



Larval development of *Euphausia superba* Dana, 1852 and a phylogenetic analysis of the Euphausiacea

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Received 29 May 2000; in revised form 15 January 2001; accepted 7 February 2001

Key words: morphology, ontogeny, appendages, thelycum, photophores, autapomorphy, ground pattern

Abstract

Literature data and new investigations by SEM of selected ontogenetic stages of the Antarctic Krill, *Euphausia superba* Dana, 1852 revealed morphological characters that are either missing in, or significantly changed towards, the adult. Besides adult features, such ontogenetic characters enabled us to propose a hypothesis of the phylogenetic relationships of and within the Euphausiacea on the basis of a computer aided cladistic analysis. These are of the form (*Bentheuphausia amblyops* + Euphausiidae = ('*Thysanopoda*' + *Nematobranchion* + Euphausiinae = (*Meganyciphanes norvegica* + Euphausiini, new name + *Nematoscelini*, new name = (*Nyciphanes* + *Nematoscelina*, new name))). From this analysis the taxon names 'Euphausiina', 'Nematoscelini', and 'Nematoscelina' are introduced for in-groups of the taxon Euphausiacea as representing monophyletic units. The position of a set of ontogenetic characters remains relatively uncertain due to the still unknown larval development of *Bentheuphausia amblyops* (G. O. Sars, 1883).

Introduction

The eumalacostracan taxon Euphausiacea comprises approximately 90 exclusively marine and mostly planktonic species. Since no phylogenetic system has been presented yet, our aim was to search for structures that could strengthen hypotheses on phylogenetic relationships of and within the Euphausiacea. The major data sources of our study were (1) our own examinations of specimens of various larval stages of the Antarctic Krill, *Euphausia superba* Dana, 1852 (see Baker et al. 1990), using light microscopy and SEM, and (2) the available literature, providing ontogenetic and adult characters. It was not intended to prepare a complete morphological re-description of the larval development of *E. superba*, since this has been done in detail already by Fraser (1936). The usefulness or prospects of ontogenetic features for investigating systematic relationships within the Crustacea has been demonstrated variously for extant (e.g. Dahms 1991, 2000; Jensen et al. 1994; Walossek et al. 1996) and fossil Crustacea (e.g. Müller & Walossek 1988; Walossek 1993). Such characters

should fulfil at least the following criteria: (1) being well documented in the literature for as many species as possible; (2) showing prominent changes during ontogeny but remaining conservative in themselves, i.e. having little to no individual variability; (3) providing information and explanations for understanding adult morphological structures.

For our study of the Euphausiacea, we selected mainly the appendages since they are amongst the best-investigated and documented structures in this group, and in Crustacea in general. All previous studies of the larval development of euphausiids used exclusively light microscopy. We wished also to check if SEM, which in modern apparatuses provides digital pictures of structures that can directly be used for documentation, yields more detailed information of surface structures, such as, e.g. segment boundaries or joints. Since SEM-images are new for documenting details of Euphausiacea, we have not included drawings that are available in various articles (e.g. Fraser 1936; Knight 1975, 1976, 1980; Weigmann-Haass 1977; Mauchline 1980).

Materials and methods

The ontogeny of *Euphausia superba* starts, according to Fraser (1936), with two stages called Nauplius I, which is a true Orthonauplius, and Nauplius II plus a metanauplius stage. The next three instars are called Calyptopis I–III stages. The last part of the larval sequence, the Furcilia phase, consists of six stages. Subsequent instars (of unknown number) are called postlarvae or juveniles. Fraser (1936) has regarded the term ‘Cyrtopia’ of Sars (1885) as a later form of furciliae, thus being superfluous; this view is followed herein. The morphological terminology follows Fraser (1936) for euphausiaceans and Walossek (1993) for general crustacean morphology.

Seven developmental instars of *E. superba* were available for our investigation: Calyptopis I–III and Furcilia I–IV, and the adult. The Calyptopis larvae were kindly provided by Prof. Dr Krzysztof Jazdzewski, University of Lodz, Poland. They were caught during a cruise of the Polish research vessel ‘Professor Siedlecki’ in the Drake Passage at 61° 51' S and 58° 59' W with a Nansen-net (diameter 70 cm, mesh width 26 µm) on June 26th, 1981. They were stored in 95% ethanol for preservation. Eight specimens per instar were prepared for SEM. The Furcilia larvae were kindly provided by Dr Sigrid Schiel, Alfred-Wegener-Institute for Polar Research, Bremerhaven, Germany. These larvae were caught during a cruise of the German research vessel ‘Polarstern’ off Princess-Martha-Coast at 69° 49.8' S and 07° 19.9' W with a multi-net 4, on April 12th, 1992, and stored in 90% formalin. Eight specimens of the material of Furcilia I – III and one of Furcilia IV were prepared for SEM. The appendages of the specimens were isolated under a stereo microscope, critical point dried and documented by a Zeiss scanning electron microscope DSM 962.

Suitable of the recognised characters were encoded in a data matrix (Table 3, see Table 4 for list of all coded characters) using MacClade (Maddison & Maddison 1992) and were run in PAUP (Swofford 1990) with unordered characters. We got three trees of 24 steps and checked how the program optimised the autapomorphies. We rejected those trees with sister group relationship for which the program could not detect a definite autapomorphic character. This made the use of any consensus tree unnecessary. Eventually, we settled on a single tree that we considered to be the best assessment of the interrelationships within the Euphausiacea (Fig. 22).

Description and discussion of morphological characters

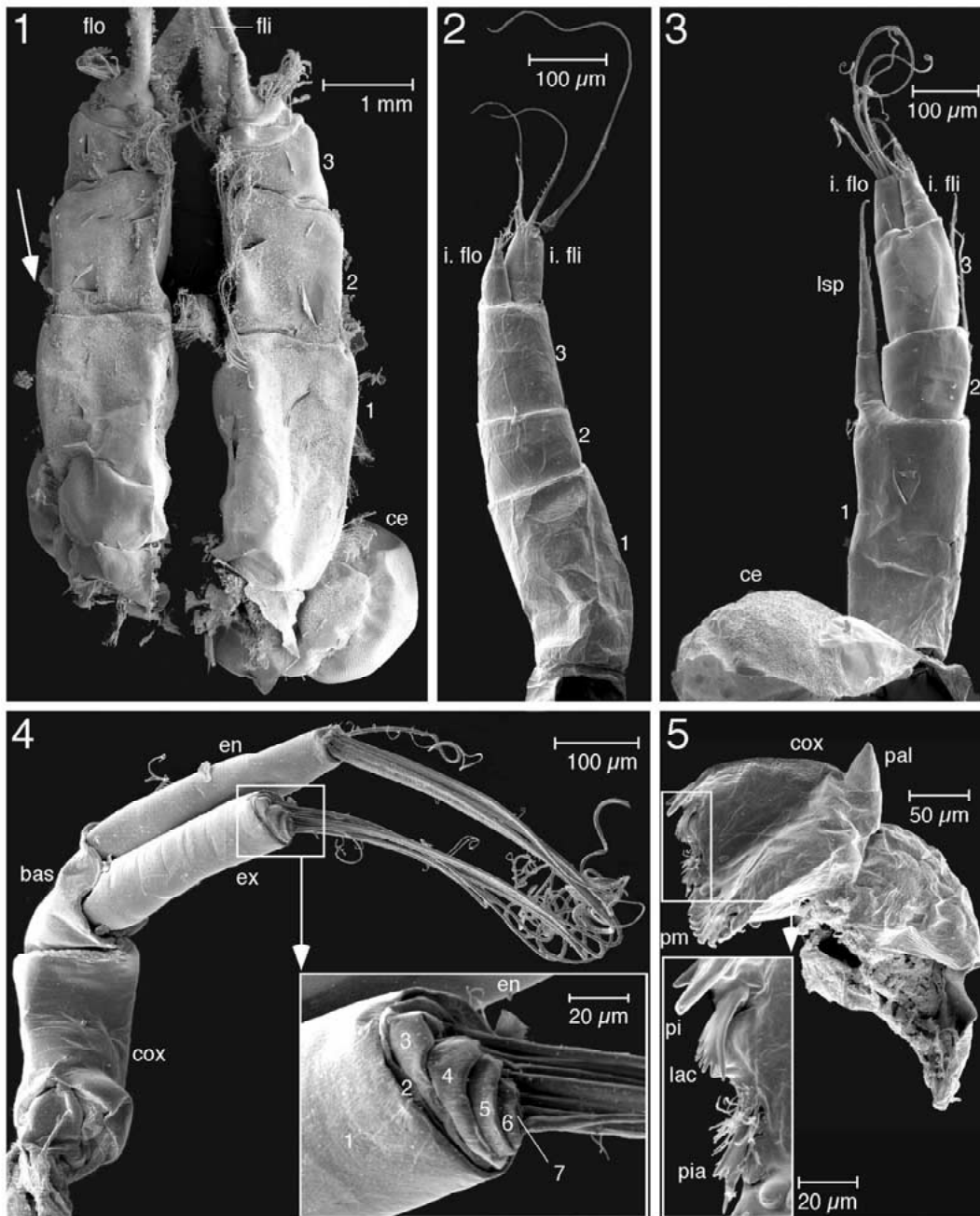
In the following, selected data from the larval development of *Euphausia superba*, completed by data from the literature are checked against other euphausiid species, providing the background for a phylogenetic analysis of the Euphausiacea including larval characters (Table 1). The Decapoda and Lophogastrida were chosen as the out-group. The Decapoda are traditionally seen as the sister group to euphausiaceans, both embraced in the Eucarida (the only clear synapomorphy is the carapace attached to 7 – not 8 – thoracomeres).

Antennula

The adult antennula of all Euphausiacea is antero-posteriorly flattened and held forwardly, parallel to the body. It consists of a peduncle with three divisions of the same thickness and two multi-annulated outgrowths, flagella, distally that are twice as long as the peduncle. The peduncle bears an excavation for the compound eyes at the anterior edge of its proximal portion. The outer flagellum is thickened at its base (Fig. 1 for *Euphausia superba*).

In the first Calyptopis of *E. superba*, the peduncle is still undivided, but we found some individuals anticipate already the tripartite condition of the subsequent stage. From Calyptopis II on, the peduncle always consists of three portions (Figs 1, 2 and 3), as in the adult. All portions are rod-shaped, and the shortest one in the middle carries one bristle medially. Subsequently more bristles are added gradually, especially along the inner margin of the ramus. The third peduncular portion bears two small conical, undivided outgrowths, the initial inner and outer flagella (Fig. 2). The initial flagella begin to grow out in the next stage to achieve their definite shape by Furcilia II. From Calyptopis III onwards, the proximal portion of the antennular peduncle is drawn out laterally into a spine, which is as long as the following two portions (Fig. 3). This spine persists, according to Fraser (1936), until Furcilia VI (Table 1, second column, Figs 1–3). It is assumed that its reduction occurs during postlarval development, which was not studied here; the spine is absent in the adult (Fig. 1; Table 1, see Fraser, 1936, Figs 23b, 25b, for Furciliae V and VI).

A lateral spine is also developed in larvae of *Thysanopoda tricuspidata* H. Milne-Edwards, 1837 (Knight 1973) and of *Euphausia hanseni* Zimmer,



Figures 1–5. **Figure 1.** Adult antennulae from the anterior. There is no trace of the larval lateral spine (arrow; numbers indicate the portions of the peduncle, abbreviations see Table 2).

Figure 2. Right antennula of *Calyptopis* II from the anterior.

Figure 3. Right antennula of *Calyptopis* III from the anterior.

Figure 4. Right antenna of *Calyptopis* III from lateral. High magnification of the tip of the exopod with its six distal annuli indicated by rectangle on lower right.

Figure 5. Right mandible of *Calyptopis* II from the anterior. The left mandible looks similar but lacks the *lacinia mobilis* (*lac*). The marked rectangular section with the *lacinia mobilis* and the *processus incisivus accessorius* (*pia*) is magnified below.

