, which is also confirmed by adult characters (e.g. Mdenp setation, P1 setation, A2enp setation).

- Both examined species of *Parathalestris* as well as *Thalestris longimana* share a number of naupliar apomorphies (Dahms, 1990a), supporting their unification in the Thalestrinae.

- The naupliar morphology of *Parastenhelia megarostrum*, which has been examined during this study, confirms the position of the Parastenheliidae at the basis of the Thalestridimorpha. They show a 4-segmented A2exp (being still 3-segmented at NI) with 2-1-1-4 setae, a 3-segmented A1 and a 3-segmented Mdexp with 2-1-2 setae, which are the most plesiomorphic states found in the species of Podogennonta investigated up to now, and which can still be regarded as primitive within the Oligoarthra. All examined representatives of the Thalestridimorpha show much less setae and segments on the above-mentioned appendages (compare Dahms, 1990).

The following results on the other hand are in need of a discussion:

1. In *Zaus spinatus*, *Harpacticus uniremis* and *H. obscurus* (but not in *Tigriopus brevicornis*; all above-mentioned species belong to the Harpacticidae) as well as *Parathalestris harpactoides* and "*Thalestris brunnea*" (Thalestridae sensu lang, 1948) and "the Diosaccidae" (however, no actual examples are listed in Dahms, 1990a) the innermost of the 4 antennal basal setae in NI and NII is modified to support the masticatory function. This seta is replaced at the NIII stage by a newly developed seta on the gnathobase, which is modified in exactly the same way. The originally modified seta is transformed at the NIII stage to a "normal" seta again. This quite specialised phenomenon suggests a phylogenetic connection between the Thalestridae sensu Lang and the Harpacticidae.
2. Another indication for such a connection is the presence of a strong single spine on the inner projection of the Mdenp in the investigated Thalestridae sensu Lang as well as in the Harpacticidae. A single spine is a derived state compared with the presence of 2 or more spines (e.g. in *Phyllognathopus viguieri*, *Scutellidium hypolytes*, *Tachidius discipes*, *Paramphiascella fulvofasciata* (Diosaccinae)). The same character is listed by Dahms (1990) also as a common character of the Thalestridae sensu Lang. It can also be observed in the Miraciinae and Metidae, which have been placed by Lang into the Thalestridimorpha or in their proximity.

3. All nauplii of Thalestridae sensu Lang investigated by Dahms, except the Pseudotachidiinae, show an only 1-segmented antennule as a potential autapomorphy.
4. The foreshortened shape of all naupliar stages, connected with an inability to swim and with sideways locomotion, is restricted to the Diosaccinae and Stenheliinae. Subtaxa of the latter with a "normal" elongated shape are the genera *Amphiascopsis* and *Amonardia* within the Diosaccinae and Miraciinae. The Miraciinae are highly specialised and adapted to a pelagic life style. These results would be an argument that the Stenheliinae arose within Diosaccinae instead being the sistergroup of a taxon Diosaccinae/Miraciinae. Dahms & Bresciani (1993) interpret the numerous autapomorphies of Stenheliinae as an argument for their exclusion from Diosaccidae sensu Lang. However, a highly derived morphology does not necessarily speak against phylogenetic relationships.
5. Further common naupliar characters of Thalestridae and Harpacticidae are the elongated distal seta on antennule segment 2 (which is, however, also present in representatives of Tisbinae), a strongly serrated gnathobase, 2 fused setae on Mdexp in *Harpacticus uniremis, Zaus spinatus* and *Parathalestris harpactoides* (the latter character is also found in Tisbinae).
6. In Dahms′ view the affinity of the Metidae to the Thalestridimorpha is confirmed by the presence of a single spine on the "inner" Mdenp (see 2.) and the morphological similarity with the nauplii of *Diarthrodes* (Thalestridae sensu Lang), as there are a funnel shaped mouth, an elongated Md protopodite with insertion of the coxal seta behind the labral margin, a 1-segmented Mdexp.

To

1. The presence of the modified "replacement seta" was observed in the course of this study in the nauplius of *Parathalestris harpactoides* (as it had already been described by Dahms) and the single NIII, which has been determined as *Thalestris brunnea*, but not in *Diarthrodes nobilis*, *Parastenhelia megarostrum*, and *Thalestris longimana*. For the

Diosaccinae this phenomenon is not described in any of the publications of Dahms, and no actual example is given by him. Therefore it is maybe restricted to the Thalestrinae only. The analysis of the adult characters (see chapters 4 + 7) speaks against a direct phylogenetic relationship with the Harpacticidae. The Thalestrinae are more closely related to the other taxa of Thalestridimorpha, in which this setal replacement could not be observed up to now. The Harpacticidae undoubtedly have to be removed from Tachidiidimorpha and assigned to Podogennonta (shape of P1, Mxl, Mx), but there is no evidence for a closer relationship of Harpacticidae and Thalestridimorpha so far. Therefore the presence of the modified "replacement seta" in the nauplius has to be interpreted either as convergence or maybe as a plesiomorphy. Since it is only known from 2 taxa (Harpacticidae, Thalestrinae) up to now, the latter seems to be rather unlikely.

2. There are indications of an independent development of the single spine on the "inner" Mdenp in the taxa mentioned above. During a re-examination of *Diarthrodes nobilis*, 2 more, however, not explicitly spine-like setae were observed. In NI of the strongly derived species *Metis ignea* (Dahms, 1990, fig. 16A) outer and inner part of the Mdenp are fused, leaving the exact homology of the spine, which occurs together with an additional seta, unclear. In Miraciinae the Md and also other appendages are strongly reduced because of the adaptation to a pelagic substrate (Cyanobacteria). The same is true for *Pseudotachidius* spec. (Dahms, 1990a, fig. 15A) being a lecithotrophic nauplius. Further arguments can be deduced from the adult morphology (see chapters 4 + 7). The Thalestrinae, for which the single spine on Mdenp of the nauplius indeed may be an autapomorphy, belong without doubt to the Thalestrioidea, which show the plesiomorphic state with at least 2 spines in their groundpattern (*Paramphiascella fulvofasciata*, Diosaccinae, description of Dahms, 1990a). The Pseudotachidiidae as well as the Harpacticidae cannot be placed into Thalestridimorpha. The nauplii of *Parastenhelia megarostrum* –the Parastenheliidae take in a position at the basis of the Thalestridimorpha in the new system- still show 2 spines on Mdenp, which represents most likely also the condition in the groundpatterns of Thalestridimorpha, Thalestrioidea and Dactylopusiidae. For the more primitive Rhynchothalestridae no data on the naupliar development are available as yet.

