Evolution of Morphology, Ontogeny and Life Cycles within the Crustacea Thecostraca

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> Abstract

We use a previously published phylogenetic analysis of the Thecostraca to trace character evolution in the major lineages of the taxon. The phylogeny was based on both molecular (6,244 sites from 18S rna, 28S rna and H3 genes) and 41 larval morphological characters with broad taxon sampling across the Facetotecta (7 spp.), Ascothoracida (5 spp.), and Cirripedia (3 acrothoracican, 25 rhizocephalan and 39 thoracican spp.). Morphological apomorphies are identified in larval morphology for almost all major branches within the Thecostraca. Characters from the cypris larva provide a long suite of apomorphies for the Cirripedia and reinforce the concept that this larva was a prerequisite to the tremendous success of that taxon. The evolution of parasitism, obligatory in three major taxa, is discussed. We conclude that the last common ancestor to the Cirripedia was most likely a suspension feeder, and the advanced metamorphosis and endoparasitism known from the Rhizocephala and strongly indicated for the Facetotecta are the result of convergent evolution. We also discuss reproductive systems, which range from separate sexes, over hermaphrodites combined with a separate male sex (androdioecy), to pure hermaphroditism. It is concluded, as envisaged by Darwin, that the Thecostraca provide excellent opportunities for studying the evolution of a wide range of complex life history traits which can now be better analyzed and understood in a robust phylogenetic framework.

> Key words

1. Introduction

The taxon Thecostraca (class or subclass) encompasses three major groups: the Cirripedia, the Ascothoracida and the Facetotecta (Martin & Davis 2001). Due to evolving ideas of relationships and taxonomy within these groups, we do not use absolute rank in this paper; rather, we discuss relationships of these taxa only in terms of relationships of lineages. We then use these relationships to discuss morphological and life history trends in the different lineages.

The modern concept of the Thecostraca was not conceived until Grygier (1987a) but has nevertheless won almost universal acceptance and is reproduced in most text books (Brusca & Brusca 2002; Ruppert et al. 2004). While the monophyly of the Thecostraca is

rarely challenged, it has been particularly difficult to analyze the intrinsic phylogeny of the taxon, because it is one of the most variable groups within all Crustacea. This variability, present both within and among the three major lineages, concerns ontogeny, adult morphology, mode of life and especially the reproductive systems, and it renders the Thecostraca excellently suited for studying and testing theories on the evolution of a host of biological traits.

All thecostracans are sessile as adults. The larval development normally comprises a series of pelagic nauplii and is terminated by the cypridoid stage, which is specialized for attaching to a substratum and initiating the juvenile phase. Following Høeg et al. (2004), the cypridoid stage is called 'y-cyprid' in the Facetotecta, 'a-cyprid' in the Ascothoracida and simply 'cyprid' in the Cirripedia (Electronic Supplement video clip 1).

The **Cirripedia** (barnacles) comprises the Acrothoracica (burrowing barnacles), the Rhizocephala (parasitic barnacles) and the Thoracica (pedunculated and sessile barnacles). Like all other thecostracans, cirripedes are sessile as adults (Anderson 1994). The acrothoracicans and thoracicans have become specialized suspension feeders, using their six pairs of highly modified thoracopods (cirri) as a highly specialized basket for food capture. As a consequence, they contain modifications in the orientation of the body and the entire morphology. The acrothoracicans burrow into calcareous substrata, but most thoracicans are freely exposed, and their body is more or less completely armed by a system of mineralized shell plates. Thoracicans therefore sport a highly modified mode of moulting and growth, and Louis Agassiz is alleged to have described them as *"Nothing but a tiny little shrimp-like animal, standing on its head in a lime stone house and kicking food into its mouth"* (Ruppert & Barnes 1994). The Rhizocephala are all parasitic, their hosts being other Crustacea. The adult, developing from an internal parasitic phase, is highly reduced and has lost almost all arthropod traits such as segmentation and appendages. But within this highly modified body morphology, adult rhizocephalans display a remarkable morphological variation including forms where multiple parasites are produced by asexual budding from a common internal system of rootlets, a situation unique in the Arthropoda. The only morphological evidence that the Rhizocephala belong to the Cirripedia comes from the development of the larvae (Thompson 1836; Høeg & Møller 2006).

The **Ascothoracida** are also parasites, but the least modified members of the taxon have a morphology with few if any obvious adaptations to this mode of life. More advanced forms can be extensively modified to parasitism although they always retain some

basic arthropod traits (Grygier 1996a; Grygier & Høeg 2005).

The **Facetotecta** were known until recently only as pelagic nauplius and cypris larvae of type 'y' (Grygier 1996b). But Glenner et al. (2008) managed to induce metamorphosis of the y-cyprid stage and obtained results indicating that the adult is a highly modified parasite with early endoparasitic stages that bear a remarkable resemblance to those found in the life cycle of rhizocephalan cirripedes. This, and the general uncertainty about thecostracan phylogeny, puts special emphasis on tracing the evolution of parasitism within this taxon (Pérez-Losada et al. 2009).

As a further complication, the Tantulocarida are often mentioned as the most likely sister group to the Thecostraca. The tantulocarids are also highly advanced parasites and, especially given the lack of knowledge about facetotectan adults, it cannot be excluded that they are nested somewhere within the Thecostraca (Boxshall 2005a).

2.   Variation within the Thecostraca

2.1.   Larval development

Details of larval development vary both among and within the major taxa. The cypridoid stage is always non-feeding. In the Thoracica, most species have planktotrophic nauplii, but lecitotrophy is prevalent or obligatory in several families such as the Scalpellidae. All Rhizocephala and Acrothoracica have lecitotrophic nauplii. This is also the prevalent mode of development in the Ascothoracida and the Facetotecta, but both these taxa also have species with planktotrophic nauplii. There is accordingly no obligatory link between parasitism and naupliar mode of feeding in the Thecostraca. Some ascothoracids and cirripedes have an abbreviated development. In the Thecostraca many taxa have six naupliar instars just as in the Copepoda, so this could be the ground pattern, but some forms, such as the Rhizocephala, have only five or four. There is no obligatory relation between numbers of instars or feeding mode and the duration of the naupliar phase as shown by some cold water rhizocephalans that use almost 30 days to reach the cyprid stage (Walossek et al. 1996). Pelagic nauplii are absent in many groups. In the Cirripedia this seems always to involve larvae hatching as cyprids, but in the Ascothoracida some species seem to brood the hatched nauplii in the mantle cavity and later release them as a-cyprids. As a further complication, some ascothoracids have two consecutive a-cyprid stages, with only the latter performing settlement on the host (Kolbasov et al. 2007). Finally,
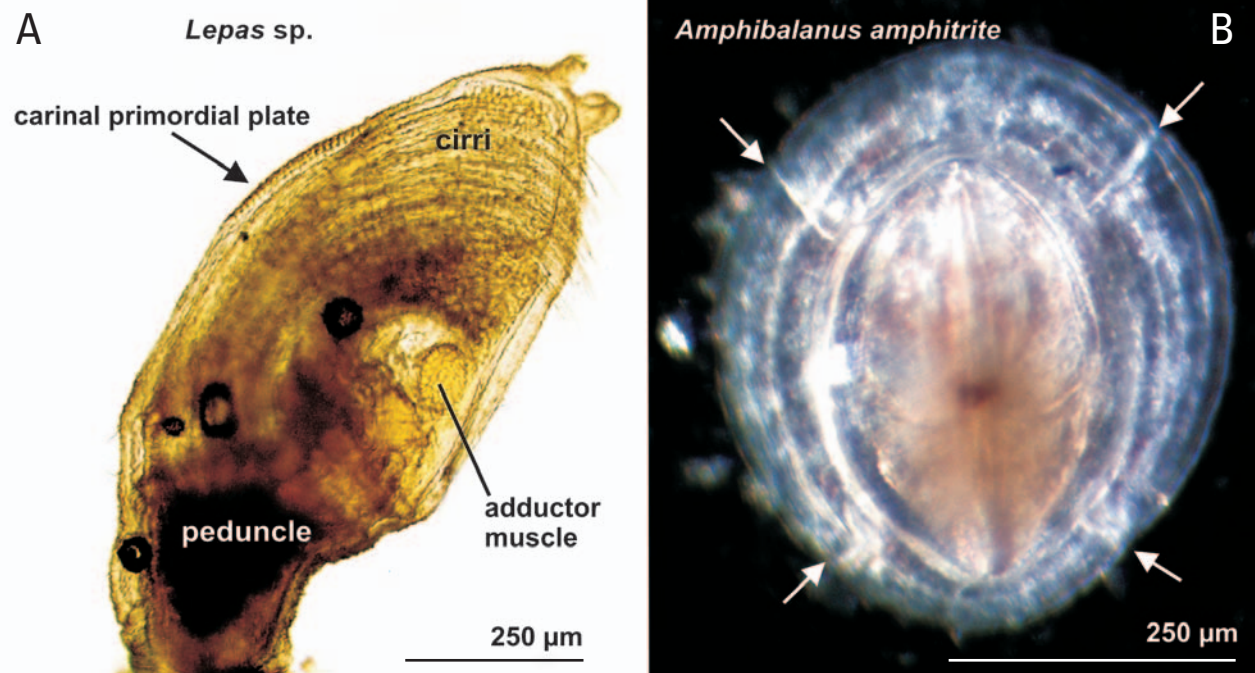
Fig. 1. Metamorphosis in the Cirripedia Thoracica. Recently settled, but fully metamorphosed specimens. **A**: *Lepas* sp., presumably *L. pectinata*. Note the distinct similarity with a cypris larva although the appearance of annulated cirri and a true peduncle are clear post-metamorphic traits. The specimen has not yet developed shell mineralization, but the cuticular primordium of the carinal plate is clearly visible. **B**: *Amphibalanus (Balanus) amphitrite* < 12 hours after settlement but already without any resemblance to a cyprid (see Fig. 2). The separation into wall plates and opercular plates has already taken place although mineralization has not yet commenced. Arrows show borders between the wall plates.
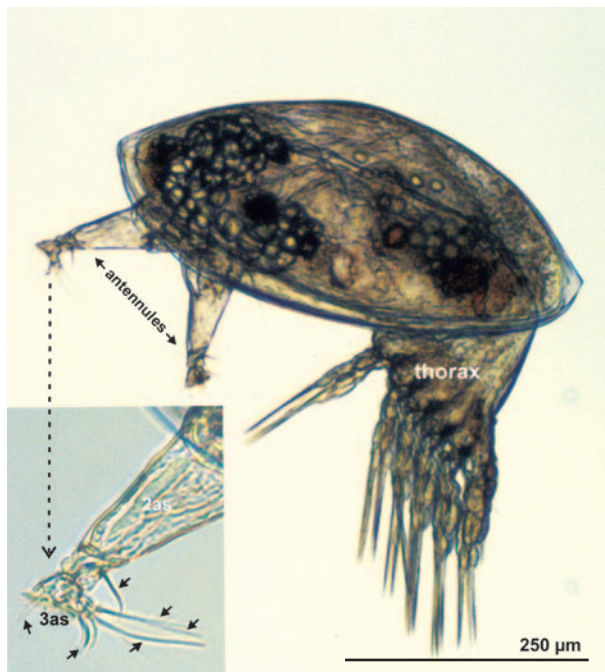