Table 1. Changes of larval characters during development of *Euphausia superba* (Character exists = +, Character is missing = -, ∞ = numerous, Character is missing because of lacking of the extremity etc. = 0). Data completed after Fraser (1936) for Furcilia V and VI

	Lateral spine at antennula	Part of the protopod of the complete length of the antenna	Right mandible with <i>Lacinia mobilis</i>	Number of setae on coxa of the maxillula	Number of setae on basipod of the maxillula	Number of endopod portions of the maxillula	Number of setae on the endopod of the maxillula	Part of the protopod of the complete length of thoracopod I	Part of the protopod of the complete length of thoracopod II – VI	Spine at protopod of the uropods	Complete number of spines on the hind body without laterocaudal spines
Nauplius I	-	60%	-	0	0	0	0	0	0	0	0
Nauplius II	-	60%	-	0	0	0	0	0	0	0	4
'Metanauplius'	-	60%	-	0	0	0	0	0	0	0	12
Calytopis I	-	60%	+	7	4	2	1	60%	0	0	12
Calytopis II	-	60%	+	7	5	2	1	60%	30–60%	0	13
Calytopis III	+	60%	+	7	5	2	1	60%	30%	+	13
Furcilia I	+	60%	+	8	7	2	1	60%	25%	+	13
Furcilia II	+	50%	+	8	7	2	1	50%	25%	+	13
Furcilia III	+	<50%	+	10	9	1	1	40%	25%	+	13
Furcilia IV	+	40%	+	10	9	1	2	30%	25%	+	11
Furcilia V	+	40%	+	>10	>9	1	9	30%	25%	-	9
Furcilia VI	+	40%	+	∞	∞	1	>10	25%	15%	-	7
Adultus	-	40%	-	∞	∞	1	∞	20%	15%	-	2

1915 (Weigmann-Haass 1977). As in *E. superba*, it appears in Calytopis III in both species and persists until the last Furcilia stage. It is thus assumed that in the larval sequence of Euphausiacea, generally a lateral spine is present at Calytopis III, and becomes progressively reduced until the adult (see, e.g. Boden 1950, 1951; Gopalakrishnan 1973; Fevolden 1980). Such a spine has never been reported for any other Crustacea. In consequence, it is postulated that a lateral spine developed on the first antennular segment at Calytopis III, persisting until the last Furcilia stage but reduced during the postlarval (=juvenile) phase, is part of the ground pattern at least of the Euphausiidae. It remains uncertain if it represents an autapomorphy of the Euphausiidae or the Euphausiacea until the larvae of *Bentheuphausia amblyops* are described (1a in Fig. 22).

In the taxa *Nyctiphanes*, *Nematoscelis*, *Stylocheiron*, *Thysanoessa* and *Tessarabrachion oculatum*, the two distal portions of the antennular peduncle of the females are distinctly narrower than the

proximal portion. In all other euphausiaceans, the females have, like the males, an antennular peduncle with three portions of the same thickness (Zimmer & Gruner 1956). The presence of a narrow tip of the antennular peduncle in the five mentioned taxa is seen as an autapomorphy for a group consisting of these taxa, a group for we propose the name *Nematoscelini*, new name (7 in Fig. 22). In *Nematoscelis*, *Stylocheiron*, *Thysanoessa* and *Tessarabrachion oculatum*, the antennular flagella are as long as the peduncle or slightly longer, and their number of annuli is low, while all other euphausiaceans have flagella at least twice as long as the peduncle and with numerous annuli (Zimmer & Gruner 1956). The reduction of the number of flagellar annuli and the shortness of the flagella are seen as an autapomorphy of a group consisting of *Nematoscelis*, *Stylocheiron*, *Thysanoessa* and *Tessarabrachion oculatum* (9 in Fig. 22). Furthermore, the females of these four taxa lack the endopods on their sixth and seventh thoracopods, a combination that can not be seen in any other euphausiacean. We

Table 2. List of abbreviations used in the figures

<i>an</i>	anus
<i>bas</i>	basis
<i>ce</i>	compound eye
<i>cox</i>	coxa
<i>en</i>	endopod
<i>ep</i>	epipodite
<i>ex</i>	exopod
<i>fli, flo</i>	inner/outer flagellum
<i>gif</i>	gill filaments
<i>i.</i>	initial
<i>lac</i>	<i>lacinia mobilis</i>
<i>lcsp</i>	laterocaudal spine
<i>lsp</i>	lateral spine
<i>pal</i>	palp of mandible
<i>pi</i>	<i>pars incisivus</i> of mandible
<i>pia</i>	<i>processus incisivus accessorius</i> of mandible
<i>ped</i>	peduncle of antennula
<i>plsp</i>	posterolateral spines
<i>pm</i>	<i>pars molaris</i> of mandible
<i>prp</i>	limb stem
<i>sscl</i>	secondary sclerite
<i>ste</i>	sternite

regard this as a further autapomorphy of this taxon group for which the name *Nematoscelina*, new name, is proposed here for the first time (9 in Fig. 22).

Character coding (Table 4):

Character 1: antennular peduncle of larvae:

- 0: without spines,
- 1: with a lateral spine.

Character 2: antennular peduncle of adults:

- 0: all segments equally,
- 1: distal segments narrower than proximal segment.

Character 3: antennular flagella:

- 0: at least twice as long as the peduncle and with numerous annuli,
- 1: length equal to peduncle, with low number of annuli.

Antenna

The adult antenna of all Euphausiacea consists of an undivided limb stem, an undivided endopod, and an undivided, flat exopod, the scaphocerite.

In *Euphausia superba*, which we examined, and in all larval Euphausiacea the coxa and basis are distinct portions (e.g. Gopalakrishnan 1973, for *Nematoscelis*

difficilis Hansen 1911; Knight 1973, for *Thysanopoda tricuspadata*). This reflects the plesiomorphic state because a subdivision should be present in the ground pattern of Malacostraca and even Eucrustacea (cf. Walossek 1999). A fused limb stem in adult Euphausiacea is, hence, considered as an autapomorphy of this group (1 in Fig. 22). In early larvae, we realised that the limb stem is rather long relative to the whole antenna, but this relation changes later on. Between Calyptopis I and Furcilia I, the limb stem measures 60% of the whole limb in *E. superba* (Table 1, third column). The stem measures 50% in Furciliae II and III, and 40% from Furcilia IV on, which is also the adult condition. In the Decapoda, the limb stem seems to be relatively shorter with less than 50% throughout development (e.g. Cockcroft 1985 for the penaeid *Macropetasma africanum* (Balss, 1913)). A similarly large stem is also present in larval rhizocephalans such as *Briarosaccus tenellus* Boschma, 1970 (Walossek et al. 1996, particularly Fig. 11). Gauld (1959), however, considered a limb stem representing 50% of the whole limb, or more, as characteristic only of the larvae of Branchiopoda, hence differentiating between a branchiopod nauplius and a non-branchiopod nauplius. It is more likely that large antennal limb stems in crustacean nauplii developed more than once due to specific needs.

The endopod is undivided in all stages examined by us for *Euphausia superba* (e.g. Fig. 4, for Calyptopis III) while the exopod consists of a proximal article more than twice as long as the following six short annuli. Each of the proximal five ringlets bears one seta, the distal annulus two (Fig. 4, for Calyptopis III). This design remains unchanged until Furcilia III, but from Furcilia IV onwards, the ramus becomes progressively flattened to attain its characteristic scaphocerite shape in the adult. The same is known from other Malacostraca. The scaphocerite is long accepted to be an autapomorphy of the Caridoida Calman, 1904 (but *sensu* Calman 1909 now embracing only Peracarida, Syncarida and Eucarida) and, therefore, represents a plesiomorphy of Euphausiacea.

Character coding (Table 4):

character 4: limb stem of antenna:

- 0: unfused coxa and basis,
- 1: fused coxa and basis.

Table 3. Data matrix of the characters that have been used for PAUP. See text or Table 4 for information on the coding of the characters

Taxon	Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	Decapoda	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Lophogastrida	?	0	0	0	2	1	0	0	?	0	0	0	0	0	0	?	0	2	2
3	<i>Bentheuphausia amblyops</i>	?	0	0	1	1	0	0	0	?	0	0	0	1	0	0	?	0	1	0
4	<i>Thysanopoda</i>	1	0	0	1	3	2	0	0	1	0	0	0	2	0	1	1	1	1	0
5	<i>Nematobranchion</i>	1	0	0	1	3	2	0	0	1	0	0	0	2	0	1	1	1	1	0
6	<i>Meganyctiphanes norvegica</i>	1	0	0	1	3	2	0	0	1	1	1	0	2	1	1	1	1	1	0
7	<i>Euphausia</i>	1	0	0	1	3	2	0	0	1	3	3	2	2	2	1	1	1	1	0
8	<i>Pseudeuphausia</i>	1	0	0	1	3	2	0	0	1	3	3	2	2	2	1	1	1	1	1
9	<i>Nyctiphanes</i>	1	1	0	1	3	2	0	0	1	1	3	0	2	1	1	1	1	1	1
10	<i>Thysanoessa raschi</i>	1	1	1	1	3	2	0	0	1	2	2	1	2	1	1	1	1	1	0
11	<i>Thysanoessa spinifera</i>	1	1	1	1	3	2	0	0	1	2	2	1	2	1	1	1	1	1	0
12	other <i>Thysanoessa</i>	1	1	1	1	3	2	1	0	1	2	2	1	2	1	1	1	1	1	0
13	<i>Stylocheiron</i>	1	1	1	1	3	2	0	1	1	2	2	1	2	1	1	1	1	1	1
14	<i>Nematoscelis</i>	1	1	1	1	3	2	1	0	1	2	2	1	2	1	1	1	1	1	1
15	<i>Tessarabrachion oculatum</i>	1	1	1	1	3	2	1	1	1	2	2	1	2	1	1	1	1	1	1

Mandible

The adult mandible of all Euphausiacea consists of a proximal portion, coxa and the so-called palp, resting on the peak of the coxal body and made of three, more or less, rod-shaped articles (see Olesen & Walossek 2000 for a new interpretation of this structure at least for leptostracans). In early larval stages of *Euphausia superba*, the palp is only a small, undivided cone (Fig. 5). Not earlier than from Furcilia IV, the palp becomes elongated, relative to that of earlier stages, a feature recognizable also in other euphausiids and eumalacostracans.

The coxal body is somewhat spindle-shaped, being more rounded medially and extending far on to the sides of the animal's head laterally. Accordingly, the abaxially oriented joint is very long and narrow. The coxal body is slightly excavated on the anterior and posterior sides. Disto-medially, the coxal body is extended into an antero-medially pointing, shovel-shaped gnathobase, with a concave distal surface. The almost straight inner margin of the gnathobase is subdivided into a thicker *pars molaris* anteriorly and a dentate *pars incisivus* posteriorly. Right and left mandibular coxae are of similar shape.

By contrast, the medially projecting gnathobase of the right mandibular coxa of the Calyptopis phase of *Euphausia superba* is subdivided, from anterior to posterior, into the *pars molaris*, the *processus incisivus accessorius* (spine row), as a dentate, movable spine with many hairs around its insertion, the *la-*

cinia mobilis, as another dentate, movable spine, but with a naked basis, and the *pars incisivus* (Fig. 5, for Calyptopis II of *E. superba*). The left mandible lacks the *lacinia mobilis*. The right mandibular coxal gnathobase of larval *E. superba* bears, at its inner edge, a mobile denticulate spine close to the *pars incisivus*, the *lacinia mobilis* (Fig. 5 for Calyptopis II). Weigmann-Haass (1977) stresses that the larval *lacinia* of the taxa *Euphausia* Dana, 1852, *Thysanoessa* Brandt, 1851, *Nematoscelis* G. O. Sars, 1883, and *Stylocheiron* G. O. Sars, 1883, should be developed only on the left mandible. Her own illustrations (Figs. 1 and 2) present, however, only right coxae. Accordingly, a right *lacinia* on the larval mandible seems to characterise, at least, the four taxa mentioned above. Larval *laciniae* are also known from Decapoda and Peracarida (Brandt and Wilson, pers. comm.). Peracarida may have two adult *laciniae* in the ground pattern, but this is unclear because such a condition occurs, according to Schram (1986), only in two isopod taxa, the Amph-isopodidae and Cirolanidae, but there is no detailed study on this feature available at present. All other Peracarida have only one *lacinia*, and always the left one (Schram 1986).

Because of the still unknown status of the *lacinia mobilis* within the Eumalacostraca, it is even uncertain if the *laciniae* of Euphausiacea and Decapoda are homologous structures.

No characters coded.

Table 4. List of all coded characters

Character 1: antennular peduncle of larvae:
 0: without spines,
 1: with a lateral spine.

Character 2: antennular peduncle of adults:
 0: all segments equally,
 1: distal segments narrower than proximal segment.

Character 3: antennular flagella:
 0: at least twice as long as the peduncle and with numerous annuli,
 1: length equal to peduncle, with low number of annuli.

Character 4: limb stem of antenna:
 0: unfused coxa and basis,
 1: fused coxa and basis.

Character 5: endopod of maxillula:
 0: consists of more or equal to 4 podomeres,
 1: consists of 3 podomeres,
 2: consists of 2 podomeres,
 3: undivided.

Character 6: endopod of maxilla:
 0: consists of 3 podomeres,
 1: consists of 2 podomeres,
 2: undivided.

Character 7: length of second thoracopod:
 0: subequal to others,
 1: longer than others.

Character 8: length of third thoracopod:
 0: subequal to others,
 1: longer than others.

Character 9: larval thoracopods II – VI:
 0: like thoracopod I, unlike that of adults,
 1: unlike thoracopod I, like that of adults.

Character 10: endopod of thoracopod VII of males:
 0: consists of 5 podomeres,
 1: consists of 2 podomeres but long,
 2: very short,
 3: lacking.

Character 11: endopod of thoracopod VII of females:
 0: consists of 5 podomeres,
 1: consists of 2 podomeres but long,
 2: very short,
 3: lacking.

Table 4. Continued

Character 12: exopod of thoracopod VII:
 0: equal to exopods of thoracopods I to VI,
 1: shorter than to exopods of thoracopods I to VI,
 2: small and undivided.

Character 13: endopod of thoracopod VIII:
 0: consists of 5 podomeres,
 1: consists of 4 podomeres,
 2: lacking.