3. In all available nauplii specimens of *Diarthrodes nobilis* a 2-segmented antennule was observed, in contrast to Dahms (1990a), who described an only 1-segmented A1. *Diarthrodes* belongs to the Dactylopusiidae, which in the new system have been removed from the Thalestridae. *Parastenhelia megarostrum*, occupying a position at the base of the Thalestridimorpha, possesses a 3-segmented antennule. A 1-segmented antennule is therefore only an autapomorphy of the Thalestrinae (no data are available for *Eudactylopus*).
5. The additional common naupliar characters of the Thalestridae and Harpacticidae mentioned by Dahms (1990) also occur in several species of the not closely related Tisbidae. A "strongly dentate" gnathobase of the Md is used as character for the Thalestridae and at the same time for uniting the Tachidiidae and Harpacticidae. Dahms himself also observed a remarkable variability in the morphology of the mandibular gnathobase even on a lower taxonomic level, which is interpreted as an adaptation to the different food preferences of the respective nauplii.
6. Because of their adult morphology (chapter 7.3), the Metidae most probably cannot be placed near Thalestridimorpha.

The knowledge of naupliar morphology of the Harpacticoida is still very incomplete. For the analysis of adult characters a much broader data basis is available which makes the results more reliable. This point of view is also shared by Dahms, Lorenzen & Schminke (1991), who obtained incongruent results when analysing phylogenetic relationships within the genus *Tisbe*, using both adult and naupliar characters.

11. Taxonomy of the new system

11.1 List of taxa

Pseudotachidiidae Lang, 1936
Paranannopinae Por, 1986
Paranannopus Lang, 1936
Cylindronannopus Coull, 1973
Danielssenia Boeck, 1872
Jonesiella Brady, 1880
Psammis Sars, 1910
Carolinicola Huys & Thistle, 1989
Leptotachidia Becker, 1974
Micropsammis Mielke, 1975
Fladenia Gee & Huys, 1990
Telopsammis Gee & Huys, 1991
Archisenia Huys & Gee, 1993
Bathypsammis Huys & Gee, 1993
Mucrosenia Huys & Gee, 1994
Sentiropsis Huys & Gee, 1996
Peltisenia Huys & Gee, 1996
Afrosenia Huys & Gee, 1996
Prionos Huys & Gee, 1996
Anapophysia Huys & Gee, 1996
Paradanielssenia Soyer, 1970
Pseudomesochrinae Willen, 1996
Pseudomesochra T. Scott, 1902
Donsiellinae Lang, 1944
Donsiella Stephensen, 1936
Pseudonsiella Hicks, 1988
Apodonsiella Hicks, 1988
Xylora Hicks, 1988
Oligoxylora Hicks, 1988
„Pseudotachidiinae"
Pseudotachidius T. Scott, 1898 (1897?)
Idomene Philippi, 1843
Dactylopodella Sars, 1905

Parastenheliidae Lang, 1944
Parastenhelia Thompson & A. Scott, 1903
Karllangia Noodt, 1964

Dactylopusiidae Lang, 1936
Dactylopusia Norman, 1903
Diarthrodes Thomson, 1882
Paradactylopodia Lang, 1944
Dactylopusioides Brian, 1928

Sewellia Lang, 1965
Dactylopodopsis Sars, 1911

Rhynchothalestridae Lang, 1948
Rhynchothalestris Sars, 1905
Pelthestris Monard, 1924
Ambunguipes Huys, 1990
Lucayostratiotes Huys, 1990
Hamondia Huys, 1990

Thalestridae Sars, 1905
Thalestrinae Sars, 1905
Thalestris Claus, 1863
Amenophia Boeck, 1865
Parathalestris Brady & Robertson, 1873
Phyllothalestris Sars, 1905
Paramenophia Lang, 1954
Eudactylopusiinae subfam. nov.
Eudactylopus A. Scott, 1909
Neodactylopus Nicholls, 1945

Diosaccidae Sars, 1906
Diosaccinae Sars, 1906
Diosaccus Boeck, 1872
Antiboreodiosaccus Lang, 1944
Pseudodiosaccopsis Lang, 1944
Robertsonia Brady, 1880
Amphiascus Sars, 1905
Amphiascopsis Gurney, 1927
Amonardia Lang, 1944
Pseudamphiascopsis Lang, 1944
Metamphiascopsis Lang, 1944
Paramphiascopsis Lang, 1944
Bulbamphiascus Lang, 1944
Robertgurneya Lang, 1944
Typhlamphiascus Lang, 1944
Rhyncholagena Lang, 1944
Amphiascoides Nicholls, 1941
Paramphiascella Lang, 1944
Haloschizopera Lang, 1944
Schizopera Sars, 1905
Eoschizopera Apostolov, 1982
Ialysus Brian, 1927
Teissierella Monard, 1935
Parialysus Nicholls, 1941
Psammotopa Pennak, 1942

  - *Pholenota* Vervoort, 1964
  - *Paramphiascoides* Wells, 1967
  - *Actopsyllus* Wells, 1967
  - *Schizoperoides* Por, 1968
  - *Protopsammotopa* Geddes, 1968
  - *Balucopsylla* Rao, 1972
  - *Helmutkunzia* Wells & Rao, 1976
  - *Miscegenus* Wells, Hicks & Coull, 1982
  - *Schizoperopsis* Apostolov, 1982
  - *Paradiosaccus* Lang, 1944
  - *Dactylopodamphiascopsis* Lang, 1944
  - *Pararobertsonia* Lang, 1944
  - *Tydemanella* A. Scott, 1909
  - *Pseudodiosaccus* T. Scott, 1906
  - *Diosaccopsis* Brian, 1925
- Stenheliinae Brady, 1880
  - *Stenhelia* Boeck, 1865
  - *Pseudostenhelia* Wells, 1967
  - *Cladorostrata* Shen & Tai, 1963
  - *Onychostenhelia* Itô, 1979
  - *Melima* Por, 1964
- Miraciinae Dana, 1846
  - *Miracia* Dana, 1846
  - *Oculosetella* Dahl, 1895
  - *Macrosetella* A. Scott, 1909
  - *Distioculus* Huys & Böttger-Schnack, 1994