Fig. 2. Live cyprid of *Amphibalanus amphitrite* performing exploratory walking on its two antennules. The thorax and six pairs of thoracopods are extended to the maximum extent. Insert shows the distal part of an antennule and its attachment disc on the third segment (3as). Both this and antennular segment 4 carry numerous sensory setae (arrows in insert) that can potentially be coded as separate characters in a phylogenetic analysis. See BIELECKI et al. (2009) for details on antennular morphology.

the sexually mature ascothoracid can in some families be morphologically almost identical to an a-cyprid, but it remains uncertain if this represents a plesiomorphic condition or a case of paedomorphosis.

2.2. Sessility

The Thecostraca are normally stated as being sessile after the pelagic larval stages, but this may be an over-simplification. The most primitive Ascothoracida are ectoparasites and exhibit remarkably little morphological adaption to this mode of life except for having a mouth cone with piercing-sucking mouth parts, and the morphology of the adult seems to differ little from the preceding a-cyprid larva (GRYGIER 1996a). Most likely, the female parasite is permanently affixed to its host, but the males do not feed from the host, and could, at least in principle, shift from one female parasite to another (M.J. Grygier pers. comm.). The ur-thecostracan may therefore not have been truly sessile but capable of at least some movement.

In both the Facetotecta and the Ascothoracida the cypridoid larva can only attach by mechanical means. In contrast, the cirripede cyprid employs its antennules to attach by secretion of cement from a specialized multicellular gland. Prior to this they attach reversibly to the substratum during their exploratory walk-

Tab. 1. Variation of key morphological and life cycle traits within the Crustacea Thecostraca. The table lists variation within the taxa, not assumed ground patterns. (1) All Rhizocephala, and assumedly also the Facetotecta, have an endoparasitic phase in the life cycle. The most primitive Ascothoracida are little modified ectoparasites. (2) The Ascothoracida had separate sexes in the ground pattern, but hermaphroditism evolved within the group as a derived condition in the Ascothoracida (Grygier 1987b).

Taxon	Nauplii	Cypridoid larva	Shell plates	Metamorphosis	Feeding	Reproduction
Facetotecta	planktotrophy lecitotrophy	y-cyprid	?	extreme	endoparasite?(1)	?
Ascothoracida	planktotrophy lecitotrophy	a-cyprid	naked	none	ectoparasite endoparasite	separate sexes hermaphroditism(2)
Rhizocephala	lecitotrophy	cyprid	naked	extreme	endoparasite(1)	separate sexes
Acrothoracica	lecitotrophy	cyprid	naked	strong	suspension	separate sexes
Thoracica	planktotrophy lecitotrophy	cyprid	naked armed	moderate - strong	suspension parasite	separate sexes androdioecy hermaphroditism

ing on the substratum by means of unicellular antennular glands, but secretion of the cyprid cement is an irreversible process that initiates the juvenile and adult phases (Walker 1992; Electronic Supplement video clip 2).

2.3. Metamorphosis and parasitism

In all Cirripedia a profound metamorphosis separates the cyprid and the first juvenile stage. The stage resulting from metamorphosis differs extensively among taxa. In some pedunculated cirripedes such as the Lepadidae (Fig. 1), the metamorphosis seems to involve only moderate changes. In balanomorphan barnacles, and especially in the Acrothoracica, the remodeling is more profound although some organs and tissues are carried through (Walley 1969; Anderson 1994; Glenner & Høeg 1993, 1995). The Rhizocephala pass through the most profound metamorphosis resulting in an extremely simplified, slug-shaped stage called the vermigon (Høeg 1985; Glenner & Høeg 1995; Glenner et al. 2000; Glenner 2001). But irrespective of details, the metamorphosis is always a highly specialized moult (Glenner & Høeg 1994). The remodeling of the body commences only after settlement of the cyprid, after which metamorphosis can proceed with remarkable speed.

The most primitive ascothoracids do not metamorphose, since the attached parasite is very similar to a pelagic a-cyprid. Uncertainty exists as to whether a moult separates the two phases, since a-cyprid larvae have never been observed during the process of attachment.

The facetotectan adults remain unknown, but we know that the settled y-cyprid metamorphose into a stage, the ypsigon, that bears remarkable resem-

blance to the rhizocephalan kentrogon (Glenner et al. 2008). We therefore code similarly for the presence of the vermigon and the ypsigon in the character matrix to indicate that they are potentially homologous stages.

2.4. Feeding

The juvenile and adult Acrothoracica and the Thoracica are suspension feeders in which the natatory thoracopods of the cyprid have become extensively modified into cirri that form the feeding basket. The rami of cirri consist of many small annuli that probably cannot be considered true segments. They are retracted by muscles but extended by haemocoelic pressure. The mandibles, maxillules and maxillae form the "trophi" slightly separated from the thoracopods and the detailed morphology of these mouth appendages varies between the taxa. In addition, up to three pairs of anterior thoracopods can be specialized as mouth cirri that do not form part of the feeding basket (Anderson 1994; Høeg et al. 1994; Chan et al. 2008; Electronic Supplement video clip 3). These specializations have not yet been formally coded as characters, but it would be surprising indeed if the morphological specializations associated with this mode of feeding were not homologous in all acrothoracicans and thoracicans. Clearly, the phylogenetic position of the Rhizocephala becomes critical in determining whether these parasites evolved from a suspension feeding ancestor or not.

Little is known about feeding in the Ascothoracida. The most primitive forms use piercing and sucking mouth parts, but in advanced forms absorption of nutrients seems to take place through the highly modified mantle (Bresciani & Jespersen 1985). Rhizocephalans

lack any trace of an alimentary canal, and food is obtained by ramified rootlets inside the host that absorb nutrients directly across the integument as in a gut epithelium (Bresciani & Høeg 2001). How such a system could evolve from a more conventional crustacean ancestor is almost impossible to trace, since the rhizocephalans, unlike the Ascothoracida and many parasitic copepods (Boxshall 2005b), do not have species that exemplify intermediate stages of this evolutionary process.

2.5. Growth, appendages and tagmata

In the Ascothoracida it is unknown whether growth in the parasitic stage takes place by moulting or whether the parasite just increases in size without ever shedding the cuticle. Growth without moulting is known to occur in rhizocephalans, tantulocarids and some parasitic copepods (Høeg & Lützen 1995; Boxshall 2005a,b). The Thoracica have what is probably the most modified mode of growth in all Crustacea due to the presence of mineralized shell plates. These plates are never shed and moulting occurs only in special cuticular zones on the external surface (Anderson 1994; Blomsterberg et al. 2004). Only the lining of the mantle cavity and the soma with its appendages is shed entirely at the moults. Some thoracicans (e.g., *Heteralepas* and *Paralepas*) lack shell plates altogether and, by outgroup comparison, such a "naked" form could be the ancestral state.