Character 14: exopod of thoracopod VIII:
 0: like in thoracopods I to VII,
 1: short but divided,
 2: short and undivided.

Character 15: pleopods I and II:
 0: Petasma absent,
 1: Petasma present.

Character 16: limb stem of uropod of larvae:
 0: without spines,
 1: with a spine.

Character 17: exopod of uropod:
 0: with diarsis (suture),
 1: no diarsis (suture).

Character 18: adult telson:
 0: without spines,
 1: one big spine present,
 2: several subequal spines.

Character 19: brood care:
 0: not made,
 1: made without oöstegites,
 2: made with oöstegites.

Maxillula

The antero-posteriorly flattened limb stem of the adult maxillula of all Euphausiidae consists of two portions, the coxa and the basis, the endopod is undivided, and the exopod is missing. In both coxa and basis, the median edge is equipped with a longitudinal row of setulous setae; the joint between both elements is indistinct laterally. At the postero-lateral edge of the limb two flat and undivided lobes insert either on the coxa or proximally on the basis (exact position uncertain), the so-called proximal lobe more posteriorly and

the elongated, lobate so-called pseud-exopod more laterally. Both structures bear setae along their inner margins, yet their homology is uncertain.

During the Calyptopis phase of *Euphausia superba*, which we examined, the coxa carries seven bristles at its median edge in a row from proximal to distal, eight in Furcilia I and II, 10 in Furcilia III and IV, and more than 10 in Furcilia V. From Furcilia VI on, the coxa bears numerous setae (Table 1). On the basis, the pattern of bristles changes similarly from four in Calyptopis I, to five in Calyptopis II and III, seven in Furcilia I and II, nine in Furciliae III and IV, and more than 10 in Furcilia V. There are numerous setae from Furcilia VI on (Table 1). We observed that the numbers of setae on the maxillular coxa and basis of *E. superba* increase very slowly at the beginning of larval development and rather rapidly at the end (Table 1, fifth and sixth columns). The numbers of setae and the process of attaining the final number seem to be rather uniform within the Euphausiacea, but this was not checked in detail.

The endopod of the maxillula of *E. superba* consists of two podomeres from Calyptopis I until Furcilia II (Fig. 6), and is an undivided lobe subsequently (Fig. 7). In all larval stages, the exopod remains an undivided hemispherical element with four setulate setae around its tip (Figs 6 and 7). Until Furcilia IV there are no traces of the proximal lobe and the pseud-exopod. As in *E. superba*, all other Euphausiidae have, according to Zimmer & Gruner (1956), an undivided maxillular endopod; its development, however, always starts with a two-segmented state (e.g. Knight 1975; Table 1, sixth column, for *E. superba*; Figs 6 and 7). Adult *Bentheuphausia amblyops* have a maxillular endopod, which consists of three podomeres (Sars 1885; Einarsson 1942). In the Decapoda and Peracarida, the endopod of the adult maxillula probably consists of four segments (e.g. Williamson 1982; Cockcroft 1985, for the penaeid *Macropetasma africanum*), possibly also representing the minimum number in the ground pattern of the Eumalacostraca. The maxillular endopod of the Lophogastrida has presumably two podomeres. The presence of three endopodal podomeres, as developed in adult *Bentheuphausia amblyops*, is hence considered as a reductive modification, and autapomorphy of Euphausiacea (1 in Fig. 22). Consequently, the presence of only one portion in adults represents an autapomorphy of the Euphausiidae (3 in Fig. 22).

Character coding (Table 4):

Character 5: endopod of maxillula:

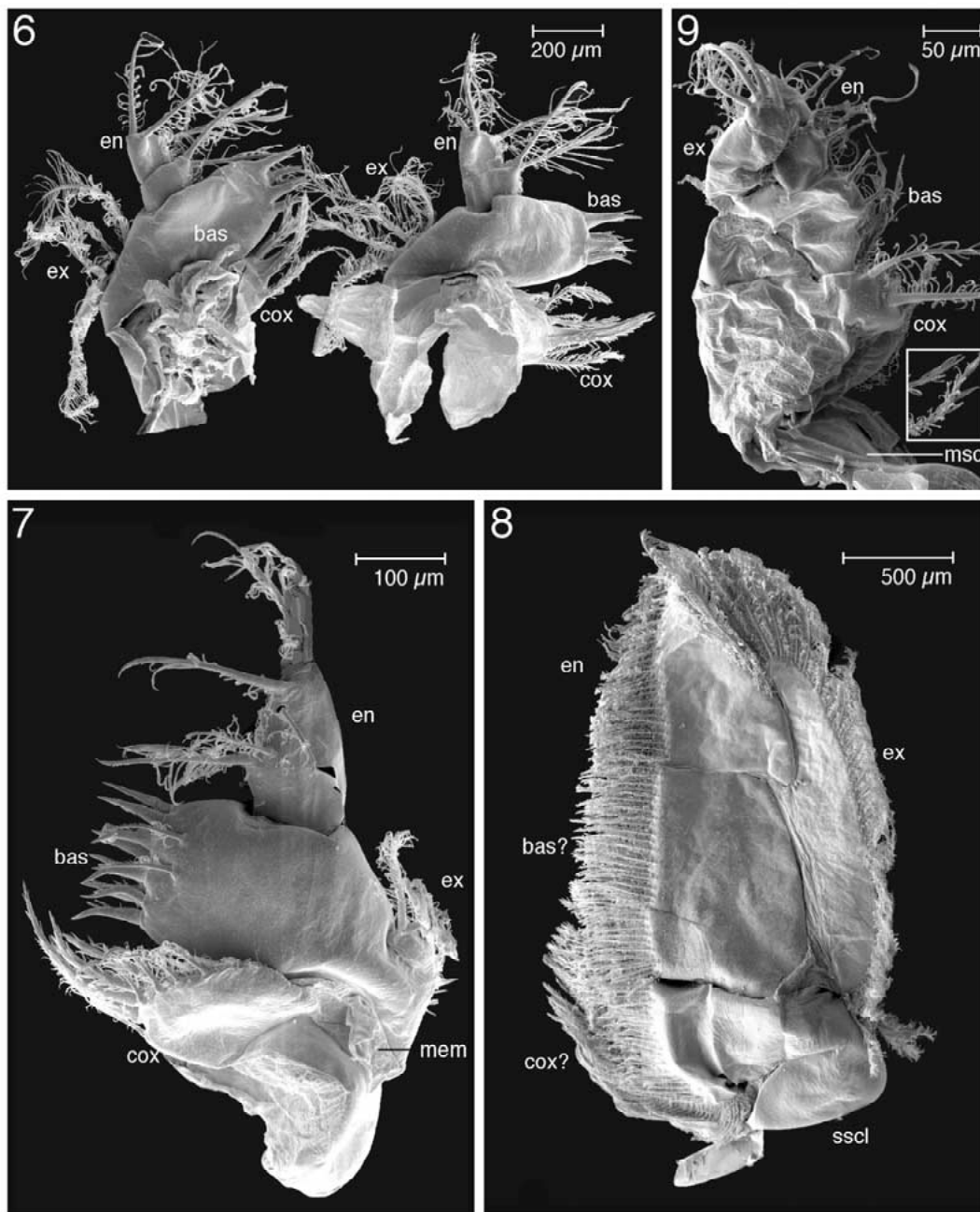
- 0: consists of more than, or equal to, 4 podomeres,
- 1: consists of 3 podomeres,
- 2: consists of 2 podomeres,
- 3: undivided.

Maxilla

The antero-posteriorly flattened adult maxilla of all Euphausiacea has a prominent limb stem split into two portions, both with setiferous median margins (two rows) and divided incompletely medially, which causes a subdivision mainly of the setiferous margins (Fig. 8). The undivided, lobate endopod arises from the medio-distal edge of the longer and trapezoidal distal part of the limb stem. The endopodal setation is, more or less, the continuation of the seta row of the limb stem. The flat, elongated and uniform exopod, with a setation along its outer and distal margins, inserts at the steeply sloping outer margin of the limb stem, the joint reaching proximally to the boundary between the two portions of the limb stem.

The maxilla of all investigated larval stages of *Euphausia superba* consists of a limb stem with five distinct, lobate endites medially and an undivided elongate endopod. The exopod is a small bud, which rests on the sloping outer edge of the limb stem and is, more or less, only the socket of a setiferous seta. In Furcilia IV, there are two setae arising from the exopod. In adult *Bentheuphausia amblyops* the endopod is divided into three portions (see, e. g. Sars 1885). Among the Decapoda, at least all Dendrobranchiata have a five-segmented maxillary endopod during the protozoal phase, while the adult endopod is undivided in all Decapoda. A five-segmented endopod, at least on postmaxillular limbs, characterises the ground pattern of the Crustacea (Walossek & Müller 1990); possibly an autapomorphy of the Crustacea. Accordingly, the three-segmented condition of adult *B. amblyops* would be apomorphic with regard to the possible sister group of the Euphausiacea but plesiomorphic among the Euphausiidae, while the undivided state of the maxillary endopod of the Euphausiidae represents an autapomorphy of this taxon (3 in Fig. 22). Consequently, the undivided state would have evolved, *via* reduction or fusion, convergently within the different eucrustacean taxa.

The interpretation of the subdivision of the proximal part of the maxilla of *E. superba* remains an unsolved problem, which directly relates to the terminology of the subdivisions of crustacean limbs. Hansen



Figures 6–9. **Figure 6.** Maxillulae of Calyptopis III from the anterior. Breakage of the coxa exposes many muscles (msc) running from the body into this limb portion.

Figure 7. Left maxillula of Furcilia III from the posterior.

Figure 8. Right maxilla of adult from the anterior.

Figure 9. Somewhat deformed left thoracopod I of Calyptopis I from the anterior. The exopod covers part of the endopod. The continuing bristles from the coxa are documented in the white-bordered box.

(1925) postulated a tripartite stem for the limbs of (all) Arthropoda, which was the basis for many subsequent studies of arthropod limbs. In consequence, Hansen (1925) called the sclerotic element at the outer proximal edge of the maxillae of euphausiids a 'praecoxa'. The interpretation of Hansen (1) severely influenced and even confused the crustacean terminology, and later authors even termed the entire arthrodistal membrane (2) a 'praecoxa' or 'precoxa' (not a sclerotic element), while others used this term, in a third sense (3), for the coxa itself and the term 'coxa' for the membrane between coxa and basis, such as Kaestner (1967, Fig. 661, only left side illustration of a copepod mandible).

Heegaard (1948: Table 4), however, called this maxillary structure of Euphausiacea a 'secondary sclerite'. In our view, this expresses its function as a lateral sclerite within the arthrodistal membrane more neutrally, possibly serving to limit the range of movability of the maxilla. Similar sclerotisations of arthrodistal membranes are widespread among Crustacea and Arthropoda in general. Again, according to Walossek (1993) the limb stem in the ground pattern of Arthropoda consisted of only a single portion, the basis. This basis continues into the endopod medio-distally and carries the exopod on its outer sloping rim, as the only extension or exite (i.e. no further exites at this stage). Amongst the first steps in crustacean evolution, a small outgrowth, the proximal endite, developed on postantennular limbs (Walossek & Müller 1990; Walossek 1993). This endite subsequently developed into a coxal portion underneath the basis on the two anterior post-antennular limbs, the antenna and the mandible (autapomorphy of NN = Phosphatocopina and Eucrustacea, see Walossek 1999). More coxal structures developed subsequently and independently in the different eucrustacean groups, hence not characterising a 'basic' or 'typical' feature of Crustacea, as stated in various textbooks.

Since it is not possible to distinguish the portions of the maxillary limb stem of euphausiids, it is uncertain if (a) this limb bears a coxa-basis subdivision (with two endites each in the adult), or if (b) the proximal one of the median endites should represent the proximal endite, while the others belong to the basis.

Character coding (Table 4):

Character 6: endopod of maxilla:

- 0: consists of 3 podomeres,
- 1: consists of 2 podomeres,
- 2: undivided.

Thoracopods I–VI

The antero-posteriorly flattened limb stem of the first adult thoracopod of all Euphausiacea consists of two distinct portions, the coxa and the longer, subtrapezoidal basis. Both parts have a median edge, which, in long axis, is equipped with two rows of setulous setae. At the lateral edge, an uni-lobed and bristleless epipodite inserts at the coxa. The endopod is composed of five podomeres and carries two rows of different setae along its inner edge, continuing the seta row of the limb stem: long plumose setae directed anteriorly and short plumose setae projecting inwards. The exopod has a rod-shaped proximal portion containing the musculature and a multi-annulated portion distally, with each annulus carrying one seta on its inner and outer sides.