Balaenophilidae Sars, 1910

- *Balaenophilus* P.O. Aurivillius, 1879

Genera incertae et incertae sedis

- *Flavia* Brady, 1899
- *Dactylopina* Brady, 1910
- *Mawsonella* Brady, 1918
- *Tisemus* Monard, 1928

11.2 Notes on the changes of the taxonomy

There are many characters (compare chapters 4 + 7) clearly showing the Pseudotachidiidae to be monophyletic. Within the family some monophyletic subtaxa can already be identified, e.g. Paranannopinae/Pseudomesochrinae, Donsiellinae, or the "*Pseudotachidius*-lineage" as well as the taxa *Pseudotachidius* (compare Veit-Köhler & Willen, 1999) and *Idomene*. Several genera are provisionally unified as "Pseudotachidiinae" (compare chapter 11.1), for

which, however, no automorphies have yet been found. The Paranannopinae show the following autapomorphies: - segment 3 ("Oligoartha segment") of the male antennule without aesthetasc (fig. 21), - Mxenp 1-segmented with at most 4 setae (fig. 39), - spine like seta of pseudotachidiid groundpattern (fig. 44) at the distal lobe of the praecoxal endite missing, single seta of the proximal lobe enlarged (fig. 44), - P1enp2 + 3 of the pseudotachidiid groundpattern fused, 1 homologous seta missing on "enp3" (fig. 56), - P2enp2 of the male with an outer segmental projection (fig. 77). For Pseudomesochrinae no adult male has been described up to now (only the male CV of *Pseudomesochra meridianensis*, see Willen, 1996). Therefore, the male paranannopinine characters could not yet be verified for the Pseudomesochrinae. However, the remaining characters are shared with Paranannopinae, so that Pseudomesochrinae may eventually be synonymised with Paranannopinae, when male characters are known.

The "*Pseudotachidius* lineage" is characterised as follows: -female antennule with homologous setae modified (figs. 11 + 13), - P1exp3 with whole setation displaced terminad, exp3 itself shortened (fig. 55), - praecoxal apical spines of MxI strongly sclerotised and spread out (fig. 35), - P2-P4enp1 ornamented with spinule patch (fig. 60), - terminal outer spines of P2-P4exp3 furnished with strong spinules (fig. 60). The reconstruction of the relationships within the Pseudotachidiidae is beyond the scope of the present study and has to be done elsewhere. In the Weddell Sea samples unknown taxa have been found (e.g. Pseudotachidiidae gen. 1 + 2), which have to be taken into account. A summary of the present status of the Pseudotachidiidae is given by Willen (1999).

The genus *Karllangia* can easily be placed into the Parastenheliidae in view of their new diagnosis (see chapters 4, 5, 7) and has to be removed from the Ameiridae. Mielke (1994) already suggested such a relationship.

The recently established families Ambunguipedidae Huys, 1990 and the monotypic Hamondiidae Huys, 1990 have been reunited with Rhynchothalestridae, because new characters have been found for this taxon, which instead of remaining as a subfamily within the Thalestridae has been elevated to family rank.

Paramenophia is listed under the Dactylopusiinae (by mistake?) in Bodin's catalogue (1997), although Lang (1954), who established this genus, had assigned it to the Thalestrinae. A comparison of the descriptions (Gamô, 1969, Lang, 1954, George, 1993) and specimens of *Paramenophia chilensis* (which were kindly made available for study by K. George) with the newly established diagnosis of Thalestrinae (see chapters 4, 5, 7) showed that Lang was right.

Eudactylopus shares the male P2enp and other characters with Thalestrioidea and, within the latter, with Thalestrinae (chapters 4-7). This justifies their removal from the Dactylopusiinae sensu Lang.

The Dactylopusiidae themselves do not share any of the autapomorphies of the Thalestrioidea and therefore had to be removed from Thalestridae. They are placed as taxon of a higher rank near the basis of Thalestridimorpha (chapters 4-7).

Pseudomesochra had been removed from the Diosaccidae sensu Lang and placed into the Pseudotachidiidae, being closely related with the Paranannopinae (Willen, 1996). The genera *Stenhelia*, *Onychostenhelia*, *Pseudostenhelia*, and *Cladorostrata* are assigned to a common taxon Stenheliinae. The Miraciinae have been recognised as a subtaxon of Diosaccidae. There are several apomorphic characters supporting a taxon Diosaccidae, within which the subtaxa Diosaccinae, Stenheliinae, and Miraciinae can be identified (chapters 4-7). Most probably the Balaenophilidae also belong to the Diosaccidae (compare the description of *Balaenophilus unisetosus* of Vervoort & Tranter, 1961). They show the respective characters, in spite of a derived shape and setation of the appendages **9, 88**. Since no material was available for examination, the Balaenophilidae were omitted from the present study.

Dactylopusia peruana Becker, 1974 most probably neither belongs to the Thalestridimorpha nor even to the Podogennonta. P1exp3 carries an inner seta and the intercoxal sclerites lack the paired projections. Instead, the shape of the Mxp, the male P2enp, the female P5, P1enp, and the habitus described by Becker (1974) suggest a closer relationship with Idyanthinae (Tisbidae).

12. Summary

1. The monophyly of the Podogennonta Lang, 1948 (excluding the Paramesochridae) as superordinated taxon of the Thalestridimorpha can be confirmed by the special shape of P1, but also by mouthpart characters. The Pseudotachidiidae (which are elevated into family rank) can be clearly assigned to the Podogennonta mainly because of their shape of the P1.