The detailed phylogeny of the Cirripedia therefore becomes critical in deciding whether the ur-cirriped was naked or armed with plates that became secondarily lost in some taxa (Høeg et al. 2009). The analysis of Pérez-Losada et al. (2008) showed that armed forms (*Ibliformes*, Calanticidae) stand at the base of the thoracican tree and that extant naked thoracicans (*Heteralepas* and *Paralepas*) evolved by secondary loss of plates. The Rhizocephala lack shell plates altogether and the same is true for the Acrothoracica, although the latter can have a mineralized element of uncertain homology (Grygier & Newman 1985). Whether or not these groups were ancestrally naked or evolved from armed forms remains uncertain (Høeg et al. 2009).

Another interesting question concerns the tagmata and appendages of the adult cirriped. The non-feeding cyprid carries only antennules, six pairs of thoracopods and a pair of caudal rami, while the antennae and the mouth parts are lacking, at least as articulated appendages. Nevertheless a full set of mandibles, maxillules and maxillae reappears in the metamorphosed acrothoracicans and thoracicans. The Ascothoracida have a well developed and segmented abdomen, but the only vestige of an abdomen in the Cirripedia is a small hump on the acrothoracican cyprids. Both rhizo-

cephalans and thoracicans lack an abdomen altogether in both cyprids and adults and, interestingly this is also reflected in the expression of Hox genes (Gibert et al. 2000). Whether an abdomen is present or not, the cirripede cyprids always carry a pair of unsegmented caudal rami, and in adult acrothoracicans and many adult thoracicans these are retained as multi-articulated caudal appendages.

2.6. Sexual biology

Thecostraca have a wide range of sexual systems. Nothing is known about the Facetotecta. Most ascothoracids have separate sexes, but hermaphroditism does exist and is argued to have evolved secondarily (Grygier 1987b). Little is known about sex determination in this group, but the presence of sexually dimorphic a-cyprids in *Ulophysema oresundense* shows that at least this species has a genetic sex determination system (GSD) (Melander 1950). All Acrothoracica and Rhizocephala have separate sexes, and the males are always non-feeding and highly modified dwarfs (Anderson 1994; Høeg 1995). In the Rhizocephala, the males receive nutrition from the female tissue in which they are permanently embedded (Høeg 1992a). Where studied in detail, rhizocephalans have a GSD system with sexually dimorphic larvae, but the situation is unclear for the highly variable suborder Akentrogonida (Høeg 1990, 1995). The system of sex determination is unknown for the Acrothoracica. The Thoracica displays the most variable situation, since species can either have separate sexes, be pure hermaphrodites, or have hermaphroditism combined with a free male sex (Charnov 1987; Høeg 1995; Høeg & Møller 2006). Where males occur, they are always dwarfs and normally highly reduced, but in a few cases they retain thoracopods and may be capable of feeding (Klepal 1987). At least in the Scalpellidae, separate sexes may have evolved secondarily from an ancestral hermaphroditic state. Sex determination is little studied in the Thoracica, but both environmental sex determination (ESD) and GSD systems seem to occur (Gomez 1975; Svane 1986). Although the presence of a separate male sex must qualify as a phylogenetic character by itself (Høeg 1995), it is by no means straightforward that all dwarf males are homologous within the Cirripedia or even within the Thoracica, and due to the disparate morphologies and life cycles in the taxon it is a challenge to establish evolutionary histories. Cirripedes, especially the thoracicans, are therefore obvious testing grounds for theories on the evolution of sexual systems (Charnov 1987; Buhl-Mortensen & Høeg 2006). Indeed, this became one of the principal reasons why Darwin (1851, 1852, 1854a,b) spent close to ten years on this

taxon culminating in his four famous monographs. He was the first to find the cirripede dwarf males and understand and discuss their evolutionary significance (Darwin 1873).

3.   Phylogeny

It follows from the above that analyzing thecostracan evolution entails complex biological problems such as: Did sessility evolve convergently or in the stem line? How did the advanced suspension feeding evolve from an ancestor that most likely used the thoracopods for locomotion as in most other Crustacea? How was the traditional arthropod moulting transformed into the one incorporating mineralized shell plates that are not shed? What was the sexual biology of the ancestors at the various key nodes of the phylogenetic tree? How did an assumed ancestor with separate sexes evolve into hermaphroditism and how was this keyed to the evolution of sessility, feeding and parasitism? What selection pressures drove the evolution of the various types of dwarf males and to what extent are these convergent? What, if any, is the relationship among the various forms of parasitism in the Thecostraca, and why is parasitism obligatory in some major groups while being almost absent in other such as the Thoracica? Answering these questions requires first a formal characterization of the various morphological and biological traits found in the taxon. Second, these characters, whether used in tree generation or not, must be mapped on a well-resolved and robust cladogram to trace homology and homoplasy in their evolution. Only on this background can we test theoretical models and predictions concerning the evolution of complex traits such as the sexual systems and parasitism.

Since Grygier (1987a), there has been no study of the intrinsic phylogeny of the Thecostraca using a formal morphology based matrix and the reason for this is clear: adults of the Facetotecta are unknown and those of the remaining major taxa, notably the Rhizocephala, cannot be compared due to their widely differing morphology. Consequently, only larval characters can accurately be compared for all taxa, and, until very recently, detailed knowledge of such traits was not available except for a few species in the taxa concerned. Schram's benchmark (1986) analysis furnishes an excellent illustration of the problem. He placed the Rhizocephala far outside the Cirripedia, in fact near the base of the Arthropoda. This surprising tree topology arose because the only character linking rhizocephalans to other cirripedes was the presence of fronto-lateral horns in the nauplii, while analysis interpreted all the reductions in adult morphology of these parasites as primary absence. While "obviously" erroneous, Schram's (1986) analysis only demonstrated the need to formally code characters into an explicit matrix for subsequent study of the evolutionary ordering of events.

Using molecular markers has been similarly impeded by a lack of taxon sampling, especially outside the Thoracica, and early attempts were also marred by methodological problems leading to phylogenies where the Acrothoracica were linked to the Ascothoracica (Spears et al. 1994). Pérez-Losada et al. (2002) presented the first molecularly based phylogeny that encompassed all major taxa within the Thecostraca, but taxon sampling was still limited, especially outside the Cirripedia Thoracica, where only a single sample represented the Facetotecta. Other recent phylogenetic studies, whether molecular or morphology based, have been confined to one of the major thecostracan taxa such as the Thoracica (Glenner et al. 1995, 1999; Harris et al. 2000; Perl-Treves et al. 2000; Newman & Ross 2001; Pérez-Losada et al. 2004, 2008) or Rhizocephala (Glenner & Hebsgaard 2006).

In this paper, we discuss character evolution in the Thecostraca based on the first in depth analysis of its phylogeny. Pérez-Losada et al. (2009) compiled a matrix using molecular and larval morphological characters and with broad taxon sampling including seven facetotectans, five ascothoracidans, three acrothoracicans, 25 rhizocephalans and 39 thoracicans. The molecular dataset used comprised 6,244 sites from the 18S, 28S and H3 genes. The morphological dataset listed below comprised 41 characters from nauplii and cypridoid larvae and the metamorphosis of the latter. A selection of copepods and malacostracans was used as outgroup taxa (Regier et al. 2008). The matrix is shown in Appendix 1 (Electronic Supplement). Trees were presented from a maximum parsimony (MP) analysis on the morphological characters, a maximum likelihood analysis (ML) on the molecular dataset and a combined analysis using both datasets and Bayesian Inference (BMCMC) methods. The morphological tree was very poorly resolved. It did return the Facetotecta, Ascothoracida and Cirripedia as monophyletic, but there was almost no resolution beyond that. Here we use the trees from the molecular (ML) and combined (BMCMC) analyses, which had almost identical topologies, to trace the evolution of the 41 morphological characters (the insignificant differences in tree topology did not affect the character evolution). Figures 3 and 4 show collapsed trees for simplicity, since we are not here concerned with detailed branching patterns. The fully resolved tree is seen in the tracings of the evolution of all 41 characters (Electronic Supplement). The tree topology in Fig. 3 confirms previous analyses of the Cirripedia and of the Thecostraca

in general (GLENNER et al. 2006; PÉREZ-LOSADA et al. 2002, 2008) but is now based on a much broader dataset in terms of taxa and characters, and with much new insight in intrinsic branching patterns in the major taxa concerned. In addition PÉREZ-LOSADA et al. (2009) was the first phylogenetic analysis of intrinsic phylogeny in the Ascothoracida, the Acrothoracica and the Facetotecta, although taxon sampling remains moderate in these groups.

