

Postembryonic Apomorphies Proving the Monophyletic Status of the Copepoda

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(Accepted February 15, 2004)

Hans-U. Dahms (2004) Postembryonic apomorphies proving the monophyletic status of the Copepoda. *Zoological Studies* 43(2): 446-453. Postembryonic characters were screened for their relevance for providing apomorphies for major maxillopodan groups with an emphasis on the Copepoda. The analysis used characters which have previously been suggested in the literature, as well as hitherto unemployed ones based on own observations. A cladogram based on postembryonic characters partly confirms and partly contradicts previous hypotheses about phylogenetic relationships within/of the Copepoda, which are mainly based on adult characters. Hypothesized naupliar apomorphies confirm the monophyletic status of the Thecostraca, Copepoda, Podoplea, Harpacticoida Oligoarthra (the Harpacticoida Polyarthra were excluded from this comparison and treated separately due to their overall plesiomorphic character states), and Calanoida. A sister-group relationship based on naupliar characters is hypothesized for the Copepoda/Thecostraca. As for copepod nauplii, the following autapomorphies are suggested: 3-segmented antennule, 2 antennal coxal setae, 1-segmented antennal endopod, postmaxillar limb buds juxtaposed medially, legs 1 and 2 present at N VI, and 6 caudal setae. A swimming mode of locomotion is suggested to represent the underived mode of locomotion among copepod nauplii and results directly in naupliar feeding. The metamorphosis to the copepodid phase in particular is unprecedented among extant Crustacea: involving somite and limb addition, and transformation of limbs which become reduced, functional, or follow changes from a locomotive to a feeding function. This provides copepod ontogeny with a peculiar way of anagenetic development, including both the naupliar and the copepodid phase, which differs from those of other Crustacea in several respects.
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Key words: Phylogeny, Ontogeny, Larval characters, Systematics, Maxillopoda.

In organisms with larval development, both early and late developmental stages show characters of the same genotype. However, in most cases, only the adults have so far been used for reconstructing phylogenetic relationships, although larvae provide a rich source of additional morphological, behavioral, and ecological characters. Therefore, evidence from postembryonic stages may complement those gained from adult characters since an individual exhibits different and significant characters at all phases of its ontogeny which can be used as holomorphological species-specific character patterns of evolutionary species (Hennig 1966, Ax 1987).

Until now, mostly characters of adult morphology have been used to characterize the Copepoda

as a monophylum. However, postembryonic instars, both early (i.e., nauplii) and later stages (i.e., copepodids), do provide a rich source of additional morphological, behavioral, and ecological characters for evolutionary hypotheses. Qualitative and quantitative structural additions as well as reductions or functional transformations take place during postembryonic ontogeny in the Copepoda. Furthermore, besides structural, meristic, and allometric differences and the mere number of stages, postembryonic development contributes another type of character: developmental allometry and the sequence of changes during development.

The present study provides insights into constituent naupliar and copepodid characters of the

Copepoda. The postembryonic stages of the Copepoda are compared with homologous stages, and structures of non-maxillopodan Crustacea, such as the Cephalocarida and Branchiopoda, and maxillopodan groups such as the Thecostraca, Mystacocarida, and Ostracoda. The Tantulocarida is omitted from this comparison because it does not develop naupliar stages.

MATERIALS AND METHODS

Nauplii were collected from the field or were reared from ovigerous females. Collection sites are given in the references cited below. Rearing and preparation techniques are described by Dahms (1990). The cladogram (Fig. 1) was generated by hand, and the character states are based on out- and in-group comparisons, as summarized in table 1. Replacing or dependent characters (e.g., loss of caudal process vs. asymmetry of the hind body) are treated as discrete characters rather than as multistate characters (Pleijel 1996).