2. Because of the P1 shape also the Harpacticidae (former members of the Exanechentera, Tachidiidimorpha after Lang, 1948) and Latiremidae are placed into the Podogennonta. Moreover, the Harpacticidae show the typical "double spinules" on the maxillule praecoxal arthrite. None of these basal podogennontan taxa, including the Pseudotachidiidae, are suitable candidates for a sistergroup position of the Thalestridimorpha

3. A possible common apomorphic character of the Thalestridimorpha and Tetragonicipitidae is the shape of the Mxenp. However, a "taxon II" can be recognised within the Podogennonta (compare fig. 82), to which not only the Thalestridimorpha, Tetragonicipitidae, and *Protolatiremus* belong, but also the "classic" family groups of Lang (1948) (Ameiridimorpha, Cletodidimorpha). Since the latter two superfamilies generally possess strongly derived mouthparts and *Protolatiremus* a strongly derived Mxenp, the above-mentioned apomorphic condition of the Mxenp is possibly already a groundpattern character of this more inclusive taxon.

4. The Paranannopinae show numerous common apomorphies with the Pseudotachidiidae (compare 14.) and are integrated into this family as monophyletic subtaxon. They clearly have to be assigned to the Podogennonta and not to the Tachidiidimorpha.

5. On the level of the Thalestridimorpha and their subtaxa as well as of the Pseudotachidiidae, Podogenonnta, and Oligoarthra to some extent groundpatterns of the mouthparts, antennules, and swimming legs are reconstructed.

6. After the exclusion of the Pseudotachidiidae from the Thalestridae sensu Lang (1948), the Thalestridimorpha can be characterised as monophylum.

7. Autapomorphic characters have been found for all newly established and/or already valid taxa mentioned in the following.

8. Several autapomorphies speak in favour of a monophyletic taxon Thalestrioidea, which has the following consequences for the system of the Thalestridimorpha:
   - the only subfamily of Lang left in the Thalestridae are the Thalestrinae. The Dactylopusiinae, except *Eudactylopus/Neodactylopus*, have to be placed outside the more inclusive taxon Thalestrioidea. By way of contrast, the genera *Eudactylopus* and *Neodactylopus* show autapomorphies of the Thalestrioidea. They form the sister taxon Eudactylopusiinae of the Thalestrinae within the Thalestridae.
   - The fourth thalestridan subfamily of Lang, the Rhynchothalestrinae, can not be placed into the Thalestrioidea, either.
   - The amended taxon Diosaccidae (see 9.) is the sister taxon of the Thalestridae within the Thalestrioidea.

9. Autapomorphies have been found, which unite the Diosaccinae, Miraciinae, and Stenheliinae as monophylum Diosaccidae. Within the Diosaccidae a sistergroup relation of the Diosaccinae and the morphologically strongly specialised Miraciinae is proposed. Both taxa together form again the sister group of the Stenheliinae, which contain the supraspecific taxa related to *Stenhelia* (i.e. *Onychostenhelia*, *Pseudostenhelia*, *Cladorostrata*, *Stenhelia*, *Melima*). Furthermore, the Balaenophilidae can probably be assigned to the Diosaccidae, although they are not included into the system before further examination.

10. The Rhynchothalestridae are elevated into family rank and form the sister taxon of the Thalestrioidea. The families Hamondiidae and Ambunguipedidae established by Huys in 1990, have been dissolved and unified with *Rhynchothalestris* in the Rhynchothalestridae.

11. On the basis of the Thalestridimorpha either the Dactylopusiidae or the Parastenheliidae are the possible candidates for a sistergroup position in relation to all other Thalestridimorpha. Both share setal reductions on homologous appendages convergently with subtaxa within the Thalestrioidea. However, the Parastenheliidae show such primitive character states in the shape of the male P2, the male and female P5 (also within the Oligoarthra) and in naupliar morphology, that they are considered the sistergroup of all other Thalestridimorpha, which show the respective apomorphic state of these characters without exception.

12. The Thalestridimorpha are relatively primitive representatives of the Podogennonta. During groundpattern reconstruction this fact, and the integration of the Harpacticidae and Pseudotachidiidae lead to the impression that the stem species of the Podogennonta in many aspects was a quite primitive representative of the Oligoarthra.

13. A suitable candidate for the sistergroup position of the Thalestridimorpha is *Protolatiremus sakaguchii* Itô, 1974. This species also shows at least a slightly elongated P1exp2 as well as modified setae on the male P2enp3, which is, however, still 3-segmented.

14. The internal phylogenetic relationships within the Pseudotachidiidae still need a further analysis. The Paranannopinae, *Idomene* (excluding the species which belong to the new genera mentioned below) and *Pseudotachidius* have been characterised as monophyla so far. Furthermore, a "*Pseudotachidius* lineage" can be distinguished consisting of 2 newly identified taxa from the Weddell Sea and *Pseudotachidius*. Maybe this lineage together with *Idomene* ("Pseudotachidiinae") represents the sister group of the Parannopinae. However, no synapomorphies have been found so far. *Dactylopodopsis* and *Dactylopodella* are in need of a revision. *Dactylopodella incerta* Vervoort, 1964 is assigned to *Paradactylopodia* (Dactylopusiidae).

15. A hypothesis on the homology of the "prehensile" maxilliped in the Podogennonta and representatives of the Tisbidae is developed.

16. It is shown, that the ontogenetic development of the female oligorarthran antennule is delayed in such a way that the adult stage retains a copepodite morphology. This is considered as an autapomorphy of the Oligoarthra. It is therefore hypothesised that the oligoarthran female antennule does not represent the groundpattern of the Harpacticoida.

17. The morphological types subchirocer, chirocer, and haplocer of the male antennule established by Lang (1948) are redefined. They are only descriptions of actual, derived (or plesiomorphic in the case of the haplocer antennule) states, but first of all are not indicative of a phylogenetic relationship. There are still additional derived, taxon-dependent states, which cannot be assigned to any of the above-mentioned morphotypes.

18. The shape of the male oligoarthran antennule is not independent of the "taxonomic level", as postulated by Huys & Boxshall (1991), but, on the contrary, is a suitable character complex to identify taxa.