4. Morphological characters

Several characters are adapted from GRYGIER (1987a) and GRYGIER (1991). See PEREZ-LOSADA et al. (2009) for details. See also GRYGIER (1996a,b) for characters from facetotectans and ascothoracidans.

4.1. Characters from the nauplius
(6 and 8 also concern the cypridoid larva)

01. *Naupliar cephalic shield continuous with free trunk dorsum*: (0) no; **(1)** yes.
02. *Naupliar cephalic shield ridges of common (facetotectan) plan*: (0) no; **(1)** yes.
03. *Nauplius with dorsal window plate in common position*: (0) no; **(1)** yes.
04. *Nauplius with ventral side of cephalic region flat, round and with wide rim*: (0) no; **(1)** yes.
05. *Nauplius with furcal setae; excluding furcal spines which apparently all taxa can have*: (0) absent; **(1)** present.
06. *Frontolateral pores and glands*: (0) absent; **(1)** present. – In nauplii with frontolateral horns, the two gland cells exiting in the terminal pore on each horn are always carried into the cyprid, where they exit in a complex pore situated fronto-ventrally on the head shield (WALKER 1973; HØEG 1987; GLENNER et al. 1989). We score (1) for species without nauplii, when these glands and pores are present in the cyprid. Occasionally the glands also exit on a small horn in the cyprid, but we have not used this as a separate character.
07. *Frontal filaments in nauplius*: (0) absent; **(1)** present.
08. *Antennular segment number expressed in entire life cycle*: (0) 8 or more; **(1)** less than 8. – This character is taken verbatim from GRYGIER (1987a), who, like the present authors, found it wanting in clarity. It concerns pronounced differences between the taxa, but we lack detailed information on the segment by segment homology in the thecostracan antennules, especially of the cypridoid larvae.

09. *Antennular segments in stage 1 nauplii*: (0) more than 3; **(1)** 3 or fewer.
10. *Nauplii with at most two segments in naupliar endopods of antennae and mandibles*: (0) no; **(1)** yes.

4.2. Characters from the cypridoid larva

11. *Head shield with distinct hinge line*: (0) absent; **(1)** present.
12. *Lattice organs*: (0) absent; **(1)** present. – Lattice organs are normally present in 5 pairs, but some taxa lack specific pairs, normally some of the posterior ones. A more detailed coding would therefore split character 12 into the presence of specific lattice organ pairs. For details on lattice organs (characters 12–17) see JENSEN et al. (1994), HØEG et al. (1998), HØEG & KOLBASOV (2002), RYBAKOV et al. (2003), and HØEG et al. (2009).
13. *Lattice organs (Lo) shape*: (0) with more or less distinct crest in trough; **(1)** no distinct crest.
14. *Lattice organ pair 1 (Lo1) large terminal pore position*: (0) posterior; **(1)** anterior. – The single large, terminal pore dealt with in characters 14 and 15 is a distinctive feature in lattice organ morphology. It differs from the large or small pores that may cover the general surface of the organ (characters 16–17) and derives ontogenetically from the terminal pore in the seta that is a precursor for the lattice organ in the nauplius (RYBAKOV et al. 2003). In the cypridoid larva the large terminal pore communicates directly with the cuticular chamber that houses the ciliary (outer-dendritic) part of the two sensory cells (HØEG et al. 1998). Some species lack the large terminal pore altogether and are therefore coded (?).
15. *Lattice organ pair 2 (Lo2) large terminal pore position*: (0) posterior; **(1)** anterior.
16. *Lattice organs with pores (large or small)*: (0) absent; **(1)** present. – Aside from the large terminal pore, the general surface of the lattice organ can be covered with numerous small or large (character 17) pores. We consider the presence of such pores, irrespective of their size, as a potentially homologous character.
17. *Lattice organs with large deep pores (pits)*: (0) absent; **(1)** present. – With SEM these structures resemble pores, but TEM reveals that they are actually deep pits, separated from the cuticular chamber of the lattice organ by a thin layer of epicuticle. Pores (whether small or large) on the general surface of the lattice organ facilitate the diffusion of compounds into the cuticular chamber housing the chemosensory cells (HØEG et al. 1998). In lattice organs without such pores, diffusion must take place by means of the single, large terminal pore dealt with in characters 14 and 15.

18. ***Frontal filaments in cypridoid larva***: **(0)** absent; **(1)** present.

19. ***Basal part of antennule consisting of two articulating sclerites = Y-rod and U-plate sensu Høeg (1985)***: **(0)** absent; **(1)** present. – This concerns the specialized morphology of first antennular segment in cirripede cyprids, which likely represents two sclerites derived from two originally fused segments. For details on this, and other features in the antennular morphology of the cirripede cyprid, see Høeg (1985), Glenner et al. (1989), Walker (1992), Lagersson & Høeg (2002), Høeg et al. (2004), and Bielecki et al. (2009).

20. ***A hand, hoof or bell shaped antennular segment (with disc or claw for attachment)***: **(0)** absent; **(1)** present.

21. ***Antennule with an attachment disc covered with cuticular villi***: **(0)** absent; **(1)** present.

22. ***Distal element of antennule as a cylindrical, movable sensory "palp" (from two segments or two fused segments)***: **(0)** absent; **(1)** present.

23. ***Antennular sensory palp undivided (segments fused)***: **(0)** no; **(1)** yes. – In cirripede cyprids the "palp" in characters 22 and 23 is the 4th antennular segment.

24. ***Antennule with (motile) distal claw***: **(0)** absent; **(1)** present. – We score "?" for facetotectans other than *Hansenocaris itoi*, because the y-cyprids of the undescribed species used in our analysis have not yet been studied for this feature.

25. ***Aesthetascs***: **(0)** on almost every antennular segment; **(1)** only one or two aesthetascs.

26. ***Distal antennular musculature***: **(0)** complex; **(1)** simple. – This character derives from Grygier (1987a), who phrased it as "reduction of the distal musculature", which entails an a priori assumption of polarity. A revision of this character is warranted in terms of the presence/absence and detailed disposition of individual muscles, but such a scheme is not yet available. In cirripede cyprids, the distal antennular musculature is represented only by the single, small muscle that operates the fourth segment (Lagersson & Høeg 2002).

27. ***Multicellular cement gland exiting on antennule***: **(0)** absent; **(1)** present.

28. ***Filamentary tuft-like cephalic sensory appendage in post-naupliar stage***: **(0)** absent; **(1)** present.

29. ***Mouthparts and gut***: **(0)** retained after metanauplius; **(1)** lost or reduced in cypridoid stage, but can reappear.

30. ***Postoral adductor muscle (for any post-naupliar stage)***: **(0)** absent; **(1)** present.

31. ***General condition of thoracopodal musculature***: **(0)** well developed; **(1)** poorly developed.

32. ***Fusion of the two basal segments of endopods in post-naupliar thoracopods 2 and following***: **(0)** absent; **(1)** present. – This refers to the fusion of the basal two segments of a three-segmented endopod (excluding thoracopod 1, which can differ). We omit to code for the special character state seen in some Facetotecta, where fusion of the distal two segments leads to two-segmented endopods. These two-segmented conditions are not homologous and the latter is an ingroup facetotectan condition.

33. ***Seta on first exopodal segment of thoracopods in post-naupliar instars***: **(0)** absent; **(1)** present.

34. ***Single seta on first exopodal segment of thoracopods in post-naupliar instars is a serrated grooming seta***: **(0)** no; **(1)** yes. – A seta is present in the Ascothoracida and Copepoda, but not as a distinctly serrated seta.

35. ***Abdominal development; excluding telson***: **(0)** well developed; **(1)** rudimentary or absent. – Details on the abdomen and telson in cirripede cyprids are provided in Kolbasov & Høeg (1999, 2007).

36. ***Abdominal segment number, excluding telson***: **(0)** four; **(1)** less than four. – We score similarly **(1)** for the Facetotecta and the Cirripedia. But facetotectans have a well developed abdomen while cirripedes have an abdomen that is either diminutive or indistinguishably fused with a small telson.

37. ***Telson-abdomen development relative to thorax***: **(1)** not pronouncedly narrower and not set off from thorax; **(2)** always distinct but narrower and set off from thorax. – In state 2 acrothoracicans have an intervening abdomen isodiametrical with the telson [states 35(1) and 36(0)], whereas other cirripedes have but a single element representing the telson or a fused abdomen-telson.

38. ***Telson cleft***: **(0)** absent; **(1)** distinct, shallow to almost reaching the base. – The latter state has occasionally been misunderstood as two-segmented caudal rami, see Kolbasov & Høeg (2002).

4.3. Characters from metamorphosis

39. ***Profound metamorphosis after cypridoid stage***: **(0)** absent; **(1)** present. – See Glenner & Høeg (1994) for details on the homology of metamorphosis in the Cirripedia.