Characters were assembled from personal observations and various sources in the literature, including especially and if not stated otherwise, for Cephalocarida (Sanders 1963), Branchiopoda (Walossek 1993, Olesen 1999), Mystacocarida (Delamare Deboutteville 1954, Olesen 2001), Ostracoda (Kesling 1951, Swanson 1989), Thecostraca (Bassindale 1936, Ito 1986, Grygier 1987, Glenner et al. 1995), Harpacticoida (Dahms 1990, 1991), Cyclopoida (Koga 1984, Dahms and Fernando 1992, Ferrari 2000, Ferrari and Ivanenko 2001), Poecilostomatoida (Izawa 1986), and Calanoida (Song and Jinchuan 1990, Dahms and

Fernando 1993). The following contributions were used for general information about crustacean nauplii or maxillopodan phylogeny: Koga (1984), Bjørnberg (1986), Izawa (1986), Schram (1986), Grygier (1987), and Boxshall and Huys (1989). Nauplii are defined as those ontogenetic stages which still bear the antennal enditic process, while metanauplii have more than the 3 appendages of A1, A2, and Md developed, if only as limb buds.

Abbreviations used: N I to N VI, 1st to 6th naupliar stage; C I to C VI, 1st to 6th copepodid; A1/A2, antennule/antenna; Md, mandible; Mx1/Mx2, maxillule/maxilla; Mxp, maxilliped; naup, nauplius; enp/exp, endopod/exopod; seg I, II, 1st, 2nd segment; metamorph, metamorphosis; develop, development; and >, larger, more or later.

RESULTS

An evaluation of postembryonic characters yielded several synapomorphies for the taxa under consideration (Fig. 1, Table 1).

Three naupliar synapomorphies are hypothesized to unite Thecostraca Gruvel, 1905 (comprised of Cirripedia, Ascothoracida, and Facetotecta (see Grygier 1987), and its sister-taxon Copepoda as a monophylum (characters 1-3).

Table 1. Character evaluation for the analysis of copepod relationships based on nauplii

Character	Plesiomorphic state	Apomorphic state
1 No. of naupliar stages	> 6	6
2 Somite borders	present	absent
3 Pronounced metamorph.	absent	present
4 Frontal filaments	absent	present
5 Postmaxillary limbs	present	absent
6 A2 coxa	?	2 setae at N III
7 A2 enp.	3-segmented	1-segmented
8 Postmaxillary limbs	with medial gap	juxtaposed medially
9 Legs 1, and 2	present > N VI	present at N VI
10 No. of caudal setae	< 6	6
11 Legs 2, and 3	different	biramous at C I

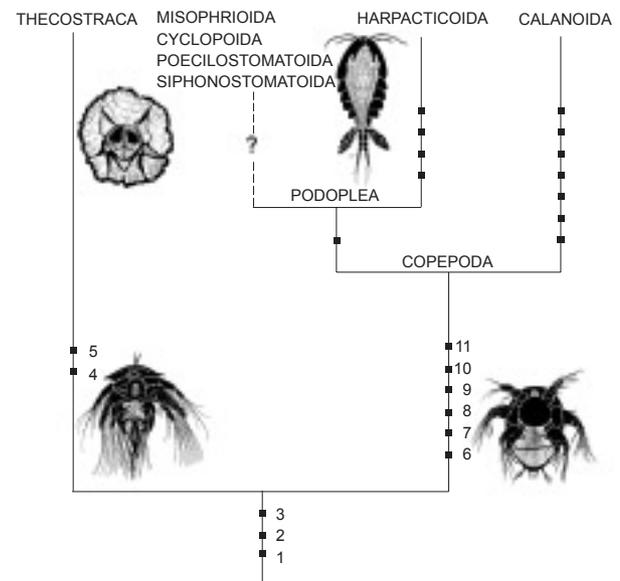


Fig. 1. Cladogram depicting the phylogenetic relationships of the Copepoda and Thecostraca based on postembryonic apomorphies (for the phylogenetic evaluation of the character states, see also table 1).