Thoracopod I of the investigated adult of *Euphausia superba* resembles thoracopods II to VI, which are, however, slightly more slender and longer. Their epipodites are also much more differentiated in that they consist of an asymmetrical, slightly curved main branch from which several tubular lobes, serving as gills, arise. Thoracopods II–VI of *E. superba* are similar to that in all species of *Euphausia*, *Pseudeuphausia* Hansen, 1910, *Nyctiphanes* Sars, 1883, *Meganyctiphanes norvegica* (M. Sars, 1857), *Thysanopoda*, *Bentheuphausia amblyops*, *Thysanoessa raschi* (M. Sars, 1864), and *Thysanoessa spinifera* Holmes, 1900 (the so-called *Rhoda*-type of *Thysanoessa*). By contrast, in *Nematoscelis* and all other *Thysanoessa*-species (the so-called *Thysanoessa*-type of *Thysanoessa*), the second thoracopod is strongly elongated. A limited number of larval and juvenile *Thysanoessa inermis* (Krøyer 1846) can also have short second thoracopods while other individuals can have elongated ones (Einarsson 1942; Zimmer & Gruner 1956). In *Nematobranchion* Calman, 1905 and *Stylocheiron*, the third thoracopod is elongated and the second and third in *Tessarabrachion oculatum* Hansen, 1911 (see Zimmer & Gruner 1956 who call these elongated thoracopods predatory limbs). This elongation of thoracopods correlates with a division of the eyes in a lateral and a frontal part (Zimmer & Gruner 1956), but there are no investigations that can prove the homology of the division of the eyes to consider this character here. The elongations of one or two thoracopods must be assumed as secondarily acquired within the Euphausiacea (autapomorphy of particular in-groups and not forming a monophyletic clade) since in Decapoda, Lophogastrida, and

other Malacostraca, there is no sign for a comparable change. At least, the elongation of the *Nematobranchion* species is different from that of the species of *Stylocheiron* because the most distal podomere is strongly elongated in *Nematobranchion* but not in *Stylocheiron* (Zimmer & Gruner 1956). Henceforce, the elongation of the third thoracopod of the three species of *Nematobranchion* is thought to be an independent development and autapomorphy of *Nematobranchion* due to the systematic position of *Nematobranchion*.

The distribution of the elongations within the other taxa can be explained by four different hypotheses (Fig. 23A–D):

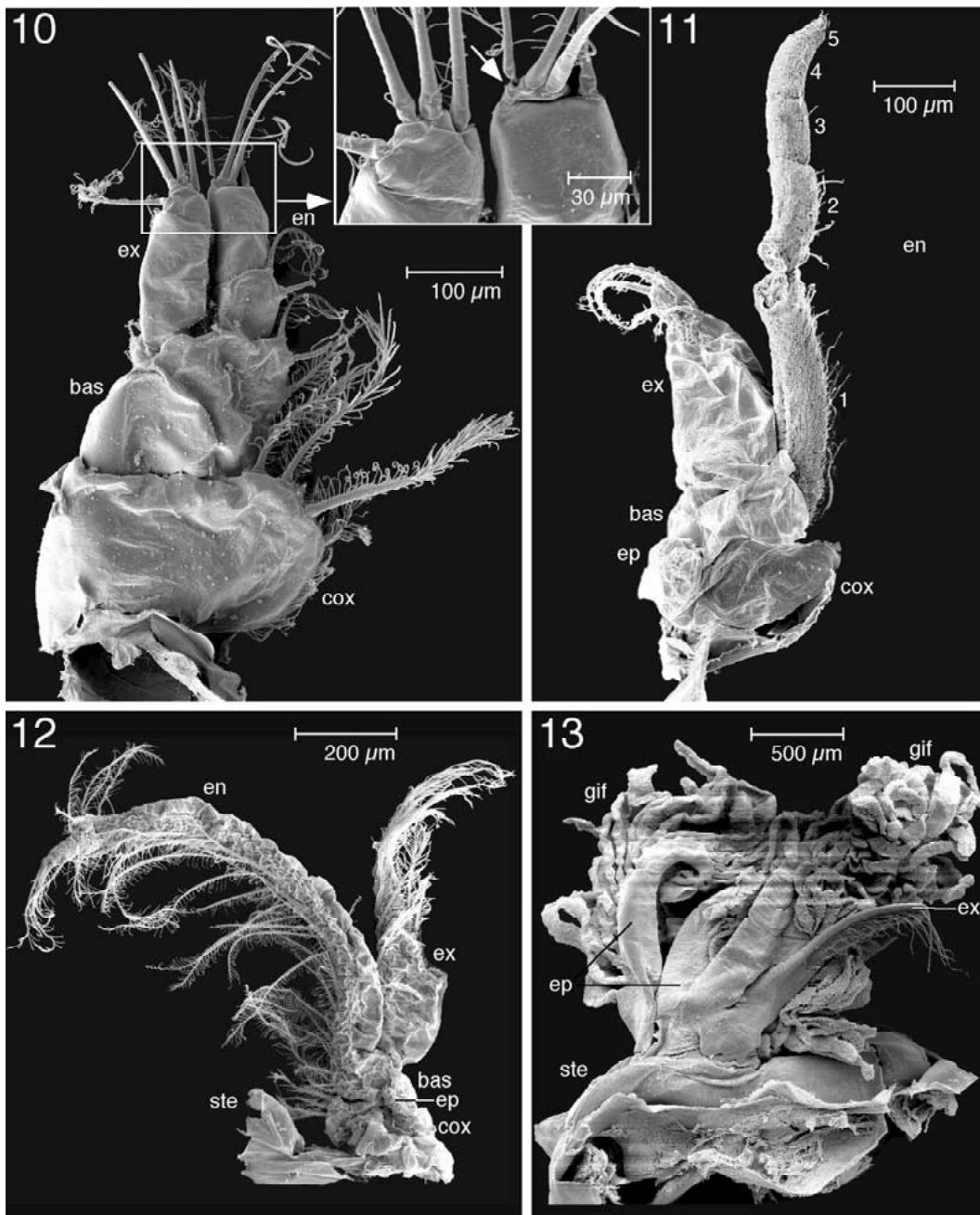
- (1) In the ground pattern of the Nematoscelina (as characterised below), there was no elongated thoracopod that is the plesiomorphic character state as found in other euphausiids. In *Stylocheiron*, the third thoracopod became elongated independently from the elongation of the second thoracopod in the ground pattern of *Thysanoessa*, except *Th. raschi* and *Th. spinifera* (no elongations at all), + *Nematoscelis* + *Tessarabrachion oculatum*. In consequence, also in *Tessarabrachion oculatum*, the third thoracopod should have become elongated autapomorphically or *vice versa*.
- (2) In the ground pattern of the *Nematoscelina* the second thoracopod was already elongated. In *Stylocheiron*, the third thoracopod became elongated but the second shortened again. *Tessarabrachion oculatum* has two pairs of elongated thoracopods, while all remaining taxa retain the plesiomorphic state of having one pair. *Thysanoessa raschi* and *Th. spinifera* having short second and third thoracopods could equally represent the sister group of all other Nematoscelina, or being a derived in-group taxon (shortening of the third thoracopod).
- (3) In the ground pattern of Nematoscelina, the third thoracopod was elongated, but not the second. Consequently, the third one should have become shortened in *Nematoscelis* and *Thysanoessa* and the second one elongated instead. *Tessarabrachion oculatum* should also have elongated its second thoracopod and have retained the long third one as a plesiomorphy. *Thysanoessa raschi* and *Th. spinifera* having short second and third thoracopods could equally represent the sister group of all other Nematoscelina, or being a derived in-group taxon (shortening of both limbs).
- (4) In the ground pattern of the Nematoscelina, both the second and third thoracopods were elongated

(as an autapomorphy of this taxon), present in this plesiomorphic state only in *Tessarabrachion oculatum*. *Thysanoessa* + *Nematoscelis* could be monophyletic in sharing a short third thoracopod, while *Stylocheiron* should have shortened the second one. *Thysanoessa raschi* and *Th. spinifera* having short second and third thoracopods could equally represent the sister group of all other Nematoscelina, or being a derived in-group taxon (shortening of both limbs).

With our present knowledge, all four hypotheses show conflicts in their interpretations and are, hence, equally difficult to judge. The shortest tree that the cladistic program suggested is in accordance with our second hypothesis (Fig. 23B). Nevertheless, more work, or a system stabilised on other characters should aid in a better understanding of this elongated-limb phenomenon.

The first thoracopod of Calyptopis I of *Euphausia superba* is antero-posteriorly flattened. It consists of a coxa and a basis (Fig. 9), which, together, make up 60% of the whole length of the limb. The endopod is three-divided, the third portion being very small relative to the others and carrying four long setae (see Fig. 10 for the third endopodal podomere in Calyptopis II). The exopod is undivided and likewise slightly flattened. In Furcilia II, the length of the limb stem measures 50% of the length of the whole limb, and the endopod is divided into five podomeres, the final number. The length of the limb stem relative to the whole limb is 40% in Furcilia III, 30% in Furcilia IV and 20% in the adult (Table 1). This is mainly due to the strong elongation of the endopod, while coxa and basis also grow, but not to any great extent. The coxal epipodite appears as an inconspicuous hump in Furcilia III. In Furcilia IV, the epipodite is uni-lobed, as in the adult. Thoracopods II–VI appear as uniform buds in Calyptopis III. They successively gain structure, but remain similar to each other in shape and size through further growth. With the moult to Furcilia II they are fully developed. Also the joint between basis and endopod, which is indistinct before (Fig. 11, for Furcilia I), is developed in Furcilia II (Fig. 12). The coxal epipodites appear as short conical humps in Furcilia I and become increasingly more lobed during ontogeny. The proportion of the limb stem relative to the limb slightly decreases from 30% in Calyptopis III to 25% in Furcilia III and 15% in the adult (Table 1).

The first thoracopod of *Euphausia superba* is used as a swimming appendage already by Calyptopis I,



Figures 10–13. **Figure 10.** Right thoracopod I of *Calyptopsis* II from the posterior. The third podomere (arrowed) of the endopod is magnified on upper right; in the magnified image, the limb is slightly tilted forward relative to the picture.

Figure 11. Thoracopod III of *Furcilia* I from the posterior. Whole limb wrinkled due to its softness. Tip of endopod almost torn off between the first and the second podomere (podomeres numbered).

Figure 12. Thoracopod IV of *Furcilia* II from the anterior. Cuticle strongly wrinkled during the drying process.

Figure 13. Thoracopod VII of the adult, embedded in the gill filaments of the epipoditeite (ep.) Endopod missing in this species (see text).

when it is still the only thoracopod present (Marschall 1985). Its morphology differs considerably from that of the adult. At the beginning of development, the limb stem is much longer, as compared to the rami (Figs 9 and 10). This proportion changes gradually during development towards a 20–80% relationship between limb stem and endopod (Table 1, ninth column). Fraser (1935) described the endopod as consisting of two podomeres, but we have been able to show that it is tripartite (Fig. 10). It is obvious that the first thoracopod develops faster than is usually presumed. Thoracopods II–VI develop in a different manner. At the beginning, they are rod-shaped and almost bristleless (Fig. 11). Later they attain the adult shape although being smaller and with fewer setae (Fig. 12). The change in the proportion of the limb stem relative to the length of the whole limb is quite different from that in thoracopod I: Here, the endopod is much longer relative to the limb stem from the beginning. This proportion changes gradually during development towards a 15:85% relationship between limb stem and endopod (Table 1, column 9, column 10). The same differences are known from other euphausiid species (cf. e.g. Mauchline 1971, 1980; Knight 1975, 1978; Gopalakrishnan 1977). Due to its differences to the following five thoracopods, and disregarding its function, which is not a maxillipedal one, the first thoracopod of the Euphausiidae has often been called ‘maxilliped’ (Sars 1885; Heegaard 1948; Mauchline 1971; Knight 1973).

Similarly, the first thoracopod of dendrobranchiate Decapoda also begins its development with a prominent limb stem of at least half the length of the limb and a leaf-shaped exopod (e.g. Cockcroft 1985 for the penaeid *Macropetasma africanum*; Oshiro & Omori 1996 for the sergestid *Acetes americanus* Ortmann, 1893). However, this also holds for the subsequent limbs and also seems to be the condition in the ground pattern of the Eumalacostraca. Differentiation of the dendrobranchiate first thoracopod into a maxilliped occurs later during morphogenesis, and the subsequent limbs attain their adult shape with a small limb stem and long endopod likewise later during development. Thus, there is a difference between decapods and euphausiaceans in that the second to sixth thoracopods are already more adult-like at the start of their development. This difference is hence regarded as a modification of the posterior thoracopods in the stem line of the Euphausiacea. Yet it remains uncertain if this includes *Bentheuphausia amblyops* due to the uncertainty about its larvae (1a in Fig. 22).

Thoracopods II–VI appear as Anlagen in Calyptopis III in *Euphausia superba*, setation is well developed in Furcilia II (Fig. 12). According to Zimmer & Gruner (1956), *E. superba* is the only species within the Euphausiacea whose thoracopods develop so early. Only *E. crystallorophias* Holt & Tattersall, 1906, develops its thoracopods II–VI in a similar rapidity: Their Anlagen also appear in Calyptopis III (Menshenina 1990), but it lasts until Furcilia V when the thoracopods are already as well developed as in *E. superba* at Furcilia II. Interestingly, these are the only taxa that are distributed off the Antarctic coast (Dzik & Jazdzewski 1978; Sheard 1953). It seems that the specific development of the second to sixth thoracopods can be considered as an autapomorphic feature of *E. superba* (7 in Fig. 22) and that *E. superba* and *E. crystallorophias* are closely related.