40. ***Preoral adductor muscle in post-cypridoid stage***: **(0)** absent; **(1)** present. – See Glenner & Høeg (1998) for details.

41. ***Primordial shell plate in first attached instar***: **(0)** no; **(1)** yes. – See discussion in Glenner & Høeg (1993) and Glenner et al. (1995).

# 5.	Apomorphies for major lineages

Pérez-Losada et al. (2009) did not discuss character evolution in the Thecostraca in any detail. This is done here by tracing all 41 characters onto their ML/ BMCMC cladogram (see Electronic Supplement Appendix 2). Figure 3 lists all the apomorphies found in the principal branches of the Thecostraca. Most apomorphies are without homoplasy. In the list below, those marked (*) have homoplastic states in another "major" branch. Those marked (**) have homoplastic apomorphic states in one or several branches nested deep within another clade.

## 5.1.	Facetotecta

1(1):	Naupliar cephalic shield continuous with free trunk dorsum.
2(1):	Naupliar cephalic ridges of common (facetotectan) plan.
3(1):	Nauplius with dorsal window plate in common position.
4(1):	Nauplius with ventral cephalic region flat, round and with wide rim.
33(0):	No seta on first exopodal segment of thoracopods in the post-naupliar instars.
36(1)*:	Less than four abdominal segments, excluding telson.

36:	State (1) of this character is convergent with Rhizocephala + Thoracica, but this clade has no abdomen at all, whilst the Facetotecta have three segments.

The apomorphies were among those listed by Grygier (1991) to uniquely diagnose the Facetotecta, being universally present within that taxon. The morphology of the y-cypris larva may well hold several additional autapomorphies for the Facetotecta, but this must await further detailed analysis of this stage with focus on the antennules and their setation.

## 5.2.	Ascothoracida + Cirripedia

7(1)**:	Frontal filaments present in the nauplius.
26(1):	Distal antennular musculature in cypridoid larva reduced.
30(1):	A postoral adductor muscle present in a post-naupliar stage.

7:	The absence of frontal filaments in the rhizocephalan *Parthenopea* (based on unpublished SEM micrographs) is exceptional. Frontal filaments are present in all ascothoracids and cirripedes that have

nauplii. They are carried into the cyprid, where they attach at the base of the compound eyes, when these are present (Walker 1974; Høeg 1985; Glenner et al. 1989). The majority of rhizocephalan cyprids lack compound eyes, but they normally retain the frontal filaments (Glenner et al. 1989; Høeg & Lützen 1993) except in most of the species that hatch as cyprids (Høeg & Rybakov 2007).
26:	This character, taken from Grygier (1987a), would benefit if formulated with consideration of homologies of specific antennular muscles, but although cyprid antennular muscles are now described in detail (Høeg 1985; Lagersson & Høeg 2002), they cannot yet be compared in homology terms to those of a-cyprids and y-cyprids.
30:	In cirripedes and ascothoracidans the cypridoid larva has a postorally situated carapace adductor muscle (Glenner et al. 1995; Glenner & Høeg 1998), while a similar muscle is lacking from the laterally extended head shield of the y-cyprids. *Bredocaris admirabilis*, which we consider as a close relative of the Thecostraca, also has a rather large head shield, but similarly laterally extending and therefore almost certainly without an adductor (Müller & Walossek 1988; Walossek et al. 1996).

## 5.3.	Ascothoracida

8(0):	Eight or more antennular segments expressed in entire life cycle.
11(1)**:	Cypridoid head shield has a distinct hinge line.
20(0):	No hand, hoof or bell shaped distal antennular segment (with disc or claw) present in the cypridoid larva.

8:	State (0) of this character is a somewhat dubious apomorphy, since the assumed plesiomorphic state would change if the Copepoda were closer related to the Thecostraca than to the Malacostraca, and, obviously, this analysis is not intended to solve copepod relationships. The character was defined by Grygier (1987a). It does not signify that any life cycle stage of the Ascothoracida shows all 8 segments simultaneously, but that a total of 8 individual segments may be discerned by following the entire ontogeny. The characters would benefit from being reformulated in terms of the presence or absence of specific segments along the lines pioneered for the copepod antennules in Huys & Boxshall (1991).
11:	The presence of a hinge line 11(1) is homoplastic with *Lepas*, *Capitulum* and *Pollicipes*. It would seem that a hinge line can evolve from an undivided head shield when the need arises, such as in very large cypridoid larvae.
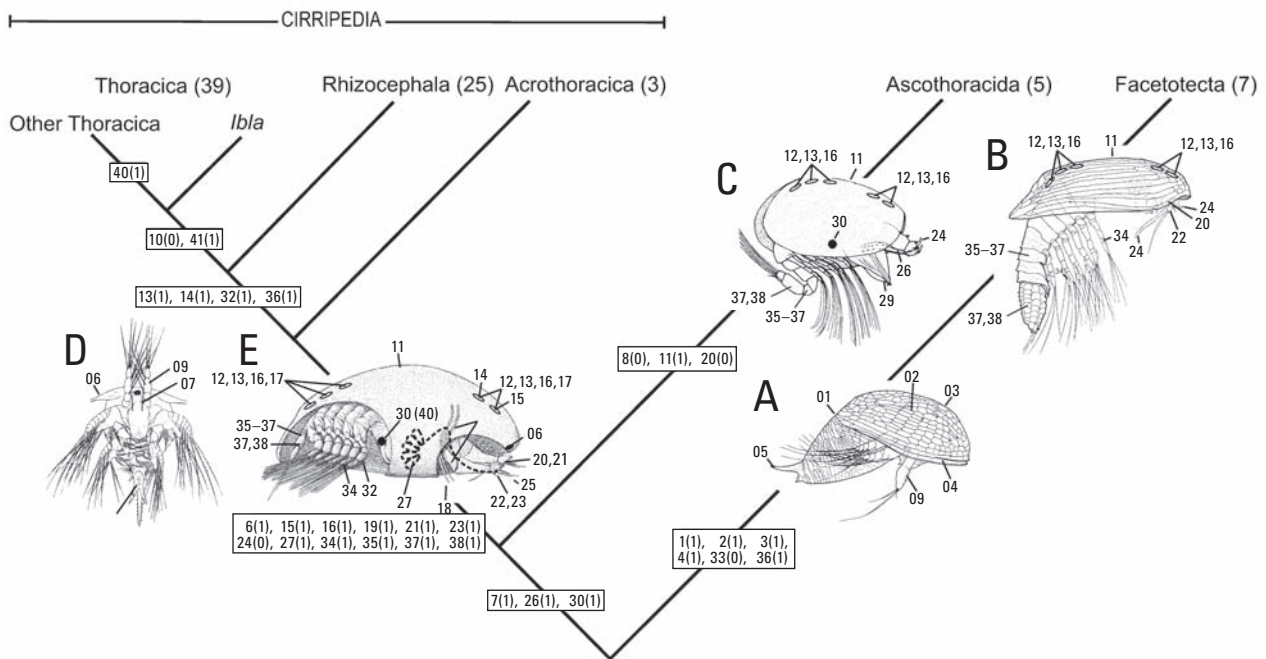
Fig. 3. Phylogeny of the Crustacea Thecostraca. From Pérez-Losada et al. (2009) with major branches collapsed. Morphological apomorphies, identified by tracing characters on the combined morphological-molecular tree, are inserted. Numbers of species included in the phylogenetic reconstruction are given behind taxon names. Vignettes of larval stages show the position of some important characters. **A**: Y-nauplius (Facetotecta). **B**: Y-cyprid (Facetotecta). **C**: A-cyprid (Ascothoracida). **D**: Cirripede nauplius. **E**: Cirripede cyprid.

20:   The shape of the attachment device 20(0) on the distal antennular segment is one of several similarities between the antennules of the y-cyprid and the cyprid, but not shared by the a-cyprid. In our phylogeny these similarities become homoplasies and thereby autapomorphies for the Ascothoracida. A priori, one might consider the multi-articulated antennule of the a-cyprid as more plesiomorphic than those in the y-cyprid and the cyprid. But our cladogram militates against this and we have no very good outgroup to solve the issue. Injecting the Tantulocarida will not help, since they lack antennules altogether except for aesthetascs sitting directly on the ventral face of the cephalon. In summary, the few apomorphies for the Ascothoracida dovetail with the observation that the most primitive forms have few obvious adaptations to parasitism.

5.4. Cirripedia

6(1):   Nauplius with frontolateral horns or frontolateral pores present in the cypridoid.

15(1):   Lattice organ pair 2 with large terminal pore in anterior position.

16(1):   Lattice organs with large or small pores in addition to the large terminal pore.

19(1):   Basal part of cypridoid antennule consists of two articulating sclerites (= Y-rod and U-plate sensu Høeg 1985).

21(1):   Cypridoid antennule with an attachment disc covered with cuticular villi.