1. Six naupliar stages (Fig. 2)

There are 10-13 naupliar stages in Cephalocarida, a variable number of stages in Branchiopoda (only 7 stages according to Sanders (1963)), and up to 10 stages in Mystacocarida (Olesen 2001). There are 6 stages in Thecostraca (while it is still uncertain whether Facetotecta comprise 5 or 6 stages, see Itô 1990). It can safely be maintained that the maximum and most common number of naupliar stages in all major groups of Copepoda is 6 as well, providing a good synapomorphy for Thecostraca and Copepoda (and possibly Mystacocarida). These groups never show more than 6 naupliar stages. Exceptions with fewer instars are known in groups with yolky eggs and lecithotrophic nauplii. Lecithotrophy is the main cause for stage reduction in several unrelated copepod taxa (see Dahms 1989). The number of naupliar stages varies from 6 to 1. For instance, *Misophria pallida* Boeck, 1865 (Misophrioida) is supposed to have only 1 lecithotrophic nauplius from which the 1st copepodid emerges (Gurney 1923). The development of yolky eggs in unrelated taxa is the major cause for abbreviated naupliar development. A decrease in naupliar stages, therefore, has evolved independently in several lineages.

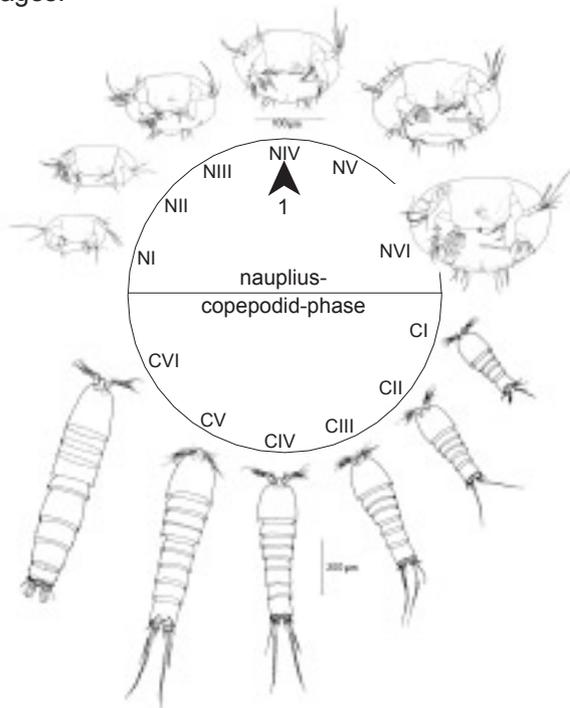


Fig. 2. Naupliar phase of the life cycle comprised of naupliar stages (1) Shown here is the life cycle of *Paramphiascella fulvofasciata* Rosenfield & Coull, 1974 (Copepoda, Harpacticoida).

2. Lack of somite borders (Fig. 3)

The metanauplii of Cephalocarida, Branchiopoda, and Mystacocarida are characterized by distinct somite borders of the postcephalic somites. In Thecostraca and Copepoda, all naupliar somites are usually fused.

3. Pronounced metamorphosis (Fig. 3)

Cephalocarida, Branchiopoda, and Mystacocarida show a rather gradual development with no striking metamorphosis in their respective series of molts (the naupliar phase ends here merely with the loss of the antennal coxal process). In Thecostraca, on the other hand, the end of the naupliar phase is marked by a molt to the cypris larva, and then to the presumably highly transformed adult (adults are not known for Facetotecta so far). Metamorphosis to the cypris larva is suggested to be homologous with that from nauplius VI to copepodid I in the Copepoda, providing a useful synapomorphy.

Thecostraca have 2 naupliar characters in common which are unique among crustacean nauplii and provide powerful synapomorphies (characters 4 and 5).