Character coding (Table 4):

Character 7: length of second thoracopod:

0: subequal to others,

1: longer than others.

Character 8: length of third thoracopod:

0: subequal to others,

1: longer than others.

Character 9: larval thoracopods II–VI:

0: like thoracopod I, unlike that of adults,

1: unlike thoracopod I, like that of adults.

Thoracopod VII

The adult thoracopod VII of *Euphausia superba* consists of a coxa with an epipodite, an inconspicuous basis, and a slightly flattened elongate exopod (Fig. 13). The endopod is missing and the joint between coxa and basis is not recognisable. Inside the coxa, a luminescent organ, the photophore, is located. The exopod is undivided, slender and bears few setae distally. The shape of the epipodite differs from that of the anterior thoracopods in consisting of an elongated major branch, from which several secondary branches arise, each carrying the tubular gill lobes. Thoracopod VII appears, as an undivided bud, in Furcilia II. By the next stage it consists of a coxa, with a luminous organ, and an uni-lobed epipodite. In Furcilia IV, the epipodite is bilobed, the basis is not distinguishable, and endopod and exopod are missing.

The adult thoracopod VII is strongly reduced in *Euphausia superba*. This seems to hold for all other species of *Euphausia* and for all members of the taxon *Pseudeuphausia* (Zimmer & Gruner 1956; Baker et

al. 1990). In all species of the two taxa, the endopod of thoracopod VII is missing and the exopod is a small, undivided device. In *Thysanoessa*, *Tessarabrachion oculatum*, *Nematoscelis* and *Stylocheiron*, the endopod is missing in the males, but is still present in the females, though small and undivided. In these four taxa, the exopod consists of a uniform proximal part and a multi-annulated distal part, but is slightly shorter than the exopod of the preceding thoracopods. *Meganyciphanes norvegica* and males of *Nyciphanes* have an endopod of two podomeres, but of the same size as all other thoracopodal endopods. Female *Nyciphanes* have lost the endopods of thoracopods VI and VII. *Thysanopoda*, *Nematobrachion* and *Bentheuphausia* have an endopod of five podomeres on the seventh thoracopod (see, e.g. Zimmer & Gruner 1956; Baker et al. 1990). In these five taxa, the exopod of thoracopod VII is as in the preceding limbs.

Considering the distribution of reduction of endopods and exopods on thoracopod VII, it seems that the rami of this limb have undergone gradual reduction during the evolution of the Euphausiacea. For the ground pattern of the Euphausiacea and also Euphausiidae, it must be assumed that the endopod consisted of five podomeres, representing a plesiomorphy in the ground pattern of the Euphausiacea (ground-pattern character of Crustacea *sensu* Walossek, 1999). Accordingly, a reduction of the endopod to two portions is interpreted as an autapomorphy of the stem species of Euphausiinae (4 in Fig. 22). The reduction in size of the two-segmented endopod in the males and the loss of the endopod in the females is seen as an autapomorphy of the Nematoscelina (9 in Fig. 22). In the common ancestor of the Euphausiini (6 in Fig. 22), comprising the sister taxa *Euphausia* and *Pseudeuphausia*, the endopod is reduced completely, and the exopod is reduced to a single element. The loss of the endopod of the sixth and seventh thoracopod in the females of *Nyciphanes* is seen as an autapomorphy of this taxon (8 in Fig. 22).

Character coding (Table 4):

Character 10: endopod of thoracopod VII of males:

- 0: consists of 5 podomeres,
- 1: consists of 2 podomeres but long,
- 2: very short,
- 3: lacking.

Character 11: endopod of thoracopod VII of females:

- 0: consists of 5 podomeres,
- 1: consists of 2 podomeres but long,

- 2: very short,

- 3: lacking.

Character 12: exopod of thoracopod VII:

- 0: equal to exopods of thoracopods I–VI,

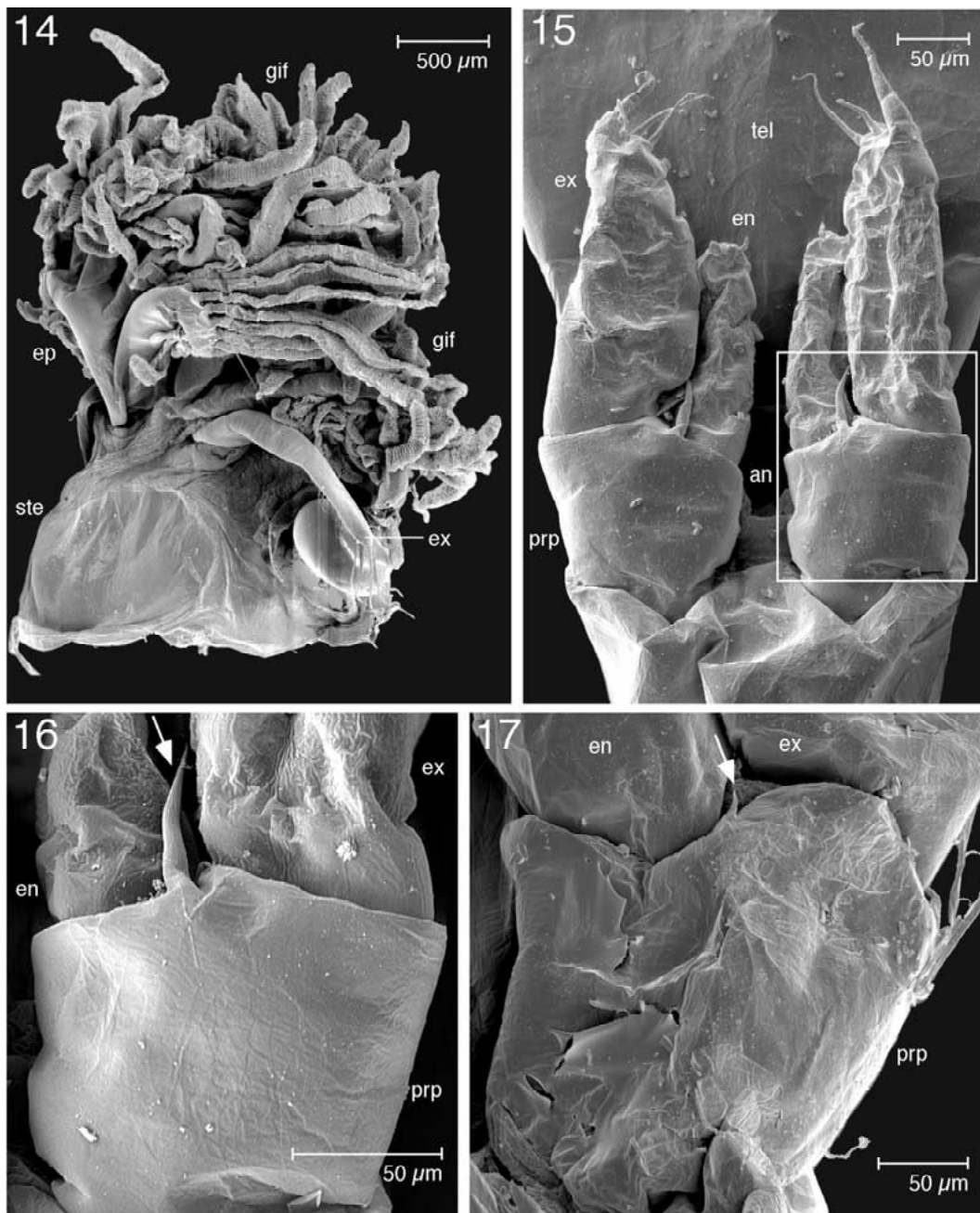
- 1: shorter than to exopods of thoracopods I–VI,

- 2: small and undivided.

Thoracopod VIII

The adult thoracopod VIII of all Euphausiidae consists of a coxa with an epipodite, a basis, and an exopod (Fig. 14 for *Euphausia superba*). The shape of the epipodite differs from that of the seventh thoracopod in having a major branch much more drawn out posteriorly and significantly larger. As in the preceding thoracopod, the boundary between coxa and basis is indistinct. Again, the endopod is missing, while the exopod is an undivided, elongate lobe bearing a few setae distally. Thoracopod VIII appears in the ontogeny of *E. superba* in Furcilia V, what we could not investigate with own material. An endopod never develops. In *Bentheuphausia amblyops*, the endopod of the eighth thoracopod is developed and distinctly four-divided. In the ground pattern of the Decapoda and, most likely, also in the stem species of Malacostraca, the endopod of thoracopod VIII consists of five podomeres, which should thus be the plesiomorphic state for this ramus (according to Walossek, 1999 representing an autapomorphy in the ground-pattern of Crustacea). Four portions, possibly podomeres, as in *Bentheuphausia amblyops*, are considered, hence, as an autapomorphy of the stem species of the Euphausiacea, but plesiomorphically retained in this species (1 in Fig. 22). In consequence, the absence of the endopod is interpreted as an autapomorphy of the stem species of Euphausiidae (3 in Fig. 22).

Within the Euphausiidae, the exopods of the eighth thoracopods of *Thysanopoda* and *Nematobrachion* are similar to that of the preceding thoracopods and similar to that of *Bentheuphausia*. Within the Euphausiinae, some species of *Thysanoessa* have a bipartite exopod, but an annulated portion is missing (Zimmer & Gruner 1956; Baker et al. 1990). All other taxa have their exopods of the eighth pair of thoracopods greatly reduced to a small rod-shaped element, as described above for *Euphausia superba* (Fig. 14). In the absence of more detailed information, it remains uncertain if in these particular species of *Thysanoessa* the annulated part of the exopod became rod-like to form the distal portion of the exopod, or if the original socket por-



Figures 14–17. **Figure 14.** Thoracopod VIII of the adult, gill filaments (gif) disguising the distal parts. Endopod missing in this species (see text).

Figure 15. Uropods of *Calyptopsis* III from the anterior. The section marked with the white bordered rectangle is shown in Figure 16.

Figure 16. Limb stem (prp) of the right uropod of *Calyptopsis* III from the anterior. Magnified from Figure 15. Arrow marks the characteristic spine on the anterodistal edge of the uniform limb stem (see text).

Figure 17. Limb stem of the right uropod of *Furcilia* IV from the anterior. Distal spine of the limb stem smaller than in Figure 16 marked by an arrow.

tion split into two. If the latter would be the case, the one-segmented state of other species of *Thysanoessa* and the rest of the Euphausiinae would be apomorphic (which would turn *Thysanoessa* into a paraphyletic assemblage). Further detailed work on these structures is necessary.

Character coding (Table 4):

Character 13: endopod of thoracopod VIII:

- 0: consists of 5 podomeres,
- 1: consists of 4 podomeres,
- 2: lacking.

Character 14: exopod of thoracopod VIII:

- 0: like in thoracopods I to VII,
- 1: short but divided,
- 2: short and undivided.

Pleopods

All anterior five pleopods of males and females of all Euphausiacea consist of an undivided limb stem, an undivided endopod and a distally annulated exopod as it is in *Euphausia superba*. The limb stem is, more or less, flattened in antero-posterior aspect. A narrow, poorly-sclerotized area extends from about the midline at the posterior side, reaching from the basal joint almost toward the insertion of the exopod. Only the short distal sector of the limb stem, from which the rami arise, is fully sclerotized. The flattened endopod and exopod are always strongly setose around their margins. In euphausiids, the endopod of pleopod I of the males is drawn out, additionally, into several lobes and processes, in contrast to the succeeding pleopods, which are all of the same shape. Every exopod annulus bears two setae terminally on opposite sides.

The appearance of pleopods of *Euphausia superba* varies individually and these limbs may occur in Furcilia I or II. The limb stem is barrel-shaped, while the undivided endopod and exopod are more or less rounded rods. Setae may be present, but this also varies individually. From Furcilia II onwards, the pleopods are always setose, and setation becomes denser during ontogeny. From Furcilia III on, the exopods are annulated distally, as in the adults.

Lobes and processes on the endopod of the first two pleopods are found in all Euphausiidae: they are called appendices masculinae and are considered as a copulatory organ, the petasma (Zimmer & Gruner 1956). Equivalent lobes are absent in *Bentheuphausia amblyops* (e.g. Einarsson 1945). Out-group comparison with, e.g. Decapoda, Syncarida and Peracarida,

indicates that in the ground pattern of Caridoida, at least, the first pleopod is not different from the succeeding pleopods (see, e.g. Schram 1986), being plesiomorphically retained in the Euphausiacea, as shown by *Bentheuphausia*. Consequently, the lobes and processes on the endopod of the first two pleopods are seen as an autapomorphy of Euphausiidae (3 in Fig. 22), and not of Euphausiacea, as stated by Schram (1986).