23(1):   Cypridoid antennular palp undivided (fused from two segments).

24(0):   Cyprid antennule without (motile) distal claw for mechanical attachment.

27(1):   Multicellular cement gland exits on the cypridoid antennule.

34(1):   Single seta on first exopodal segment of thoracopods in post-naupliar instars is a serrated grooming seta.

35(1):   Abdomen (excluding telson) is rudimentary or absent.

37(1):   Telson-abdomen distinctly narrower than thorax.

38(1):   Telson cleaved.

6:   The presence of fronto-lateral horns in the nauplius is the "classic", and until very recently only, character uniting all Cirripedia including the Rhizocephala (Thompson 1836; Høeg 1992b; Anderson 1994; Høeg & Møller 2006). Each frontolateral horn carries at the tip the exit pore for two unicellular glands and setae supplied with nerves (Walker 1973; Semmler et al. 2008). The glands and pores, but only rarely the horns, are present also in the cyprid (Walker 1973; Høeg 1987). The character state is without exception present in all cirripedes with nauplii studied until now. Even species that hatch as cyprids will normally retain
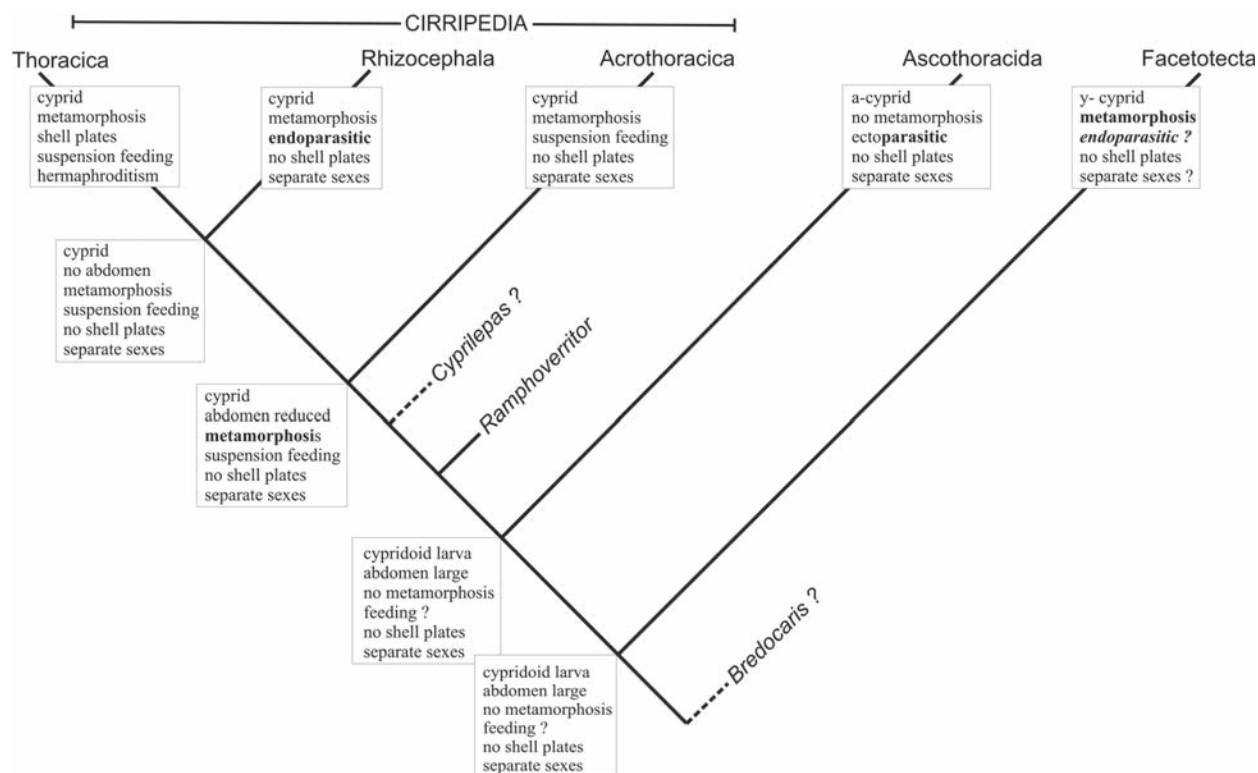
Fig. 4. The tree from Fig. 3, but with reconstructed ground pattern states for important morphological and life cycle traits in the major thecostracan lineages. Boldface indicates important homoplasies. Suspension feeding is argued to be the most probable mode of life for the cirripede ancestor. Separate sexes is concluded to be ancestral for the Thecostraca and is retained in all Rhizocephala and Acrothoracica and in most Ascothoracida. Hermaphroditism evolved convergently at least twice: As an ingroup condition in some Ascothoracida and in the stem lineage of the Thoracica. Advanced parasitism with an endoparasitic phase, characterizing the Rhizocephala and indicated (*italics*) for the Facetotecta, is here argued to be have evolved homoplastically. The vermigon (Rhizocephala) and ypsigon (Facetotecta) stages are therefore not homologous. The Silurian fossil *Ramphoverritor* is considered as sister-group to all extant Cirripedia. The Silurian *Cyprilepas* could possibly sit anywhere between the cirripede stem and the Thoracica. The position of the upper Cambrian *Bredocaris* is highly uncertain.

the glands and pores. They lack only in most species of the Rhizocephala Akentrogonida (HøEG & RYBAKOV 2007).

15+16: HøEG & KOLBASOV (2002) and HøEG et al. (2009) offered an in depth account of the evolution of lattice organs in the Thecostraca, a repetition is unwarranted here.

19:   State (1) is a characteristic feature of the cirripede cyprid, and one that forms part of the elaborate skeletal and muscular morphology that enables the cyprid to explore the substratum walking bipedally on its antennules (HøEG 1985; LAGERSSON & HøEG 2002).

21+23: The attachment disc 21(1) on the third antennular segment is a prerequisite for the surface exploration and final cementation of the cyprid. It carries both the exit pores of the glands used in attachment and numerous sensory setae. In cirripedes, the "palp" 23(1) equals the fourth antennular segment that carries two distinct groups of sensory setae (BIELECKI et al. 2009). In the Facetotecta, the palp consists of two articulating segments. The homology between the palp in these two taxa and the antennule of the Ascothorac-

ida remains uncertain. The character is ambiguous in our conservative scheme because we coded the outgroups as (?), since they do not possess this palp. But if unfused distal antennular segments are assumed for the ancestor, as indeed they are in, for example, the Copepoda, this character becomes an apomorphy for the Cirripedia. Details of the disc morphology and the sensory apparatus on both the third and fourth segments can unquestionably be formulated in terms of additional apomorphies for the Cirripedia, but it would require a homology scheme for these antennular structures, which is not yet available for comparison with the cypridoid larvae in the ascothoracidans and facetotectans.

27:   The cirripedes do not attach mechanically but using cement 27(1) secreted from the attachment disc.

37:   Facetotectan y-cyprids and ascothoracidan a-cyprids and adults have a well developed abdomen and telson 37(0), but no adult cirripede has any trace of an abdomen and only cyprids of the Acrothoracica sport a rudimentary abdomen intercalated between the

cleaved telson and the thorax 35(1). Neither cyprids nor adults of the Rhizocephala and Thoracica have any trace of an abdomen 35(1), but all cirripede cyprids have a small telson 37(1) with a distinct cleft 38(1) (Kolbasov & Høeg 2007).

Compared to the many apomorphies in cyprid morphology, y-cyprids (Facetotecta) and a-cyprids (Ascothoracida) are much less specialized (for details see Høeg et al. 2004). In the nauplius the presence of frontolateral horns is the only apomorphy identified in our analysis. The specialized morphology of the cyprid enables the advanced mechanism of substrate location and final cementation found in all cirripede taxa irrespective of the different stages that can result from the ensuing metamorphosis. We conclude that the cirripede cyprid has been a major factor in the success of the taxon as both parasites and suspension feeders compared to the two other thecostracan taxa. It is remarkable that the same type of larva can settle successfully on substrata as different as e.g., rocks, floating objects in the sea, crustacean exoskeletons, whale skin and the epidermis of corals (Moyse et al. 1995; Høeg et al. 2004; Høeg & Møller 2006; Bielecki et al. 2009).

5.5. Acrothoracica

Our analysis did not identify any autapomorphies in larval morphology for the Acrothoracica, but this taxon is well characterized by autapomorphies in adult morphology, not coded for here (Anderson 1994). Knowledge of larval morphology and its variation within acrothoracicans is still scarce, but the information in Kolbasov & Høeg (2007) gives promise that a useful database of characters from cypris larvae can be constructed. This is fortunate, because most acrothoracican species are difficult to collect, rendering it very unlikely that many more will be available for molecular analysis in the near future. Characters from nauplii are of little use, since most species hatch as cyprids.