19. The ancestral harpacticoid male antennule proposed by Huys & Boxshall (1991) in fact represents only the groundpattern of the Thalestridimorpha or, slightly amended, the groundpattern of the Oligoarthra. By way of contrast, the male polyarthran antennule shows a fundamentally different morphological structure. If a common harpacticoid groundpattern exists, it would look still different from the one postulated by Huys & Boxshall.

13. References

Apostolov, A. (1975). Les Harpacticoides marins de la Mer Noire. Description de quelque formes nouvelles. Vie et Milieu, 25 (1-4): 165-178.

Ax, P. (1984). Das phylogenetische System. Gustav Fischer Verlag: 349 Seiten.

Ax, P. (1995). Das System der Metazoa I: Ein Lehrbuch der phylogenetischen Systematik. Gustav Fischer Verlag: 226 Seiten.

Ax, P. (1999). Das System der Metazoa II: Ein Lehrbuch der phylogenetischen Systematik. Gustav Fischer Verlag: 384 Seiten.

Becker, K.H. (1974). Eidonomie und Taxonomie abyssaler Harpacticoida (Crustacea, Copepoda). I. Cerviniidae-Ameiridae. „Meteor" Forschungsergebnisse, Deutschland 18: 1-28.

Bensien, M. (1998). Anatomischer Vergleich des weiblichen Genitaltrakts von *Tachidius discipes* Giesbrecht und *Robertgurneya similis* A. Scott (Copepoda: Harpacticoida). Diplomarbeit Carl von Ossietzky Universität Oldenburg: 1-163.

Bodin, P. (1997). Catalogue of the new marine Harpacticoid Copepods. Studiedocumenten van het Koninklijk Belgisch Instituut voor Natuurwetenschappen 89: 1-304.

Boeck, A. (1865). Oversigt over de ved Norges Kyster i agttagne Copepoder henhoerende til Calanidernes, Cyclopidernes og Harpactidernes Familier. Forhandlinger i Videnskabsselskabet i Kristiania 1864: 226-282.

Boeck, A. (1872). Nye slaegter og arter af Saltvands-Copepoder. Forhandlinger i Videnskabsselskabet i Kristiania 14: 35-60.

Boxshall, G., & Huys, R. (1998). The ontogeny and phylogeny of copepod antennules. Philosophical transactions 353: 765-768.

Boxshall, G., Ferrari, F. & Tiemann, H. (1984). The ancestral copepod: towards a consensus of opinion at the First International Conference on Copepoda 1981. Crustaceana (Suppl. 7): 68-84.

Bozic B. (1969). *Latiremus eximius*, n.gen, n. sp. à position systématique incertaine (Copépode Harpacticoide): données pour une nouvelle famille. Bulletin de la Societé zoologique de France 94/2: 309-316.

Brady, G.S. (1880). A monograph of the free and semi-parasitic Copepoda of the British Islands 2. The Ray Society: 1-182.

Brady, G.S. (1880). A monograph of the free and semi-parasitic Copepoda of the British Islands 3. The Ray Society: 1-83.

Canu, E. (1892). Les Copépodes du Boulonnais: morphologie, embryologie, taxonomie. Travaux de la Station zoologique de Wimereux 6: 1-292.

Chislenko, L.L. (1980). Three new harpacticoid species (Copepoda Harpactioida) from the coasts of the Kurile Islands. In: Korotkevitch, V.S. (Hrsg.). On the progress in taxonomy of marine invertebrates. Issledovanija fauny moreij 25/33: 77-88.

Cottarelli, V. (1971). *Delamarella galateae* n.sp., nuovo Harpacticoide di acque sotteranee littorali di Sardegna. Fragmenta Entomologica 7/4: 289-301.

Coull, B. (1976). A revised key to *Stenhelia* (*Delavalia*) (Copepoda: Harpacticoida) including a new species from South Carolina, USA. Zoological Journey of the Linnean Society 59/4: 353-364.

Dahms, H.U. (1987b). Postembryonic development of *Drescheriella glacialis* Dahms & Dieckmann (Copepoda, Harpacticoida) reared in the laboratory. Polar Biology 8: 81-93.

Dahms, H.U. (1988). Development of functional adaption to clasping behaviour in harpacticoid copepods (Copepoda, Harpacticoida). Hydrobiologia 167/168: 505-513.

Dahms, H.U. (1989). Antennule development during copepodite phase of some representatives of Harpacticoida (Copepoda, Harpacticoida). Bijdragen tot de Dierkunde 59/3: 159-189.

Dahms, H.U. (1990a). Naupliar development of Harpacticoida (Crustacea, Copepoda) and its significance for phylogenetic systematics. Microfauna Marina 6: 169-272.

Dahms, H.U. (1990b). The first nauplius and the copepodite stages of *Thalestris longimana* Claus, 1863 (Copepoda, Harpacticoida, Thalestridae) and their bearing on the reconstruction of phylogenetic relationships. Hydrobiologia 202: 33-60.

Dahms, H.U. (1992). Peltidiidae (Copepoda, Harpacticoida) from the Weddell Sea (Antarctica). Zoologica Scripta 21/2: 181-195.

Dahms, H.U. (1993a). Copepodid development in Harpacticoida. Microfauna Marina 8: 195-245.

Dahms, H.U. (1993b). Comparative copepodid development in Tisbidimorpha sensu Lang, 1948 (Copepoda, Harpacticoida) and its bearing on phylogenetic considerations. Hydrobiologia 250: 15-37.

Dahms, H.U. & Bresciani, J. (1993). Naupliar development of *Stenhelia (D.) palustris* (Copepoda, Harpacticoida). Ophelia 37/2: 101-116.

Dahms, H.U. & Dieckmann, G.S. (1987a). *Drescheriella glacialis* gen. nov., sp. nov. (Copepoda, Harpacticoida) from Antarctic Sea Ice. Polar Biology 7: 329-337.

Dahms, H.U. & Schminke, H.K. (1992). Sea ice inhabiting Harpacticoida (Crustacea, Copepoda) of the Weddell Sea (Antarctica). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Biologie 62: 91-123.

Dahms, H.U., Lorenzen, S. & H.K. Schminke (1991). Phylogenetic relationships within the taxon *Tisbe* (Copepoda, Harpacticoida) as evidenced by naupliar characters. Zeitschrift für Systematik und Evolutionsforschung 29/5-6: 450-465.