There exists neither a description of the ontogeny of any euphausiacean species or of any malacostracan species at all with a detailed documentation of all pleopods throughout development, except of the petasma of males. Again, no one has ever looked at pleopods as suitable structures for a phylogenetic analysis. Comparing the figures of pleopods of adult Euphausiacea, they look quite similar to that of *Euphausia superba*. However, it is unclear when the pleopod design with undivided limb stems and exopods made of a prominent basal part and a multi-annulated distal part, have appeared during malacostracan phylogeny. Further studies have to investigate this in more detail. Since it was not part of our programme of study, there is no place herein to discuss the apparent variation in pleopod development within the ontogeny of Euphausiacea (see, e.g. Mauchline & Fisher 1969).

Character coding (Table 4):

Character 15: pleopods I and II:

- 0: petasma absent,
- 1: petasma present.

Uropods

The adult uropods of Euphausiacea consist of an undivided sub-rectangular limb stem, a lanceolate endopod and an equally lanceolate exopod. The limb stem is short compared to the rami, making up one fifth of the length of the rami. It bears many setae at its outer margin. The endopod is antero-posteriorly flattened and pointed. It bears setae along its outer edge and distally on its inner edge. The exopod is also antero-posteriorly flattened but is slightly more than twice as wide as the endopod. Its tip is straight. Setae occur only at the inner exopodal margin.

Uropods of *Euphausia superba* appear in Calyptopis III (Fig. 15), consisting of an undivided limb stem and the two rami, which are slightly flattened and undivided. The antero-distal rim of the limb stem carries a spine just between the insertion areas of the rami (Fig. 15). In Furcilia IV, this spine is shorter (Fig. 17)

than that of Furcilia III, while the adult uropodal limb stem has no such spine. On the outer margin of the limb stem, there are two setae in Furcilia IV. While the endopod is almost tubular and naked, the exopod is somewhat thicker, and its inner margin is convex, carrying three setae. The tip of the exopod is drawn out in a long spinose seta laterally. This spine remains present until Furcilia III, but is missing from Furcilia IV on. The setation of limb stem and rami becomes denser during ontogeny.

The spine on the limb stem of the uropods of noted above as an exclusively larval feature (Figs 13 and 14) has also been described from all those species of Euphausiacea with known ontogeny. As in *E. superba*, it always disappears still within the praeadult phase (e.g. Knight 1973 for *Thysanopoda tricuspidata* and Knight 1975 for *Euphausia gibboides* Ortmann, 1893; Boden 1951 for *Nyctiphanes simplex* Hansen, 1911). Since there is no comparable structure described from any other Malacostraca, the uropod spine is regarded as an autapomorphic character either of the Euphausiacea or – due to insufficient knowledge of *Bentheuphausia amblyops* – of the Euphausiidae (1a in Fig. 22).

An undivided uropodal exopod, as in *E. superba*, is found also in the other species of the Euphausiidae. *B. amblyops* alone shows a suture on the exopod, indicative of a bipartite state (Sars 1885). An uropodal exopod of two portions is, on the other hand, present in stomatopods, peracarids, bathynellids and decapods, which is assumed to represent the state already existing in the ground pattern of the Eumalacostraca. The modification of the sixth pair of pleopods into uropods has been mentioned since long as one of the autapomorphies in the ground pattern of Eumalacostraca. It is, hence, assumed that the bipartite uropodal exopods were retained in the stem species of Euphausiacea, and also being, more or less, retained in *B. amblyops*. Consequently, an undivided ramus represents an autapomorphy of Euphausiidae (3 in Fig. 22).

Character coding (Table 4):

Character 16: limb stem of uropod of larvae:

0: without spines,

1: with a spine.

Character 17: exopod of uropod:

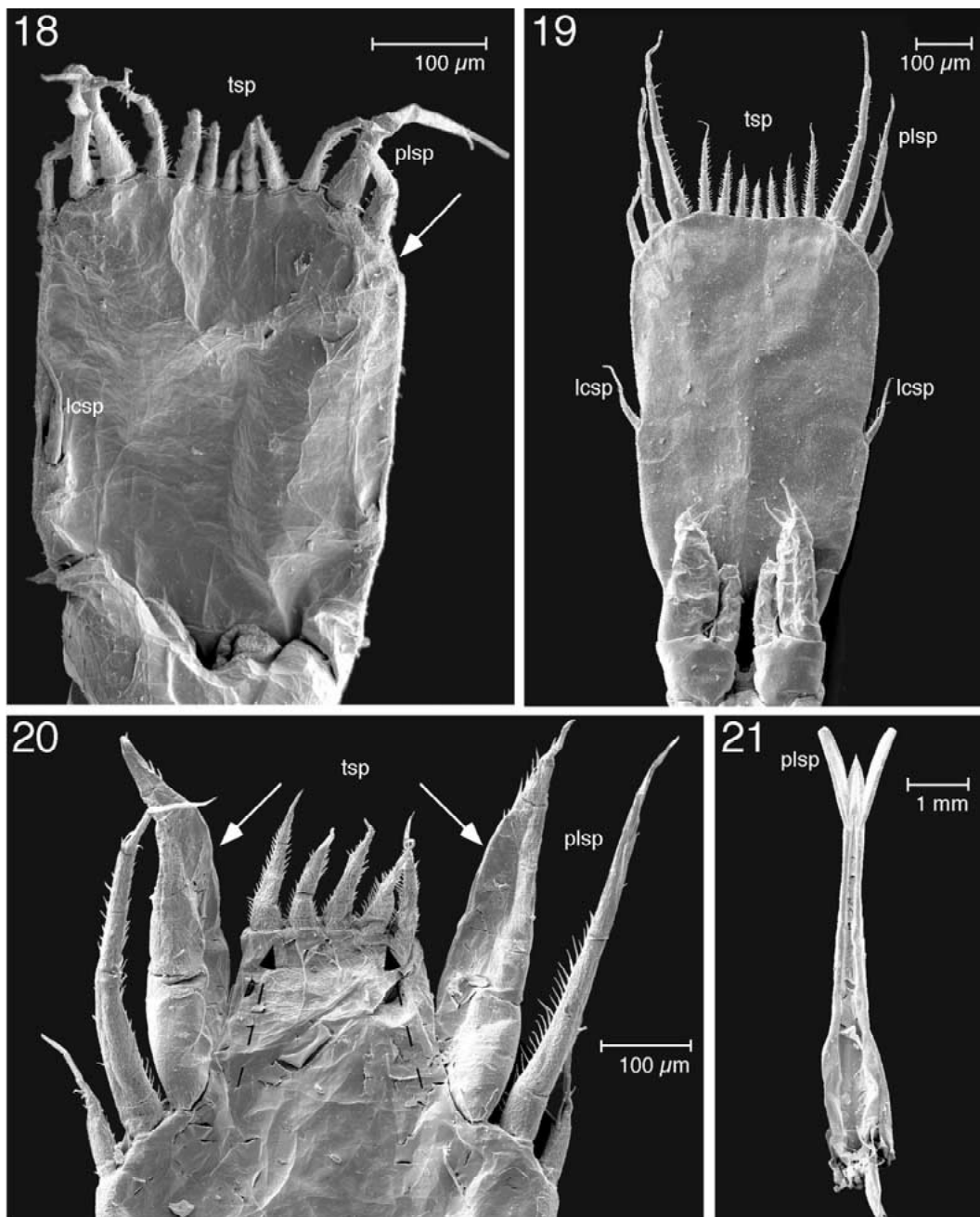
0: with diaresis (suture),

1: no diaresis (suture).

Telson

The telson of the adults of all Euphausiacea is a long, pointed and dorso-ventrally flattened element. It bears two flattened, posteriorly pointing spines in the last third of its length (Fig. 21 for *Euphausia superba*). The anus is located basally, on the ventral side of the telson. The tail of Calyptopis I of *E. superba*, from at least the first thoracomere backward, is undivided. Its cross-section is oval anteriorly. Toward its bluntly rounded and terminally slightly excavated rear, the tail becomes progressively more dorso-ventrally flattened. The caudal margin bears a row of 12 spines that are arranged in two symmetrical sets of six spines on either side: three postero-laterally, and three terminally (= six in a terminal set). Additionally, a small spine is located ventro-laterally on either side of the tail, the so-called laterocaudal spine. The anus opens on the ventral side of the telson between the laterocaudal spines. In Calyptopis II, where all thoracomeres and pleomeres are developed, the telson comprises the distinct caudal portion, demarcated off from the preceding trunk by a furrow. There is an additional spine developed in the marginal row of the end of the tail, making up seven terminal spines, and 13 in all (Fig. 18 for one of our Calyptopis II specimens). The anus opens ventrally in the first half of the telson anteriorly of the laterocaudal spines, which arise half way back on the telson.

In Calyptopis III, the pleon is progressively more depressed toward the telson, which is completely dorso-ventrally flattened and of a spatulate shape, viz. widens first and becomes narrower in the last sixth. The converging postero-lateral margins – that part behind the widest point – are, more or less, straight. The innermost postero-lateral spine is bigger than in the previous stage. From Calyptopis III onwards, the anus is located on the ventral side of the telson, almost between the insertions of the uropods (Fig. 19 for Calyptopis III). The terminal margin of the telson is straight in Furcilia II. In Furcilia IV, the postero-lateral margins are deflected and longer than before (dashed black arrows in Fig. 20). The inner postero-lateral spine is much flattened and now lanceolate, having a wide insertion area (Fig. 20). Due to the change of the postero-lateral margins, the rear of the telson appears more drawn out and pointed with the terminal margin being much shorter and carrying only five spines. This process continues until the characteristic, elongated, triangular shape of the telson is reached in the latest stages, with the inner postero-lateral spines strongly



Figures 18–21. **Figure 18.** Ventral view of hind body of *Calyptopis* II. The outermost posterolateral spine on the right side is broken off (arrow).

Figure 19. Ventral view of hind body of *Calyptopis* III.

Figure 20. Ventral view of rear of the hind body of *Furcilia* IV. The white arrows point to the median flattening of the innermost posterolateral spines (plsp). The dashed black arrows show the growing of the median end of the telson.

Figure 21. Ventral view of telson of the adult. And the paired flat spines flanking the pointed telson (plsp). Telson torn off from the body, and medially collapsed.

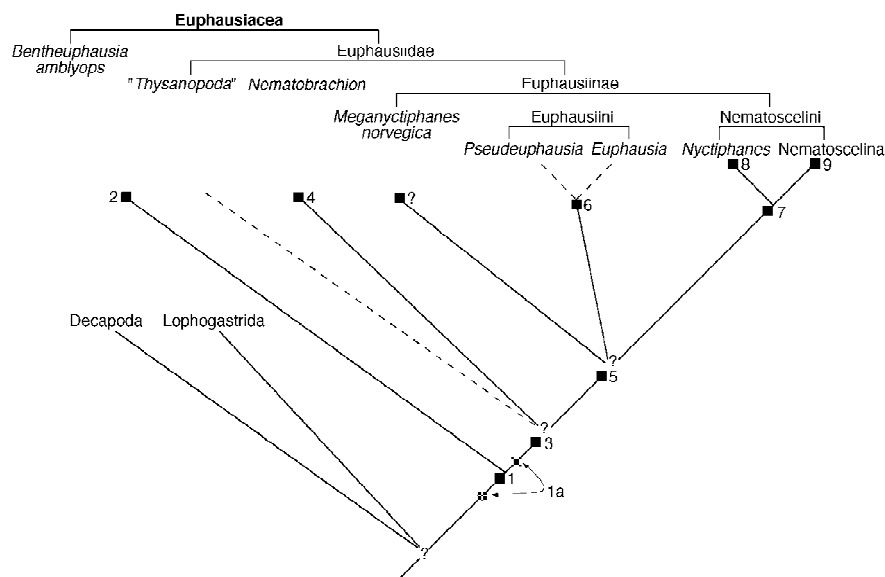


Figure 22. Hypothesised relationships within the Euphausiacea. One of three shortest trees suggested by the computer program PAUP (consistency index = 0.89; retention index = 0.92, rescaled consistency index = 0.81). See text for explanations of the numbers given for sets of autapomorphies in the ground patterns of the according stem species before a branching event. Hatched lines indicate uncertainty regarding monophyly. The taxon Nematoscelina new name comprises the genera *Nematoscelis*, *Thysanoessa*, *Tessarabrachion oculatum* and *Stylocheiron*. A monophyletic status can be confirmed only for *Stylocheiron* (see p. 164).

drawn out, the so-called 'subapical appendages' of the adult.

Spines on the hind body, as in *Euphausia superba* (Table 1, last column, Figs 18, 19 and 20), are developed in every larval stage of all other Euphausiacea with known ontogeny. However, their appearance and disappearance differ between species. The flattened spines of the adult, traditionally called 'subapical appendages', are, in fact, the innermost of the three postero-lateral furcal spines on either side of the hind body of the larvae, which, in *E. superba*, become very broad from Furcilia IV on (Fig. 20). These flattened spines are described from adults of each species (e.g. Sars 1885; Mauchline 1980; Baker et al. 1990) and have long been recognised as a 'diagnostic' character for the Euphausiacea. Leaf-shaped furcal rami, articulating with the conical telson and with marginal spines is a character, possibly an autapomorphy, of the ground pattern of Eucrustacea (Walossek 1999). This design is retained in the Leptostraca, and therefore it is at least part of the ground pattern of Malacostraca. A furca, though not articulating, with spines, occurs least in adult Bathynellacea (Schminke 1975), Thermosbaenacea (see Monod & Cals 1988, their Fig. 2), possibly also the Stomatopoda, and in the fossil eumalacostracan Belotelsonidea, Waterstonellidea, and 'eocarids'. This demonstrates that furcal rami were

also retained in the ground pattern of Caridoida, though no longer set-off. Furcal rami are lacking in all adult Decapoda, though in their larvae they are present and well developed, so that it is even possible to homologue the decapod and euphausiaceous furcal and telsonic setae. Adult lophogastrids have several small subequal spines at the telson. Therefore, the broadened postero-lateral spines of the euphausiaceous adult ('subapical appendages') are not a simple retention of furcal spines but a strong modification of the original furcal armature, thus representing a further autapomorphy of the Euphausiacea (1 in Fig. 22).