5.6. Rhizocephala + Thoracica

13(1)**: Lattice organs without a distinct longitudinal crest.
14(1):   Lattice organ pair 1 with large terminal pore in anterior position.
17(1):   Lattice organs with deep pits (pores) almost reaching the cuticular chamber.
32(1):   Basal two segments fused in the originally three-segmented endopod of thoracopods in post-naupliar stages.
36(1):   Abdominal segment number less than four.

Although adult rhizocephalans are next to impossible to compare to other cirripedes, larval morphology provides unequivocal support for a Rhizocephala + Thoracica clade.

13, **14**, **17**: The lattice organs exemplify the advantage of an exemplar approach to character coding, since "unexpected" homoplasies occur in several species. Lattice organs are putative chemoreceptors on the head shield of the cyprid and their morphology provides important large-scale phylogenetic information. They occur as five pairs straddled along the dorsal midline of the cypridoid head shield and are even present in adult males of the Ascothoracida (Jensen et al. 1994; Høeg et al. 1998; Høeg & Kolbasov 2002; Kolbasov et al. 2007). They develop from simple setae on the head shield of the nauplius (Rybakov et al. 2003). The plesiomorphic shape, found in facetotectans, ascothoracidans and acrothoracicans, is 13(0) a smooth, elongated crest, prostrate in a shallow depression and having some resemblance to a reclined seta. The apomorphic shape, seen in the Rhizocephala and Thoracica, is an elongated flat field 13(1) perforated by numerous deep pit-like pores 17(1) and without any resemblance to a seta whatsoever. But, interestingly, the plesiomorphic shape of an elongated, seta-like crest 13(0) reappears in two species in our matrix nested deep within the Thoracica (*Pollicipes* and *Capitulum*) although the crest is still perforated by pores 17(1) as in other species of that suborder. Also a species of *Chthamalus* shows this reversal (Pérez-Losada et al. 2008) although not part of the present analysis. These cases of homoplasy might be due to heterochrony in the several features involved in lattice organ morphology.

32:   The Acrothoracica and the Ascothoracida have three-segmented endopods in cypridoid larva. Some facetotectan y-cyprids also have two-segmented endopods, but this (Grygier 1987a; Kolbasov & Høeg 2003) is by fusion of the distal two segments and therefore not a homologous state in a Huys & Boxshall (1991) regime.

36:   State (1) is convergent with the Facetotecta, but the Rhizocephala + Thoracica have no abdomen at all in the cypridoid, while y-cyprids sport three distinct abdominal segments.

5.7. Rhizocephala

We found no apomorphies in larval morphology for the Rhizocephala. Their cyprid, especially its antennules, exhibits considerable variation (Glenner et al. 1989) but Pérez-Losada et al. (2009) refrained from coding this in detail because character states are still unknown for many species. All rhizocephalans have separate sexes and most have sexually dimorphic cyprids. Con-

sidering our tree topology, a possible autapomorphy for the taxon could be the presence of an aesthetasc on the third antennular segment of male cyprids (GLENNER et al. 1989). Another candidate autapomorphy is the presence of a large unicellular gland in the cyprid antennules (HØEG 1987; GLENNER et al. 1989). In contrast to rhizocephalan and acrothoracican cyprids (GLENNER et al. 1989; KOLBASOV & HØEG 2007), those of the Thoracica seem to have a much more uniform morphology, although exceptions do exist. We can possibly conclude that the specialized settlement substrata used by epibiotic and parasitic barnacles (Acrothoracica, Rhizocephala) are associated with more variation in the sensory and attachment structures than found in the Thoracica, where most species settle on inanimate surfaces. To investigate how much cypris morphology is associated with the habitat of the adult (KOLBASOV 1996), it would be interesting to study its morphology in the rather few thoracican species that attach to the soft tissues of other animals such as the coral barnacles, the whale barnacles and the very few parasitic thoracicans (HØEG et al. 2005).

5.8. Thoracica

10(0)*: Nauplii with more than two segments in the endopods of antennae and mandibles.
41(1):   Primordial shell plates present in first attached instar.

10:   State (0) is convergent with some or all Ascothoracida.
41:   Primordial plates are cuticular formations that appear during metamorphosis as primordia of the paired scuta-terga in *Ibla* and of the paired scuta-terga and the unpaired carina in the Thoracica. The homology of the phosphatic mineralization of the cuticle in *Ibla* and the calcitic type found in other Thoracica is uncertain, but the presence of cuticular primordia of the mineralized plates in both taxa indicate that some level of homology does exist (GLENNER et al. 1995; HØEG et al. 1999; PEREZ-LOSADA et al. 2004; BUCKERIDGE & NEWMAN 2006).

5.9. Thoracica exclusive of *Ibla*

40(1): A preoral adductor muscle in the post-cypridoid stage.

40:   GLENNER & HØEG (1995) found that thoracicans other than *Ibla* replace the postoral carapace adductor of the cyprid with a preoral adductor during metamorphosis. The preoral muscle connects the two scutal plates. Both muscles are present during cyprid

metamorphosis showing that they are not homologous.

An additional larval apomorphy for this clade may be a pair of plumose setae apically on the fourth antennular segment of the cyprid (see HØEG et al. 2009), but identified too late for inclusion in PÉREZ-LOSADA et al. (2009). The metamorphosis of the settled cyprid is a key event in cirripede ontogeny, but in our matrix only characters 39–41 concern this process. Future studies may well assist in understanding how metamorphosis evolved and diversified within the taxon.

6.   Character evolution & reconstruction of ground patterns

Our analysis allows us to reconstruct morphological ground patterns for some of the internal nodes in the thecostracan tree and offers a framework for discussing the evolution of complex life cycle traits not used as input data. The reconstruction of thecostracan phylogeny would benefit if the phylogenetic position of the parasitic Tantulocarida could also be fixed. It is not straightforward if the tantulus larva is homologous with the thecostracan cypridoid larva, and, in light of their complicated life cycle (BOXSHALL 2005a), the Tantulocarida could well hold morphological and biological surprises. A molecularly based analysis of tantulocarid relationships is therefore most warranted.

6.1. Evidence from fossils

Bredocaris admirabilis from the upper Cambrian "Orsten" fauna has been suggested as a close relative to the Thecostraca, although never given a precise phylogenetic position relative to both the Thecostraca and the Tantulocarida (MÜLLER & WALOSSEK 1988; WALOSSEK et al. 1996). The latest stages known of *B. admirabilis* have some resemblance to facetotectan y-cyprids, but the fossil lacks both the prehensile antennules of the thecostracan cypridoid larva and other cypridoid characteristics such as lattice organs. Therefore, whatever the position of *B. admirabilis*, it does not shed light on the origin of sessility and metamorphosis in the Thecostraca.

There are no fossils outside the Cirripedia pertinent to discussing thecostracan evolution. Most of the early cirripede fossils also provide but little information on the problems at hand because they are either of dubious affiliation or cannot be precisely placed in phylogeny (FOSTER & BUCKERIDGE 1987; GLENNER et al. 1995; HØEG et al. 1999).

Thoracica. *Praelepas jaworski* Chernyshev from the Carboniferous has five unmineralized plates and is normally claimed to be nested within the Thoracica somewhere above the *Ibla* (Ibliformes) node (GLENNER et al. 1995; HØEG et al. 1999). This fossil is therefore instructive when discussing character evolution within the Thoracica, but not for reconstructing the ground pattern of the taxon or any more inclusive clade. HØEG et al. (1999) also discussed the possibility that the Upper Jurassic *Eolepas rhaeticus* Withers is more closely related to the Ibliformes than to the other Thoracica, because it allegedly has phosphatic plates, but BUCKERIDGE & NEWMAN (2006) advanced a series of counterarguments to that claim. SCHRAM (1975) similarly suggested that the five-plated *Illilepas damrowi* (Schram) from the Carboniferous, first described as a *Praelepas*, is a close relative of the Ibliformes, a claim having gained some support (FOSTER & BUCKERIDGE 1987), but the theory was never elaborated in any detail. This means that *Ibla* (the Ibliformes) has at present only extant representatives, and it remains unknown when four-plated forms first appeared and whether they preceded five-plated forms, were secondarily derived from them or arose independently.