Dinet, A. (1974). Espèces nouvelles de Copépodes Harpacticoides (Crustacea) des sédiments profonds de la dorsale de Walvis. Archives de Zoologie Experimentale et Generale 115/4: 549-576.

Drzycimski, I. (1968). Drei neue Harpacticoida aus Westnorwegen. Sarsia 36: 55-64.

Faith, D.P. (1994). Phylogenetic pattern and the quantification of organismal biodiversity. Philosophical Transactions of the Royal Society of London B Biological Sciences 345: 45-58.

Fiers, F. (1982). New Canuellidae from the northern coast of Papuae New Guinea (Copepoda: Harpacticoida). Bulletin de l' Institut Royal des Sciences naturelles de Belgique Biologie 54/4: 1-32.

Fiers, F. (1990). *Abscondicola humesi* gen.n., sp.n. from the gill chambers of land crabs and the definition of the Cancrincolidae fam.n. (Cop.Harp.). Bulletin de l' Institut Royal des Sciences naturelles de Belgique Biologie 60: 69-103.

Fiers, F. (1992). *Metis reducta* n.sp. and *Laubieria tercera* n.sp. (Harpacticoida, Metidae) from the southern coast of Papuae, New-Guinea. Belgian Journal of Zoology 122/1: 37-51.

Fiers, F. (1995): New Tetragonicipitidae (Copepoda, Harpacticoida) from the Yucatecan continental shelf (Mexico), including a revision of the genus *Diagoniceps* Willey. Bulletin de l'Institut Royale des Sciences Naturelles de Belgique 65: 151-236.

Gamô, S. (1969). Further notes on *Paramenophia platysoma* (Thompson & A. Scott) (= *Dactylopusia platysoma* Thompson & A. Scott), harpacticoid Copepoda from Tanabe Bay, Kii Peninsula. Proceedings of the Japanese Society of Systematic Zoology 5: 19-22.

Gaston, K.J. (Hrsg.) (1996): Biodiversity.-Blackwell Science, Oxford: 1-396.

Geddes, D.C. (1969). Marine biological investigations in the Bahamas. 9. Harpacticoid copepods belonging to the family Thalestridae. Sarsia 39: 1-16.

Gee, J.M & Huys, R. (1990). The rediscovery of *Danielssenia intermedia* Wells, 1965 (Copepoda, Harpacticoida): a missing link between the "danielssenid" genera and *Paranannopus* Lang, 1936 (Paranannopidae). Journal of Natural History, 24: 1549-1571.

Gee, J.M & Huys, R. (1994). Paranannopidae (Copepoda: Harpacticoida) from sublittoral soft sediments in Spitsbergen. Journal of Natural History 28: 1007-1046.

Gee, J.M. & Huys, R. (1991). A review of Paranannopidae with claviform aesthetascs on oral appendages. Journal of Natural History 25: 1135-1169.

George, K. (1993). Harpacticoida (Crustacea, Copepoda) aus Chile und der Antarktis unter besonderer Berücksichtigung der Ancorabolidae. Diplomarbeit, Carl von Ossietzky Universität Oldenburg: 129 Seiten.

Giesbrecht, W. (1902). Resultats du voyage du S.Y. Belgica en 1897-1898-1899. Rapports Scientifiques, Publés aux frais du gouvernement Belge, sous la direction de la commission de la Belgica Vol. 8 (5) Zoologie, Copepoden. 7: 1-72.

Hamond, R. (1973). Four new copepods (Crustacea: Harpacticoida: Canuellidae) simultaneously occuring with *Dogenes senex* (Crustacea: Paguridea) near Sydney. Proceedings of the Linnean Society New South Wales 97/3: 165-201.

Hennig, W. (1966): Phylogenetic Systematics. University of Illinois press, Urbana: 263 Seiten.

Hennig, W. (1982): Phylogenetische Systematik. Verlag Paul Parey: 246 Seiten.

Hicks, G. R. F. (1988). Systematics of the Donsiellinae Lang (Copepoda, Harpacticoida). Journal of Natural History 22: 639-684.

Hicks, G.R.F. (1989). Harpacticoid copepods from biogenic substrata in offshore waters of New Zealand. 2. Partial revisions of *Dactylopodella* Sars and *Amphiascus* Sars (*varians*-group) including new species, and a new record for *Harrietella simulans* (T.Scott). National Museum of New Zealand Records 3/10: 101-117.

Hosfeld, B. (1997). Beiträge der vergleichenden Anatomie zur Stammesgeschichtsforschung der Harpacticoida (Crustacea, Copepoda). Dissertation, Carl v. Ossietzky Universität Oldenburg: 270 Seiten.

Humes, A.G. (1994). How many Copepods? In: Ferrari, F.D. und Bradley, B.P. (Hrsg.). Ecology and Morphology of Copepods. Hydrobiologia 292/293: 1-7.

Huys, R. (1987). *Paramesochra* T. Scott, 1892 (Copepoda, Harpacticoida): a revised key, including a new species from the SW Dutch coast and some remarks on the phylogeny of the Paramesochridae. Hydrobiologia 144: 193-210.

Huys, R. (1988). Sexual dimorphism in aegisthid cephalosomic appendages (Copepoda, Harpacticoida): a reappraisal. Bijdragen tot de Dierkunde 58 (1): 114-136.

Huys, R. (1990). A new family of harpacticoid copepods and an analysis of the phylogenetic relationships within the Laophontoidea T.Scott. Bijdragen tot de Dierkunde 60 (2): 79-120.

Huys, R. (1990). A new harpacticoid copepod family collected from Australian sponges and the status of the subfamily Rhynchothalestrinae Lang. Zoological Journal of the Linnean Society 99: 51-115.

Huys, R. (1992). A revision of *Danielssenia perezi* Monard, *D. paraperezi* Soyer, *D. eastwardae* Coull (Harpacticoida; Paranannopidae) and their transfer to a new genus. Zoological Journal of the Linnean Society 104: 31-56.

Huys, R. (1995). A new genus of Canuellidae (Copepoda, Harpacticoida) associated with Atlantic bathyal sea-urchins. Zoologica Scripta 24/3: 225-243.