Character coding (Table 4):

Character 18: adult telson:

- 0: without spines,
- 1: one big spine present,
- 2: several subequal spines.

Photophores

Adult *Euphausia superba* have 10 luminescent organs, photophores, of a pink colour. One pair is located within the peduncle of the compound eyes. Two more pairs are positioned inside the coxae of the second and the seventh thoracopods, and a single one is found inside each sternite of the first to fourth pleomeres,

between the insertions of the pleopods. The first photophores appear in Calyptopis I, being located behind the compound eyes. They remain Anlagen until Furcilia I, where they are now located in the peduncle of the compound eyes and represent conical luminous organs. In Furcilia II, the photophores of the coxae of the second pair of thoracopods are developed. The appearance of photophores inside the sternites of pleomeres I–IV differs individually. The photophores of the coxae of thoracopod VII appear at Furcilia III. From this stage on, all photophores are functional.

Photophores, as developed in *Euphausia superba*, are also known from other Euphausiacea (Zimmer & Gruner 1956), while *Bentheuphausia amblyops* has no photophores (Brinton 1987). All species of the taxon Euphausiinae have 10 photophores located in the peduncle of the compound eyes, in the coxae of the second and seventh thoracopods, and in the sternite of the first to fourth pleomere, with the exception of *Stylocheiron*. In this taxon, photophores are developed only in the peduncle of the compound eyes, in the coxae of the seventh thoracopod and in the sternite of the first pleomere. Since *Stylocheiron* can be interpreted, on the other characters mentioned, as an in-group member of Euphausiini, its lower number of photophores must be regarded as an autapomorphy of this taxon and not an 'intermediate' stage between zero and 10. There are some deep-sea species of *Thysanopoda* with no photophores, but all others have such organs – and also always 10. Other Crustacea with photophores are known, but photophores, in general, do not belong to a ground pattern of supraspecific taxa like the Decapoda or the Peracarida. Accordingly, the status of this character remains uncertain, viz., it is not conclusive if photophores were primarily absent in the stem species of Euphausiacea (see Brinton, 1987 for further information and discussion) and were progressively added in the evolutionary line of Euphausiidae. However, it seems clear that a set of ten photophores characterises the ground pattern of Euphausiinae.

No character coded.

Thelycum

Around the limb bases and the sternite of the sixth thoracomere of adult female Euphausiacea, there is a pouch, the thelycum, into which the gonoducts open. Only in *Nyctiphanes couchi* (Bell, 1853) a thelycum is missing and the gonopores open freely on the sternite (Guglielmo & Costanzo 1983). The thelyca differ from species to species, and it has been shown that the

special form is a diagnostic character for distinguishing species (see, e.g. Einarsson 1942; Costanzo & Guglielmo 1976; Guglielmo & Costanzo 1978, 1983, for more details). Thelycum-like structures are also found in Dendrobranchiata and some Reptantia within the Decapoda (Schram 1986), but since detailed information on their development is lacking, it is not clear if these structures are homologous to those of the Euphausiacea. Hence, it remains uncertain if this could hold as an autapomorphy of a taxon Eucarida, uniting Euphausiacea and Decapoda. The status of the Amphionidacea, which are currently also understood as a member of the Eucarida, is also unclear because the only species, *Amphionides reynaudii* (Milne-Edwards 1838) is still poorly known. A thelycum is present in *Bentheuphausia amblyops* and thus definitely part of the ground pattern of Euphausiacea. Since *Nyctiphanes couchi* is a member of the monophylum *Nyctiphanes*, which again is a member of the monophyletic Euphausiinae, it is assumed that the thelycum has been lost in *Nyctiphanes couchi*, representing an autapomorphy of this species.

No character coded

Proposed phylogeny of the Euphausiacea

The sets of characters discussed above as being autapomorphic for Euphausiacea and its subordinate taxa are summarised below and visualised in a phylogenetic diagram in Figure 22. Most of the traditional taxa can be confirmed by our work (Euphausiacea, Euphausiidae and Euphausiinae) but, in most cases, newly characterised, while more monophyletic units have been recognised. For these groups, names are proposed related to the name *Euphausia* or *Nematoscelis* but using endings to address to their in-group status. Nematoscelini respectively Nematoscelina were chosen with reference to Nematoscelinae of Colosi (1917) of the traditional classification, but with a different content of species.

Euphausiacea = *Bentheuphausia amblyops* + *Euphausiidae*

Autapomorphies of the stem species of Euphausiacea are (1 in Fig. 22):

1. adult antenna with coxae and basis fused to an unsegmented limb stem (plesiomorphic character state: coxa and basis separated, as in Decapoda, Lophogastrida and other Malacostraca);

2. adult pair of maxillulae with a three-segmented endopod (plesiomorphic state: endopod at least four-segmented, as in Decapoda);
3. adult endopod of eighth thoracopod consisting of four podomeres but as long as the five-segmented endopods of the preceding thoracopods (plesiomorphic state: endopod with five podomeres, as in Decapoda and Lophogastrida);
4. one pair of large, flattened, and broad spines ('subapical appendages') at the pointed telson of the adult, developed from smaller postero-lateral bristle-like spines of the larvae by reduction of all other larval furcal spines (plesiomorphic state: no such modification of the furcal armature paralleled by furcal morphogenesis and no such spines, as in Decapoda and Lophogastrida).

Due to the unknown larval development of *Bentheuphausia amblyops*, it remains uncertain if the following three characters can be considered as autapomorphies of either the Euphausiacea or the Euphausiidae (1a in Fig. 22). Better knowledge of the ontogeny of *B. amblyops* will solve these problems:

1. antennula with a lateral spine on proximal portion of the peduncle from Calyptopis III on to the last Furcilia stage (plesiomorphic state: no such spine throughout development);
2. stem of uropod of early larvae with a spine at the antero-distal edge just between the insertion areas of the rami (plesiomorphic state: no such spine throughout development);
3. larval second to sixth thoracopods resemble already those of the adults (plesiomorphic state: thoracopods II–VI resemble thoracopod I at first and develop gradually into adult shape).

The blind *Bentheuphausia amblyops* is a deep-sea species that lives at depths below 1000 m during its whole life. Out-group comparisons suggest that presence of fully functional compound eyes should represent the plesiomorphic character state. Hence, the lack of compound eyes should be regarded as a reduction and autapomorphy of *Bentheuphausia amblyops* (2 in Fig. 22), in contrast to its sister group, the Euphausiidae, which have retained the eyes. Reduction of compound eyes does occur in some species of Euphausiidae too, especially in the taxon *Thysanopoda*, which includes also deep-sea species, but this must, in consequence, be interpreted as convergent development.

Euphausiidae = 'Thysanopoda' + Nematobranchion + *Euphausiinae*

Autapomorphies of Euphausiidae are (3 in Fig. 22):

1. endopod of maxillula consisting of two portions in early larval stages (plesiomorphic state: more than two, as in *Bentheuphausia amblyops*);
2. endopod of maxillula undivided in late larval stages and the adult (plesiomorphic state: endopod tripartite, as in *Bentheuphausia amblyops*);
3. adult endopod of maxilla undivided (plesiomorphic state: tripartite, as in *Bentheuphausia amblyops*);
4. endopod of eighth pair of thoracopods missing (plesiomorphic state: a well-developed, quadripartite ramus, as in *Bentheuphausia amblyops*);
5. exopod of eighth pair of thoracopods reduced in size (plesiomorphic state: of same shape and size as the exopod of the preceding thoracopods, as in *Bentheuphausia amblyops*);
6. endopod of first two pleopods with lobes and processes (plesiomorphic state: all pleopods similar to each other, lacking lobes and processes, as in *Bentheuphausia amblyops*);
7. exopod of uropod undivided (plesiomorphic state: bipartite, as in *Bentheuphausia amblyops*).

No autapomorphies could be found to support the monophyletic state of the taxon *Thysanopoda* and synapomorphies to support the sister group relationship of this taxon with *Nematobranchion*, as opposed to Euphausiinae. More likely that *Thysanopoda* is a paraphyletic assemblage, but more data are needed still. One autapomorphy of *Nematobranchion* are the elongated third thoracopods of the adults. Furthermore, the second thoracopod has three little spines at its distal podomere (Zimmer & Gruner 1956, their Fig. 54) that is only developed in *Nematobranchion* (4 in Fig. 22). Moreover, there are no processes at the petasma of males and the Lobus internus and the Lobus medius of the petasma are fused, according to Weigmann-Haass (1987), but it has to be confirmed still if this is exclusive for *Nematobranchion*. The exclusion of *Thysanopoda* and *Nematobranchion* from the Euphausiinae is due to their lack of shared characters with this taxon considered as its autapomorphies (see below).

Euphausiinae = *Meganyctiphanes norvegica* + *Euphausiini* + *Nematoscelini*

Autapomorphies of the Euphausiinae are (5 in Fig. 22):

1. endopod of seventh thoracopod of adults with two podomeres, but of an equal size compared to the endopod of sixth thoracopod (plesiomorphic state: five podomeres);
2. exopod of eighth thoracopod of adults reduced and undivided (plesiomorphic state: exopod comprises a proximal, uniform portion and a distal, annulated portion with two setae per annulus).

Baker et al. (1990) diagnosed, in their identification key, *Meganctiphanes norvegica* on the basis of partly plesiomorphic characters and of features known also from other species. We could not find any clear autapomorphy in their description, but we have not investigated this species systematically. We also could not find any synapomorphic characters that would support a sister group relationship of two of the three taxa to resolve the in-group relationships of Euphausiinae.

Euphausiini = *Euphausia* + *Pseudeuphausia*

The only autapomorphy of the Euphausiini we recognised is (6 in Fig. 22):

1. endopod of seventh thoracopod of adults lost (plesiomorphic state: endopod present with five podomeres).

Colosi (1917) already combined *Euphausia* and *Pseudeuphausia* under the name 'Euphausinae'. Yet, both taxa, traditionally treated as genera, have still proven to be monophyletic.

Autapomorphies of *Euphausia superba* are (as compared to other species of Euphausiacea):

1. thoracopods II–VI as Anlagen in Calytopis III (plesiomorphic state: Anlagen earliest in Furcilia I);
2. thoracopods II–VI with distinct portions in Furcilia II (plesiomorphic state: comparable differentiation later in development).

Nematoscelini = *Nyctiphanes* + *Nematoscelina*

The only autapomorphy of the Nematoscelini we could find is (7 in Fig. 22):

1. the two distal portions of the antennular peduncle are distinctly narrower than the proximal portion (plesiomorphic state: all portions have the same thickness).

Nyctiphanes is considered as monophyletic, being characterised by the lack of exopods on the sixth

and seventh thoracopods of adult females (Zimmer & Gruner 1956). A possible additional autapomorphy is the reduction of processes of the petasma, as mentioned by Weigmann-Haass (1987) (8 in Fig. 22). Only the processus spinosus and the processus lateralis are developed in this taxon, but this has still to be investigated in more detail also for all other euphausiids.

Nematoscelina = *Thysanoessa raschi* + *Th. spinifera* + *NN*

Autapomorphies for the Nematoscelina are (9 in Fig. 22):

1. antennular flagella as long as the peduncle and with few number of annuli (plesiomorphic state: at least twice as long as the peduncle and with numerous annuli),
2. two-divided endopod of the seventh thoracopod only slightly longer than the corresponding exopod (plesiomorphic state: of an equal size compared to the endopod of sixth thoracopod, i.e. more than three times as long as the exopod, though two-divided),
3. females lacking endopods on the sixth and seventh thoracopods (plesiomorphic state: endopod of sixth thoracopod present, consisting of five podomeres; endopod of seventh thoracopod present, consisting of two podomeres).

Stylocheiron is most likely monophyletic due to the missing photophores in the coxae of the second thoracopod and within the sternites of the second to fourth pleomeres in all species. All other taxa within the Euphausiini, traditionally treated as genera, such as *Euphausia*, *Pseudeuphausia*, and *Nematoscelis*, have still proven to be monophyletic. '*Thysanoessa*' is, according to our proposed phylogenetic scheme, a paraphyletic assemblage (see above); at least *Thysanoessa raschi* and *Th. spinifera* do not belong to *Thysanoessa* s. str.