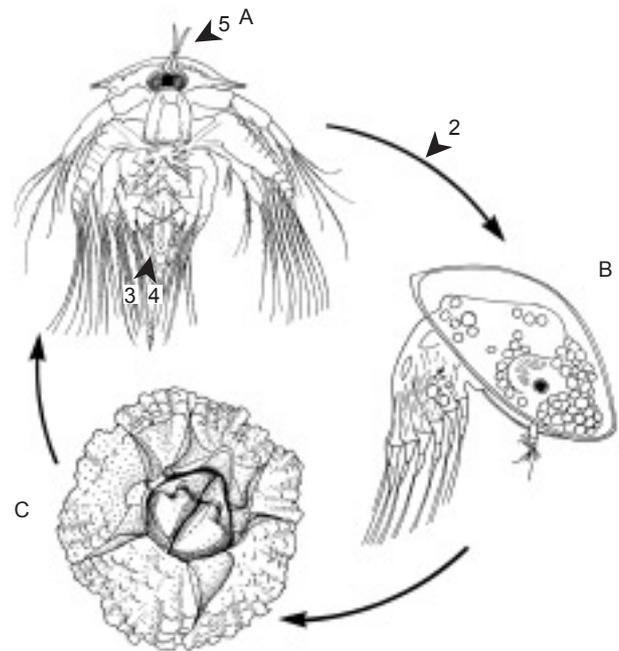


Fig. 3. Thecostracan nauplii showing a pronounced metamorphosis (2), lack of somite borders (3), lack of postmaxillary limbs, (4) and frontal filaments (5). Here the life cycle of *Semibalanus balanoides* (Linnaeus, 1758)(Cirripedia).

4. Absence of postmaxillary limbs (Fig. 3)

Postmaxillary appendages are subsequently added in the metanaupliar development of Cephalocarida, Mystacocarida, Branchiopoda, and Copepoda. In Thecostraca, there is no indication of any postmaxillary appendage.

5. Frontal filaments (Fig. 3)

The thecostracan frontal filaments are located as a pair of medial, presumably sensory organs, anteriorly to the base of the labrum. They become associated with the compound eye in later stages (see Glenner et al. 1995).

Copepod nauplii are characterized by 6 synapomorphies, related to the sequence and position of appendage development and meristic characters of the appendages (characters 6-13).

6. Two antennal coxal setae (Fig. 4)

Besides the antennal enditic process of the coxa which is present (although rudimentary in N I) throughout the phase, there is a peculiar strong seta at the base of this process which develops at the N III stage in Calanoida and Cyclopoida (Dahms and Fernando 1992). In some species of Harpacticoida, a presumably homologous seta is



Fig. 4. Copepod nauplii bearing 2 setae at N II of the antennal coxa (6) and a 1-segmented antennal endopod (7). Here the N I of *Longipedia minor* T. & A. Scott, 1893 (Harpacticoida - Polyarthra).

present throughout the phase (Dahms 1990). However, if this is strongly developed, it appears also in harpacticoids not before the N III stage (e.g., the Harpacticidae, and Thalestridae; see Dahms 1990). Its inconsistency and unsettled state compared to other Maxillopoda makes it a weak apomorphy for the Copepoda as yet.

7. One-segmented antennal endopod (Fig. 4)

The antennal endopod is 2-segmented in Cephalocarida, 3-segmented in Mystacocarida, Cirripedia, and Ascothoracida of Thecostraca, but 2-segmented in Facetotecta. Therefore, it is argued that a 1-segmented naupliar antennal endopod, which is present without exception among copepod nauplii, is a strong apomorphy for the Copepoda. There are spinule rows, possibly indicating a former 2-segmented state (or even a 4-segmented state at later stages) of this ramus in *Longipedia minor* T. & A. Scott, 1893, belonging to Polyarthra (Dahms 1991).

8. Postmaxillar limb buds juxtaposed medially (Fig. 5)

In Cephalocarida, Branchiopoda, and Mystacocarida, the postmaxillary appendages are gaped medially, probably to provide space for a medial food groove. This character is not available in

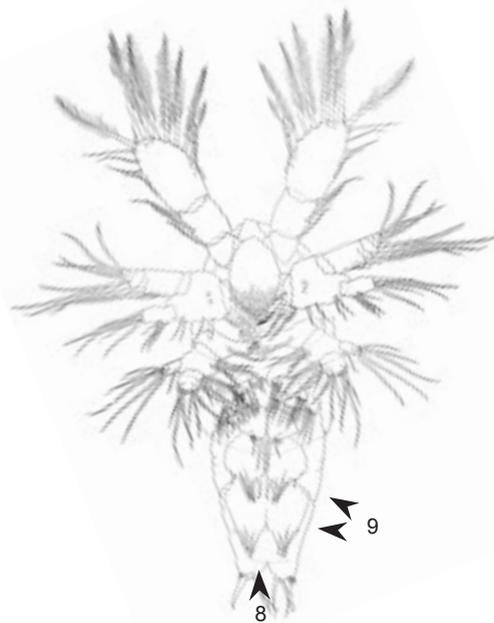


Fig. 5. Copepod nauplii with postmaxillar limbs juxtaposed medially (8), their legs 1 and 2 present at N VI stage (9), and their number of caudal setae of 6 (10). Here the N VI of *Phyllodiptomus annae* Apstein, 1907 (Calanoida).