Huys, R. & Böttger-Schnack, R. (1994). Taxonomy, biology and phylogeny of Miraciidae (Copepoda, Harpacticoida). Sarsia 79/3: 207-283.

Huys, R. & Boxshall, G. (1991). Copepod Evolution. Ray Society, London: 468 Seiten.

Huys, R. & Gee, J.M. (1990). A revision of Thompsonulidae Lang, 1944 (Copepoda: Harpacticoida). Zoological Journal of the Linnean Society 99: 1-49.

Huys, R. & Gee, J.M. (1993). A revision of *Danielssenia* Boeck and *Psammis* Sars with the establishment of two new genera *Archisenia* and *Bathypsammis* (Harpacticoida: Paranannopidae). Bulletin of the Natural History Museum (Zoology) 59 (1): 45-81.

Huys, R. & Gee, J.M. (1996a). *Sentiropsis*, *Peltisenia* and *Afrosenia*: three new genera of Paranannopidae (Copepoda: Harpacticoida). Cahiers de Biologie Marine 37: 49-75.

Huys, R. & Gee, J.M. (1996b). *Prionos* gen.nov. from the meiofauna of a Malaysian mangrove forest and the status of *Psammis borealis* (Copepoda, Harpacticoida, Paranannopidae). Cahiers de Biologie Marine 37: 227-248.

Huys, R. & Willems, K.A. (1989). *Laophontopsis* Sars and the taxonomic concept of the Normanellinae (Copepoda: Harpacticoida): A revision. Bijdragen tot de Dierkunde 59 (4): 203-227.

Huys, R. et al. (1996). Marine and brackish water harpacticoid copepods. Part 1. In: Synopses of the British Fauna (New Series), DM. Kermack, R.S.K. Barnes & J.H. Crothers (Hrsg.), London: 352 Seiten.

Itô, T. (1970). Description and records of marine harpacticoid copepods from Hokkaido, III. Annotationes Zoologicae Japonenses 43/4: 211-218.

Itô, T. (1974). Description and records of marine harpacticoid copepods from Hokkaido, V. Journal of the Faculty of Science Hokkaido University Series VI Zoology 19/3: 546-640.

Itô, T. (1976). Description and records of marine harpacticoid copepods from Hokkaido, VI. Journal of the Faculty of Science Hokkaido University Series 20/3: 448-567.

Itô, T. (1980). Two species of the genus *Longipedia* Claus from Japan, with reference to the taxonomic status of *L. weberi* previously reported from Amakusa, southern Japan (Copepoda: Harpacticoida). Journal of Natural History 14: 17-32.

Itô, T. (1983). Harpacticoid copepods from the Pacific abyssal off Mindanao.II. Cerviniidae (cont.), Thalestridae and Ameiridae. Publications of Seto Marine Biological Laboratory 28 (1/4): 151-254.

Itô, T. & Kikuchi, Y. (1977). On the occurrence of *Harpacticella paradoxa* (Brehm) in Japan; a fresh-water copepod originally described from a chinese lake. Annotationes Zoologicae Japonenses. 50/1: 40-56.

Kitching, I.J. et al. (1998). Cladistics. The Theory and Practice of Parsimony Analysis. Oxford University Press: 228 Seiten.

Lang, K. (1935). Über Umfang und systematische Stellung einiger Harpacticidengenera. Kunglia Fysiografiska Saellskapets i Lund Foerhandlinger 5/21: 209-216.

Lang, K. (1936). Copepoda Harpacticoida. In: Bock, S. (Hrsg.): Further results of the Swedish Antarctic Expedition, 1901-1903. 3 (3): 1-68.

Lang, K. (1944). Monographie der Harpacticiden (Vorläufige Mitteilung). Almquist & Wiksells Boktryckeri A.B. (Uppsala): 1-39.

Lang, K. (1948). Monographie der Harpacticiden I und II. Reprint Otto Koeltz Science Publication, Koenigstein, West Germany: 1-1682.

Lang, K. (1954). Eine neue Harpacticidengattung und die systematische Stellung von *Dactylophusia platysoma* Thompson & A. Scott. Arkiv foer Zoologi 2/6: 597-601.

Lang, K. (1965). Copepoda Harpacticoidea from the Californian Pacific Coast. Kungliga Svenska vetenskapsakademiens handlingar, 10 (2), 1-560.

Maddison, W.P. & Maddison, D.R. (1992). MacClade: Analysis of phylogeny and character evolution. Version 3.0. Sinauer Associates, Sunderland, Massachusetts: 1-404.

Martinez Arbizu, P. & Moura, G. (1994). The phylogenetic position of the Cylindropsyllinae Sars (Copepoda, Harpacticoida) and the systematic status of the Leptopontiinae Lang. Zoologische Beiträge N. F. 35/1: 55-77.

Martinez Arbizu, P. & Moura, G. (1998). Atergopedidae, a new family of harpacticoid copepods (Crustacea) from oligotrophic Arctic Sediments. Zoologische Beiträge N. F. 38/2: 189-210.

Martinez Arbizu, P. & Seifried, S. (1996). The phylogenetic position of *Arctimisophria bathylaptevensis* gen. et sp. n. (Crustacea, Copepoda) a new misophrioid from hyperbenthic deep-sea waters in the Laptev Sea (Arctic Ocean). Sarsia 81: 285-295.

McMillan, G.J. (1989). Description of the life-history stages of *Amphiascus undosus* Lang (Copepoda, Harpacticoida). Canadian Journal of Zoology 69: 512-527.

Mielke, W. (1975). Systematik der Copepoda eines Sandstrandes der Nordseeinsel Sylt. Mikrofauna des Meeresbodens 52: 41-174.

Mielke, W. (1984). Interstitielle Fauna von Galapagos. XXXI. Paramesochridae (Harpacticoida). Microfauna Marina 1: 63-147.

Mielke, W. (1989a). Interstitielle Fauna von Galapagos. XXXVI. Tetragonicipitidae (Harpacticoida). Microfauna Marina 5: 95-172.

Mielke, W. (1989b). Interstitielle Fauna von Galapagos. XXXVII. Metidae (Harpacticoida). Microfauna Marina 5: 173-188.