Some difficulties remain with the phylogenetic diagram, as presented (Fig. 22). One problem is the mode of egg release. Taxa, such as *Bentheuphausia amblyops*, *Thysanopoda*, *Meganctiphanes norvegica*, *Euphausia*, and at least two lines of the paraphylum '*Thysanoessa*' release their eggs into the water column. Free egg release also occurs in the Dendrobranchiata (Decapoda). By contrast, the females of *Nyctiphanes*, *Pseudeuphausia*, *Nematoscelis*, *Stylocheiron* and *Tessarabrachion oculatum* carry their

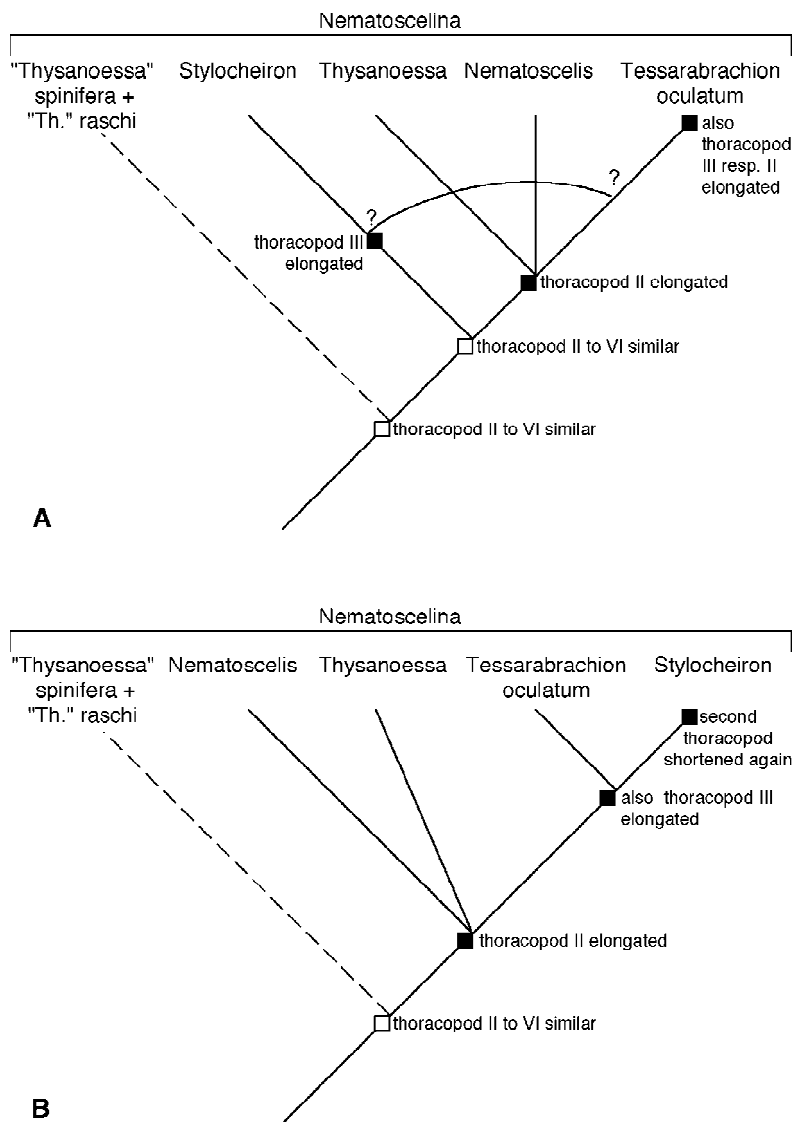


Figure 23. Four hypotheses for the distribution of elongated thoracopods within the Nematoscelina (see text for explanation). Figure 23A refers to hypothesis 1, Figure 23B to hypothesis 2 and so on. The other characters discussed for each taxon (genus) are not named.

eggs by their posterior thoracopods until hatching. There are no additional structures evolved like for instance the oöstegites in Peracarida incl. Lophogastrida. This is also in contrast to the Pleocyemata (Decapoda) that carry their eggs and young by their pleopods.

Assuming that free release of eggs and no brood care represents the plesiomorphic state, the resulting phylogenetic diagram implies that egg carriage (brood care) could have developed four times independently within the Euphausiidae, viz. in *Nematobrachion*, in *Nyctiphanes*, in *Pseudeuphausia*, and in *Nematoscelis*

+ *Stylocheiron* + *Tassarabrachion oculatum* among the Nematoscelina.

Alternatively, egg carriage on thoracopods might have been developed, as an autapomorphy, in the stem species of a taxon N.N. embracing all Euphausiidae except '*Thysanopoda*', while the taxa *Meganyctiphanes norvegica*, *Euphausia*, and at least two lines of the paraphylum '*Thysanoessa*' must have lost this carriage capability again. A problem is that the mechanisms of holding the eggs and the number of limbs involved seem to differ between the taxa. Unfortunately, the available literature gives no clues

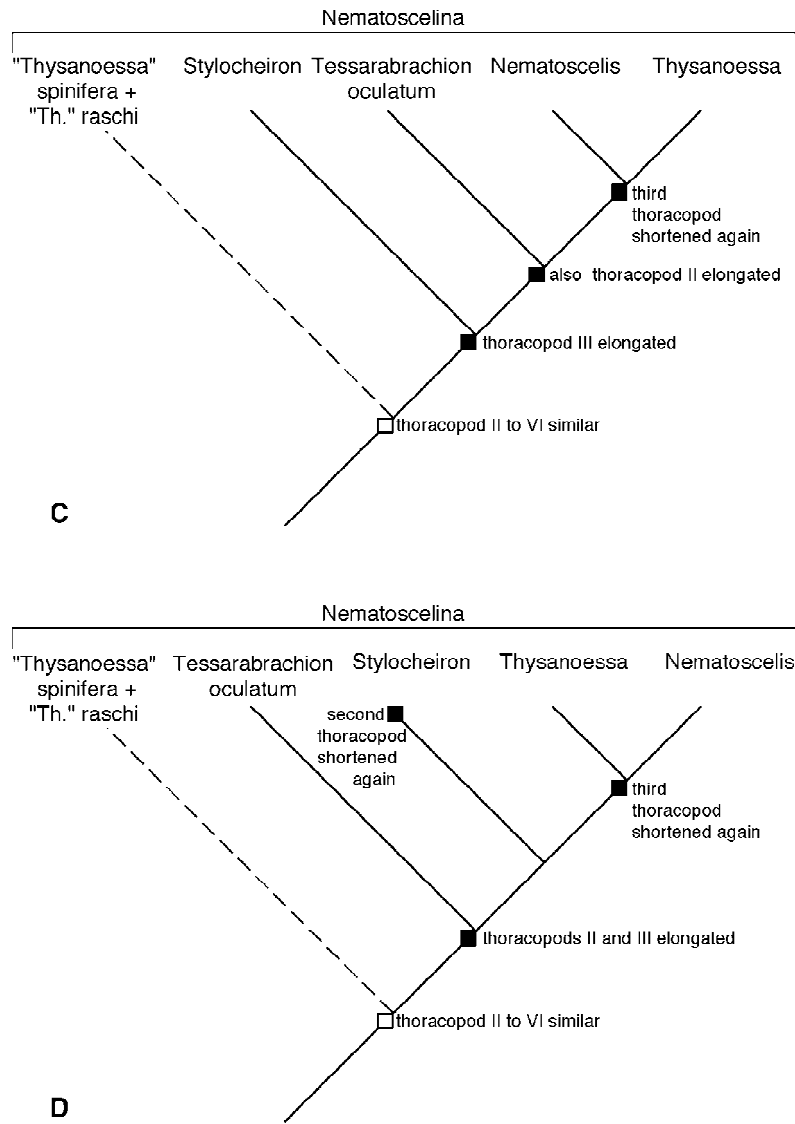


Figure 23. Continued.

about the detailed mechanism of carrying the eggs in the different taxa that could support more strongly the one or other alternative. Since we investigated *Euphausia superba* and all species of *Euphausia* do not do brood care, we can not contribute additional facts to this question.

If, as an alternative, egg carriage on thoracopods represents the plesiomorphic state for Euphausiacea, this would imply that loss of this habit should have occurred at least six times independently within the Euphausiacea, i.e. in *Bentheuphausia amblyops*, in *Thysanopoda*, in *Meganycitiphanes norvegica*, in *Euphausia*, and, at least twice, in the paraphylum

'*Thysanoessa*'. This would only hold if *Thysanopoda* would represent a monophylum, which is at the least uncertain. This problem cannot be solved on the basis of our investigations and the currently available data. Since brood care is done in many different ways among the Euphausiacea (by thoracopods), by the Peracarida (by thoracopods with oöstegites) and by Pleocyemata (by pleopods), all three methods have presumably evolved independently from each other. We coded the character due to the evidence that brood care together with the elongated thoracopods within the Nematoscelina can be used to answer the question

how the four taxa within the Nematoscelina are related to each other.

Character coding (Table 4):

Character 19: brood care:

- 0: not made,
- 1: made without oöstegites,
- 2: made with oöstegites.

Conclusions

One significant process in the evolution of the Euphausiacea is seen in the gradual reduction of the seventh and eighth thoracopods, paralleled by an increase in size of the epipodite of these limbs. To explain this phenomenon, one had to compare the life of different species with different reduction states of thoracopods VII and VIII. A rearing of euphausiacean species would also be very helpful, but the past has shown that the Antarctic Krill is a very difficult species for rearing, since the animals die very fast after setting them into an aquarium (Gopalakrishnan 1973). It would be interesting to know more about egg release and brood care, which is a critical character in the interpretation of the systematic relationships within Euphausiacea and is also related to the particular design and development of the thoracopods, especially the also critical elongation phenomenon.

Our results demonstrate that larval features may well aid in the phylogenetic analysis of crustacean groups. Even more, one of the major problems for a better understanding of the phylogeny of Euphausiacea and its systematic relationships to other eumalacostracan taxa remains the lack of data on larval development, particularly that of *Bentheuphausia amblyops*.

Concerning our methodological approach, using SEM for documentation, it became evident that the material often has shrunk during the drying process, a special problem we faced immediately when trying to fix the fragile and soft-integumented larvae of *Euphausia superba*. Anyway, SEM yielded very detailed information of cuticular structures, such as segment boundaries, joints, pores, setation and surface ornamentations. All of these have proven to represent useful data for phylogenetic analyses, as evident from the studies of the Cambrian 'Orsten' fossils (e.g. Walossek & Müller 1990; Walossek 1993). However, they have not yet been accumulated for extant crustaceans as could have been done. SEM is a very

up-to-date method for comparative morphology (see, e.g. Olesen & Walossek 2000) and should be applied to similar studies to a much larger extent, especially in regard to considering larval stages (Dahms 2000).

Fossil record of Euphausiacea

There is no fossil species known that has been assigned beyond doubt to the Euphausiacea. Taxa such as *Anthracophausia* Peach, 1908, *Crangopsis* Salter, 1864, or *Palaeomysis* Peach, 1908 had been thought to be euphausiaceans (cf. Schram 1986). They are certainly eumalacostracans but clearly cannot be assigned with any certainty to any particular in-group except from *Crangopsis* that is now assigned to the Aeschronectida (Hoplocarida) (Schram, pers. commun., 2000).

Presented phylogenetic system of the Euphausiacea

Euphausiacea Dana, 1852

Bentheuphausia amblyops (G. O. Sars, 1883)

(= *Bentheuphausia* G. O. Sars, 1885

= *Bentheuphausiidae* Colosi, 1917)

Euphausiidae Dana, 1852

Thysanopoda H. Milne-Edwards, 1837

Nematobranchion Hansen, 1911

Euphausiinae Holt & Tattersall, 1905

Meganyctiphanes norvegica (M. Sars, 1857)

(= *Meganyctiphanes* Holt & Tattersall, 1905)

Euphausiini, new name (*Euphausia* Dana,

1852, *Pseudeuphausia* Hansen, 1911)

Nematoscelini, new name

Nyctiphanes G. O. Sars, 1883

Nematoscelina, new name ('*Thysanoessa*'
raschi (M. Sars, 1864),

'*Thysanoessa*' *spinifera* Holmes, 1900,

Thysanoessa Brandt, 1851,

Nematoscelis G. O. Sars, 1883,

Stylocheiron G. O. Sars, 1883,

Tessarabrachion oculatum Hansen, 1911

(= *Tessarabrachion* Hansen, 1911).

Acknowledgements

We are grateful to Prof. Dr Krzysztof Jazdzewski, University of Lodz, Poland, and Dr Sigrid Schiel, Alfred-Wegener-Institute for Polar Research, Bremerhaven, for supply of specimens of larval and adult

Euphausia superba. Thanks are also due to Dr Wilko Ahlrichs, University of Ulm, and to Prof. Dr Euan N. K. Clarkson, University of Edinburgh, for critical revision of this paper. We also want to thank Prof. Dr Angelika Brandt, University of Hamburg, and Dr George Wilson, Australian Museum, Sydney, for their information about the *lacinia mobilis* of the Peracarida. Special thanks go to Prof. Dr Frederick R. Schram, University of Amsterdam, for his critical review of the manuscript, his support with the PAUP program during a visit of AM at his institute, and stimulating discussions about Euphausiacea and Crustacea in general.

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