Thecostraca since their nauplii lack postmaxillary appendages. Postmaxillary appendages are juxtaposed medially in Cyclopoida, Polyarthra, and Calanoida, whereas they are widely spaced secondarily in the derived Harpacticoida Oligoarthra. This positional peculiarity indicates a striking difference between copepod cephalic (A1 to Mx2) and thoracic (Mxp to P2) appendages (see Izawa 1987).

9. Legs 1 and 2 present at N VI (Fig. 5)

The sudden external appearance of the 2nd and 3rd thoracic appendages as limb buds, as a rule not before N VI in all major copepod taxa, is a unique character compared to other crustacean nauplii (see Walossek 1993) and, therefore, a strong apomorphy for the Copepoda. It is doubtful that any further limb bud will develop in copepod nauplii as proposed by Izawa (1987), who observed leg 3 at N VI in the descriptions of various authors. This pair of limbs belong to the 1st copepodid, becoming visible through the naupliar cuticle of intermolt stages only (see Dahms 1992). Exceptions in the form of reductions are provided by certain Harpacticoida Oligoarthra (e.g., *Macrosetella gracilis* (Dana, 1847)) where naupliar postmaxillary limb formation is reduced (Dahms 1990).

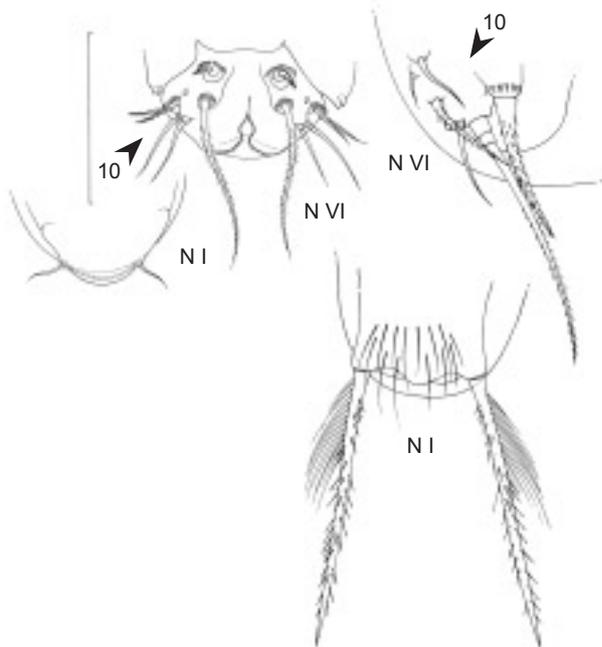


Fig. 6. Copepod nauplii with 6 caudal setae (10). Shown here are: A. *Phyllognathopus viguieri* (Maupas, 1892) and B. *Canuella perplexa* T. & A. Scott, 1893 (Harpacticoida)(scale bar, 50 μm).

10. Six caudal setae (Fig. 6)

The caudal armature of non-copepod nauplii is difficult to ascertain, since spiniform processes may or may not have setal precursors. However, Cephalocarida, Branchiopoda, Mystacocarida, and Thecostraca have fewer than 6 caudal setae on each prospective caudal ramus. Six naupliar setae are widespread, and this is the maximum number among all major copepod taxa. Six setae are present in primitive groups of Harpacticoida, but often become reduced in derived Harpacticoida. Caudal setae are often reduced in Calanoida. A “full-set condition” of 6 caudal setae cannot be an apomorphy of Poecilostomatoida, as suggested by Izawa (1987), because it is the plesiomorphic attribute already present in the ancestral copepod nauplius.

11. Biramous legs 1 and 2 of copepodid I stage (Fig. 7)

The anameric mode of somite addition during the naupliar and copepodid phases and especially the presence of biramous legs 1 and 2 at copepodid I (see Dahms 1993, Ferrari 2000) are unprecedented among the Crustacea (see also Walossek 1993).