Mielke, W. (1990). A *Parastenhelia* species from Bahia Lapataia, Ushuaia, Terra del Fuego (Argentina). Microfauna Marina 6: 157-167.

Mielke, W. (1994). Two co-occurring new *Karllangia*-species (Copepoda: Ameiridae) from the Caribbean coast of Costa Rica. Revista de Biologia Tropical 42 (1/2): 141-153.

Monard, A. (1927). Synopsis universalis gernerum Harpacticoidarum. Zoologische Jahrbücher 54: 139-176.

Monchenko, V.I. (1967). Über das Vorkommen von *Dactylopodia euryhalina* (Monard) in der Ostsee und Bemerkungen über ihre Morphologie und Synonymik (Crustacea, Harpacticoida). Academia Polaccadelle Science 15/2: 95-100.

Montagna, P.A. (1980). Two new bathyal species of *Pseudotachidius* (Copepoda: Harpacticoida) from the Beaufort Sea (Alaska, U.S.A). Journal of Natural History 14: 567-578.

Montagna, P.A. (1981). A new species and a new genus of Cerviniidae (Copepoda: Harpacticoida) from the Beaufort Sea, with a revision of the family. Proceedings of the Biological Society of Washington 93/4: 1204-1219.

Noodt, W. (1955). Marine Harpactcoiden (Crustacea Copepoda) aus dem Marmara Meer. Revue de la Faculté des Sciences de l'Université d'Istanbul 20 1-2: 49-94.

Pallares, R.E. (1970). Copepodos marinos de la ria Deseado (Santa Cruz, Argentina). Contribucion sistematico-ecologica. III. Physis 30/80: 255-282.

Pallares, R.E. (1975). Copepodos marinos de la ria Deseado (Santa Cruz, Argentina). Contribucion sistematico-ecologica. IV. Physis 34/88: 67-83.

Pallares, R.E. (1982). Copepodos harpacticoides de Tierra del Fuego (Argentina) IV. Bahia Thetis. Contributions Cientifica III. CIBIMA 186: 1-39.

Por, F.D. (1969). The Canuellidae in the waters around the Sinai peninsula and the probem of „Lessepsian“ migration of this family. Israel Journal of Zoology 18: 169-178.

Por, F.D. (1983). A note on two species of Canuellidae (Copepoda, Harpacticoida) from the Red Sea. Crustaceana 44/2: 187-197.

Por, F.D. (1986). A re-evaluation of the family Cletodidae Sars, Lang (Copepoda, Harpacticoida). In: Schriever, G. et al. (Hrsg.). Proceedings of the Second International Conference on Copepoda. Ottawa, Canada, 13.-17. August 1984. National Museums of Natural Sciences Ottawa 58: 420-425.

Sars, G.O (1903-1911). An Account of the Crustacea of Norway. Copepoda Harpacticoida. Parts 1-36. Bergen Museum 5: 1-443.

Sars, G.O (1906). An Account of the Crustacea of Norway. Copepoda Harpacticoida. Parts 11-16. Bergen Museum 5: 133-196.

Sars, G.O (1910). An Account of the Crustacea of Norway. Copepoda Harpacticoida. Parts 29-30. Bergen Museum 5: 337-368.

Sars, G.O (1919-1921). An Account of the Crustacea of Norway. Copepoda, supplement. Parts 1-10. Bergen Museum 7: 1-121.

Shen, C.J. & Tai, A.Y. (1963). On five new species, a new subgenus and a new genus of freshwater Copepoda (Harpacticoida) from the delta of the Pearl River, South China. Acta Zoologica Sinica 15/3: 417-432.

Soyer, J. (1971). Bionomie benthique du plateau continental de la côte catalane francaise. III. Les peuplement de Copépodes Harpacticoides (Crustacea). Vie et Milieu 21/2-B: 337-511.

Sudhaus, W. & Rehfeld, K. (1992). Einführung in die Phylogenetik und Systematik. Gustav Fischer Verlag: 241 Seiten.

Tiemann, H. (1984). Studies on Copepoda II. Is the taxon Harpacticoida a monophyletic one? Crustaceana Suppl. 7: 47-59.

Veit-Köhler G. & Willen E. (1999). *Pseudotachidius jubanyensis* (Copepoda: Harpacticoida): A new species from antarctic shallow waters and its ecology. Senckenbergiana maritima 30 (1/2): 27-45.

Vervoort, W. & Tranter, D. (1961). *Balaenophilus unisetus* P.O.C. Aurivillius (Copepoda, Harpacticoida) from the Southern Hemisphere. Crustaceana 3/1: 70-84.

Wägele, J.W. (1994). Review of methodological problems of „Computer cladistics“ exemplified with a case study on isopod phylogeny (Crustacea: Isopoda). Zeitschrift für Systematik und Evolutionsforschung 32: 81-107.

Warwick R.M. & Clarke K.R. (1998): Taxonomic distinctness and environmental assessment. Journal of Applied Ecology 35 (4): 532-543.

Wells, J.B.J. (1980). A revision of the genus *Longipedia* Claus (Crustacea: Copepoda: Harpacticoida). Zoological Journey of the Linnean Society 70: 103-189.

Wells, J.B.J. & Rao, G.C. (1987). Littoral Harpacticoida from Andaman and Nicobar Islands. Memoirs of the Zoological Survey of India 16 (4): 1-385.

Willen, E. (1995). *Archilaophonte maxima* gen.n., spec.n., a new taxon of Laophontidae (Copepoda, Harpacticoida) from the high Antarctic (Weddell Sea). Hydrobiologia 302 (2): 241-255.

Willen, E. (1996). *Pseudomesochra* T. Scott 1902 as a member of the Paranannopidae Por, 1986 (Copepoda, Harpacticoida) with a description of three new species. Senckenbergiana maritima 28: 81-109.

Willen, E. (1996). Two new genera of Laophontidae (Copepoda Harpacticoida) from the high Antarctic Weddell Sea. Journal of Natural History 30: 1297-1327.

Willen, E. (1999). Preliminary revision of the Pseudotachidiidae. Courier Forschungsinstitut Senckenberg 215: 221-225.

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