Acrothoracica and the stem lineage. Boring barnacles are known as trace fossils from the Devonian (GLENNER et al. 1995). The Silurian *Cyprilepas holmi* Wills has a peduncle and a capitulum enclosed in two valves but no mantle mineralization and no differentiated shell plates. It could well predate the divergence of the Acrothoracica, but *Cyprilepas* might equally sit in any position on the stem lineage from the cirripede base to the thoracican base. The Burgess Shale form *Priscansermarinus barnetti* Collins & Rudkin has been claimed to be a heteralepadid (COLLINS & RUDKIN 1981), but it is doubtful whether this very early fossil has any cirripede or even arthropod affiliation (Jakob Vinther, Yale University, pers. comm.). In contrast, the Silurian *Ramphoverritor reduncus* Briggs et al., recently described in BRIGGS et al. (2005) based on a cypridoid larva and a metamorphosed specimen, seems to hold essential clues for reconstructing the cirripede ground pattern. The larval form exhibits a series of putative synapomorphies with a true cirripede cyprid sensu HØEG et al. (2004), especially in the antennules. BRIGGS et al. (2005) argued that *R. reduncus* is a crown group cirripede, meaning that it diverged no lower than the Acrothoracica. But its cypridiform stage has a well developed, segmented abdomen, something never present in any extant cirripede cypris according to our analysis (Figs. 3, 4). Instead, it must be the only fossil known to date that can be reliably placed on the cirripede stem lineage, i.e., below the split between the Acrothoracica and Rhizocephala + Thoracica clades. In agreement, the *R. reduncus* larva lacks several of the apomorphies characterising a

crown group ("complete") cyprid *sensu* HØEG et al. (2004). The metamorphosed form has no mineralized parts, but from their state of the art 3D reconstruction BRIGGS et al. (2005) claim to have found evidence for five plates or their precursors. If true, this entails that five-plated forms evolved in the cirripede stem lineage no later than the Silurian and therefore predate both the plate-less Acrothoracica (known as trace fossils from the Devonian), the Rhizocephala and the four-plated Ibliformes. Clearly, therefore, *Ramphoverritor reduncus* holds essential information for reconstructing the cirripede ground pattern.

6.2. Ground patterns for major lineages

(Fig. 4)

The cypris larva. The morphology of the cyprid exhibits a long series of apomorphies for the Cirripedia. This also suggests that sessility by irreversible cement secretion is a cirripede apomorphy.

Feeding biology and parasitism. If parasitism is naively coded as a single character, a parasitic or a suspension feeding ancestor become equally parsimonious solutions for the Cirripedia. But as explained above this would entail a convergent evolution of numerous similarities associated with suspension feeding in thoracicans and acrothoracicans. Moreover, the parasitism of the Ascothoracida involves few specializations and shows no similarity to either the Rhizocephala or the Facetotecta. We conclude that suspension feeding is an apomorphy for all Cirripedia, whence the parasitism in the Rhizocephala must have evolved from this mode as also argued by GLENNER & HØEG (2003). As argued by PÉREZ-LOSADA et al. (2009), the slug-shaped vermigon (Rhizocephala) and ypsigon (Facetotecta) stages must have evolved convergently. The two taxa are separated by two other lineages (Acrothoracica, Ascothoracida) neither of which has such stages and in ascothoracidans there is even no metamorphosis at all. In summary, the Thecostraca is a taxon where parasitism has evolved several times and in at least two lineages (Rhizocephala and Facetotecta) reached a climax of morphological specialization. All thecostracan taxa, except the Thoracica, are epibiotic and if this was also true for the stem lineages it could have favored the evolution of parasitism, but there is no simple explanation as to why the species rich Thoracica have so few parasitic forms.

Shell plates. By simple parsimony, we infer that mineralized shell plates evolved only in the thoracican stem line. Cuticular primordial plates are not present in the Acrothoracica, but *Ramphoverritor* seems to have five such plates. If this fossil is a cirripede, it indicates that five primordial plates were present already in the cir

ripede stem line, and this would have far reaching consequences. Not only must acrothoracicans and rhizocephalans have lost these cuticular primordia, but the presence of only four plates in *Ibla* (Ibliformes) must also have evolved from a five-plated state.

Sexual biology. Sexual biology in the Cirripedia and Thecostraca was already discussed by Høeg (1995). By parsimony, separate sexes is the ancestral state and hermaphroditism evolved only in the thoracican stem lineage. It is at present impossible to reconstruct the sexual biology of the (suspension feeding) ur-cirripede. Did it have equal-sized male and females or were female-associated dwarf males already present? Copulation between equal-sized male and female partners would have required at least some level of gregarious settlement. It is interesting that all cirripedes have filiform, motile sperm that swim through seawater to accomplish fertilization, although this occurs within the confines of the mantle cavity. Even the advanced rhizocephalan parasites fertilize the eggs like this and it constitutes one of the very few similarities between adults of these parasites and other barnacles. With motile sperm present, could the ur-cirriped have been a free spawner as in many other sessile and filter feeding invertebrates?

7. Characterisation of the Thecostraca

Without a reference phylogeny for all Crustacea it is difficult or impossible to list morphological apomorphies for the Thecostraca even if the taxon appears to be monophyletic based on molecular evidence. Grygier (1987a) listed three tentative autapomorphies for the taxon:

i)   No post-maxillular limb buds in the nauplii. This entails a unique one step appearance of the six pairs of natatory thoracopods in the cypridoid. New information of the ontogeny of the Tantulocarida could affect this character.

ii)   Compound eyes with three crystalline cones per ommatidium. The value of this character depends critically on what is considered plesiomorphic for the Crustacea in general, and it obviously cannot be scored for the Copepoda.

iii)   Strongly developed frontal filaments associated with compound eyes in the cypridoid larva. This is character state 18(1) in our analysis and seems to be a solid apomorphy. Frontal filaments are even present in most rhizocephalans, although their cyprids normally lack compound eyes (Glenner et al. 1989). Facetotectan nauplii lack frontal filaments, so in our analysis

their presence in cirriped and ascothoracidan nauplii becomes a synapomorphy, character state 7(1), for these two taxa.

To this list we add the following three characters:

iv)   Antennule with distally situated attachment device. This combines character states 21(1) and 24(1) in our analysis. Grygier (1987a) listed it as a synapomorphy for the Thecostraca and the Branchiura, but in light of recent studies we find this unlikely (Møller et al. 2008). It is reasonable to assume that the thecostracan cypridoid changed from attaching mechanically to chemically in the stem lineage, but the details of this transformation cannot be worked out until segment homologies between cyprid, a-cyprid and y-cyprid antennules have become better understood.

v)   Five pairs of lattice organs in the head shield of the cypridoid (post-naupliar) larva. This is character state 12(1) and seems to be a very strong autapomorphy for the Thecostraca. Lattice organs have not been found in any other Crustacea including tantulocarids and *Bredocaris*. The claim they occur in the extinct Thylacocephala needs a closer study. Lattice organs range from an almost seta-like shape to some advanced shapes but always with the same TEM level structure (Høeg et al. 1998) and always organized as two anterior and three posterior pairs, although secondary loss of pairs occurs nested within lineages.

vi)   One or two aesthetascs situated distally on the cypridoid antennule. True aesthetascs are specialized, chemoreceptive setae found only on antennules, and they occur widespread in the Crustacea. They are sac-shaped, with a very thin cuticle and contain profusely branched cilia from the sensory cells (Hallberg et al. 1992). Normally, aesthetascs occur many together, i.e., hundreds in malacostracans and in copepods typically one per antennular segment. Those found in cypridoid larvae are aesthetasc-like at the TEM level (Lagersson et al. 2003; Pasternak et al. 2004), but the limitation in number to one (or two as in rhizocephalan male cyprids) is unique also compared to the Tantulocarida. We therefore suggest character state 25(1) as an autapomorphy for the Thecostraca.

8. Outlook

Morphological comparison of thecostracan cypridoid larvae can undoubtedly reveal more potential apomorphies for this taxon that include some of the most transformed forms known in all Arthropoda. This would also assist in developing morphological matrices for the analysis of the intrinsic phylogenies of the Facetotecta, Ascothoracida, and Acrothoracica, which

are all poorly known. Finally, characters from juvenile and adult (post-cypridoid) stages should be combined with larval and molecular data. This would both provide more robust and detailed phylogenies and facilitate the reconstruction of ground pattern states for all stages in the life cycle.

9.   Acknowledgements & participation

10.   References

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Electronic Supplement Files

at http://www.arthropod-systematics.de/ ("Contents")

Appendix 1:   Morphological matrix used for tracing character evolution.

Appendix 2:   01–41. Tracings of the morphological characters (1–41) on the phylogeny of Pérez-Losada et al. (2009). Squares above terminal branches indicate taxa not scored with (?).

Video clip 1:   3D visualization of a generalized cirripede cyprid. Note the complex shape of the antennules and their musculature, enabling the exploratory behaviour shown in Video clip 2; modeled in the 3D Studio Max® software package by N. Lagersson and J.T. Høeg.

Video clip 2:   Surface exploration in the field of cyprids of *Semibalanus balanoides*. Note the speed with which the cyprid can walk and the presence of several attached and metamorphosing specimens. Recorded at the Menai Bridge Marine Science laboratories by J.T. Hoeg and N. Lagersson.

Video clip 3:   Suspension feeding in *Balanus improvisus* from the Danish Isefjord documented with an underwater endoscope. Note how the thoracopods are divided into a feeding basket of the three posterior pairs of thoracopods and three anterior pairs of (white-coloured) mouth cirri that transfer food from the cirral net to the mouth cone and appear white in this video.