DISCUSSION

	C I	C II	C III	C IV	C V	C VI
P1						
P2						
P3						
P4						
P5						

Fig. 7. Copepodid development showing biramous legs 1, and 2 at copepodid I (11). Here a schematic illustration of leg segment formation is shown during copepodid development.

Phylogenetic relationships of and within the Copepoda

The cladogram of copepod relationships based on naupliar characters (Fig. 1) does not consider all maxillopodan taxa, due either to the lack of nauplii (Branchiura, if they belong to the Maxillopoda at all, see Abele et al. 1992; Tantulocarida) or the limited data available (Ostracoda and Mystacocarida). The proposed sister-group relationship and monophyletic status of the Thecostraca and Copepoda was previously suggested by Schram (1986) who based his conclusions mainly on adult characters. His cladogram results in an unresolved tritomy, with the Tantulocarida as 1 branch, the Thecostraca and its sister-taxon Copepoda as the 2nd, leaving the Branchiura, Mystacocarida, and Ostracoda as the 3rd branch. The approach of Grygier (1987), using mainly naupliar characters, unites the Cirripedia, Ascothoracida, and Facetotecta into the monophyletic Thecostraca. He suggested that Branchiura was the sister-group of Thecostraca. The Copepoda, showing the most plesiomorphic character states, were regarded as the sister-group of the Branchiura-Thecostraca clade. Grygier (1987) provides no synapomorphy uniting the Branchiura, Thecostraca, and Copepoda. Boxshall and Huys (1989) recognized 2 main lineages within the Maxillopoda, one leading to the Copepoda (comprising the Copepoda, Mystacocarida, and, Skaracarida) and the other to the Thecostraca (comprising Thecostraca, Branchiura, and Ostracoda). The latter 2 studies basically agree and support a 2-lineage concept within the Maxillopoda, which is also suggested by the present study. The present study, however, is largely based on hitherto unconsidered naupliar characters.

Despite its preliminary nature, naupliar synapomorphies of the present study indicate that the Thecostraca and Copepoda of the "Maxillopoda" are closely related.

As for adult characters, there was a previous suggestion for an "ancestral copepod" (Boxshall et al. 1986). Recent approaches suggest the Calanoida (Boxshall 1986), Platycopioida and Calanoida (Ho 1990), or the Platycopioida (Huys and Boxshall 1991) as the sister-group of all remaining copepod taxa combined.

The author is aware of the fact that the possession of a number of strong synapomorphies as such does not provide full proof of a monophylum, because it could also pertain to a paraphyletic

assemblage if not all descendants of the ancestor have been included.

Obstacles to the phylogenetic use of postembryonic characters

There are several reasons why naupliar characters have thus far been widely neglected in systematic and phylogenetic studies: 1) - the difficulty in obtaining detailed information on naupliar characters; 2) - the fact that nauplii provide fewer characters than later ontogenetic instars and adults; 3) - the lack of appropriate comparative data; 4) - the fact that non-feeding nauplii mask or lack phylogenetically valuable structures; 5) - conflicting evidence when comparing adult and naupliar character states.

1) Like other instars, nauplii can be collected from the field, using fine-mesh nets, for instance. However, species identification is usually a problem, since no adequate descriptions exist, or accurate keys for their identification are lacking. Hence, it is most reliable to rear ontogenetic stages from isolated ovigerous females in the laboratory. In sensitive species, this requires a costly setup and rearing experience. On the other hand, as larvae are small organisms with miniature appendages, the latter are often superimposed on each other in microscopic preparations, and therefore difficult to accurately observe in sufficient detail. Oil immersion and interference-/phase contrast optics are indispensable in those cases. SEM is helpful but provides little evidence for structures hidden by superimposed limbs. Due to their small size, manual dissection is impossible with many nauplii.

2) Also due to their smaller size and number of appendages, nauplii offer fewer qualitative and quantitative characters than do later ontogenetic stages. For example adults in addition provide primary and secondary sexually dimorphic characters.

3) Nauplii of entire copepod orders and subordinate taxa are still unknown. Even when nauplii are described, the lack of detail, due to inadequate microscopes, experience, and/or illustration effort, frequently prevents the use of meaningful comparative data. Moreover, species descriptions are based only on adults and traditionally have been the main subject of systematic investigations. For this reason the database available for comparison is much larger for adults than for preadult stages.

4) Non-feeding, mostly as a result of lecithotrophy, causes certain structures to atrophy,

thus masking phylogenetically valuable characters (see Bjørnberg 1986). Lecithotrophy often, but not necessarily, leads to an abbreviation of naupliar stages (see Matthews 1964, Izawa 1987). Structural reductions are most pronounced in the feeding parts of the antenna and mandible. As demonstrated for a lecithotrophic harpacticoid nauplius (Dahms 1989), the armature of the coxa and basis as well as the medial protrusions and spines on the endopods are lacking; the labrum is reduced; neither mouth nor anal perforations are detectable; and there are no signs of a tubular gut. However, an oligomeric antennule as well as extreme reductions of the paired caudal armature, which is commonly found in yolky nauplii of strictly parasitic forms (see Izawa 1987), seem to be secondary acquisitions and possibly are not dependent on lecithotrophy. On the other hand, it is stated here that lecithotrophy can provide a situation where plesiomorphic character states are conservatively unchanged. This hypothesis is based on the assumption that no structural or behavioral adaptations are necessary for the otherwise important functional "feeding" complex. This may leave lecithotrophic nauplii conservatively unadapted to "feeding niche" requirements (Dahms 1989). Besides obligate lecithotrophic nauplii, most nauplii do not feed in the 1st stage. In the Harpacticoida, therefore, the antennal gnathobase is not differentiated in the 1st stage (Dahms 1990). In some unrelated harpacticoids, nauplii become non-feeding in the 6th stage. They show peculiar reductions in the oral structures from N V to N VI, such as loss of the labrum and ventral body wall ornamentation, as well as antennal and mandibular protopod armature. This holds for all nauplii of the Tachidiidae and Harpacticidae so far studied (Dahms 1991) and for the *Tisbe holothuriae* group (Dahms et al. 1991).

5) Different selection forces may act on different ontogenetic stages causing a divergent evolution of characters. This can be due to a different degree or pace of evolutionary radiation in either the naupliar or the copepodid phase. Also, either the naupliar or copepodid (and adult) organization may comprise characters leading to conflicting evidence when comparing phylogenetic character states of both phases. Bjørnberg (1986) argued that due to their small size and lower differentiation, nauplii have fewer structures which can be modified, whereas adults provide a larger number of characters. If this is true, nauplii of closely related taxa are more likely to conserve synapomorphies than their adults. It seems to me, on the

other hand, that naupliar characters could then mainly be represented by plesiomorphic states.

CONCLUSIONS

Maxillopodan and copepodan larval characters contribute in 2 ways to the elucidation of phylogenetic relationships. First, they can be used as independent plesio- or apomorphies in cladistic analyses. Also, a gradient (i.e., morphocline) can be traced from larval character states. Second, a polarity criterion for the direction of evolution can be gained, most reliably from characters that are reminiscent of former conditions. Even more valuable in this respect are characters that recapitulate former character states in the course of ontogeny.

The present analysis relied only on naupliar characters, some of which are unsatisfactory, since they either do not hold for all taxa belonging to a proposed monophylum or occur in other taxa as well. This is due in part to the pronounced radiation of maxillopodan nauplii where characters were diversified, lost, or are likely to have evolved by convergence. Furthermore, the status of the Mystacocarida and Ostracoda remains unresolved as far as nauplii are concerned. The Branchiura and Tantulocarida do not possess a free-living naupliar stage. Eventually, for a sufficient view of the phylogenetic relationships of and within the Copepoda, both postembryonic and adult characters should be considered and evaluated. Despite its preliminary nature, the present analysis indicates that there are 2 main lineages within maxillopodan nauplii, the 1st leading to the Thecostraca, and the 2nd to the Copepoda. Both taxa together compose a monophylum.

Acknowledgements: Parts of this study were funded by grants from the Deutsche Forschungsgemeinschaft to the author as principal investigator (DFG Da 256-7/1 and Da 256-10/1-3).

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